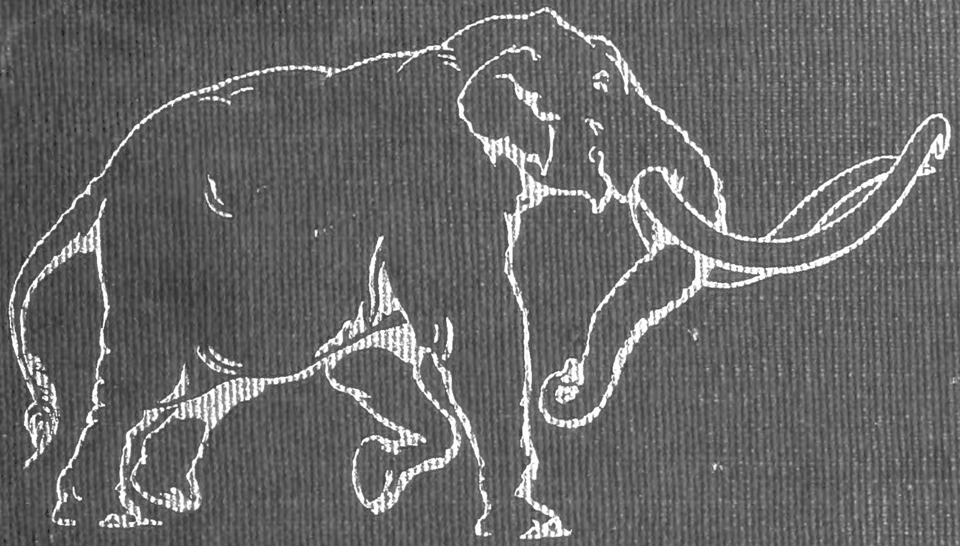
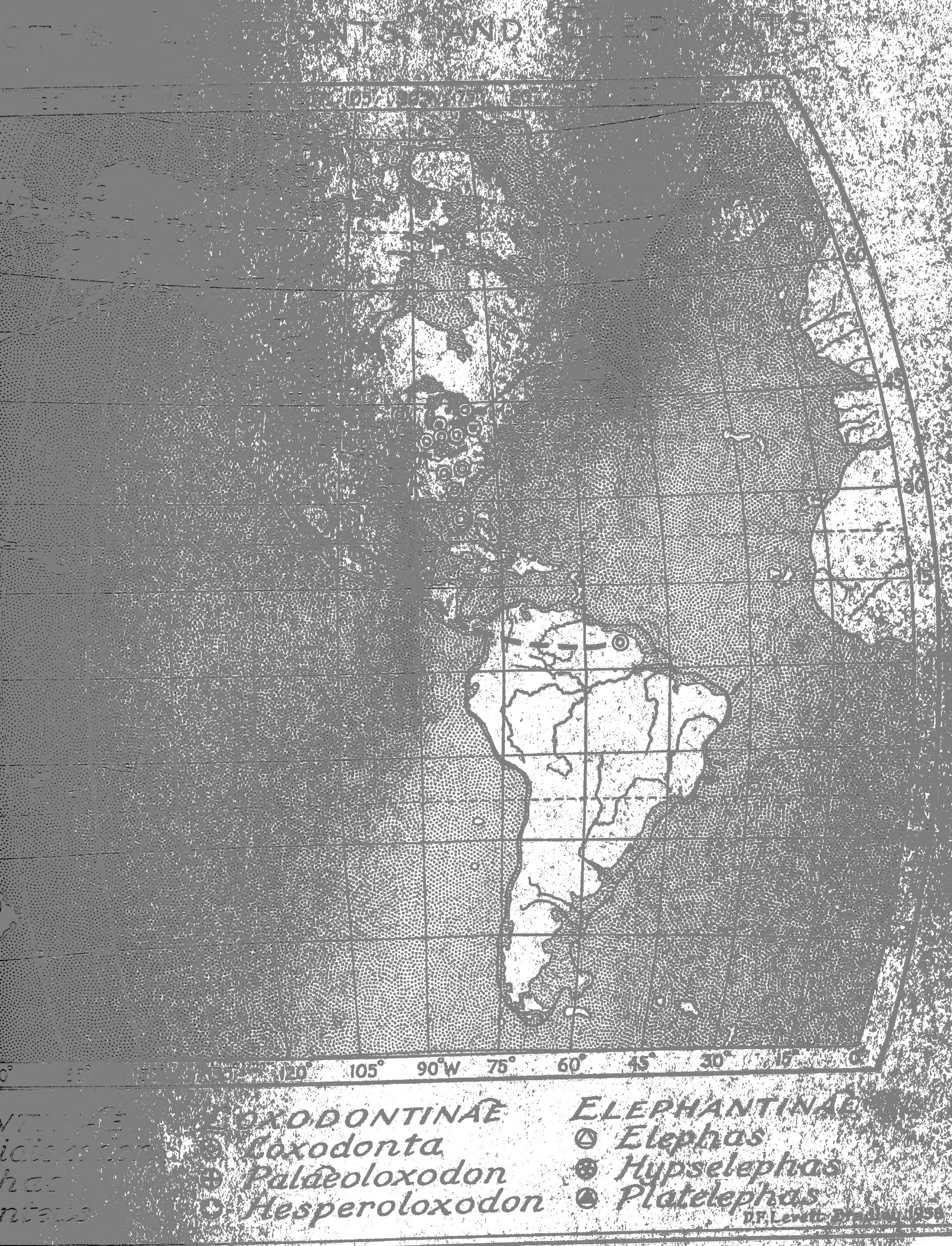


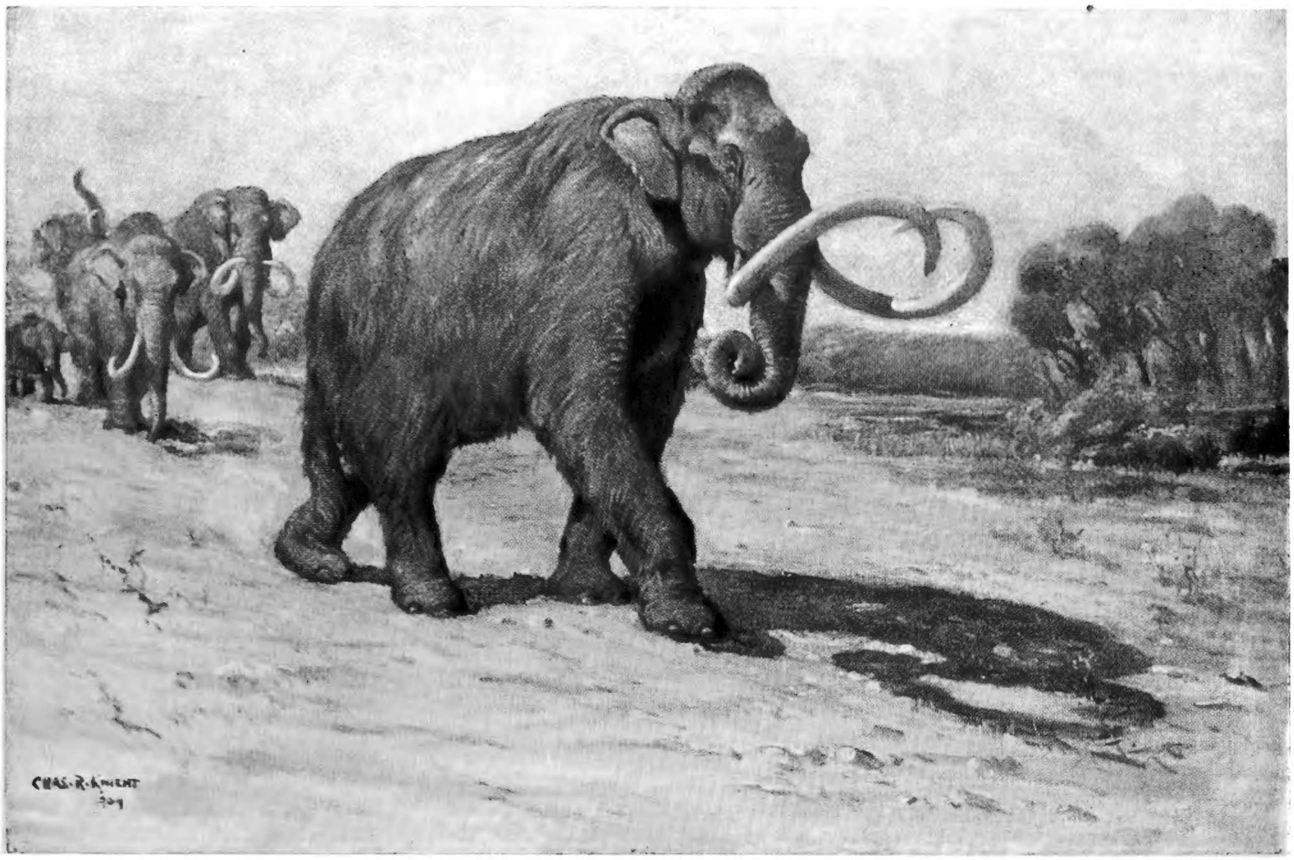
PROBOSCIDEA

HENRY FAIRFIELD OSBORN


WORLD DIST
165°
Present coast line

ODONTS, AND ELEPHANTS
105°
90°W
75°
60°
45°
30°
15°
0°
120°
60
45
30
15
LOXODONTINAE
Loxodonta
Palaeoloxodon
Hesperoloxodon
ELEPHANTINAE
Elephas
Hypselephas
Platelephas
P.F. Lewis ... 1936

PROBOSCIDEA



RESTORATION OF THE JEFFERSONIAN MAMMOTH (*PARELEPHAS JEFFERSONII*)

After a painting by Charles R. Knight in 1909, under the direction of Henry Fairfield Osborn

The skeleton on which this painting was based is mounted in the American Museum of Natural History, Hall of the Age of Man. It was found near Jonesboro, Indiana, on the farm of Dora E. Gift, in 1903; purchased for the American Museum with the Jesup Fund in 1904; mounted in 1906; first described and figured by the present author in 1907. As found the skeleton was embedded in a muck deposit of late Pleistocene age, fifteen feet below the surface. This deposit is probably of post(?)-Wisconsin age (according to the geologic time scale having been laid down about 15,000 years ago). Representatives of the Parelephas phylum appeared in Europe in the early Pleistocene and persisted into the Third Interglacial. This Third Interglacial period may mark the time of migration across Asia into North America. In fact, it is suggested by the present author that such migration might have occurred in Second or even in First Interglacial time.

The most striking features of this individual are the complete incurvation and crossing of the tusks, indicating that it is an old bull, and the relatively small size of the head. It is here represented with a hairy covering, as Parelephas is characteristic of the north temperate region, both of Europe and the United States.

PROBOSCIDEA

A MONOGRAPH OF THE DISCOVERY, EVOLUTION, MIGRATION AND EXTINCTION OF THE MASTODONTS AND ELEPHANTS OF THE WORLD

BY

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ELEPHANTOIDEA

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I. INTRODUCTION

1. HISTORY OF CLASSIFICATION

[The name Stegodontoidea first appeared in a diagram by Professor Osborn in his article of June, 1935, entitled, "The Ancestral Tree of the Proboscidea. Discovery, Evolution, Migration and Extinction over a 50,000,000 Year Period" (Osborn, 1935.937, p. 407, fig. 2), in which superfamily he included both *Stegolophodon* and *Stegodon* under the family Stegodontidæ of Young-Hopwood, thus removing them from the Elephantoidea.

In Volume I of the present Memoir (published Aug. 15, 1936) Professor Osborn confirmed his separation of the Stegodontoidea from the Elephantoidea (pp. 22, 25) but he withdrew the Stegolophodonts, placing them in the superfamily Mastodontoidea, family Mastodontidæ, and creating a new subfamily, the Stegolophodontinæ (see pp. 700, 737, and Pl. IV), to embrace the various species, owing to the "intermediate position of [the] molars between the true Mastodontidæ . . . and the true Stegodontoidea," and suggesting (p. 191) the "possible derivation of the grinding teeth of the Stegodontoidea from those of *Stegolophodon*." The true Stegodonts he retained in the superfamily Stegodontoidea, subfamily Stegodontinæ.

As early as 1857 Falconer observed (1857.1, p. 314) that "The Stegodons constitute the intermediate group of the Proboscidea from which the other species diverge through their dental characters, on the one side into the Mastodons, and on the other into the typical Elephants." Later Falconer (in Murchison, Pal. Mem., 1868, Vol. II, footnote, p. 268) remarked that "The Indian fossil species, which have been ranged under the designation of *Stegodon*, establish, through their molar teeth, a manifest and nearly unbroken passage from the Mastodons into the true Elephants." Also, as recently as 1932, van der Maarel (1932.1, p. 162) expressed the opinion that "all the species of *Stegolophodon* . . . being all very primitive forms . . . may as well be reckoned to the family of the *Mastodontidæ*."

Therefore, while various scientific observers have regarded certain of the Stegodonts as transitional between the Mastodontidæ and the Elephantidæ, it remained for Professor Osborn to assign the superfamily name Stegodontoidea to the true Stegodonts and to remove the Stegolophodonts to the superfamily Mastodontoidea, under the new subfamily name Stegolophodontinæ, the members of which he designated (Vol. I, p. 690) as "pro-stegodonts."

The regrettable death of Professor Osborn in November of 1935 precludes the full treatment of these groups as contemplated by him (see Vol. I, p. 197); it is deemed best, therefore, to allow the present chapter to remain as first written by him, making such changes (either in square brackets or in editorial notes) as are consistent with the known opinions of the author, namely, as deduced from published statements, accumulated notes, and interlined text.

The classification of the genera *Stegolophodon* and *Stegodon*, now to be described, would appear, therefore, to be as follows:

SUPERFAMILY: STEGODONTOIDEA Osborn, 1935, 1936

Separated by Osborn (Vol. I, 1936, pp. 22, 25, of the present Memoir) from the Elephantoidea Osborn, 1921, as a distinct stock, but without diagnosis. However, according to his observations on the sectioned molars, the valleys separating the adjacent ridges are closed or V-shaped at the bottom in the Stegodontoids (Fig. 764) and open or U-shaped in the Elephantoids (Fig. 1231). He also considered that the extremely short face of the Stegodontoids could not have given rise to the longer face of the Elephantoids.

FAMILY: STEGODONTIDÆ Young-Hopwood, 1935

This name appears in Young (1935.1, p. 5) but without definition. Later in 1935, Hopwood, in his Memoir on the "Fossil Proboscidea from China," defines the family as follows (p. 71): "The animals included in this family have skulls which resemble those of the true elephants but which are more primitive. They have very long sockets for the tusks, and the grinding teeth and palate are well below the plane of the occipital condyles. The grinding teeth remain brachyodont throughout the whole of their evolutionary history, but they parallel the teeth of the true elephants in showing a progressive increase in the number of ridges. This is especially true of the third molars. With this increase in the number of ridges, and its accompanying increase of length, there is an ever increasing curvature of the occlusal surface which reaches its maximum in certain specimens referred to *S. airawana* and *S. insignis*. Owing to the short palate, it was impossible for the whole of the very long teeth to be accommodated in the upper jaw at one time. The curvature of the crown allowed the tooth to follow a more or less circular path which brought it from a position practically parallel to the plane of the occiput to the correct position for mastication. There is an ever increasing amount of cement, and the ridges show an increasing number of mammillæ on their crests."

"This sub-family comprises two groups[1] of animals. One, with compressed, tectiform, ridges is given the generic name *Stegodon* Falconer & Cautley. The other, in which the ridges are blunter, and composed of rounded conules, is known as *Stegolophodon* Schlesinger. Both genera occur in India, but, so far as is known, *Stegodon* is the only genus found in China."

SUBFAMILY: STEGODONTINÆ Osborn, 1918, 1921

Original reference: Bull. Geol. Soc. Amer., 1918, Vol. XXIX, pp. 135, 136 (Osborn, 1918.468); Amer. Mus. Novitates, 1921, No. 1, pp. 12, 13 (Osborn, 1921.515).

> SUBFAMILY DEFINITION (Osborn, 1918.468, p. 136): "The *Stegodontinæ* may be distinguished as a phylum confined to Asia, in which the grinding teeth remain brachyodont, short-crowned, although a very large number of cross crests evolve, especially on the posterior grinding teeth. From an early member of this subfamily, perhaps of Middle Miocene time, were given off one or more branches of the elephant and mammoth phyla."
>
> (Osborn, 1921.515, pp. 12 and 13): "We observe that the Stegodonts are persistent browsers, probably tropical, forest-living proboscideans. According to Pohlig, from the skeleton discovered in

---

[1] [According to Osborn, 1936, Vol. I, p. 700, by removal of the Stegolophodonts to the family Mastodontidæ, the Stegodontidæ embrace the true Stegodonts (*Stegodon* Falconer and Cautley) only.—Editor.]

Trinil, Java, they have short, massive bodies like those of the Mastodontinæ of the north temperate forests. The skull and tusks do not lead into either the Elephantinæ or the Mammontinæ types . . . The distinctive feature of the grinding teeth is the rapid multiplication of transverse crests which rise from the formula 4.5.6.6.7-8 in *S.* [*Stegodon*] *cliftii* (Lower Pliocene) to 5.9.10.12.13 in *S. insignis* (Lower Pleistocene). Jaw rapidly abbreviated. Upper tusks straight, parallel, slightly upcurved (adapted to dense forests). Grinders brachyodont to subhypsodont, crests breaking up into small mammillæ, valleys filling with cement."

In the first article, namely, "A Long-jawed Mastodon Skeleton from South Dakota and Phylogeny of the Proboscidea," 1918, Osborn placed the Stegodontinæ under the Elephantidæ (p. 135), and in an accompanying table mentioned the species *Stegodon ganesa*, *S. cliftii*, *S. bombifrons*, and *S. latidens*. The last-mentioned species was made by Schlesinger the genotype of *Stegolophodon*.

The above definitions were based on both *Stegolophodon* and *Stegodon*. After the removal of the former genus to the superfamily Mastodontoidea, family Mastodontidæ, subfamily Stegolophodontinæ, no revised definition of the subfamily Stegodontinæ was given by the author.

LATE TERTIARY GEOLOGY OF INDIA

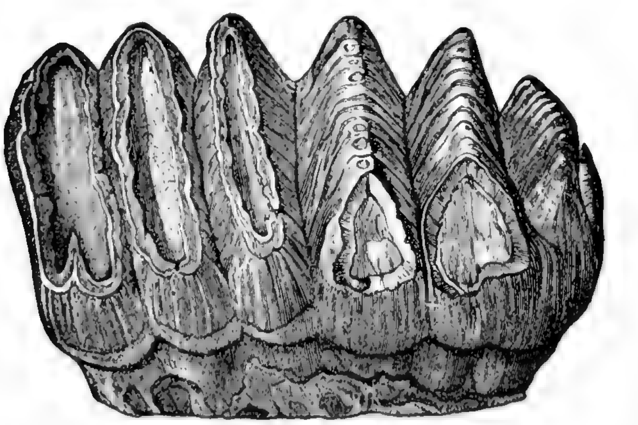
The latest opinion regarding the geology of India (the Siwalik Hills and Perim Island) will be found in Edwin H. Colbert's Memoir of 1935 on "Siwalik Mammals in The American Museum of Natural History," pages 6 to 55; in a summary on page 21 it will be noted that Doctor Matthew in 1929 assigned to the Siwalik beds a somewhat higher position in the geologic time scale than Doctor Pilgrim in 1927. Compare also Chapter XXII of the present Memoir, "Geologic Succession of the Proboscidea," which has been written by Doctor Colbert.

Throughout the present Volume, therefore, the later determinations will be inserted in square brackets or added in footnotes. It should be recalled that the chapters constituting this Volume were written about eight to ten years ago and were awaiting final revision by Professor Osborn.—Editor.]

2. HABITS AND GENERAL CHARACTERS

We observe that this subfamily [Stegodontinæ[1]] includes forest-living browsers, which probably developed in a forested or semi-forested oriental region, ranging through India into Burma, China, Japan, and southward into Java, Borneo,[2] and the Philippines. The ancestors of the subfamily may be found in Miocene deposits of western Europe[3]. A single tooth, named *Mastodon* (*Bunolophodon*) *longirostre* Kaup *forma sublatidens*, has been de-

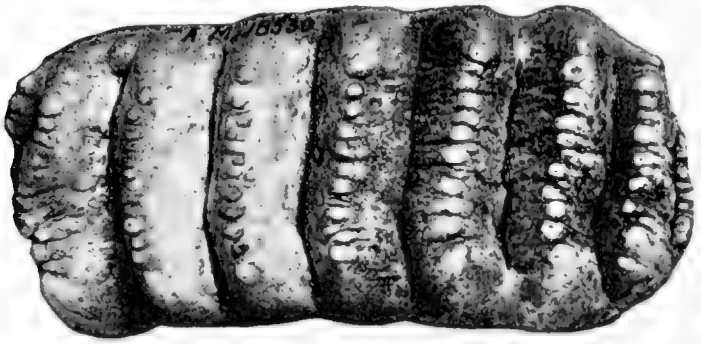
Fig. 20.



Elephas clifti.—The first (?) left upper true molar; from the Siwaliks of Burma. ½. The lower border of the figure is the inner border of the specimen. (From Gaudry's 'Enchainements.')

Cotype of Stegodon elephantoides Clift (=cliftii Falconer)

Fig. 683. Type of *Elephas cliftii* Falconer and Cautley, 1846, a first left upper true molar, l.M^1, one-half natural size. The same six crested tooth appears in figures 686, 700, and 701. After Lydekker, 1886.2, p. 81, fig. 20 (taken from a woodcut in Gaudry, 1878, p. 176, fig. 232).



Referred superior Molar of Stegodon orientalis grangeri

Fig. 684. Referred first right superior molar, r.M^1 (rev.) of *Stegodon orientalis grangeri* (Amer. Mus. 18536—wrongly numbered 18530). Actual median length 181 mm.

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[1] [At the time this chapter was written the subfamily Stegodontinæ was thought to embrace both the Stegolophodonts (now removed to the Mastodontoidea subfamily Stegolophodontinæ, p. 700) and the true Stegodonts.—Editor.]

[2] [Type locality of *Stegolophodon lydekkeri* Osborn, 1936 (see Vol. I, p. 700).—Editor.]

[3] [See Vol. I, p. 197.—Editor.]

scribed by Schlesinger from near Teschen (Schlesien), Austria; this resembles *Mastodon* [=*Stegolophodon*] *latidens* of Burma and is referred in the present Memoir to *Stegolophodon sublatidens* (see Vol. I, p. 737; Vol. II, p. 846).

The skull is subelephantine in type, brachycephalic, brachyopic, the rostrum being elongated to support the tusks; the grinding teeth and palate are depressed far below the occipital condyles (bathycephalic). As in the elephants, the jaw is greatly abbreviated. The upper tusks are straight or slightly upcurved, elongating, without trace of enamel band, to a length of about 10 ft. Considering the large size of the tusks the skull is relatively small. The grinding teeth are brachyodont to subhypsodont, yet the ridge-crests in the posterior molars, M3, multiply from five plus [*Stegolophodon*] to fifteen plus [*Stegodon*], each crest breaking up into small nipples, mamillæ, or conelets. The lower incisors disappear very early.

As in certain of the Mastodontidæ and as in all the Elephantidæ, the grinding teeth increase the number of their ridges by adding crests both in front and behind, as first observed by Falconer. Thus in M 1 of *Stegodon orientalis grangeri* (Fig. 684) the ridge formula may be written: $\frac{\tfrac{1}{2}-6-7-\tfrac{1}{2}}{8}$. The descending scale of the ridge formulæ in the premolars and molars of the principal species of Stegodonts is approximately as below.

3. APPROXIMATE DESCENDING RIDGE FORMULÆ, AFTER FALCONER, LYDEKKER, MARTIN, AND OSBORN

Observe that (1) the maximum *upper* ridge-crests, rising from 21e to 51e, are, so far as known, less numerous than the maximum *lower* ridge-crests which probably rise to more than 51; (2) this is compensated for by the fact that the *upper molars* are throughout broader than the *lower molars;* (3) the differences in width and in the number of ridge-crests of the *upper molars* in comparison with the *lower molars* are beautifully shown in figure 687, also in figures 759 and 762, the type of *Stegodon orientalis grangeri*. See also details of progressive ridge-crest formulæ, talons and half ridge-crests, under each species.

	Dp 2	Dp 3	Dp 4	M 1	M 2	M 3	Maximum conelets per ridge-crest	Estimated maximum upper and lower ridge-crests Dp 3–M 3	
								U.	L.
Stegodon airâwana	$\frac{2}{}$	$\frac{5-6}{}$	$\frac{7-9}{}$	$\frac{7-9}{}$	$\frac{9-11}{}$	$\frac{12-14}{13-15\tfrac{1}{2}}$	13–20+	51e	
Stegodon insignis *Stegodon ganesa*	$\frac{2}{2}$	$\frac{5-6}{6}$	$\frac{7-7\tfrac{1}{2}}{7\tfrac{1}{2}-9}$	$\frac{7\tfrac{1}{2}-8}{7\tfrac{1}{2}-10}$	$\frac{7\tfrac{1}{2}-\tfrac{1}{2}-8}{7\tfrac{1}{2}-8-\tfrac{1}{4}-9-\tfrac{1}{4}}$	$\frac{\tfrac{1}{2}-11-\tfrac{1}{2}}{12\tfrac{1}{2}-13}$	11	42	49
Stegodon orientalis grangeri	$\frac{\tfrac{1}{2}-2-\tfrac{1}{2}}{2}$	$\frac{5\tfrac{1}{2}-6}{+5\tfrac{1}{2}}$	$\frac{\tfrac{3}{4}-6-\tfrac{1}{2}}{7\tfrac{1}{3}}$	$\frac{\tfrac{1}{2}-6-7-\tfrac{1}{2}}{8}$	$\frac{\tfrac{1}{3}-8-\tfrac{1}{3}}{(?)\ 9\tfrac{1}{3}}$	$\frac{\tfrac{1}{8}-11-\tfrac{1}{8}}{\tfrac{1}{3}-13+}$	–11	41	46
Stegodon bombifrons		$\frac{4}{4}$	$\frac{5-6}{7}$	$\frac{6}{7\tfrac{1}{2}}$	$\frac{7}{7\tfrac{1}{2}-8}$	$\frac{9\tfrac{1}{2}}{9\tfrac{1}{2}}$	11+		34e
Stegodon elephantoides				$\frac{6\tfrac{1}{4}}{}$	$\frac{6\tfrac{1}{4}}{}$	$\frac{}{10}$	5–8		
Stegodon elephantoides (=*cliftii*)		$\frac{4}{}$	$\frac{6}{}$	$\frac{6\tfrac{1}{4}}{}$	$\frac{6\tfrac{1}{2}}{}$	$\frac{6\tfrac{1}{2}}{8\tfrac{1}{2}}$	10–12	28e	
Stegolophodon stegodontoides						$\frac{6\tfrac{1}{2}}{}$	5–6		
Stegolophodon latidens		$\frac{2}{}$	$\frac{4}{}$	$\frac{\tfrac{1}{4}-4-\tfrac{1}{4}}{}$	$\frac{4\tfrac{1}{2}-5}{4\tfrac{1}{2}-5}$	$\frac{\tfrac{1}{4}-5-\tfrac{1}{2}}{\tfrac{1}{2}-6-\tfrac{1}{2}}$	4–5	23(?)	
Stegolophodon cautleyi			$\frac{\tfrac{1}{2}-3-\tfrac{1}{2}}{}$	$\frac{\tfrac{1}{2}-4-\tfrac{1}{2}}{}$	$\frac{4}{}$	$\frac{5-\tfrac{1}{2}+}{}$	4–5	21e	

FORMULA: RIDGE-CRESTS OR LOPHS (DP 2–M 3).—The above ridge-formula table, assembled from several sources, is approximate, first, because various observers differ in the method of counting the ridge-crests, second, because within each species the ascending mutations may lead up to the next higher progressive stage, as, for example, in the transition of *Stegodon insignis-ganesa* to *S. airâwana* of Trinil, Java.

The individual number of ridge-crests from Dp 2 to M 3 is mainly assembled from a very careful collation of the ridge-crest formulæ given by Falconer (see below), supplemented by the observations of Lydekker, of Martin, and of Osborn.

Conelets.—The conelets of *Stegolophodon* and of *Stegodon* arise chiefly by binary, rarely by ternary, fission of the primary cones. Starting with the original loph of the *Palæomastodon* stage, consisting of two cones, normal binary fission would produce:

2—4+ (*S. cautleyi*)—8 (*S. elephantoides*)—20+ (*S. airâwana*), *etc.*

But the binary fission is not so regular as this. The newer anterior and posterior crests exhibit fewer conelets than the older mid-crests, so that the highest number of conelets usually will be found in the third and fourth crests.

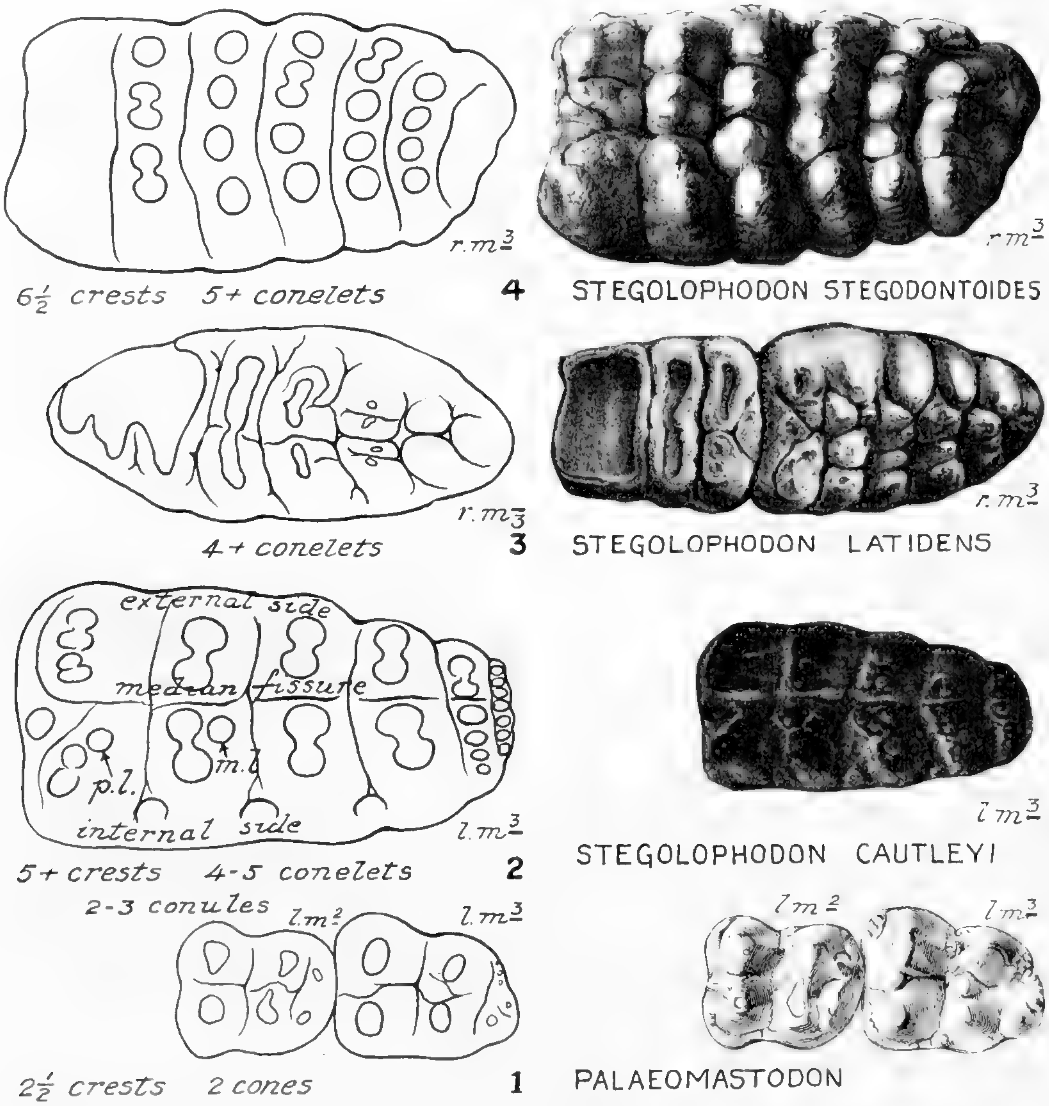

Fig. 685. Structural Evolution of the Cones, Conelets, and Ridge-crests in the Stegolophodon Phylum, in comparison with Palæomastodon

(1) Palæomastodon, Primary Type. Four primary cones; ridge-crests, proto-, meta-, and rudimentary tritoloph. [See pp. 143 and 691 of Vol. I, for subfamily position of *Palæomastodon*.—Editor.]

(2–4) Stegolophodon Phylum. Binary fission of *primary cones* into four to five *conelets*, vestigial conules in *S. cautleyi* and *S. latidens* (protoconule = p.l., metaconule = m.l.); addition of trito-, tetarto-, penta-, and hexalophs. Gradual loss of *median sulcus*, presistent, however, in the first two anterior crests.

Stegolophodon latidens (3, left) is a third lower molar, r.M_3, inserted for comparison, and has seven plus (7½) ridge-crests, four plus conelets, and median sulcus.

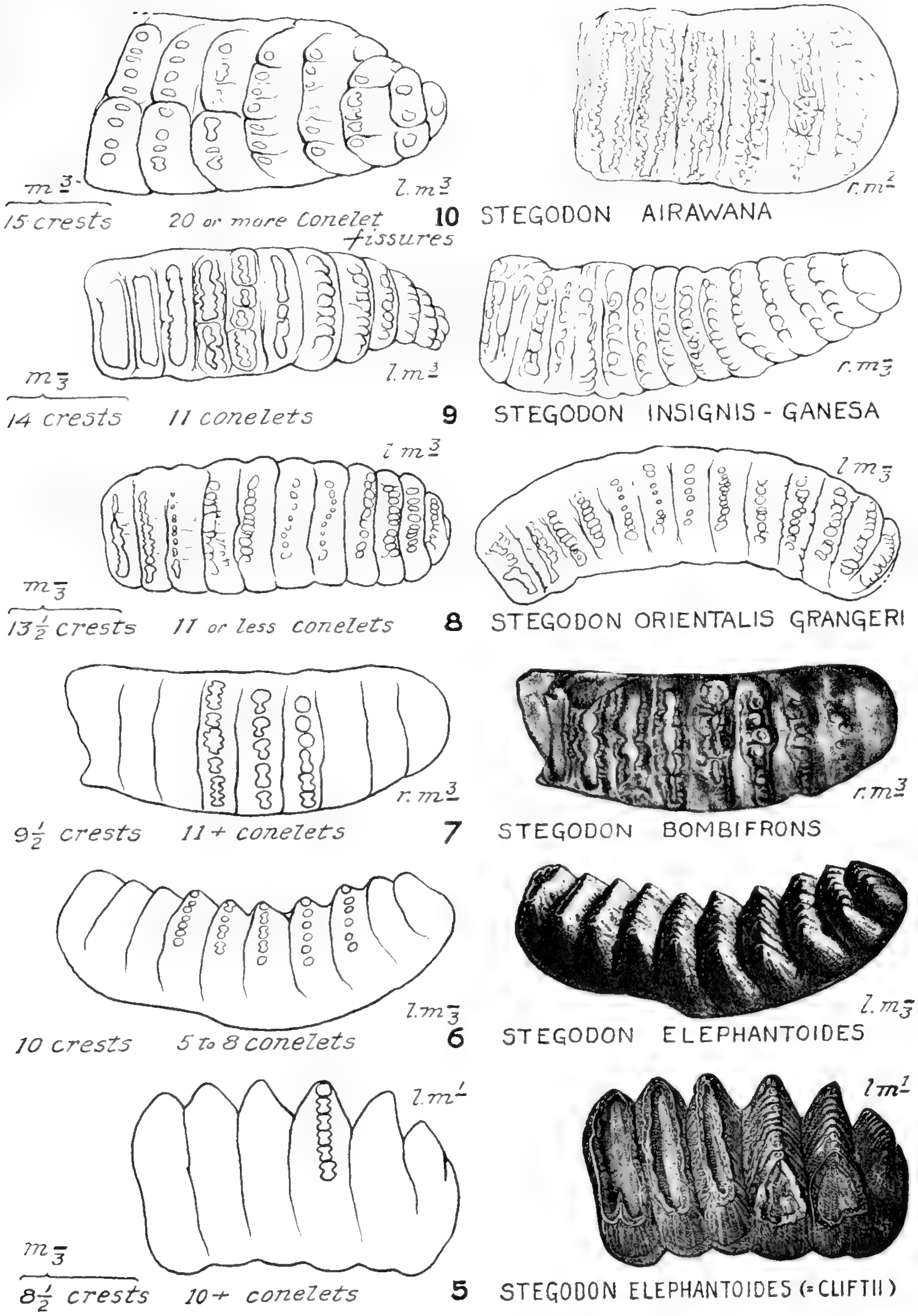

Fig. 686. Structural Evolution of the Cones, Conelets, and Ridge-crests in the Stegodon Phylum, in Ascending Order (5–10).

(5–10) Stegodon Phylum. Binary or ternary fission of the cones into conelets (5–20); addition of anterior and posterior ridge-crests (10–15 in M 3); addition of cement.

(5) *Stegodon elephantoides* (= *cliftii*) with six and a quarter ridge-crests and ten plus conelets (M^1).
(6) *Stegodon elephantoides* with ten ridge-crests and five to eight conelets (M_3).
(7) *Stegodon bombifrons* with nine and a half ridge-crests and eleven plus conelets (M^3).
(8) *Stegodon orientalis grangeri* with thirteen and a half ridge-crests and eleven or less conelets (M_3).
(9) *Stegodon insignis-ganesa* with fourteen ridge-crests and eleven conelets (M_3).
(10) *Stegodon airâwana* with fifteen ridge-crests and twenty plus conelets (M^3).

FIGURES 685 AND 686.—Particularly interesting and significant in the Stegodontinæ is the transformation of the original *cones* by fission into *conelets*. Thus in the archetypal *Palæomastodon* molar there are two cones in the protoloph, in *Stegolophodon latidens* and *S. cautleyi* each cone splits into two, making four plus conelets in the metaloph; in *S. stegodontoides* each of these four conelets tends to split into two, tending to form from five to eight conelets, but this splitting is not regular and no loph actually attains eight. In *Stegodon elephantoides* the equal splitting gives rise to from *five* to *eight* conelets; in *S. elephantoides* (=*cliftii*), *S. bombifrons*, and *S. insignis-ganesa* the fission gives rise to from *eleven* to *twelve* conelets, hence each ridge is finally surmounted by *twelve* conelets which, when slightly worn, present eight loops. In *Stegodon airâwana*, the most progressive species, the conelets range from thirteen to twenty plus. Thus the maximum number of cones and conelets in each crest runs as follows:

Molar cones and conelets: Primitive (*Palæomastodon*) 2–4–6–8–12–20+ progressive (*Stegodon airâwana*).

RIDGE-CREST EVOLUTION.—The Stegodontinæ also furnish a beautiful example of the evolution through which each ridge passes in turn, from the primitive submastodontoid type seen in *Palæomastodon* into the highly progressive subelephantoid type seen in *Stegodon insignis-ganesa* and *S. airâwana*. The superior (-loph) and inferior (-lophid) ridge-crests may receive a brief numerical terminology, namely:

Pro-protoloph—id =One-half, anterior rudimentary ridge
Post-metaloph—id =One-half, posterior rudimentary ridge
Protoloph—id =First primary ridge=protocone and paracone of Ungulata
Metaloph—id =Second primary ridge=hypocone and metacone of Ungulata
Tritoloph—id =Third ridge
Tetartoloph—id =Fourth ridge
Pentaloph—id =Fifth ridge
Hexaloph—id =Sixth ridge
Heptaloph—id =Seventh ridge
Octaloph—id =Eighth ridge
Ennealoph—id =Ninth ridge
Decaloph—id =Tenth ridge
Endecaloph—id =Eleventh ridge
Dodecaloph—id =Twelfth ridge

CREST ADDITION.—In *Stegolophodon* and in the Mastodontidæ the homology of the protoloph and of the metaloph is simple as compared with other ungulates, but since the increment of ridge-crests in the elephantine molar is by addition to both the anterior and posterior ridges, namely, the pro-protoloph and the post-metaloph, it soon becomes difficult to determine which ridge-crests correspond with the primary protoloph and metaloph of *Palæomastodon* and of other ungulates.

INTERMEDIATE MOLARS UNIFORM.—A constant feature in the Proboscidea appears to be the uniformity of the three 'intermediate molars,' namely, Dp 4, M 1, M 2, which tend to have the same ridge-crest formula in each species, for example:

Stegodon insignis-ganesa	Dp 4	7½	M 1	7½	M 2	7½–8	=intermediate molars
Stegolophodon latidens	Dp 4	4	M 1	4½	M 2	4½–5	=intermediate molars
Trilophodon angustidens	Dp 4	3	M 1	3	M 2	3	=intermediate molars

Consequently it may be difficult to distinguish these 'intermediate molars' from each other by the ridge formula alone; whereas they may be distinguished by the character of wear, by the width of the crowns, and by the condition of the fangs.

RIDGE-CREST ELEVATION.—The progressive elevation of the ridge-crests in the Stegodontinæ is illustrated in two diagrammatic figures (Figs. 687, 688), which demonstrate the constant progressive heightening of the ridge-crests as we ascend from the Lower(?) Pliocene *Stegodon sinensis* and [Middle Pliocene] *S. bombifrons* into the Middle Pleistocene *S. airâwana* stage. The early phases of ridge-crest elevation (Fig. 687) may be compared with the later phases (Figs. 688, 781) as follows:

Stegodon orientalis Owen
Stegodon orientalis grangeri Osborn
Stegodon bombifrons Falconer and Cautley
Stegodon sinensis Owen

Stegodon auroræ Matsumoto
Stegodon airâwana Martin
Stegodon insignis Falconer and Cautley

Descending Order of Species.—(1) At the summit of the known Stegodontinæ is *Stegodon airâwana*, the most progressive both in ridge-crests and in conelets—a Lower to Middle Pleistocene stage. The following extract from a letter by Doctor Dietrich (March 10, 1924, and notes) confirms the Middle Pleistocene age of this species:

> For a long time I have been trying to prove that the *Stegodon* [*airâwana*] species from the *Pithecanthropus* strata [Trinil, Java] are the very youngest, that is, young Pleistocene. In detail: "*Geologisches Alter*. Aus morphologischen Gründen muss die javanische Art jünger sein als die chinesische und alle bekannten kontinentalen Stegodon-Arten. Dass St. Airawana im Pleistocän lebte, wird von fast allen Autoren angenommen; ihr *pleistocänes* Alter dürfte gesichert sein. Erweist sich die chinesische Stegodontenfauna als alt-pleistocän, dann ist die Trinilfauna jünger als alt-pleistocän. Ich halte es aus geologischen und anderen Gründen sogar für wahrscheinlich, dass die Trinilfauna (und damit Pitheacanthropus) *jung*-pleistocän ist; das wird sich mit Hilfe des St. Airawana bei besserer Kenntnis der kontinentalen Stegodonformen vielleicht erweisen lassen."

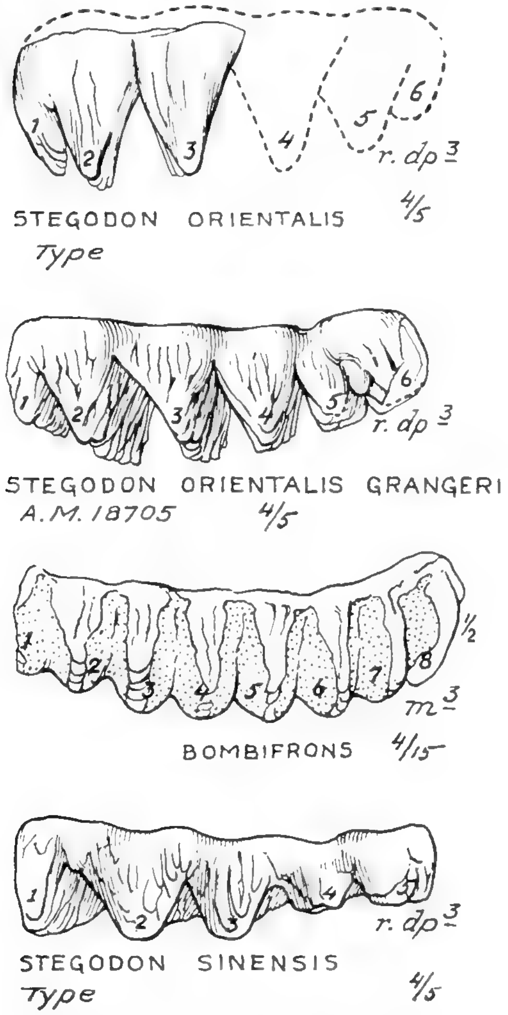

Fig. 687. Gradual Progressive Hypsodonty in Superior Grinders

Stegodon orientalis Owen, type. Superior deciduous premolar, r.Dp^3.

Stegodon orientalis grangeri Osborn. Superior deciduous premolar, r.Dp^3.

Stegodon bombifrons Falconer and Cautley. Third superior molar, M^3.

Stegodon sinensis Owen, type. Superior deciduous premolar, r.Dp^3.

All figures four-fifths natural size, excepting *Stegodon bombifrons* which is four-fifteenths natural size. Observe that the ridge-crests (1–5) in transition from *S. sinensis* type to *S. orientalis* type are broad, progressively elevated, and approximated.

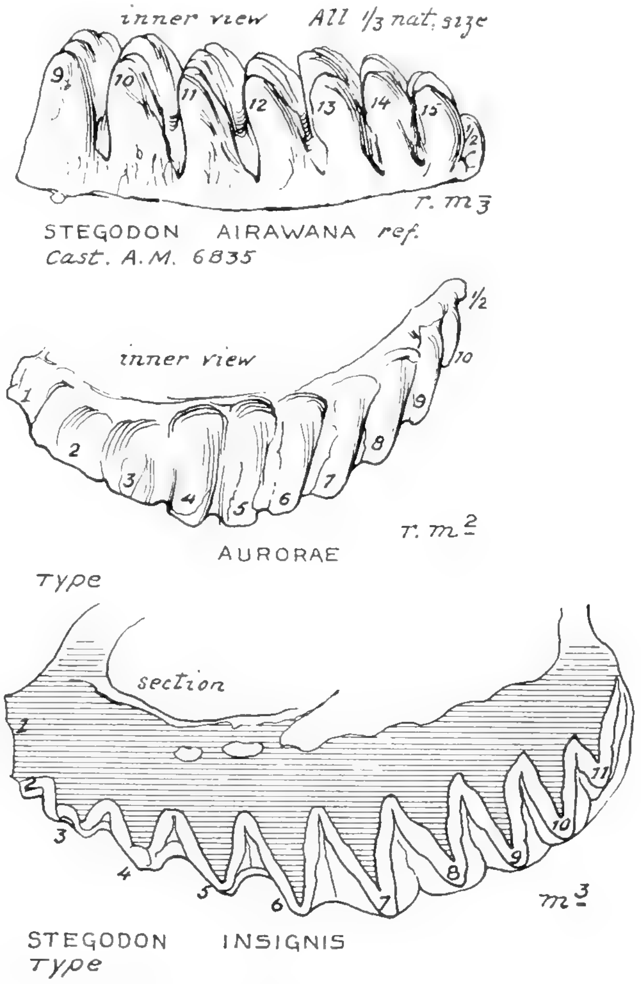

Fig. 688. Gradual Progressive Hypsodonty in Superior and Inferior Grinders

Stegodon airâwana Martin. Middle Pleistocene of Java. Elevated and approximated ridge-crests (9–15½), right third inferior molar, r.M$_3$.

Stegodon auroræ Matsumoto, type. Middle Pleistocene [?Upper Pliocene] of Japan. Elevated and closely approximated ridge-crests, right second superior molar, r.M^2.

Stegodon insignis Falc. and Caut., type. Lower Pleistocene, Upper Siwaliks, Boulder Conglomerate, of India. Third superior molar, M^3, with eleven+ridge-crests.

All figures to same scale, one-third natural size. Observe that in *Stegodon airâwana* and *S. auroræ* the ridge-crests are much more elevated and approximated than in *S. insignis*, but that *S. insignis* is less elevated than *S. orientalis* (Fig. 687).

TABLE III	STEGOLOPHODON PHYLUM			STEGODON PHYLUM		
	India, Burma	Japan	Borneo	India, Burma	China, Japan	Philippine Islands, Java
UPPER PLEISTOCENE				*Stegodon insignis* ref. *Stegodon ganesa* ref.		
MIDDLE PLEISTOCENE					*Stegodon orientalis shodoënsis* type	*Stegodon airâwana* type *Stegodon ganesa* var. *javanicus* type = *S. airâwana* or *S. trigonocephalus* *Stegodon (Archidiskodon?) mindanensis* type
LOWER PLEISTOCENE				*Stegodon pinjorensis* type	*Stegodon orientalis* type *Stegodon orientalis grangeri* type	*Stegodon trigonocephalus* type
Upper Pliocene to Lower Pleistocene				*Stegodon insignis* lectotype and ref. *Stegodon ganesa* lectotype and ref.		
UPPER PLIOCENE	*Stegolophodon stegodontoides* type		*Stegolophodon lydekkeri* type	*Stegodon insignis birmanicus* type[1] *Stegodon bombifrons* ref.	*Stegodon auroræ* type	
MIDDLE PLIOCENE	*Stegolophodon cautleyi* lectotype *Stegolophodon latidens* ref. [AUSTRIA *Stegolophodon sublatidens* type]			*Stegodon bombifrons* lectotype *Stegodon bombifrons* ref.	*Stegodon bombifrons* ref.	
LOWER PLIOCENE	*Stegolophodon latidens* lectotype and cotype[1] *Stegolophodon latidens* ref.[1]	*Stegolophodon latidens* ref.		*Stegodon elephantoides* lectotype[1] *Stegodon elephantoides* (=*cliftii*) cotype[1]	*Stegodon sinensis* type	
MIO-PLIOCENE	*Stegolophodon cautleyi progressus* type *Stegolophodon nathotensis* type					

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[1] [See note on page 824 below, in which the geologic age of *Stegolophodon latidens* is given as Lower Pleistocene. As *S. elephantoides* and *S. elephantoides* (=*cliftii*) were found in the same locality and at the same geologic level, they should also be regarded as of Lower Pleistocene age. Note also that *S. birmanicus* is placed in the Lower Pleistocene. Compare Colbert, Chap. XXII, pp. 1450, 1451.—Editor.]

(2) Next in descending order are referred *Stegodon insignis* and *S. ganesa*, of Lower to Middle [Upper] Pleistocene age. (3) Third in descending order is *Stegodon orientalis grangeri*, slightly more primitive than *S. insignis* both in ridge-crest and conelet progression—probably of Lower Pleistocene age. (4) Next is the [?Upper Pliocene] *Stegodon auroræ* of Mt. Tomuro, Japan. (5) Far more primitive both in ridge-crests and conelets are *Stegodon bombifrons* [of the Middle Pliocene] and *S. elephantoides* (= *cliftii*), known to be of Lower Pliocene (type) age.[1] It is probable that the referred *S. bombifrons* of the Middle [Upper] Pliocene, Tatrot horizon, will prove to be somewhat more progressive than the lectotype of *S. bombifrons* of the Middle Pliocene, Dhok Pathan horizon.

(6) Representing the *Stegolophodon* phylum is the Upper(?) Pliocene *Stegolophodon stegodontoides* type, of approximately the same age as *Stegodon ganesa* lectotype and *S. orientalis grangeri* type. (7) *Stegolophodon latidens* ref. is recorded in the same Middle Pliocene (Dhok Pathan) geologic level as *Stegodon bombifrons* lectotype. (8) The Upper Miocene [Middle Pliocene] yields *Stegolophodon cautleyi* lectotype of Perim Island (Dhok Pathan). (9) The Middle Miocene [Mio-Pliocene] yields *Stegolophodon cautleyi progressus* and *S. nathotensis*.

4. GEOLOGIC AND DIPHYLETIC ORDER OF THE STEGODONTINÆ

The geologic level of Falconer's types of *Elephas* [= *Stegodon*] *ganesa* and *E.* [= *S.*] *insignis*, although unrecorded, is probably Pinjor (see Vol. I, Fig. 413). Pilgrim writes (letter of January 26, 1927): "I am now almost convinced that the bulk of the fossils were collected from that zone, i. e., Upper Pliocene [Pinjor zone, Moginand], but that some came from the Boulder Conglomerate zone Falconer distinctly states." As observed by Barnum Brown, the exact geologic horizon of the type and referred specimens of *S. insignis* and *S. ganesa* is uncertain, because apparently in the Pinjor horizon are obtained jaws and skulls redeposited from the Boulder Conglomerate above.

5. HISTORY OF DISCOVERY OF THE SUBFAMILY STEGODONTINÆ. PRINCIPLES OF TYPE REVISION OF THE SPECIES

GENERA.—Up to 1924 sixteen species of [Stegolophodonts and] Stegodonts had been discovered and described between the years 1828 and 1917, in the order shown in the list in Section II below. In 1924 Matsumoto described a new subspecies from Japan, namely, *Stegodon orientalis shodoënsis*. In 1929 Osborn described *Stegodon orientalis grangeri* from the pits near Wanhsien, Szechuan, China, *Stegodon insignis birmanicus* from the Pliocene of Burma, Irrawaddy River, and *Stegodon pinjorensis* from the Lower Pleistocene (?Pinjor) of India; also two Stegolophodonts (*Stegolophodon nathotensis* and *S. cautleyi progressus*). All the early species were described either as *Mastodon* (*e.g.*, *Mastodon latidens*, *Mastodon elephantoides*) or as *Elephas* (e.g., *Elephas insignis*, *Elephas ganesa*). Although the name *Stegodon* appears as early as 1847 ("Fauna Antiqua Sivalensis," Falconer and Cautley, Pl. XLII), it was not until the year 1857 (pp. 314, 318, table opp. p. 319) that Falconer ventured to select *Elephas cliftii*, *E. bombifrons*, *E. ganesa*(?), and *E. insignis* as representing a new subgenus, *Stegodon*.

It was in 1922 that Matsumoto in a letter to the present author announced his intention of making *Mastodon latidens* the type of a new genus, *Prostegodon*. The name, however, is preoccupied by the *Stegolophodon* of Schlesinger, 1917 (genotype *Mastodon latidens* Clift), in which genus Osborn united (1929) the four species *M. latidens* Clift, *M. cautleyi* Lydekker, *M. stegodontoides* Pilgrim, and *M.* (*Bunolophodon*) *longirostre* Kaup *forma sublatidens* Schlesinger, also *Stegolophodon nathotensis* Osborn from the lower Middle Siwaliks and *Stegolophodon cautleyi progressus* Osborn from 2,000 feet above the base of the Lower Siwaliks, India.[2]

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[1] [See footnote on preceding page (p. 814) regarding the Lower Pleistocene age of *Stegodon elephantoides* (= *cliftii*).—Editor.]

[2] [To these six species should be added *Stegolophodon lydekkeri* Osborn, described in Volume I of the present Memoir, page 700.—Editor.]

[Recently six additional species of *Stegodon* have been described, namely, *Stegodon bondolensis* van der Maarel 1932, and *S. trigonocephalus praecursor* von Koenigswald, 1933, from Java, *S. officinalis*, *S. zdanskyi* Hopwood, 1935, and *S. yüshensis* Young, 1935, from China, also *Parastegodon* [*Stegodon?*] *sugiyamai* Tokunaga, 1935, from Japan. The generic determination of Tokunaga's species *Parastegodon? kwantoensis*, 1934, has not been given in the present Memoir, owing to Professor Osborn's views regarding the genus *Parastegodon* (see next paragraph).—Editor.]

The genus *Parastegodon* of Matsumoto, 1924, belongs to the genus *Archidiskodon* or to a progressive *Stegodon*, as the genotypic species, *Elephas* (*Parastegodon*) *auroræ*, is slightly more primitive than *Archidiskodon planifrons*.

Principles of Type Revision.—The consideration of these matters of descent and phylogeny, however, must be preceded by a very rigid review of each species of Stegodont in the order of its original description, following the standard methods of type analysis established throughout this Memoir, namely:

1) Determination of the actual *type specimen* or the specimen first mentioned among a series of cotypes.
2) Fixation of the original *type figure*, the one first published by the author or selected by the author from other publications.
3) Enumeration of the *type characters* observed in the type specimen by the author or by subsequent observers.
4) Elimination from the type list of characters founded on *referred* specimens which do not actually belong to the same species as the type.
5) Determination of the type locality and distinction of the topotypes.

Original Descriptions.—The revision of these various species of Stegodonts, on the strict application of the five rules above, has been a long and very difficult task. In order to establish absolutely the original author's intention, the author's *original description* is cited in full. When too prolix, as in the case of many descriptions by Owen and by Lydekker, excerpts are made in the author's own language.

This revision and establishment of *type* characters must be followed by a restudy and revision of *referred* specimens, which in most cases can only be done in future by monographic research directly upon the specimens themselves, amplified by knowledge afforded by fresh materials. Consequently the present Stegodont chapter lays no claim to completeness or finality; it leaves many questions wholly undecided, for example, the sexual or specific dental or cranial distinctions between *Stegodon insignis* and *S. ganesa*.

In the meantime our present establishment of the types and of the type specific characters based upon the type specimens themselves as well as of characters derived from properly referred specimens in the same geologic horizon, as in the case of *Stegodon bombifrons*, may lay a firm foundation for future monographic research.

6. THE STEGODONTINÆ AND MASTODONTINÆ OF CHINA

Two species of Stegodonts described by Owen in 1870, namely, *Stegodon orientalis* and *S. sinensis*, were determined from collections brought in by dealers for medicinal purposes and not procured *in situ* by palæontologists.

a) Koken's Notes of 1885 and Schlosser's Notes of 1903

Koken, "Ueber fossile Säugethiere aus China," 1885, pp. 31–44; Schlosser, "Die fossilen Säugethiere Chinas," 1903, pp. 43–49

Koken's specimens were also probably collected from the caverns of Yunnan by dealers for von Richthofen; his list is as follows (Koken, 1885, p. 33):

Proboscidia.

1.	*Mastodon perimensis* var. *sinensis*	Yünnan.
2.	*Mastodon* aff. *Pandionis*	Yünnan.
*3.	*Stegodon Cliftii*	Shanghai; oberer Hoangho (West-Kansu).
*4.	*Stegodon insignis*	Yünnan; Szechuen.
5.	*Stegodon* aff. *bombifrons*	Yünnan.

Schon früher beschriebene oder erwähnte Arten sind durch *ausgezeichnet.

The type fragments all appear as though they had been brought in by native collectors, for medicine dealers, since they consist of broken teeth only; the same is true of the Schlosser collection. Consequently we regard the specific and generic determinations made from these imperfect materials as of provisional value. The species of Proboscidea contained in Schlosser's article of 1903, following Koken's review of 1885, are as follows:

		Reference in Present Memoir
Fokien, Kansu	*Stegodon orientalis* Owen, 1870 = *Stegodon insignis* Falconer (*fide* Koken, 1885, *fide* Schlosser)	*Stegodon orientalis*
?Shanghai	*Stegodon sinensis* Owen, 1870 = *Stegodon clifti* Falconer (*fide* Koken, 1885), = *Elephas clifti* (*fide* Lydekker, 1886)	*Stegodon sinensis*
	Stegodon bombifrons Falconer, 1846 = *Stegodon* aff. *bombifrons* (*fide* Koken, 1885), = *Elephas bombifrons* (*fide* Lydekker, 1886)	?*Stegodon bombifrons*
Rothe Thone = Shansi	*Mastodon latidens* Clift, 1828 = *Mastodon* aff. *latidens* (*fide* Schlosser)	?*Stegolophodon latidens*
Röthliche Sande = Tientsin, Honan, etc.	*Mastodon Lydekkeri* Schlosser, 1903, related to *Mastodon latidens* (*fide* Schlosser, 1903), to *Serridentinus* (*fide* Osborn)	?*Serridentinus lydekkeri*
	Mastodon perimensis var. *sinensis* Koken, 1885 = *Tetralophodon* (*Lydekkeria*) *sinensis* (*fide* Osborn)	*Tetralophodon* (*Lydekkeria*) *sinensis*
Rothe Thone = Shansi	*Mastodon pandionis* Falconer (*fide* Koken, 1885) = *Incertæ sedis* (*fide* Osborn)	*Incertæ sedis*

b) American Museum Discovery of Stegodon orientalis grangeri near the Yangtze River, China

The first scientific party to collect fossils *in situ* in China, with records of the actual locality and geologic level, was that of the American Museum, under Walter Granger, in 1920–1921.

In a preliminary notice of a collection secured during the winter of 1920–1921 by Dr. Granger of the Central Asiatic Expedition, Matthew and Granger (1923) described the material as occurring in a series of pits or fissures at the village of Yenchingkou in the vicinity of Wanhsien, province of Szechuan, about one hundred and forty miles distant in an air line from Chungkingfoo, the type locality of *Stegodon orientalis* Owen. This Yenchingkou material includes a fairly complete adult skull, two young skulls, a series of palates and lower jaws, and many teeth, which Matthew and Granger figured and partly described (pp. 567–571, figs. 3–6). They remark (p. 567): "*Stegodon orientalis* Owen. Schlosser regards this species as identical with *S. insignis* of India, basing the reference upon the fragmentary teeth described by Owen. Matsumoto regards it as distinct, upon the evidence of the referred material which he describes and figures. The Yen-ching-kao material includes a fairly complete adult skull, two young skulls, a series of palates and lower jaws and many teeth. It should enable us to estimate the affinities of the species more exactly when it has been cleaned up and studied." They deferred further description of this fine material to Osborn (see below, pp. 875-881).

Geologic Age of Stegodon orientalis and S. orientalis grangeri Types.—Matthew and Granger (1923, pp. 563, 565) observe:

> The Chinese fossil mammals described by Owen in 1870 [Footnote: 'Quar. Journ. Geol. Soc., London, XXVI, pp. 417–436, Pls. xxvii–xxix.'] came from 'a cave near the city of Chung-king-foo in the province of Sze-chuan.' Chung-king is on the Yang-tse-kiang above Wan-hsien, about one hundred and forty miles distant [southwest from the Granger locality of Yenching-kou] in an air line. . . . Possibly the Chinese informants of Consul Swinhoe, who sent the fossils to Owen, misled him, unintentionally or deliberately, as to the locality. . . . Owen regarded the [Chungkingfoo] fauna as Pliocene and described the following species:

[Chungkingfoo]		[Yenchingkou]
Stegodon orientalis [type].	Parts of molars.	[*S. orientalis grangeri* type
Rhinoceros sinensis [type].	Parts of 4 upper and 4 lower molars.	*R. sinensis* ref.
Tapirus sinensis [type].	Parts of 3 upper and 4 lower teeth.	*Tapirus sinensis* ref.
Chalicotherium sinense [type].	Part of an upper molar.	*Chalicotherium sinense* ref.
Hyæna sinensis [type].	Canine, 2 premolars.	*Hyæna sinensis* ref.]

> Owen's descriptions and figures accord very well with some of the species in our collection [the Yenchingkou collection of the American Museum], so that we have referred them to his species, whether or not later investigation proves them to be exact topotypes.

7. PLIOCENE TO PLEISTOCENE PROBOSCIDEA OF JAPAN

Discovery.—Matsumoto's discoveries and descriptions of the Japanese Proboscidea up to 1924 are recited in more detail at the close of this chapter (pp. 901 to 909). His *Elephas* (*Prostegodon*, *Parastegodon*) *auroræ*, 1915, 1918, 1924, from a comparison with *Stegodon airâwana* of Java, appears to belong to *Stegodon auroræ* rather than to represent a distinct genus, i. e., *Parastegodon.* Matsumoto (1918, pp. 51, 52) gives the history of discovery of *Stegodon* and *Elephas* in Japan, beginning with Leith Adams (1868), Naumann (1881), Brauns (1883), Lydekker (1886), Martin (1886 [1887]), Tokunaga (1906), Sato (1914), Kato (1914), Matsumoto (1915, 1918). The Japanese species of *Stegodon* referred by Naumann to *S. cliftii* and *S. insignis* have been transferred by Matsumoto to Owen's Chinese species *Stegodon sinensis* and *S. orientalis.* Matsumoto remarks as to sexual characters (*op. cit.*, 1918, p. 52):

> Thus, the present writer's opinion [Footnote: 'This Vol., p. 10.'] that, *St. sinensis,* as well as *St. orientalis,* is geologically younger than *St. cliftii,* evidently holds true also in the Japanese specimens. One evidence noticeable is that the Stegodont species are usually found in couples. For example, *St. cliftii* and *bombifrons* are found associated with each other from the Dhok Pathan to the Tatrot horizon, *St. ganesa* and *insignis* from the Boulder Conglomerate horizon and the Lower Pleistocene of Narbada, *St. orientalis* and *sinensis* from the Uppermost Pliocene to Lower Pleistocene of China and Japan, and *St. airâwana* and *trigonocephalus* from the Lower [to Middle] Pleistocene of Java. One may imagine the possibility, that each couple of species represent sexual dimorphism of one and the same species.

Matsumoto (1924, 1926, 1927) continues the history of discovery of the Stegodonts and Elephants of Japan up to the year 1927, as set forth in detail in this chapter, and presents his recent views as to the phylogeny of these animals as shown in figures 791, 792, and 793. To the fossil fauna of Japan he adds the following five referred and new species (*op. cit.*, 1926.1, p. 1):

> Genus *Stegodon* Falconer & Cautley. 4. *S. clifti* Falconer & Cautley, *ibid.* [Journ. Geol. Soc. Tokyo, Vol. XXXI], 1924 [1924.3], p. 327. Akira-mura, Kage District, Province of Ise—possibly Plaisancian-Astian. 5. *S. sinensis* Owen, *ibid.*, 1924, p. 328. Island of Shôdo (Shôdo-shima or Shôzu-shima), Inland Sea—Milazzian-Tyrrhenian. 6. *S. orientalis* Owen, *ibid.*, 1924, p. 330. (Also as *S. bombifrons, ibid.*, p. 329.) Nagahama, Minato Town, Province of Kazusa; Togane Town, same province—Calabrian. Riuge, Ikadachi-mura, Province of Omi—Calabrian or possibly Cromerian. Okimisome, Ube Coal-Field, Province of Suwô—Cromerian. 7. *S. orientalis shôdoënsis,* nov., *ibid.*, p. 333. Islands of Mitsugo (Mitsugo-shima) and Island of Shôdo, Inland Sea; off Nagasaki, Eastern Sea—Milazzian-Tyrrhenian. Kashiwazaki, Province of Echigo (?this form).

Of the above the genus *Parastegodon* Matsumoto, 1924, is regarded in the present Memoir as belonging to the genus *Archidiskodon* or to a progressive *Stegodon.*

8. PHYLOGENETIC DISCUSSION OF THE THIRTY DESCRIBED SPECIES OF STEGODONTS AND STEGOLOPHODONTS

Double or Multiple Phyla of the Stegodonts. Schlosser, 1903.—Schlosser (1903, p. 191), in his revision of the Stegodonts of China, doubtfully suggested that west European species, originally described as *Mastodon turicensis* [= *M. tapiroides, M. pyrenaicus*, etc.], separated as *Zygolophodon* by Vacek in 1877 and (1926) by Osborn as *Turicius* (*M. turicensis, M. tapiroides*) and *Zygolophodon* (*M. pyrenaicus*), may have given rise to such Upper Miocene [Middle Pliocene] Stegodonts of India as *Stegolophodon cautleyi.*

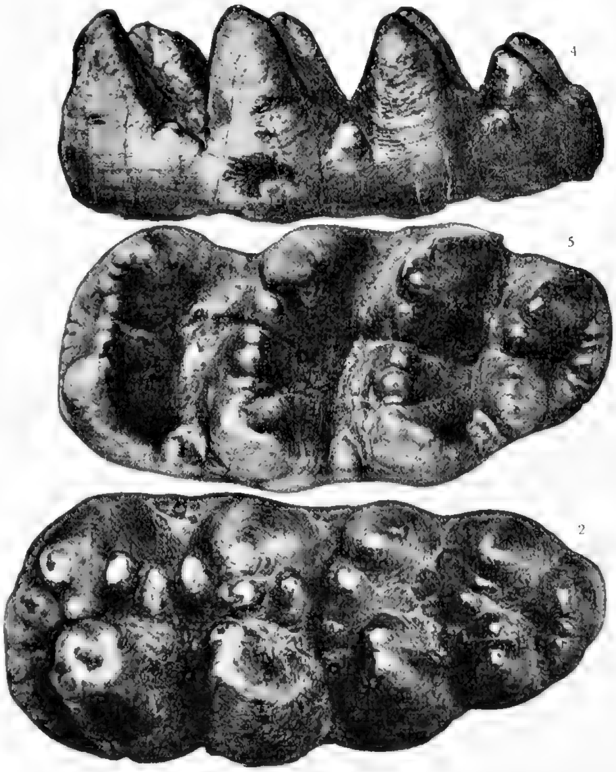
Schlosser was also the first to suggest (*op. cit.*, p. 191) that *Mastodon turicensis* [= *Turicius tapiroides*] of the Lower Miocene of Europe may have given rise to the *Mastodon* [=*Stegolophodon*] *latidens* of the Lower Pliocene[1] of Asia from which in turn sprang off the true Stegodonts, such as *Stegodon insignis.*

More in detail, Schlosser, who was the first to discuss the double phylogeny of the Stegodonts (*op. cit.*, p. 206), separated them into two divisions as follows:

Mastodon latidens Clift
Mastodon cautleyi Lydekker

Stegodon ganesa Falconer and Cautley
Stegodon insignis Falconer and Cautley
Stegodon cliftii Falconer and Cautley
Stegodon bombifrons Falconer and Cautley

Two Phyla Suggested by Pilgrim, 1913.—The second to discuss the phylogeny of the Stegodonts was Pilgrim. The foundations of a *diphyletic* arrangement of the Stegodonts were laid by his observation (1913, pp. 293, 294) that *Mastodon* [= *Stegolophodon*] *latidens* occurs in the same Lower [Middle] Pliocene beds with *Stegodon bombifrons.* Pilgrim's discussion of the phylogeny of the Stegodonts may be paraphrased as follows:



Lower Miocene. Turicius (4,5) compared with Trilophodon (2)

Fig. 689. Left third inferior molar, l.M$_3$. Comparison of *Turicius turicensis* [=*tapiroides*] (upper 4,5) with *Trilophodon pontileviensis* (lower 2), one-half natural size. After Mayet, 1908, Pl. xi, figs. 2, 4, and 5.

These molar teeth exhibit the profound difference between the zygolophodont molar (above), resembling that of a primitive Stegodont with uninterrupted, widely open valleys, and the bunolophodont molar (below), in which the valleys are closed by the *central conules.*

(Upper) Figs. 4, 5.—"*Mastodon turicensis* [= *T. tapiroides*]. Pontlevoy. Dernière molaire inférieure. Paris Muséum. Grandeur naturelle." Fig. 5.—"*Id.* vue d'en haut." See also figure 138C, C1.

(Lower) Fig. 2.—"*Mastodon angustidens.* Falun de Pontlevoy. Dernière molaire supérieure. Communiquée par M. Jean de Bodard, Pontlevoy. Grandeur naturelle." [= *Trilophodon pontileviensis.*]

(a) In the lower deposits of Perim Island there appears a species *Mastodon cautleyi* representing a line of evolution which in all its earlier stages is entirely unknown in Europe [see *Turicius* (?) and *Zygolophodon* (?)]. The lectotype of *M. cautleyi* is a last upper molar, figured by Lydekker in 1886 (1886.1).

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[1] [See note on page 824 below where *Stegolophodon latidens* is given as of Lower Pleistocene age.—Editor.]

(b) In the higher Perim levels, as well as in the Middle Siwaliks of Lower [Middle] Pliocene age, is found a further development of this type in the species *Mastodon latidens*, with an increased number of ridges. The larger form of *M. latidens* is to be regarded as a direct descendant of *Mastodon cautleyi*. The last species of mastodont to be referred to this line is represented by a tooth from Lehri, for which Pilgrim proposed the name *Mastodon* [*Stegolophodon*] *stegodontoides*.

(c) The type tooth of *M. stegodontoides*, of which the horizon is uncertain but may possibly be Upper Siwalik, is distinguished from that of *M. latidens* by the almost entire absence of accessory columns [conules of Osborn]; *M. stegodontoides*, like *M. latidens*, carries on each of its ridges four columns [=conelets of Osborn], while the anterior ridges of the next higher stage, *Stegodon elephantoides* (=*cliftii*),[1] carries nine or ten mamillæ [=conelets of Osborn].

(d) So close is *M. stegodontoides* to *S. elephantoides* (=*cliftii*) that it is hard to separate the two genera.

(e) The true *Stegodon* type represented by *S. bombifrons* appears in the Lower [Middle] Pliocene, Dhok Pathan horizon, before the extinction of the *Mastodon* [=*Stegolophodon*] *cautleyi-latidens-stegodontoides* phylum which is parallel with it.

Pilgrim accordingly divides the Stegodontinæ into two generic phyla: to the first he applies the name *Mastodon* [=*Stegolophodon*], to the second he applies the name *Stegodon*. This may be graphically represented as follows:

MASTODON SERIES [=STEGOLOPHODON]	STEGODON SERIES [=STEGODON]
Upper Pliocene *Mastodon stegodontoides*	*Stegodon bombifrons* [Middle Pliocene]
Lower Pliocene[1] *Mastodon latidens*	*Stegodon cliftii* [=*Stegodon elephantoides* (=*cliftii*), Lower Pliocene][1]
Upper Miocene [Middle Pliocene] *Mastodon cautleyi*	

SCHLESINGER, 1917.—Schlesinger recognized the distinctness of *Stegolophodon*, basing his type on *Mastodon latidens* Clift.

MATSUMOTO, 1922.—The fact that *Mastodon latidens* appears in the same Lower [Middle] Pliocene geologic horizon as *S. bombifrons* is very significant; it tends to support the idea that the Stegodonts were diphyletic. This idea is perhaps carried a step further by Matsumoto who writes (letter, Nov. 20, 1922): "In my report just in preparation on the Japanese 'Mastodonts,' I follow you to refer '*Mastodon*' *latidens* to the genus *Stegodon* creating however a subgenus *Prostegodon* for it. *Prostegodon* is the primitive representative of the *Stegodon*-phylum, representing half bunomastodontine and half stegodontine dental characters. Schlosser's opinion, that *Prostegodon* might be ? a descendant of '*Mastodon*' *turicens*, does not appear to be correct at all."

OSBORN, 1923.—Osborn (1923.601, p. 2) erroneously adopted the generic name *Prostegodon* Matsumoto, based on the genotypic species *Mastodon latidens* Clift. *Prostegodon*, however, is preoccupied by *Stegolophodon* Schlesinger, 1917. Thus the diphyletic arrangement of the Asiatic and European species and genera would appear as follows:

Stegolophodon stegodontoides	*Stegodon ganesa*
Stegolophodon cautleyi	*Stegodon insignis*
Stegolophodon latidens	*Stegodon bombifrons*
Turicius (?) sp.	*Stegodon elephantoides* (=*cliftii*)
Zygolophodon (?) sp.	

MATSUMOTO, 1924, 1926.—A more recent step is that of Matsumoto in a diagram embodied in a letter dated Sendai, November 20, 1924, in which the polyphyletic Stegodontinæ are divided theoretically into *five*

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[1] [See footnote on page 824 regarding the Lower Pleistocene age of *Stegodon elephantoides* (=*cliftii*).—Editor.]

phyla (Fig. 792), and *Trilophodon* [=*Zygolophodon*] *pyrenaicus* (Fig. 791) is placed as ancestral to *Tetralophodon falconeri, Parastegodon* [=*Stegolophodon*] *latidens, P.* [=*S.*] *stegodontoides,* and *Stegodon.*

In other words: (1) The type of *Mastodon* [=*Zygolophodon*] *pyrenaicus* of the Middle Miocene or its ancestors *Zygolophodon pyrenaicus aurelianensis* Osborn of the Lower Miocene of western Europe may be ancestral to the *Stegolophodon* and *Stegodon* species of southern Asia.

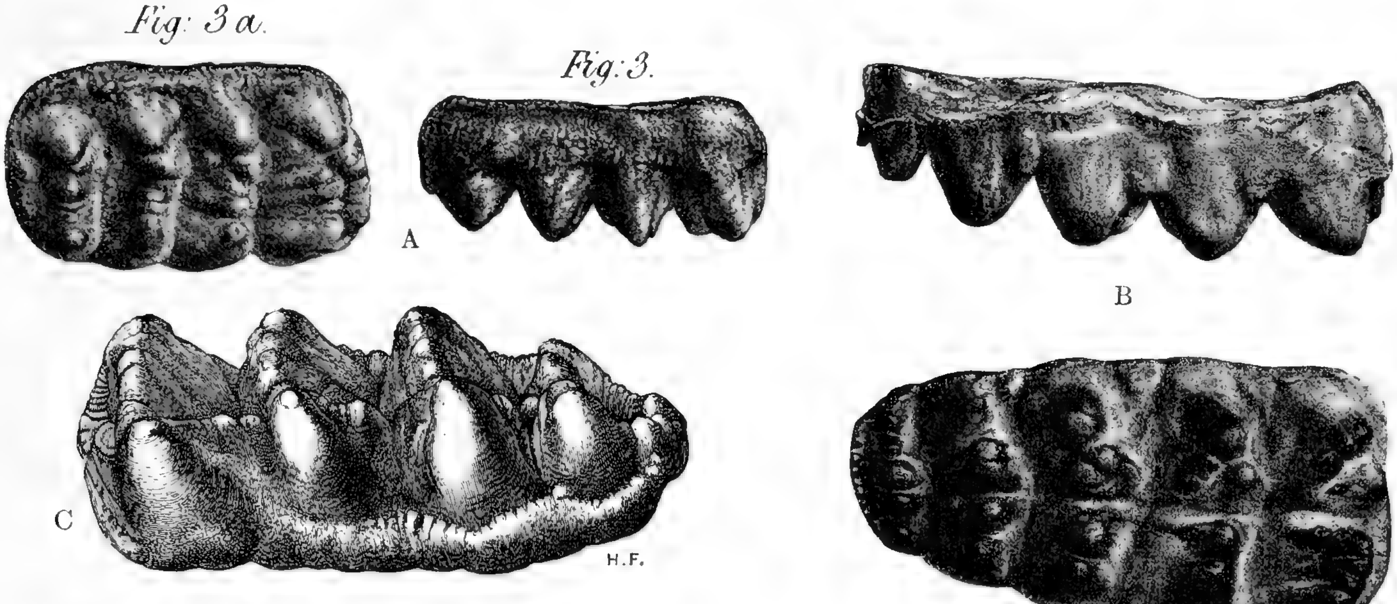

Fig. 230. — Dernière molaire inférieure du *Mastodon turicensis* (*tapiroides*), aux 2/5 de grandeur. — Miocène moyen de Simorre, Gers. (D'après Lartet.)

Turicius (C) and Stegolophodon (A, B) Form of Grinding Teeth
Compare with Stegodon Molars (Fig. 686)

Fig. 690. (C) Type third right inferior molar, r.M_3, of *Turicius turicensis simorrensis* Osborn, 1926, erroneously determined by Lartet (1859, Pl. xv, fig. 3) as *Mastodon tapiroides*, two-fifths natural size. Upper Middle Miocene of Simorre. After Gaudry, 1878, p. 174, fig. 230. Reversed in drawing. See also Vol. I, pp. 207 and 220 of the present Memoir.

Cotype and lectotype of *Mastodon* [=*Stegolophodon*] *cautleyi* Lydekker, 1886.

A (Cotype). First superior molar of the left side, l.M^1, one-third natural size. After Falconer and Cautley, 1846 [1847, Pl. xl, figs. 3, 3a], as "*Mastodon latidens.*" Length 4 inches, width 2.3 inches. Brit. Mus. M.2817. Cast Amer. Mus. 26965. Perim Island. See Lydekker, 1886.1, p.xv, fig. 5.

B (Lectotype). Third superior true molar of the left side, l.M^3, one-third natural size. After Falconer and Cautley, 1846 [1847, Pl. xxxi, figs. 6, 6a] as "*Mastodon latidens.*" Length 8.5 inches, width 4.5 inches. Brit. Mus. M.2705. Cast Amer. Mus. 26966. Perim Island. See also Lydekker, 1886.1, p. xv, fig. 6, and 1886.2, p. 73, fig. 18. Same as figures 141 and 142 of Volume I of the present Memoir.

(2) Matsumoto held (1924) that the Stegodonts are not merely *diphyletic* (e. g., *Stegolophodon* and *Stegodon*), but polyphyletic by subdivision of the species of *Stegodon* into five distinct lines of descent, as clearly displayed in figure 792.

Osborn, 1927.—The present author (1927) takes the more conservative view that there are certainly two distinct phyla, namely: (a) *Stegolophodon cautleyi, S. latidens, S. stegodontoides,* and (b) *Stegodon elephantoides* (=*cliftii*) to *S. airâwana.* The latter appear to present a progressive series in the increasing number of conelets and ridge-crests or lophs, but without very marked divergence, as shown in the geologic succession table (Table III, p. 814).

SUGGESTED EUROPEAN-ASIATIC ORIGIN AND MIGRATION OF THE PRIMITIVE STEGODONTS

The suggestion by Schlosser (1903), rejected by Matsumoto (1922), that the species of *Stegolophodon* may be derived from mastodonts related to the *Turicius* or *Zygolophodon* of western Europe, should not be lightly dismissed. These west European animals have been grouped in the genus *Zygolophodon* by Vacek (1877), based on the three species *Mastodon borsoni*, *M. turicensis*, and *M. tapiroides* (= *M. pyrenaicus*). The genus *Zygolophodon* embraces a type molar tooth fundamentally homologous and analogous, as shown in the accompanying comparison of the lectotype of *Mastodon* [= *Stegolophodon*] *cautleyi* from the Middle Pliocene of Perim Island, with a third inferior molar erroneously referred by Lartet (1859) to *M. tapiroides* [= type of *Turicius turicensis simorrensis* Osborn, 1926—Fig. 690] from the Middle Miocene of Simorre. Molars of the *Turicius turicensis* [= *tapiroides*] type occur in the Lower Miocene, Burdigalian, of the Falun de Pontlevoy, contemporaneous with the referred *Trilophodon angustidens* [= *T. pontileviensis*—Fig. 689, 2].

Actual relationship to primitive Stegodonts [Stegolophodontinæ] of Asia is represented by the *Mastodon* (*Bunolophodon*) *longirostre* Kaup *forma sublatidens* of Schlesinger from the Pliocene of Teschen (Schlesien), Austria (Fig. 722). A striking analogy to the *Stegodon* type is seen in the molar teeth referred by von Meyer to *M.* [*Turicius*] *turicensis* from the lignites of Elgg and Kapfnach, and finally in the strictly stegodont *Mastodon* [*T.*] *virgatidens* of von Meyer (Fig. 168). The only way to test this theory, however, is to place models or casts of the teeth of *Zygolophodon*, of *Turicius*, and of *Stegolophodon* side by side to see whether they compare in close detail, in which case the genus *Zygolophodon* Vacek would replace the genus *Stegolophodon* Schlesinger.

CONCLUSION: PROBABLE AFRICAN-EUROPEAN-ASIATIC ORIGIN AND MIGRATION OF THE PRIMITIVE STEGODONTS

Osborn, 1927[1]: If, as now appears probable, (1) the *Trilophodon* phylum first arrived in southern Europe and migrated eastward into India, (2) it is also probable that certain primitive species of the forest-living *Zygolophodon* or *Turicius* phyla gave rise in Lower Miocene time to forest-living animals which spread into the forests of southern Asia and developed into the *Stegodon* series, as first adumbrated by Schlosser (1903).

The European species actually resembling these animals is the *Mastodon* (*Bunolophodon*) *longirostre* Kaup *forma sublatidens* Schlesinger from Schlesien, Austria (Fig. 722), as described below.

II. TYPE REVISION OF THE SPECIES IN ORDER OF ORIGINAL DISCOVERY AND DESCRIPTION

In the previous Section I of the present Chapter XIV we have discussed the habits and general characters, the ridge formulæ, the geologic order, the history of discovery, the principles of type revision of the species, the Stegodonts of China, Japan, and the East Indies, the phylogenetic succession, and, finally, the probable origin of the Stegodontinæ [and Stegolophodontinæ] in western Europe, and hence more remotely in Africa.

We now pass in Section II to the very complicated subject of the type revision of the species on the principles enumerated above (p. 816). For this purpose we will review the thirty species described in the years between 1828 and 1936 in the order of their description, quoting extensively from the original type descriptions and reproducing every available type or lectotype figure directly after the original author.

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[1] [Compare Vol. I, pp. 195, 197, also Pls. II to IV.—Editor.]

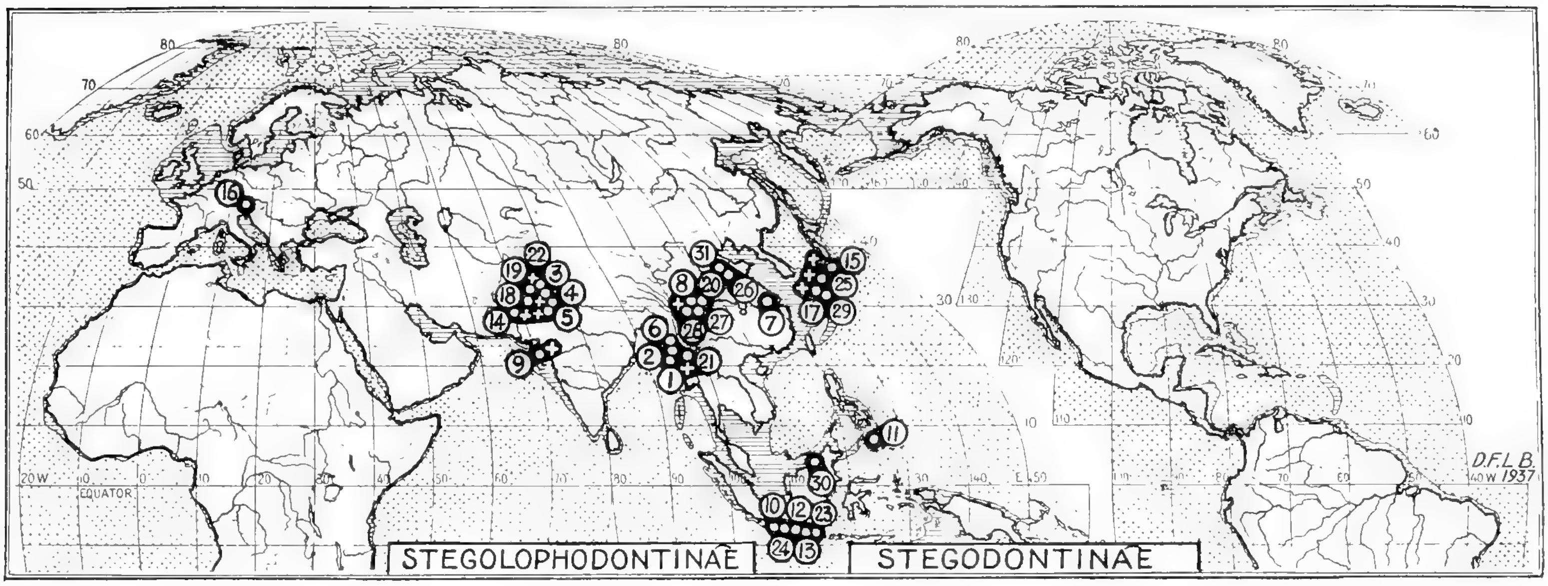

Fig. 691. Geographic distribution of the principal species of *Stegolophodon* and *Stegodon*. The white dots within the black areas represent the approximate localities where the types of these thirty species were discovered. Numbers 1, 9, 14, 16, 18, 19 and 30 are Stegolophodonts (see also Fig. 1228). The white crosses represent referred specimens.

STEGODONTS [AND STEGOLOPHODONTS] IN ORDER OF THEIR DISCOVERY AND DESCRIPTION
See Figure 691

			Original Name	Specific Reference in Present Memoir
1.	Burma	1828	*Mastodon latidens* Clift, Irrawaddy River, Burma	= *Stegolophodon latidens*
2.	Burma	1828	*Mastodon elephantoides* Clift, Irrawaddy River, Burma	= *Stegodon elephantoides*
3.	India	1846 [1845]	*Elephas insignis* Falconer and Cautley, Siwalik Hills, India	= *Stegodon insignis-ganesa*
4.	India	1846 [1845]	*Elephas ganesa* Falconer and Cautley, Siwalik Hills, India	= *Stegodon insignis-ganesa*
5.	India	1846	*Elephas bombifrons* Falconer and Cautley, Siwalik Hills, India	= *Stegodon bombifrons*
6.	Burma	1846	*Elephas cliftii* Falconer and Cautley, Irrawaddy River, Burma	= *Stegodon elephantoides* (= *cliftii*)
7.	China	1870	*Stegodon sinensis* Owen, vicinity of Shanghai, China	= *Stegodon sinensis*
8.	China	1870	*Stegodon orientalis* Owen, Chungkingfoo, province of Szechuan, China	= *Stegodon orientalis*
9.	India	1886	*Mastodon cautleyi* Lydekker, Perim Island, India	= *Stegolophodon cautleyi*
10.	Java	1887	*Stegodon trigonocephalus* Martin, ?vicinity of Surakarta, Java	= *Stegodon trigonocephalus*
11.	Philippines	1890	*Stegodon mindanensis* Naumann, Mindanao, Philippine Islands	= *Stegodon* (*Archidiskodon?*) *mindanensis*
12.	Java	1890	*Stegodon Airâwana* Martin, Alas-Tuwa, Java	= *Stegodon airâwana*
13.	Java	1908	*Stegodon Ganesa* var. *javanicus* Dubois, Trinil, Java	= *Stegodon airâwana* [or *S. trigonocephalus*]
14.	India	1913	*Mastodon stegodontoides* Pilgrim, Lehri, Punjab, India	= *Stegolophodon stegodontoides*
15.	Japan	1915, 1918, 1924	*Elephas* (*Prostegodon, Parastegodon*) *auroræ* Matsumoto, Mt. Tomuro, Kaga, Japan	= *Stegodon auroræ*
16.	Austria	1917	*Mastodon* (*Bunolophodon*) *longirostre* Kaup *forma sublatidens* Schlesinger, Teschen (Schlesien), Austria	= *Stegolophodon sublatidens*
17.	Japan	1924	*Stegodon orientalis shodoënsis* Matsumoto, Island of Mitsugo (Mitsugo-shima) and Island of Shôdo, Inland Sea; off Nagasaki, Eastern Sea, Japan	= *Stegodon orientalis shodoënsis*
18.	India	1929	*Stegolophodon nathotensis* Osborn, near Nathot, India	= *Stegolophodon nathotensis*
19.	India	1929	*Stegolophodon cautleyi progressus* Osborn, near Chinji Bungalow, India	= *Stegolophodon cautleyi progressus*
20.	China	1929	*Stegodon orientalis grangeri* Osborn, Yenchingkou, China	= *Stegodon orientalis grangeri*
21.	Burma	1929	*Stegodon insignis birmanicus* Osborn, Mingoon opposite Mandalay, Burma	= *Stegodon insignis birmanicus*
22.	India	1929	*Stegodon pinjorensis* Osborn, near Siswan, India	= *Stegodon pinjorensis*
23.	Java	1932	*Stegodon bondolensis* van der Maarel, Bondol, near Kuwung	= *Stegodon bondolensis*
24.	Java	1933	*Stegodon trigonocephalus praecursor* von Koenigswald, Bumiaju	Not determined by the present author
25.	Japan	1934	*Parastegodon? kwantoensis* Tokunaga, Kakio, Kanagawa Prefecture	
26.	China	1935	*Stegodon yüshensis* Young, Yüshe	
27.	China	1935	*Stegodon officinalis* Hopwood, Szechuan(?)	= *Stegodon officinalis*
28.	China	1935	*Stegodon zdanskyi* Hopwood. Exact locality unknown	= *Stegodon zdanskyi*
29.	Japan	1935	*Parastegodon sugiyamai* Tokunaga, Iruhi in Saida Village, Shikoku	Not determined by the present author
30.	Borneo	1936	*Stegolophodon lydekkeri* Osborn, near Bruni	= *Stegolophodon lydekkeri*

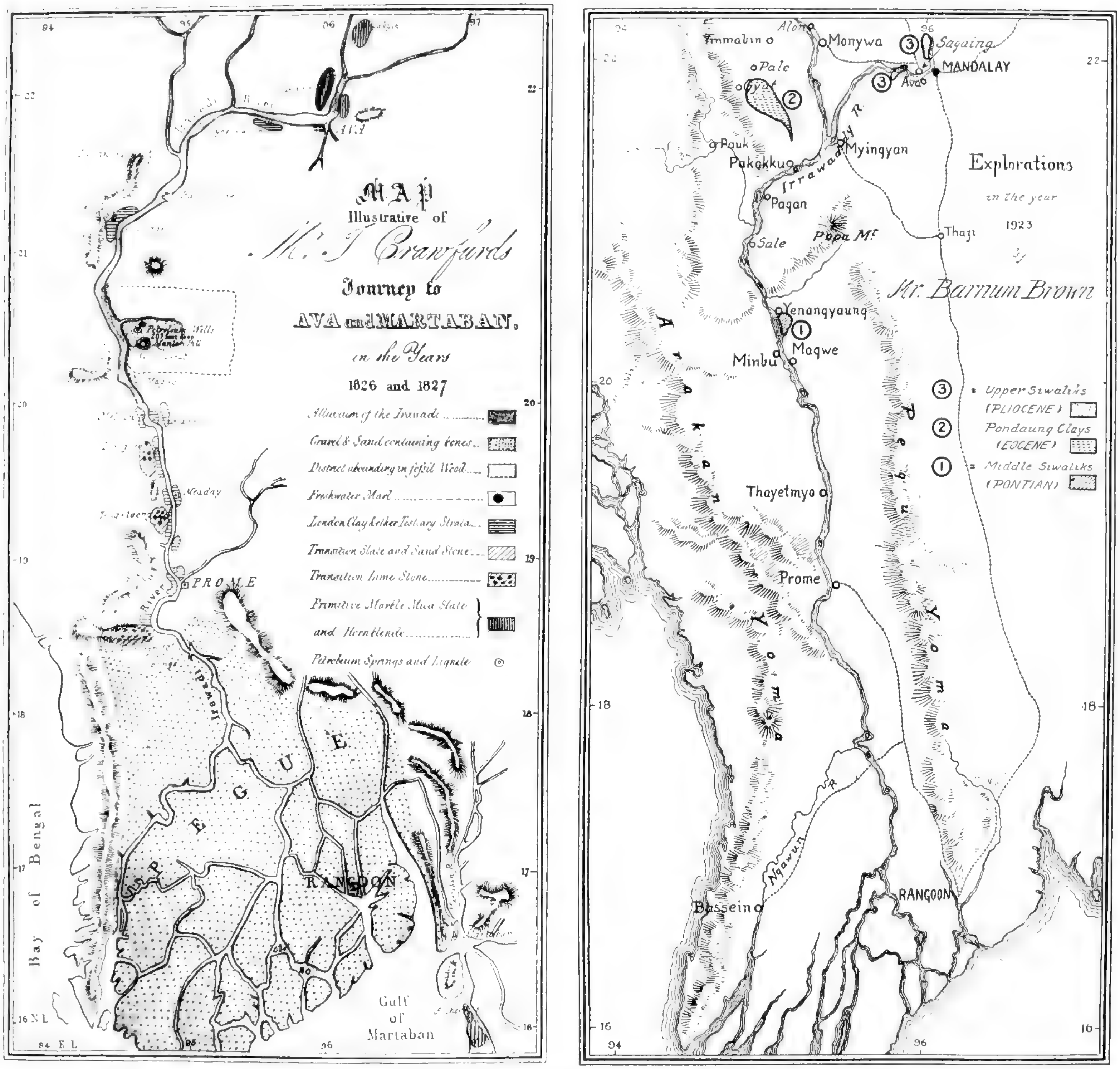

Fig. 692. Fossil-bearing Horizons along the Irrawaddy River, Burma

(Left) Map illustrating J. Crawfurd's journey to Ava and Martaban in the years 1826 and 1827. After William Clift, 1828, Pl. xliv. (Right) Map illustrating the explorations of Barnum Brown for the American Museum of Natural History in the year 1923. Based on the official Indian Survey Gazetteer.

3-3. Ava, upper levels of the Irrawaddy Series (600 feet in thickness) = Upper Pliocene, Upper Siwaliks of India, containing *Stegodon birmanicus* Osborn and undetermined *Bos*. [Lower Pleistocene (cf. Colbert, chap. XXII, pp. 1450, 1451 of the present Memoir.—Editor.]

2. Pondaung Clays (50 feet in thickness) = Upper Eocene, containing the suilline Anthracotheriidæ; also of the Order Perissodactyla: Fam. Titanotheriidæ, Gen. *Sivatitanops*, sp. *S. cotteri*, *S. birmanicum*, *S. rugosidens*, Gen. *Eotitanotherium*, sp. *E. lahirii*; Fam. Amynodontidæ, Gen. *Paramynodon*, sp. *P. cotteri*, *P. birmanicus*; Fam. Tapiridæ [=Lophiodontidæ], Gen. *Indolophus*, sp. *I. guptai*, Gen. *Chasmotherium*, sp. *C. birmanicum*. [For additional members of the Pondaung fauna, see Colbert, 1938.1, pp. 255–398.—Editor.]

1. Yenangyaung (250 miles south of Ava), lowest levels of the Irrawaddy Series (estimated at 1500 feet in thickness), base of the Middle Siwaliks, containing *Stegolophodon latidens* type, *Stegodon elephantoides* type, *S. cliftii* type [*Stegodon elephantoides* (=*cliftii*)].

[Note by Edwin H. Colbert:—The total thickness of the Irrawaddy Series is estimated at 5,000 feet, of which the upper levels only (about 600 feet), so far as known, are mammal bearing and are now regarded by recent geologists and palæontologists as of Lower Pleistocene age. Stamp (1922, pp. 497, 498), for example, has shown that *Mastodon* [*Stegolophodon*] *latidens* and *Hippopotamus irravaticus* are probably limited to the upper Irrawaddy beds (Lower Pleistocene). He considers that Pilgrim erred (1910, p. 196) in placing these species in the lower Irrawaddy fauna (cf. Colbert, Chap. XXII, pp. 1450, 1451, of the present Memoir). Colbert places all the proboscideans discovered in Burma up to the present time, namely, *Stegolophodon latidens*, *Stegodon elephantoides*, *S. elephantoides* (=*cliftii*), and *S. birmanicus*, in the upper Irrawaddy Series, thus assigning them to the Lower Pleistocene. The lowest levels of the Series are considered of Middle to Upper Pliocene age. Likewise the Pondaung clays are of a total thickness of 6,500 feet, the mammal-bearing portion apparently not exceeding 50 feet.—Editor.]

1. THE FIRST TWO STEGODONTS, DISCOVERED IN BURMA, 1828

Geology, Irrawaddy River, Burma.—In the years 1826 and 1827, J. Crawfurd, F.R.S., while on an embassy to Ava, Burma, discovered an extensive deposit of organic remains in that unknown and distant region. On the Irrawaddy River, 250 miles below Ava, a gravel and sand deposit contained fossil bones, as mapped and described by Buckland (1828). This is the type region of *Mastodon latidens* Clift, 1828, and of *Mastodon elephantoides* Clift, 1828, also of "*Elephas cliftii*" Falconer and Cautley, 1846. According to Buckland (1828, p. 378) the exposure is an extensive one:

> These plants were found most abundantly in the same region with the fossil bones, but occur also along nearly the whole course of the Irawadi from Ava to Prome. They were principally collected from a tract of country [Footnote: 'See annexed map, Plate xliv.'] extending over a square of more than twenty miles on the east bank of the Irawadi, near the town of Wetmasut, about half-way between Ava and Prome, between lat. 20° and 21° N. The occurrence of bones was most abundant in a small space near the centre of this district, occupying about one third of the above-named area, the surface of which is composed chiefly of barren sand hills mixed with gravel; beneath these are strata containing shells and lignite, through which they sink wells about two hundred feet to collect petroleum.

This indicates that the cotype specimens came from lower and higher geologic levels, a fact not realized in Buckland's paper, nor in subsequent descriptions excepting those of Pilgrim.[1] Referring to Clift's paper of 1828, Buckland mentions (p. 380):

> . . . two new and strongly characterized species, one of which, from its approximation to the elephant in the structure of the teeth, Mr. Clift proposes to designate by the name of *Mastodon elephantoides*: to the other he has given the name of *Mastodon latidens*.

Lydekker (1886.2, p. 81) states that the type of *E. cliftii*, l.M^1, "was obtained near Yenankhoung, on the left bank of the Irawadi in Upper Burma, by Crawfurd in 1826, and is preserved in the Museum of the Geological Society."[2]

D. N. Wadia (1919, p. 213) includes this Burmese [Yenangyaung] deposit in the "Irrawaddy system" [series], which combines marine and fluviatile strata. The upper part (=2,000 feet), composed of "sands and clays with abundance of fossil wood and mammals," is of fluviatile origin and corresponds to the Manchhars of Baluchistan and to the Siwaliks of the sub-Himalayas.

Barnum Brown visited this region in 1923 for the American Museum of Natural History and prepared a new map (Fig. 692, right) of this classic collecting ground which should be compared with Crawfurd's original map (Fig. 692, left). The three geologic levels, discovered along the Irrawaddy River, Burma, are shown in these maps.

HISTORY OF DISCOVERY OF BURMESE STEGODONTS

Clift, 1828.—The first proboscidean described from Burma was *Mastodon latidens* Clift (1828, p. 371), the second species was *Mastodon elephantoides* Clift (1828, p. 372), both species founded on excellent cotypes with the excellent figures which are reproduced herewith (Figs. 693, 694, 695, 696).

Mastodon latidens.—The cotypes of *M. latidens* (Figs. 693, 694) were found in 1826 on the Irrawaddy River, 250 miles below Ava, near Yenangyaung, Burma. Clift's figured specimens include: Plate xxxvi, upper jaw (palate with anterior molar teeth, M^2 much worn), which rightly (Osborn) belongs to *Mastodon* [=*Stegodon*] *elephantoides;* Plate xxxvii, upper molar teeth of the right side, M^2, M^3 (a younger animal), also Plate xxxviii, fig. 1, anterior part of the lower jaw; these certainly are the cotypes, because they conform with Clift's description—all from the left bank of the Irrawaddy.

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[1] [See this Volume, Chapter XXII, p. 1450, by Edwin H. Colbert.—Editor.]

[2] [Now in British Museum (Brit. Mus. M. 10520)].

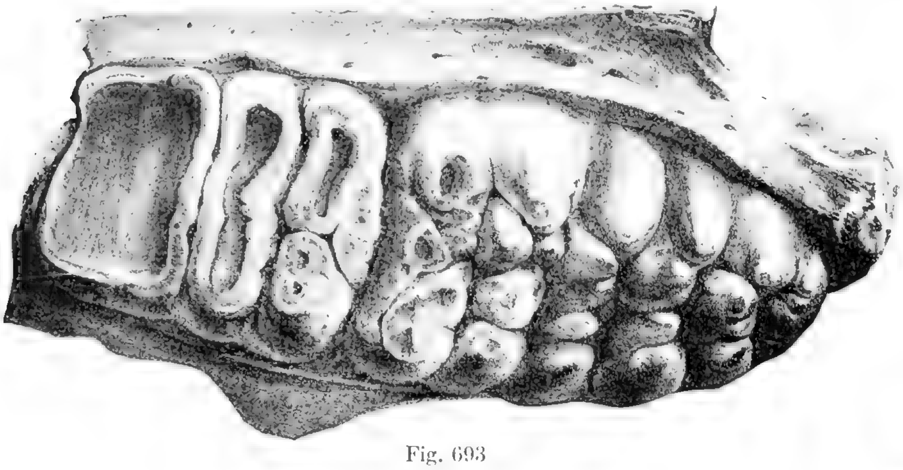

Fig. 693

LECTOTYPE PALATE OF STEGOLOPHODON LATIDENS

Fig. 693 (left). Lectotype palate (perspective of r.M^3) of *Mastodon latidens* Clift, 1828, Pl. XXXVII, fig. 1, with r.M$^{2-3}$ *in situ*, about one-third natural size. Inverted to show natural position of molars. From near Yenangyaung, Burma.

Observe beginnings of binary fission of cones in tritoloph. An accurate scale drawing of these teeth is shown in figure 716 from a cast (Amer. Mus. 21978).

COTYPE THIRD INFERIOR MOLAR OF STEGOLOPHODON LATIDENS

Fig. 694 (right). Cotype third right inferior molar, r.M$_3$, of *Mastodon latidens* Clift, 1828, Pl. XXXVIII, fig. 1, one-third natural size. Jaw omitted. From near Yenangyaung, Burma.

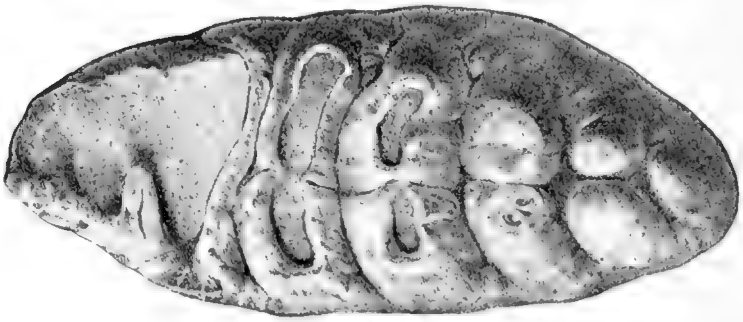

Fig. 694

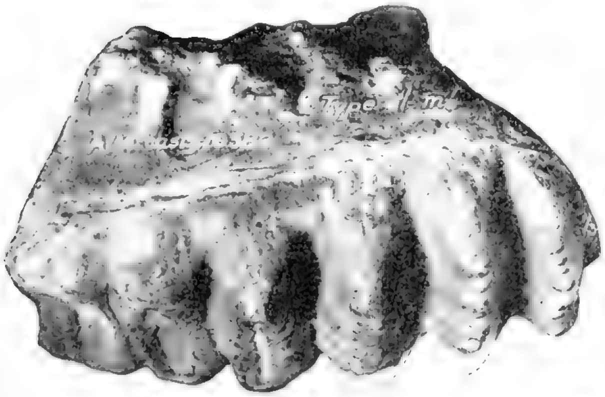

Fig. 695

COTYPE OF STEGODON ELEPHANTOIDES CLIFT (=CLIFTII FALCONER)

Fig. 695 (left). Type first left superior molar, l.M^1, of *Elephas cliftii* Falconer and Cautley, 1846, after photograph of cast Amer. Mus. Warren Coll. 10382, one-half natural size. Inverted to show the molar in natural position. From near Yenangyaung, Burma. See also figure 683. Compare Clift, 1828, Pl. XXXIX, fig. 6. Original in British Museum (Natural History) M.10520.

LECTOTYPE LOWER JAW OF STEGODON ELEPHANTOIDES

Fig. 696 (right). Lectotype second and third left inferior molars, l.M$_{3-2}$, of *Mastodon elephantoides* Clift, 1828. Pl. XXXVIII, fig. 2, one-third natural size. From near Yenangyaung, Burma,

Fig. 696

> MASTODON LATIDENS (OP. CIT., P. 370).—On comparing the teeth of our Mastodon latidens with those of the Mastodon of the Ohio (M. giganteum), we shall find the elevated points or ridges in the tooth of the former more numerous, less distant, and the interstices less deep than in those of the latter; in short, we shall observe that the teeth begin to assume the appearance of those of the elephant. On advancing to Mastodon elephantoides, we shall find all these features of similarity more strongly developed;—the points and ridges are still more numerous, and the structure, were it not for the absence of crusta petrosa, becomes almost that of the tooth of the elephant.

MASTODON ELEPHANTOIDES.—This species (Fig. 696) was found in the same locality as the cotypes of *M. latidens.* Clift's figured specimens include: Plate XXXVIII, fig. 2 (lower jaw with M_2, M_3 *in situ*); Plate XXXVI (palate figured by Clift as *M. latidens*), and Plate XXXIX, fig. 6 (a first superior molar, l.M^1) afterward made the type of *Elephas cliftii* by Falconer and Cautley, referred in the present Memoir to *Stegodon elephantoides* (*=cliftii*).

> MASTODON ELEPHANTOIDES (OP. CIT., P. 372).—The tooth [Fig. 696], which is eleven inches long and three inches and a half broad, has no less than ten denticules [i.e., ridges], and each of these denticules is mammillated with small points; five being the smallest number, and eight the greatest on any one denticule. In front of this beautiful tooth we have a remnant of the preceding one, . . .

Osborn, 1924: Pending final revision, which can only be made by a reëxamination of the specimens and the localities from which they came, we may designate these Stegodonts from Burma as follows:

Mastodon [=*Stegolophodon*] *latidens*	Clift, 1828, founded upon a palate from near Yenangyaung, Burma, with five and a half ridge-crests in the third superior molar, four and a half to five in the second superior molar, and with four to five mamillæ (or conelets) on each crest. See Clift, 1828, Pl. XXXVII, fig. 1 (Fig. 693 of the present Memoir). Also a lower jaw (see Clift, Pl. XXXVIII, fig. 1), r.M_3 with seven ridge-crests (Fig. 694 of the present Memoir).
Mastodon [=*Stegodon*] *elephantoides*	Clift, 1828, founded upon a third inferior molar of the left side, l.M_3, from near Yenangyaung, Burma, with ten ridge-crests, five to eight conelets on each. See Clift, 1828, Pl. XXXVIII, fig. 2 (Fig. 696 of the present Memoir). Also a palate showing r.M^2 and l.M^2, with six and a quarter ridge-crests (see Clift, 1828, Pl. XXXVI), erroneously marked "Upper Jaw of *Mastodon latidens.*" (Not figured in the present Memoir.)
Stegodon elephantoides (=*cliftii*)	Also a left first superior molar, l.M^1, with six and a quarter ridge-crests, from near Yenangyaung, Burma. See Clift, 1828, Pl. XXXIX, fig. 6, marked "Upper molar of *M. Elephantoides.*" Afterward made the type of *Elephas cliftii* by Falconer and Cautley. (Figs. 683, 695, of the present Memoir.)

ORIGINAL COTYPES OF MASTODON LATIDENS CLIFT (FIGS. 693, 694)

FIRST SPECIES.—Clift's designation (1828) of *Mastodon latidens* as including a lower jaw (Pl. XXXVIII, fig. 1—Fig. 694 of the present Memoir) and a palate containing M^2, M^3 (Pl. XXXVII, fig. 1—Fig. 693 of the present Memoir) establishes these specimens as the cotypes. The same superior teeth, r.M^2, r.M^3, were sectioned and figured by Falconer and Cautley (1846, p. 48 [1845, Pl. III, fig. 8]):

> The last tooth shows five principal ridges with a posterior talon ridge and a subordinate ridge in front. The ridges are transverse, and divided by a longitudinal cleft into two pairs of principal points without intermediate mammillæ in the hollows. The enamel is very thick, and the cement is reduced to a thin layer which is only observable in the bottom of the hollows. . . . The anterior tooth [M^2] had been a long time in use, and the ridges are nearly all worn out. They were four in number, in this as well as in the two teeth which preceded it in the jaw. We believe this to be a small or dwarf variety of M. latidens. . . .
>
> (Clift, 1828, p. 371): Dentition.—Each tooth of the lower jaw [Fig. 694] consists of seven denticules, which are elevated, rounded, and mammillated: the mammillæ being from three to four in number. The dentition both in this species and in M. elephantoides, very much resembles that of the elephant. We have the molar tooth gradually protruded forward, and rising as the fangs are added, according to the demand made by the abrasion of the exposed crown, and the consequent absorption of the anterior fang; the posterior part of the tooth not having cut the gum, while the anterior portion is completely worn away. The relics of the preceding tooth, the place of which the tooth in use was progressively supplying, are plainly to be seen [Footnote: 'See Plate XXXVII. fig. 1. Plate XXXVIII. fig. 2.'].

According to the above, the ridge formula is as follows:

Ridge formula of *Mastodon* [=*Stegolophodon*] *latidens*: Dp $4\frac{4}{7}$ M $1\frac{4}{7}$ M $2\frac{4}{4}$ M $3\frac{5\frac{1}{2}}{7}$.

Osborn, 1927: The above is the main ridge formula given by Falconer, omitting the anterior and posterior talon ridges (compare tables above, Section I, No. 3, and below Section IV of this chapter, also full description).

ORIGINAL COTYPES OF MASTODON ELEPHANTOIDES CLIFT (Fig. 696)

SECOND SPECIES.—The second species is *Mastodon elephantoides* Clift.

> CLIFT, 1828, P. 372.—*Mastodon elephantoides*.—M. dentibus molaribus latis, denticulis numerosis, compressis. This species must have been smaller than the last; and though we have one fine example of the lower jaw, showing the tooth in the highest degree of perfection, that is the only portion of the animal from which we can safely draw any inference as to its structure and habits. The tooth, which is eleven inches long and three inches and a half broad, has no less than ten denticules [i. e., ridge-crests], and each of these denticules is mammillated with small points [conelets]; five being the smallest number, and eight the greatest on any one denticule. . . . The denticules of the tooth are much more compressed than those in the species last described; they are closer together [Footnote: 'Eight denticules of M. elephantoides occupy the same space as five denticules of M. latidens.'], and the enamel appears to be not so thick. They form a series of plates mucronated with small points. There is no apparent commissure, neither is there any central depression: on the contrary, the plates rather rise in the middle.

Clift uses the word denticules in the sense of ridges, or crests, or lophs; subsequently Falconer uses the word denticles in the sense of "mammillæ" or conelets. Osborn introduces the word *conelets*, because these small, rounded "mammillæ" appear on the summits of the primary *cones*, as explained above (p. 812).

(Clift, 1828, "Explanation of Plates," Pl. XXXIX, fig. 6): "Upper molar tooth of Mastodon elephantoides." [No mention of this tooth is found in the text.] As reproduced herewith (Fig. 695) this molar corresponds closely in scale and structure with Clift's *type* of *M. elephantoides* (Fig. 696).

Osborn, 1927: From these two teeth, figured and described together by Clift, 1828, not improbably representing the same species, also from the palate with r.M^2 and l.M^2 *in situ* (Clift's figure, Pl. XXXVI), the following ridge formula may be written:

Ridge formula of *Mastodon* [=*Stegodon*] *elephantoides:* M $1\frac{6\frac{1}{4}}{?}$ M $2\frac{6\frac{1}{4}}{?}$ M $3\frac{?}{10}$.

The above ridge formula is similar to that of *Stegodon bombifrons* and much more primitive than that of *S. insignis-ganesa*. Consequently *Mastodon elephantoides* Clift, 1828, of Lower Pliocene age,[1] based upon two figured specimens (Figs. 695, 696), appears to be well established as the second species of *Stegodon* described from Burma in 1828. The name *elephantoides* was dropped, however, by Falconer and Cautley in 1846 and a new name, *Elephas cliftii*, was applied to the second specimen (Fig. 695 of the present Memoir) figured by Clift, Pl. XXXIX, fig. 6.

SPECIES M. ELEPHANTOIDES DROPPED BY FALCONER AND LYDEKKER.—In 1846, Falconer and Cautley erroneously alleged that Clift had confused the remains of the two species *Mastodon latidens* and *M. elephantoides* under the name *M. elephantoides;* they accordingly (*op. cit.*, p. 47) dropped the name *elephantoides* and proposed a new name for the species of "transitional Mastodons," which had been partly confused with *Mastodon latidens*. Thus to the Stegodonts with six ridges on the intermediate molars they gave the name of *Elephas cliftii* (Figs. 683, 695), and to the Stegodonts with a greater number of ridges the name of *E. insignis* (Fig. 697). In a subsequent paper (Falconer, 1857, p. 314), these and other species appeared under the subgeneric name of *Stegodon* Falconer. Lydekker (Palæontologia Indica, 1880, pp. 256, 257) also set aside the prior specific name *elephantoides* Clift, 1828, and made it a synonym of *Stegodon cliftii* Falc. and Caut., 1846. In subsequent literature (e. g., Pilgrim) the Falconer-Lydekker usage is followed, i.e., *M. elephantoides* is dropped.

M. ELEPHANTOIDES REVIVED.—In the present Memoir the specific name *elephantoides* is revived by Osborn for reasons given in the systematic revisions above and below.

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[1] [See note on page 824 above regarding the Lower Pleistocene age of *Stegodon elephantoides*.—Editor.]

2. DISCOVERIES IN INDIA AND BURMA (1845, 1846)

Third Species.—The third species of Stegodont (*Elephas insignis*) was described (Falconer and Cautley, 1846, p. 37) as follows (see Fig. 697):

> . . . the four anterior ridges being affected by wear, and the six posterior ridges entire, . . . The white mass in the centre [dentine] represents the body of ivory, which is projected upwards in ten angular lobes terminating in a sharp edge. . . . The interspaces of the five posterior ridges of enamel are completely filled up by a mass of cement, or 'cortical,' much exceeding the enamel in thickness; and in quantity in nearly as great an amount of development as the ivory core of the ridge.

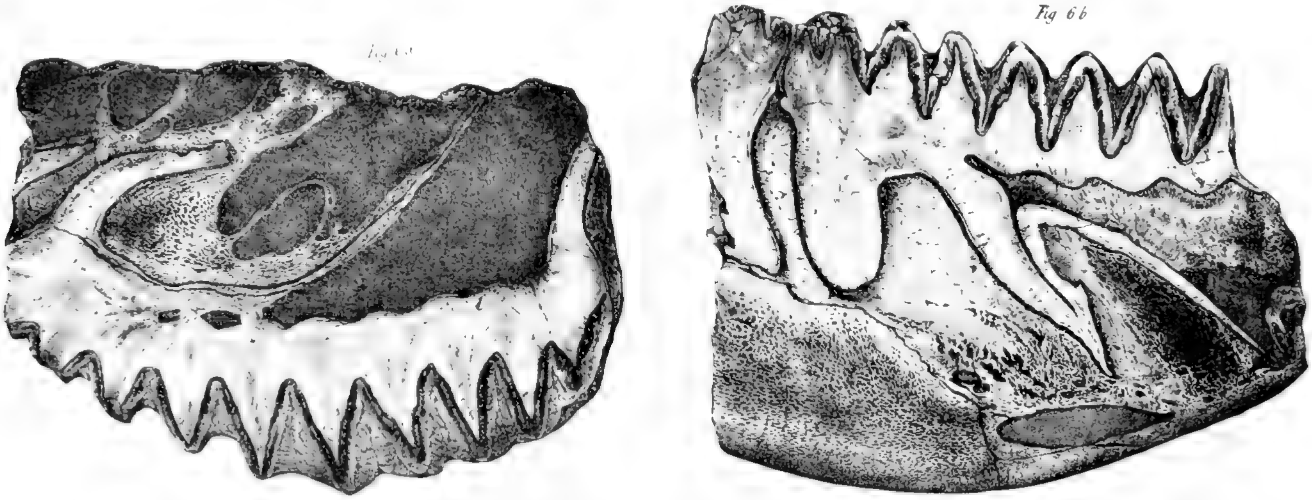


Fig. 697. Lectotype and Cotype of Stegodon insignis

(Left) Lectotype superior molar, l.M^3, of *Elephas insignis* Falconer and Cautley, 1846 [1845, Pl. II, fig. *6a*], one-third natural size. Probably Pinjor horizon, Upper Pliocene [Lower Pleistocene], Upper Siwaliks, India. Inverted to show natural position of molar.

(Right) *Elephas* [= *Stegodon*] *insignis* cotype. Anterior portion of a third inferior molar, M_3. After Falconer and Cautley, *op. cit.*, Pl. II, fig. *6b*.

Falconer distinguished this species as possessing a ridge formula of $\mathrm{M}\,3\,\frac{10}{}$, with valleys between acute ridges deeply filled with cement, as compared with *Stegodon elephantoides* which has ten less acute ridges without cement (Fig. 696). Lectotype ridge formula (Fig. 697) of *Elephas* [= *Stegodon*] *insignis:* $\mathrm{M}\,3\,\frac{10}{}$.

Fourth Species.—The fourth species of Stegodont (described by Falconer and Cautley, 1846, p. 45) was named *Elephas ganesa:*

> Fig. 7*a*, pl. 3., represents a section of the last upper molar of an undescribed Indian fossil species, named *E. Ganesa*, in this work. The crown consists of ten principal ridges, with a subordinate 'talon' ridge in front and behind [i.e., $\mathrm{M}\,3\frac{\frac{1}{4}\text{-}10\text{-}\frac{1}{4}}{}$]. The anterior seven ridges have their summits worn, the two in front being ground down to the common base of ivory, the tooth having been a considerable time in use. A small portion is broken off at the anterior end. The disposition and relative proportions of the ivory, enamel, and cement, bear the closest resemblance to those of the corresponding tooth of *E. insignis* (pl. 2, fig. 6*a*), and the number of ridges agrees. The section presents the same chevron-formed character in the ridges, but the interspaces are narrower, the cement is in less quantity, and the layer of enamel is thicker.

Lectotype of Stegodon ganesa

Fig. 698. Lectotype M^3 of *Elephas Ganesa* Falconer and Cautley, 1846, [1845, Pl. III, fig. 7*a*], one-third natural size. Probably Pinjor horizon, Upper Pliocene [Lower Pleistocene]. Upper Siwaliks, India.

Lydekker observes (Lydekker, 1880.1, p. 268): . . . "these latter teeth, however, cannot be distinguished from those named *Stegodon insignis*, and as we shall see subsequently, it is only the adult skulls of these two very closely allied species that can be distinguished." This has led to the opinion that *S. insignis* may represent a female and *S. ganesa* a male of the same species.

The ridge formula of the lectotype third superior molar of *Stegodon ganesa* (Fig. 698) appears to be practically the same as that of the lectotype of *S. insignis* (Fig. 697). Other more progressive ridge formulæ are shown in the comparative ridge formulæ tables above and below in this Memoir.

Ridge formula (Fig. 698) of *Elephas* [=*Stegodon*] *ganesa:* $M\ 3\ \frac{\frac{1}{2}\text{-}10\text{-}\frac{1}{2}}{\quad}$.

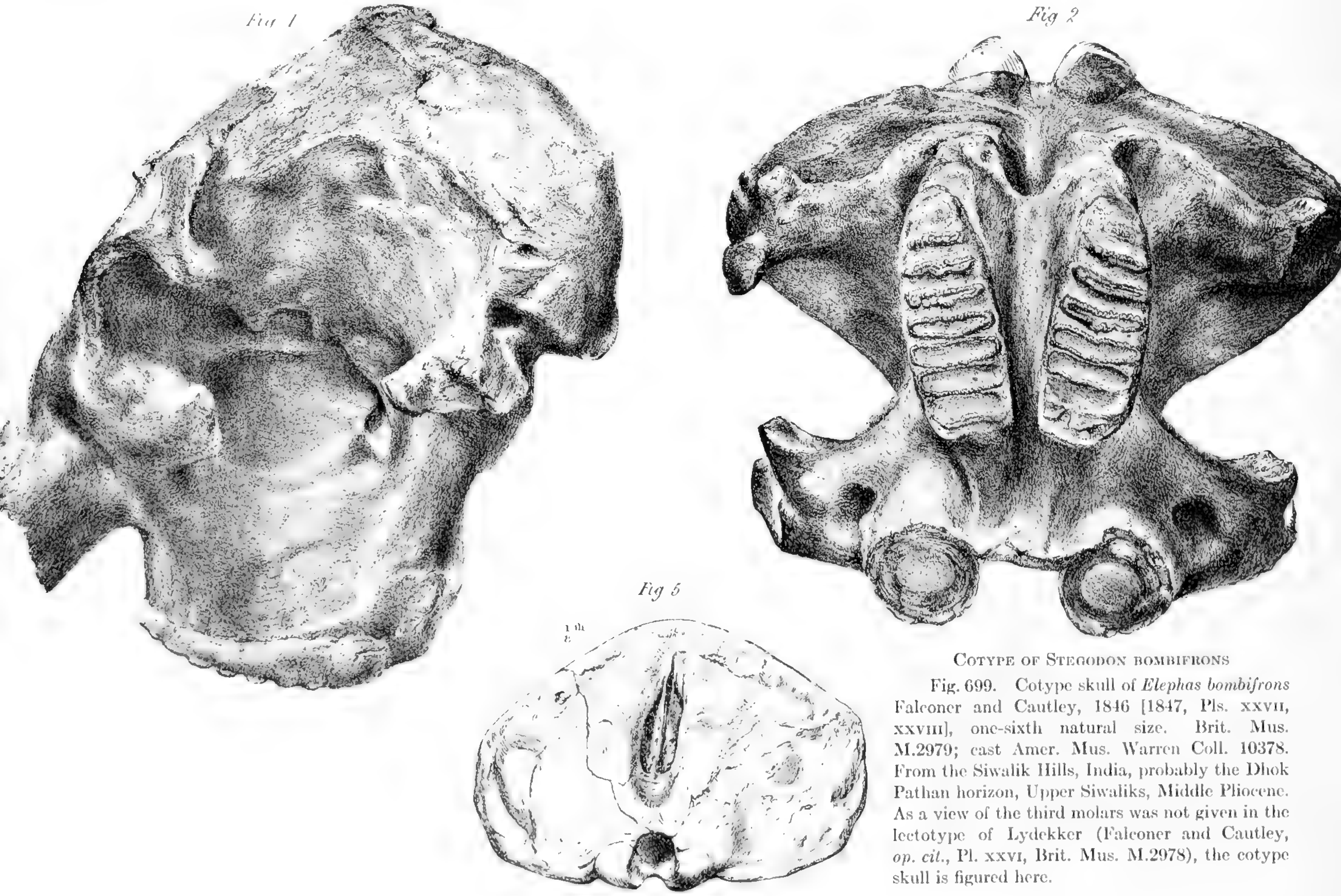
Fifth Species.—Falconer described (Falconer and Cautley, 1846, p. 46) *Elephas bombifrons*, the fifth species of Stegodont, as follows:

> This species, of the distinctness of which we are assured, by possessing several crania containing perfect teeth, belongs to the same group [*Stegodon*] as the two species last described. The crown is divided into similar transverse ridges, composed of numerous mammillæ, which yield a corresponding chevron-shaped section, and the interspaces are occupied by a thick coat of cement; but they differ, in being broader and less elevated, with more open hollows. The principal ridges of the last molar [M^3] do not exceed eight in the upper jaw, and nine in the lower [M_3]; while in *E. insignis* they amount to ten in the former [M^3], and reach as many as thirteen in the latter [M_3]. The last tooth of the upper jaw measures eleven inches in length, by four and a half in width.

Falconer and Cautley (1846 [1847, Pl. xxviii]) assign to M^3 nine ridges and a heel.

Lectotype ridge formula of *Stegodon bombifrons:* $M\ 3\ \frac{8}{9}$.

Sixth Species.—A sixth species of Stegodont (Figs. 683 and 695) was erroneously proposed by Falconer and Cautley in 1846 (1846, p. 47) under the name of '*Elephas cliftii.*' They selected the type of this species as follows:

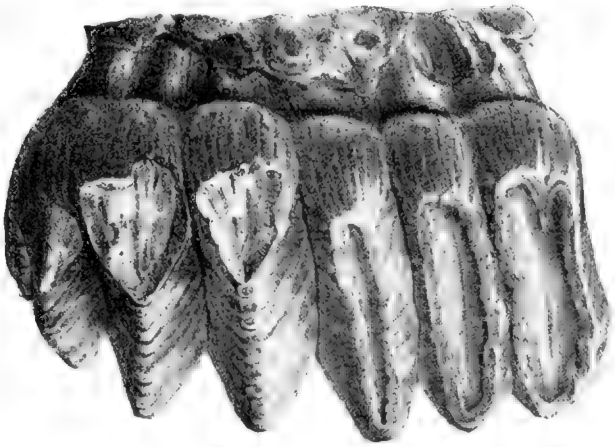


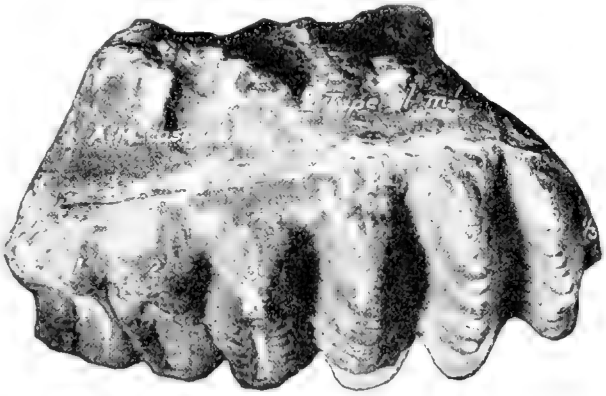
Cotype of Stegodon bombifrons

Fig. 699. Cotype skull of *Elephas bombifrons* Falconer and Cautley, 1846 [1847, Pls. xxvii, xxviii], one-sixth natural size. Brit. Mus. M.2979; cast Amer. Mus. Warren Coll. 10378. From the Siwalik Hills, India, probably the Dhok Pathan horizon, Upper Siwaliks, Middle Pliocene. As a view of the third molars was not given in the lectotype of Lydekker (Falconer and Cautley, *op. cit.*, Pl. xxvi, Brit. Mus. M.2978), the cotype skull is figured here.

> In our view, the tooth represented in pl. 39, fig. 6, of Mr. Clift's memoir in the Geological Transactions [Clift, 1828], under the name of *Mastodon Elephantoides,* and the palate specimen represented in pl. 36 of the same memoir, under the name of *M. latidens,* belong to this species.

This was an unfortunate error. As explained above, the tooth in Pl. 39, fig. 6, of Clift's Memoir, measuring 155 mm. in length, 83 mm. in breadth, has a ridge formula of $\mathrm{M}\ 1\,\frac{6\frac{1}{4}}{}$; the palate specimen (Pl. 36), erroneously identified by Clift as "*Mastodon latidens,*" also has a ridge formula of $(?)\mathrm{M}\ 2\frac{6\frac{1}{4}}{}$. Consequently they belong to the same species, namely, *Stegodon elephantoides,* but to preserve the name *cliftii,* which runs all through the previous literature, they are designated in the present Memoir as *Stegodon elephantoides* (=*cliftii*).





Stegodon elephantoides (=cliftii)

Fig. 700. Original type figure of *Elephas cliftii* Falconer and Cautley, 1846, a first superior molar of the left side, $\mathrm{l.M}^1$, one-half natural size. From near Yenangyaung, Burma. After Clift, 1828, Pl. xxxix, fig. 6, figured as an "Upper molar of *M. Elephantoides.*" Original in the British Museum (Brit. Mus. M.10520); cast Amer. Mus. Warren Coll. 10382. Inverted to show natural position.

Fig. 701. New figure of type of *Elephas cliftii* Falconer and Cautley, 1846, a first superior molar of the left side, $\mathrm{l.M}^1$, described and figured as *M. Elephantoides* by Clift, 1828, Pl. xxxix, fig. 6. Subsequently selected by Falconer and Cautley as the type of *Elephas cliftii.* After photograph of type cast (Amer. Mus. Warren Coll. 10382). One-half natural size. Observe that the molar is here placed in its natural position. Original in the British Museum (Brit. Mus. M.10520).

3. THE STEGODONTS OF CHINA, INDIA, JAVA, THE PHILIPPINE ISLANDS, AUSTRIA, JAPAN, AND BURMA

Seventh Species.—The seventh species of Stegodont described (Fig. 702) was the *Stegodon sinensis* of Richard Owen (Owen, 1870, p. 417), alleged to be (p. 421) "from marly beds in the vicinity of Shanghai," China, which has been mistakenly regarded by some authors as close to, or as a synonym of, *Stegodon cliftii* (Owen, *op.*

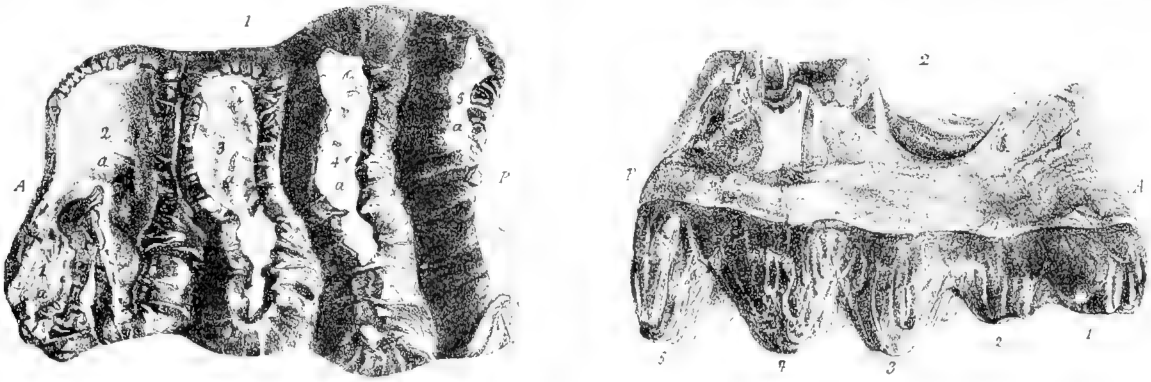


Fig. 702. Type $\mathrm{r.Dp}^3$ of *Stegodon sinensis* Owen, 1870, Pl. xxvii, figs. 1, 2, natural size. From "marly beds in the vicinity of Shanghai," China, of Upper Miocene [Lower Pliocene] age.

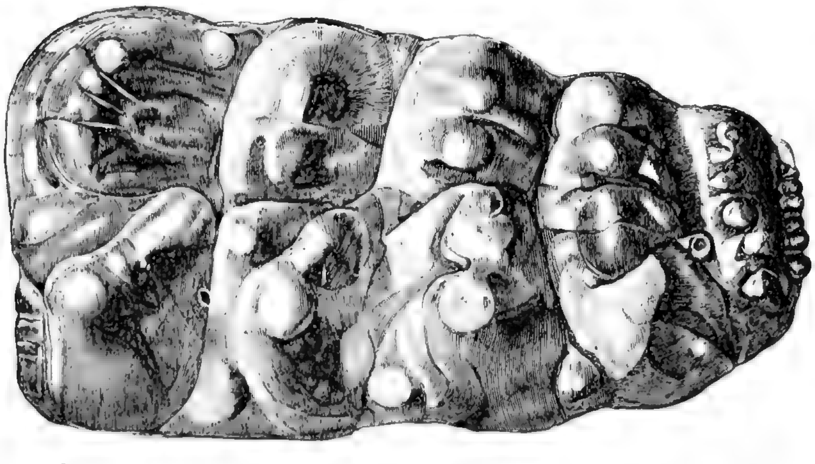
cit., p. 418; Brauns, 1883, p. 44). This synonymy is not borne out by careful comparison with the type figures, because *S. sinensis* is much more primitive than *S. cliftii*.

EIGHTH SPECIES.—In the same paper Owen (*op. cit.*, 1870, p. 421) describes *Stegodon orientalis*, the eighth species of Stegodont (Fig. 703), "from a cave, near the city of Chung-king-foo, in the province of Sze-chuen," based upon molar fragments which he rightly observes "more resemble the teeth of *Stegodon Cliftii*, *St. insignis*, and *St. ganesa* of Falconer than does the *St. sinensis;* and in the apparent quantity of coronal cement . . . as well as in the evidence of a hinder talon . . . they are more like *St. insignis* than *St. Cliftii.*"

Fig. 703. Type of *Stegodon orientalis* Owen, 1870, Pl. XXVIII, figs. 1–4. "Portion of true molar" (figs. 1, 2) and "hind end of milk-molar" (figs. 3, 4). From near Chungkingfoo, China, probably of Lower Pleistocene age.

NINTH SPECIES.—*Mastodon cautleyi* Lydekker, 1886 (1886.1), was founded on five teeth of the upper jaw, of which we select as the type (Fig. 704) the third left upper true molar, from Perim Island, India, a tooth first figured by Falconer and Cautley and referred to the species *Mastodon latidens* Clift (Pl. XXXI, figs. 6, 6a —see Vol. I, fig. 142 of present Memoir, the caption of which is erroneous—corrected in present chapter, p. 821). The four cotypes, obviously smaller and much more primitive teeth than the type of *Mastodon latidens*, are also from Perim Island and are recorded, like the lectotype, from an older geologic horizon, namely, Upper Miocene [now (1935–1938) regarded as Middle Pliocene, Dhok Pathan]. According to these specimens, the ridge formula of *Mastodon* [=*Stegolophodon*] *cautleyi* is about the same as that of *Mastodon* [=*Stegolophodon*] *latidens*.

Fig. 18.



Mastodon cautleyi.—The third left upper true molar, in an unworn condition; from the Siwaliks of Perim Island. $\frac{1}{2}$. The lower border of the figure is the inner border of the specimen.

LECTOTYPE OF STEGOLOPHODON CAUTLEYI

Fig. 704. Third left superior molar of *Mastodon cautleyi* Lydekker, 1886, selected as the type (see Pilgrim, 1913, p. 294). Reproduced after Lydekker, 1886 (1886.2, p. 73, fig. 18), one-half natural size.

Mastodon [=*Stegolophodon*] *cautleyi:* $M\,2^{\underline{4}}\ M\,3^{\underline{5\text{-}\frac{1}{2}+}}$.

TENTH SPECIES.—In 1887 Martin described ("Fossile Säugethier-reste von Java und Japan") from Java a species to which he gave the name *Stegodon trigonocephalus* (Fig. 705), in reference to the triangular shape of the head. The geologic level is regarded by Matsumoto as equivalent to the Lower Pleistocene, Boulder Conglomerate beds of India. It may be of the same geologic age as the type of *Pithecanthropus erectus*. The juvenile type does not admit of giving the mature ridge formula; the ridges are closely compressed, buried in cement, and each ridge is surmounted with ten to twelve conelets, the exact number being indeterminable from the figures.

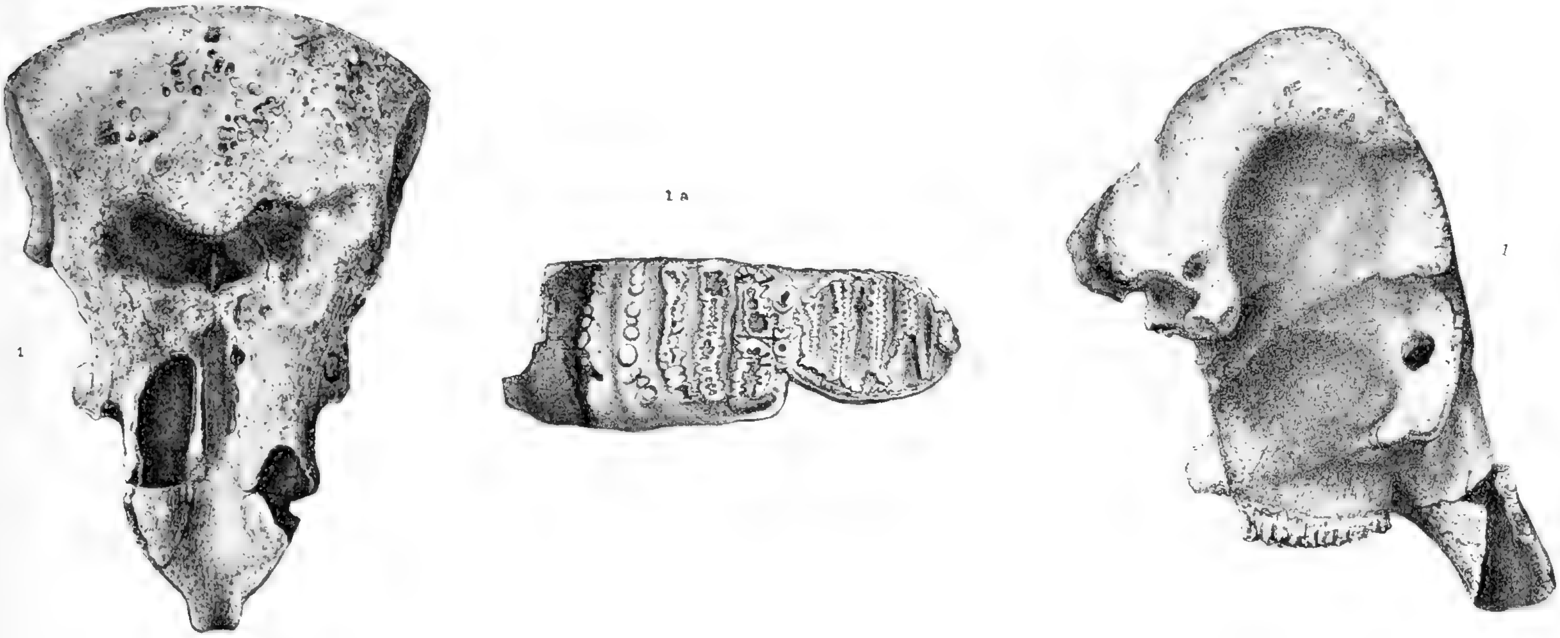
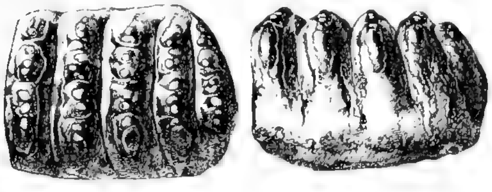


Fig. 705. Type of *Stegodon trigonocephalus* Martin, 1887, immature skull, one-eighth natural size. From vicinity of Surakarta, Java, probably of Lower Pleistocene age. (Right figures) Tab. II, figs. 1, 1*a*; (left figure) Tab. III, fig. 1.

ELEVENTH SPECIES.—The eleventh species (Fig. 706) was described by Naumann in 1890 from Mindanao, Philippine Islands, as *Stegodon mindanensis*. It was first referred to *Stegodon trigonocephalus* by Naumann in 1887, but subsequently was made the type of a distinct species. The compressed cement-covered ridges with multiple conelets indicate a Lower to Middle Pleistocene stage of evolution, similar to that of *S. trigonocephalus*.

TWELFTH SPECIES.—A twelfth species, *Stegodon airâwana* (Fig. 707), was described by Martin in 1890 from Alas-Tuwa, Java, based upon a type jaw containing the right and left third inferior molar teeth, M_3. In its high ridge formula the author compared it to *Stegodon insignis* and *S. ganesa*. In a later paper by Janensch (1911, p. 187), he distinguished *S. airâwana* from both *S. insignis* and *S. ganesa* and wrote the ridge formula as follows, according to the present writer's understanding of the Janensch system [cf. Table V]:



TYPE OF STEGODON (ARCHIDISKODON?) MINDANENSIS

Fig. 706. Type of *Stegodon mindanensis* Naumann, 1890, molar tooth. Mindanao, Philippine Islands, Lower to Middle Pleistocene age. After Naumann, 1887, Taf. I, figs. 1 and 2, under the name *Stegodon trigonocephalus*.

Ridge formula of *Stegodon airâwana:* Dp 3 $\frac{?\ 5\text{-}\frac{1}{2}}{}$ Dp 4 $\frac{\frac{1}{2}\text{-}7\text{-}\frac{1}{2}}{}$ M 1 $\frac{\frac{1}{2}\text{-}7\text{-}\frac{1}{2}}{}$ M 2 $\frac{\frac{1}{2}\text{-}9\text{-}\frac{1}{2}}{}$ M 3 $\frac{\frac{1}{2}\text{-}11\text{-}12\text{-}\frac{1}{2}}{\frac{1}{2}\text{-}13\text{-}\frac{1}{2}}$.

This species is important because it is highly characteristic of the Trinil *Pithecanthropus erectus* beds.

THIRTEENTH SPECIES.—In 1908 Dubois described from the Trinil Kendeng-Schichten, Java, *Stegodon ganesa javanicus*, as a variety of *S. ganesa* [which proves to be a synonym of either *S. airâwana* or *S. trigonocephalus* (see p. 889 below)].

FOURTEENTH SPECIES.—Very important is the *Mastodon stegodontoides* of Pilgrim, 1913, from Lehri, Punjab, India (Fig. 708), which Pilgrim described as follows (p. 294):

> The last species of *Mastodon* which can be referred to this line [the *M. cautleyi-M. latidens* line] is the tooth from Lehri, of which the horizon is uncertain but may be possibly Upper Siwalik, figured by Lydekker in Pal. Ind. ser. 10, Vol. I, Plate 39, as *M. latidens* but which is better recognized as a new species, owing to the almost entire absence of accessory columns, for which I propose the name *Mastodon stegodontoides*. So close is this to *Stegodon clifti* that it is hard to separate the two genera. It will be seen that *Mastodon stegodontoides* carries on none of its ridges more than the usual four columns while anterior ridges of *Stegodon clifti* carry nine or ten mammillæ.

FIFTEENTH SPECIES.—Very progressive is the *Elephas* (*Prostegodon, Parastegodon*) *auroræ* of Matsumoto, 1915–1924, from Mt. Tomuro, Kaga, Japan (Fig. 709), which Matsumoto first regarded as a stage

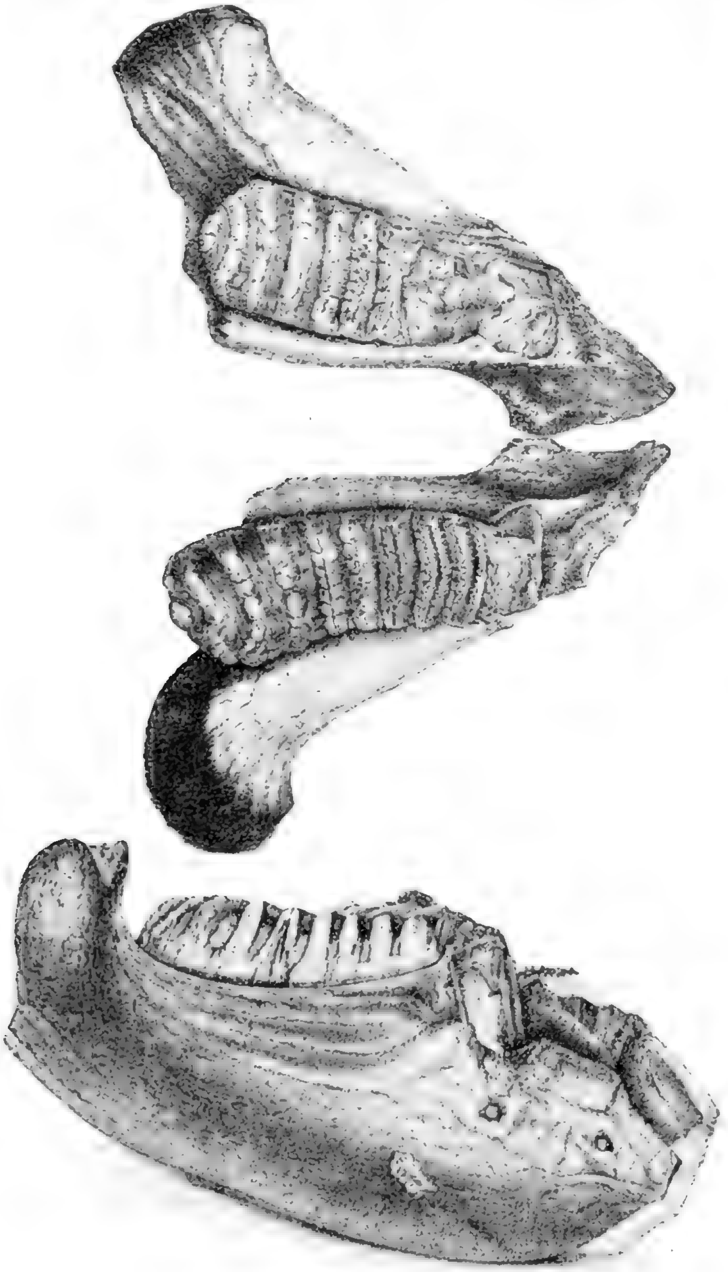
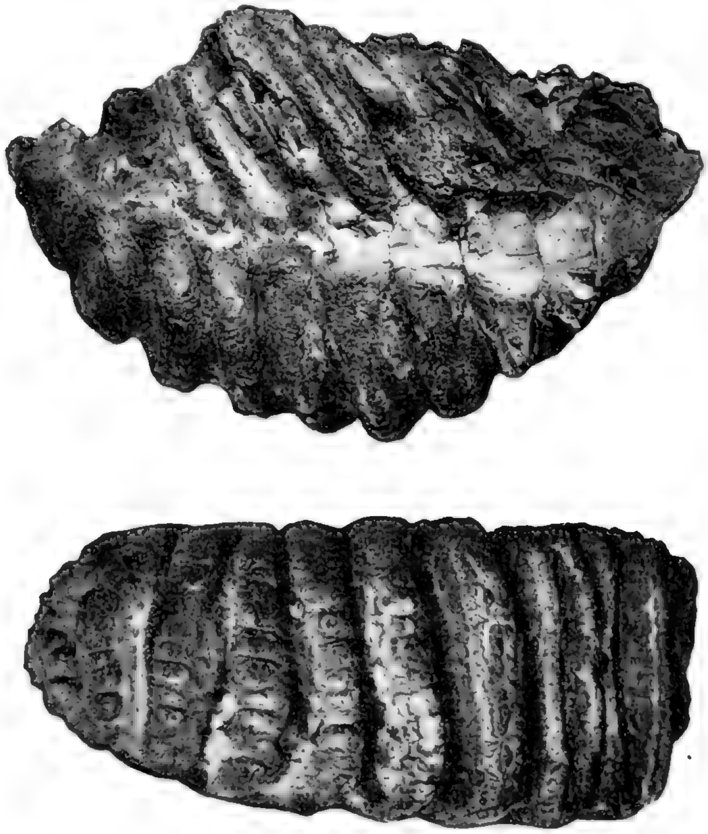


Fig. 707. Type of *Stegodon Airâwana* Martin, 1890, Tab. I, figs 1, 2, lower jaw, one-fourth natural size. From Alas-Tuwa, Trinil, Java. Kendeng-Schichten horizon (*Pithecanthropus erectus* zone), Middle Pleistocene.

TYPE OF STEGOLOPHODON STEGODONTOIDES

Fig. 708. Type r.M^3 of *Mastodon stegodontoides* Pilgrim, 1913. After Lydekker, 1880, Pl. XXXIX: "*Mastodon* (*Tetralophodon*) *latidens*, Clift. The third right upper true molar: from Lehri, in the Punjab. The specimen is drawn of the natural size, and is viewed from the inner [outer] side." Ind. Mus. A.86. Reduced to one-half natural size. Provisionally placed in the Upper Pliocene, Pinjor formation (see Fig. 413, also Pl. XIII).

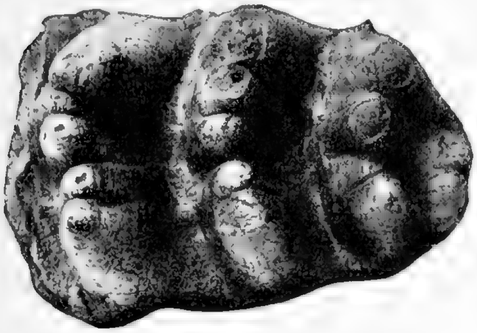


TYPE OF STEGODON AURORÆ

Fig. 709. Type r.M^2 of *Elephas* (*Prostegodon, Parastegodon*) *aurora* Matsumoto, 1918, Pl. XX, figs. 1 and 3, one-half natural size.

in *Elephas* close to the Upper Pliocene *Elephas* [=*Archidiskodon*] *planifrons* of India, but which he subsequently made the genotype of a new genus *Parastegodon*. With our fuller knowledge of *Stegodon airâwana*, the present species may be placed in the true *Stegodon* phylum, distinguished by cranial characters from species of the Elephantidæ, as *Stegodon auroræ*.

Sixteenth Species.—The subspecies *Mastodon* (*Bunolophodon*) *longirostre* Kaup *forma sublatidens* Schlesinger, 1917, from near Teschen (Schlesien), Austria (Fig. 710), appears to be very close to the *Mastodon* [=*Stegolophodon*] *stegodontoides* of Pilgrim; consequently it is removed to this genus, namely, *Stegolophodon sublatidens*.



Type of Stegolophodon sublatidens

Fig. 710. Type of *Mastodon* (*Bunolophodon*) *longirostre* Kaup *forma sublatidens* Schlesinger, 1917, one-half natural size. Compare full legend below of figure 722.

Seventeenth Species.—The subspecies *Stegodon orientalis shodoënsis* of Matsumoto, 1924, named from the Island of Shôdo, Inland Sea, is regarded by its author as a descendant of *S. orientalis* Owen, of China, contemporaneous with the referred *S. insignis* of the Middle [Upper] Pleistocene, Narbada of India. Not figured in present Memoir.

Eighteenth Species.—The type of *Stegolophodon nathotensis* Osborn, 1929, consists of fragmentary molars (Fig. 724) collected by Barnum Brown in 1922 in the Lower Chinji horizon, near Nathot, India.

Nineteenth Species.—Somewhat more advanced than *Stegolophodon cautleyi* of the Upper Miocene [Middle Pliocene] is the *Stegolophodon cautleyi progressus* Osborn, 1929 [of the Mio-Pliocene], the type of which (Amer. Mus. 19446) is a complete cranium (Figs. 725, 727) collected at the summit of the Lower Chinji horizon, 2,000 feet above the base of the Lower Siwaliks, India. This is a young individual in which the molar ridge-crests are intermediate in formula and pattern between the '*Mastodon*' *cautleyi* of Lydekker and the '*M.*' *latidens* of Clift.

Twentieth Species.—Somewhat more primitive and ancient than the Upper Pliocene [Lower Pleistocene] *Stegodon insignis* Falconer type is the subspecific stage *Stegodon orientalis grangeri* Osborn, 1929 (Fig. 762) of the Yangtze River region near Wanhsien, Sezchuan, 140 miles northeast of the type locality of *S. orientalis* Owen. This subspecies is now very fully known and is amply illustrated and defined in the present Memoir. See type figures on pages 876, 877, 879, and 881 below.

Twenty-first Species.—*Stegodon insignis birmanicus* Osborn, 1929 (Fig. 758), from the Upper Pliocene of Burma. See type figure on page 875.

Twenty-second Species.—*Stegodon pinjorensis* Osborn, 1929, from the Lower Pleistocene of India, upper levels of the Pinjor horizon (Figs. 711, 765, 767).

[The following species have been described since the author's intensive review of the true Stegodonts, consequently the determinations of Professor Osborn cannot be given and the spe-

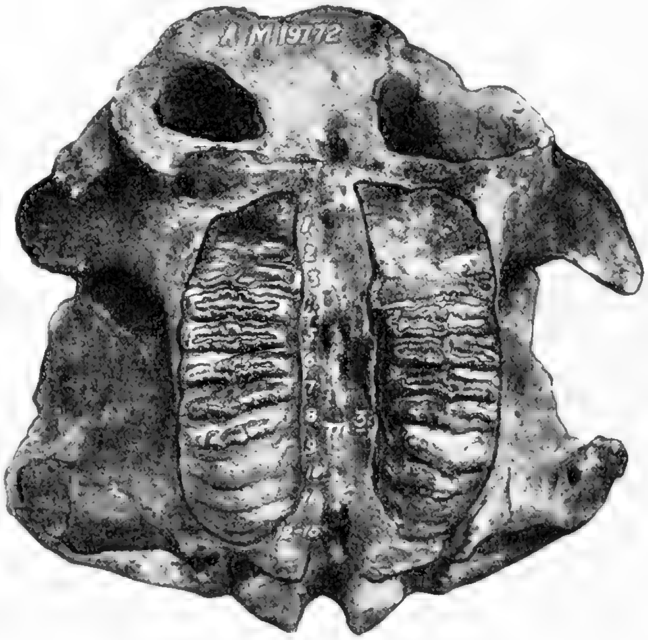


Fig. 711. Photographic reproduction of type palate of *Stegodon pinjorensis* Osborn, 1929 (Amer. Mus. 19772), collected by Barnum Brown three miles north of Siswan, India. About one-eighth natural size. See figure 765 below.

Table IV	INDIA	BURMA	CHINA	JAPAN	PHILIPPINE ISLANDS	JAVA	BORNEO
Upper Pleistocene	*Stegodon insignis* ref. *Stegodon ganesa* ref.						
Middle Pleistocene				*Stegodon orientalis shodoënsis* type	*Stegodon* (*Archidiskodon?*) *mindanensis* type	*Stegodon airâwana* type *Stegodon ganesa* var. *javanicus* type [=*S. airâwana* or *S. trigonocephalus*]	
Lower Pleistocene	*Stegodon pinjorensis* type		*Stegodon orientalis* type *Stegodon orientalis grangeri* type			*Stegodon trigonocephalus* type	
Upper Pliocene to Lower Pleistocene	*Stegodon insignis* lectotype and ref. *Stegodon ganesa* lectotype and ref.						
Upper Pliocene	*Stegolophodon stegodontoides* type *Stegodon bombifrons* ref.	*Stegodon insignis birmanicus* type[1]		*Stegodon auroræ* type			*Stegolophodon lydekkeri* type
Middle Pliocene	*Stegodon bombifrons* lectotype and ref. *Stegolophodon cautleyi* lectotype *Stegolophodon latidens* ref.	[AUSTRIA *Stegolophodon sublatidens* type]		*Stegodon bombifrons* ref.			
Lower Pliocene		BURMA *Stegolophodon latidens* lectotype, cotype, and ref.[1] *Stegodon elephantoides* lectotype[1] *Stegodon elephantoides* (=*cliftii*) cotype[1]	*Stegodon sinensis* type	*Stegolophodon latidens* ref.			
Mio-Pliocene	*Stegolophodon cautleyi progressus* type *Stegolophodon nathotensis* type						

[Seven species from Java, China, and Japan described since 1929 are omitted here owing to the fact that the horizons were not determined by the present author.—Editor.]

[1] [See note on page 824 above where these three species are now regarded as of Lower Pleistocene age.—Editor.]

cies are listed here according to the nomenclature of the various authors, without comment, with the exception of *Parastegodon? kwantoensis* and *P. sugiyamai.*

Twenty-third Species.—The type of *Stegodon bondolensis* van der Maarel, 1932, is a fragment of a mandible with what is inferred to be the third molar of each side, found at Bondol, Java (Fig. 782 of the present Memoir).

Twenty-fourth Species.—In 1933 von Koenigswald described from Bumiaju, Java, a lower jaw with third molar of both sides complete, which he named *Stegodon trigonocephalus praecursor* (Fig. 783 of the present Memoir).

Twenty-fifth Species.—The species *Parastegodon? kwantoensis* Tokunaga, 1934, Pl. ix, a portion of a jaw with second right molar *in situ*, is indeterminate, owing to the fact that Professor Osborn regarded *Parastegodon* as either a progressive *Stegodon* or a primitive *Archidiskodon.* See type figure 784 on page 897 below.

Twenty-sixth Species.—*Stegodon yüshensis* Young, 1935, from Yüshe, China. Type, a well preserved upper left third molar, Pl. v, fig. 1 (Fig. 785 of the present Memoir).

Twenty-seventh Species.—The type of *Stegodon officinalis* Hopwood, 1935, is a fragment of an unworn lower molar, said to have come from Szechuan, China. This is figured in Hopwood, 1935, Pl. vii, fig. 3 (Fig. 786 of the present Memoir).

Twenty-eighth Species.—The type of *Stegodon zdanskyi* Hopwood, 1935, is a fragment of a right third lower molar, consisting of the first four ridges, and figured in Hopwood, Pl. vii, fig. 5 (Fig. 788 of the present Memoir).

Twenty-ninth Species.—The type of *Parastegodon sugiyamai* Tokunaga, 1935 [*Stegodon? sugiyamai*] is either a first or a second molar, probably of the upper left side, found in Shikoku, Japan (Fig. 789 of the present Memoir).—Editor.]

Thirtieth Species.—In Volume I of the present Memoir (p. 700, fig. 660) will be found the type description of *Stegolophodon lydekkeri,* dedicated by the present author to his friend Richard Lydekker. The type is a third left superior molar from Borneo, "much more progressive than the *S. latidens* type."

III. SYSTEMATIC ARRANGEMENT OF THE STEGOLOPHODONTS AND STEGODONTS IN PHYLOGENETIC ORDER

1. CHARACTERS OF THE SUBFAMILY STEGODONTINÆ[1]

Subfamily Characters.—(1) Habits chiefly browsing; tropical forest living; crushing of coarse leafage, herbage, and wood fiber; not progressing to the grazing type. (2) Cranium relatively abbreviated, mesocephalic, bathycephalic; grinding-tooth plane deeply depressed to occipital condyles; occipitofrontal plane neither elevated nor expanded, non-acrocephalic, non-hypsicephalic. (3) Tusks straight or slightly curved, horizontal or subhorizontal in direction, continuously serving in browsing habits. (4) Grinding teeth brachyodont to subhypsodont, ridge-plates of M 3 increasing from $\frac{5\frac{1}{2}-6\frac{1}{2}}{\frac{1}{2}-6-\frac{1}{2}}$ [*Stegolophodon*] to $\frac{9\frac{1}{2}-14}{15\frac{1}{2}}$ [*Stegodon*].

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[1] [In Volume I (1936) of the present Memoir, the author separated the Stegodontoidea (true Stegodonts) from the Elephantoidea (pp. 22, 25), also the genus *Stegodon* from *Stegolophodon*, placing all the Stegolophodonts in the superfamily Mastodontoidea, family Mastodontidæ, new subfamily Stegolophodontinæ (p. 700) and the true Stegodonts in the superfamily Stegodontoidea, family Stegodontidæ, subfamily Stegodontinæ (see pp. 806–808 above).—Editor.]

These characters are observed in the species and subspecies discovered since 1828, many of which were originally referred to the genus *Mastodon* and the genus *Elephas* and are now referred to the primitive genus *Stegolophodon* and to the more progressive genus *Stegodon*.

2. HISTORY OF THE GENERIC NAMES ASSIGNED TO THE STEGOLOPHODONTS AND TO THE STEGODONTS

The history of the generic term *Stegodon* Falconer is fully given in Chapter XXI, also in the present Chapter XIV, which may be summarized as follows: (1) The name *Stegodon* applies chiefly to the more progressive Stegodonts. (2) To the more primitive Stegodonts, e.g., the Upper Miocene [Middle Pliocene] *Mastodon cautleyi*, the Lower Pliocene[1] *M. latidens*, and the Pliocene *M. stegodontoides*, the name *Stegolophodon* Schlesinger is applicable. The name *Stegolophodon* also applies to the *Mastodon* (*Bunolophodon*) *longirostre* Kaup *forma sublatidens* Schlesinger of Austria. The name *Stegolophodon* Schlesinger, 1917, preoccupies the name *Prostegodon* Matsumoto, 1922–1924. (3) The name *Parastegodon* Matsumoto, 1924, based on the genotypic species *Elephas auroræ*, appears to be in part a synonym of *Archidiskodon*. These interpretations of the generic names adopted in the present Memoir are displayed in the following table.

PHYLOGENY. STEGOLOPHODONTS AND STEGODONTS ARRANGED BY COUNTRIES IN APPROXIMATE ASCENDING ORDER OF EVOLUTION, THE MOST PRIMITIVE FORMS BELOW, THE MOST PROGRESSIVE FORMS ABOVE

[The species described by various authors since 1929 are omitted here owing to the fact that they had not been studied in detail by Professor Osborn.—Editor.]

		STEGODON	
Japan	1924	*Stegodon orientalis shodoënsis* Matsumoto, Island of Shôdo, Inland Sea, Japan	= *Stegodon orientalis shodoënsis*
	1915 1924	*Elephas* (*Prostegodon, Parastegodon*) *auroræ* Matsumoto, Mt. Tomuro, Kaga, Japan	= *Stegodon auroræ*
Philippines	1890	*Stegodon mindanensis* Naumann, Mindanao, Philippine Islands	= *Stegodon* (*Archidiskodon?*) *mindanensis*
Java	1908	*Stegodon ganesa* var. *javanicus* Dubois, Kendeng, Trinil, Java	[= *Stegodon airâwana* or *S. trigonocephalus*]
	1887	*Stegodon trigonocephalus* Martin, vicinity of ?Surakarta, Java	= *Stegodon trigonocephalus*
	1890	*Stegodon Airâwana* Martin, Alas-Tuwa, Kendeng, Trinil, Java	= *Stegodon airâwana*
China	1870	*Stegodon orientalis* Owen, Chungkingfoo, Szechuan, China	= *Stegodon orientalis*
	1929	*Stegodon orientalis grangeri* Osborn, Yenchingkou, Szechuan, China	= *Stegodon orientalis grangeri*
	1929	*Stegodon pinjorensis* Osborn, near Siswan, India	= *Stegodon pinjorensis*
India	1846 [1845]	*Stegodon Ganesa* Falc. and Caut., Siwalik Hills, India	= *Stegodon insignis-ganesa*
	1846 [1845]	*Stegodon insignis* Falc. and Caut., Siwalik Hills, India	= *Stegodon insignis-ganesa*
Burma	1929	*Stegodon insignis birmanicus* Osborn, Mingoon opposite Mandalay, Burma	= *Stegodon insignis birmanicus*
India	1846	*Elephas bombifrons* Falc. and Caut., Siwalik Hills, India	= *Stegodon bombifrons*
Burma	1828	*Mastodon elephantoides* Clift, near Yenangyaung, Irrawaddy River, Burma	= *Stegodon elephantoides*
	1846	*Elephas cliftii* Falc. and Caut., near Yenangyaung, Irrawaddy River, Burma	= *Stegodon elephantoides* (= *cliftii*)
China	1870	*Stegodon sinensis* Owen, near Shanghai, China	= *Stegodon sinensis*
		STEGOLOPHODON	
India	1913	*Mastodon stegodontoides* Pilgrim, Lehri, Punjab, India	= *Stegolophodon stegodontoides*
Austria	1917	*Mastodon* (*Bunolophodon*) *longirostre* Kaup *forma sublatidens* Schlesinger, Teschen (Schlesien), Austria	= *Stegolophodon sublatidens*
Borneo	1936	*Stegolophodon lydekkeri* Osborn, near Bruni, Borneo	= *Stegolophodon lydekkeri*
Burma	1828	*Mastodon latidens* Clift, near Yenangyaung, Irrawaddy River, Burma	= *Stegolophodon latidens*
India	1929	*Stegolophodon cautleyi progressus* Osborn, near Chinji Bungalow, India	= *Stegolophodon cautleyi progressus*
	1886	*Mastodon cautleyi* Lydekker, Perim Island, India	= *Stegolophodon cautleyi*
	1929	*Stegolophodon nathotensis* Osborn, near Nathot, India	= *Stegolophodon nathotensis*

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[1] [See note on page 824 above regarding the Lower Pleistocene age of *Mastodon* [= *Stegolophodon*] *latidens*.—Editor.]

SUPERFAMILY: MASTODONTOIDEA Osborn, 1921
FAMILY: MASTODONTIDÆ Girard, 1852
SUBFAMILY: STEGOLOPHODONTINÆ Osborn, 1936

GENUS: **STEGOLOPHODON** Schlesinger, 1917

Original reference: Denk. Naturhist. Hofmus., 1917, I, p. 115.
Genotypic species: *Mastodon latidens* Clift, 1828.
Compare *Stego (lopho) don* Pohlig, 1888, p. 252.
Syn.: *Prostegodon* Matsumoto MS., in Osborn, 1923; Matsumoto, 1924, p. 325.

GENERIC CHARACTERS.—(Schlesinger, 1917, p. 115, footnote): "Ich schlage für *M. latidens*, das sich durch seine kurze Symphyse von dem Subgenus *Bunolophodon*, durch seinen Molarenbau von *Dibunodon* entfernt, den Untergattungsnamen *Stegolophodon* vor. Der Name bringt einerseits die nahen Beziehungen zum Genus *Stegodon*, anderseits die Loslösung der Untergattung von *Bunolophodon* und ihre Sonderstellung gegenüber *Dibunodon* zum Ausdruck."

Osborn, 1926: (1) Six[1] species of *Stegolophodon*, namely, *Mastodon latidens*, the more primitive *M. cautleyi*, and the more progressive *M. stegodontoides;* also *S. cautleyi progressus*, *S. nathotensis*, and *Mastodon* (*Bunolophodon*) *longirostre* Kaup *forma sublatidens*. As defined by the teeth, these species have in common the following generic characters: (2) Lophs as in *Mastodon* and *Zygolophodon*, tendency to form from four to six transversely arranged cones and conelets (conelets somewhat irregular) and to consolidate into ridge-crests; (3) molar pattern transitional between the *Zygolophodon* type and the *Stegodon* type; (4) ridge-crest formula known in *Stegolophodon latidens* as follows, $\mathrm{Dp}\,3^{\underline{2}}$ $\mathrm{Dp}\,4^{\underline{4}}$ $\mathrm{M}\,1\,\frac{\frac{1}{4}\text{-}4\text{-}\frac{1}{4}}{}$ $\mathrm{M}\,2\,\frac{4\frac{1}{2}\text{-}5}{4\frac{1}{2}\text{-}5}$ $\mathrm{M}\,3\,\frac{\frac{1}{4}\text{-}5\text{-}\frac{1}{2}}{\frac{1}{2}\text{-}6\text{-}\frac{1}{2}}$. [Anterior ridge-crests with persistent median sulcus (see Vol. I, p. 700).—Editor.]

This genus resembles *Trilophodon* and *Tetralophodon* in the retention of a broad enamel band on the straight superior incisive tusks (Figs. 725 and 727); it differs widely from *Trilophodon* in the presence of *four* ridge-crests on the intemediate molars (Fig. 726); it also differs from *Tetralophodon* in the absence of trefoils and in the progressive tendency of the cones and conelets to form regular transverse ridge-crests surmounted by regular conelets, as seen in the genotypic species *Mastodon* [= *Stegolophodon*] *latidens*, also in *Mastodon* [= *Stegolophodon*] *stegodontoides*.

Four of the known species are provisionally distinguished as follows:

Middle Pliocene	Lower Pliocene[2]	Middle(?) Pliocene	Upper Pliocene
Stegolophodon cautleyi	*Stegolophodon latidens*	*Stegolophodon sublatidens*	*Stegolophodon stegodontoides*
$\mathrm{M}\,2^{\underline{4}}$ $\mathrm{M}\,3\,\frac{5\text{-}\frac{1}{2}+}{}$	$\mathrm{M}\,2\,\frac{4\frac{1}{2}\text{-}5}{4\frac{1}{2}\text{-}5}$ $\mathrm{M}\,3\,\frac{\frac{1}{4}\text{-}5\text{-}\frac{1}{2}}{\frac{1}{2}\text{-}6\text{-}\frac{1}{2}}$	(?) $\mathrm{M}\,3\,\frac{6\frac{1}{2}}{}$	$\mathrm{M}\,3\,\frac{6\frac{1}{2}}{}$
4–5 conelets on each ridge-crest, very irregular.	4–5 conelets on each ridge-crest, more regular.	4–5 conelets on fourth, fifth, and sixth ridge-crests. Posterior ridge-crests arched or slightly convexo-concave.	5–6 conelets on each ridge-crest, very regular. Posterior ridge-crests arched or convexo-concave.

Stego(*lopho*)*don* (see Pohlig, 1888, p. 252). By strict rules this term may be regarded as a *nomen nudum* and should not stand in the way of Schlesinger's excellent name *Stegolophodon*.

Prostegodon. (1) For the first printed use of the name *Prostegodon*, see Osborn, 1923.601, p. 2: "*Prostegodon*, new genus, Matsumoto. In a letter from Dr. H. Matsumoto, dated November 20, 1922, from Sendai, Japan, he writes: 'In my report just in preparation on the Japanese 'Mastodonts,' I follow you to refer "*Mastodon*" *latidens* to the genus *Stegodon*, creating however a subgenus *Prostegodon* for it. *Prostegodon* is the primitive representative of the *Stegodon*-phylum, representing half bunomastodontine and half stegodontine dental characters. Schlosser's opinion, that *Prostegodon* might be ? a descendant of "*Mastodon*" *turicens*, does not appear to be correct at all.' Genotypic species *Mastodon latidens* Clift. This genus should be credited to Doctor Matsumoto."

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[1] [Seven species including *Stegolophodon lydekkeri* described in Vol. I, p. 700, of the present Memoir.—Editor.]

[2] [See page 824 above where it is stated that *S. latidens* is limited to the upper Irrawaddy beds (Lower Pleistocene).—Editor.]

(2) In 1924 Matsumoto's report on the Japanese Mastodonts, referred to above, appeared in the Journal of the Geological Society of Tokyo, Volume XXXI, in which he defined the genus *Prostegodon* (p. 325). This, however, was published in the Japanese language.

(3) In 1926 Matsumoto published his English text on this genus ("On Two New Mastodonts and an Archetypal Stegodont of Japan," 1926, p. 9), from which the following is a direct quotation:

> Skull and mandible only imperfectly known, brevirostral. Lower incisor-tusks might be absent, or abortive if present at all. Intermediate molars four- or five-ridged, last molars five- or six-ridged. Grinders essentially lophodont, though their first and second ridges may show a slight tendency of bunodonty and of trefoil pattern of cusps; mesial longitudinal cleft evident; inner and outer cusps opposite, instead of being alternate; valleys widely open, free of cement.

(4) Thus *Prostegodon* Matsumoto-Osborn, 1923, 1924, 1926, becomes a synonym of *Stegolophodon* Schlesinger, 1917.

(5) The genus *Parastegodon* Matsumoto, 1924 (1924.2), founded upon the genotypic species *Elephas* (*Prostegodon*) *auroræ* Matsumoto (Fig. 709), also probably [in part] becomes a synonym of *Stegodon,* because as shown below the genotypic species *E.* (*P.*) *auroræ* [= *Stegodon auroræ* of the present Memoir] is somewhat more primitive than *Stegodon airâwana* Martin of the Middle(?) Pleistocene and quite distinct from *E.* [*Archidiskodon*] *planifrons.* The name *Parastegodon* was originally published by Matsumoto in 1924, pp. 256, 257: *Parastegodon* gen. nov. = *Stegodon mindanensis-Elephas auroræ* group; type *Elephas auroræ;* it was subsequently cited by Matsumoto (1926.1, p. 1). *Elephas auroræ* was originally figured in 1918, Pl. xx, as reproduced in figure 709 of the present Memoir. From the isolated type second superior grinder of the right side, r.M^2, it was difficult to determine whether this was a progressive *Stegodon* like *S. airâwana* or whether it was transitional to a primitive elephant like *Archidiskodon planifrons.* We have finally referred it to the genus *Stegodon.*

SYSTEMATIC DESCRIPTION OF SPECIES OF STEGOLOPHODON

Stegolophodon cautleyi Lydekker, 1886

Figures 142, 685, 690, 704, 712–715, Pl. XIII

Lectotype: Middle Pliocene, Perim Island, India; referred, Salt Range, Simla Hills, India.

Falconer's very accurate figure of the lectotype (Fig. 713) displays clearly (1) the characteristic *median fissure* [or sulcus], a primitive character (cf. Fig. 685, 2–4), (2) vestigial median conules, also observable in *Stegolophodon latidens,* and (3) internal conelets blocking the valleys. If *S. cautleyi* is not really ancestral to *S. latidens,* it is certainly a much more primitive and less perfect Stegolophodont, retaining certain resemblances to the less regular molars of primitive species of *Zygolophodon.* The species is represented in the present Memoir by the lectotype (Figs. 712 and 713), also by the cotype of Lydekker (Fig. 714), and by the referred upper molar (Fig. 715). Compare the superior grinding teeth with the somewhat more progressive species *Stegolophodon cautleyi progressus* (Figs. 725–727).

Specific Characters (Osborn).—Distinguished by median fissure [or sulcus], irregular formation of ridge-crests surmounted by from four to five 'conelets' each, with small 'conules' or 'accessory tubercles' in the valleys, as shown in the lectotype and cotype figures (Figs. 714 = cotype, 712 = lectotype). M^3 with 5+ ridge-crests; ap. 210 mm., tr. 112 mm.

Geologic Horizon.—According to Pilgrim-Osborn (see Fig. 413 of Vol. I), the type of *Stegolophodon cautleyi* from the Perim Island formation is of Middle Pliocene Dhok Pathan age, equal approximately to the Plaisancian (of France) and Levantin (of Austria and Hungary). In the same formation occur the types of *Anancus perimensis, Deinotherium indicum,* and *D. angustidens,* also *Hipparion perimense* type. Referred specimens of *S. cautleyi* occur again in the Salt Range, Simla Hills, in the same level with specimens of *Anancus perimensis,* of *Hipparion theobaldi,* and of *Aceratherium perimense.* In the Lower Pliocene[1] it is replaced by *Stegolophodon latidens.*

Mastodon cautleyi Lydekker, 1886. "Addenda to Synopsis of Siwalik & Narbada Mammalia." Mem. Geol. Surv. Ind., Pal. Indica, 1886, Ser. X, Vol. III, pp. xiv–xix. Lectotype and cotypes.—(*Op. cit.,* p. xiv): "The specimens on which this provisional species is founded are five in number, and are all cheek-teeth of the upper jaw; four of them being in an unworn condition." The third superior molar of the left side (Lydekker, 1886.1, p. xv, fig. 6) has been selected as the type (see Pilgrim, 1913, p. 294). Horizon and Locality.—Perim Island, India; Middle Pliocene. Lectotype and Cotype Figures.—(*Op. cit.,* p. xv, figs. 5 and 6): Fig. 5 (Brit. Mus. M.2817, cast Amer. Mus. 26965), figured in the "Fauna Antiqua Sivalensis," Pl. XL, figs. 3, 3a, as

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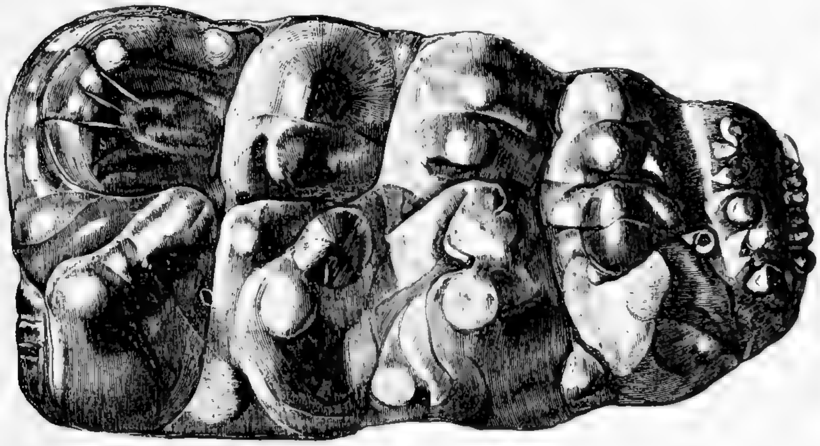
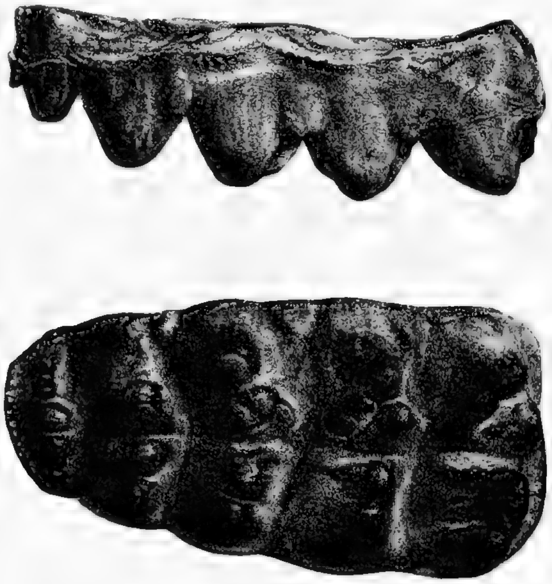
[1] [See note on page 824 above regarding the Lower Pleistocene age of *Stegolophodon latidens.*—Editor.]

M. latidens (appears as *M. cautleyi*, Lydekker, 1886.2, p. 72, fig. 17); Fig. 6 (Brit. Mus. M.2705, cast Amer. Mus. 26966), figured in the "Fauna Antiqua Sivalensis," Pl. XXXI, figs. 6, 6a, as *M. latidens* (appears as *M. cautleyi*, Lydekker, 1886.2, p. 73, fig. 18) chosen as the type (by Pilgrim); Brit. Mus. M.2884 (no history), figured in the "Fauna Antiqua Sivalensis," Pl. XL, figs. 2, 2a, as *M. latidens* (appears as *M. cautleyi*, Lydekker, 1886.2, p. 71); Ind. Mus. A.48 (cast Brit. Mus. M.3428),[1] figured in Lydekker, 1880, Pl. XL, as *M. perimensis* (appears as *M. punjabiensis*, Lydekker, 1886.2, p. 60); Ind. Mus. A.437 (cast Brit. Mus. 2887), figured in Lydekker, 1884.3, Pl. XVI, fig. 2, as *M. perimensis* (appears as *M. cautleyi*, Lydekker, 1886.2, p. 72).

Fig. 18.



Mastodon cautleyi.—The third left upper true molar, in an unworn condition; from the Siwaliks of Perim Island. ½. The lower border of the figure is the inner border of the specimen.



LECTOTYPE OF STEGOLOPHODON CAUTLEYI

Fig. 712. Lectotype (see Pilgrim, 1913, p. 294) of *Mastodon cautleyi* Lydekker, 1886, l.M^3, one-half natural size. Middle Pliocene, Perim Island, India. Brit. Mus. M.2705. After Lydekker, 1886.2, p. 73, fig. 18; same as Lydekker, 1886.1, p. xv, fig. 6. See also four cotype figures of Lydekker, namely, Lydekker, 1886.1, p. xv, fig. 5; Pl. XVI, fig. 2 (as *M. perimensis*); Lydekker, 1880.1, Pl. XL (as *M. perimensis*), 1886.2, p. 60 (as *M. punjabiensis*); Falconer and Cautley, 1846 [1847, Pl. XXXI, figs. 6, 6*a* (as *M. latidens*)].

Observe the irregular character of the ridge-crests and the presence of rudimentary intermediate conules in the first and second valleys (Lydekker, 1884.3, Pl. XVI, fig. 2, *a*, *a*, *b*, *a*).

Fig. 713. Lectotype of *Mastodon cautleyi* Lydekker (same lectotype tooth as that shown in figure 712). Third upper true molar of the left side, l.M^3, from Perim Island, one-third natural size. Originally figured by Falconer and Cautley, 1846 [1847, Pl. XXXI, figs. 6, 6a] as *Mastodon latidens*, and described as follows (Falconer, 1868, Vol. I, p. 463): "Figs. 6 and 6*a*.—*M. latidens*. Upper true molar, very perfect.—B.M. Length, 8.5 in. Width, 4.5 in." Brit. Mus. M.2705.

ORIGINAL DESCRIPTION (LYDEKKER, 1886.1, P. XIV).—"Mastodon cautleyi, *n. sp. Lyd.*— . . . In recently describing a molar of *Mastodon latidens* from Borneo, the present writer [Footnote: 'Proc. Zool. Soc. 1885, pl. XLVIII.'] referred to certain Siwalik specimens in the British and Indian Museums which appeared to indicate a more or less complete transition between typical molars of that species on the one hand and those of *M. perimensis* on the other. A subsequent examination of the specimens in question has however led to the conclusion that they cannot apparently be satisfactorily referred to either one of those species; and as there can be no question as to the strongly marked distinction between typical molars of those two species, it has been thought, after considerable hesitation, advisable to provisionally apply a distinct specific name to the aberrant form, which may be called *M. cautleyi*. . . . The specimens on which this provisional species is founded are five in number, and are all cheek-teeth of the upper jaw; four of them being in an unworn condition. Three of these teeth, which are all from Perim Island, are in the British Museum, and are figured in the 'Fauna Antiqua Sivalensis,' under the name of *M. latidens*: the first (pl. XL. figs. 2, 2a [Brit. Mus. M.2884]) is the right $\frac{\text{mm.4}}{}$; the second (pl. XL. figs. 3, 3a [Brit. Mus. M.2817]) is the left $\frac{\text{m.1}}{}$, and is refigured of the natural size in woodcut fig. 5; while the third (pl. XXXI. figs. 6, 6a [lectotype, Brit. Mus. M.2705]) is the left $\frac{\text{m.3}}{}$, and is refigured on a larger scale in woodcut fig. 6. The other two specimens are in the Indian Museum, and are figured in the present work under the name of *M. perimensis*; the first[1] [Footnote: ' "Cat. Siwalik Vert. Ind. Mus." pt. I, p. 97. No. A.48. (1885). *M. perimensis*.'] (vol. I. pl. XL.) being the partially-worn left $\frac{\text{m.1}}{}$, with the associated $^{\text{pm.4}}$, the former [Footnote: 'When describing this specimen in Calcutta the writer could not identify it with the one figured in the "F.A.S." pl. XL. fig. 3, owing to the small size of the figures in that work, which renders them almost useless for comparison.'] of which apparently agrees precisely with the homologous British

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[1] [Lydekker subsequently (1886.2, p. 60) made this (cast Brit. Mus. M.3428) a cotype of *Mastodon* [=*Tetralophodon*] *punjabiensis* (cf. Vol. I, p. 363, of the present Memoir).—Editor.]

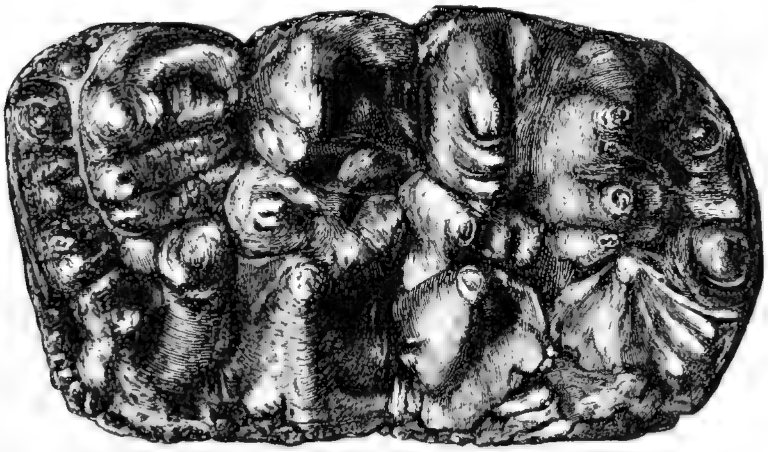
Museum specimen, and the other[1] [Footnote: '"Cat. Siwalik Vert. Ind. Mus." pt. I. p. 97. No. A.437 (1885). *M. perimensis.*'] (vol. III. pl. xvi. fig. 2) the imperfect right $\frac{\text{m.2}}{}$, in an unworn condition."

Specific Characters (Lydekker, 1886.1, p. xv).—"All these five specimens agree so exactly with one another that there can be little or no hesitation in referring them to one and the same species. Their essential characters are that the ridges are moderately tall, and inclined forwards; the valleys partially blocked by accessory tubercles, of which there are none on the outer side of the median longitudinal cleft. The first inner column always has accessory tubercles on both sides, and there are similar tubercles on the hinder side of both the second and third inner columns; the hind talon of the 'intermediate' molars (woodcut fig. 5) is relatively small; while in unworn examples the hinder aspect of the outer column of the first ridge is deeply concave, and the arrangement of the tubercles on the inner column of the same ridge forms a V. The third true molar (woodcut fig. 6) is very wide, tapers but little posteriorly, and carries five ridges and a simple hind talon, the latter consisting of a narrow ridge with six small tubercles. All the teeth are relatively wide, with a well-marked median longitudinal cleft; they appear to have no appreciable quantity of cement in the valleys, and when worn . . . present trefoils on their inner columns." The cotype figure reproduced above (Fig. 714) is a first left superior true molar from Perim Island; the lectotype (Figs. 712 and 713) is a third left superior true molar, also from Perim Island. According to these specimens, the ridge formula of *Mastodon* [=*Stegolophodon*] *cautleyi* is as follows:

Ridge formula: Dp $4\frac{\frac{1}{2}-3-\frac{1}{2}}{}$ M $1\frac{\frac{1}{2}-4-\frac{1}{2}}{}$ M $3\frac{5-\frac{1}{2}+}{}$.

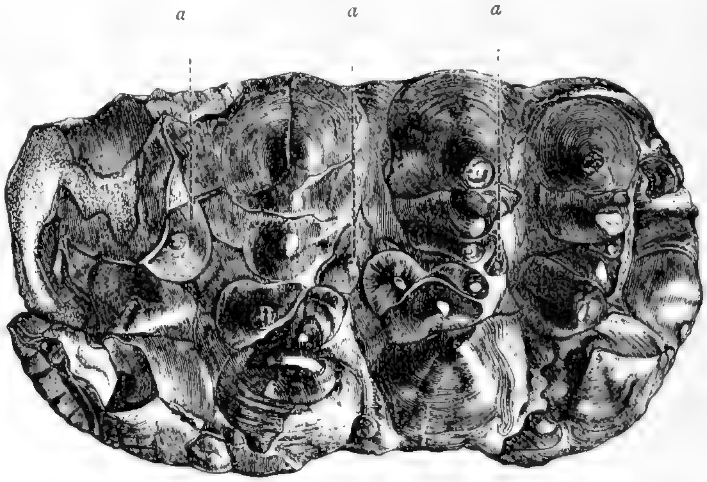
According to Falconer and Lydekker, (1) the same ridge formula is observed in specimens of *Mastodon* [=*Stegolophodon*] *cautleyi* from Perim Island (type locality) and from the Dhok Pathan, namely, M 2^{4} M $3\frac{5\frac{1}{2}}{}$; (2) the open and irregular ridge structure of the molar teeth in *S. cautleyi* is more primitive than the close-set, regular ridge structure in the type of *S. latidens*, as is seen at once by comparison of the type figures of the two species; (3) Lydekker separated the species *Mastodon cautleyi* from specimens in the Perim Island beds which had been referred by Falconer to *Mastodon latidens*; (4) Pilgrim (1913, p. 294) accepted this species, regarding it as a direct ancestor of one of the larger forms of *M. latidens*.

Fig. 17.



Mastodon cautleyi.—The first left upper true molar in an unworn condition; from the Siwaliks of Perim Island. $\frac{1}{1}$. The lower border of the figure is the inner border of the specimen.

Fig. 14.



Mastodon perimensis.—The second left upper true molar, in an unworn condition; from the Siwaliks of Perim Island. $\frac{2}{3}$. *a.* External accessory tubercles. The lower border of the figure is the inner border of the specimen. (From the 'Palæontologia Indica.')

Cotype First and Referred Second Superior Molars of Stegolophodon cautleyi

Fig. 714. Cotype of *Mastodon cautleyi* Lydekker, 1886 (Brit. Mus. M.2817), p. xv, fig. 5. Compare "Fauna Antiqua Sivalensis," Falc. and Caut., 1846 [1847, Pl. xl, figs. 3, 3*a* (*M. latidens*)]. After Lydekker, 1886.2, p. 72, fig. 17.

Compare type of *S. cautleyi progressus* (Fig. 726).

Fig. 715. *Mastodon perimensis* (Ind. Mus. A.355, cast Brit. Mus. M.2851). After Lydekker, 1886.2, pp. 57 and 58, fig. 14.

Referred by Osborn to *Stegolophodon cautleyi*. Compare type of *S. cautleyi progressus* (Fig. 726).

Stegolophodon latidens Clift, 1828

Figures 685, 693, 694, 716–721, 757, Pl. xiii

Lectotype: Lower Pliocene, lowest levels of the Irrawaddy Series (fluviatile)[2] near Yenangyaung, Burma; referred, Middle Pliocene of India (Dhok Pathan zone), and Lower (?) Pliocene of China and Japan.

This is the characteristic Lower Pliocene[2] stage of the Irrawaddy Series, Burma (lectotype and cotypes) and of the Middle Pliocene stage of the Siwaliks and Perim Island, India (referred specimens).

Specific Characters (Osborn).—Distinguished by more regular formation of the ridge-crests than in *Stegolophodon cautleyi*,

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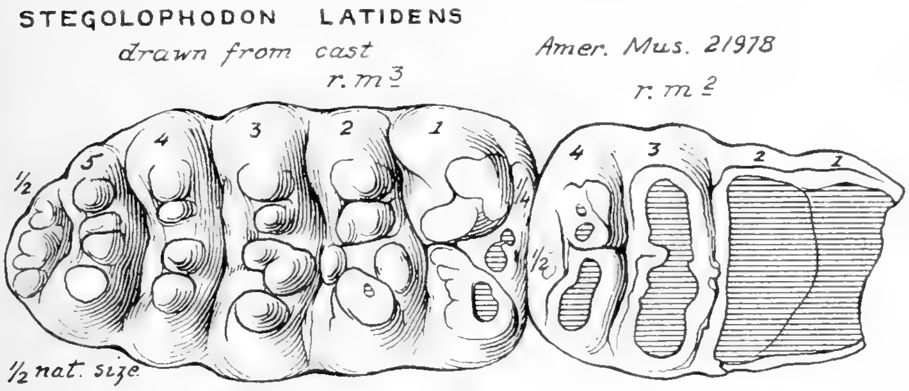
[1] [Cast Brit. Mus. M.2887.]

[2] [See note on page 824 above regarding the Lower Pleistocene age of *Stegolophodon latidens*.—Editor.]

surmounted by four to five conelets each, with two vestigial 'conules'; median fissure [or sulcus] in anterior ridge-crests; ridge-crests more stegodontoid. Ridge-crest formula: $M\,2\,\frac{4\frac{1}{2}-5}{4\frac{1}{2}-5}\,M\,3\,\frac{\frac{1}{2}-5-\frac{1}{2}}{\frac{1}{2}-6-\frac{1}{2}}$.

This important stage, originally described as *Mastodon* by Clift and as *Stegodon* by Falconer, has been aptly chosen as the genotypic species of *Stegolophodon* Schlesinger, and subsequently of *Prostegodon* Mastumoto-Osborn. The crown of the superior molar teeth, r.M², rM³, from Burma, represents an advance upon the species *Stegolophodon cautleyi* towards the true *Stegodon* type of molar; the three anterior ridges are closely compacted, closing the bottom of the three valleys (see Fig. 719). Each ridge consists of four plus compressed, rounded conelets, as shown in the protoloph and metaloph of M³; these conelets soon wear into uniform, transverse ridges (see tritoloph of M²). None of the specimens referred by Falconer, from Perim Island, agrees in these characters with the cotypes of *S. latidens;* some of the specimens referred by Falconer and Lydekker, from the Middle Pliocene Dhok Pathan, and other beds, also do not agree with the cotypes of *S. latidens.* We must accordingly define the species from the lectotype, following closely the original definition of Clift, together with the characters displayed in the several views of the lectotype molar, M³, reproduced herewith.



New Figure of Lectotype of Stegolophodon latidens Superior Molars

Fig. 716. New figure of lectotype of *Mastodon latidens* Clift, 1828, Pl. xxxvii, fig. 1, r.M², r.M³. Strong *orthogonal projection* after cast (Amer. Mus. 21978), one-half natural size. Compare figure 693. From near Yenangyaung, Burma. Original in British Museum.

The measurements of these molars (Figs. 718, 716, 719, 720, 717) in millimeters (with equivalents in inches) are as follows:

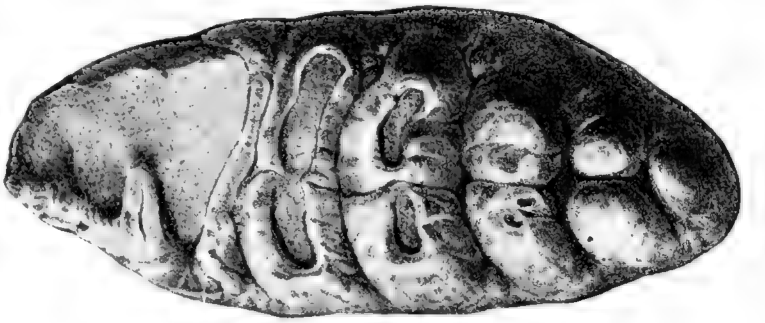
Second right superior molar, r.M²	
Anteroposterior	98 = 3⅞ inches
Transverse	68 = 2¾
Third right superior molar, r.M³	
Anteroposterior	140 = 5½
Transverse	76 = 3
Third right inferior molar, r.M₃	
Anteroposterior	300 = 11¾
Transverse	101 = 4

Mastodon latidens Clift, 1828. "On the Fossil Remains of two New Species of Mastodon, and of other vertebrated Animals, found on the left Bank of the Irawadi." Trans. Geol. Soc. London. (2), II, Pt. III, 1828, pp. 369-375. Lectotype.—Palate containing right M², M³. Cotype.—Right lower jaw with M₃ *in situ*. Originals in British Museum (Natural History), London; cast of r.M², r.M³ (Amer. Mus. 21978). Horizon and Locality.—Left bank of the Irrawaddy River, near Yenangyaung, 250 miles below Ava, Burma; Lower Pliocene, lowest levels of the Irrawaddy Series (fluviatile).[1] Lectotype Figure.—*Op. cit.*, Pl. xxxvii, fig. 1. Cotype Figure.—Pl. xxxviii, fig. 1.

Characters (compare Falconer and Cautley, 1846, p. 48).—Five and a half ridges in the third superior molar, including a posterior talon ridge and a subordinate ridge in front; four ridges in the second superior molar; four plus mammillæ on each ridge; ridges transverse, divided by a longitudinal cleft into two pairs of principal points [conelets], without intermediate mammillæ [conules] in the hollows. Enamel very thick; cement reduced to a thin layer, observed in the bottom of the hollows.

(Clift, 1828, p. 371): "Each tooth of the lower jaw [Fig. 717] consists of seven denticules, which are elevated, rounded, and mammillated; the mammillæ being from three to four in number."

Characters Shown in Three Figures of the Cotypes.—The three figures of the cotype molar teeth reproduced herewith show that Clift's original figure (Fig. 693) gives a somewhat wrong impression as to the rounded character of the conelets of which the ridges are composed. The more acuminate character of these conelets is displayed in Falconer's section reproduced herewith (Fig. 719, fig. 8) in which it appears that the three anterior valleys tend to close in at the bottom, unlike the open valleys in *Mastodon americanus* (Fig. 719, fig. 9). Thus a more accurate figure than Clift's is that of Gaudry (Fig. 720) probably made directly from a cast of Clift's specimen. This figure shows traces of trefoil conules in the anterior and second valleys and altogether presents a closer resemblance to the *Stegolophodon cautleyi* form of molar tooth, justifying Pilgrim's statement that a large form of *M. latidens* is derivable directly from *M. cautleyi.*



Cotype Third Inferior Molar of Stegolophodon latidens

Fig. 717. Cotype third right inferior molar, r.M₃, of *Mastodon latidens* Clift, 1828, Pl. xxxviii, fig. 1, about one-third natural size. Jaw omitted. From near Yenangyaung, Burma.

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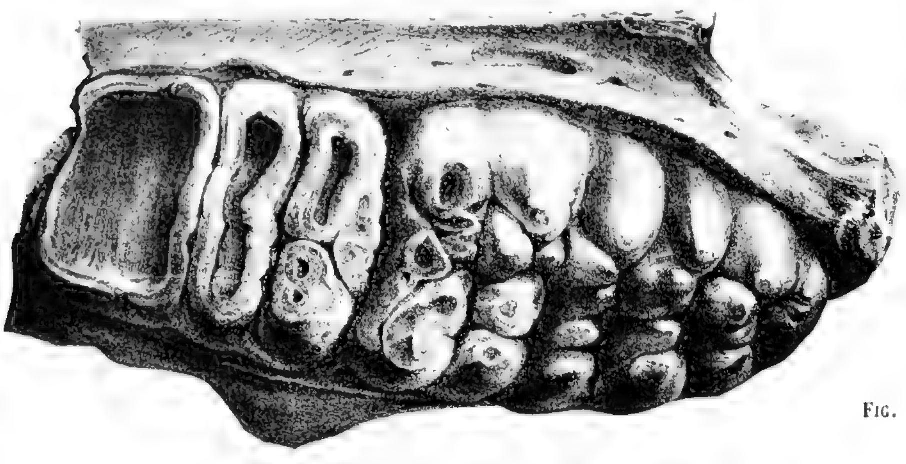
[1] [See note on page 824 above.—Editor.]

History of Discovery.—The history of discovery of this species (*Stegolophodon latidens*) in 1826 by Clift is very fully set forth in this Memoir (pp. 825, 827 above) and need not be repeated here; also Clift's original description and ridge formula as abbreviated above. Attention should be concentrated on the characters of the cotype specimens as shown in the four figures of the superior molars reproduced above (Figs. 718, 719, 720, 716), and in the lower jaw (see Fig. 717 for r.M_3).



Lectotype Molars of Stegolophodon latidens

Fig. 718. [Perspective.] Lectotype of *Mastodon latidens* Clift, 1828, reduced from Clift's Pl. xxxvii, fig. 1, to one-half natural size. Found on the left bank of the Irrawaddy River, below Ava, Burma. (Clift, 1828, p. 371 and Explanation of Plates): "The palate, and molar teeth of the right side of Mastodon latidens (a younger animal than the last). The anterior tooth is very much worn. The anterior part of the posterior tooth appears to have been just brought into use." These teeth include a right M^2 and M^3. The ridge-crests are: $\mathrm{M}\,2^{\underline{4-\frac{1}{2}}}\ \mathrm{M}\,3^{\underline{\frac{1}{2}-5-\frac{1}{2}}}$. Cast Amer. Mus. 21978. See orthogonal projection (Fig. 716).

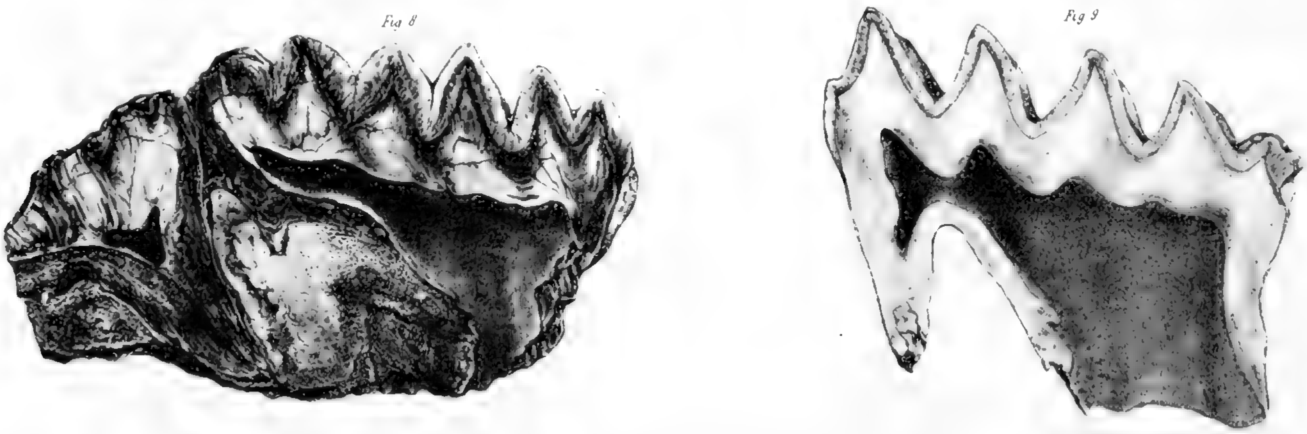


Fig. 719. (Left) Section of molars, M^2, M^3 (*fide* Falconer, Pal. Mem., 1868, Vol. I, p. 424) of *Mastodon latidens* Clift, 1828 [*Stegolophodon latidens*, lectotype], reduced to one-third natural size. After Falconer and Cautley, 1846 [1845, Pl. iii, fig. 8]. Compare with the crown view of same molar reproduced above.

(Right) Section of M^3 of *Mastodon americanus*, from Missouri, *op. cit.*, Pl. iii, fig. 9, inserted by Falconer for comparison. Brit. Mus. 17420.

Geologic Age.—The type of *Stegolophodon latidens*, according to Pilgrim (notes of April 3, 1923), probably occurs in the lowest levels of the Irrawaddy Series (fluviatile), near Yenangyaung, Burma, of Lower Pliocene age.[1] In beds of the same age in the Salt Range, Pabbi Hills, Jammu, and Kangra, are also found *Tetralophodon punjabiensis, Hipparion punjabiense, Tetraconodon magnus,* and *Taurotragus latidens.*

Referred specimens of *Stegolophodon latidens,* according to Pilgrim, also occur in the overlying Dhok Pathan beds (Salt Range) associated with the types of *Tetralophodon punjabiensis, Tetrabelodon* [= *Synconolophus*] *corrugatus, Mastodon* [= *Synconolophus*] *hasnoti,* and *Stegodon bombifrons.* It is probable that specimens referred by Falconer to *Stegolophodon latidens* from the Upper Miocene [Middle Pliocene] of Perim Island belong rather to *S. cautleyi.*

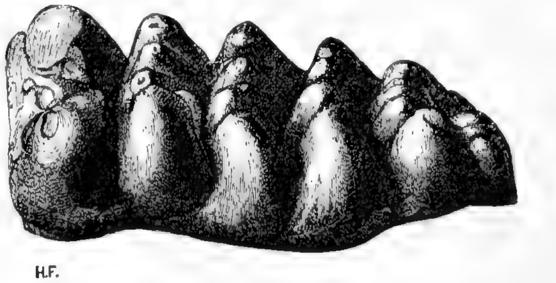


Fig. 231. — Première arrière-molaire supérieure du *Mastodon latidens,* à 1/2 grandeur, découverte par Crawfurd, dans l'Ava.

Fig. 720. Lectotype M^3 of *Mastodon* [*Stegolophodon*] *latidens* Clift, 1828, reproduced from an engraving by Gaudry (1878, p. 175, fig. 231). The third superior molar discovered by Crawfurd below Ava.

Geologic and Geographic Distribution.—The cotypes of *Stegolophodon latidens* are from the Irrawaddy River, 250 miles below Ava, near Yenangyaung, Burma. (1) In the Calcutta Museum are listed by Lydekker (1885, pp. 94–97) thirty-three specimens referred to *M. latidens* Clift, as follows: (a) Burma—six specimens of grinding teeth; (b) Asnot, Punjab—five grinding teeth; (c) Sind—five grinding teeth; (d) the remainder are from the Punjab, Potwár district, Gadari, Lehri, Jabi, Niki. (2) In the British Museum collections are listed by Lydekker (1886.2, pp. 74–78) eleven specimens from: (a) The

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[1] [See note on page 824 above.—Editor.]

Pliocene Siwaliks of the Punjab; (b) from near Yenangyaung, upper Burma; (c) Perim Island, Gulf of Cambay; (d) the Pliocene of Bruni, northwest Borneo [made by Osborn (1936, Vol. I, p. 700, of this Memoir) the type of *Stegolophodon lydekkeri*]; (e) Lehri, Punjab.

Lower Pliocene[1] Age.—Pilgrim assigns (Chap. XXII below) *Stegolophodon latidens* cotypes to Burma, Irrawaddy Series, lowest levels (fluviatile), and referred specimens to the Jammu and Kangra beds of India, also to the Salt Range and Pabbi Hills. According to Pilgrim the species ranges upwards into the upper Irrawaddy levels (fluviatile), Burma, and into the Salt Range, Hasnot, Dhok Pathan zone of India, equivalent to the Middle Pliocene Plaisancian (of France) and Levantin (of Austria and Hungary). *Stegolophodon latidens* may be regarded therefore as a characteristic Lower Pliocene[1] stage of the Stegodonts; whereas the more primitive *Stegolophodon cautleyi* specific type belongs in the Middle Pliocene of Perim Island, also referred specimens of the Salt Range, Simla Hills.

NOTES OF FALCONER, 1868, ON MASTODON [STEGOLOPHODON] LATIDENS, ALSO OF LYDEKKER, 1886

Falconer, "Palæontological Memoirs," Vol. I, pp. 424, 463, 471, Pls. III, XXX, XL of the "Fauna Antiqua Sivalensis"; Lydekker, "Catalogue of the Fossil Mammalia in the British Museum (Natural History)," Part IV, 1886, p. 74, and "Siwalik & Narbada Proboscidia," 1880, p. 236.

Stegolophodon latidens. Lectotype. Plate III, fig. 8, M^2 ridges 4½, M^3 ridges ¼-5-½, 4 conelets or denticles, enamel thick, cement thin.

Upper Molars.—Plate XL, figs. 1, 1a, ?second upper milk molar, Dp^3, with 2 ridges; figs. 2, 2a, ?third upper milk molar, Dp^4, with 4 ridges; figs. 3, 3a, M^1 ridges 4 and back and front heel (¼-4-¼ ridges), length 4 in. = 101 mm., width 2.3 in. = 59 mm. Lower Molars.—Plate XXX, fig. 6, lower jaw, $l.M_3$, 5 ridges and a double heel (5½ ridges), no cement, length of molar 11.3 in. = 288 mm., width 4.5 in. = 114 mm.

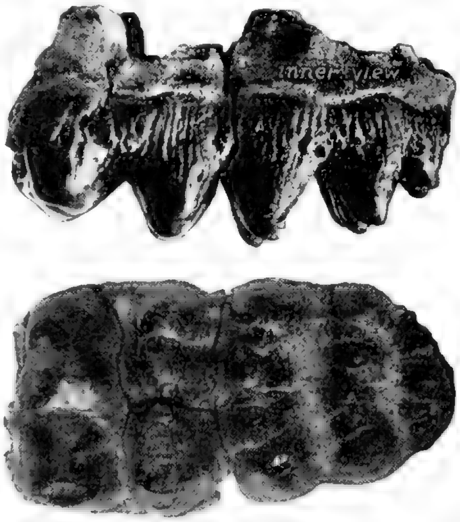
From these observations of Falconer, and from those of Lydekker below, we may write the following collective formula, primitive and progressive:

Stegolophodon latidens: Dp $3\frac{2}{}$ Dp $4\frac{4}{}$ M $1\frac{¼\text{-}4\text{-}¼}{}$ M $2\frac{4½\text{-}5}{4½\text{-}5}$ M $3\frac{¼\text{-}5\text{-}½}{½\text{-}5\text{-}½}$.

Osborn, 1927: Clift's figures (Figs. 717 and 718) as well as his description assign to M 3 the following ridge-crests $\frac{5½}{7}$ which should be interpreted as $\frac{¼\text{-}5\text{-}½}{½\text{-}5\text{-}½}$. This is approximately in accordance with Falconer and Lydekker's formula, although, as in all the Stegodonts, it is difficult to count the new or rudimentary ridge-crests.

Characters (Falconer, 1868.1, Lydekker, 1886.2).—(1) The presence of a median furrow between the primitive inner and outer lobes, (2) of four conelets or denticles on each ridge, (3) of thick enamel and thin cement, and (4) of conules in the two anterior valleys—these are the chief characters assigned by Falconer, 1868. Lydekker (1886.2, p. 74) characterizes the dentition as follows: "The mandibular symphysis is not certainly known, but it was probably short and tuskless. The upper molars are very wide, with no cingulum and relatively low transverse ridges, the median longitudinal cleft being frequently indistinct, the accessory tubercles small and the valleys comparatively open, the trefoils on the worn ridges imperfect, and the worn dentine surfaces on the inner and outer columns soon uniting. The hind talons are very large, while the inner border of the crown is concave and without a distinct cingulum; a fifth ridge is sometimes present in $\frac{\text{m. }2}{}$ . . . ; and the hind talon of $\frac{\text{m. }3}{}$ is always large, and may sometimes be reckoned as a sixth ridge. The enamel is very thick, and in the hinder teeth quite smooth; cement is usually absent, and premolars were probably developed."

Summary of Characters (Lydekker, 1880.1, p. 236).—"Having now passed in review the molar series of *M. latidens*, we may sum up what is known regarding the species. The adult cranium is unfortunately quite unknown; the palate is noticeable from the extent to which the molars converge anteriorly. The mandible is known by a specimen of the greater part of the right ramus, containing the two last molars, in the collection of the Indian Museum. This mandible is very long and slender, and sub-circular in cross-section, in the middle its vertical diameter at the penultimate molar being 5.8 inches and its transverse diameter 5.6 inches. The lower border is nearly straight up to the symphysis, with a slight convexity in the middle. From the extremely small size and circular section of the ramus where broken off at the commencement of the symphysis, the latter must have been short, and was probably unprovided with incisors."



Referred Stegolophodon latidens of Japan, a very Primitive Stage

Fig. 721. Referred 4½+ ridge-crested *Stegolophodon latidens* (*cautleyi*?) from Shiwogama, Miyagi District, Province of Rikuzen, Japan; "probably of typical Pontian age [Lower Pliocene]." Cast Amer. Mus. 22616. Inner and superior aspects of a third right upper molar, $r.M^3$, with 4½+ ridge-crests. (Upper) Internal aspect; (lower) crown aspect. After Matsumoto, 1926, Pl. V, figs. 1 and 3: "Fig. 1. *Prostegodon latidens* (Clift); right D^4 or M^1; inner view; natural size. . . Fig. 3 . . . [crown] view; natural size." Reduced in the present figure to one-half natural size. Length of $r.M^3$ along median line 115 mm. Compare *Mastodon* (*Bunolophodon*) [=*Stegolophodon*] *sublatidens* Schlesinger (Fig. 710).

"The ridge formula of the milk-molars is constant, and conforms to the normal tetralophodont order; in the true molars, however, there is not an unfrequent tendency to assume a pentalophodont type, the hind-talon of many of these teeth not unfrequently, partly or entirely, taking the form of a fifth ridge. In the following ridge-formula these varieties are indicated:—

Milk-molars.	True molars.
$\frac{2+3+4}{2+3+4}$	$\frac{(4\text{-}5)+(4\text{-}5)+(5\text{-}6)}{4+(4\text{-}5)+5}$

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[1] [See note on page 824 above.—Editor.]

This tendency to the production of an additional ridge in the true molars of *M. latidens* will be subsequently shown to be a character which it possesses in common with *M. sivalensis*. This tendency to variation enables us easily to comprehend how the passage from the tetralophodont *Mastodons* to the hexalophodont *Stegodons* (*S. cliftii*) was effected."

STEGOLOPHODON LATIDENS IN CHINA AND JAPAN

According to Schlosser (1903, p. 45), in the Munich collection, from an unknown locality, is a fragment of a lower molar tooth referable to *M. latidens*. Schlosser's figure of this fragment is reproduced in figure 770, 7.

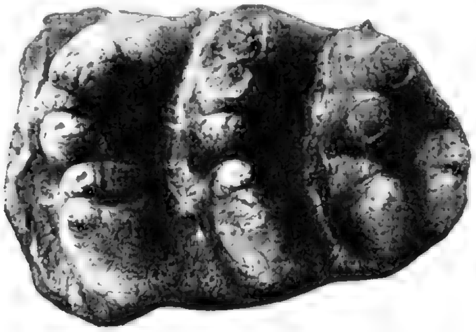
A primitive Japanese stage (Fig. 721) has been referred to this species by Matsumoto; it apparently possesses but four and a half ridge-crests and thus approaches the *S. cautleyi* stage (cf. Figs. 713 and 712).

Stegolophodon sublatidens Schlesinger, 1917

Figures 710, 722, Pl. xiii

Middle(?) Pliocene age. From near Teschen (Schlesien), Austria.

This species (Fig. 722) is founded upon the posterior half of a superior molar quite closely comparable to Pilgrim's type (Fig. 723) of *Mastodon* [=*Stegolophodon*] *stegodontoides*; it is more primitive in every way but the affinity is very striking; it thus appears to represent the first true *Stegolophodon* discovered in Europe.



Type of Stegolophodon sublatidens

Fig. 722. Type of *Mastodon* (*Bunolophodon*) *longirostre* Kaup *forma sublatidens* Schlesinger, 1917, posterior half of a third right superior molar, r.M^3. From near Teschen (Schlesien), Austria, Middle(?) Pliocene. Collection of the Royal Museum of Natural History, Vienna ("alter Sammlungs bestand"). Photograph loaned by Doctor Schlesinger. Reproduced one-half natural size. Compare Schlesinger, 1917, Taf. xvii, fig. 2.

The five conelets, of which two of the ridge-crests are composed, are arched transversely, a character not observed in *Stegolophodon latidens*, in which the ridge-crests are directly transverse, but seen in the type of *Stegolophodon stegodontoides*.

Specific Characters.—Inferior in size to *Stegolophodon stegodontoides*; valleys between ridge-crests more open, four to five conelets on fourth, fifth, and sixth ridge-crests; each posterior ridge-crest arched or convexo-concave; width of tetartoloph 82 mm., width of tetartoloph in *S. stegodontoides* 107 mm.; rudimentary cement in the valleys.

Mastodon (*Bunolophodon*) *longirostre* Kaup *forma sublatidens* n.f. Schlesinger. "Die Mastodonten des K. K. Naturhistorischen Hofmuseums." Denk. Naturhist. Hofmus., I, 1917, pp. 101, 102. Type.—A third right superior molar, r.M^3. Collection of the Royal Museum of Natural History, Vienna (alter Sammlungs bestand). Horizon and Locality.—From near Teschen (Schlesien), Austria; Middle(?) Pliocene. Type Figure.—*Op. cit.*, Taf. xvii, fig. 2.

Type Description.—(Schlesinger, 1917, pp. 101, 102): "Es wäre unmöglich, diesen Zahn, den ich als Typus einer *forma sublatidens* n.f. auffasse, innerhalb der Variationsbreite von *M. longirostre* anzuführen, wenn nicht die vorbeschriebenen Molaren direkt zu ihm überleiten würden. Praktisch ist der Zahn—stegodont, d.h. er weist jene Form von Jochzähnigkeit auf, die im Gegensatze zu den Verhältnissen bei den tapiroiden Mastodonten durch Umbildung der Sperrhöcker zu Nebenpfeilern und Einordnung in die Flucht gleichgrosser. Mammillen erreicht wird, während jene Arten Haupt- und Nebenhöcker verschmelzen und die Sperrhöcker als Crista nach aussen drängen und dann unterdrücken [Footnote: 'Ich kann nicht umhin, auf die Bestätigung des "Gesetzes der Nichtumkehrbarkeit der Entwicklung" (L. Dollo) hinzuweisen, die darin liegt, dass eine funktionelle Zygodontie von der Bunodontie aus nicht durch offene Rückkehr zum Urtypus (*M. pygmaeum*), sondern durch die Bildung der ganz anderen Stegodontie erreicht wird.']."

History.—In defining the genus *Stegolophodon*, with the genotypic species *Mastodon latidens* Clift, of Burma, Schlesinger implies, but does not so state with definiteness, the inclusion of his species '*Mastodon sublatidens*' within the genus *Stegolophodon*. His type of *Mastodon sublatidens* (Fig. 722) is an imperfect third superior molar of the right side, r.M^3, from Schlesien, Austria, of Pliocene age. The *five conelets*, of which two of the crests are composed, are arched transversely; this *arcuate* character is exceptional and does not appear in the two species of *Zygolophodon* (*Z. borsoni*, *Z. pyrenaicus*) nor in the genotypic species of *Stegolophodon*, namely, *Mastodon latidens* of Burma, in which the ridge-crests are directly transverse. The resemblance to *Stegolophodon stegodontoides* is much closer, although *S. sublatidens* is a smaller and more primitive form, with more open valleys and less distinct division of the cones into five conelets, as admirably shown in the accompanying figures 722 and 723, the types of these two species.

Stegolophodon stegodontoides Pilgrim, 1913

Figures 685, 708, 723, Pl. xiii

Lehri, in the Punjab, India, possibly Upper Siwaliks. Upper(?) Pliocene.

This is the characteristic Upper(?) Pliocene stage of the Pinjor horizon, Upper Siwaliks.

Specific Characters (Osborn).—Larger and much more progressive than *Stegolophodon latidens*. M^3 measures ap. 210 mm., tr. 110 mm., approximately same dimensions as the type of *Mastodon* [=*Stegolophodon*] *cautleyi*. Ridge-crests 6½ with five to six conelets. Valleys compressed or partly closed, less open than in *S. latidens*. Vestige of median fissure on three anterior ridge-crests (Fig. 723).

The type tooth of this species is transitional between the *Stegolophodon* and the *Stegodon* pattern, yet the species belongs to an independent line of descent contemporaneous in the Upper Pliocene with an advanced stage of *Stegodon* such as *Stegodon insignis*. From Lehri, in the Punjab, India, Pilgrim (1913) selected a six and a half crested third right upper true molar, r.M³, as the type of a new species *Mastodon stegodontoides*. He remarked (*op. cit.*, p. 294): "The last species of *Mastodon* which can be referred to this [*cautleyi-latidens*] line is the tooth from Lehri, of which the horizon is uncertain but may be possibly Upper Siwalik." The type specimen was originally figured natural size by Lydekker in "Palæontologia Indica," ser. 10, Vol. I, 1880, Pl. xxxix, as: "*Mastodon* (*Tetralophodon*) *latidens*, Clift. The third right upper true molar: from Lehri, in the Punjab. The specimen is drawn of the natural size and is viewed from the inner [outer] side."

Mastodon stegodontoides Pilgrim, 1913. "The Correlation of the Siwaliks with Mammal Horizons of Europe." Rec. Geol. Surv. India, Vol. XLIII, Pt. 4, p. 294. Type.—A third superior molar of the right side, r.M³, Ind. Mus. A.86. Horizon and Locality.—Possibly Upper Siwaliks, Pinjor formation, Upper(?) Pliocene; Lehri, Punjab, India. Type Figure.—Lydekker, 1880.1, Pl. xxxix, figured as *Mastodon* (*Tetralophodon*) *latidens*.

Type of Stegolophodon stegodontoides

Fig. 723. Type r.M³ of *Mastodon stegodontoides* Pilgrim, 1913. After Lydekker, 1880, Pl. xxxix: "*Mastodon* (*Tetralophodon*) *latidens*, Clift. The third right upper true molar: from Lehri, in the Punjab. The specimen is drawn of the natural size, and is viewed from the inner [outer] side." Ind. Mus. A.86. Reduced to one-half natural size. Provisionally placed in the Upper Pliocene, Pinjor formation (see Vol. I, fig. 413, also Pl. xiii).

Type Figure.—This fine half-size drawing of the type tooth measures: ap. 210 mm., tr. 110 mm. The ridge formula is $\mathrm{M}\ 3\frac{6\frac{1}{2}}{}$. In the anterior three ridges of the tooth there is still a trace of subdivision into inner and outer lobes, which disappears in the posterior three ridges. The conelet formula is: protoloph—six, metaloph—five to six, tritoloph—four to five, tetartoloph—five, pentaloph—five, hexaloph—four; the conelets are more or less discrete, the valleys apparently open. Consequently this molar crown appears to be descended from that of *Stegolophodon latidens* and represents a marked advance towards the true *Stegodon* type.

Specific Characters (Pilgrim).—(1) Owing to the almost entire absence of accessory columns the name *Mastodon stegodontoides* is proposed. (2) It will be seen that the type molar carries on none of its ridges more than the usual four columns [characteristic of *Stegolophodon latidens*], while the anterior ridges of *Stegodon elephantoides* (=*cliftii*) carry nine or ten mammillæ [i.e., conelets].

Osborn, 1924: While we recognize the usual four columns in this molar tooth, we observe in Lydekker's figure that the summits of the two inner columns tend to subdivide; thus in the tetartoloph and the pentaloph there are *five* distinct conelets, as compared with *four* plus observed in *Stegolophodon latidens* and in *S. cautleyi*.

Lydekker's Description (1880.1, pp. 235–237).—"*Third upper true molar.*—The large tooth represented in Plate xxxix is a specimen of the last upper molar of the right side of *M. latidens*, collected by Mr. A. B. Wynne near the village of Lehri, in the Punjab. This specimen is implanted in a fragment of the maxilla, which also contains the two last ridges of the preceding or penultimate tooth. The figured tooth is entirely unworn, and was still covered by the gum at the death of the animal. The crown carries six transverse ridges, the hindmost of which is considerably smaller than the others, and probably represents an ultra-developed talon, as we saw to be the case in the penultimate molar represented in fig. 1 of Plate xxxviii. The tooth consequently belongs to a 'pentalophodont' type of dentition. The ridges are low and simple, and with the exception of the first, are slightly convex anteriorly, and as concave posteriorly. Each ridge is divided by a longitudinal cleft placed somewhat externally to the mesial antero-posterior axis of the tooth. The internal moiety of each ridge, with the exception of the second and sixth, bears three mammillæ or cusps, while the external moiety bears only two on each ridge. The valleys are quite simple and uninterrupted. In this tooth, as also in all the previously described specimens, there is no trace of cement. The length of the specimen is 8.6 inches, and its greatest width 4.2 inches."

Lydekker's description and figure concur in giving five conelets as characteristic of each ridge and as showing the three posterior ridges more progressive than the three anterior.

Also exhibiting this six+ ridged, five to six conelet condition, is a third left upper true molar from Borneo erroneously referred by Lydekker to *Mastodon latidens*.[1]

Stegolophodon nathotensis Osborn, 1929

Figure 724, Pl. xiii

Lower Chinji horizon, near Nathot, India; Mio-Pliocene.

This type was discovered by Barnum Brown in 1922 in the Lower Chinji horizon, near Nathot, India, the exact level being unrecorded. As shown in figure 413 the species is of approximately the same geologic age as *Trilophodon chinjiensis* type, *Deinotherium pentapotamiæ* type, and *Serridentinus browni* type. The Chinji horizon, of a total thickness of 2,400 feet, doubtless represents a very long period of geologic time.

Stegolophodon nathotensis Osborn, 1929. "New Eurasiatic and American Proboscideans," Amer. Mus. Novitates, No. 393, Dec. 24, pp. 13–15 (Osborn, 1929.797). Type.—Amer. Mus. 19455. Posterior half of a fragmentary right third superior molar, r.M³ (Fig. 724, C, C1); posterior half of a right third inferior molar, r.M₃ (A, A1); anterior half of a left second superior molar, l.M² (B, B1). Horizon and Locality.—Found near Nathot, India, "Lower Chinji horizon, the exact level being unrecorded, lower Middle Siwaliks; Middle to Upper Miocene [Mio-Pliocene]." Type Figure.—*Op. cit.*, 1929.797, p. 14, fig. 14.

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[1] [Made by Professer Osborn in 1936 the type of *Stegolophodon lydekkeri* (see Vol. I, p. 700, fig. 660).—Editor.]

TYPE CHARACTERS.—Ridge-crests low, blunted, with four to five blunted conelets (Fig. 724 B, A) on each crest; ridge-crests transversely arcuate or arched, as in *Stegolophodon stegodontoides*. Enamel thick with slightly indented border. Rugose external cingulum. Ridge-crest formula unknown, probably M 3 $\frac{?4\frac{1}{2}}{?5\frac{1}{2}}$; characters of ridge-crests and conelets quite distinct from those of *Stegolophodon latidens*, ridge-crest formula probably lower than in *S. latidens*. Species at present known by the type specimen only, which belongs in a lower geologic level, namely, Mio-Pliocene, than the type of *S. latidens*, which belongs in the Lower Pliocene.[1] See measurements in legend (Fig. 724).

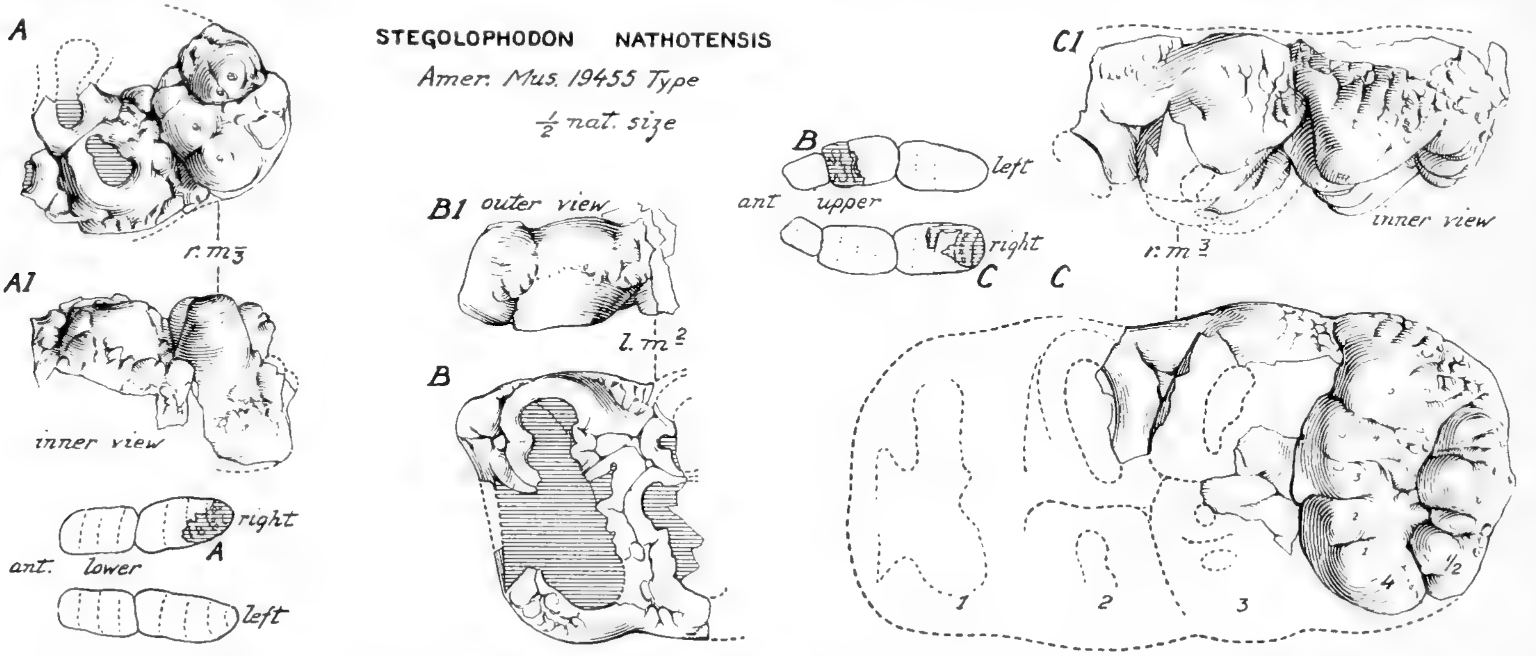

Fig. 724. Type of *Stegolophodon nathotensis* Osborn, 1929 (Amer. Mus. 19455), Lower Chinji horizon, from near Nathot, India. One-half natural size. A third superior molar of the right side, r.M^3, probably with four and a half ridge-crests. Meas.: ap. 180e mm., tr. 88e mm.; height of metaloph 38e mm.; l.M^2 (protoloph) tr. 73 mm., (metaloph) 36e mm.; r.M$_3$, tetartolophid and pentalophid (talon only). Ridge-crest of tetartoloph of r.M^3 with five arcuate conelets. Massive, brachyodont. Osborn, 1929.797, p. 14, fig. 14.

Stegolophodon cautleyi progressus Osborn, 1929

Figures 725–727, Pl. XIII

Summit of Lower Chinji horizon, 2,000 feet above base of Lower Siwaliks, twelve miles east of Chinji Bungalow, India; Mio-Pliocene.

This type is of great importance and interest as yielding for the first time a knowledge of the cranial structure of *Stegolophodon* in its Miocene stage of evolution. Distinguished as *Stegolophodon* by its four-crested intermediate molars, its superior tusks, and its cranial profile, which remind us strongly of the primitive type of skull and tusks seen in *Trilophodon* and in *Serridentinus*; the four-crested intermediate molars parallel those observed in *Tetralophodon*, a genus from which the present *Stegolophodon* is sharply removed by the *absence* of trefoils, vestiges of which appear only in the valleys between the ridge-crests. Altogether *Stegolophodon cautleyi progressus* (probably of the summit of the Miocene or lower levels of the Pliocene) is a *progressive ascending mutation* of the typical *Stegolophodon cautleyi* of Perim Island, which we regard as of Middle Pliocene age.

Stegolophodon cautleyi progressus Osborn, 1929. "New Eurasiatic and American Proboscideans," Amer. Mus. Novitates, No. 393, Dec. 24, pp. 13–15 (Osborn, 1929.797). TYPE.—Amer. Mus. 19446. A juvenile cranium (Figs. 725 and 727), containing right and left superior tusks with broad enamel band, also *in situ* third and fourth superior deciduous premolars and first molar of both sides (see Fig. 726, r.Dp$^{3-4}$, r.M^1). HORIZON AND LOCALITY.—"Twelve miles east of Chinji Bungalow, India . . . Collected by Barnum Brown in 1922 at summit of Lower Chinji horizon, 2,000 feet above base of Lower Siwaliks. Middle Miocene [Mio-Pliocene]." TYPE FIGURE.—*Op. cit.*, 1929.797, p. 14, fig. 15. See also figures 725 to 727 of present Memoir.

TYPE CHARACTERS.—Superior tusks laterally compressed, with broad external enamel band; ridge-crest formula as compared with that of *Stegolophodon cautleyi*, as follows:

Stegolophodon cautleyi progressus: r.Dp $3^{\underline{3}}$ r.Dp $4^{\underline{4\text{-}\frac{1}{2}}}$ r.M $1^{\underline{\frac{1}{2}\text{-}4\text{-}\frac{1}{2}}}$
Stegolophodon cautleyi (typical): r. Dp $3^{\underline{(3?)}}$ r. Dp $4^{\underline{\frac{1}{2}\text{-}3\text{-}\frac{1}{2}}}$ r.M $1^{\underline{\frac{1}{2}\text{-}4\text{-}\frac{1}{2}}}$.

Four ridge-crests in intermediate molars, r.Dp^4, r.M^1, with four irregular conelets on each crest; rudimentary anterior and posterior ridge-crests in r.M^1; conelets less blunt and crowns less brachyodont than in *Stegolophodon nathotensis*; median fissure in r.M^1 wanting, as shown in comparison of figure 726 with figure 714, cotype of *Stegolophodon cautleyi*, or decidedly less distinct than in *S. cautleyi* lectotype from Perim Island (Fig. 712) and the referred l.M^2 (Fig. 715); traces of irregular internal trefoil conelets on r.Dp^4 and r.M^1.

Of very great importance and interest is the presence of superior incisive tusks with lateral enamel band as well as other evidence in the structure of the superior grinding teeth of the affinities of this tetralophodont type with the much more primitive trilophodont mastodonts of the Lower Miocene of France (cf. also Figs. 725–727).

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[1] [See notes on pages 814 and 824 above.—Editor.]

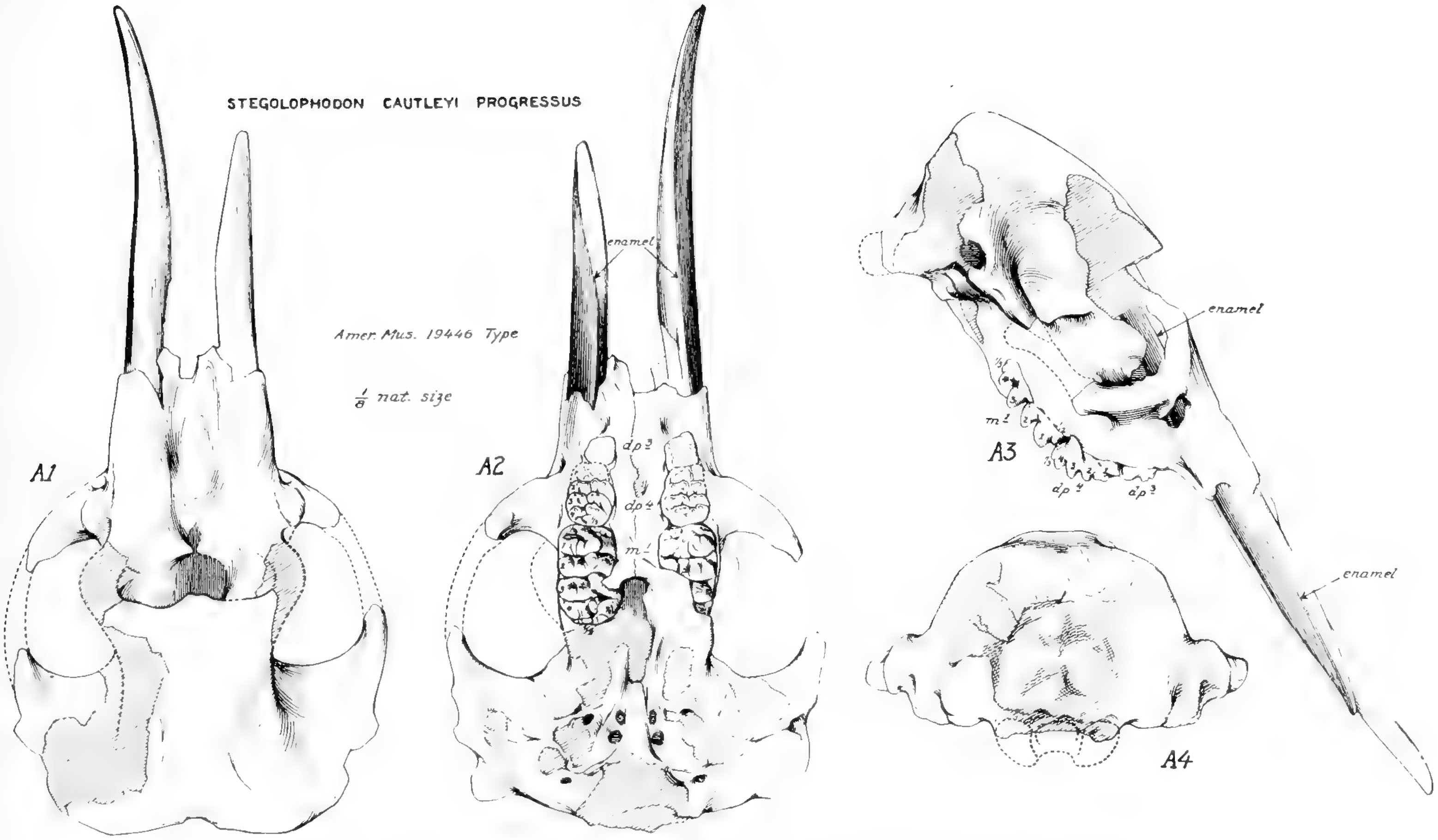


Fig. 725. Type cranium of *Stegolophodon cautleyi progressus* Osborn, 1929 (Amer. Mus. 19446), same specimen as figure 727.

A1, Superior aspect, exhibiting cranium with anterior narial opening and premaxillaries.

A2, Palatal view, exhibiting lateral enamel band of tusks, much worn Dp^3 with remnants of 3+ ridge-crests, Dp^4 with 4+ ridge-crests, M^1 with 4+ ridge-crests, also posterior narial opening and basicranial foramina.

A3, Right lateral aspect, exhibiting enamel band on tusk.

A4, Occipital aspect, slightly compressed by crushing.

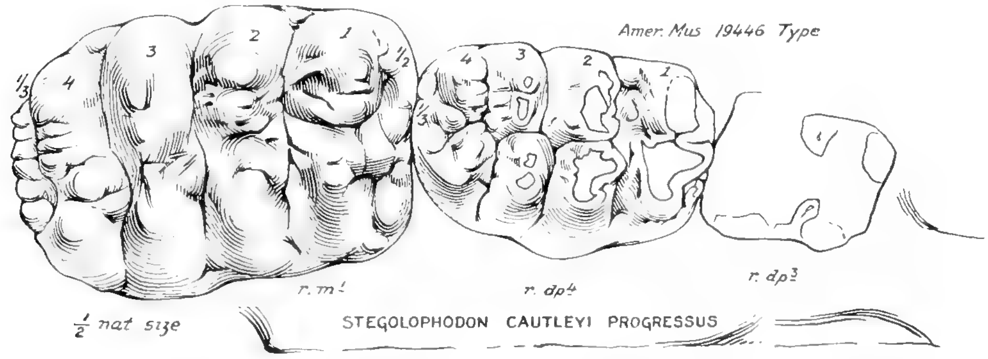
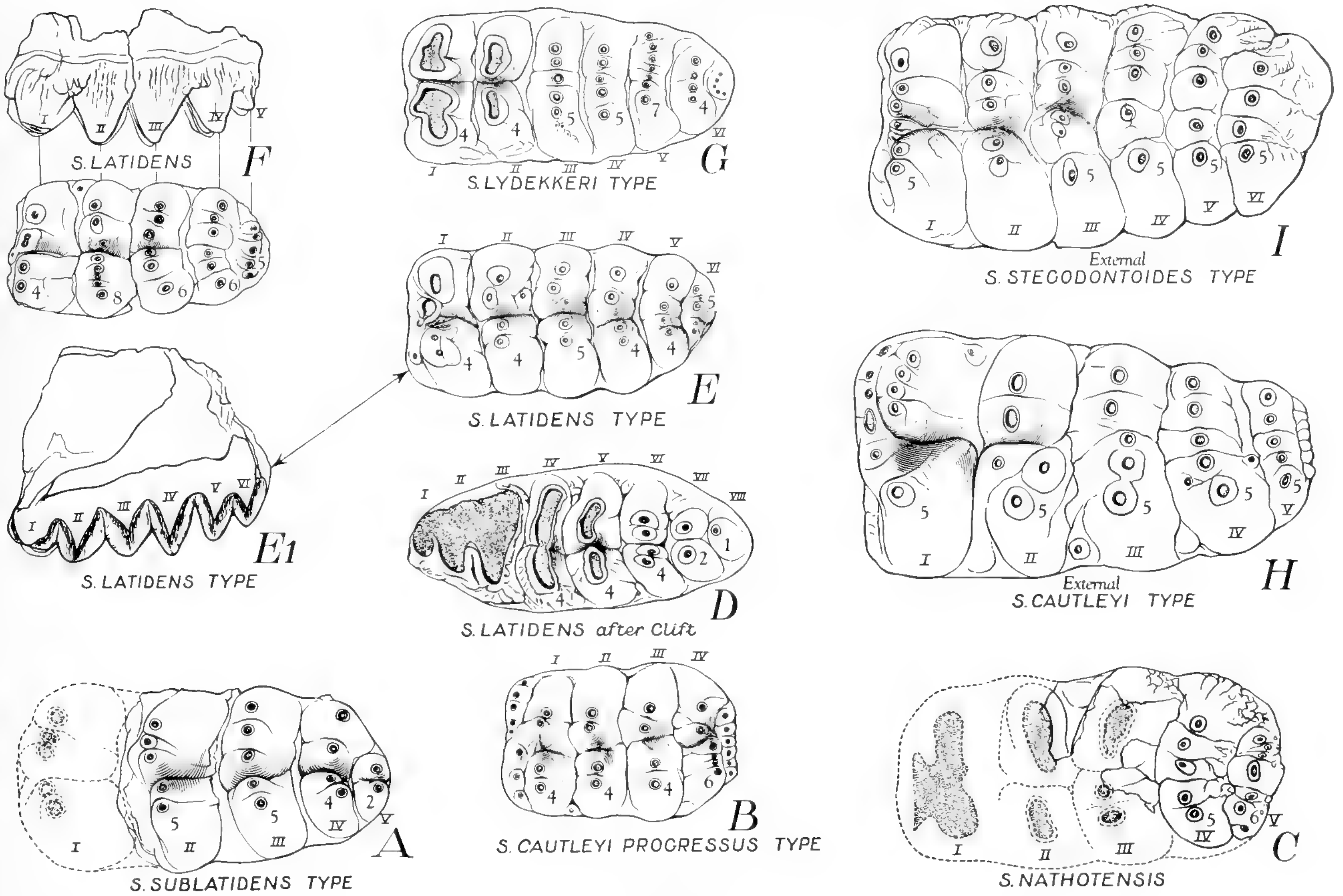


Fig. 726. Type of *Stegolophodon cautleyi progressus* Osborn, 1929. Detailed study of right superior dentition, Dp^3-M^1, combination drawing of two sides. Coronal ridge-crests intermediate in formula and pattern between the typical *Mastodon* [=*Stegolophodon*] *cautleyi* Lydekker and *M.* [=*Stegolophodon*] *latidens* Clift; similar in the regular disposition of the cones and conelets.

Fig. 727. Type skull (Amer. Mus. 19446) of *Stegolophodon cautleyi progressus* Osborn, 1929, collected by Barnum Brown twelve miles east of Chinji Bungalow, summit of the Lower Chinji horizon, 2,000 feet above the base of the Lower Siwaliks, India. This skull, containing the right and left superior tusks, third and fourth superior deciduous premolars, and the first superior molars (partly erupted), shows the laterally compressed tusks with enamel band, 4+ ridge-crests on Dp^4, 4+ ridge-crests on M^1; it is somewhat more progressive than the type of *Mastodon* [=*Stegolophodon*] *cautleyi* Lydekker.

Left lateral, palatal, and right lateral aspects, one-fifth natural size.

STEGOLOPHODON



S. LATIDENS

S. LYDEKKERI TYPE

S. STEGODONTOIDES TYPE

S. LATIDENS TYPE

S. LATIDENS TYPE

S. LATIDENS after Clift

S. CAUTLEYI TYPE

S. SUBLATIDENS TYPE

S. CAUTLEYI PROGRESSUS TYPE

S. NATHOTENSIS

PLATE XIII

Stegolophodontinæ, Stegolophodon: Primitive Longitudinal Sulcus, Shaded (A, B), Persisting in I–IV Anterior Ridge-crests (E, E1), in I–III Anterior Ridge-crests (F), Vestigial in Ridge-crests I–III (G, H, I). Conelets Rounded, Increasing from 4–5 (A, D), 5–7 (C, H, I, G). Posterior Ridge-crests IV–VI Progressive, with Conelets 5–7 (G), Conelets not Exceeding 5 (H, I)

Mio-Pliocene B, *Stegolophodon cautleyi progressus* type, r.M^1. Amer. Mus. 19446, near Chinji Bungalow, India. Summit of Lower Chinji horizon, 2,000 feet above base of Lower Siwaliks.

C, *Stegolophodon nathotensis* type, r.M_3. Conelets 5–6. Amer. Mus. 19455, near Nathot, Lower Middle Siwaliks, India. Lower Chinji horizon.

Lower Pliocene[1] D, *Stegolophodon latidens* cotype, r.M_3. Ridge-crests I–VIII, conelets 4, sulcus on ridge-crests I–IV. After Clift, 1828, Pl. xxxviii, fig. 1, near Yenangyaung, Burma.

E, *Stegolophodon latidens* cotype, r.M^3. Ridge-crests I–VI, sulcus on ridge-crests I–IV. E 1 (section), ridge-crests coalescent at base (I–III). After cast (Amer. Mus. 21978) of Clift's type, 1828, Pl. xxxvii, fig. 1, near Yenangyaung, Burma.

F, *Stegolophodon latidens* ref., r.M^1. Sulcus on ridge-crests I–III, conelets 4–6, ridge-crests 4½. After Matsumoto, 1926.1, Pl. v, figs. 1 and 3 (*Prostegodon*), Shiwogama, Miyagi District, Province of Rikuzen, Japan.

Pliocene (?) G, *Stegolophodon lydekkeri* type, l.M^3. Ridge-crests I–VI, conelets 4–7, sulcus on ridge-crests I and II only. After Lydekker, 1886.2, fig. 19 (as *M. latidens*), Borneo.

Middle(?) Pliocene A, *Stegolophodon sublatidens* type, r.M^3. Conelets 4–5. After Schlesinger, 1917, Taf. xvii, fig. 2, Teschen (Schlesien), Austria.

Middle Pliocene H, *Stegolophodon cautleyi* lectotype, l.M^3. Ridge-crests I–V, sulcus on ridge-crests I and II, conelets 5. After Lydekker, 1886.1, p. xv, fig. 6, Perim Island, India

Upper(?) Pliocene I, *Stegolophodon stegodontoides* Pilgrim, type, r.M^3. Ridge-crests I–VI, sulcus on ridge-crests I–III, conelets 5. After Lydekker, 1880, Pl. xxxix, Lehri, Punjab, India, possibly Upper Siwaliks.

Comparative Observations (1935)

Molars of *Stegolophodon* are readily distinguished from those of the *Mastodon*, *Zygolophodon*, and *Turicius* phyla by the following characters:

First, by the persistence of the *median sulcus* separating the inner and outer pairs of cones of all the crests (A, B, D), of the three to four anterior crests (E, F, I), of the two anterior crests (G, H).

Second, by the rounded, bunoid conelets separated by median sulcus (A–H).

Third, by the closure of the enamel in the base of the transverse valleys, as seen in section (E1), very characteristic of *Stegodon*.

The second and third of the *Stegolophodon* characters enumerated above link this genus with the genus *Stegodon*. But we must remember that *Stegolophodon cautleyi* is of Middle Pliocene age (Perim Island), contemporary with the true Middle Pliocene *Stegodon bombifrons* (Dhok Pathan).

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[1] [See note on page 824 above regarding the Lower Pleistocene rather than Lower Pliocene age of *Stegolophodon latidens*.—Editor.]

evidence in the structure of the superior grinding teeth of the affinities of this tetralophodont type with the much more primitive trilophodont mastodonts of the Lower Miocene of France (cf. also Figs. 725 and 727).

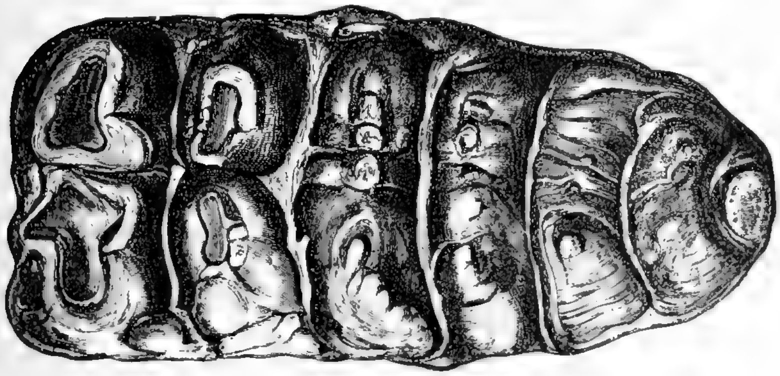
Stegolophodon lydekkeri Osborn, 1936

Figure 728, Pl. XIII

From vicinity of Bruni, northwest coast of Borneo.

[In an intensive reexamination of various species of *Stegolophodon*, Professor Osborn discovered wide differences between the types of *Stegolophodon sublatidens* Schlesinger, 1917 (Pl. XIII, A) and *S. latidens* Clift, 1828 (Pl. XIII, E) and a molar tooth from Borneo described and figured by Lydekker as '*Mastodon latidens*' Clift (1885.2, 1886.1, 1886.2). This molar Professor Osborn selected as the type of a new Pliocene species, namely, *Stegolophodon lydekkeri* (Vol. I, p. 700).

Fig. 19.



Mastodon latidens.—The third left upper true molar of a small individual in a partially-worn condition; from the Pliocene (?) of Borneo. $\frac{2}{3}$. The lower border of the figure is the inner border of the specimen. (From the 'Palæontologia Indica.')

Fig. 728. *Stegolophodon lydekkeri* Osborn, 1936, Volume I, p. 700, fig. 660, of the present Memoir. Third left superior molar exhibiting six ridge-crests and a talon. Figured by Lydekker, 1886.2, fig. 19, as *Mastodon latidens*. Compare Lydekker, 1885.2, Pl. XLVIII, also Pl. XIII of the present Memoir. Two-thirds natural size.

TYPE.—Third superior molar of the left side, l.M^3, original in the Zoological Society of London; cast in the British Museum (M.2498). HORIZON AND LOCALITY.—(Lydekker, 1885.2, p. 777): "The specimen forming the subject of the present notice was forwarded from Borneo to the Secretary of this Society by Mr. A. H. Everett, C.M.Z.S., who stated that it was found during the early part of the present year [1885] by a Kadayan in the jungle in the vicinity of Bruni, on the north-west coast of Borneo." Pliocene (?). TYPE FIGURE.—Lydekker, 1885.2, Pl. XLVIII, figs. 1 and 2; see also Lydekker, 1886.1, fig. 7, 1886.2, fig. 19, as well as Pl. XIII and figures 660 and 728 of the present Memoir.

DESCRIPTION.—(Lydekker, 1885.2, pp. 777–779): "The specimen is the crown of the last left upper true molar of a tetralophodont *Mastodon*, and agrees so closely with Indian teeth of the Siwalik *Mastodon latidens*, Clift [Footnote: 'Trans. Geol. Soc. ser. 2, vol. ii, pt. 3, p. 371 (1828).'], that it may be safely referred to that species, although it indicates a very small individual. . . . It will be seen that the Borneo specimen agrees [with *M. latidens* of the Punjab—made by Pilgrim in 1913 the type of *Mastodon stegodontoides*] in the number of ridges (although the hind talon is considerably smaller), but is of greatly inferior size, the dimensions of the two specimens being as follows, in inches:—

	Punjab	Borneo.
Extreme length	8.6	6.3
Width of first ridge	4.2	2.95"]

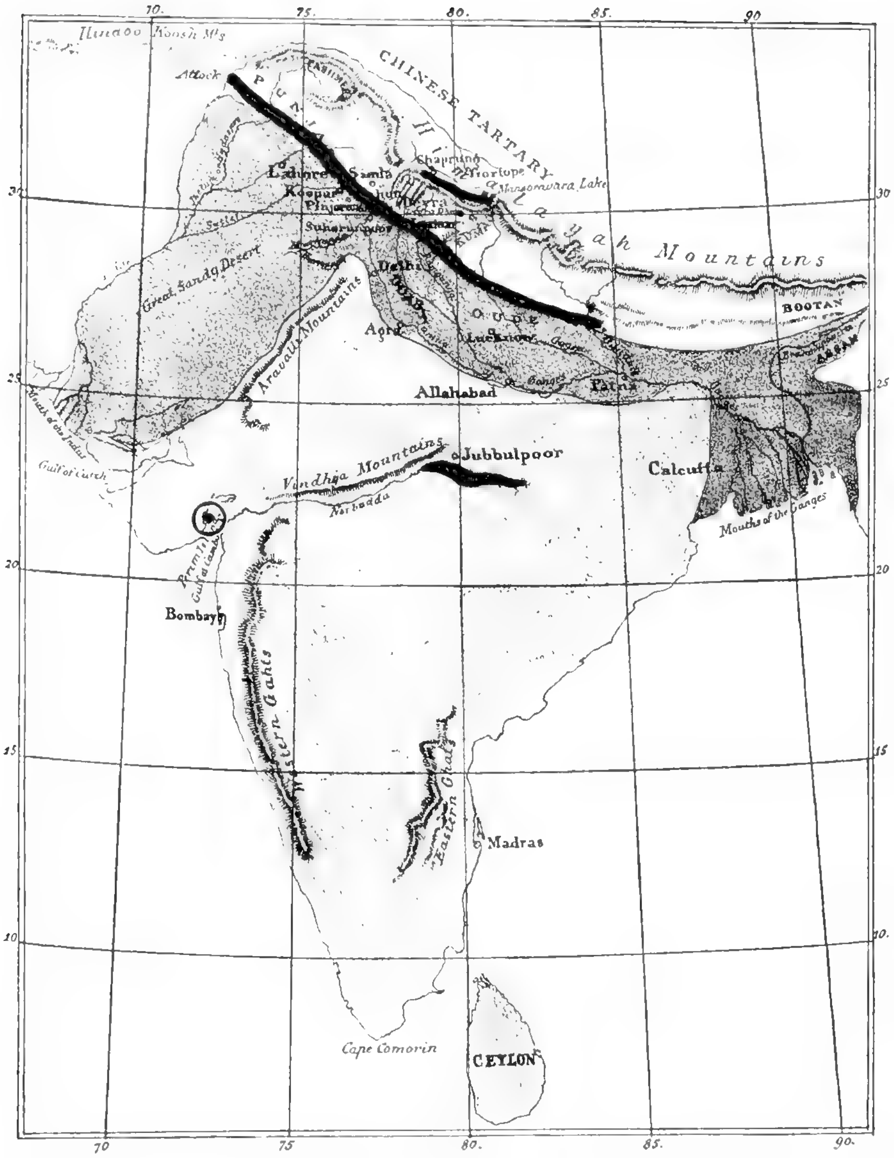


Fig. 729. Falconer's map of the geology of India (see "Palæontological Memoirs," 1868, Vol. I, description of Pl. II). The *red* fossiliferous areas, here colored black, are described by Falconer as follows:

"The *red* [black] stripe represents the Sewalik Hills, stretching from the Hydaspes to the Gunduck River, 800 miles. The small *red* [black] patch behind the Himalayahs represents the ossiferous plain of Tibet about 16,000 feet above the sea. The other *red* [black] patches represent the Nerbudda [Pleistocene], and the [black dot within the circle the] Gulf of Cambay [Perim Island—Middle Pliocene] fossil tracts."

The following is Falconer's interpretation of the geology of India:

"The great mass of *light shading* represents the supposed *insular* form of the continent of India at an early period of the Tertiary epoch, the island forming a sort of triangle, of which the eastern and western Ghats formed the sides and the great Vindhya range the base, with an irregular patch of mountainous country stretching north forming the Aravalli range."

"The *dark shading* represents the plains of India, forming the valley systems of the Ganges and Indus drainage, which were formerly narrow ocean straits. These straits were the recipients of the silt and alluvium washed out of the Himalayahs, and were at length elevated above the sea, so as to form the existing continent. The Sewalik Fauna then spread over the continent, from the mouth of the Irrawaddi to the Gulf of Cambay 2,000 miles, and north to the Jhelum 1,500 miles. After the long establishment of the Sewalik Fauna, a great upheavement took place along the line of the Himalayahs, elevating a narrow belt of the plains into the Sewalik Hills, and adding many thousand feet to the height of the Himalayahs."

IV. SUCCESSION OF SPECIES OF THE GENUS STEGODON

Superfamily: STEGODONTOIDEA Osborn, 1935, 1936
Family: STEGODONTIDÆ Young-Hopwood, 1935
Subfamily: Stegodontinæ Osborn, 1918, 1921

Genus: **STEGODON** Falconer and Cautley, 1847, 1857

Original reference: Falconer and Cautley, "Fauna Antiqua Sivalensis," 1846 [1847, Pl. xlii]; also Falconer, Quart. Journ. Geol. Soc. London, 1857, Vol. XIII, pp. 314, 318, and Synoptical Table opposite page 319.

Genotypic species: *Elephas Cliftii, E. bombifrons, E. ?Ganesa, E. insignis.*[1]

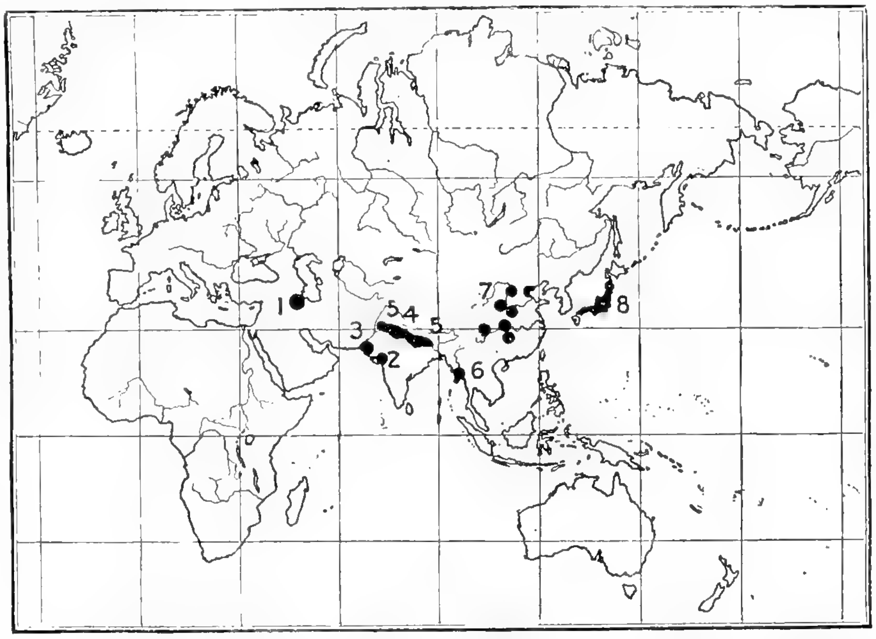
Syn.: *Emmenodon* Cope, 1889; *Parastegodon* Matsumoto, 1924 (in part).

Generic Definition.—(Falconer, 1857, p. 318): "Dentium molarium 3 utrinque intermediorum coronis complicata colliculis hypisomeris (*e.g.* 7+7+8), mammillatis, tectiformibus. Praemolares nondum observati."

Generic Characters.—Ridge-crests intermediate between *Stegolophodon* and *Archidiskodon planifrons* types, progressively multiplying from six to eleven in the intermediate molars, from nine to fifteen and a half in the posterior molars. Cones rapidly subdividing by binary or ternary fission into multiple conelets. Ridge-crests elevating from brachyodont (*Stegodon sinensis*) to subhypsodont (*S. airawâna* and *S. auroræ* stages). Cement developing in the valleys. Crania of mastodontoid (*S. bombifrons*) to extremely abbreviated, female? (*S. insignis*), more elongated, male? (*S. ganesa*), more triangular (*S. trigonocephalus*) form. Tusks attaining great dimensions (*S. ganesa*). Phylum parallel to that of the true *Archidiskodon* and *Elephas*, not directly ancestral, readily distinguished by cranial and dental characters.

The generic name *Stegodon* was first printed in the "Fauna Antiqua Sivalensis" of Falconer and Cautley, 1846 [1847, Pl. xlii]. It was ten years later that it appeared as a subgenus (Falconer, 1857, pp. 314, 318, table opp. p. 319) to include the following species, *Elephas cliftii, E. bombifrons, E. ganesa*(?), and *E. insignis*, and has subsequently been used as a genus by all the principal authors, except Lydekker who clung to the Cuvierian division of the mastodonts and elephants into the two genera *Mastodon* and *Elephas*. Pohlig in 1888, p. 252, wrote the genus in this way: *Stego(lopho)don.* Schlesinger, 1917, p. 115, separated the species *M. latidens* as the type of a new genus *Stegolophodon.*

Fig. 730. After Osborn, 1910.346, p. 323, fig. 154. Compare figures 729 and 826 of present Memoir.



—Chief Miocene and Pliocene fossil mammal deposits of Asia. **1.** Maragha, Persia. **2.** Perim Island. **3.** Manchhar Beds of Sind. **4.** Siwaliks of the Punjab. **5.** Subhimalayan Siwaliks (River Brahmaputra to River Jhelum). **6.** Valley of the Lower Irawadi, Burma. **7.** Miocene and Pliocene deposits of China (Provinces of Shan-si, Shen-si, Sze-chuan, Kwang-Tung, Ho-nan, Hu-nan, Hu-peh). **8.** Miocene and Pliocene deposits of Japan.

Stegodon (omitting the six[2] species described above under *Stegolophodon*) is readily definable and readily distinguishable from any genus of the Mastodontidæ, on the one hand, or of the Elephantidæ, on the other (see Vol. I, p. 25), by the *brachyodonty* to subhypsodonty of its ridge-crests, in contrast to the hypsodonty in all the species of the *Elephas* and *Loxodonta* phyla. The relative height attained is shown in figures 687 and 688. While the ridge-

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[1] [Hopwood in his Memoir of 1935 on the "Fossil Proboscidea from China," p. 72, remarks: "According to the modern school of priority-purists this necessitates the selection of *E. cliftii* as genotype as a matter of course. Fortunately, we can do so and adhere to the author's original intention, for, in his later writings Falconer expressly says that *Stegodon* corresponds 'with the forms collectively designated *Mastodon elephantoides* by Clift', (1857, p. 314)." —Editor.]

[2] [To these six species should be added the *Stegolophodon lydekkeri* Osborn, described in Volume I of the present Memoir (p. 700).—Editor.]

crests are composed exactly as we know that we shall find them in the direct ancestors of *Elephas*, they remain short crowned, even in the progressive species *Stegodon insignis* and *S. ganesa*, and in the still more progressive *S. orientalis* and *S. airâwana*. This is undoubtedly an adaptation to browsing on leaves and softer kinds of food, which leads us to believe that the Stegodonts were persistent browsers rather than grazers, as in all the phyla of *Elephas* and of *Loxodonta*.

Table V. Species in Approximate Ascending Order of Collective Maximum and Minimum Ridge-crests

Falconer (1868), Lydekker (1886), Martin (1890), Matsumoto (1918), Osborn (1929)

	Dp 2	Dp 3	Dp 4	M 1	M 2	M 3
STEGOLOPHODON *cautleyi*			½-3-½	½-4-½	4	5-½ +
cautleyi progressus		3	4-½	½-4-½		
latidens		2	4	¼-4-¼	4½-5 / 4½-5	¼-5-½ / ½-6-½
lydekkeri						6 +
sublatidens						?6½
stegodontoides						6-½
STEGODON *sinensis*		½-4				
elephantoides (=*cliftii*, *fide* Falc.)		4	5-6	6-6¼	6½	6½ / 8-½
elephantoides Clift				6¼	6¼	10
bombifrons		4 / 4	5-6 / ½-5-½-6½-7	6 / 7-7½	6-7 / 7-7½-8	7½-8-8½-9-9½ / 8-9-9½
trigonocephalus		4	7			
mindanensis (*Archidiskodon?*) Fragments, far more progressive in the direction of *Archidiskodon* than either *insignis* or *ganesa*.						
insignis	2 / 2	5-6 / 6	7½ / 7½-9	6½-7-7½-8 / 4-7-7½-10	7-½-7-½-½-8 / 7-8-¼-9-¼-?12	9-10-11-11½-½-11-½ / 9-10-½-11-½-12-12½-13
ganesa	2	5	7 / 7½	6½-7 / 5½-7½	7-7½ / 7½-8	6½-10-¼—10-½ / 7½+-8-¼-8-½
pinjorensis						11½-15
insignis birmanicus						12-½
orientalis grangeri	½-2-½ / 2	5-½ / +5½	¾-6-½ / 7-½	½-6-½ / 8	½-8-½ / (?)-9-½	⅛-11-⅛ / ½-13
auroræ					10½	
airâwana	2	5-6	7-9	7-9	9-11	12-14 / 13-15-½

The order of ridge-crest addition and development (Table V) corresponds approximately with the phylogenetic and geologic ascending order as shown in Table IV above of the present chapter, in which the species are grouped partly by geographic distribution. The ridge-crest formulæ of certain species, e.g., *Stegodon sinensis*, *S. ganesa javanicus*, *S. orientalis*, and *S. orientalis shodoënsis*, are too imperfectly known to determine precisely their phylogenetic position. In general, *S. sinensis* appears to be the most primitive, while *S. airâwana* appears to be the most progressive and geologically recent.

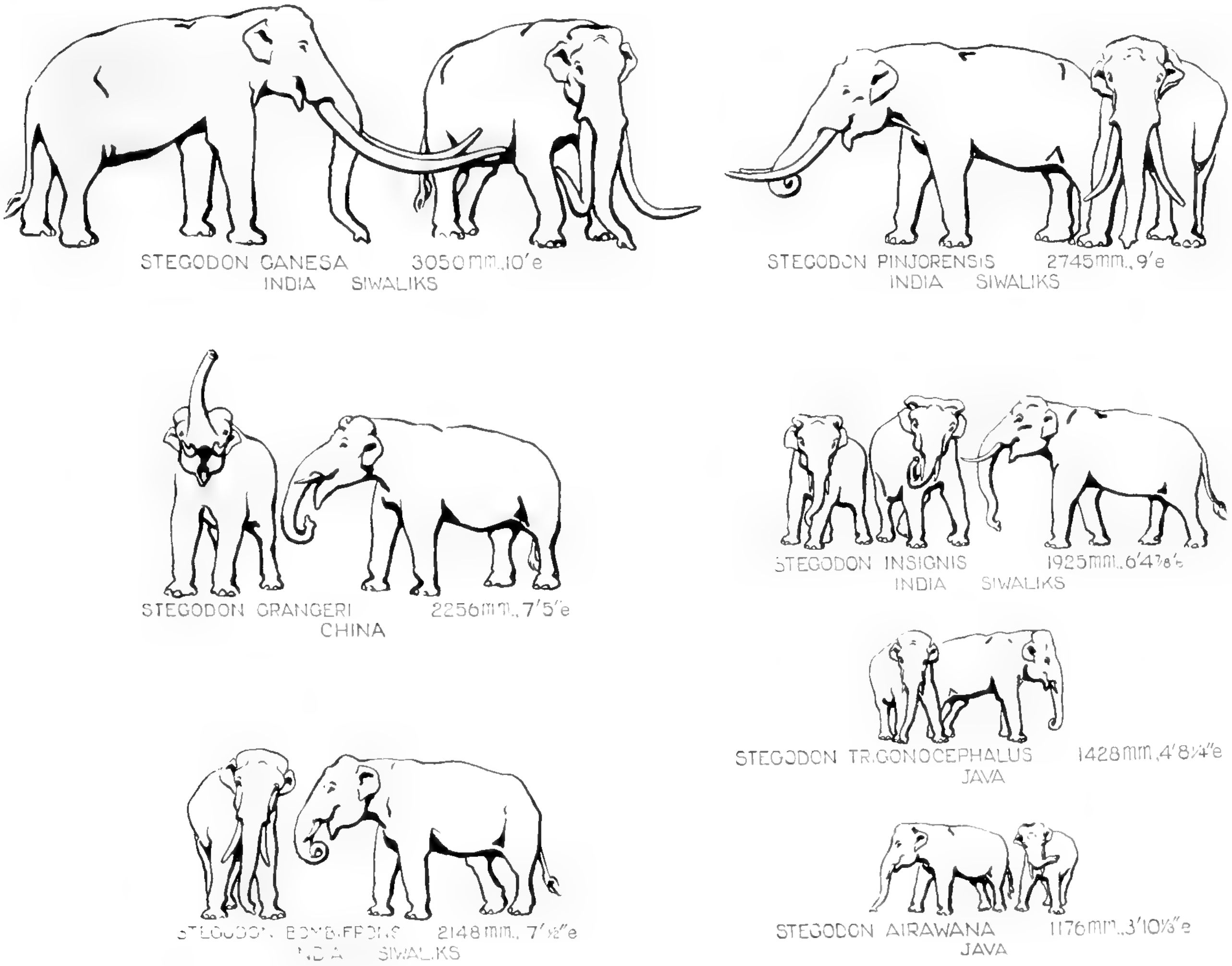


Fig. 731. Species of Stegodon from India, China, and Java
Restorations by Margret Flinsch, under the direction of Henry Fairfield Osborn, One one-hundredth Natural Size

Skulls of Stegodon bombifrons, S. insignis, and S. ganesa in the British and Indian Museums

Before considering in detail the succeeding species of *Stegodon*, it is necessary to examine and compare the known crania of various species with each other, as assembled in figure 732 from Falconer and Cautley's beautiful plates, with the crania of other Stegodonts from the East Indies, e.g., *Stegodon airâwana* (Fig. 773) and *S. trigono-*

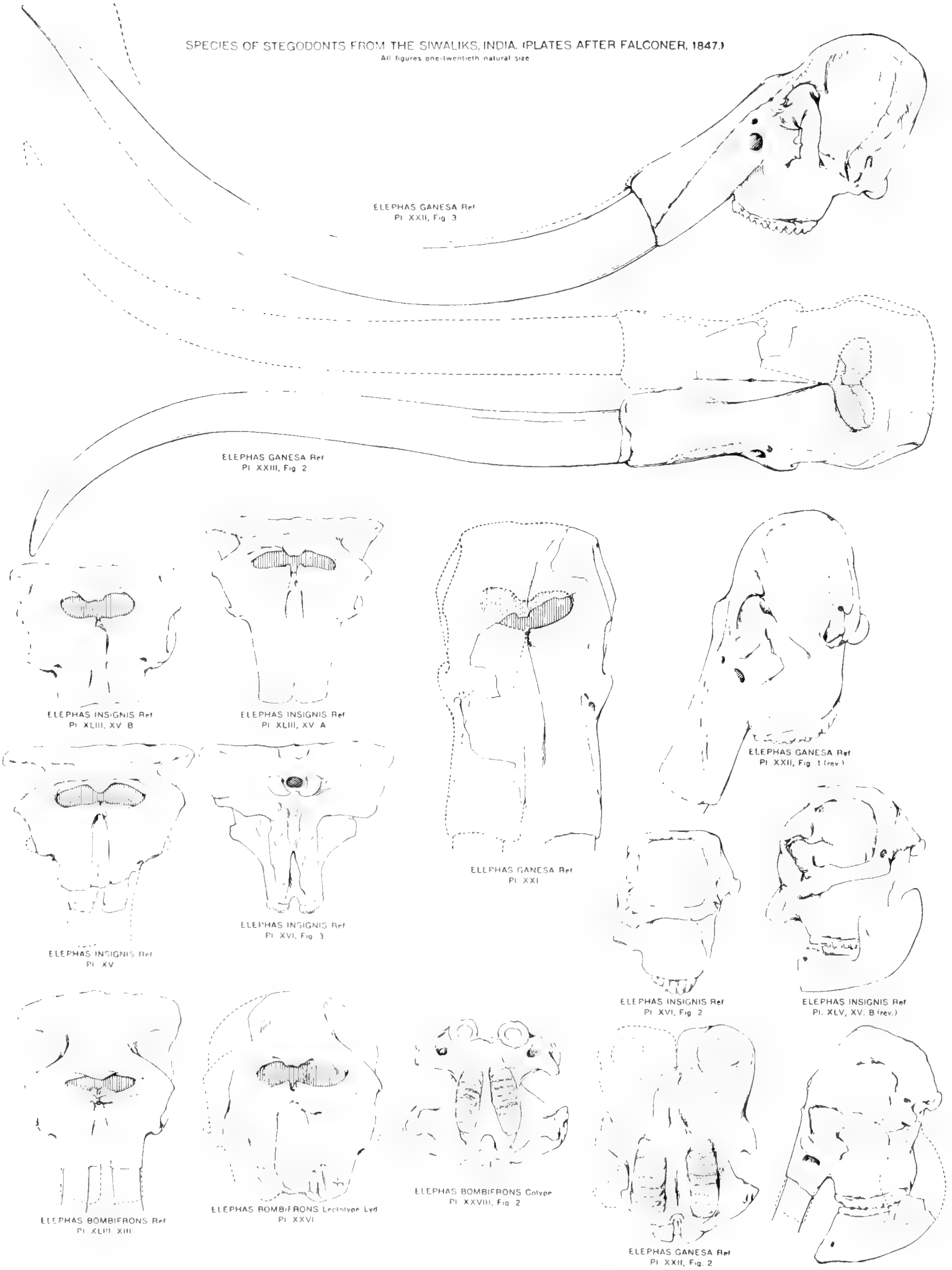


Fig. 732. The three species of Stegodonts of which the crania were known to Falconer are illustrated in this comparative plate in such a manner that their distinctive characters may be readily contrasted. Throughout the *Stegodon* crania are of relatively small size, lacking the cancellate structure characteristic of *Elephas*. All one-twentieth natural size. Compare figure 777.

Elephas [= *Stegodon*] *bombifrons*, a Middle [to Upper] Pliocene stage of evolution, is illustrated in the lower line. [The cranium of *E. bombifrons* at extreme right should read: Pl. XLV, XIII (rev.).]

Elephas [= *Stegodon*] *insignis*, a Lower to Middle [Upper] Pleistocene stage of evolution, is illustrated in the middle of the diagram.

Elephas [= *Stegodon*] *ganesa*, a Lower to Middle [Upper] Pleistocene stage of evolution, is illustrated in the top lines. It is extraordinary that tusks of such enormous length and width should be supported by a cranium of such small size. The extremities of the tusks should probably be turned *inward*, instead of outward as figured by Falconer and Cautley; the left tusk is complete; a portion of the right tusk is omitted in this drawing. [Compare figure 733 for revised restoration of the tusks.]

cephalus (Fig. 776) of Java, also with the newly found *S. orientalis grangeri* (Fig. 763) of China. These Stegodont crania should be compared with the large cranium of *Archidiskodon planifrons* (Fig. 830), one of the most primitive of the true elephants.

In general the cranium of *Stegodon bombifrons* (Fig. 732, bottom row, also Fig. 742 and Fig. 744) is more generalized and subelephantine in character, whereas the crania of *Stegodon ganesa* and *S. insignis* are very highly specialized, of relatively small size, and bear little resemblance to the crania of the true Elephantidæ. Quite different are the small, triangular crania of *Stegodon trigonocephalus* and *S. airâwana* of the East Indies.

Sexual Divergence very Marked.—The referred giant skull of *Stegodon ganesa* obviously belongs to a full-grown male Stegodont (as shown in four aspects in Fig. 732). On the contrary, the crania *referred* to *S.*

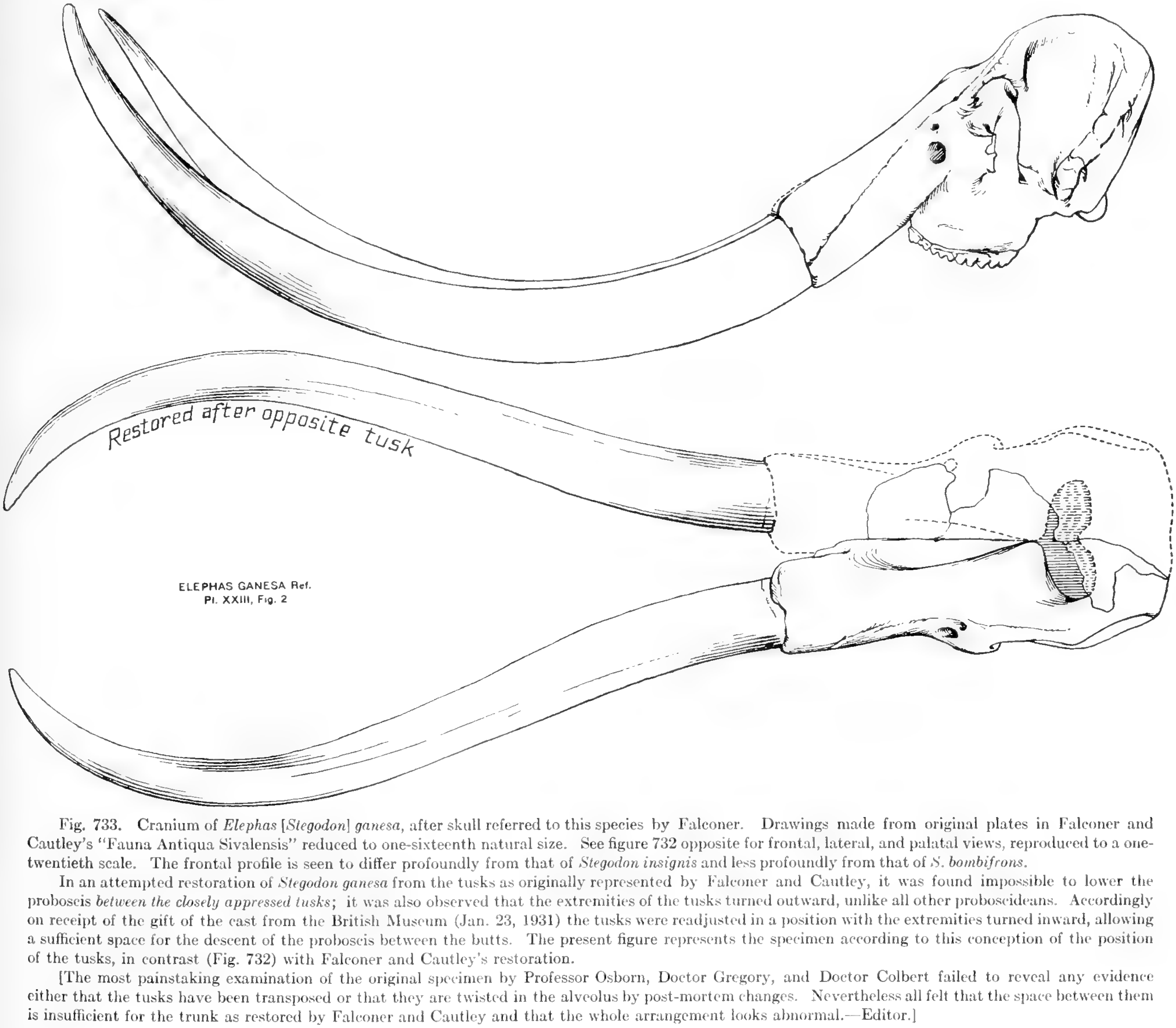


Fig. 733. Cranium of *Elephas* [*Stegodon*] *ganesa*, after skull referred to this species by Falconer. Drawings made from original plates in Falconer and Cautley's "Fauna Antiqua Sivalensis" reduced to one-sixteenth natural size. See figure 732 opposite for frontal, lateral, and palatal views, reproduced to a one-twentieth scale. The frontal profile is seen to differ profoundly from that of *Stegodon insignis* and less profoundly from that of *S. bombifrons*.

In an attempted restoration of *Stegodon ganesa* from the tusks as originally represented by Falconer and Cautley, it was found impossible to lower the proboscis *between the closely appressed tusks*; it was also observed that the extremities of the tusks turned outward, unlike all other proboscideans. Accordingly on receipt of the gift of the cast from the British Museum (Jan. 23, 1931) the tusks were readjusted in a position with the extremities turned inward, allowing a sufficient space for the descent of the proboscis between the butts. The present figure represents the specimen according to this conception of the position of the tusks, in contrast (Fig. 732) with Falconer and Cautley's restoration.

[The most painstaking examination of the original specimen by Professor Osborn, Doctor Gregory, and Doctor Colbert failed to reveal any evidence either that the tusks have been transposed or that they are twisted in the alveolus by post-mortem changes. Nevertheless all felt that the space between them is insufficient for the trunk as restored by Falconer and Cautley and that the whole arrangement looks abnormal.—Editor.]

insignis (Fig. 732) obviously belong to small-tusked females, because the alveolar processes for the insertion of the tusks are extremely small and narrow.

If, as seems possible, all the crania referred by Falconer and Cautley to *Elephas* [=*Stegodon*] *insignis* are females, and the great cranium referred to *Elephas* [=*Stegodon*] *ganesa* is a male, there is in *Stegodon* a far greater sexual *disparity* and *difference* than prevails between the female and male crania of either *Elephas indicus* or *Loxodonta africana*, as figured below in the present Memoir. If this be true, the sexual disparity in cranial characters constitutes an important specific distinction of *Stegodon insignis* and *S. ganesa.*

In the present Memoir we treat the two species separately but agree with the theory suggested by more than one author, especially Lydekker and Matsumoto, that the crania of *S. insignis* represent the females of the same collective species as the referred male cranium of *S. ganesa.*

British Museum, W. D. Matthew, September, 1920.—The skull of *Stegodon bombifrons* is essentially elephantine, the shortness of the enamel plates being the chief distinction; the skull is apparently shorter than in *Loxodonta;* the jaw is deeper; the symphyseal process may be a little heavier. In contrast, the skull of *S. insignis* has a supranarial region with a great thickening of the cellular tissue which appears to round back into the occiput, the occipital crest being very little developed; a very curiously shaped head and very small tusks.

Characters of Referred Skulls of Indian Stegodonts, after Falconer, 1868

(See Figs. 732-736, 754, 777)

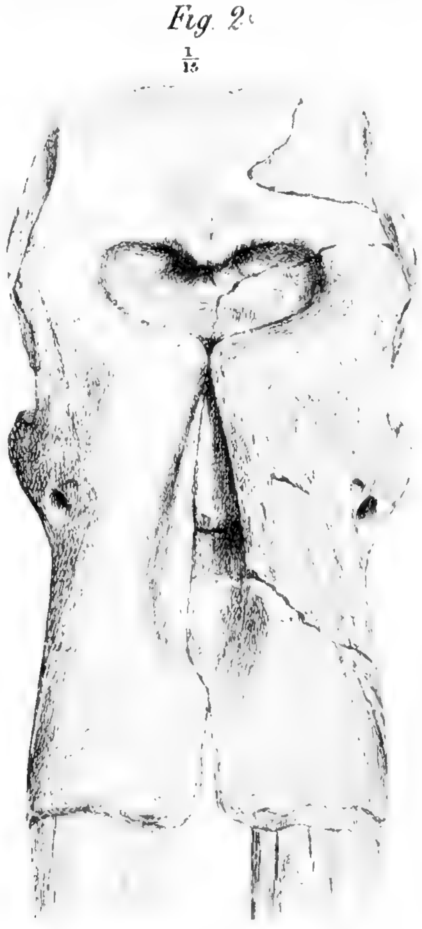
Skull of *Elephas* [=*Stegodon*] *bombifrons* (Falconer, 1868, Vol. I, p. 458, Pl. xxvii): "Very fine and perfect skull, anterior view. Four other views of same skull are given in Plate xxviii. This head is very marked; it is convex from occiput to front and also across, and is very narrow at the temporal contraction. The bounding ridges sweep round by a


A Generalized Cranium

Fig. 734. *Elephas* [=*Stegodon*] *bombifrons.* Front view of cranium, one-twelfth natural size. Brit. Mus. M.2979; cast Amer. Mus. 10378. After Falconer and Cautley, 1846 [1847, Pl. xxvii].


A Specialized Cranium

Fig. 735. *Elephas* [=*Stegodon*] *insignis,* one-twelfth natural size. After Falconer and Cautley, 1846 [1847, Pl. xv].



A Specialized Male Cranium

Fig. 736. Restoration: *Elephas* [=*Stegodon*] *ganesa,* one-twelfth natural size. Brit. Mus. M.3008. After Falconer and Cautley, 1846 [1847, Pl. xxiii].

bold curve into the post-orbitary processes, as in *E.* [=*Archidiskodon*] *meridionalis.* There is a deep furrow between the tusks. The nasal opening for the trunk is above the line (or nearly so) of the post-orbitary processes of the frontal bone. Above the infra-orbitary foramen on the right side there is another smaller opening."

Skulls of *Elephas* [=*Stegodon*] *insignis* (Falconer, 1868, Vol. I, p. 448, Pl. xv): "This is the most remarkable of all the Indian fossil Elephants. The cranium is as singular and grotesque in construction as that of the *Dinotherium giganteum.* The cranium is seen to differ remarkably from that of *E. Ganesa* (Plates xxi. and xxii.) notwithstanding that the molars of the two species agree so closely. That of *E. insignis* is flattened at the top, elongated from side to side and singularly modified, so as to bear an analogy to the cranium of *Dinotherium giganteum,* while that of *E. Ganesa* does not differ much from the ordinary type of the Elephants."

(*Op. cit.,* p. 449, Pl. xvi, fig. 1): "This head is very cubical in form, is old, very concave in front and vertically; teeth broken. Interval between incisive sheaths deep. No tusks."

(*Op. cit.,* p. 449, Pl. xvii, figs. 3 and 4): "Anterior and lateral view of another cranium. Both zygomatic arches are missing, and the left side of the cranium is deficient. Shows the great length of the incisive sheaths."

Skulls of *Elephas* [=*Stegodon*] *ganesa* (Falconer, 1868, Vol. I, p. 453, Pl. xxi): "Large skull, with fragment of left incisive *in situ,* and corresponding fragment of right incisive detached. The incisive alveoli are remarkably elongated, as in *E. primigenius.* The plane of the incisives is continuous with that of the frontal, but with a tendency to obliquity forwards. The skull is very imperfect on right side."

(*Op. cit.,* p. 454, Pl. xxii): "Fig. 1.—*Elephas Ganesa.* Lateral view of large skull figured in Pl. xxi.—B.M. Fig. 2.—*E. Ganesa.* Palate view of same skull. The right incisive is seen in section. The posterior true molar is seen on either side of palate. It has ten plates and a heel behind, and a small talon in front; the hind heel has few denticles; the four front ridges are worn. The alveoli are parallel as in the Mammoth.—B.M. Fig. 3.—*E. Ganesa.* Sketch showing restoration of skull, with tusks, of *E. Ganesa,* profile view, one-thirteenth of natural size."

(*Op. cit.,* p. 454, Pl. xxiii): *Restoration.* "Sketch showing restoration of skull, with tusks, of *E. Ganesa,* oblique antero-lateral view, one-thirteenth of natural size."

(*Op. cit.,* p. 455, Pl. xxiv.a.): "Figs. 1 and 1*a.*—*Elephas Ganesa.* Fragment of skull with palate and back molars on both sides. This is a most remarkable specimen. I have called it *E. Ganesa* (H. F.), and it much resembles the molar of the big *Ganesa* specimen (Plate xxii. fig. 2) in form and in the compression of the ridges, but the ridges are few. . . . B.M."

Stegodont Crania of China and of the East Indies

(See Figs. 763, 776, 773, 777)

A most fortunate discovery from the pits along the Yangtze River near Wanhsien, Province of Szechuan, China, is the extensive series of Stegodont crania in all stages of development, infantile, juvenile, young adult, and mature adult. This priceless collection made by Walter Granger of the Central Asiatic Expedition of the American Museum illustrates in a perfect manner (Figs. 759, 761–763, 686) the complete ontogeny, dental succession, and metamorphosis of the cranial form. The young adult and mature adult crania, together with the inferior mandible (Fig. 763), apparently resemble the cranium of *S. bombifrons* more closely than the crania of *S. insignis* and *S. ganesa.* This material was described by the present author as belonging to a new subspecies, namely, *Stegodon orientalis grangeri.*

The cranium of the East Indian species *Stegodon airâwana* (Fig. 773) of Java belongs to a very advanced mid-Pleistocene stage, resembling *S. bombifrons* and *S. orientalis grangeri* in profile but differing in the frontal aspect, which is flattened. The cranium of *S. trigonocephalus* (Fig. 776), as its specific name indicates, has a triangular rather than a rounded superior profile, and, although of the same geologic age as *S. insignis* and *S. ganesa*, it is entirely different from the Siwalik species in its profile and proportions. Consequently it appears that both in cranial and dental characters the East Indian species represent a distinct and somewhat dwarfed side-branch of the northerly continental species.

SYSTEMATIC DESCRIPTION OF SPECIES OF STEGODON

Stegodon sinensis Owen, 1870

Figures 687, 702, 737

Alleged to be "from marly beds in the vicinity of Shanghai," China. This animal (Figs. 687, 702) is probably of Upper Miocene [Lower Pliocene] age, for it is more primitive than *Stegodon bombifrons*, and possibly ancestral to the *S. bombifrons* stage.

SPECIFIC CHARACTERS.—This little-known true Stegodont, *Stegodon sinensis* (Dp 3 $\frac{\frac{1}{2}-4}{\ }$), is somewhat more primitive than *S. bombifrons* (Dp $3^{\frac{4}{\ }}$), since the ridge-crests are less elevated or hypsodont as compared (Figs. 687, 688) with *S. bombifrons*, *S. orientalis grangeri*, and *S. insignis*. Estimated number of conelets on fourth ridge thirteen to fifteen. Falconer, Lydekker, and Martin ascribe (see Table V above) four ridge-crests to Dp^3 of *S. elephantoides* (=*cliftii*), *S. bombifrons*, and *S. trigonocephalus*.

HISTORY.—(1) After comparing the type deciduous molar with all the Siwalik specimens in the British Museum, Owen concluded (1870, p. 420) that the above Chinese tooth was most closely related to undetermined Siwalik specimens which he compared with the *M. elephantoides* of Clift. These two undetermined specimens are described by Falconer (1868, Vol. I, p. 460) as follows: Plate XXIX. A, "Fig. 5.—*E. bombifrons*? Fragment of molar, from lower jaw, right side, with four ridges.—B.M. Length, 5.8 in. Width, 4.5 in. Fig. 6.—*E. bombifrons*? Fragment of molar with three ridges and a heel. 'Doubtful what figs. 5 and 6 are.'—H. F. Length, 4.4. in. Width, 4.5 in." This shows that Falconer regarded these Siwalik teeth as doubtfully related to *E. bombifrons* and that Owen also indirectly compared them with *E. bombifrons*. *Stegodon bombifrons* lectotype is of Middle Pliocene age.

(2) One should also compare Owen's type tooth with figure 700 above of *Mastodon* [*Stegodon*] *elephantoides* (=*cliftii*). This comparison is strengthened by the fact that Koken (1885) referred the *Stegodon sinensis* of Owen to the species *Stegodon cliftii* of Falconer.

(3) Lydekker (1886.2, p. 79) also referred *S. sinensis* Owen to *Elephas cliftii* Falc. (*Op. cit.*, p. 80): Brit. Mus. 41925. "A third right upper milk-molar, provisionally referred to this species; from the Pliocene near Shanghai, China. This specimen is the type of *Stegodon sinensis*, and is described and figured under that name by Owen in the Quart. Journ. Geol. Soc. vol. xxvi. p. 417, pl. xxvii.; it is also figured and provisionally referred to the present species [*Elephas cliftii*] by the writer, in the 'Palæontologia Indica,' ser. 10, vol. i. p. 257, pl. xlv. fig. 2. There are four complete ridges, and a large anterior talon, which is reckoned by Owen as a fifth ridge. The median longitudinal cleft is very indistinct. *Presented by Prof. Sir R. Owen, K.C.B.*, 1870."

(4) Osborn (1924) prefers to retain the name *Stegodon sinensis* until further local material can be secured for comparison.

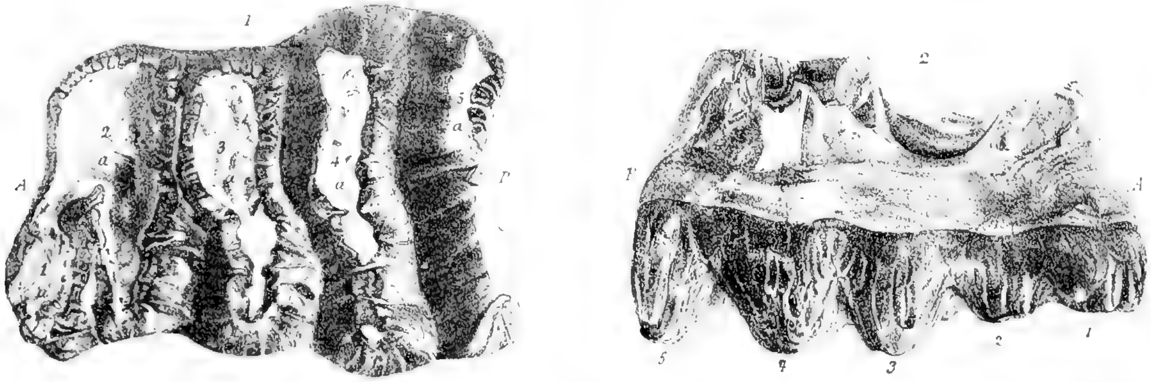
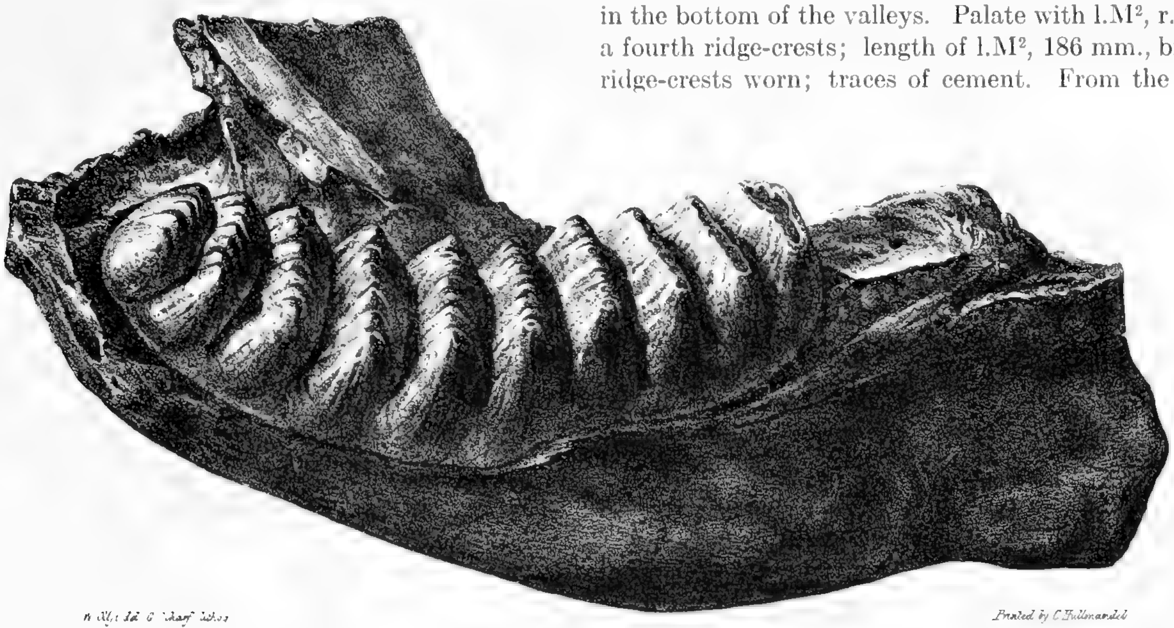


Fig. 737. Type of *Stegodon sinensis* Owen, 1870, Pl. XXVII, figs. 1 and 2, natural size. Alleged to be from "marly beds" near Shanghai, China. (*Op. cit.*, p. 417): "The tooth in question is the second upper molar (*d*3 of the type series) from the right side. Its crown, in a length of three inches, is divided into five transverse ridges."

Falconer, Lydekker, and Martin (Table V above) ascribe four ridge-crests to Dp^3 of *Stegodon elephantoides* (=*cliftii*), *S. bombifrons*, and *S. trigonocephalus*.

Stegodon sinensis Owen, 1870. "On Fossil Remains of Mammals found in China." Quart. Journ. Geol. Soc. London, Vol. XXVI, p. 417. TYPE.—(*Op. cit.*, p. 417): ". . . Second upper molar (*d* 3 of the type series) from the right side [Dp^3]." Brit. Mus. 41925. HORIZON AND LOCALITY.—Alleged to be "from marly beds in the vicinity of Shanghai," China. Probably Upper Miocene [Lower? Pliocene]. TYPE FIGURE.—*Op. cit.*, Pl. XXVII, figs. 1–3.

TYPE DESCRIPTION.—(Owen, *op. cit.*, pp. 417, 418): "*Stegodon sinensis*, Ow. The tooth in question is the second upper molar (*d* 3 of the type series) from the right side. Its crown, in a length of three inches, is divided into five transverse ridges, the proportions of which, as to height and basal breadth, with the ridged and wrinkled character of the enamel, suffice for its reference to a species of the group of Proboscidians discovered by Crawfurd in the Irrawadi Tertiaries of Ava, and described by Clift in the second volume of the second series of the Transactions of the Geological Society (p. 369, pls. 36–39, 1828). . . . In the present tooth the first or foremost ridge (Pl. XXVII. figs. 1 & 2, 1) is defined by a cleft on the outer side of the tooth, but not on the inner side, fig. 3; here the abraded surfaces or ridges 1 and 2 are blended by wear into a common hollow field of smooth dentine (fig. 1, *a*). There is a slight constriction near the part where the worn surface of the first ridge blends with that of the second; and this constriction, which may be detected in the succeeding ridges, I take to be a trace of that stronger one which more completely divides the transverse coronal ridge in the molars of better Mastodons into an inner and an outer part. A well marked tubercle (figs. 1 and 2, *f*) projects at the outer side of the base of the first ridge, 1, near the interspace between that and the second ridge. . . . Nevertheless in the number of ridges in a given tract of the grinding-surface, in their height and breadth of base, and in the absence of intervening cement, the conformity of the Chinese molar with the grinders of the *Mastodon elephantoides* is close. The enamel also shows the same vertical linear impressions and ridges, by which we may reckon that the summit (say, of the fourth ridge in the tooth here described), if it were unworn, might be cleft into from thirteen to fifteen small mamillæ." Owen did not compare this specimen with Clift's original type lower molar of *Mastodon elephantoides,* but with specimens referred by Clift to that species.



LECTOTYPE OF STEGODON ELEPHANTOIDES

Fig. 738. Lectotype left M_2, M_3, of *Mastodon elephantoides* Clift, 1828, Pl. XXXVIII, fig. 2, one-third natural size. (*Op. cit.*,p. 372 and Explanation of Plates): "Left side of the lower jaw of Mastodon elephantoides. The remains of the anterior molar tooth [l.M_2] are seen, and behind it, the posterior tooth which was advancing, and which, in consequence of the jaw-bone being broken away, is seen through its whole length. This tooth is eleven inches long and three and a half broad."

Stegodon elephantoides Clift, 1828

Figures 683, 686, 695, 696, 700, 701, 738, 739-741

Lower Pliocene, lowest levels of the Irrawaddy Series (fluviatile),[1] near Yenangyaung, 250 miles below Ava, Burma.

Syn.: *Elephas cliftii* Falconer, 1846 [=*Stegodon elephantoides* (=*cliftii*) of the present Memoir.]

SPECIFIC CHARACTERS (CLIFT, 1828, OSBORN, 1929).—Third inferior molar, M_3, with nine complete ridge-crests and a well-developed half ridge, equaling ten; five to eight conelets on each ridge-crest; length 11 inches = 280 mm., est. breadth 3½ inches = 90 mm.; no apparent cement. Superior molar, l.M^1 (= Falconer's type of *Elephas cliftii*) with six and a fourth ridge-crests, length 155 mm., breadth 83 mm., ten to twelve conelets on each; cement in the bottom of the valleys. Palate with l.M^2, r.M^2, with six and a fourth ridge-crests; length of l.M^2, 186 mm., breadth 102 mm.; ridge-crests worn; traces of cement. From the three specimens enumerated below the lectotype and cotype ridge formula is compiled as follows: $\mathrm{M}\ 1\frac{6\frac{1}{4}}{\ }\ \mathrm{M}\ 2\frac{6\frac{1}{4}}{\ }\ \mathrm{M}\ 3\frac{\ }{10}$.

Osborn, 1927: This Stegodont is similar to *S. bombifrons* in ridge-crest formula.

HISTORY.—As fully explained above (pp. 855, 856), *Stegodon elephantoides* Clift is the second species of Stegodont based by Clift on a lower jaw (Pl. XXXVIII, fig. 2) and on an upper molar (Pl. XXXIX, fig. 6). Unfortunately Falconer was led to abandon '*Mastodon elephantoides*' and to substitute '*Elephas cliftii*'; consequently all the literature subsequent to Clift's original description and most of the reproductions of his illustrations appear under the specific name *Elephas cliftii,* which is actually a synonym of *Stegodon elephantoides.* Falconer's mistake partly arose through Clift's error in entitling the palate of *Mastodon* [=*Stegodon*]

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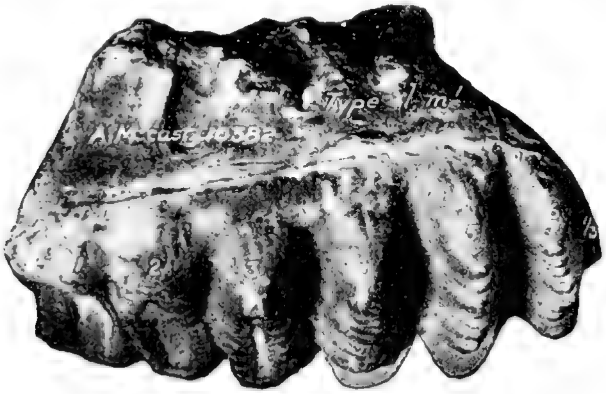
[1] [See note on page 824 above regarding the Lower Pleistocene age of *Stegodon elephantoides.*—Editor.]

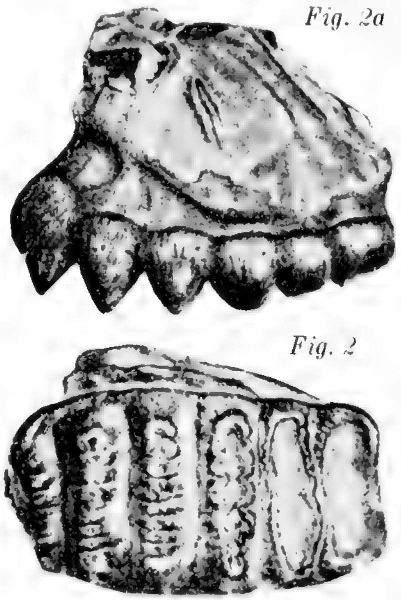
elephantoides (figured in Pl. XXXVI) as '*Mastodon latidens.*' Consequently Clift's species *M.* [=*Stegodon*] *elephantoides* rests upon three specimens:

Lectotype:	"Left lower jaw, *Mastodon Elephantoides*" (Clift, 1828, Pl. XXXVIII, fig. 2 = figures 696 and 738 of the present Memoir).
Cotype:	First left superior molar, l.M^1, "Upper molar of *M. Elephantoides*" (Clift, 1828, Pl. XXXIX, fig. 6 = figures 700, 739, and 740 of the present Memoir), subsequently made the type of *Elephas cliftii* by Falconer and Cautley.
Referred:	Palate, with l.M^2 and r.M^2, "Upper jaw of *Mastodon latidens*" (Clift, 1828, Pl. XXXVI), not figured in the present Memoir.

Mastodon elephantoides Clift, 1828. "On the Fossil Remains of two New Species of Mastodon, and of other vertebrated Animals, found on the left Bank of the Irawadi." Trans. Geol. Soc., London, (2), II, Pt. III, 1828, pp. 372, 373. LECTOTYPE.—(1) Left side of lower jaw with M$_2$, M$_3$; original in Museum of Geological Society of London; cast Brit. Mus. 7393 [referred by Falconer and Cautley in the "Fauna Antiqua Sivalensis," Pl. XX, figs. 9, 9a, Pl. XX.A, fig. 6, to *E. insignis*].[1] COTYPE.—(2) First upper molar of the left side, l.M^1 (original in the British Museum (Brit. Mus. M.10520), cast Amer. Mus. Warren Coll. 10382); same tooth was selected by Falconer and Cautley as the type of *Elephas cliftii*. REFERRED (Osborn).—Palate with l.M^2 and r.M^2 (figured as *Mastodon latidens* by Clift). HORIZON AND LOCALITY.—Left bank of the Irrawaddy River, near Yanangyaung, 250 miles below Ava, Burma. Lower Pliocene, lowest levels of the Irrawaddy Series (fluviatile).[2] LECTOTYPE FIGURE.—Clift, 1828, Pl. XXXVIII, fig. 2. COTYPE FIGURE.—Clift, 1828, Pl. XXXIX, fig. 6 [=*Stegodon elephantoides* (=*cliftii*).] REFERRED PALATE.—Clift, 1828, Pl. XXXVI.

CLIFT'S ORIGINAL DESCRIPTION OF 'MASTODON' ELEPHANTOIDES.—We refer to Clift's clear and consistent description quoted in full above (p. 827) together with the beautiful lectotype figure reproduced in our figure 738 herewith. Clift's specimen comes from Burma and his figureagrees exactly with his description, namely, M 3_{10}, with five to eight conelets on each ridge.





COTYPE OF STEGODON ELEPHANTOIDES CLIFT (=CLIFTII FALCONER)

Fig. 739. New figure of type (l.M^1) of *Elephas cliftii* Falconer and Cautley, 1846, first figured by Clift, 1828, Pl. XXXIX, fig. 6, as an "Upper molar of *M. Elephantoides.*" Reproduced herewith from cast (Amer. Mus. Warren Coll. 10382) one-half natural size. Original in British Museum (Brit. Mus. M.10520). From near Yenangyaung, Burma.

Fig. 740. Cotype l.M^1 of *Stegodon elephantoides* (=*cliftii*), after Falconer and Cautley, 1846 [1847, Pl. XXX, figs. 2, 2a], left M^1, said to be the same molar (see Pal. Mem., 1868, Vol. I, p. 461) as that figured in Clift, 1828, Pl. XXXIX, fig. 6, although the drawing does not agree well with Clift's original illustration nor with the reproduction from the cast (Fig. 739 opposite).

Observe rudimentary anterior ridge (pro-protoloph) and rudimentary seventh ridge (heptaloph), also the six ridge-crests (proto-, meta-, trito-, tetarto-, penta-, and hexalophs), the ridge-crest summits each crowned with from ten to twelve conelets.

COTYPE CHARACTERS OF STEGODON ELEPHANTOIDES (=CLIFTII) FALCONER AND CAUTLEY, 1846, PAGE 47, BASED ON CLIFT'S SPECIMEN AND FIGURE

Falconer's designation of this type (?left M^1) and of this species is as follows: "The same group comprises a fourth extinct Indian species, named in this work, *E. Cliftii*, which furnishes the next link in the chain of forms presented by the molars of the Elephantidæ. . . . In our view, the tooth represented in pl. 39, fig. 6, of Mr. Clift's memoir in the Geological Transactions [Clift, 1828], under the name of *Mastodon Elephantoides*, and the palate specimen represented in pl. 36 of the same memoir, under the name of *M. latidens*, belong to this species. . . . The penultimate and antepenultimate molars in the upper jaw have only six transverse

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[1] [See Chakravarti, D. K., Quart. Journ. Geol., Mining, Metallurg. Soc. India, 1937.1, p. 34, who referred it to *S. elephantoides.*—Editor.]

[2] [See note on page 824 above regarding the Lower Pleistocene age of *Stegodon elephantoides.*—Editor.]

ridges, continuous, and chevron shaped, with numerous mammillæ, as in *E. insignis* and *E. Ganesa*; but the cement does not fill up the interspaces of the ridges, being reduced to a comparatively inconsiderable quantity in the bottom of the hollows. *E. Cliftii*, in the reduced number of the coronal ridges, and in the other characters of the teeth, appears to constitute the dental link which forms the immediate passage from *Elephas* into *Mastodon*."

ADDITIONAL CHARACTERS OF THE COTYPE SPECIMEN OF STEGODON ELEPHANTOIDES (=CLIFTII)

(Falconer, 1868, Vol. II, p. 84): "But the detached tooth [Fig. 740] on the upper jaw is seen entire, and beautifully preserved, in the specimen fig. 2 of the same plate [i.e., Pl. XXX], presenting six ridges and a small hind talon. The same tooth is represented by fig. 6 of Pl. XXXIX. of Mr. Clift's Memoir (Geol. Trans., vol. ii. 2nd series). It is there described as an upper molar tooth of *Mastodon Elephantoïdes*, under which title Mr. Clift included specimens that are referred in our arrangement to two distinct forms. . . . The Elephantine affinities of this tooth are indicated by the absence of a longitudinal line of division along the crown, and by the great number of points (about eleven in each) that enter into the composition of the ridges." Of the same cotype molar, Lydekker (1886, p. 81) observes: "7388. Cast of the first (?) left upper true molar in an early stage of wear (woodcut, fig. 20). The original was obtained near Yenankhoung, on the left bank of the Irawadi in Upper Burma, by Crawfurd in 1826, and is preserved in the Museum of the Geological Society;[1] . . . There is scarcely any trace of the median cleft, the cement is slight, and there are numerous cusps. *Mantell Collection. Purchased*, 1836."

FALCONER'S NOTES OF 1868 ON STEGODON ELEPHANTOIDES (=CLIFTII)

Falconer, "Palæontological Memoirs," Vol. I, 1868, pp. 461, 462, Plate XXX of the "Fauna Antiqua Sivalensis."

It is very important to observe that the four specimens described by Falconer, including the cotype of *S. elephantoides* from Burma, agree with each other both in the number and character of the ridges and in the number of conelets on each ridge.

UPPER JAWS.—Burma, left bank of the Irrawaddy River, 250 miles below Ava. Plate XXX, figs. 1, 1*a*, *E. cliftii* F. & C., palate, Dp^4, ? ridges; figs. 2, 2*a*, type,[1] Burma, 250 miles below Ava, $l.M^1$, ridges 6¼, beautifully preserved, "six ridges and a small hind talon . . . as many as eleven to twelve denticles. . . . Its elephantine affinities are indicated by the . . . great number of points [denticles]"; fig. 3, superb palate, M^2, ridges 6½, little cement (referred by Clift, 1828, Pl. XXXVI, to *M. latidens*); figs. 4, 4*a*, 4*b*, fragment of M^2, right side, 5 ridges, cement moderate in quantity, from near Yenangyaung, upper Burma. LOWER JAWS.—Burma. Plate XXX, figs. 5, 5*a*, $l.M_3$, "eight ridges and a talon," little cement.

COTYPE CHARACTERS.—From the above it appears that the four specimens described by Falconer from near Yenangyaung, 250 miles below Ava, Burma, exhibit the following characters: (1) Denticles very numerous, eleven to twelve on each ridge; (2) ridges moderately high with little cement; (3) ridge formula as follows:

Stegodon elephantoides (=*cliftii*): $M\ 1\frac{6-6\frac{1}{4}}{}M\ 2\frac{6\frac{1}{2}}{}\ M\ 3\frac{}{8\frac{1}{2}}$.

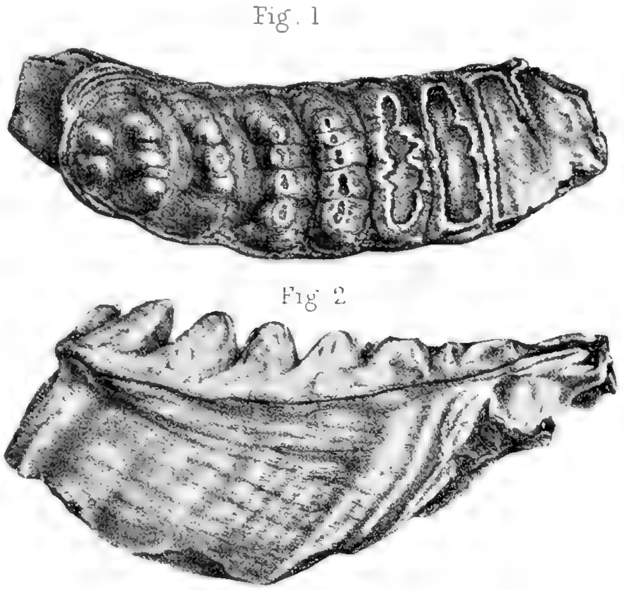
PHYLETIC CONCLUSIONS

Osborn, 1927: Falconer considered Clift's Lower Pliocene[2] type of *Mastodon* [=*Stegodon*] *elephantoides* as close to his Upper Pliocene *S. insignis*, but *S. elephantoides* proves rather to be close to the Middle Pliocene *S. bombifrons*, as shown in the comparative ridge formulæ table above, the two formulæ abbreviated being as follows:

S. bombifrons: $Dp\ 3\frac{4}{4}\ Dp\ 4\frac{6}{6\frac{1}{2}-7}\ M\ 1\frac{6}{7\frac{1}{2}}\ M\ 2\frac{7}{8}\ M\ 3\frac{9\frac{1}{2}}{9\frac{1}{2}}$.

S. elephantoides: $Dp\ 3\frac{?}{?}\ Dp\ 4\frac{?}{?}\ M\ 1\frac{6\frac{1}{4}}{?}\ M\ 2\frac{6\frac{1}{4}}{?}\ M\ 3\frac{?}{10}$.

Elephas cliftii [=*Stegodon elephantoides* (=*cliftii*)], *fide* Falc. and Caut.: $Dp\ 3\frac{4}{?}\ Dp\ 4\frac{6}{?}\ M\ 1\frac{6\frac{1}{4}}{?}\ M\ 2\frac{6\frac{1}{2}}{?}\ M\ 3\frac{6\frac{1}{2}}{8\frac{1}{2}}$.



REFERRED STEGODON ELEPHANTOIDES (=CLIFTII)

Fig. 741. Referred l.M_3 of *Elephas cliftii*, after Falconer, 1868, Vol. II, Pl. v, figs. 1, 2, "Views in plan and profile of last true molar, lower jaw, left side, rather less than one-fourth (two-ninths) of the natural size." See also the "Fauna Antiqua Sivalensis," Falconer and Cautley, 1846 [1847, Pl. XXX, figs. 5, 5*a*]. From Burma, presented to the British Museum by Colonel Burney (Brit. Mus. 14759).

The ridge formula of l.M_3, namely, $\frac{}{8\frac{1}{2}}$, assigned by Falconer and Lydekker, actually occurs in an aged specimen from Burma, Falconer's figure of which (Falconer and Cautley, 1846 [1847, Pl. XXX, figs. 5, 5*a*] is reproduced herewith in our figure 741; this grinder is so old that the two anterior ridge-crests may have worn off, consequently the ridge formula is uncertain; the dimensions (length 12.7 in. = 323 mm., breadth 4.5 in. = 115 mm.) considerably exceed those of the type of *Stegodon elephantoides* given above. There is no substantial basis, therefore, for the assignment to the synonymous *Elephas* [=*Stegodon*] *cliftii* of a ridge formula inferior to that of *Mastodon* [=*Stegodon*] *elephantoides* Clift.

Stegodon bombifrons Falconer and Cautley, 1846

Figures 686, 687, 699, 731, 732, 734, 742-746, 777, Pl. XX

Lectotype: Siwalik Hills (*fide* Falconer), probably from the Dhok Pathan horizon, Lower [Middle] Pliocene, India, in which this species is very abundant and characteristic (Pilgrim-Brown).

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[1] Now in the British Museum (Natural History), M.10520 = *Stegodon elephantoides* (=*cliftii*).

[2] [See note on page 824 above regarding the Lower Pleistocene age of *Stegodon elephantoides*.—Editor.]

This is an early Lower [Middle] Pliocene stage of the true *Stegodon* based on types from the Dhok Pathan zone which also contains *Stegolophodon latidens*. From this species some of the earlier authors believed that the genus *Elephas* originated. Referred *Stegodon bombifrons* occurs in the Tatrot horizon, Middle [Upper] Pliocene. A superior molar from the Dhok Pathan horizon (Fig. 746) exhibits very clearly the cone and conelet structure of the crown.

E. [*Elephas*] *bombifrons* Falconer and Cautley, 1846. "Fauna Antiqua Sivalensis" . . . letterpress, 1846, pp. 46, 47. Lectotype and Cotypes.—(*Op. cit.*, p. 46): ". . . several crania containing perfect teeth," of which the lectotype is figured in Pl. xxvi. Horizon and Locality.—Siwalik Hills, India, probably from the Dhok Pathan horizon, Lower [Middle] Pliocene. Lectotype and Cotype Figures.—*Op. cit.*, 1846 [1847, Pls. xxvi (lectotype), xxvii, xxviii], figures 742 and 744 of the present Memoir.

Falconer and Cautley, 1846, p. 46 (see above p. 858) based this species on "several crania containing perfect teeth," described as "from the Sewalik Hills." Of these Lydekker (1886.2, p. 83) designated as the lectotype Brit. Mus. M.2978. The exact locality is not given. According to Pilgrim (Vol. I, fig. 413, also Chap. XXII below) this species occurs abundantly in the Dhok Pathan horizon of Lower [Middle] Pliocene age, a horizon which also contains *Tetralophodon punjabiensis*, *Synconolophus corrugatus*, and *S. hasnoti*. Falconer assigned to this species a low ridge formula, namely: M 3 $\frac{8\text{-}9\frac{1}{2}}{9\frac{1}{2}}$.

Characters (Falconer and Cautley, 1846, p. 46); see Osborn above, pp. 855–859.—(1) Type based on several crania containing perfect teeth. (2) Crown divided into transverse ridges, composed of numerous mammillæ [conelets] of chevron-shaped section. (3) Interspaces occupied by a thick coat of cement. (4) Principal ridges of third upper and lower molars, M 3$\frac{9}{9}$, in contrast to [*S.*] *insignis*. (5) Third upper molar measures 11 inches (279 mm.) in length by 4½ inches (114 mm.) in width. (6) The lower third molar of the left side, with nine [9½] ridge-crests, measures 13.4 inches in length (=340 mm.) by 4.2 inches in breadth (=105 mm.), considerably exceeding the dimensions of the lectotype of *S. elephantoides*, namely, length 280 mm., breadth 90 mm. (7) The collective (Falconer, Lydekker, Osborn) ridge-crest formula (not including the unexposed ridge-crests) is as follows:

Stegodon bombifrons: Dp 3 $\frac{4}{4}$ Dp 4 $\frac{5\text{-}6}{\frac{1}{2}\text{-}5\text{-}\frac{1}{2}\text{-}6\frac{1}{2}\text{-}7}$ M 1 $\frac{6}{7\text{-}7\frac{1}{2}}$
M 2 $\frac{6\text{-}7}{7\text{-}7\frac{1}{2}\text{-}8}$ M 3 $\frac{7\frac{1}{2}\text{-}8\text{-}8\frac{1}{2}\text{-}9\text{-}9\frac{1}{2}}{8\text{-}9\text{-}9\frac{1}{2}\ [11+]}$.

FALCONER'S NOTES OF 1868 ON ELEPHAS [=STEGODON] BOMBIFRONS

Falconer, "Palæontological Memoirs," Vol. I, 1868, pp. 456, 458–461, Plates xxv–xxix.b of the "Fauna Antiqua Sivalensis."

[Errors of determination indicated by Osborn in square brackets.]

Elephas bombifrons Falconer and Cautley, 1846 [1847, Plates xxvi, xxvii, xxviii]. Lectotype and Cotypes.—Cranium represented in Plate xxvi (Lydekker's lectotype); Plate xxvii, very fine skull, M³, ridges 9½, length of molar, 10.2 in. = 257 mm., width 3.7 in. = 93 mm., and Plate xxviii, fig. 2, same skull.

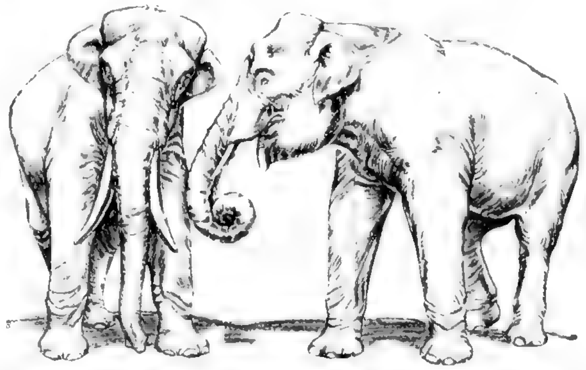
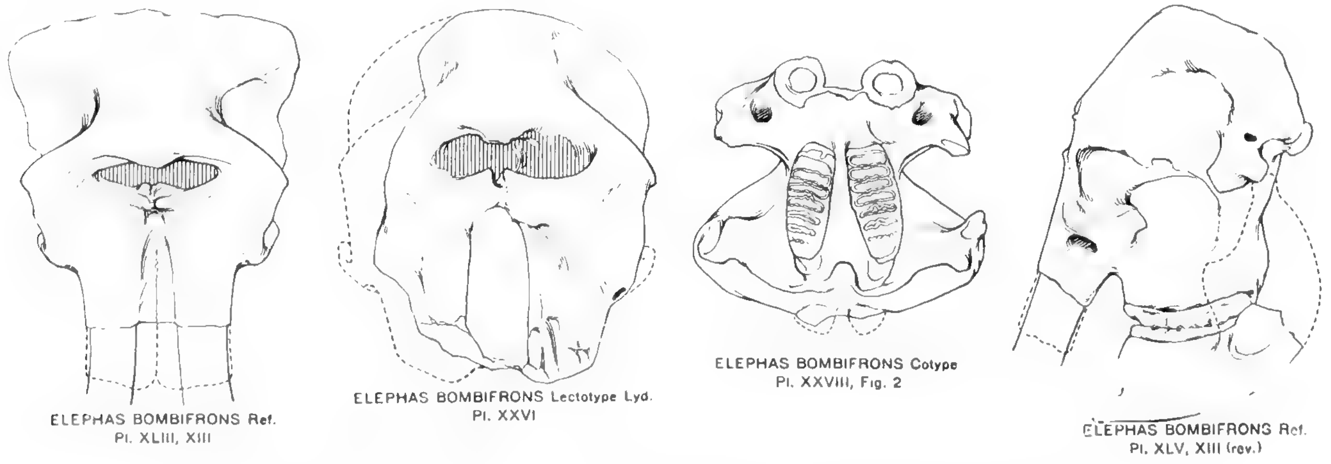


Fig. 743. *Stegodon bombifrons.* Much more primitive than *S. insignis.* Observe transverse ridges of trunk to elevated nasals, extreme broadening of summit of occiput. Ears conjectural. Limbs given the same proportions as the Stegodonts throughout, without knowledge of skeletal material. Female to right, directly after lectotype skull; no inferior tusks. Male to left. Restoration by Margret Flinsch, 1930. One-fiftieth natural size.

Upper Jaws.—Plate xxix, fig. 1, broken cranium, M³, ridges 8½, length of molar 10 in. = 253 mm., width 4 in. = 101 mm.; figs.



Stegodon Crania, after Falconer and Cautley's Illustrations in the "Fauna Antiqua Sivalensis"

Fig. 742. Crania of *Stegodon* (*Elephas*) *bombifrons*, lectotype, cotype, and referred. Outlines assembled from original plate drawings of this species in Falconer and Cautley's "Fauna Antiqua Sivalensis," frontal, palatal, and lateral aspects. All one-sixteenth natural size.

2, 2*a*, cranium, M^3, 8 ridges; figs. 4, 4*a*, r.M^3, 8+ ridges; figs. 5, 5*a*, upper jaw, r.M^3, 7½ ridges; figs. 6, 6*a*, palate with r.M^3, 9½ ridges, length 10.9 in. = 276 mm., width 3.8 in. = 97 mm. (at ends), 4.3 in. = 112 mm. (in middle).

Lower Jaws.—Plate xxv, figs. 3, 3*a*, lower jaw, r.M_3, 9½ ridges, enamel very thick, scanty cement. Plate xxix.a, figs. 1, 1*a*, lower jaw with Dp_4, ridges 6½, "probably the third [fourth] milk molar"; figs. 2, 2*a*, lower jaw, r.M_1, ridges 7½, "certainly the first true molar"; figs. 3, 3*a*, lower jaw, l.M_2, ridges 7½; figs. 4, 4*a*, lower jaw, M_2, ridges 7½; figs. 7, 7*a*, lower jaw, M_1, ridges 7. Plate xxix.b, figs. 5, 5*a*, lower jaw, r.Dp_4 "with 5 ridges and an anterior and posterior talon"; figs. 6, 6*a*, lower jaw, r.M_1, ridges 7½; figs. 7, 7*a*, lower jaw, l.M_3, ridges 9½ [11+].

In the two plates (xxix.a, xxix.b) of the "Fauna Antiqua Sivalensis" about sixteen specimens of inferior molar teeth are beautifully figured; they exhibit six to ten conelets on the unworn crown and a maximum of eleven conelets on the worn crown; five of the conelets double by dichotomy. Thus the number of conelets is approximately the same as in *Stegodon elephantoides* (= *cliftii*).

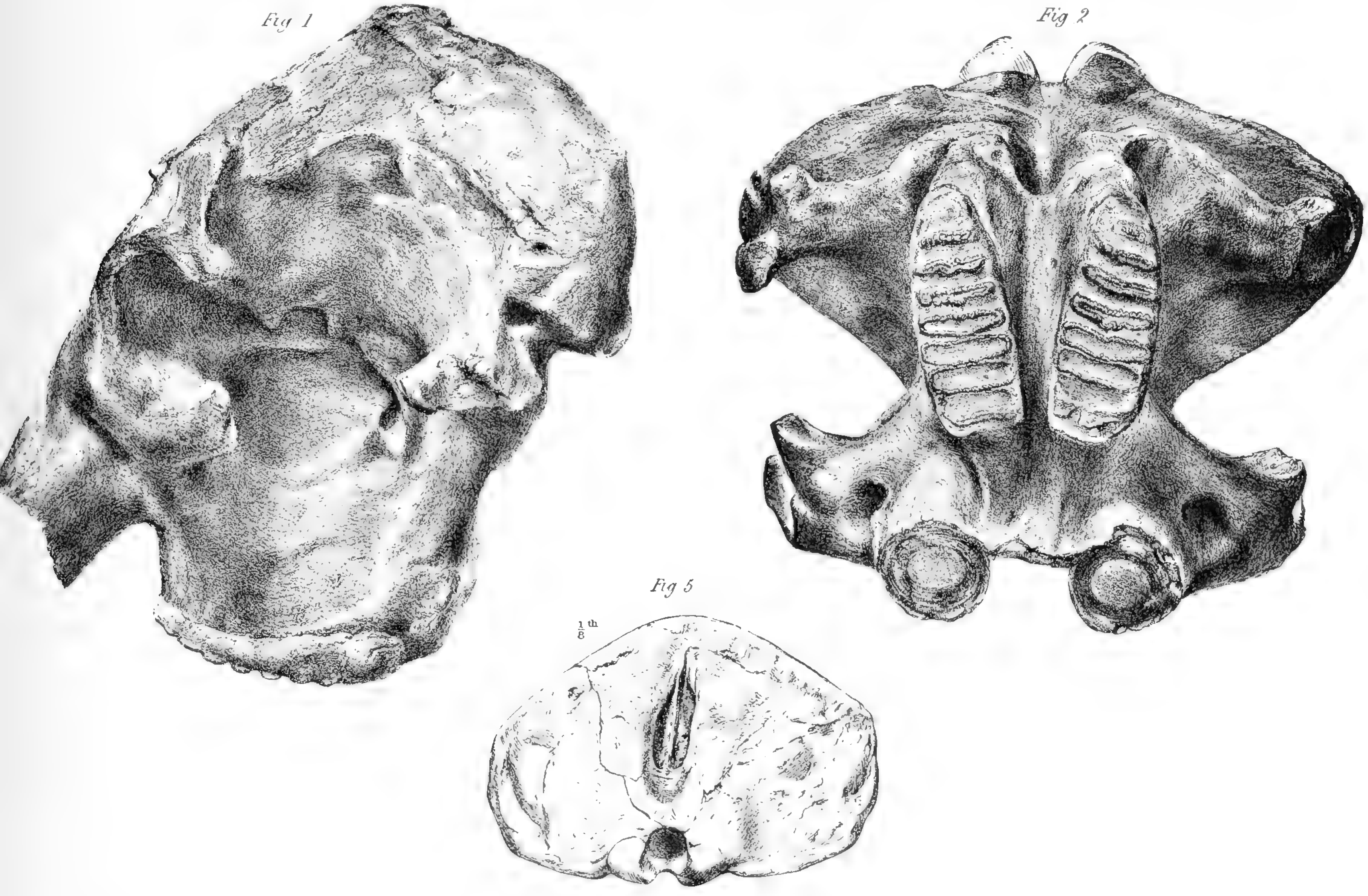
From the above observations we deduce the ridge formula of *Stegodon bombifrons* practically as above under "Characters."

LYDEKKER'S NOTES OF 1886 ON ELEPHAS [= STEGODON] BOMBIFRONS

"Catalogue of the Fossil Mammalia in the British Museum (Natural History)," Part IV, 1886, pp. 82–88

Lydekker (1886.2, p. 83) designates as his lectotype Brit. Mus. M.2978: "The cranium, showing the third true molars of both sides in an early stage of wear. This specimen is the type, and is figured by Falconer and Cautley in the 'Fauna Antiqua Sivalensis,' pl. xxvi"; reproduced in figure 742 of the present Memoir.

Lydekker's notes are based on forty-four specimens in the British Museum referred to this species, chiefly from the Cautley



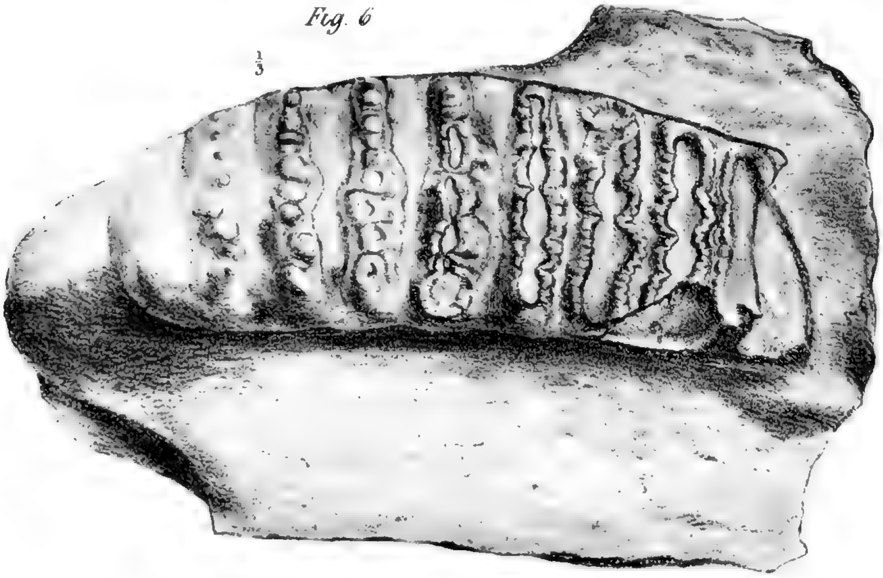
Cotype of Stegodon Bombifrons

Fig. 744. Cotype of *Elephas bombifrons* Falconer and Cautley, 1846. After Falconer and Cautley, 1846 [1847, Pls. xxvii, xxviii], one-sixth natural size. Brit. Mus. M.2979; cast Amer. Mus. 10378. From the Siwalik Hills, India.

Falconer, Pal. Mem., 1868, Vol. I, p. 458: (Pl. xxvii) "Very fine and perfect skull, anterior view." (Pl. xxviii) Fig. 1. "Lateral view of same skull, as figured in Plate xxvii.—B. M. Fig. 2. . . Palate view of same skull, showing sections of tusks, and last ? true molar on either side, with 9 ridges and a heel; the 8 front ridges worn. The interval between the molars in front is very narrow; behind they are extremely divergent.—B.M." Fig. 5. Occipital view of another skull.

Collection (1842); the specific references therefore are based on Falconer's determinations.

Specific Characters.—(Lydekker, 1886.2, p. 82): "The ridges are rather taller, somewhat wider apart, and more numerous than in *E. clifti* [=*Stegodon elephantoides* (=*cliftii*)], and the valleys are generally completely filled with cement; it is, however, sometimes very difficult to distinguish between the hinder teeth of the two species, while in the opposite direction it is often difficult to distinguish between those of *E. bombifrons* and *E. insignis*. The teeth figured by Falconer and Cautley under the name of *E. ganesa* cannot be distinguished from those of the present species, and are therefore provisionally classed under the same head. The teeth are frequently very large, and the ridges are often curved; a trace of the median longitudinal cleft can often be observed in the first two or three ridges, and the inner columns of these ridges occasionally show accessory tubercles near the longitudinal cleft, where they assume a *Mastodon*-like shape. The plane of wear of the teeth of this and the following species [*E. ganesa*] is similar to that of the true Elephants. The mandibular symphysis is produced into a spout-like termination, as in *E. indicus*. The cranium has the fronto-parietal region very convex, the constriction of the frontals by the temporal fossæ being more marked than in the other species. *Hab.* India (Punjab to Siwalik Hills) and (?)China [Footnote: 'Koken, Pal. Abhand. vol. iii. pt. 2, p. 12 (1885).']. The species may perhaps also occur in Java."



Referred Right Third Superior Molar of Stegodon bombifrons

Fig. 745. A partly worn right superior molar, r.M^3, referred by Falconer and Cautley to *Elephas bombifrons* and corresponding very closely in all details to Falconer's description of the cotypes of this species, namely: M 3 with nine and a half ridges; conelets—six dividing into eleven. After Falconer and Cautley, 1846 [1847, Pl. xxix, fig. 6], one-third natural size.

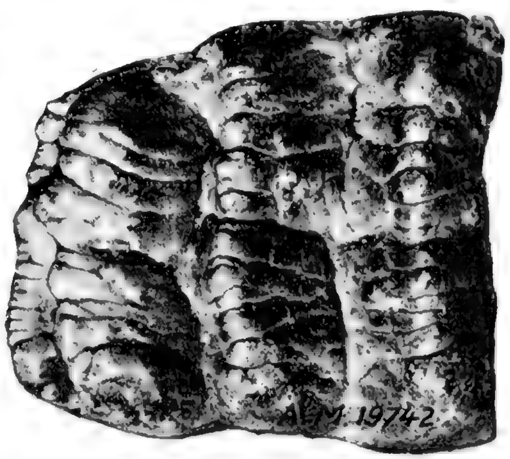


Fig. 746. Referred fragment of superior molar of *Stegodon bombifrons* collected by Barnum Brown in 1922 in the Dhok Pathan horizon, Lower [Middle] Pliocene, two and a half miles northeast of Hasnot, India. This specimen is wrongly numbered; it should read Amer. Mus. 20044.

Three anterior ridge-crests of a right third superior molar, r.M^3 (compare Fig. 759 of *Stegodon orientalis grangeri* type).

The *ridge formula* of Lydekker (*op. cit.*, 1886.2, p. 82), namely, Mm. [Dp] $\frac{?.?.(5\text{-}6)}{?.4(5\text{-}7)}$, M $\frac{6.(6\text{-}7).(8\text{-}9)}{7.(7\text{-}8).(8\text{-}9)}$, is less precise in not referring to the half-ridges but does not otherwise differ excepting in the superior ridges (^{4}) of Dp 3 from the type ridge formula gathered from Falconer's observations above. Lydekker's observations fully substantiate Falconer's formula of 1868, and, omitting the half-ridges, enable us to write the standard *maximum* formula as follows:

Maximum ridge formula of *Elephas* [=*Stegodon*] *bombifrons*: Dp $2^{?}_{?}$ Dp 3^{4}_{4} Dp 4 $\frac{6}{7}$ M 1 $\frac{6}{7}$ M $2^{7}_{7\text{-}8}$ M 3 $\frac{9}{9}$.

Stegodon insignis Falconer and Cautley, 1845, 1846

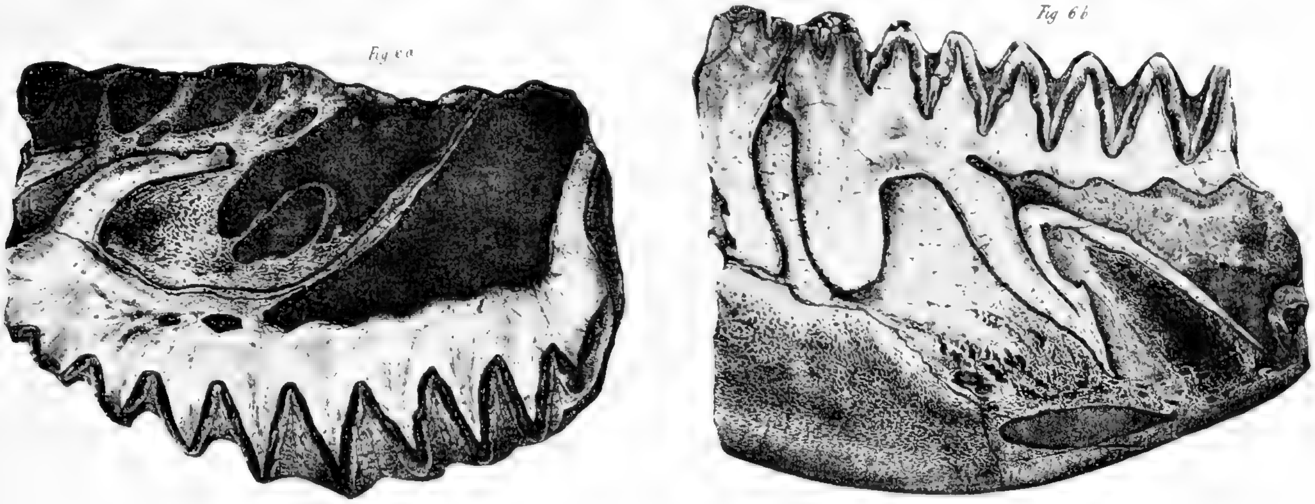
Figures 686, 688, 697, 731, 732, 735, 747–753, 756, 760, 764, 766, 776, 819, Pl. xx

Siwalik Hills, India, Upper Pliocene, Pinjor horizon, to Lower Pleistocene, Boulder Conglomerate (*fide* Falconer and Pilgrim), to Upper Pleistocene. In the present Memoir (see Fig. 413) the upper levels of the Pinjor horizon are of Lower Pleistocene age (*fide* Barnum Brown).

Falconer's types of this species agree in the ridge-crest formula with the type which he subsequently described as *Stegodon ganesa* but they exhibit profoundly different characters in the cranium, as shown in a comparison of figures 735 (*S. insignis*) and 736 (*S. ganesa*), or in a comparison of figures 752 (*S. insignis*) and 732 (*S. ganesa*). This profound difference, as explained above and below, is attributed to the fact that all the crania referred by Falconer and Cautley to *Stegodon insignis* represent small-tusked and probably female individuals, while crania referred to *S. ganesa* represent large-tusked and probably male individuals.

Falconer originally described *Elephas insignis* in 1846, p. 37, and in the same communication (p. 45) he named a fourth species *Elephas Ganesa*, describing a third superior molar (which had been figured in 1845, Pl. iii, fig. 7a) and remarking that the tooth bears the closest resemblance to the corresponding tooth in *E. insignis*. This doubt always remained in Falconer's mind, for in his notes of 1867, p. 4, and of 1868, Vol. I, p. 424, he remarked: "In fact, there are no good characters by which the teeth of these two species can be satisfactorily distinguished, although the crania are so remarkably different." In Falconer's mind, therefore, *Elephas* [=*Stegodon*] *insignis* possessed a cranium of the type he figured in Pl. xv of the "Fauna Antiqua Sivalensis," reproduced herewith in our figure 735, in contrast to *Elephas* [=*Stegodon*] *ganesa* which possessed a cranium of the type figured in Pl. xxiii, reproduced in our figure 736.

Sexual Disparity.—As explained above in the discussion of the crania, Falconer apparently selected the *female* crania as referable to *Elephas* [=*Stegodon*] *insignis* and the *male* crania as referable to *E.* [*S.*] *ganesa.* A detailed comparison of all the referred specimens has failed to establish any true specific distinction between these two species. Consequently we may regard the lectotype and referred specimens from the Pinjor, Boulder Conglomerate, and Godávari, Narbada Alluvium, as 'collective species' including a number of ascending mutations or subspecies which will be recognizable by profound monographic research; it is not probable that a single true specific stage passed from the Pinjor into the Narbada Alluvium horizon.



Lectotype and Cotype of Stegodon insignis

Fig. 747. Lectotype left superior molar, l.M^3, of *Elephas insignis* Falconer and Cautley, 1846, from the Siwalik Hills, India, after Falconer and Cautley, 1846 [1845, Pl. ii, fig. 6*a*], also cotype third inferior molar, M$_3$, after Falconer and Cautley, 1846 [1845, Pl. ii, fig. 6*b*]; both figures one-third natural size.

(Falconer and Cautley, 1846, p. 37): "Fig. 6*a*, pl. 2 [lectotype l.M^3—Brit. Mus. M.3015], represents a vertical and longitudinal section of the last upper molar of an Indian fossil species, which we have named *Elephas insignis* in this work." Length of this tooth 10.3 inches. Inverted to show natural position. (Falconer, "Palæontological Memoirs," 1868, I, p. 423): "The four anterior ridges are affected by wear; the six posterior ridges are entire, the fangs are fully developed, and their mode of implantation in the jaw is distinctly shown." Fig. 6*b* (cotype M$_3$—Brit. Mus. M.3039) is a vertical section of a third lower molar of *E. insignis*, one third natural size (cf. Falconer, 1867.1, p. 4; 1868.1, I, p. 424; also caption to figure 697 above).

In the present Memoir we shall first treat Falconer's descriptions of the types and referred specimens of these two species separately and then unite them under the collective species name *Stegodon insignis-ganesa.*

Cranium.—The *lectotype* cranium of the third species of Stegodont, described as *Elephas insignis* by Falconer and Cautley, 1846, is from the Cautley Collection but is without record as to its exact geologic level. The specimen is now in the British Museum. Lydekker (1886.2, p. 91) designates it as "M. 3015. An imperfect cranium, showing the third true molar of either side."

Elephas insignis Falconer and Cautley, 1846. "Fauna Antiqua Sivalensis," letterpress, 1846, p. 37. Lectotype.—A third superior molar of the left side, l.M^3, in an imperfect cranium (Brit. Mus. M.3015) containing the third true molar of either side. Horizon and Locality.—Siwalik Hills, India, probably Pinjor horizon, Upper Pliocene or Lower Pleistocene. Lectotype Figure.—*Op. cit.*, 1846 [1845, Pl. ii, fig. 6*a*]. Cotype.—*Op. cit.*, 1846 [1845, Pl. ii, fig. 6*b*]. Description.—Falconer's original description of 1846, p. 37, quoted in part above in this Memoir (p. 829) was restated in 1868, Vol. I, p. 423, fig. 6*a* of Pl. ii, as follows: "*Elephas insignis*, from the Sewalik Hills [Fig. 747 of the present Memoir]. Vertical section of last upper molar. The four anterior ridges are affected by wear; the six posterior ridges are entire, the fangs are fully developed, and their mode of implantation in the jaw is distinctly shown. The white mass in the centre represents the body of ivory, which is projected upwards in ten angular lobes, terminating in a sharp edge. The height of these lobes does not much exceed the width of their base, and closely applied over them is a thick layer of enamel reflected up and down in a continuous zig-zag plate. The interspaces of the five posterior ridges of enamel are completely filled up by a mass of cement much exceeding the enamel in thickness (*vide* Plate vi. fig. 7). This is the best illustration of the intermediate type of a proboscidean molar tooth, from which those of the other species diverge in opposite directions. It belongs to the *Mastodon Elephantoïdes* of Clift. The dark granulated shade below the portion of the ivory nucleus sustaining the five posterior ridges indicates the hollow of their common fang, which in the fossil is occupied by a core of sandstone.—B.M. (Reproduced in Pl. iv. fig. 1.) Length of tooth, 10.3 in."

Characters of Elephas [=Stegodon] insignis.—(Lydekker, 1886.2, p. 89): "The apparent impossibility of distinguishing the dentition of this species from that of *E. ganesa* has been already mentioned. . . . The ridges of the cheek-teeth are usually rather

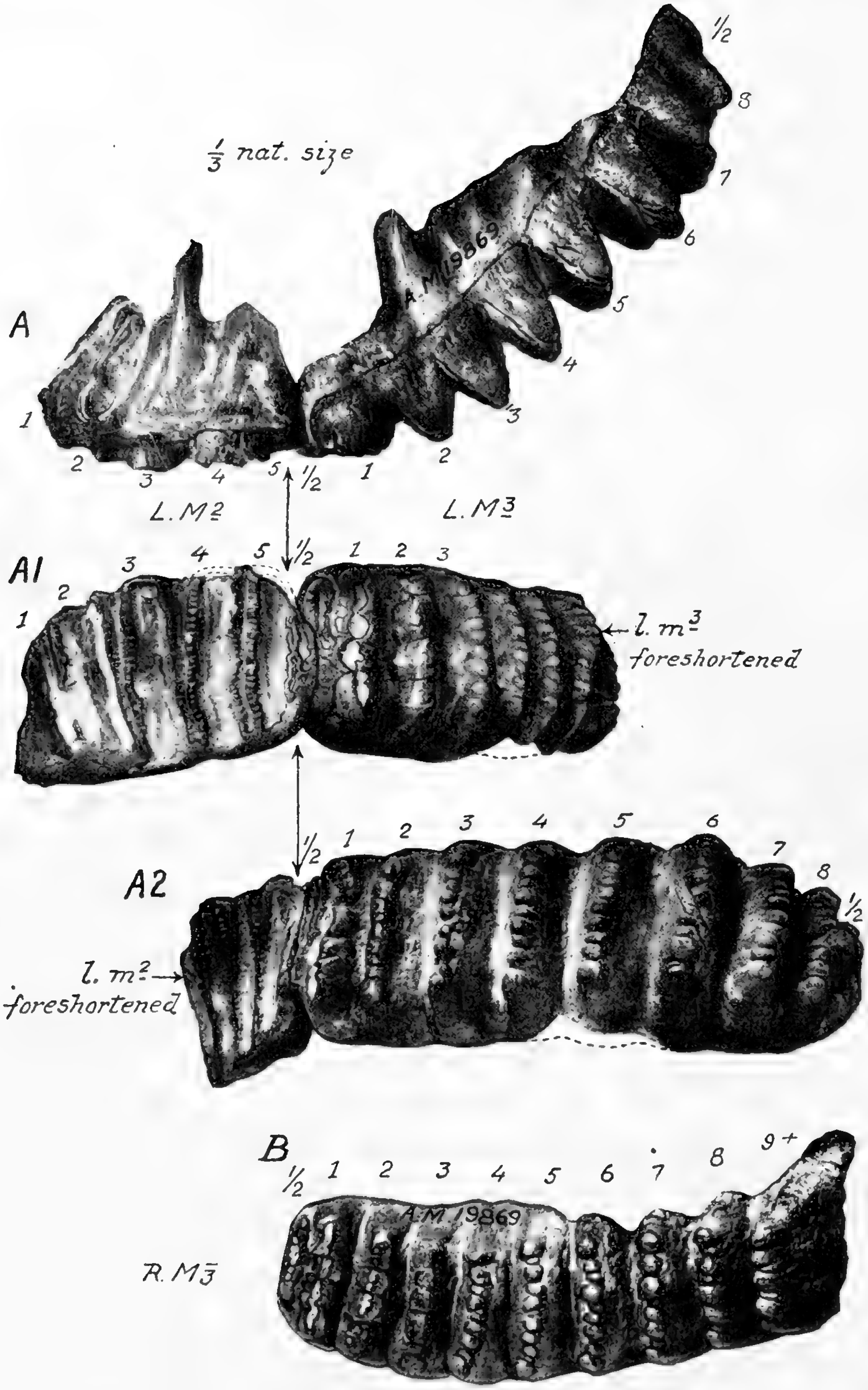


Fig. 748. *Stegodon insignis* ref. (Amer. Mus. 19869) superior and inferior molars probably belonging to the same individual as the mandible shown in figure 750. Pinjor horizon, Upper Siwaliks, near Siswan, India. One-third natural size.

A, A1, A2, Imperfect second superior molar, l.M^2, with +5½ ridge-crests much worn; a complete third superior molar, l.M^3, with ½-8-½ ridge-crests, of which the two anterior are slightly worn.

B, Right third inferior molar, r.M_3, displaying ½-9+ ridge-crests, of which the three anterior are slightly worn (compare Fig. 750). The l.M_3, now completely exposed, displays a total of 12 ridge-crests.

taller and narrower than in *E. bombifrons*, their average number greater, and the cement still more abundant. It is, however, not always easy to distinguish between the two. The third molar is usually narrower posteriorly, and the enamel frequently thinner. The taller and more numerous ridges indicate that the present species is intermediate in respect of dental characters between *E. bombifrons* and *E. planifrons*. The adult cranium is remarkable for the great depression of the fronto-parietal region, although this feature is less marked in some specimens than in others [Footnote: 'Compare "Fauna Antiqua Sivalensis," pl. xliii. figs. 15, 15*b*.']; but in the young cranium the contour is indistinguishable from that of the adult *E. ganesa* [Footnote: 'It is of course self-evident that these young crania (like detached teeth) might equally well have belonged to *E. ganesa*.']."

Referred Materials in the American Museum.—A typical individual (Amer. Mus. 19869—Figs. 748, 750), in the primitive *S. insignis-ganesa* stage, was found by Barnum Brown near Siswan (Pinjor horizon), India, in which the upper and lower jaws are fortunately associated; this specimen exhibits the following ridge-crest formula:

$$\mathrm{M}\,2\,\frac{+5\tfrac{1}{2}(=7)}{}\quad \mathrm{M}\,3\,\frac{\tfrac{1}{2}\text{-}8\text{-}\tfrac{1}{2}}{12}.$$

Also recorded from Siswan are two other specimens, namely, a second superior molar, r.M^2 (Amer. Mus. 19804—Fig. 749), in which the ridge-crests ($\frac{\frac{1}{2}\text{-}7\text{-}\frac{1}{2}}{}$) agree closely with the typical formula of *Stegodon insignis*, and a third left inferior molar, l.M_3 (Amer. Mus. 19859—Fig. 753) with $\frac{}{+12\frac{1}{2}}$ ridge-crests. A juvenile right lower jaw (Amer. Mus. 19858—Fig. 751) exhibits Dp_4 with 7 ridge-crests; a young adult lower jaw (Amer. Mus. 19964—Fig. 752B) shows l.M_2 in full use, l.M_3 coming into place; the ridge-crest formula of l.M_2 is 7. Still another specimen from the same locality of Siswan is a lower jaw, also a right upper tusk complete (Amer. Mus. 19773—Fig. 766).

Fig. 749. Referred *Stegodon insignis* (Amer. Mus. 19804), a second superior molar, r.M^2, taken from palate found below the conglomerates, three miles northeast of Siswan, Upper Siwaliks, India. Ridge-crests, namely, ½–7–½, agree closely with *S. insignis*, somewhat too progressive for *S. bombifrons*.

The grinding teeth of these three individuals in the American Museum collection (see Figs. 748, 749, 750, and 753), all recorded from the Pinjor horizon, Upper Pliocene [or Lower Pleistocene], exhibit progressive variation in the ridge count, as indicated by numerals in these figures; according to Doctor Brown, it is not certain that they belong in the Pinjor horizon proper, but may have come in by erosion from the conglomerates above.

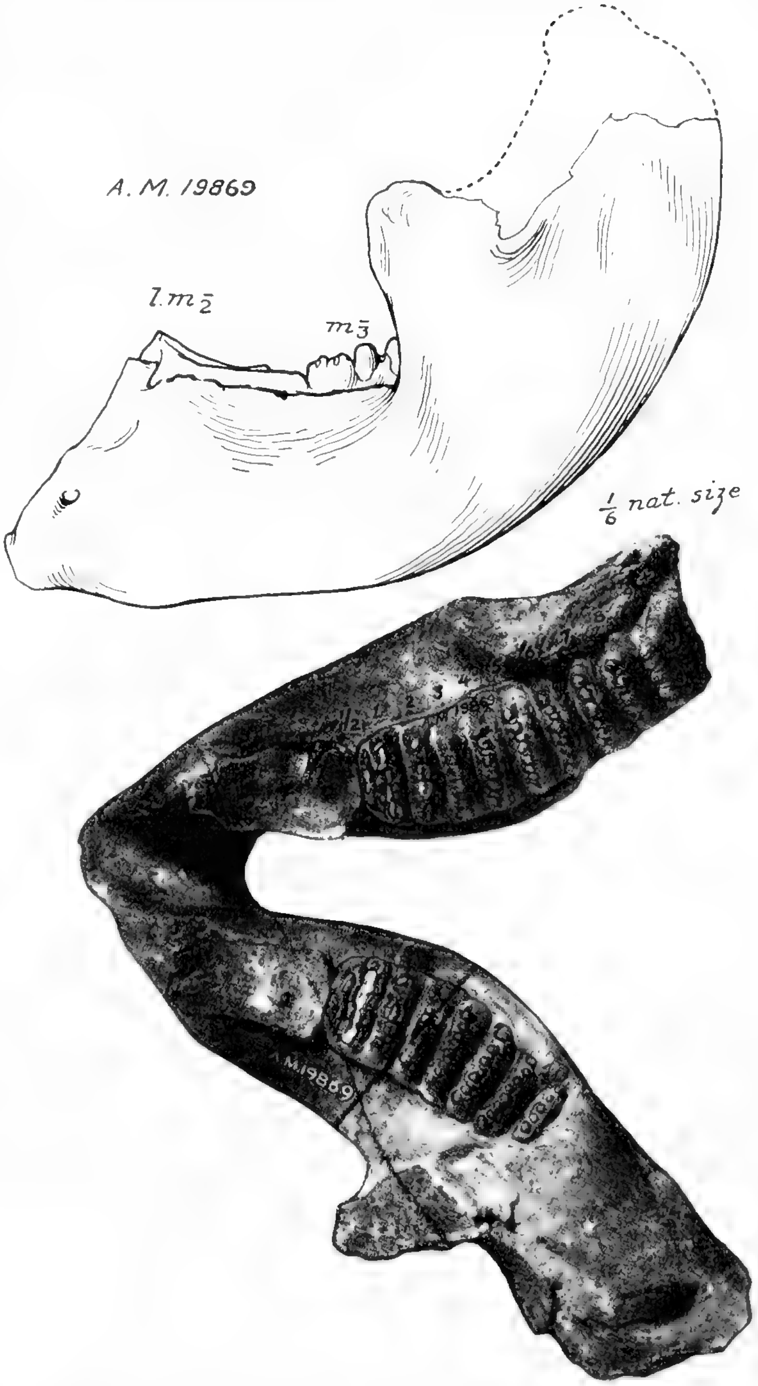


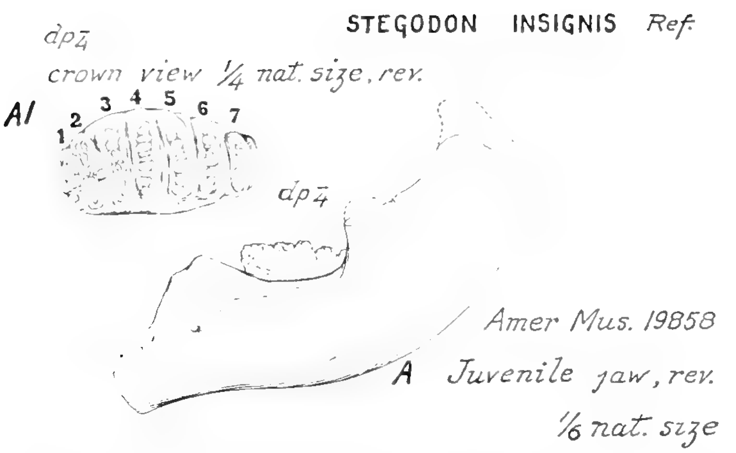
Fig. 750. Referred inferior mandible, associated with two upper teeth, of *Stegodon insignis* (Amer. Mus. 19869), collected by Barnum Brown in the Pinjor horizon, Upper Siwaliks, near Siswan, India; it contains both second inferior molars, M_2, well worn, also right and left third inferior molars, M_3, little worn, with ½-9+ ridge-crests; the l.M_3, after removal of the bone, displays 12 ridge-crests (compare Fig. 748, probably of the same individual).

Stegodon ganesa Falconer and Cautley, 1845, 1846

Figures 686, 698, 731–733, 736, 754, 755, 757, 760, 766, 819, Pl. xx

Siwalik Hills, India, Upper Pliocene Pinjor horizon, to Lower Pleistocene, Boulder Conglomerate (*fide* Falconer and Pilgrim), to Upper Pleistocene. In the present Memoir (Fig. 413) the upper levels of the Pinjor horizon are of Lower Pleistocene age (*fide* Barnum Brown).

This species (*fide* Falconer, Lydekker) exhibits the same dental characters (Fig. 757) as *Stegodon insignis* but is distinguished by



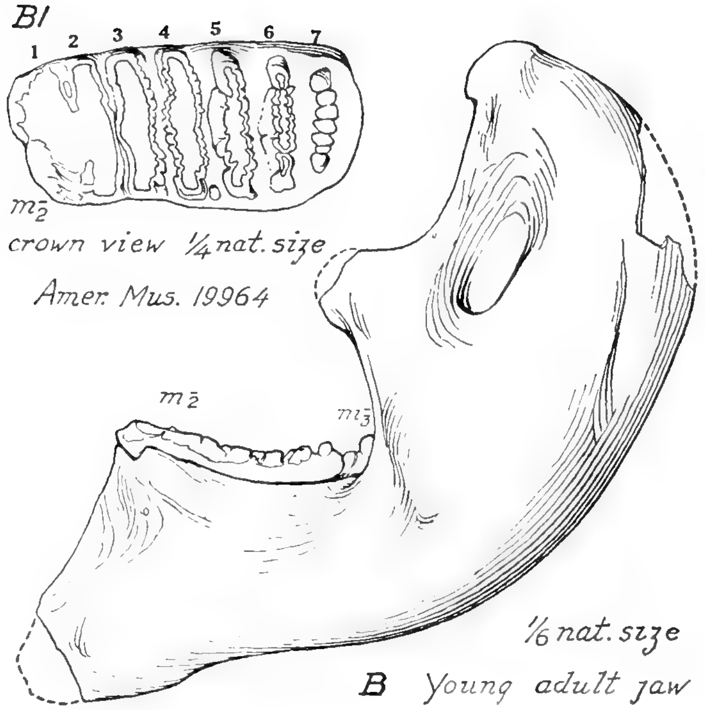
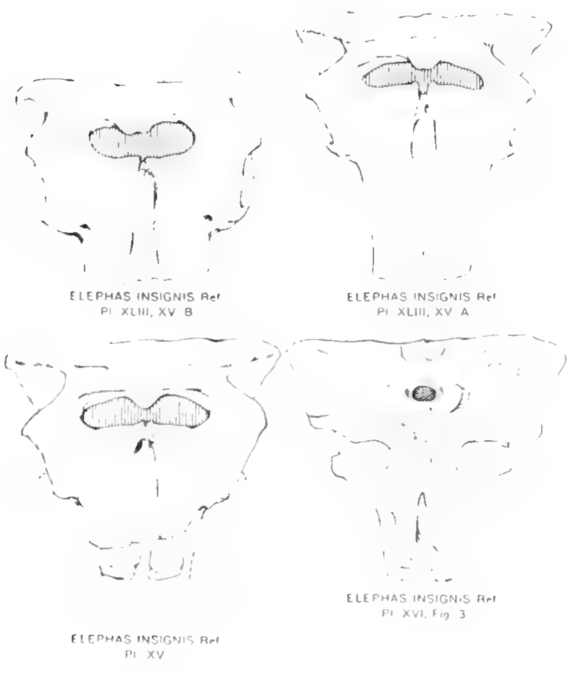


Fig. 751. Referred lower jaw, left aspect, of *Stegodon insignis* (Amer. Mus. 19964), mature adult, collected by Barnum Brown in 1922 in the upper clays below the conglomerates, three miles north of Siswan, Pinjor horizon, Upper Pliocene, India. The juvenile right lower jaw of *S. insignis* (Amer. Mus. 19858), collected by Dr. Brown also in the upper clays but two miles north of Siswan, summit of the Pliocene, is inserted for comparison.

The ramus (Amer. Mus. 19964) exhibits a fully adult form, with abbreviated symphysis, l.M_2 in full use, l.M_3 coming into place. The ridge-crest formula is $M\ 2^{?}_{7}$, $M\ 3^{?}_{?}$. One-sixth natural size.

Observe Dp_4 of Amer. Mus. 19858 which exhibits seven ridge-crests as compared with the typical Dp_4 of *S. insignis* with seven to nine ridge-crests (cf. Table V, p. 854 above). One-fourth natural size.



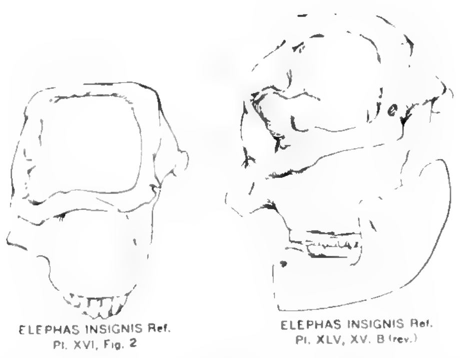


Fig. 752. Referred crania of *Elephas* [=*Stegodon*] *insignis*. Specimens reproduced in outline from original plates in Falconer and Cautley's "Fauna Antiqua Sivalensis," as indicated in the printed legends. Frontal aspect of four crania, lateral aspect of one cranium, and posterior aspect of one cranium. All one-twentieth natural size. Compare figures 732 and 777.

profoundly different cranial contours, profile and facial aspects (compare Figs. 732, 752). Falconer, immediately after describing *Elephas insignis* (1846, p. 37), described *Elephas ganesa* (1846, p. 45); apparently he was very much puzzled by the exact similarity in the structure of the teeth as contrasted with the profound difference in the character of the skull, for in the "Palæontological Memoirs" of 1868 (Vol. II, p. 84) appears the following statement:

"Regarding the specific distinctness of *E.* (*Steg.*) *Ganesa* I am by no means so well assured; this species is chiefly founded on a huge cranium in the British Museum with long tusks, presented by Colonel Baker. I have not been able to reconcile the form of this cranium with either that of *E.* (*Steg.*) *insignis* or *E.* (*Steg.*) *bombifrons*; but at the same time I must confess that I have failed in tracing its dentition satisfactorily as a distinct form through different ages."

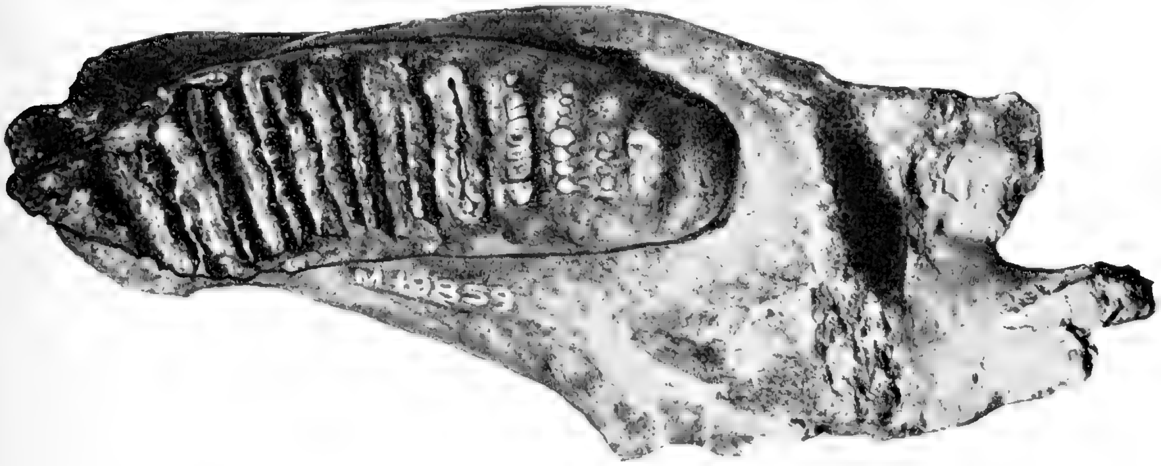


Fig. 753. Referred *Stegodon insignis* (Amer. Mus. 19859), collected by Barnum Brown in 1922 two and a half miles south of Charnian, near Siswan, India, below the conglomerates, probably Pinjor horizon, Upper Pliocene.

A third left inferior molar, l.M_3; length 291 mm., width 93 mm.; ridge-crests of M 3 $\overline{+12\frac{1}{2}}$. One-third natural size.

E. [*Elephas*] *Ganesa* Falconer and Cautley. "Fauna Antiqua Sivalensis," letterpress, 1846, p. 45. Lectotype.—A last upper molar, M^3. Brit. Mus. 18489. Horizon and Locality.—Siwalik Hills, India, Pinjor horizon, Upper Pliocene or Lower Pleistocene. Lectotype Figure.—*Op. cit.*, 1846 [1845, Pl. iii, fig. 7*a*—see figures 698 and 757 of the present Memoir].

Lectotype Description.—(*Op. cit.*, 1846, p. 45): "The crown consists of ten principal ridges, with a subordinate 'talon' ridge in front and behind. The anterior seven ridges have their summits worn, the two in front being ground down to the common base of ivory, the tooth having been a considerable time in use."

Characters.—Falconer (1868, Vol. I, p. 424) remarks of this molar, M^3: "Plate iii, Fig. 7*a*.—*Elephas Ganesa*, a fossil Indian species. Vertical section of last upper molar. The crown consists of ten principal ridges, with a subordinate talon ridge in front and behind. The anterior seven ridges have their summits worn. A small portion is broken off at the anterior end. The disposition and relative proportions of the ivory, enamel, and cement bear the closest resemblance to those of the corresponding tooth of *E. insignis*, and the number of ridges agrees. In fact, there are no good characters by which the teeth of these two species can be satisfactorily distinguished, although the crania are so remarkably different.—B. M. . . . Length of tooth, 9.25 in."

Lydekker (1886.2, p. 89) erroneously selects Brit. Mus. M.3008 as the type of *E. ganesa*: "The imperfect cranium, showing the partially-worn third true molar of either side, the base of the left and the greater portion of the right incisor; from the Pliocene of the Siwalik Hills. This specimen (the missing portions of which have been restored in wood) is the type, and is figured by Falconer and Cautley in the 'Fauna Antiqua Sivalensis,' pls. xxi., xxii., xxiii., and xliii. fig. 14. It is remarkable for the enormous size of the incisors. *Presented by Gen. Sir W. E. Baker, K.C.B.*, 1848."

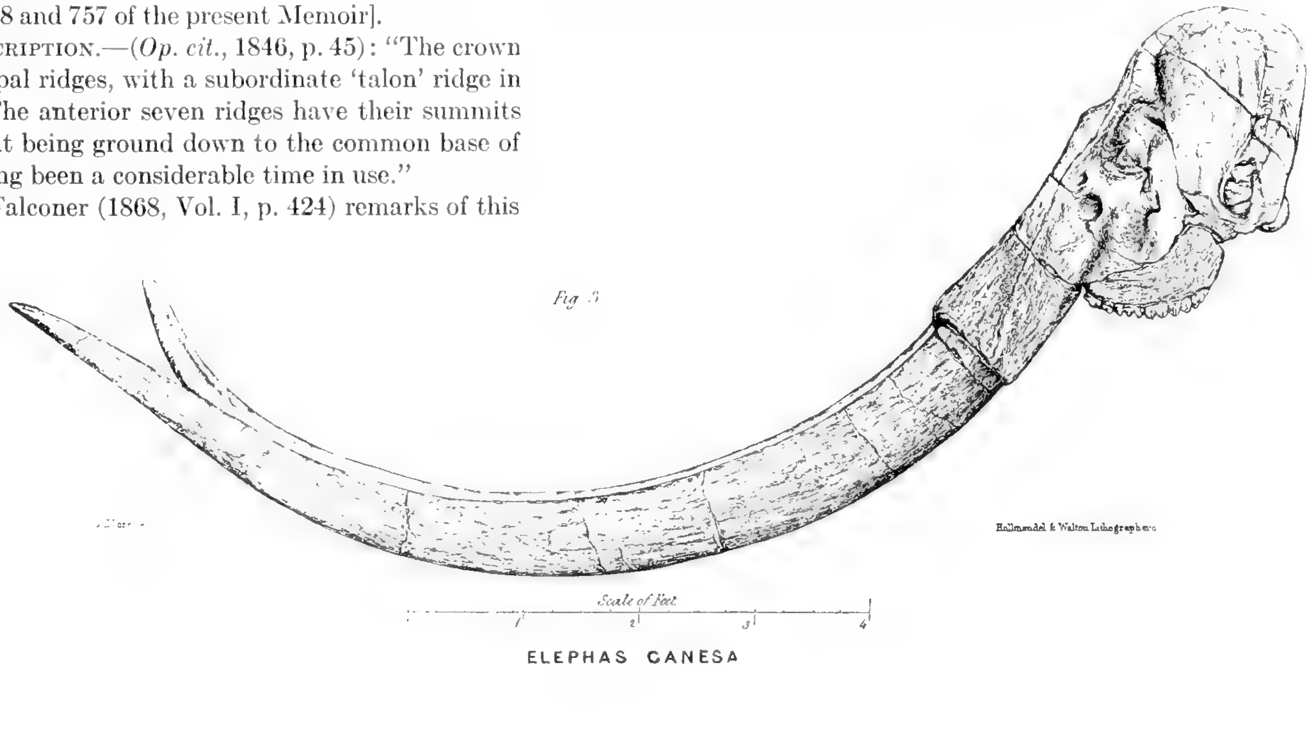


Fig. 754. This is the famous and oft-reproduced referred skull and tusks of *Elephas* [=*Stegodon*] *ganesa* Falconer and Cautley, 1845–1847, reproduced from Plate xxii, fig. 3, of the "Fauna Antiqua Sivalensis." Same skull figures 732, 733, and 736. Original in the British Museum (M.3008).

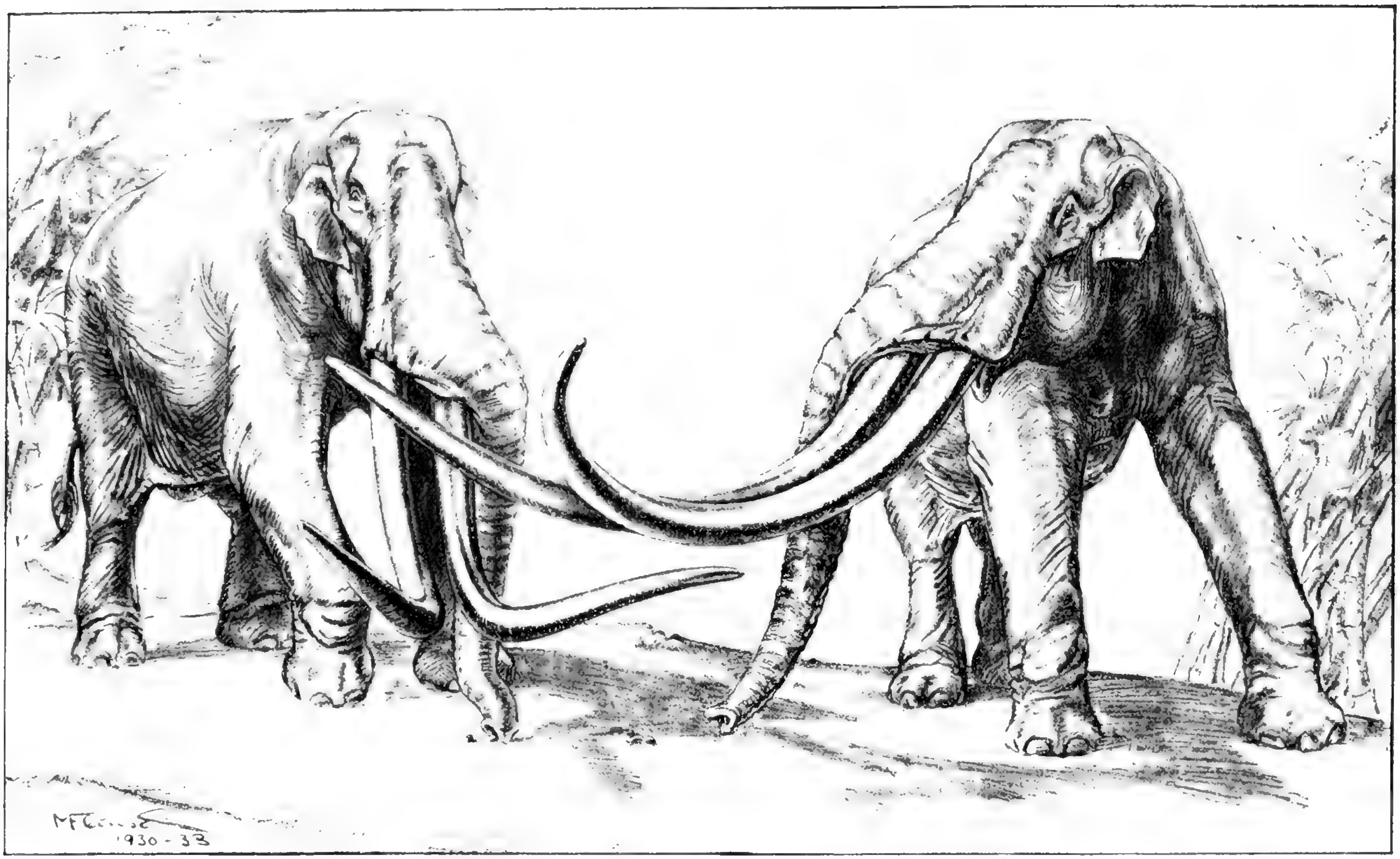


Fig. 755. Restoration (1930–1933) of *Stegodon ganesa,* to a one-thirty-fifth scale, by Margret Flinsch, under the direction of Henry Fairfield Osborn. Based on Falconer's figures of the skull and tusks [see also Fig. 733.]

Fig. 756. Restoration (1934) of *Stegodon insignis,* by Margret Flinsch, under the direction of Henry Fairfield Osborn. All figures about one thirty-sixth natural size. Restoration based on crania figured in the "Fauna Antiqua Sivalensis" by Falconer and Cautley. Aged individual at left (Pl. XVI, fig. 1), center (Pl. XLIII, fig. XV.A, cf. Pl. XV), right (Pl. XLIII, fig. XV.B, cf. Pl. XVII, figs. 1 and 2).

FALCONER'S NOTES OF 1868 ON STEGODON INSIGNIS AND S. GANESA

Falconer, "Palæontological Memoirs," Vol. I, 1868, pp. 423, 424, 452, Plates II–XXV of the "Fauna Antiqua Sivalensis"

Stegodon insignis. LECTOTYPE of *Stegodon insignis* from the Siwalik Hills. Plate II, fig. 6*a*, M^3 with 10 ridges, the height of these ridges does not much exceed the width at the base, closely covered with a thick layer of enamel, interspaces of five posterior ridges of enamel completely filled with cement. (Falconer and Cautley, 1846.1, p. 37): "This tooth belongs to one of the forms which have been included under the name of *Mast. Elephantoides*, by Mr. Clift; and which Professor Owen names 'Transitional Mastodons.' "

Stegodon ganesa. LECTOTYPE. Plate III, fig. 7*a*, M^3, length 9.25 in. = 235 mm.; ". . . ten principal ridges, with a subordinate talon ridge in front and behind. . . . The disposition and relative proportions of the ivory, enamel, and cement bear the closest resemblance to those of the corresponding tooth of *E. insignis*, and the number of ridges agrees. In fact, there are no good characters by which the teeth of these two species can be satisfactorily distinguished, although the crania are so remarkably different.—B.M."

UPPER JAWS AND GRINDING TEETH

STEGODON INSIGNIS.—Plate XIX, figs. 1, 1*a*, upper jaw with Dp^2 and Dp^3, Dp^3 with 6 ridges; figs. 4, 4*a*, skull, M^1 with 7½ ridges; figs. 6, 6*a*, skull with M^{2-3}, M^3 with 11½ ridges, abundant cement, length of M^3 11 in. = 280 mm., width 3.8 in. = 97 mm. Plate XIX.A, figs. 2, 2*a*, palate with M^2, M^3; M 2 ridges 7, M 3 ridges ½-11-½. Plate XXIV, figs. 6, 6*a*, M^1 ridges 7½, M^2 ridges ½-8, ridges very high and compressed, ten points or denticles on 5th ridge. Plate XXIV.A, fig. 2, skull fragment, M^1 ridges 6½, M^2 ridges ½-7-½, little cement.

STEGODON GANESA.—Plate XXII, fig. 2, fine large skull, M^3 ridges 10½, small talon in front. Plate XXIV, fig. 1, upper jaw, M^1 ridges 6½; fig. 2, upper jaw, (?) M^2 ridges 7; fig. 3, upper jaw, M^2 ridges 7½; fig. 4, upper jaw, M^3 ridges 6½, last ridge with 7 denticles; fig. 5, imperfect upper molar—6 ridges with 9 denticles on fourth ridge.

LOWER JAWS AND GRINDING TEETH

STEGODON INSIGNIS.—Plate XVIII.A, figs. 3, 3*a*, lower jaw, M_3 with 12½ ridges, 9 denticles on the 7th ridge; figs. 4, 4*a*, lower jaw with M_1, M_2, M_1 with 4 ridges, M_2 with 7 ridges, plates very deep; figs. 5, 5*a*, lower jaw, l.M_3 with 11½ ridges. Plate XX, fig. 6, 6*a*, lower jaw, M_2 with 9 ridges and front and back heel; figs. 7, 7*a*, lower jaw, M_3 with 12 or 13 ridges; figs. 9, 9*a*, lower jaw, M_2 with 9½ ridges. Plate XX.A, fig. 6, lower jaw, M_2 7 to 8 ridges. Plate XXIV.A, fig. 3, M_2 [M_3] ridges 12½, length 11.5 in. = 291 mm., width 4 in. = 101 mm. Plate XXV, fig. 4, lower jaw, M_1 ridges 7½.

STEGODON GANESA.—Plate III, fig. 7*b*, M_3 [?M_2] "appears to have consisted of eight principal ridges, with a talon ridge behind, and a subordinate ridge in front. . . . It bears a close resemblance to the corresponding inferior tooth of *E. insignis* in the form of the ridges, thickness of enamel, and proportion of cement.—B.M." Plate XX.A, figs. 1, 1*a*, lower jaw, M_1 with 5½ ridges, M_2 with 8 ridges; figs. 2, 2*a*, M_2 with 7½ ridges. Plate XXV, fig. 1, M_3 ridges +8. Plate XXV.A, fig. 1, lower jaw, M_3 ridges 7½+. Plate XXIX.B, figs. 2, 2*a*, lower jaw, Dp_4 ridges 7½.

SKULLS OF S. INSIGNIS AND S. GANESA

Stegodon insignis. Plate XV. "The cranium is seen to differ remarkably from that of *E. Ganesa* (Plates XXI. and XXII.) notwithstanding that the molars of the two species agree so closely. That of *E. insignis* is flattened at the top, elongated from side to side and singularly modified, so as to bear an analogy to the cranium of *Dinotherium giganteum*, while that of *E. Ganesa* does not differ much from the ordinary type of the Elephants." Plate XVI, figs. 1, 2, 3. "Fig. 1.—*Elephas insignis.* Broken cranium, oblique antero-lateral view. Left orbit, &c., gone. This head is very cubical in form, is old, very concave in front and vertically; teeth broken. Interval between incisive sheaths deep. No tusks. A black specimen in Cautley's collection.—B.M." Fig. 4, skull with M^3, number of ridges +10½, length of M^3 9.4 in. = 239 mm. Plate XVII, figs. 1, 2, same skull as Plate XVI, fig. 3. Extreme length from occipital bulge to plane of molars 23 in. = 583 mm., extreme width of occiput 25.5 in. = 647 mm., width of naso-maxillary opening 11.3 in. = 288 mm., occipital condyles to anterior end of palate 22 in. = 560 mm. See also Plate XVII, figs. 3, 4, and Plate XVIII, figs. 1, 2, 3, 4.

SUMMARY OF RIDGE FORMULÆ

The above observations on ridge formulæ include teeth in different stages of development and of attrition, hence the many discrepancies. The adult ridge formulæ are indistinguishable in the two species. Consequently we may combine the ridge numbers observed by Falconer (in Murchison) in the following collective ridge formula of *Stegodon insignis-ganesa.*

Stegodon insignis-ganesa: $\mathrm{Dp}\ 3\frac{6}{-}\ \mathrm{Dp}\ 4\frac{}{7\frac{1}{2}}\ \mathrm{M}\ 1\ \frac{7\frac{1}{2}}{7\frac{1}{2}}\ \mathrm{M}\ 2\ \frac{7\frac{1}{2}\text{-}\frac{1}{2}\text{-}8}{8\text{-}9\frac{1}{4}}\ \mathrm{M}\ 3\ \frac{10\frac{1}{2}\text{-}\frac{1}{2}\text{-}11\text{-}\frac{1}{2}}{12\frac{1}{2}\text{-}13}$.

This collective ridge formula includes the *maxima* numbers only; whereas that given below by Lydekker (1886.2, p. 89, under *E. insignis*) includes both maxima and minima. In a *collective ridge formula* we include ascending mutations, i.e., successive geologic stages in the evolution of the ridges, some more primitive, some more progressive, all constituting a collective species.

LYDEKKER'S (1886) COMPARISON OF STEGODON BOMBIFRONS, S. INSIGNIS, AND S. GANESA

"Catalogue of the Fossil Mammalia in the British Museum (Natural History)," Part IV, 1886, pp. 88, 89

CHARACTERS OF E. [= STEGODON] GANESA.—(Lydekker, 1886.2, p. 88): "The third true molars in the type cranium of this species contain ten ridges, and thereby agree with the corresponding teeth of *E. insignis* rather than of *E. bombifrons*, a conclusion confirmed by a second cranium, in which there appear to be either ten or eleven ridges in the same tooth [Footnote: 'See Rec. Geol. Surv. Ind. vol. ix. p. 48 (1876).']. This close resemblance between the last molar of this form and of *E. insignis* renders it apparently impossible to draw any distinction between the earlier teeth of the two forms [Footnote: 'The majority of the teeth figured in the "Fauna Antiqua Sivalensis" under the name of *E. ganesa* have the low ridge-formula of *E. bombifrons* (*q. v.*).'], and all such teeth are therefore referred to the latter. Falconer [Footnote: 'See "Palæontological Memoirs," vol. ii. p. 84.'] had considerable doubts as to the specific distinctness of the present form, and as the resemblance between the type cranium and the young cranium of *E. insignis* [Footnote: 'See "Fauna Antiqua Sivalensis," pl. xliii. figs. 14, 15.'] indicates that the two are closely related, it is possible that *E. ganesa* may be the male form of *E. insignis*. The adult cranium does not differ very widely from the type of *E. indicus*, although the frontal constriction is less marked."

Lydekker's ridge formula of *Elephas* [=*Stegodon*] *insignis-ganesa*, namely, Mm. [Dp] $\frac{2.(5\text{-}6).7}{2.5.(7\text{-}9)}$, M $\frac{(7\text{-}8).(7\text{-}8).(9\text{-}11)}{(7\text{-}10).(8\text{-}12).(9\text{-}13)}$, omits the half-ridges; it also gives a higher ridge formula to M 1 and M 2. Consequently the following maximum ridge formula according to Lydekker is higher than that of Falconer; this ridge formula, however, is not sustained by Lydekker's own observations on fifty-nine specimens of the Cautley Collection in the British Museum, many of which are described and figured by Falconer.

Lydekker's combined ridge formula of *Elephas* [=*Stegodon*] *insignis-ganesa* may be written as follows:

$$\text{Dp 2}\ \tfrac{2}{2}\ \text{Dp 3}\ \tfrac{5}{5}\ \text{Dp 4}\ \tfrac{7}{9}\ \text{M 1}\ \tfrac{8}{10}\ \text{M 2}\ \tfrac{8}{8\text{-}?12}\ \text{M 3}\ \tfrac{11}{13}.$$

Stegodon insignis-ganesa

Falconer and Cautley (1846)–Osborn (1928)

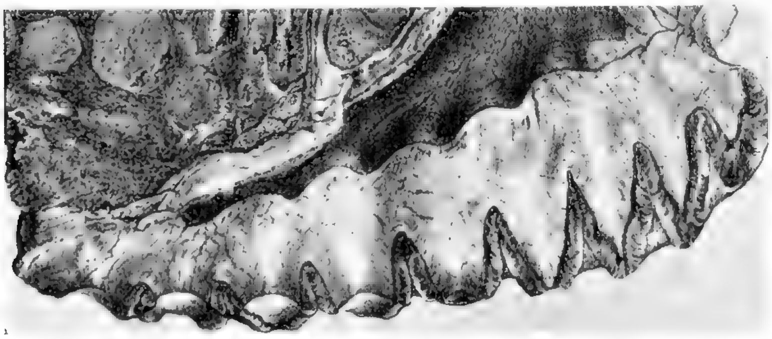
Having now reviewed in detail the observations of Falconer and of Lydekker, we appear to be forced to the conclusion that *Stegodon insignis* and *S. ganesa* are respectively female and male representatives of a single 'collective species' which first appears in the Lower Pleistocene, Pinjor horizon, extending into the Boulder Conglomerate, while specimens at present *referred* to the same species occur in the Middle [Upper] Pleistocene Godávari, Narbada Alluvium, contemporaneous with *Elephas* (*Hypselephas*) *hysudricus* and *Palæoloxodon namadicus* of the Godávari.

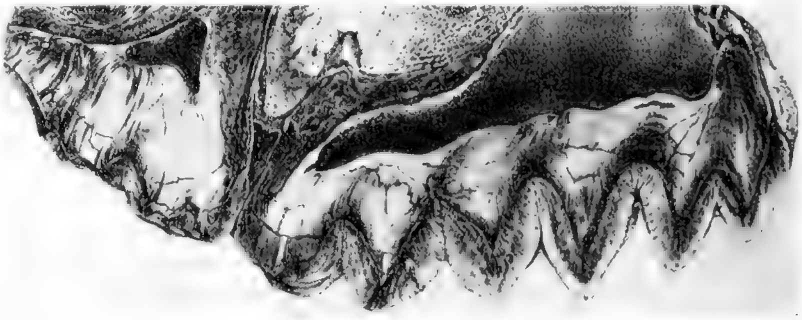
Doubtless we are dealing with a series of ascending mutations which in time may be distinguished by valid constant specific or subspecific characters; meanwhile we regard these ascending mutations as a collective species *Stegodon insignis-ganesa*. The collective ridge formula is probably as follows, indicating as minima the ridge-crests characteristic of the more primitive stages and as maxima the ridge-crests characteristic of the more progressive stages so far as known:

S. insignis-ganesa: $\text{Dp 2}\ \tfrac{2}{2}\ \text{Dp 3}\ \tfrac{5\text{-}6}{6}\ \text{Dp 4}\ \tfrac{7\text{-}7\frac12}{7\text{-}7\frac12\text{-}9}\ \text{M 1}\ \tfrac{7\frac12\text{-}8}{7\frac12\text{-}10}$ $\text{M 2}\ \tfrac{\frac12\text{-}7\text{-}\frac12\text{-}\frac12\text{-}8}{\frac12\text{-}9\text{-}\frac12}\ \text{M 3}\ \tfrac{\frac12\text{-}11\text{-}\frac12}{\frac12\text{-}11\text{-}\frac12\text{-}12\text{-}12\frac12\text{-}13}.$

The survival in India of referred *Stegodon insignis-ganesa* in the same Middle [Upper] Pleistocene levels with the true elephants and Loxodonts, such as *Elephas* (*Hypselephas*) *hysudricus* and *Palæoloxodon namadicus*, is paralleled in the East Indies by the presence of *Stegodon airâwana* in the same Kendeng-Schichten or Trinil horizon [Middle Pleistocene] of Java with *Palæoloxodon hysudrindicus*, which, according to Stremme (1911) and Janensch (1911) is comparable to *Elephas antiquus* (i.e., *P. namadicus*). See note on the fauna of the Kendeng-Schichten below.

In summation, the phylum *Stegodon insignis-ganesa* of India and the phylum *Stegodon airâwana* (=*javanicus*)[1] of Java represent the last surviving Lower and Middle Pleistocene [to Upper Pleistocene] members of the southern forest-browsing Stegodonts. These two Stegodont phyla were geologically contemporaneous with the forest- and plains-browsing Loxodonts, and with the grazing ancestral true elephants, such as *Archidiskodon*.





SECTIONED MOLARS OF STEGODON GANESA AND STEGOLOPHODON LATIDENS

Fig. 757. (Left) Vertical section of lectotype left third superior molar, l.M³, of *Elephas* [=*Stegodon*] *ganesa* Falconer and Cautley, 1846 [1845, Pl. III, fig. 7a], less than one-half natural size. Brit. Mus. M.18489 (erroneously referred by Lydekker, 1886.2, p. 84, to *E. bombifrons*). From Siwalik Hills, India. (Falconer and Cautley, 1846.1, p. 45): "The crown consists of ten principal ridges, with a subordinate 'talon' ridge in front and behind. The anterior seven ridges have their summits worn, the two in front being ground down to the common base of ivory, the tooth having been a considerable time in use." Molar inverted to show natural position.

(Right) Vertical section of two last upper molars of the right side, r.M²⁻³, of *Mastodon* [=*Stegolophodon*] *latidens* Clift, after Falconer and Cautley, 1846 [1845, Pl. III, fig. 8], less than one-half natural size. Same molars as those figured by Clift in 1828, Pl. XXXVII, fig. 1. From Irrawaddy River, Burma. Compare figure 719 above.

Stegodon insignis birmanicus Osborn, 1929

Figures 758, 760

Mingoon, opposite Mandalay, Burma; upper levels of the Irrawaddy Series, Upper Pliocene.[2]

This left ramus (Amer. Mus. 20002), collected by Barnum Brown in 1922, agrees with *Stegodon insignis* in the number of the ridge-crests of the third molar but greatly exceeds this typical Siwalik species in size; the jaw and inferior grinder appear to be one of the largest of the Stegodonts heretofore described (Figs. 758 760); the tooth indicates a higher degree of specialization than the typical *S. insignis-ganesa* and a specialization different from that of *S. orientalis grangeri*; the *S. insignis birmanicus* molar is of gigantic

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[1] [Synonym of *Stegodon airâwana* or *S. trigonocephalus* (see footnote on page 889 below).—Editor.]

[2] [See note on page 824 above regarding the Lower Pleistocene age of the upper levels of the Irrawaddy Series.—Editor.]

size, there are many ridge-crests, far apart, with a medium number of conelets, and considerable cement; the *S. orientalis grangeri* molar is of medium to large size, there are many ridge-crests, approximated, many conelets, and moderate development of cement.

Fig. 758. Type of *Stegodon insignis birmanicus* Osborn, 1929 (Amer. Mus. 20002), a twelve and a half crested third left inferior molar, l.M$_3$, in the same ridge-crest stage as *Stegodon insignis-ganesa*. One-third natural size. From Mingoon, opposite Mandalay, Burma.

Stegodon insignis birmanicus Osborn, 1929. "New Eurasiatic and American Proboscideans." Amer. Mus. Novitates, No. 393, Dec. 24, 1929, pp. 15, 16. Horizon and Locality.—Upper Pliocene [now regarded as of Lower Pleistocene age]. Mingoon, opposite Mandalay, Burma. Type Figure.—*Op. cit.*, 1929.797, p. 16, fig. 16.

Type.—Amer. Mus. 20002, a very large and massive left inferior jaw containing the left third inferior molar, l.M$_3$. The ridge-crests of l.M$_3$, namely, $\frac{}{12\text{-}\frac{1}{2}}$, are the same in number as in *Stegodon insignis*, but the elongation of this inferior molar and the open character of the ridge-crests are quite distinctive from *S. insignis*; the jaw is more massive and the inferior grinding teeth surpass in length measurement those of any other Stegodont type known; the grinders are larger and exhibit fewer conelets. The principal measurements (in millimeters) are as follows:

Total length of third inferior molar, l.M$_3$	
At the crown	333
At the base	362
Total maximum breadth of l.M$_3$	97
Breadth-length index of l.M$_3$	29–27
Length of mandibular ramus from base of l.M$_3$ to tip of symphysis	560
Horizontal thickness of mandibular ramus	204
Height of ramus at symphysis	208

In detail, the entire jaw and posterior grinder are very massive. Of the total of 12-½ ridge-crests, the anterior pair are deeply worn and widely open; the tritolophid and tetartolophid, or second pair, are partly worn, ridge-crests slightly open; this is followed by ridge-crests pentalophid to octalophid (5th to 8th), partly worn; conelets still separate; the ninth to twelfth ridge-crests are entirely unworn. The conelets are few and stout; they vary in number from four to twelve on each ridge-crest. Cement is present all the way back.

Stegodon orientalis grangeri Osborn, 1929

Figures 682, 684, 686, 687, 731, 759–764, 777, 1231, Pl. xx

Upper Pliocene [Lower Pleistocene] of Yenchingkou, near Wanhsien, Province of Szechuan, China.

The subspecies *Stegodon orientalis grangeri*, as shown in figure 687 is more primitive than the type of *S. orientalis*, also from a cave in Szechuan; the ridge-crests are less elevated and wider apart at the base and seem to be even more primitive than those of the *S. insignis* type (Figs. 688, 747); the cranium is much smaller and simpler than that of *S. insignis-ganesa* (Figs. 735, 736) and resembles in its contour rather that of *S. bombifrons* (Figs. 732, 734, 777).

Stegodon orientalis grangeri Osborn, 1929. "New Eurasiatic and American Proboscideans." Amer. Mus. Novitates, No. 393, Dec. 24, 1929, pp. 16 and 17. Type.—Amer. Mus. 18714, a left third superior molar, l.M^3, and right and left third inferior molars, r.M$_3$, l.M$_3$, of the same individual. Horizon and Locality.—Upper Pliocene [now regarded as of Lower Pleistocene age]. Yenchingkou, near Wanhsien, Province of Szechuan, China. Type Figure.—*Op. cit.*, Osborn, 1929.797, p. 16, fig. 16.

Type and Referred Figures.—Aside from the type (Figs. 759, 760, 762) there is very abundant referred material from the same locality, including the complete superior and inferior dentition, Dp 2–Dp 4, M 1–M 3, in various stages of attrition and dental succession, as illustrated in figures 687, 759, 763, 761, 762 of the present Memoir, constituting the most complete material of dental succession known in the fossil Proboscidea.

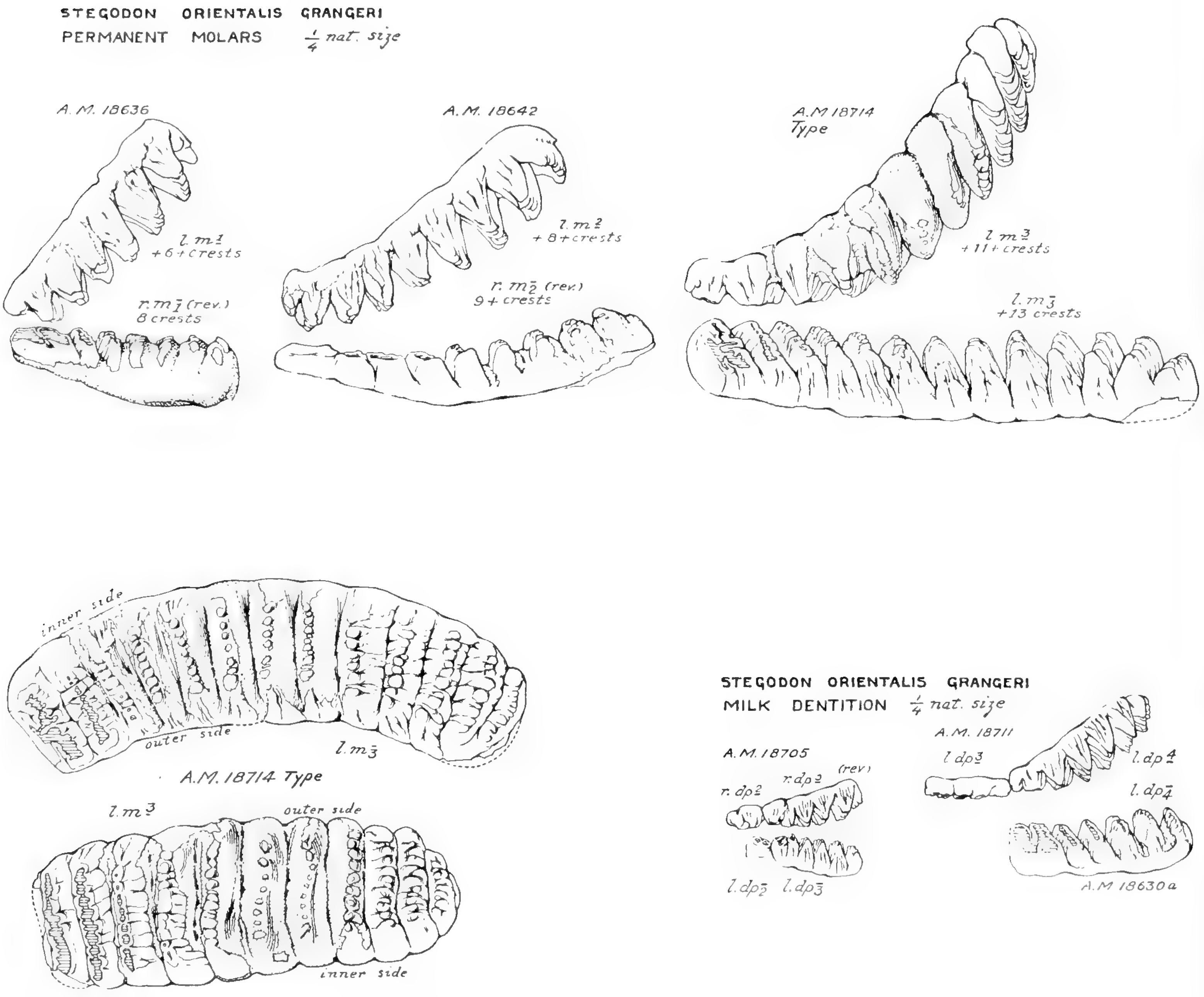


Fig. 759. Type (Amer. Mus. 18714) and referred specimens (Amer. Mus. 18705, 18711, 18630*a*, 18636, 18642) of *Stegodon orientalis grangeri*, part of the collection from Yenchingkou, Province of Szechuan, China, made by Walter Granger during the winter of 1920–1921. All figures one-fourth natural size. (Cf. Figs. 761 and 762 for crown views, giving ridge-crests and conelets.) The specimens bearing number 18642 have been sent to Peking, China, in exchange.

Left lateral aspect of:

R.Dp^2, r.Dp^3 (rev.)—l.Dp$_2$, l.Dp$_3$ (Amer. Mus. 18705)

L.Dp^3, l.Dp^4 (Amer. Mus. 18711), and l.Dp$_4$ (Amer. Mus. 18630*a*)

L.M^1, r.M$_1$ (rev.) (Amer. Mus. 18636)

L.M^2, also r.M$_2$ (rev.) (Amer. Mus. 18642)

L.M^3, l.M$_3$ (Amer. Mus. 18714)—type.

Crown view of:

Type third left inferior molar, l.M$_3$, strongly concavo-convex, outwardly arched. Amer. Mus. 18714.

Type third left superior molar, l.M^3, strongly convex, parallel sides. Amer. Mus. 18714.

Materials of Stegodon orientalis grangeri, Type and Referred.—Collected by Walter Granger in 1920–1921, all from the same pit; estimated specimens:

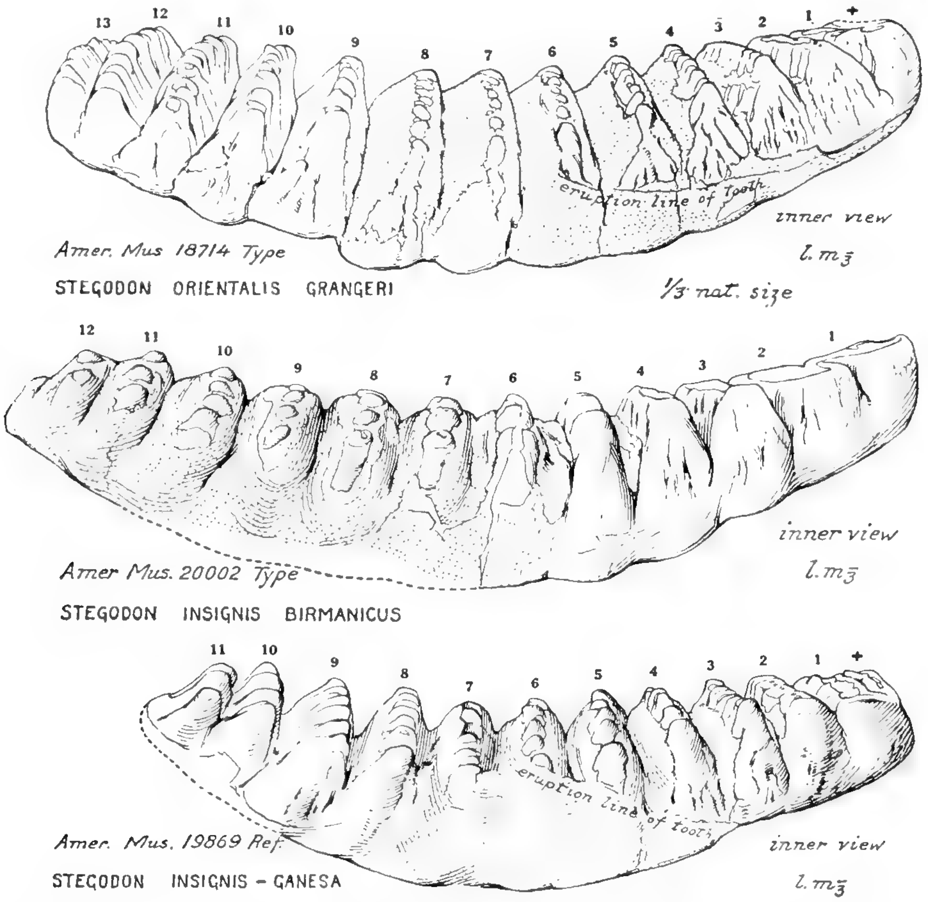
Separate crania, more or less complete	6
Separate crania, more or less fragmentary	7
Right and left mandibular rami and complete inferior jaws	28
Separate superior and inferior grinding teeth in various stages of succession	49
Skeletal bones, very few, not exceeding	3–4

Characters.—An ascending mutation or a subspecific stage regarded as somewhat more primitive than the type of *Stegodon orientalis* Owen (Fig. 769) which is recorded from a cave in the Province of Szechuan, northwest China, and much more progressive than Owen's type of *Stegodon sinensis* which appears to be comparable to *S. bombifrons.* The ridge-crest formula, beautifully shown in figure 759, is as follows:

$$\mathrm{Dp}\,2\,\frac{\frac{1}{2}\text{-}2\text{-}\frac{1}{2}}{2}\ \ \mathrm{Dp}\,3\,\frac{5\frac{1}{2}}{+5\frac{1}{2}}\ \ \mathrm{Dp}\,4\,\frac{\frac{1}{4}\text{-}6\text{-}\frac{1}{2}}{7\frac{1}{2}}\ \ \mathrm{M}\,1\,\frac{\frac{1}{2}\text{-}6\text{-}\frac{1}{2}}{8}\ \ \mathrm{M}\,2\,\frac{\frac{1}{2}\text{-}8\text{-}\frac{1}{2}}{(?)\text{-}9\frac{1}{2}}\ \ \mathrm{M}\,3\,\frac{\frac{1}{2}\text{-}11\text{-}\frac{1}{2}}{\frac{1}{2}\text{-}13}.$$

Comparison with other Chinese Stegodonts.—On closely comparing Owen's types of *Stegodon sinensis* (Figs. 687, 702) and *S. orientalis* (Figs. 687, 769) with the *Stegodon orientalis grangeri* teeth (Figs. 687, 759, 761) collected by Doctor Granger at Yenchingkou, it is certain that we have to do with three distinct specific and subspecific stages broadly distinguished as follows:

Upper Miocene [Pliocene] stage.	Lower Pleistocene stage.	(?) Lower Pleistocene stage.
Owen's type of *Stegodon sinensis*	Osborn's type of *Stegodon orientalis grangeri*	Owen's type of *Stegodon orientalis*
Brachyodont.	Subhypsodont (first stage).	Subhypsodont (second stage).
Lophs compressed, far apart.	Lophs more compressed, more elevated.	Lophs still more compressed, still more elevated.
Compare *Stegodon bombifrons.*	Compare the typical *Stegodon orientalis.*	Compare the referred *Stegodon orientalis* and *S. airâwana.*



Comparison of Stegodon insignis-ganesa, S. insignis birmanicus, and S. orientalis grangeri

Fig. 760. Left third inferior molars, to a one-third scale, from the internal aspect, showing the eruption line of the grinder and exposing the six anterior ridge-crests in *Stegodon orientalis grangeri* (upper) and *S. insignis ganesa* (lower). After Osborn, 1929.797, p. 16, fig. 16.

Stegodon orientalis grangeri, type (Amer. Mus. 18714). Large size with 13+ ridge-crests of which 6+ anterior were erupted while 7–13 were buried in the jaw.

Stegodon insignis birmanicus, type (Amer. Mus. 20002), with 5–6 ridge-crests erupted, 6–12 buried in the jaw and encased in cement (dotted).

Stegodon insignis-ganesa ref. (Amer. Mus. 19869), with +1–6 ridge-crests erupted, 7–11 buried in the jaw, mostly lacking cement.

This comparative figure illustrates the gigantic size attained; the largest (*S. insignis birmanicus*) slightly exceeds in length the corresponding grinder of *S. orientalis grangeri.*

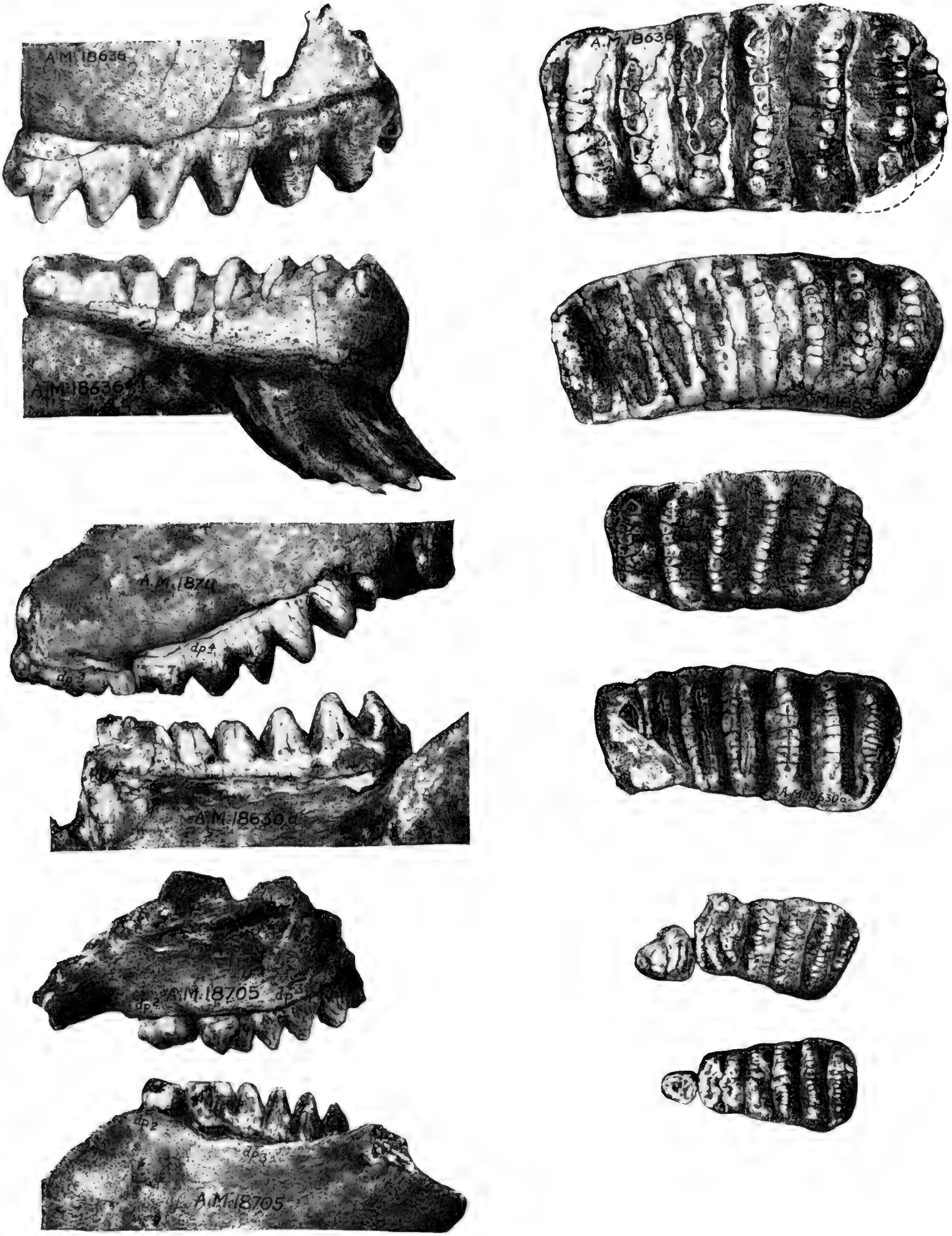


Fig. 761. Superior and inferior second, third, and fourth premolars and first molar; (Dp 2—M 1) of *Stegodon orientalis grangeri* (Amer. Mus. 18636, 18711, 18630*a*, 18705), side and crown views, one-half natural size (cf. Fig. 759).

(Upper pair). First superior and inferior molars (Amer. Mus. 18636), l.M^1 with +6+ ridge-crests, conelets 10 maximum, r.M$_1$ (rev.) with 8 ridge-crests, conelets 9.

(Middle pair). Fourth superior and inferior deciduous premolars, l.Dp^4 (Amer. Mus. 18711) with $\frac{3}{4}$-6 $\frac{1}{2}$ ridge-crests, conelets 12–13, l.Dp$_4$ (Amer. Mus. 18630*a*) with 7-$\frac{1}{3}$ ridge-crests, conelets 12 maximum.

(Lower pair). Second and third superior and inferior deciduous premolars (Amer. Mus. 18705), r.Dp^2 (rev.) with +3+ ridge-crests, r. Dp^3 (rev.) with 6+ ridge-crests, conelets 15 maximum, l.Dp$_2$ with 2 ridge-crests, l.Dp$_3$ with 6+ ridge-crests, conelets 16 maximum.

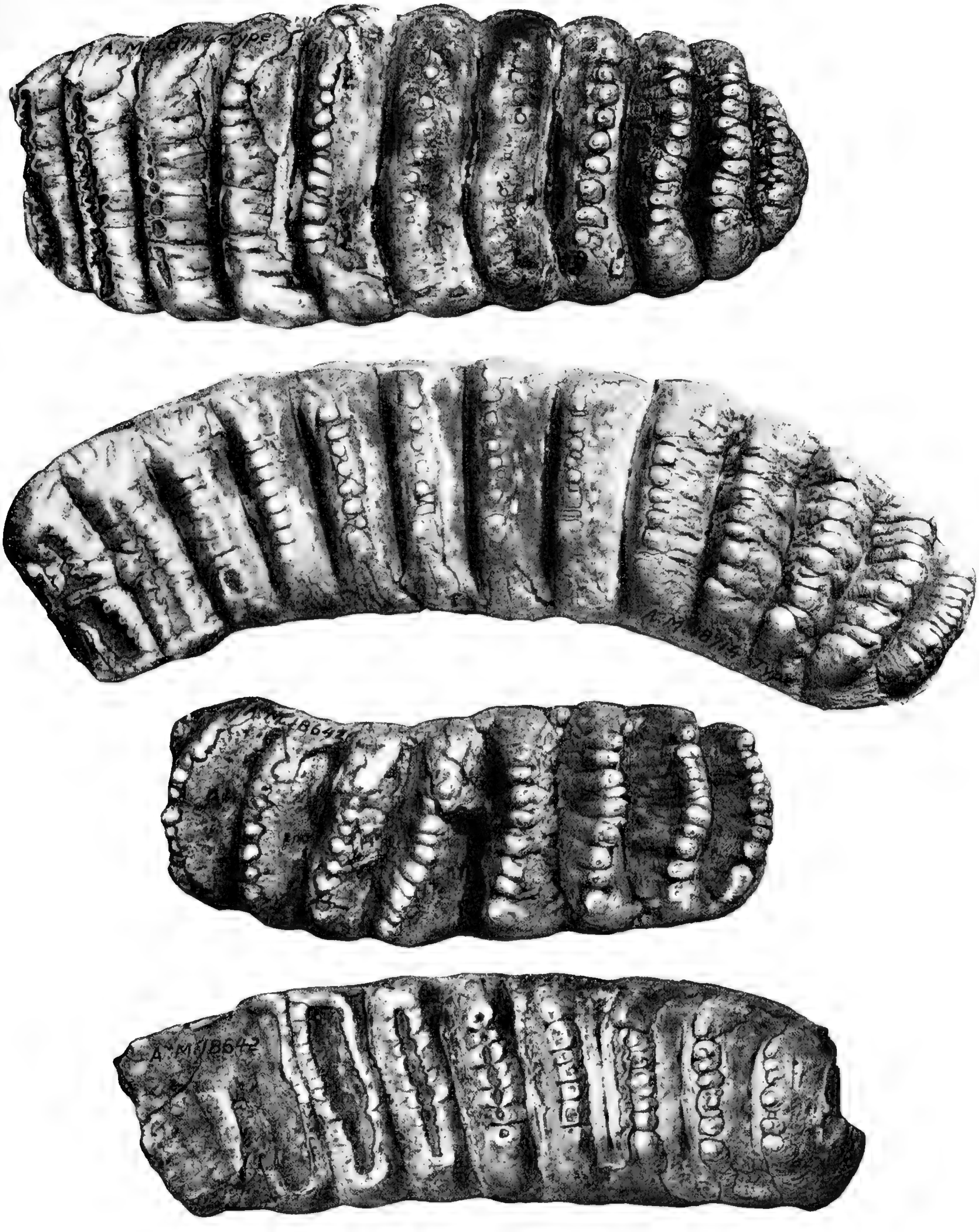


Fig. 762. Type and referred superior and inferior molars of *Stegodon orientalis grangeri*. Crown views (cf. Fig. 759). After retouched photographs, one-half natural size.

(Upper pair) Type (Amer. Mus. 18714), left third superior molar, l.M^3, with +11½ ridge-crests. Left third inferior molar, l.M$_3$, with ½–13 ridge-crests; inner side strongly convex, outer side strongly concave, in contrast to the parallel sides of the upper molar.

(Lower pair) Amer. Mus. 18642. Left second superior molar, l.M^2, with +8+ ridge-crests. Right second inferior molar, r.M$_2$ (rev.) with 9+ ridge-crests. These molars have been sent to Peking, China, in exchange.

CRANIAL CHARACTERS OF STEGODON ORIENTALIS GRANGERI

(Figs. 759, 761, 763, 777)

The *infantile* cranium of *Stegodon orientalis grangeri* (Amer. Mus. 18638, 18702), as represented in the composition drawing (Fig. 763), exhibits the small deciduous superior incisors and the deciduous premolars, Dp 2–4 (for crown views of these deciduous premolars, compare Fig. 761); the rounded profile, of subtriangular form, should be compared with the infantile cranium of *Mastodon acutidens* (Fig. 131) and that of *Elephas indicus* (Fig. 799).

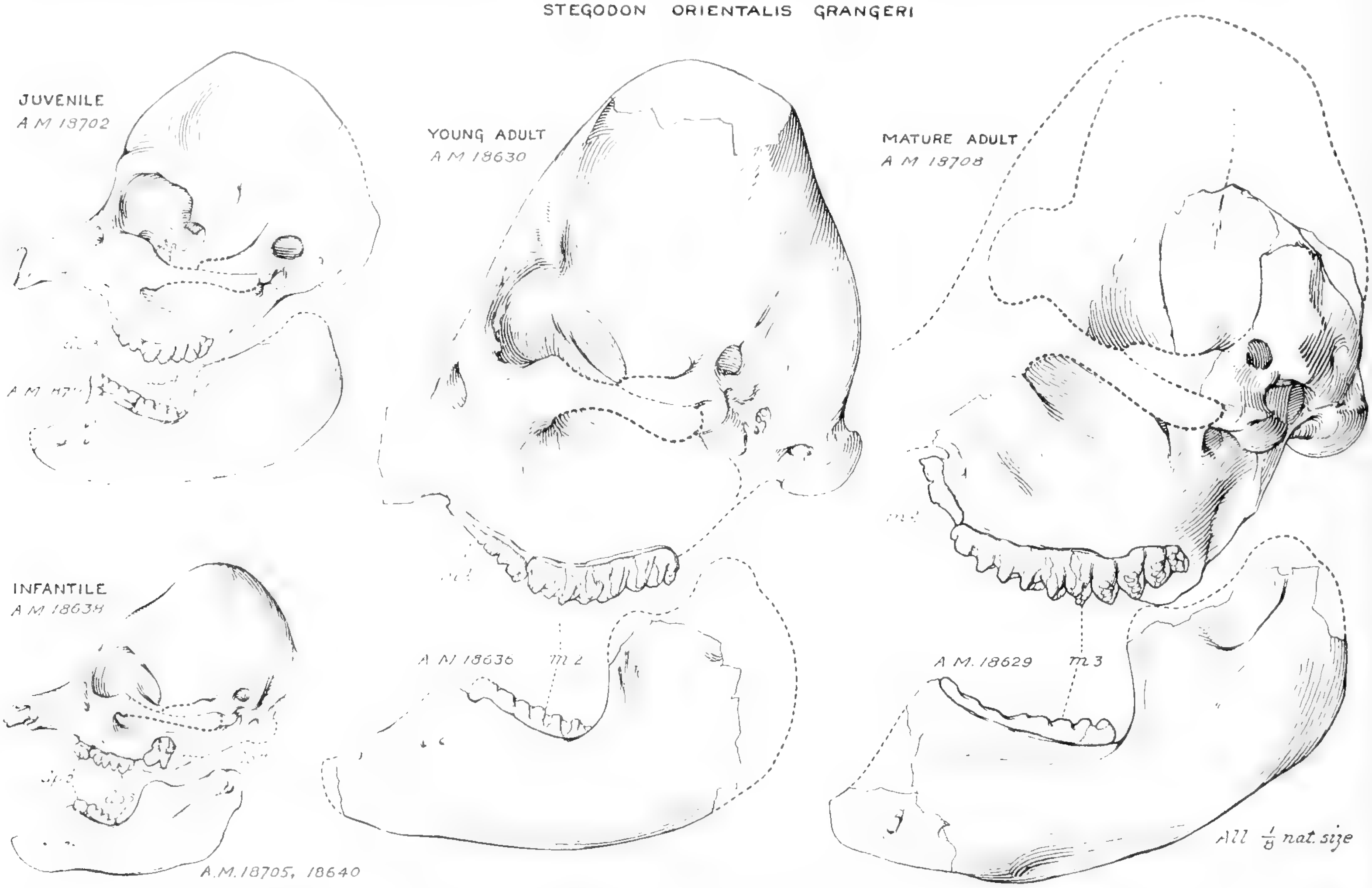


Fig. 763. Infantile, juvenile, young adult, mature adult crania showing eruption of Dp^3—M^3, Dp_3—M_3. Yenchingkou, Province of Szechuan, China.
Infantile cranium (Amer. Mus. 18638) showing succession of Dp^2—Dp^4, also Di^2, together with jaw (Amer. Mus. 18640) belonging to this skull, showing Dp_2—Dp_4.
Juvenile cranium (Amer. Mus. 18702), jaw (Amer. Mus. 18711), showing eruption of Dp3, Dp4.
Young adult cranium (Amer. Mus. 18630) showing M^1 and M^2. Jaw (Amer. Mus. 18636) with M_2 *in situ*, sent to British Museum.
Mature adult cranium (Amer. Mus. 18708), jaw (Amer. Mus. 18629—sent abroad in exchange), showing M^2, M^3, and M_3 *in situ*.

The *juvenile* cranium (Amer. Mus. 18702, skull, 18711, jaw—a composition drawing) has lost the deciduous incisors, also Dp 2, but retains the functional Dp 3–Dp 4 (cf. Figs. 759 and 761).

The *young adult* cranium (Amer. Mus. 18630, skull, 18636, jaw) exhibits the rounded and greatly elevated dome of the brain case; all the deciduous teeth, Di^2, Dp 2–4, have disappeared and the grinding function is now assumed by the first and second true molars, M 1–M 2 (cf. Figs. 761, 763). It would appear that the grinders M^{1-2}, with ridge-crests 6 and 8 respectively, are opposed to lower grinders, M_{1-2}, with ridge-crests 8 and 9 respectively (cf. Figs. 759, 762 lower); these ridge-crests, partly bathed in cement, of moderate hypsodonty, exhibit the characteristic *convex* coronal curvature of the upper ridge-crests, the *concave* coronal curvature of the lower ridge-crests, a feature much more strongly marked in the third molars (Fig. 759). In the *mature adult* cranium (Amer. Mus. 18708, skull, 18629 jaw) the second superior molar, M^2, is disappearing, while the third superior and inferior molars, M^3, M_3, are fully functional, their reciprocal convexo-concave relations being beautifully shown in figure 763 (right). The upper portion of this mature adult cranium is fractured, leaving the exact profile contour in doubt.

The third superior and inferior molars of this subspecies grandly represented in the *type* specimen (Amer. Mus. 18714) seen in both lateral and crown views in figures 759 and 762, add a great deal to our knowledge of the Stegodont dentition and show very marked mechanical contrasts between the superior and inferior grinders as follows:

THIRD SUPERIOR MOLARS

Lateral profile strongly convex.

Posterior ridge-plates elongated, partly or wholly bathed in cement.

Sides of crown parallel.

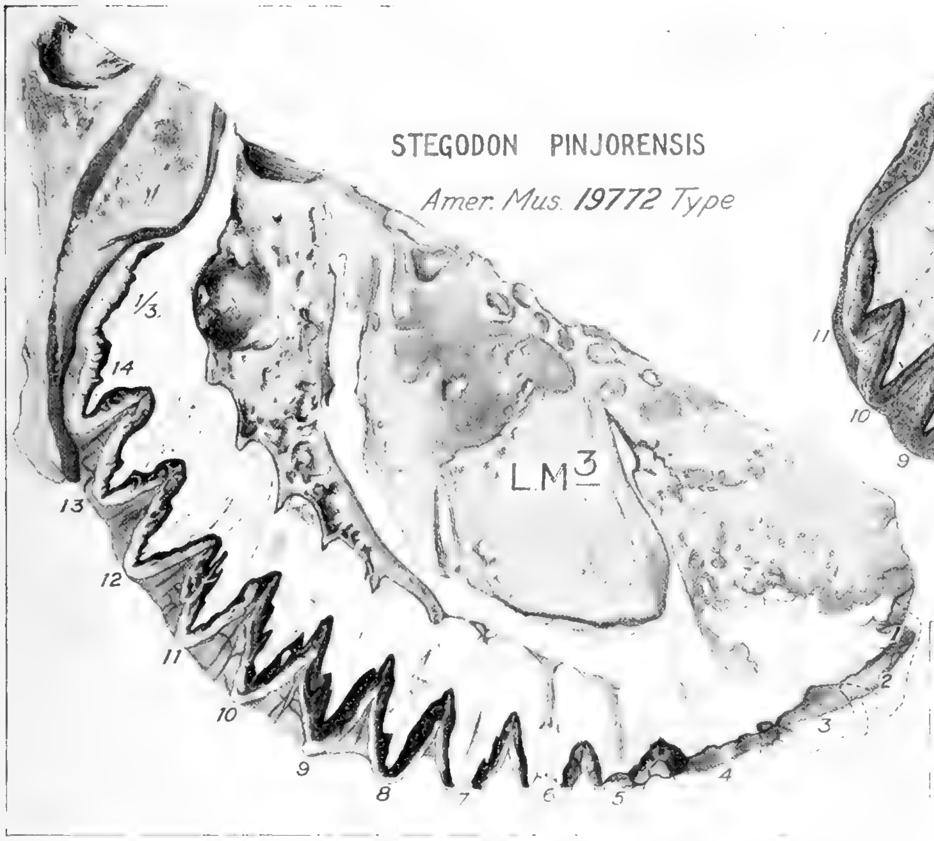
THIRD INFERIOR MOLARS

Lateral profile horizontal.

Anterior and posterior ridge-plates of uniform height; cement chiefly in median plates.

Sides of crown strongly arched, *convex* inner side, *concave* outer side.

A very careful study of these four ontogenetic stages of the cranium, namely, infantile, juvenile, young adult, and mature adult, reveals resemblances and contrasts with the *Mastodon* and *Elephas* crania which will probably prove of phyletic or generic value. Similarly, the remarkable ridge-crest succession, the mechanical warping of the superior and inferior grinders, the gradual increase in height (hypsodonty) of the superior ridge-crests from Dp 2–M 3, indicate that the *highest and most progressive ridge-crests* are reserved for the extremely adult stages in which the posterior ridge-crests of the eleven and a half crested third superior molar grind against the less hypsodont ridge-crests of the thirteen crested third inferior molar.



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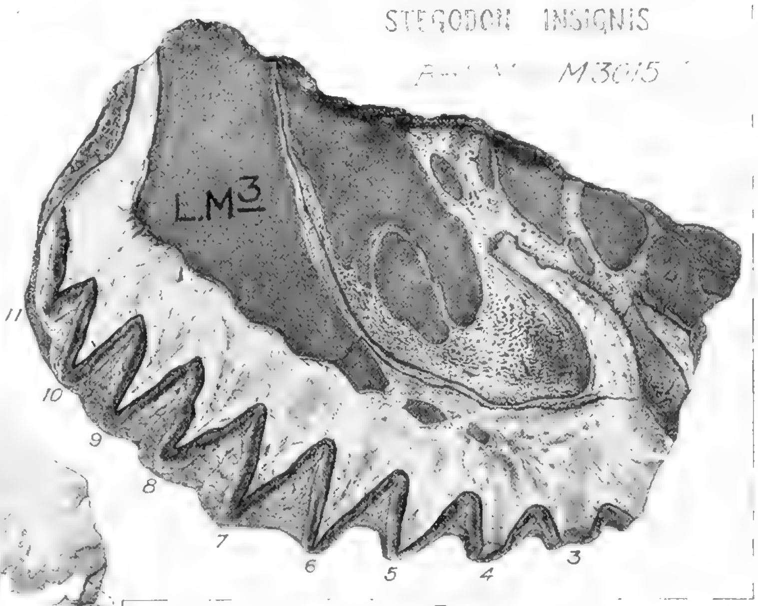

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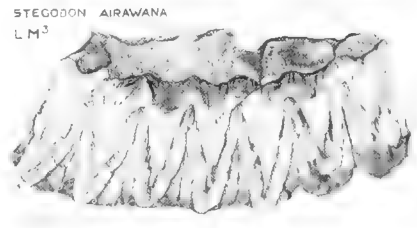

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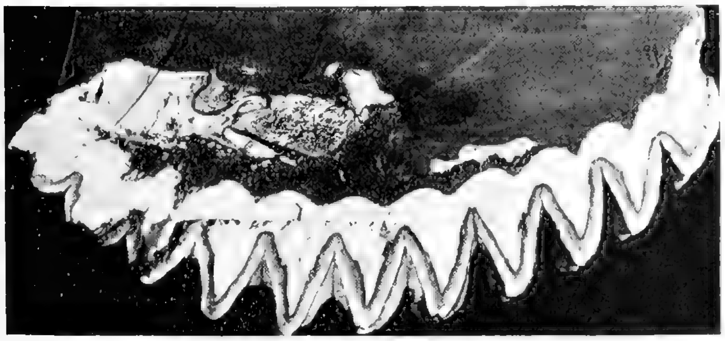


D

Fig. 764. Comparative sections of third left superior molars of Stegodonts of India, Java, and China, all to a one-third scale.

A, *Stegodon pinjorensis* Osborn, type. A 14+ ridge-crested l.M³, from near Siswan, India. Amer. Mus. 19772.

B, *Stegodon insignis* Falconer and Cautley, lectotype. A 11 ridge-crested l.M³, from the Siwalik Hills, India. After Falconer and Cautley, 1846 [1845, Pl. II, fig. 6a]. Brit. Mus. M.3015.

C, *Stegodon airâwana* Martin, ref. Portion of an l.M³ of the Middle Pleistocene of Trinil, Java, exhibiting 7 of the 12–14 ridge-crests; much more recent in structure than the molars of *Stegodon insignis* of the Lower Pleistocene. This tooth was presented to the American Museum by the Geological-Palaeontological Institute and Museum of the University of Berlin, Germany, through the courtesy of Geheimrat Pompeckj and Doctor Dietrich. Amer. Mus. 22636.

D, *Stegodon orientalis grangeri* Osborn, type. An l.M³ with +11 ½ ridge-crests, from near Wanhsien, Province of Szechuan, China. Amer. Mus. 18714.

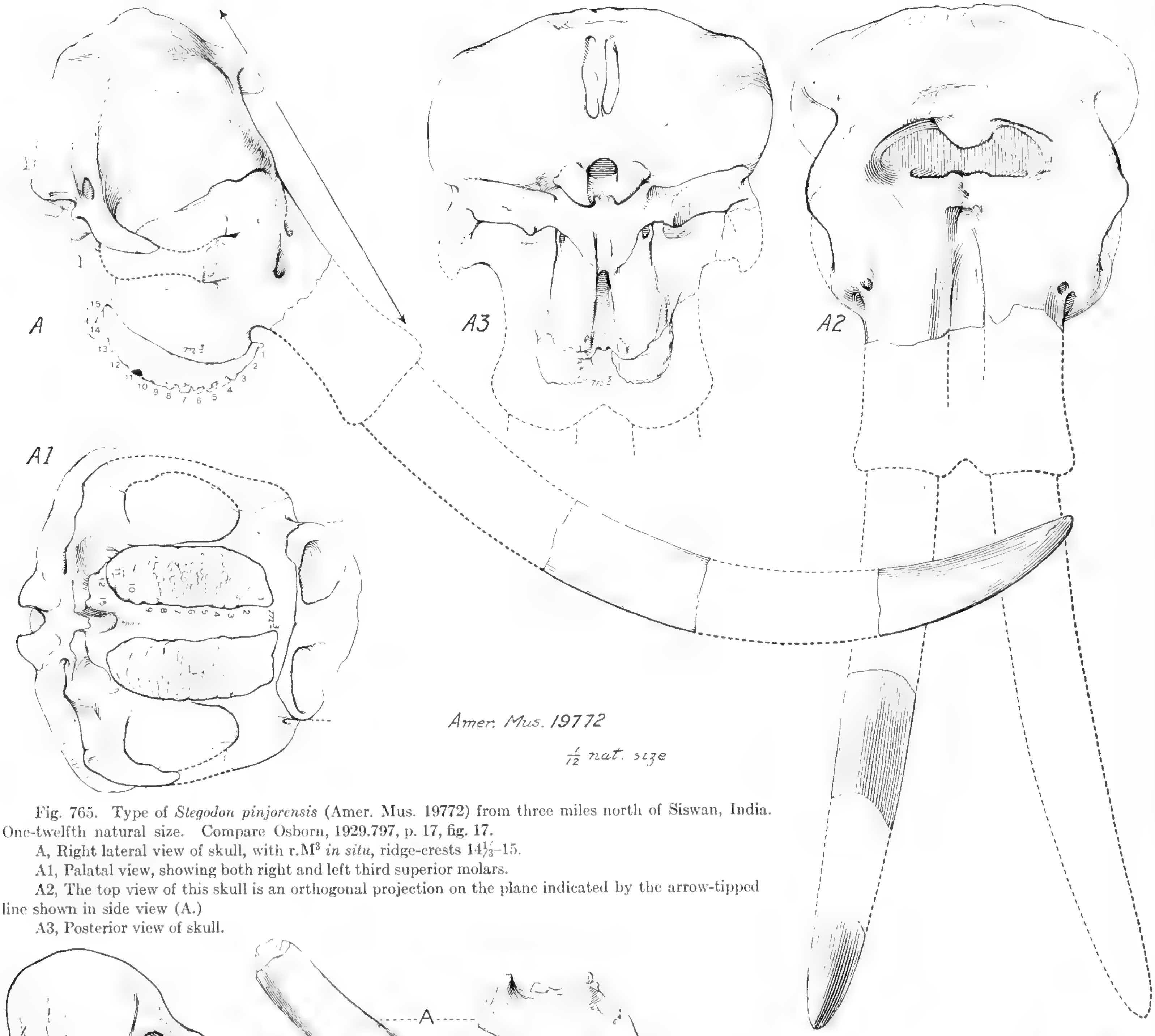


Fig. 765. Type of *Stegodon pinjorensis* (Amer. Mus. 19772) from three miles north of Siswan, India. One-twelfth natural size. Compare Osborn, 1929.797, p. 17, fig. 17.

A, Right lateral view of skull, with r.M^3 *in situ*, ridge-crests 14⅓–15.

A1, Palatal view, showing both right and left third superior molars.

A2, The top view of this skull is an orthogonal projection on the plane indicated by the arrow-tipped line shown in side view (A.)

A3, Posterior view of skull.

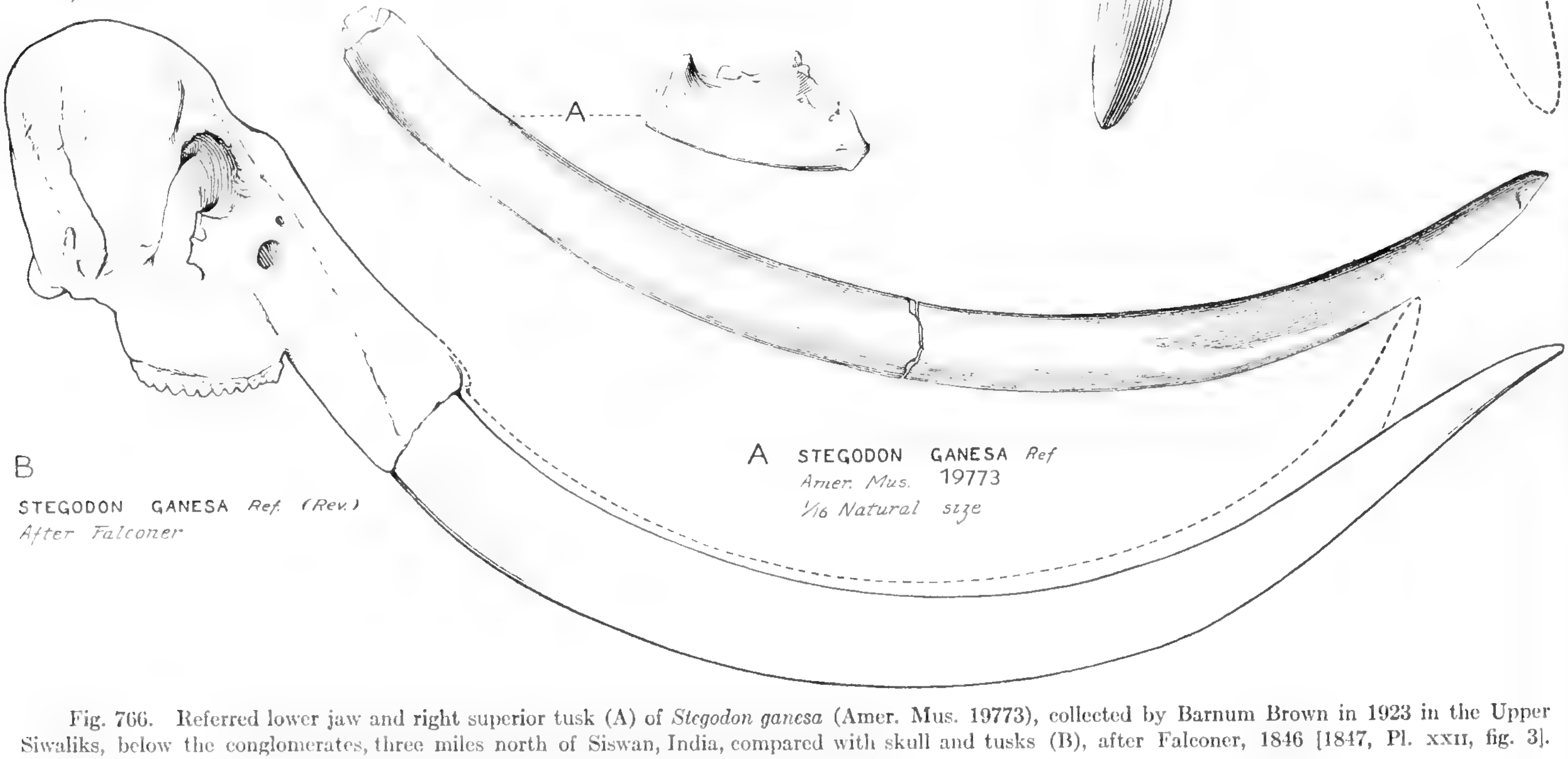


Fig. 766. Referred lower jaw and right superior tusk (A) of *Stegodon ganesa* (Amer. Mus. 19773), collected by Barnum Brown in 1923 in the Upper Siwaliks, below the conglomerates, three miles north of Siswan, India, compared with skull and tusks (B), after Falconer, 1846 [1847, Pl. XXII, fig. 3]. Original in British Museum (Brit. Mus. M.3008). Both figures one-sixteenth natural size.

Stegodon pinjorensis Osborn, 1929

Figures 711, 731, 764, 765, 767, 768, 777, 817, 1217, Pl. xx

"Three miles north of Siswan, India." Upper levels of the Pinjor horizon, Lower Pleistocene.

Stegodon pinjorensis Osborn, 1929. "New Eurasiatic and American Proboscideans." Amer. Mus. Novitates, No. 393, p. 18. TYPE.—"Amer. Mus. 19772. A male cranium, rostrum wanting; portions of right inferior tusk preserved." HORIZON AND LOCALITY.—"Recorded by Barnum Brown as follows: 'Skull. Just below Conglomerate beds, Upper Siwaliks, three miles north of Siswan, India.' This progressive cranium does not belong in the Pinjor (Upper Pliocene) horizon, as the specific name *pinjorensis* suggests, but was probably deposited from the overlying Boulder Conglomerate beds of Lower Pleistocene age." TYPE FIGURE.—Osborn, 1929.797, p. 17, fig. 17.

TYPE DESCRIPTION.—"Superior grinding teeth distinguished from those of *Stegodon insignis-ganesa* by their superior size, much more numerous ridge-crests, progressive hypsodonty; the comparative ridge formulæ of M 3 are as follows:

Stegodon pinjorensis: M 3 $\frac{14\frac{1}{2}\text{-}15}{}$
Stegodon insignis birmanicus: M 3 $\frac{}{12\text{-}\frac{1}{2}}$
Stegodon insignis-ganesa: M 3 $\frac{\frac{1}{2}\text{-}11\text{-}\frac{1}{2}}{12\frac{1}{2}\text{-}13}$

This type male cranium resembles that of the male type of *Stegodon ganesa* Falc., namely, with small rounded parieto-occipital crest, lofty and greatly abbreviated frontonasal surface, anterior nares correspondingly elevated, grinding surface of the large molars very strongly arched, but the cranium is relatively more depressed or bathycephalic than in *S. ganesa*."

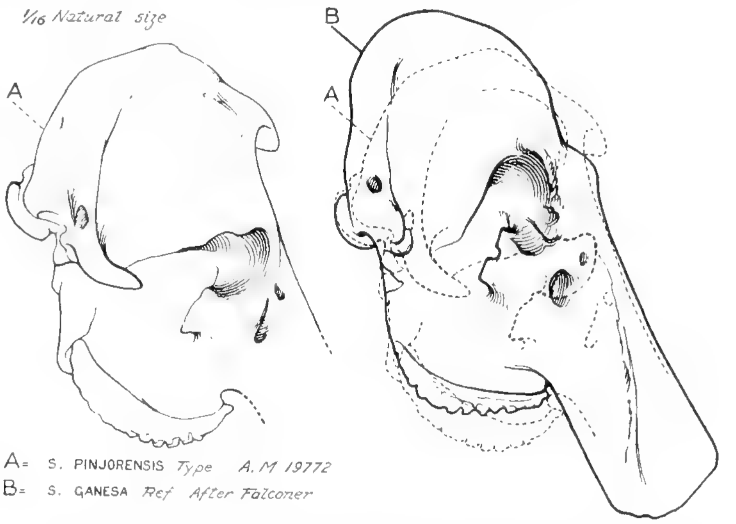


Fig. 767. Type skull (Amer. Mus. 19772) of *Stegodon pinjorensis* (A), also skull of same individual (A) superimposed (dotted lines) on referred skull of *S. ganesa*, after Falconer (B). One-sixteenth natural size.

Observe the extreme bathycephaly in the skull of *Stegodon ganesa* in comparison with the more typical Stegodont form, as exemplified by the skull of *S. pinjorensis*.

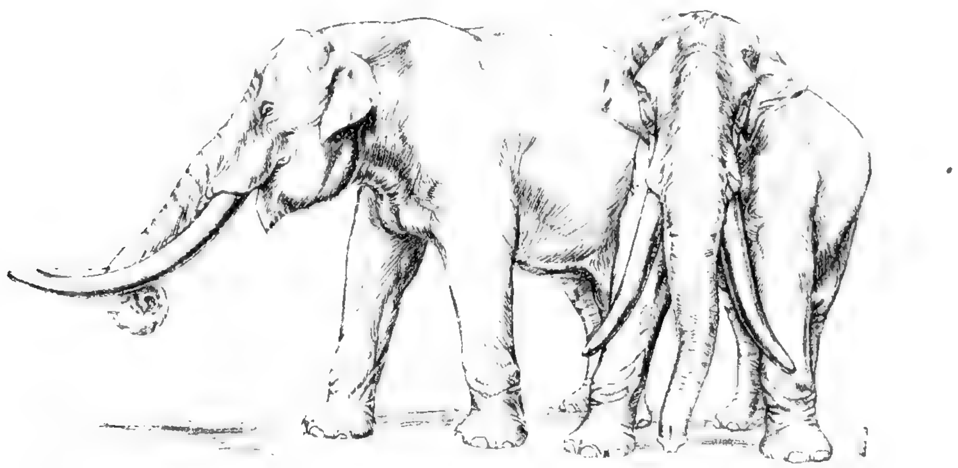


Fig. 768. Front view of *Stegodon pinjorensis* before present arrangement of the tusks, which now are regarded as possibly turning inward, as in new restoration of *Stegodon ganesa* (see Fig. 733, p. 857 above); otherwise head true to present proportions. Forelimbs entirely conjectural, drawn in proportion to size of head. Ungues 5 and 5. Restoration by Margret Flinsch, May, 1930. One-fiftieth natural size.

Stegodon orientalis Owen, 1870

Figure 687, 703, 769, 770

Szechuan, northwest China, near the city of Chungkingfoo. Probably Lower Pleistocene. Swinhoe Collection of 1870.

The imperfectly known *Stegodon orientalis*, as shown in comparison of figures 687, 688, 697, and 769, is apparently more progressive, with more elevated ridge-crests, than the type of *S. insignis* (Fig. 697); the ridge-crests (Fig. 769) are more acute and more compressed at the base, and the summits are more closely approximated; with numerous conelets and strong layers of cement in the valleys. It is, however, impossible clearly to define and separate this species until further material is found in the type locality. It is somewhat more progressive than *S. orientalis grangeri*.

This species described by Owen from an imperfect type figure (Fig. 769) is regarded by Lydekker (1886.2, p. 97) as a synonym of *Stegodon insignis* (see citation below). Koken (1885) also regarded *S. orientalis* as a synonym of *S. insignis*, Schlosser (1903) agreeing with Koken. In Osborn's opinion, the imperfect character of the type molar (Fig. 769) and associated milk molar renders it difficult to determine whether these specimens are in the *Stegodon insignis* stage; in both specimens the lophs are elevated. From another cave locality, 140 miles distant, near Yenchingkou, comes the superb material collected by Granger, which proves to be somewhat more primitive than Owen's type of *Stegodon orientalis* and is described as *Stegodon orientalis grangeri* (see p. 875 above).

Fig. 769. Type of *Stegodon orientalis* Owen, 1870, from a cavern in Szechuan, northwest China. After Owen, 1870, Pl. XXVIII, figs. 1–4. Original in the British Museum (41926–7). (*Op. cit.*, p. 433, fig. 1): "Portion of true molar, grinding-surface." Fig. 2. Same, "side view." Fig. 3. "Hind end of milk-molar, *d* 3, grinding-surface." Fig. 4. Same, "side view."

Locality.—(*Op. cit.*, p. 421): "These fragments form part of the series of teeth obtained by Mr. Swinhoe, and said to be 'from a cave, near the city of Chung-king-foo, in the province of Sze-chuen.' The condition of the fragments agrees with the statement, viz. that they were from a cavern. . . . [p. 434] Mr. H. Woodward stated that Mr. Swinhoe had himself obtained a series of these fossils from a cave many miles inland—he believed, on the course of the Yang-tse-kiang."

Owen's type description is in part as follows:

Stegodon orientalis Owen, 1870. "On Fossil Remains of Mammals found in China." Quart. Journ. Geol. Soc. London, Vol. XXVI, Pt. 1, p. 421. Type.—Molar fragments (Brit. Mus. 41926–7). Horizon and Locality.—(*Op. cit.*, p. 421): ". . . obtained by Mr. Swinhoe, and said to be 'from a cave, near the city of Chung-king-foo, in the province of Sze-chuen.'" Type Figure.—*Op. cit.*, Pl. XXVIII, figs. 1–4.

Type Description.—(*Op. cit.*, p. 421): "The dentine retains its original white colour, . . . the enamel also has its recent pearly tint; a thick mass of cement appears to have been retained in the intervals of the coronal ridges. One of these ridges, with the contiguous halves of two others, form a molar two inches nine lines in breadth (Pl. XXVIII. figs. 1 & 2); a portion of a posterior ridge with a low basal heel, from the same, or the same-sized tooth, and the last two ridges, with a terminal half ridge or talon, of a milk-molar, one inch and a half in breadth (ib. figs. 3 & 4), represent the present species. . . . The condition of the fragments agrees with the statement, viz. that they were from a cavern. . . . The ridge (ib. fig. 1) *a a* runs straight, or nearly so, across the tooth; the entire ridge is cleft at the summit into about a dozen mamillæ by as many vertical grooves; the dentine rises into the base of each mamilla. The enamel (*c*) averages two lines in thickness."

"From the above-defined characters it is plain that we have here, also, parts of a 'transitional Mastodon,' in other words, a species of *Stegodon*, Fr. In the straight, or nearly straight, direction of the coronal ridges, and the absence of any trace of mid cleft, these molar fragments more resemble the teeth of *Stegodon Cliftii*, *St. insignis*, and *St. ganesa* of Falconer than does the *St. sinensis*; and in the apparent quantity of coronal cement (ib. fig. 2 *c*) as well as in the evidence of a hinder talon (ib. fig. 3 *t*), they are more like *St. insignis* than *St. Cliftii*. Yet the two hinder ridges, with the terminal talon of the tooth (ib. figs. 3 & 4), which, in breadth, corresponds with the second upper deciduous molar of *St. insignis* and *St. sinensis*, clearly differ from both. The last two ridges run straighter across, are of the same extent, and are divided by more numerous vertical grooves into smaller and correspondingly numerous apical mamillæ. The second of these ridges is cleft in the middle. From the alleged conditions of discovery, and the little-altered condition of the above-described portions of proboscidian molars, one would be led to deem them to be of as comparatively recent geological age as our ordinary British Cave-fossils."

LYDEKKER'S NOTES OF 1886 ON STEGODON ORIENTALIS

"Catalogue of the Fossil Mammalia in the British Museum (Natural History)," Pt. IV, 1886, p. 97

Lydekker (1886.2, p. 97) treated this species as follows: "[Brit. Mus.] 41926–7. The last two ridges and talon of an unworn fourth lower milk-molar and portions of two other cheek-teeth, provisionally referred to the present species. These specimens, which were obtained from a cavern in Sechuen, northwest China, are the types of Owen's *Elephas* (*Stegodon*) *orientalis*, and are described and figured by him under that name in the Quart. Journ. Geol. Soc. vol. xxvi. pl. xxviii. figs. 1–4. They show, however, no characters by which they can be distinguished from the teeth of the present species [i.e., *Stegodon insignis*], as the writer has already observed in the 'Palæontologia Indica,' ser. 10, vol. i. p. 269. *Purchased from R. Swinhoe, Esq.*, 1870."

Stegodon airâwana Martin, 1890

Figures 686, 688, 707, 731, 764, 771, 773, 774, 777, 779, Pl. xx

Kendeng-Schichten, *Pithecanthropus erectus* zone, Middle(?) Pleistocene, Alas-Tuwa, Trinil, Java.

This is the most progressive Stegodont known, surpassing *Stegodon orientalis* and greatly surpassing *S. insignis-ganesa* in the elevation (hypsodonty) and number of the ridge-crests. As shown in figures 687 and 688, the fourteen to fifteen ridge-crests of the third right inferior molar, r.M_3, are almost columnar in side view and much more elevated than in *S. orientalis* (Figs. 687, 779, and 769). In front view the cranium (Figs. 773, 777) resembles that of *S. trigonocephalus* (Fig. 776) and differs widely from that of *S. insignis-ganesa* or *S. bombifrons*. This is a dwarfed insular form, very progressive in molar structure.

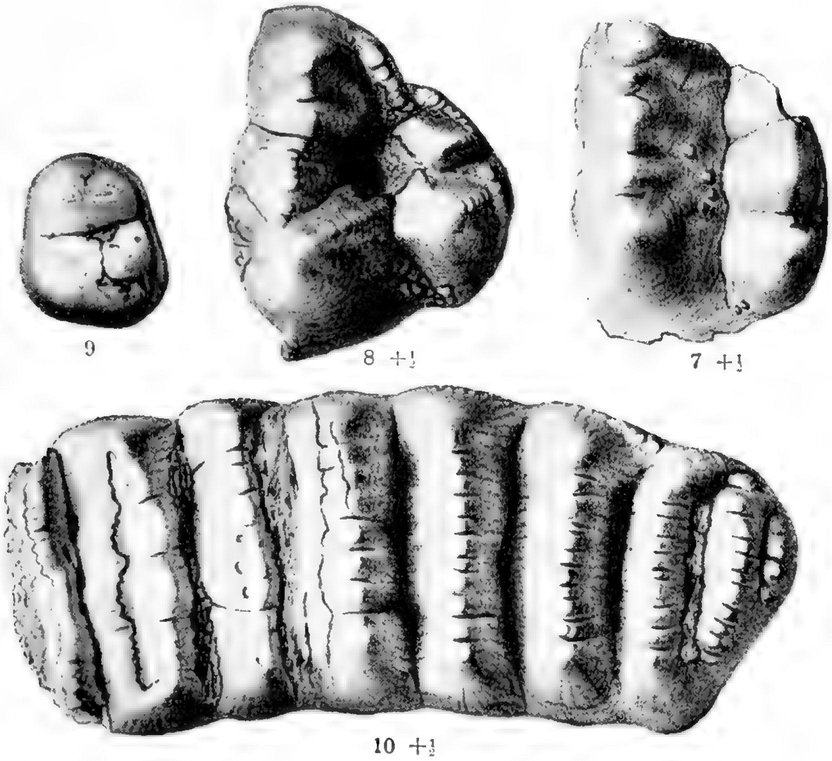


Fig. 770. Referred Stegodon insignis(?) = orientalis(?) and Type of Serridentinus lydekkeri. After Schlosser, 1903, Taf. xiv, Figs. 7–10

Fig. 7. Tooth referred by Schlosser to *Mastodon* aff. *latidens* Clift, from the rothe Thone = Schansi; fig. 10, a left inferior molar, ?M_3, from ?Fokien, referred by Schlosser to *Stegodon insignis*.

Fig. 8. Type of *Mastodon* [= *Serridentinus*] *lydekkeri* Schlosser, from the röthliche Sande = Tientsin, Honan, north China, presumably a left M^3 (cast Amer. Mus. 10374); fig. 9, supposed inferior premolar referred by Schlosser to *Mastodon lydekkeri* [= *Serridentinus lydekkeri* of the present Memoir].

History.—This species was named by Martin in 1890 and regarded by Janensch (compare Janensch, 1911, p. 171, fig. 12, also Taf. xxiii, fig. 3) as differing in skull structure both from *Stegodon insignis* and *S. ganesa* while similar in jaw structure. The assigned ridge formula is: $\mathrm{Dp}\ 3\frac{5}{}\ \mathrm{Dp}\ 4\frac{7}{}\ \mathrm{M}\ 1\frac{7}{}\ \mathrm{M}\ 2\frac{9}{}\ \mathrm{M}\ 3\frac{11\text{-}12}{13}$. Dubois in his Trinil-Fauna (1908, p. 1256) observes that this species of *Stegodon* is highly characteristic of the Trinil *Pithecanthropus* beds, also that the third lower molar rises to fourteen ridges, i.e., $\mathrm{M}\ 3\ \overline{14}$, and is more progressive than that of *insignis.* This would tend to place *Pithecanthropus erectus* as of Middle Pleistocene age. Dietrich (letter, March 10, 1924, and notes), as cited above in this Memoir (p. 813), on morphological grounds, regards this Javanese species as more recent than any of the known continental species of Stegodonts.

Stegodon Airâwana Martin, 1890. "Ueber Neue Stegodon-Reste Aus Java," Verh. Kon. Akad. Wetensch. Afdeel Natuurk., Amsterdam, Deel XXVIII, p. 4. TYPE.—Incomplete mandible with third molar of either side in place. HORIZON AND LOCALITY.—Kendeng-Schichten, *Pithecanthropus erectus* zone, Middle(?) Pleistocene, Alas-Tuwa, Trinil, Java. TYPE FIGURE.—Martin, 1890, Tab. I, figs. 1 and 2 (mandible), also Tab. II, figs. 3 and 4 (type M_3).

TYPE DESCRIPTION.—(*Op. cit.*, p. 4): "Nur von Java in einer unvollständigen Mandibel und darin steckenden Molaren bekannt. Letztere mit 9 Jochen und 2 Talons. Durch den mastodonartigen Charakter der Kronenspalte und die geringen Cementmengen schliesst sich die Art an *St. Cliftii* und *St. bombifrons*, durch die höheren Joche an *St. insignis* und *St. ganesa* an; sie nimmt somit, gleich dem ebenfalls auf Java beschränkten *St. trigonocephalus* [Footnote: 'Vgl. Sammlgn. Ser. I, Bd. 4, pag. 102.'], eine Mittelstellung zwischen beiden Gruppen ein."

Janensch, 1911 ("Die Proboscidier-Schädel der Trinil-Expeditions-Sammlung") concludes his detailed description of the skull, dentition, and skeleton of *Stegodon airâwana* with the statement (p. 192) that while *Stegodon insignis* and *S. ganesa* are closest in their dentition to *S. airâwana*, yet in certain details they are somewhat more primitive; also in skull structure *S. airâwana* differs both from *S. insignis* and *S. ganesa*, while in jaw structure the three species are similar.

Stremme ("Die Säugetiere mit Ausnahme der Proboscidier," 1911, p. 143) observes: "*Stegodon Airâwana* Mart. ist nach Janensch mit *Stegodon ganesa* und *Stegodon insignis* am nächsten verwandt, die im indischen Pliocän und Pleistocän vorkommen." Janensch (1911, p. 192) determines the Trinil *Stegodon* as *Stegodon airâwana* Martin, and observes regarding the ridge formula (*op. cit.*, p. 187): "Die Jochformel [Footnote: 'In dieser Formel bedeutet x den Talon.'] lautet, soweit bis jetzt bekannt:

$$\mathrm{Mm}^{?5\times\ \times7\times}\ \mathrm{M}^{\times7\times\cdot9\times\cdot\frac{11\text{-}12\times}{\times13\times}}.$$

Dubois gibt neuerdings (Trinil-Fauna S. 1256) an, dass die Zahl der Joche der letzten unteren Molaren bei dem *Stegodon* von Trinil bis zu wenigstens 14 gehe, doch ist aus seiner Angabe nicht zu ersehen, ob er die Talons etwa mitzählt." He also observes that this species of *Stegodon* is highly characteristic of the Trinil *Pithecanthropus* beds. The other Javan species, *Stegodon trigonocephalus* Martin, does not occur at Trinil.

Osborn, 1922: Our knowledge of this very progressive Javan type has been greatly extended by the researches of Janensch (1911) on the rich collection discovered by the Selenka-Blanckenhorn Expedition in the Trinil beds in which the type of *Pithecanthropus erectus* occurs. The fauna of these beds, as described by Stremme (1911, pp. 82–150) includes (pp. 141, 142) the following.

STEGODON AIRÂWANA FAUNA OF THE KENDENG-SCHICHTEN LAYER, JAVA, AS LISTED BY STREMME, 1911

This fauna was first regarded as of Lower Pleistocene age (=Boulder Conglomerate zone of Pilgrim), or transitional to Middle [Upper] Pleistocene (=Godávari Alluvium, Nerbudda of Pilgrim) which contains *Stegodon insignis* ref., *S. ganesa* ref., and *Palæoloxodon namadicus.* Stremme remarks (1911, p. 144): "Ein wichtiges Leitfossil wäre eventuell *Elephas*, dessen Zahnbruchstück Janensch dem *Elephas antiquus* am nächsten stellt. Das Stück

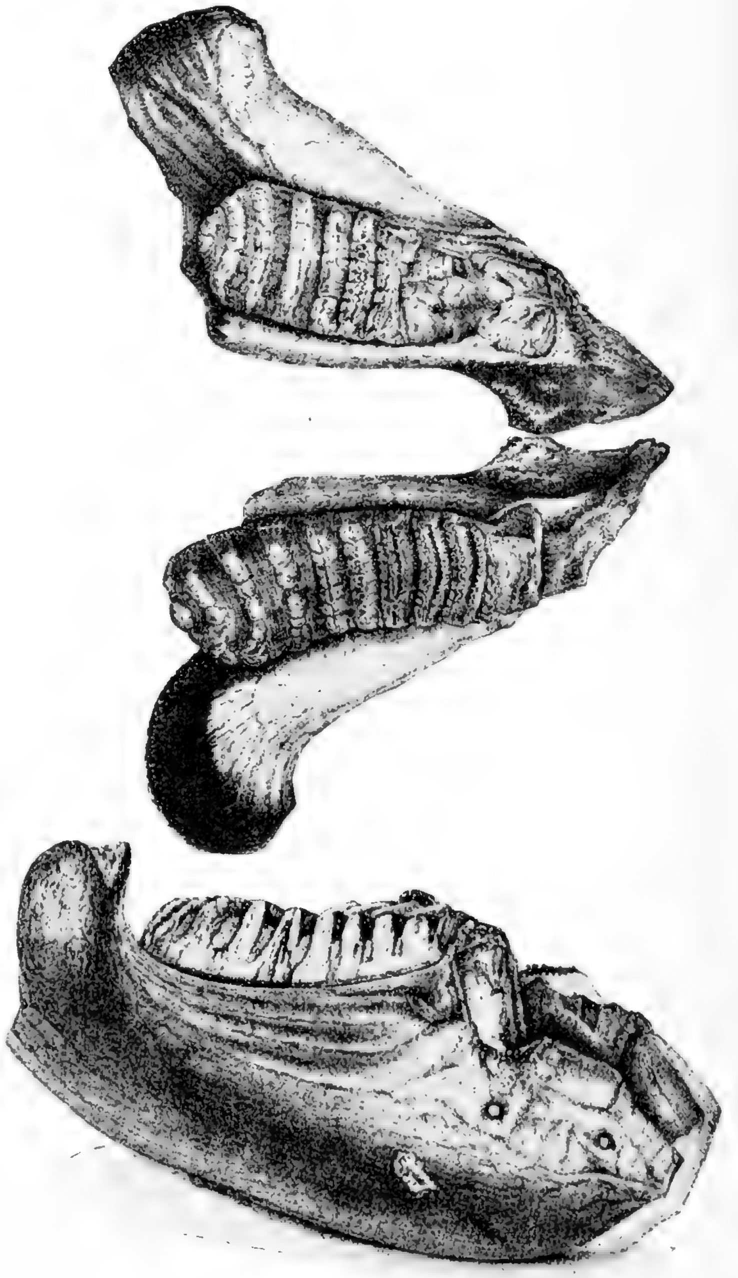


Fig. 771. Type of *Stegodon Airâwana* Martin, 1890, Tab. I, figs. 1 and 2, one-fourth natural size. The type right inferior molar, r.M_3, is also figured in Tab. II, figs. 3 and 4, two-thirds natural size. (Martin, *op. cit.*, p. 4): "Nur von Java in einer unvollständigen Mandibel und darin steckenden Molaren bekannt. Letztere mit 9 Jochen und 2 Talons."

stammt nicht von Trinil; auch Dubois hat keine *Elephas*-Reste von Trinil in seiner grossen Sammlung."

Primates: *Pithecanthropus erectus* Dubois.
Macacus nemestrinus saradana, related to existing Zati of Sumatra and *Nemestrinus* of Borneo.

Ungulata: *Stegodon ganesa javanicus* Dubois = [*Stegodon Airâwana* or *S. trigonocephalus* Martin].
Elephas hysudrindicus Dubois = *Elephas* sp. *antiquus* [*namadicus*] Falconer (*fide* Stremme, 1911, and Janensch, 1911).
[It is important to note that *E. hysudrindicus does not occur* at the locality of Trinil.]
Rhinoceros sivasondaicus Dubois, intermediate between *R. sivalensis* and *R. sondaicus*.[1]
Rhinoceros kendengindicus Dubois.
Tapirus pandanicus Dubois.

Artiodactyla: *Sus brachygnathus* Dubois, related to recent *Sus verrucosus* of Java.
Sus macrognathus Dubois.
Hippopotamus (*Hexaprotodon*) *sivajavanicus* Dubois, related to *Hexaprotodon sivalensis*.
Cervulus kendengensis Stremme, related to existing muntjac.
Cervus (*Axis*) *liriocerus* Dubois = *Cervus* (*Axis*) *Lydekkeri* Martin.
Cervus (*Rusa*) *kendengensis* Dubois.
Cervus (*Rusa*) *palæomendjangan* Dubois.
Duboisia (*Tetraceros*) *Kroesenii* Dubois, related to existing *Boselaphus* and *Tetraceros*.
Leptobos Groeneveldtii Dubois.
Leptobos dependicornis Dubois.
Bibos palæosondaicus Dubois, related to the existing *Bibos sondaicus*.[1]
Bibos protocavifrons Dubois.
Buffelus (*Bubalus*) *palæokerabau* Dubois, related to existing Javan *Buffelus*.[1]

Rodentia: *Hystrix*.

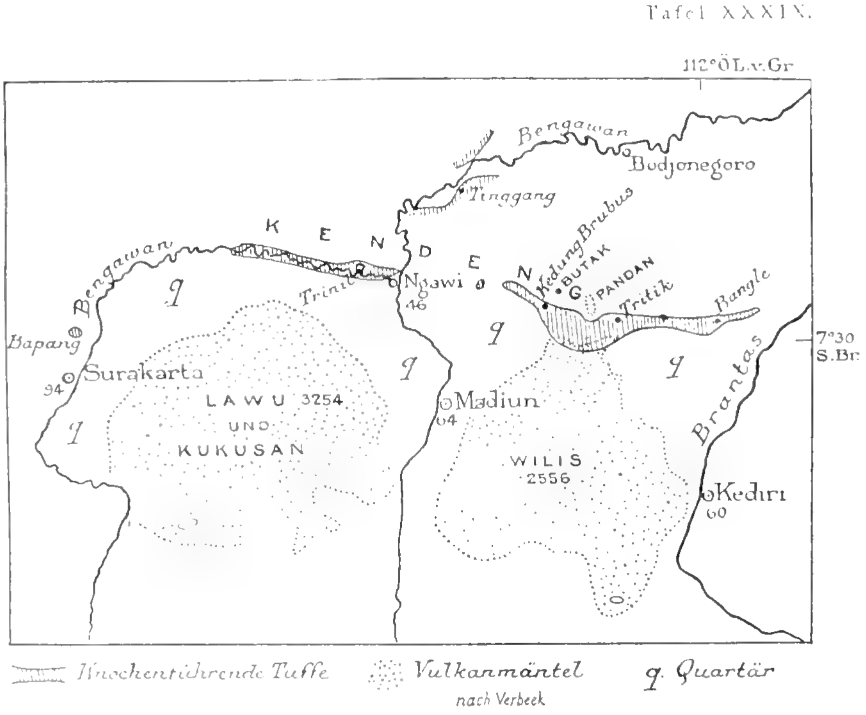
Edentata: *Manis palæojavanica* Dubois.

Carnivora: *Mececyon trinilensis*, related to recent *Mececyon javanicus*.
Felis oxygnatha Dubois.
Felis trinilensis Dubois.
Felis microgale Dubois = *Feliopsis palæojavanica* Stremme.
Hyæna bathygnatha Dubois.
Lutra palæoleptonyx Dubois.

More recently (letter, 1924) Dietrich determined that the species *Stegodon airâwana*, which the Kendeng horizon contains, is somewhat more progressive and consequently more recent geologically than *S. insignis-ganesa*.

The last word by Dietrich (1926.1, p. 139) makes it still more recent, namely: "Selbst wenn das Entwicklungstempo rascher geworden ist, kommen wir für *Airawana* zu einem sehr viel jüngeren Alter als bisher für ihn und damit für die Trinilschichten festgesetzt wurde, nämlich zu Jung- bis Jüngstpleistocän. Diese Auffassung des geologischen Alters der Pithecanthropusschichten bahnt der von Dubois 1923 gewonnenen Erkenntnis, dass *Pithecanthropus* ein Glied der Hominiden ist, den Weg zu dem weiteren Schritt, das *P.* bereits zur Gattung *Homo* gehört."

Osborn, 1928: It now seems probable that *Stegodon airâwana* is of lower Middle Pleistocene age, somewhat more ancient than the Godávari, Narbada Alluvium, and with a more early fauna, including the rhinoceroses related to the *R. sivasondaicus* and lacking the *R. unicornis* and *Equus namadicus* forms as well as the *Palæoloxodon namadicus* of the Godávari, Narbada Alluvium.



a. Kartenskizze der Umgebung von Trinil. Masstab 1 : 1 500 000.

Fig. 772. Sketch of the Kendeng horizon (vertical shading), Trinil, Java, containing the type of *Pithecanthropus erectus* Dubois and the type of *Stegodon ganesa* var. *javanicus* (=*S. airâwana* or *S. trigonocephalus*), also referred specimens of *Stegodon airâwana*. After Dubois, 1908, Taf. XXXIX. Middle Pleistocene.

Comparison of the beautiful figures of Janensch (1911, figs. 1–16, Taf. XXI–XXV) together with casts (Amer. Mus. 6835) indicates that *Stegodon airâwana* is a much more progressive species than the *S. insignis* type of the Upper Pliocene [to Lower Pleistocene], and referred of the Lower and Middle [Upper] Pleistocene; it is nearly as progressive as the *Stegodon auroræ* type from Mt. Tomuro, Japan, as shown in the comparative figure (Fig. 688). Consequently we are justified in accepting Dietrich's recent conclusion that *Stegodon airâwana* and *Pithecanthropus erectus* are

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[1] [(Maarel, 1932, p. 193) ". . .we do not doubt that Stremme would have come to a pleistocene age, had he as we arrived at the conclusion that the Trinil fauna contains at least three still living species viz., *Bibos sondaicus fossilis*, *Buffelus bubalus* var. *sondaicus fossilis*, and *Rhinoceros sondaicus fossilis*."]

of Middle rather than of Lower Pleistocene age. While the vertical heightening or hypsodonty of the molar crown approaches that of the *Archidiskodon planifrons* type, the entire conformation of the *S. airâwana* cranium (Fig. 773) is totally different and demonstrates afresh that *the most progressive Stegodontinæ are parallel with, rather than ancestral to, the Elephantidæ.*

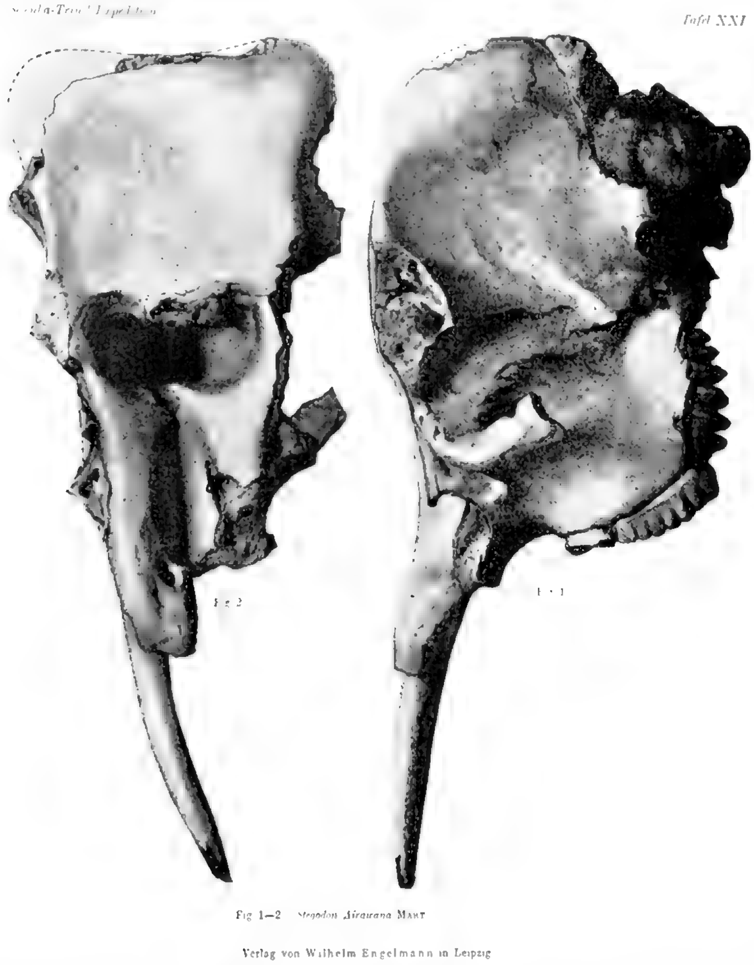

Fig. 773. Front and side views of referred *Stegodon airâwana* Martin, as figured by Janensch in his memoir of the Selenka-Blanckenhorn Trinil-Expedition, 1911, Taf. XXI, figs. 1 and 2. One-sixth natural size.

COMPARISON OF STEGODON AIRÂWANA MARTIN WITH STEGODON INSIGNIS-GANESA

Translated from the German of Dr. W. O. Dietrich with interpolations by H. F. Osborn and corrected by Doctor Dietrich, April 18, 1924

Stegodon airâwana Martin from the Pleistocene of middle Java (*Pithecanthropus* beds of Trinil) manifests evidences of insular dwarfing; it is in all its parts, both of teeth and skeleton, smaller than the continental west Asiatic and Indian races and species. Special features of the *S. airâwana* teeth include the following characteristics: (1) Shallow longitudinal cleavage of the crowns; (2) relatively slender and narrow ridge-crests; (3) strong division of the ridge-crests into numerous mamillæ [conelets], relatively limited cement covering; (4) small, thin, and strongly folded enamel on the abrasion surfaces. (5) While *Stegodon airâwana* is a dwarfed tropical form as compared with the giant *S. insignis-ganesa*, it exhibits more numerous, more elevated, and more compressed ridge-crests.

It is in these respects the most specialized Stegodont of all known species, a terminal form based upon a Stegodont foundation. The dental formula of *S. airâwana* runs as follows:

Stegodon airâwana: Dp 2 $\frac{2}{?}$ Dp 3 $\frac{5\text{-}6}{?}$ Dp 4 $\frac{7\text{-}9}{?}$ M 1 $\frac{7\text{-}9}{?}$ M 2 $\frac{9\text{-}11}{?}$ M 3 $\frac{12\text{-}14}{13\text{-}15\frac{1}{2}}$.

The greater or lesser development of the ridge formula depends upon the anterior and posterior half-ridges or talons, as in the reckoning of Falconer and Lydekker. In contrast [Osborn] the maximal ridge formula of the best-known continental species, *Stegodon insignis*, is as follows:

[*Stegodon insignis-ganesa*: Dp 3 $\frac{6}{6}$ Dp 4 $\frac{7\frac{1}{2}}{7\frac{1}{2}\text{-}9}$ M 1 $\frac{7\frac{1}{2}\text{-}8}{7\frac{1}{2}\text{-}10}$ M 2 $\frac{8\text{-}8\frac{1}{2}}{\frac{1}{2}\text{-}9\text{-}\frac{1}{2}}$ M 3 $\frac{\frac{1}{2}\text{-}11\text{-}\frac{1}{2}}{12\frac{1}{2}\text{-}13}$].

Length of Molars.—In the following table the characteristic maximal and minimal molar tooth length is expressed in millimeters:

Upper Molars	Dp^2	Dp^3	Dp^4	M^1	M^2	M^3
Stegodon airâwana	18	54	90	126	189	221
Stegodon insignis	18	68.6	121.9	246	280	310
Stegodon elephantoides (=*cliftii*)		70.7	124.4	155	208	236
Stegodon bombifrons				150	188	250.5

Consequently *Stegodon airâwana* is two-thirds the size of *S. insignis-ganesa* and is also inferior in size to *S. bombifrons.*

The construction of a specialized stegodont molar arises through the simple outgrowth of the anterior and posterior half ridge-crests. The lengths of the molar teeth in the above table are taken from Falconer and Lydekker and from original measurements by Dietrich. The maximal length measurements of M_3 of the lower jaw compared with the width give us the indices of the third lower molar which is the longest in the series:

Stegodon airâwana	ap. tr.	$\frac{304}{14}$ mm.	= 22 length-breadth ridge index
Stegodon insignis	ap. tr.	$\frac{310}{11}$ mm.	= 28 length-breadth ridge index
Stegodon cliftii	ap. tr.	$\frac{323}{9}$ mm.	= 36 length-breadth ridge index
Stegodon bombifrons	ap. tr.	$\frac{334}{10}$ mm.	= 33 length-breadth ridge index

By this means we may calculate the length-breadth ridge quotient. Such indices may be calculated also for the third upper molar, M^3, when we secure similar figures which will enable us to

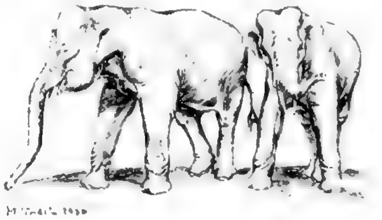

Fig. 774. *Stegodon airâwana.* Juvenile cranium with small tusks. Elevation of narial openings as in *S. trigonocephalus.* Observe the peculiar straight front of the forehead and great breadth across the top of occipitals. Skeleton conjectural as in other Stegodonts. Restorations by Margret Flinsch (1930), under the direction of Henry Fairfield Osborn. One-fiftieth natural size.

determine positively the progressive development within the Stegodont series. In order to measure the specialization of the molar teeth, including anterior addition and reduction and posterior addition and reduction, a relative proportion may be established between the development of the two anterior teeth and the two posterior teeth. It is noteworthy that the proportion between the first and second molars in the Chinese and Javanese species is the same. From careful calculations it follows that M^2 in *S. airâwana* is more strongly reduced than in the corresponding tooth of the *S. orientalis* of Owen.

On all these structural grounds Doctor Dietrich concludes that *S. airâwana* is more recent than either of the Asiatic species of the continent and that its newer Pleistocene age is rendered certain.

STEGODON GANESA VAR. JAVANICUS DUBOIS, 1908

Middle Pleistocene, Trinil, Kendeng-Schichten, Java

This subspecies, *Stegodon ganesa javanicus*, belonging in the same Kendeng beds as *S. airâwana* Martin, 1890, is to be regarded, as remarked by Stremme, as a synonym of *S. airâwana*.[1]

In his paper of 1908, entitled "Das Geologische Alter der Kendeng-Oder Trinil-Fauna," Dr. Eugen Dubois, the discoverer of *Pithecanthropus erectus*, assigns to *Pithecanthropus* and the accompanying Kendeng-Trinil Fauna at the most a Lower Pleistocene age ("alt-diluvialen Alters"). The remains occur in the fossil-bearing tufa known as the "Kendeng-Schichten," in the center of which lies Trinil, as shown in Plate XXXIX (Fig. 772 of the present Memoir). Recently Dietrich has assigned a Middle Pleistocene age to the Kendeng Trinil fauna.

Dubois (1908, p. 1257) erroneously remarks that the two skulls described by Martin as *S. trigonocephalus* really belong specifically to *Stegodon ganesa* in their cranial and dental characters, but in order to distinguish this smaller Kendeng species, as an insular variety, from the giant continental form of *ganesa*, he proposes the subspecific name *Stegodon ganesa* var. *javanicus*. He considers it probable (1908) that this Javan subspecies belonged to the Upper Pliocene fauna.

Stremme, "Die Säugetiere mit Ausnahme der Proboscidier," in "Die Pithecanthropus-Schichten auf Java," 1911, p. 142, regards this subspecies as closely related to *Stegodon airâwana* Martin, 1890.

According to Dubois (1908) the two skulls described by Martin as *Stegodon trigonocephalus* belong to this species.[1] It is important to note that the true *S. trigonocephalus* of Martin does not occur in the same level as *Pithecanthropus erectus*.

Stegodon Ganesa var. *javanicus* Dubois, 1908. "Das Geologische Alter der Kendeng-Oder Trinil-Fauna." Tijdsch. Konink. Neder. Aardrijks. Genoots. Amsterdam, Tweede Serie, Deel XXVB, No. 6, p. 1257. TYPE.—Material from Kendeng. HORIZON AND LOCALITY.—Trinil, Kendeng Schichten, Middle Pleistocene, Java.

DESCRIPTION (*Op. cit.*, 1908, pp. 1256, 1257).—"Die Untersuchung eines sehr reichlichen Stegodonten-materiales aus dem ganzen Kendeng, unter welchem auch mehrere Schädel von jungen und alten Tieren, hat mich nun zu dem Ergebnisse geführt, dass alle diese Ueberreste einer einzigen Art angehören. Diese unterscheidet sich von *Stegodon ganesa* kaum anders als durch ihre viel geringere Grösse. Der Schädel besitzt dieselbe weite Temporalgrube, ist ebenso charakteristisch stark brachycephal und auch übrigens sind beide Formen sehr ähnlich. Nur ältere Schädel weichen in einigen Beziehungen etwas von der typischen Ganesa-Form ab, indem nämlich die Frontal- und Occipitalteile sich gegeneinander abflachen und mehr oder weniger scharf von einander getrennt sind. Das braucht uns aber nicht davon abzuhalten diese Formen derselben Art zuzuschreiben, denn es kann ja bei den Elephanten die Schädelform einer und derselben Art, innerhalb gewissen Grenzen, beträchtliche Verschiedenheiten zeigen. Der Ganesa-Typus bleibt bei unserer Form doch immer erkenbar."

"Auch durch ihre Molaren ist sie von *S. ganesa* spezifisch nicht zu trennen, nur geht die Lamellenzahl im Unterkiefer bis zu wenigstens 14 anstatt 13; die Zahl der Lamellen hat aber, wie wir durch POHLIG wissen, für die Unterscheidung der Elephantenarten nicht die grosse Bedeutung welche man ihr früher zuschrieb."

"Zu dieser Art gehören auch die zwei von MARTIN als *Stegodon trigonocephalus* . . . beschriebenen Schädel. Wären diese gut erhalten gewesen, so hätten sie erkennen lassen, dass die dreieckige Form keine ursprüngliche und der Art eigentümliche ist. Der darauf Bezug nehmende Name ist also zu kassieren. Ich schlage nun vor, diese kleinere Kendeng-Form nur als Varietät von der riesigen Festlandsform, der sie deutlich sehr nahe steht, zu trennen, führe sie also als *Stegodon ganesa* var. *javanicus* ein."

CHARACTERS (*Op. cit.*, 1908, p. 1257).—"Wenn man nun auch nicht zugeben kann, dass *Stegodon ganesa* und *Stegodon insignis* einer Art angehören, so sind beide jedenfalls einander sehr nahe verwandt (die Molaren sind nicht oder kaum zu unterscheiden), *Stegodon insignis* aber kann man, mit M. SCHLOSSER . . .), geradezu als das Leitfossil der jüngeren Pliocänfauna Ostasiens ansehen. Es ist schon hierdurch wahrscheinlich, dass unsere javanische *Stegodon ganesa* der gleichen jungpliocänen Fauna angehört. Unzweifelhafte Ueberreste von *Stegodon ganesa* sind nun aber noch nicht in jüngeren als Pliocänen Schichten angetroffen worden, denn der in den Narbadá-Schichten gefundene Stosszahn kann man dieser Art nicht mit Sicherheit zuschreiben . . ."

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[1] [The following note was prepared by Dr. George Gaylord Simpson (October, 1937): "*Stegodon trigonocephalus* Martin, 1887, pp. 27, 36, 41, was founded principally on two skulls, Professor Osborn selecting the younger as type. These were probably from the vicinity of Surakarta (Solo), Java (see Martin, 1887.1, pp. 25, 27). Dubois briefly characterized abundant material from Kendeng, referring it to *Stegodon ganesa* but as a new variety *javanicus* (Dubois, 1908, pp. 1256, 1257). He also referred *S. trigonocephalus* to *S. ganesa*. He probably considered *trigonocephalus* as the same as his variety *javanicus* but he did not explicitly say so and the clear implication is that they have different types. Von Koenigswald considers *S. trigonocephalus* as distinct from *S. ganesa* but the same as *S. airawana* (1933, pp. 103–105). He implies that *S. ganesa* var. *javanicus* is the same as *S. trigonocephalus* and *S. airawana* and applies to the species the oldest of the three names, *S. trigonocephalus*. Maarel, however, considers *S. trigonocephalus* to be distinct from *S. airawana*, and this was Professor Osborn's opinion. It appears, in any case, that *S. ganesa* var. *javanicus* Dubois, 1908, is synonymous with *S. trigonocephalus*, *S. airawana*, or both, and as both names antedate it, Dubois' name is invalid."—Editor.]

Stegodon trigonocephalus Martin, 1887

Figures 705, 731, 775, 776, 777, Pl. xx

Probably vicinity of Surakarta, Java. Dubois notes that *Stegodon trigonocephalus* does not occur in the Kendeng-Schichten of Trinil; Matsumoto regards the geologic level of *S. trigonocephalus* as equivalent to the Lower Pleistocene, Boulder Conglomerate beds of India.

Stegodon trigonocephalus is a dwarfed insular Stegodont, based chiefly upon an immature cranium (Fig. 776) which has substantially the same characteristic insular form as the immature cranium of *S. airâwana* (Fig. 773), but which is very different from the crania of *S. bombifrons* or *S. insignis-ganesa*. This juvenile type represents the immature condition of the Stegodont cranium and consequently is very interesting and important. It is now regarded as in a Pleistocene stage of evolution, but the extremely immature condition of the teeth renders its specific determination very difficult. From the following description and figures of Martin, it is difficult to distinguish this immature type from *Stegodon airâwana*; it is apparently a somewhat more primitive Lower Pleistocene form.

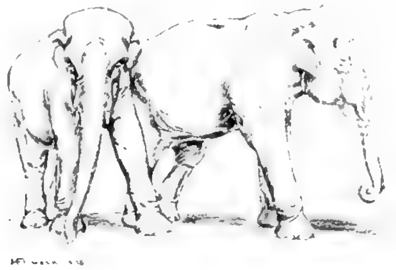


Fig. 775. *Stegodon trigonocephalus.* Rather young cranial profiles drawn directly from type. Frontal line much longer than in *S. pinjorensis.* Cranium extremely abbreviated. Skeleton conjectural, as in other Stegodonts. Restoration by Margret Flinsch (1930), under the direction of Henry Fairfield Osborn. One-fiftieth natural size.

Stegodon trigonocephalus Martin, 1887. "Fossile Säugethierreste von Java und Japan," Sammlung. Geolog. Reichs-Museums, Leiden, Beiträge z. Geolog. Ost-Asiens und Australiens, Ser. I, Bd. IV, Heft 2, pp. 27, 36 (1887); also Jaarb. Mijnw. Neder. Oost-Indië, 1887, Wetensch. Ged. 16, Palæontologie van Nederlandsch-Indië. Verhandeling No. 21, pp. 3, 12 (1887). Type.—Young skull with third and fourth deciduous premolars in the Geological Museum of Leiden. Horizon and Locality.—Probably from vicinity of Surakarta, Java; said to be associated with remains of proboscideans referred to *Stegodon bombifrons, Euelephas namadicus,* and *Euelephas hysudricus.* Type Figure.—(*Op. cit.,* Martin, 1887, Sammlung. Geolog. Reichs-Museums Leiden, Tab. ii, figs. 1, 1a, and Tab. iii, fig. 1.

Description.—The original description by Martin (1887, pp. 36–41, with figures) gives the characters of the immature type skull and teeth in great detail, and on page 45 offers the following distinctions from *Stegodon cliftii* and *S. bombifrons*: "Zunächst ist es von Bedeutung, dass die Zähne von denjenigen des *Stegodon Cliftii* so völlig verschieden gebaut sind, dass eine Vereinigung der javanischen Art mit der genannten, von der ein Schädel noch nicht bekannt ist, von vornherein ausgeschlossen wird. Ebenso bestimmt unterscheiden sich aber (soweit unsere Kenntniss bis jetzt reicht) auch die Zähne von *St. trigonocephalus* durch die Jochzahl der Praemolaren von allen anderen, bis jetzt bekannten Arten von Stegodon, . . . Bezeichnend für den 2^{ten} Praemolaren von *St. trigonocephalus* ist ferner seine ovale Form, und ebenso für den 3^{ten} Praemolaren die kaum merkliche Convergenz seiner Seitenflächen nach vorne zu, Merkmale, die von allen bekannten, entsprechenden Zähnen der übrigen Stegodontenarten abweichen. Durch die hohen, schmalen Joche und vor allem durch die feine Fältelung dürfte auch bei Bruchstücken der Molaren von *St. trigonocephalus* eine Unterscheidung von *St. bombifrons* bisweilen

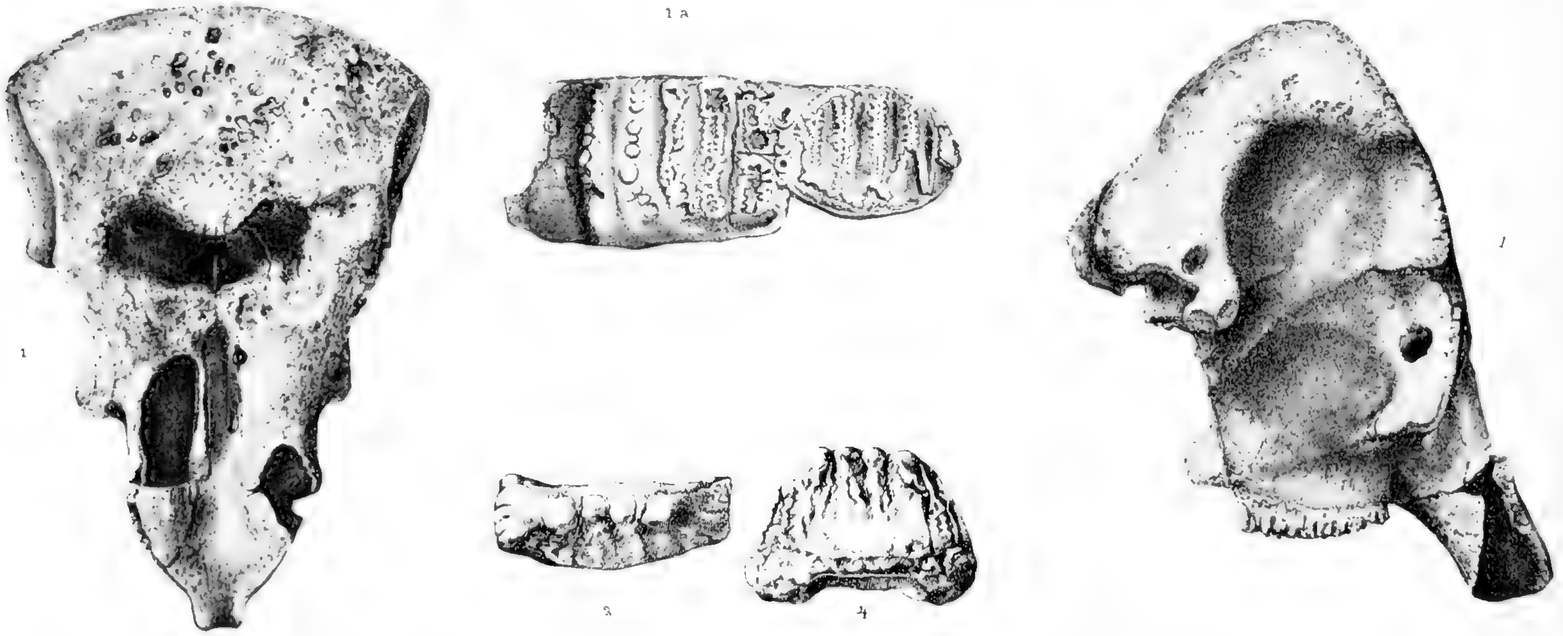


Fig. 776. Type of *Stegodon trigonocephalus* Martin, 1887, Tab. ii, figs. 1, 1a, and Tab. iii, fig. 1. The side and front views are reproduced one-eighth natural size; the crown view of the tooth is reproduced one-third natural size.

Taf. i, figs. 3 and 4 (Naumann, 1887). A single crest from Java, distinct from *S. trigonocephalus* and doubtfully referred by Naumann to *S. insignis* Falc. and Caut. (*op. cit.,* p. 9): "Das Zahnbruchstück kann nur zu *St. insignis* oder zu *St. Ganesa* gehoren."

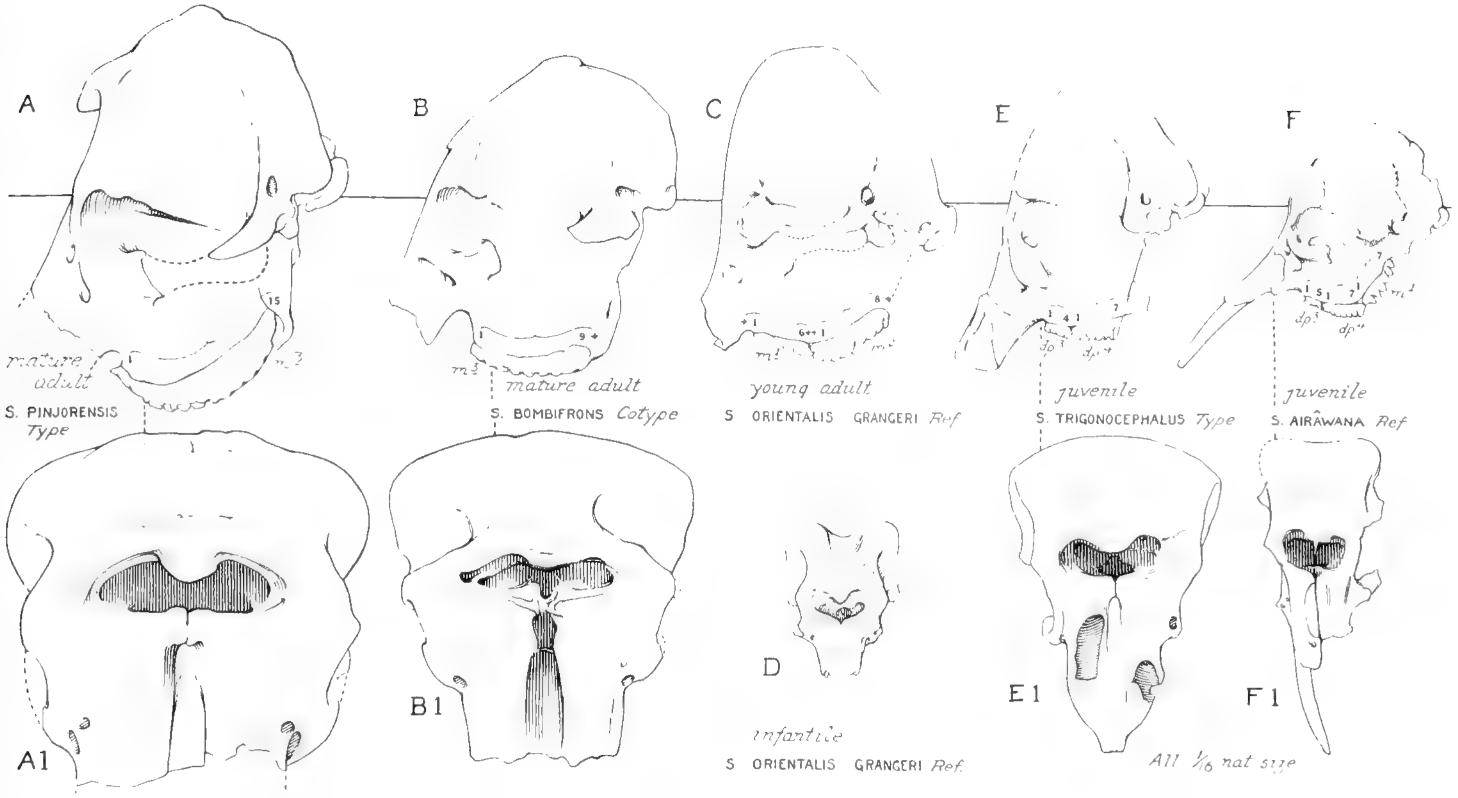


Fig. 777. Front and side view outlines to a one-sixteenth scale of Stegodont crania of:

A, A1, *Stegodon pinjorensis* type, mature adult (Amer. Mus. 19772), from near Siswan, India. See also figure 765.
B, B1, *Stegodon bombifrons* cotype, mature adult (Brit. Mus. M. 2979, cast Amer. Mus. 10378). See figure 734.
C, *Stegodon orientalis grangeri* ref., young adult (Amer. Mus. 18630) collected by Walter Granger, Wanhsien, Province of Szechuan, China. See figure 763.
D, *Stegodon orientalis grangeri* ref., infantile (Amer. Mus. 18632) collected by Walter Granger, Wanhsien, Province of Szechuan, China.
E, E1, *Stegodon trigonocephalus* type, juvenile, from vicinity of ?Surakarta, Java. Sammlung. Geolog. Reichs-Museums, Leiden. See figure 776.
F, F1, *Stegodon airâwana* ref., juvenile, Java. See figure 773.

ermöglicht werden; dagegen ist die Trennung solcher Reste von *St. insignis* und *ganesa* mit sehr grossen Schwierigkeiten verbunden."

Ridge formula of *S. trigonocephalus*: $\mathrm{Dp}\,3^{\underline{4}}\ \mathrm{Dp}\,4^{\underline{7}}$ as compared by the author with *S. cliftii*: $\mathrm{Dp}\,3^{\underline{4}}\ \mathrm{Dp}\,4^{\underline{6}}$; with *S. bombifrons*: $\mathrm{Dp}\,3^{4}_{(?)}\ \mathrm{Dp}\,4^{\underline{(?)\,5-6}}$; with *S. ganesa*: $\mathrm{Dp}\,2^{\underline{2}}\ \mathrm{Dp}\,3^{\underline{5}}\ \mathrm{Dp}\,4^{\underline{7}}$. The skull, however, is quite different in form from that of *S. insignis*. Martin inclines to compare *S. trigonocephalus* with *S. insignis* rather than with the Lower [Middle] Pliocene stage of *S. bombifrons*.

It is important to note that these characters relate both to the immature type skull and to a second older skull which is a *referred* specimen, namely: (*op. cit.*, p. 41) "*b. Alter Schädel.* (Tab. IV u. V Fig. 1)."

A specimen from northwest Mindanao, Philippine Islands, referred to this species is described in detail by Dr. Edmund Naumann of Munich University in his "Fossile Elephantenreste von Mindanáo, Sumátra und Malakka," Abhand. u. Berichte des Königl. Zoolog. Anthrop.-Ethnog. Museums zu Dresden, 1887, pp. 5–8. He subsequently (1890) made it the type of *Stegodon mindanensis*.

Stegodonts of the Philippine Islands and Japan

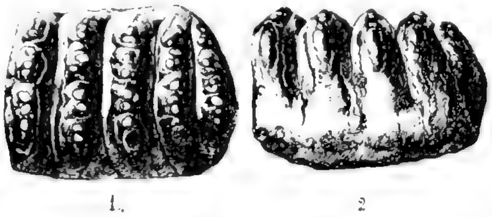
We owe to Naumann (1890) and to Matsumoto (1915, 1918) the discovery and description of three very progressive species, originally referred to *Stegodon*, which in part or wholly seem transitional in structure to *Archidiskodon* or to *Elephas*. The true affinity of these types rests upon (a) the still unknown structure of the cranium and (b) the ridge formula and height and form of the ridge-crests as now revealed in the case of the species *Stegodon auroræ* (Fig. 781). In brief, until the cranium is known, we cannot be certain whether these animals are progressive Stegodonts or primitive Archidiskodonts. The history of discovery and description is as follows.

Stegodon (Archidiskodon?) mindanensis Naumann, 1890

Figures 706, 778

Mindanao, Philippine Islands, Lower(?) to Middle Pleistocene.

Stegodon Mindanensis Naumann, 1890. "*Stegodon Mindanensis*, eine neue Art von Uebergangs-Mastodonten." Zeitschr. deutsch. geol. Ges., Bd. XLII, Heft I, pp. 166–169. Type.—Fragment of a molar tooth. Horizon and Locality.—Mindanao, Philippine Islands, (?)Lower to Middle Pleistocene. Type Figure.—Naumann, 1887, Taf. I, figs. 1 and 2. Type Description.—(Naumann, 1890, p. 167): ". . . so bleibt doch das früher erzielte Resultat, nach welchem durch die Untersuchung der beiden Zahnbruchstücke von Mindanao 'die Verbreitung der Siwalikfauna über das Gebiet der Philippinen bewiesen und die enge Verknüpfung einer wahrscheinlich jungtertiären Säugethierfauna auf Java und den Philippinen durch eine in der Entwicklungsreihe der Stegodonten und Elephanten hochwichtige Art' constatirt sein sollte, zu Recht bestehen. . . Merkwürdig ist ferner ein medianer Einschnitt der Krone, der jederseits von einem secundären Einschnitt begleitet wird. Durch diese Spaltungen werden die Mamillenreihen in Gruppen zerlegt." The type of this species was originally figured by Naumann in 1887 as *Stegodon trigonocephalus*; it was regarded by him as an outlyer of the Siwalik proboscidean fauna. A single ridge-crest from Java (see Fig. 776, lower), distinct from *S. trigonocephalus*, was doubtfully referred by Naumann to *S. insignis* or *S. ganesa* Falconer and Cautley. (Naumann, 1887, p. 9): "Das Zahnbruchstück kann nur zu *St. insignis* oder zu *St. Ganesa* gehören."



Type of Stegodon (Archidiskodon?) mindanensis

Fig. 778. Type incomplete inferior molar of *Stegodon mindanensis* Naumann, 1890, from Mindanao, Philippine Islands (originally figured by Naumann in 1887, Taf. I, figs. 1 and 2, as *Stegodon trigonocephalus*).

As compared with *Stegodon airâwana* (Fig. 779), the ridge-crests in *S. mindanensis* type are more vertically placed, as in the *Stegodon auroræ* type (Fig. 780).

If a true Stegodont, *Stegodon mindanensis* (Fig. 778) is even more progressive than *S. airâwana*, because the valleys between the ridge-crests are entirely closed up; it compares somewhat more closely with *Stegodon auroræ* (Figs. 780, 781), also an imperfectly known species possibly referable to *Archidiskodon*.

Osborn, 1924: It is very difficult to determine the characters of this type (Fig. 778) without examination of the original specimen. The type lower molar is far more progressive in the direction of *Archidiskodon* or *Elephas* than the types of either *Stegodon insignis* or *S. ganesa*; it is, in fact, a true-crested tooth in which the ridges are closely compressed and the valleys closed. Consequently this tooth should be compared with that of a primitive species of elephant or of *Archidiskodon*.

Stegodon auroræ Matsumoto, 1915, 1918

Figures 688, 709, 780, 781, 819

Upper(?) Pliocene, Mt. Tomuro, Kaga, Japan.

Like *Stegodon mindanensis*, *Elephas* (*Prostegodon*, *Parastegodon*) *auroræ* is either a highly progressive *Stegodon* or a primitive *Archidiskodon*, a point to be determined positively by the discovery of a cranium.

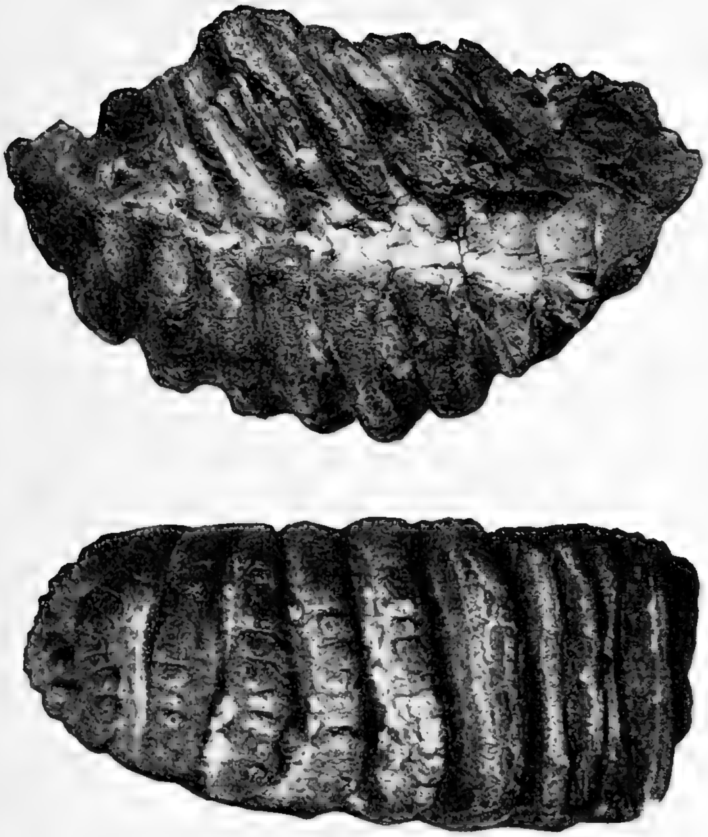
Elephas (Prostegodon, Parastegodon) auroræ Matsumoto.—In describing the type specimen, determined as a second right superior molar, r.M^2, Matsumoto remarked (1918, p. 52): ". . . this specimen represents a species new to science, being . . . a transitional form from *Stegodon* to *Elephas*." Originally described as *Elephas auroræ* Mats., 1915, also 1918, p. 52, Pl. xx, it was afterward referred by Matsumoto (in Osborn, 1923.601) to *Prostegodon*, the genotype of which is *Mastodon latidens*, and finally (1924.2) was made the genotype of *Parastegodon* Matsumoto, to include the *Stegodon mindanensis-E. auroræ* group.

Elephas auroræ Matsumoto, 1915, 1918. Preliminary reports of this species were published in the Scientific Gazette, Tokyo, Vol. III, No. 5, 1915, pp. 308–315, and in the Journal of the Geological Society, Tokyo, Vol. XXIII, No. 275, 1916, p. 294 (both in Japanese). Also (in English) "On a New Archetypal

Fig. 779. Referred by Janensch to *S. airâwana*. Nine ridge-crested second superior molar, M^2, after Janensch, 1911, p. 171, fig. 12, and ridge-crest section of a third superior molar, M^3, after Janensch, *op. cit.*, p. 174, fig. 13. One-half natural size. Both figures inverted to show the molars in natural position.

(Left) Lateral view. (Right) Ridge-crest section.

It will be observed that the convexity of the ridge-crests of the second molar crown, resulting in the wide divergence of the crests, together with the more numerous ridge-crests, tends to relate this animal to *Stegodon* rather than to *Archidiskodon*, in which the ridges are more vertical and more closely compressed.



TYPE OF STEGODON AURORÆ

Fig. 780. Type of *Elephas* (*Prostegodon, Parastegodon*) *aurora* Matsumoto, after Matsumoto, 1918, Pl. xx, figs. 1 and 3. One-half natural size. Determined by Matsumoto (1918) as a ten and a half crested second right superior molar, r.M^2. Compare figures 699 of *S. bombifrons* and figure 762 of *S. orientalis grangeri* showing convex external side and flat internal side; also figures 686, 7, and 688.

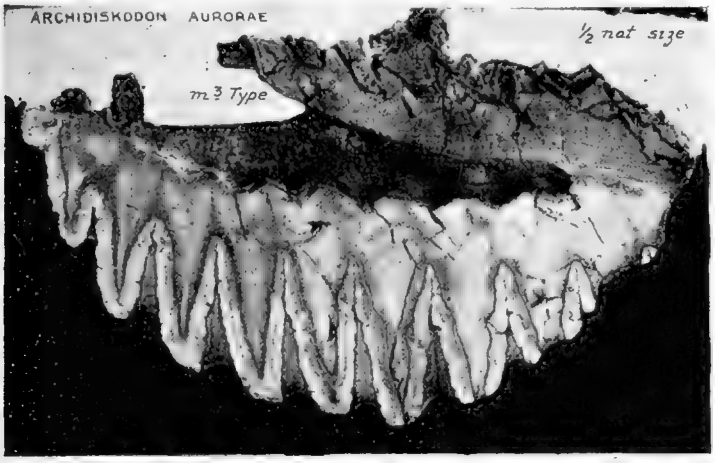


Fig. 781. Vertical section of type molar, r.M^2, of *Stegodon auroræ* (compare Fig. 780, crown and side views of type of *Elephas* (*Prostegodon, Parastegodon*) *auroræ*, also Fig. 825, lectotype of *E.* [=*Archidiskodon*] *planifrons*). One-half natural size. After photograph sent by Doctor Matsumoto.

Fossil Elephant from Mt. Tomuro, Kaga." Sci. Rept. Tôhoku Imp. Univ., 1918, (2), III, No. 2, p. 52. TYPE.—A right M^2 with ten and a half ridges, thus exceeding the ridge formula of M^2 in *Archidiskodon planifrons*, namely, $\text{M}\,2^{\underline{8-9}}$. Original in Geological Institute, Tokyo. HORIZON AND LOCALITY.—Mt. Tomuro, Kaga, Japan, (?)Upper Pliocene. TYPE FIGURE.—*Op. cit.*, 1918, Pl. xx, figs. 1–3. SUPPLEMENTARY DESCRIPTION (MATSUMOTO, 1924.2, PP. 256, 257, 262).—Made the genotype of the genus *Parastegodon* (see p. 903 of the present Memoir).[1]

TYPE DESCRIPTION (1918, PP. 52–55).—"The unique type specimen corresponds to an upper, probably penultimate, molar of the right side. It measures 180 mm. in length, 75 mm. in maximum width and 48 mm. in the maximum height of the crown." The reasons why the author referred this new species to *Elephas* and not to *Stegodon* are as follows: The ridge formula of M^2 corresponds to 10½, while that of the known species of *Stegodon* corresponds to 6 to 9. The author gives six additional reasons for separating the animal from *Stegodon*, and six additional reasons for separating it specifically from *E. planifrons*, to which he regards it as allied generically. The author concludes (p. 55): "The present species appears to the present writer to be more archetypal and more *Stegodon*-like than *E. planifrons* in the second distinctive characteristic, but just the opposite in the third, fifth and sixth distinctive characteristics. At any rate, the discovery of the present species is worthy [to] be considered as an additional datum to prove the very intimate alliance of *Stegodon* and *Elephas*."

Stegodon orientalis shodoënsis Matsumoto, 1924

Middle Pleistocene. Island of Mitsugo (Mitsugo-shima) and Island of Shôdo, Inland Sea, Japan.

Stegodon orientalis shodoënsis Matsumoto, 1924. "Preliminary Notes on the Species of Stegodon in Japan." Journ. Geol. Soc. Tokyo, XXXI, No. 373, pp. 333–335. TYPE.—A fragment of skull—left and right upper jaw bone with third molar attached. Uyeno Museum of Tokyo, No. 2194, presented by Mr. Tomekichi Ozaki. HORIZON AND LOCALITY.—Mitsugo-shima, Yoshima-mura, Nakatadotsu-gun, Province of Sanuki, Japan. Milazzian-Tyrrhenian. Middle Pleistocene. TYPE FIGURE.—Type figure not seen by the present author.[2]

Description in Japanese by Matsumoto; translation by Messrs. Shoichi Ichikawa and Ushinosuke Narahara.—(Matsumoto, 1924.3, pp. 333–335). "Materials: A fragment of skull; left and right upper jaw bone with third molar attached (found at Mitsuko-shima, Yoshima-mura, Nakatadotsu-gun, Province of Sanuki. Specimen No. 2194, Uyeno Museum of Tokyo, presented by Mr. Tomekichi Ozaki). A small fragment of third molar (found at Shôdo-shima and the property of the Tokyo Imperial University). Third upper left molar (found at Shôdo-shima, the cast is kept at Kyoto Imperial University). A fragment of an upper palate with third molar of left and right attached (found at Shôdo-shima, the property of Kyushu Imperial University and the cast kept at Kyoto Imperial University)."

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[1] [See also Matsumoto's article (in English) "On Parastegodon Mastumoto and its bearing on the Descent of Earlier Elephants," Sci. Rept. Tôhoku Imp. Univ., (2), XIII, No. 1 (Matsumoto, 1929.3).—Editor.]

[2] [Dr. Jirō Makiyama has recently reviewed the Japanese Proboscidea (see Makiyama, "Japonic Proboscidea," 1938, Mem. Coll. Sci. Kyoto Imp. Univ., (B), XIV, No. 1, pp. 1–59), in which he figures (p. 18, fig. 7) the holotype palate of *Stegodon shodoënsis*, with right and left third molars *in situ*. On page 19 he states that "The material of Matsumoto was not enough to give full details of the species, but it was named before *Parastegodon akashiensis* Takai, 1936, which seems to me to be in the nearest relation, as it may have a new name form *S. shodoensis akashiensis*." This subspecies he describes on pages 21 to 27, including three figures (Figs. 10–12).—Editor.]

"Ridge formula of molar: left, a+9× [=½-9-½]; right, a+8× [=½ 8 ½]. The exact measurement of ridges cannot be determined. The length as it is, left 226 mm., right 215 mm. The greatest width, left 97 mm. at 2nd ridge, right 96 mm. at 3rd ridge to 6th ridge. The height of crown, left 52 mm. at 6th and 7th ridges, right 49 mm. at 7th ridge. The 6th ridge of left, and 7th ridge of right shows the beginning of wear. . . . There are four ridges within 100 mm. The length of each ridge is 25 mm. and this is rather narrow as a width for third molar of *Stegodon*. The valley is narrow, and the entrance of inside of valley has supplemental cusps. The fold of enamel is very regular and fine. The cement is well developed. The interlocking of opposing surfaces of the molar is of *Mastodon* type."

"Second example: Ridge formula may probably be ×11×. Greatest width, 93½ mm. at 6th ridge, height, 55 mm. at 7th ridge. There are four ridges within 100 mm. Judging by the measurement, it looks like a second molar, but by the shape of its being attached to the palate is a third molar. Ridge formula, left a+9×; right a+8×. The exact measurements of ridges cannot be determined. Length, left 205 mm., right 200 mm. Greatest width, 85 mm. at 6th ridge from back (left), 84 mm. at 5th ridge from back (right). Height, 45 mm. at 3rd ridge (left), 50 mm. at 2nd ridge (right). There are four ridges within 100 mm. The interlocking occlusion of the molar is elephant type."

"A small fragment of third molar, which shows three ridges. I cannot determine whether it belongs to the upper or lower jaw. The length from inside to outside of each ridge is 90 to 96 mm. The width of front to back is 24 to 25 mm."

"Among these specimens, the first has comparatively low crown and the second and third have very high crowns. The fourth specimen is rather low as absolute value but as a ratio it is high. The molars are different in sizes, and this differentiation (or varieties) is the one which occurs in the last period of the existence of the species."

"These specimens resemble the *Stegodon insignis* which is found in the Narbada Valley of India."

V. RECENTLY DESCRIBED STEGODONTS FROM JAVA, CHINA, AND JAPAN

[The following species were described respectively by Dr. Franciscus Hendricus van der Maarel ("Contribution to the Knowledge of the Fossil Mammalian Fauna of Java," 1932), by Dr. G. H. Ralph von Koenigswald ("Beitrag zur Kenntnis der Fossilen Wirbeltiere Javas," 1933), by Dr. Shigeyasu Tokunaga ("Fossil Elephant teeth found at Yokohama and Kakio, Kanagawa Prefecture," Journ. Geog. (Tokyo), XLVI, No. 546, 1934, and "A New Fossil Elephant found in Shikoku, Japan," Proc. Imp. Acad. Tokyo, XI, 1935), by Dr. Chung-Chien Young("Miscellaneous Mammalian Fossils from Shansi and Honan," 1935), and by Dr. Arthur Tindell Hopwood ("Fossil Proboscidea from China," 1935). While the species of Stegodonts in these publications (other than *Parastegodon? kwantoensis* and *Parastegodon sugiyamai* of Tokunaga) were noted by Professor Osborn, they were not studied intensively by him, consequently they are listed here together with excerpts from the original descriptions, including type figures, but without comment or determinations by the author of the present Memoir.

Doctor Hopwood states on page 103 of his Memoir that "Insufficient is known of the Stegodontidæ of China to make a comparison with those of India very profitable. At present it seems as though they occur earlier in India than in China, where they are a late invasion from the South. *Palaeoloxodon*, on the other hand, may be more recent in India than in China."—Editor.]

Stegodon bondolensis van der Maarel, 1932

Figure 782

Bondol near Kuwung, district Randublatung, Regency Blora, Residency Rembang, Java.

Stegodon bondolensis van der Maarel, 1932. "Contribution to the Knowledge of the Fossil Mammalian Fauna of Java," pp. 158–164. Type.—"Fine fragment of the mandible, comprising the whole of the horizontal ramus and the lower portion of the ascending ramus of either side; containing on either side a molar which is inferred to be the M_3 from the absence of the indication of any other tooth behind." Horizon and Locality.—Bondol near Kuwung, district Randublatung, Regency Blora, Residency Rembang, Java. Type Figure.—*Op. cit.*, Pl. xiv, figs. 1, 4, 5, also text figures 24 and 25.

Description.—(Van der Maarel, 1932.1, pp. 158–164): "The mandible is broken into two in the symphysis, but both parts match exactly. The alveolar border of both molars is damaged."

"The diastema descends obliquely forwards at an acute angle of about 35° with the inferior border of the ramus. The mandibular symphysis is produced into a relatively broad, spoutlike termination. Its lower border is damaged. . . . The outer surface of the horizontal ramus presents two foramina mentalia, the one situated some 8 cm. below the anterior extremity of the alveolar margin, the other about 8 cm. in advance of the former and nearer to the inferior border of the ramus."

"Only the lower portion of the coronoid process has been preserved."

"Measurements of lower jaw in cm.
See text fig. 24.

In plane I	greatest height	=16
	greatest width	= 7.8
In plane II	greatest height	=12
	greatest width	=17
Length of B C		=47.5"

"As the front side of both molars is damaged, it seems—at first sight—impossible to ascertain the true number of ridge-crests carried by each of them. Fortunately, however, in the l.M$_3$ a small portion of the front surface of the fangs has been preserved. It is situated below the anterior side of the foremost ridge-crest, and proves with absolute certainty, that this ridge-crest is really the first one. That is to say: not a single ridge-crest has been lost. The ridge formula is, therefore, 8×."

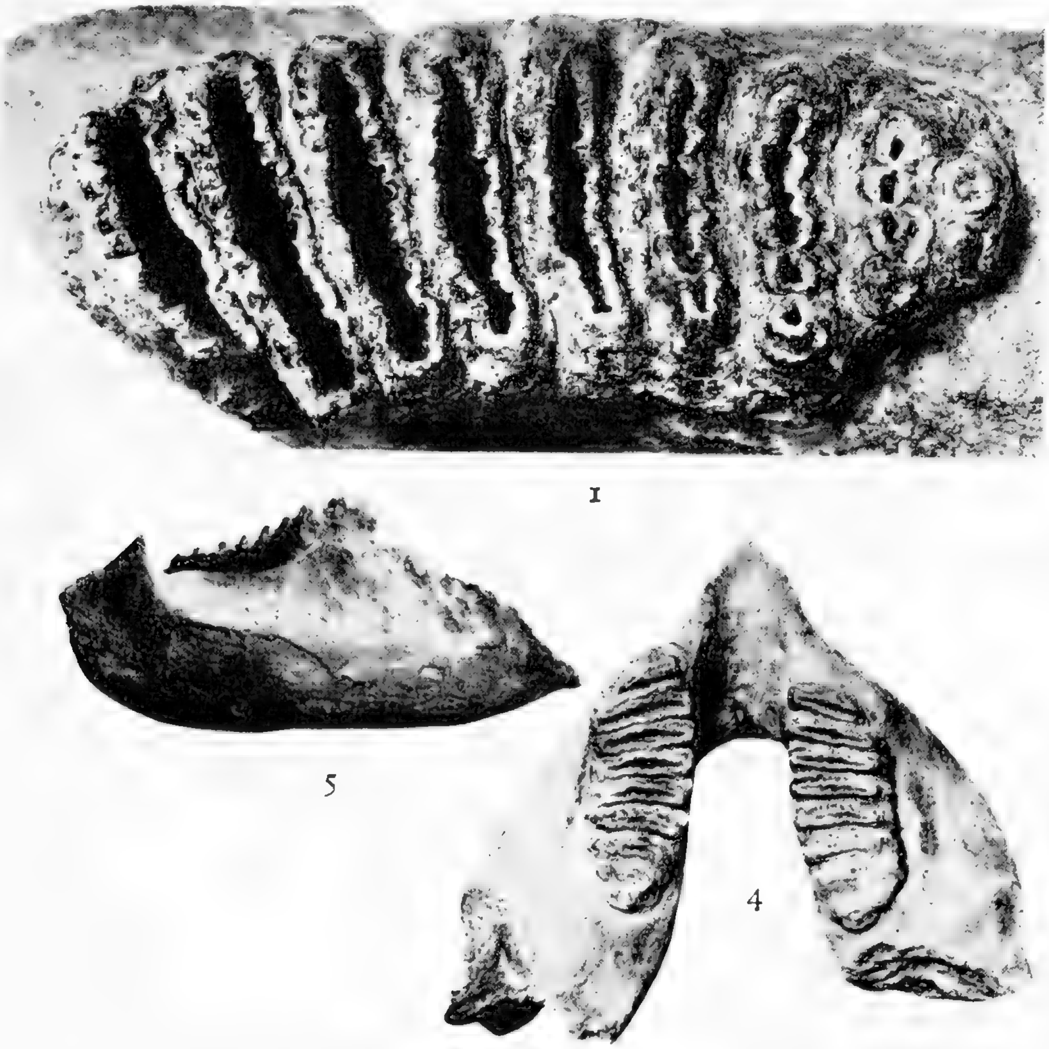

Fig. 782. Type mandible and enlargement of third left inferior molar of *Stegodon bondolensis*. After van der Maarel, 1932, Pl. XIV, figs. 1, 4, and 5. Molar about three-fifths natural size; mandible about one-seventh natural size. From Bondol, Java.

(Upper) Crown view of third left inferior molar, l.M$_3$, with 8+ ridge-crests; same molar as in accompanying lower jaw.

(Lower, right) Superior view of fragmentary lower jaw with right and left third molars *in situ*.

(Lower, left) Right lateral view of same jaw.

"The tooth is distinctly curved outwards. The base of ridge-crests 1–7 are more or less of the same length; from ridge-crest 8 inner and outer side of the molar converge suddenly backwards."

"The base of the crown and the grinding surface are strongly concave. The grinding surface slopes obliquely from the outside inwards."

"The enamel is moderately thick and consists of two layers (see the buccal cusps of ridge-crest 7). A distinct 'Stufenbildung' can, however, only be seen in the last three ridge-crests. In this connection attention may be drawn to the fact that in the molars of the present specimen enamel, cement and the greater part of the dentine had the same irregularly spotted appearance. As a result the crenulation of the enamel was very indistinct, and it was only possible to make it distinctly visible in the photograph by blackening the dentine of the tooth. Another result is, however, that 'Stufenbildung' though present, is in general not clearly exhibited."

"There is no indication of the presence of a median longitudinal cleft. Cement is present, though in small quantities. The valleys between ridge-crests 1, 2, 3, 4 and 5 possess but little cement. More backwards the amount is somewhat less small, not only the base of the valleys being filled to a greater extent, but also the lingual and buccal sides of the ridge-crests, and the posterior side of the hind talon being covered by a thin coat of cement. Noteworthy is the stronger, local development of cement near the buccal side of ridge-crest 7."

"MEASUREMENTS OF R. AND L.M_3 IN MM.

Total length of r. M_3 190 mm. } measured along median line
Ditto " l. M_3 197 " } of crown."

"As a matter of fact all the species of *Stegolophodon* may be left out of consideration, being all very primitive forms which in my opinion may as well be reckoned to the family of the *Mastodontidæ*."

"On the other hand, most of the remaining species [of *Stegodon*] are considerably more progressive than the form to which the lower jaw in question belongs."

"In my opinion we may, therefore, conclude, that the present Javan form is distinct from all other species. I propose the specific name of *bondolensis,* indicating the locality from whence it has been procured."

Fig. 783. Type left third inferior molar, l.M_3, of *Stegodon trigonocephalus praecursor*, after von Koenigswald, 1933, Taf. XXVII, fig. 2, two-thirds natural size. From Bumiaju, Java.

Stegodon trigonocephalus praecursor

von Koenigswald, 1933

Figure 783

Untere Schichten, Kali Glagah, Bumiaju, Java.

Stegodon trigonocephalus praecursor von Koenigswald, 1933. "Beitrag zur Kenntnis der Fossilen Wirbeltiere Javas." Wetenschappelijke Mededeelingen, Dienst Mijnbouw Nederl.-Indië, I Teil, No. 23, pp. 104, 105. TYPE.—Lower jaw with third molar of both sides complete. HORIZON AND LOCALITY.—Untere Schichten, Kali Glagah, Bumiaju, Java. TYPE FIGURE.—*Op. cit.,* Taf. XXVII, fig. 2 (third lower molar of the left side, l.M_3).

DESCRIPTION.—(von Koenigswald, 1933.1, pp. 104, 105): "Es liegt ein Unterkiefer vor, dessen beide M_3 noch komplet sind. M_3 rechts ist isoliert, ein Teil der starken Zementlage ist abgewittert, so dass auch die letzten noch nicht angekauten Joche und der kleine Talon hervortreten. Der linke M_3 sitzt noch auf dem leider etwas gequetschten Kieferast, der im vorderen Teil anscheinend weniger an Höhe zunahm, als es bei der typischen Form der Fall ist. Die letzten drei Joche und der Talon liegen noch dick unter Zement."

"Diesen letztaufgeführten Zahn bilde ich Taf. XXVII ab, neben dem entsprechenden Zahn von *St. t. trigonocephalus* von Pitoe, nahe Trinil. Dieser letztgenannte Zahn ist ca. 270 mm lang und gehörte einem mittelgrossen Tier. Zwei letzte Molaren von Trinil sind (nach Janensch) 304 und 303 mm lang, auch solche von Watoealang und Ngandong erreichen 300 mm, (da sie z. T. mit der Hinterhälfte noch im Kiefer stecken, kann ihre Grösse nur geschätzt werden.) Dem gegenüber müssen die Zähne von Boemiajoe mit ca. 240 mm klein genannt werden. Dabei haben sie dieselbe Breite und dieselbe Biegung, wie die anderen Zähne. Die Verkürzung kommt daher, dass die Zähne von Boemiajoe nur X 11 X Joche besitzen gegenüber X 13 X bei der jüngeren Form. Dubois (1908, pg. 1256) gibt für das Stegodon der Kendenglagen sogar 14 Joche an, doch ist aus seinen Ausführungen (Abbildungen hat er bisher nicht veröffentlicht) nicht zu ersehen ob er nicht etwa einen Talon mitgerechnet hat. Die Exemplare der SELENKA-Expedition haben alle, und auch die mir vorliegenden bis auf eines, nur 13 Joche. Dieses eine von Lepen Alit bei Tingang zeigt nur X 11 X Joche (vergl. v. d. Maarel, pg. 143) und gehört aber dennoch einem typischen *St. t. trigonocephalus.* Dieser Fund zeigt, dass noch unter den Stegodonten der Kendengschichten als Ausnahme Formen mit weniger Jochen auftreten können. Es ist eine bekannte Erscheinung, dass oft bei spezialisierteren Arten auch noch Rückschläge auftreten."

"Ein weiteres Kennzeichen der Zähne von Boemiajoe ist, dass der dicke Schmelz viel weniger intensiv gefältelt ist als bei der typischen Art (Taf. XXVII). Das lässt auch ein Vergleich mit den Abbildungen bei MARTIN und JANENSCH deutlich erkennen."

"Von Boemiajoe stammt auch noch ein auffallend grosser Stosszahn von etwa 3,50 m Länge, der seiner ganzen Form nach wohl nur einem *Stegodon* gehört haben dürfte."

Fig. 784. Type lower jaw with right second molar, r.M_2, *in situ*, of *Parastegodon? kwantoensis* Tokunaga, 1934, Pl. IX, fig. 1, one-half natural size.

Stegodon yüshensis Young, 1935

Figure 785

From Yüshe, China.

Stegodon yüshensis Young, 1935. "Miscellaneous Mammalian Fossils from Shansi and Honan." Pal. Sinica, (C), IX, Fasc. 2, 1935, pp. 26-28. TYPE.—"A well preserved upper left third molar." HORIZON AND LOCALITY.—"Pontian 'violet sands' of the Yüshe formation from Yüshe," China. TYPE FIGURE.—*Op. cit.*, Pl. v, figs. 1, 1a.

DESCRIPTION.—(Young, 1935.1, pp. 26–28): "With the exception of the fourth ridge and of a large part of the cingulum, the tooth is well preserved, including the roots. Crown composed of five ridges, not including the posterior heel and the anterior cingulum. . . . The ridges are rather closely set; the valleys not very deep; only slight traces of cement can be observed. Cingulum is very weakly indicated in the preserved parts."

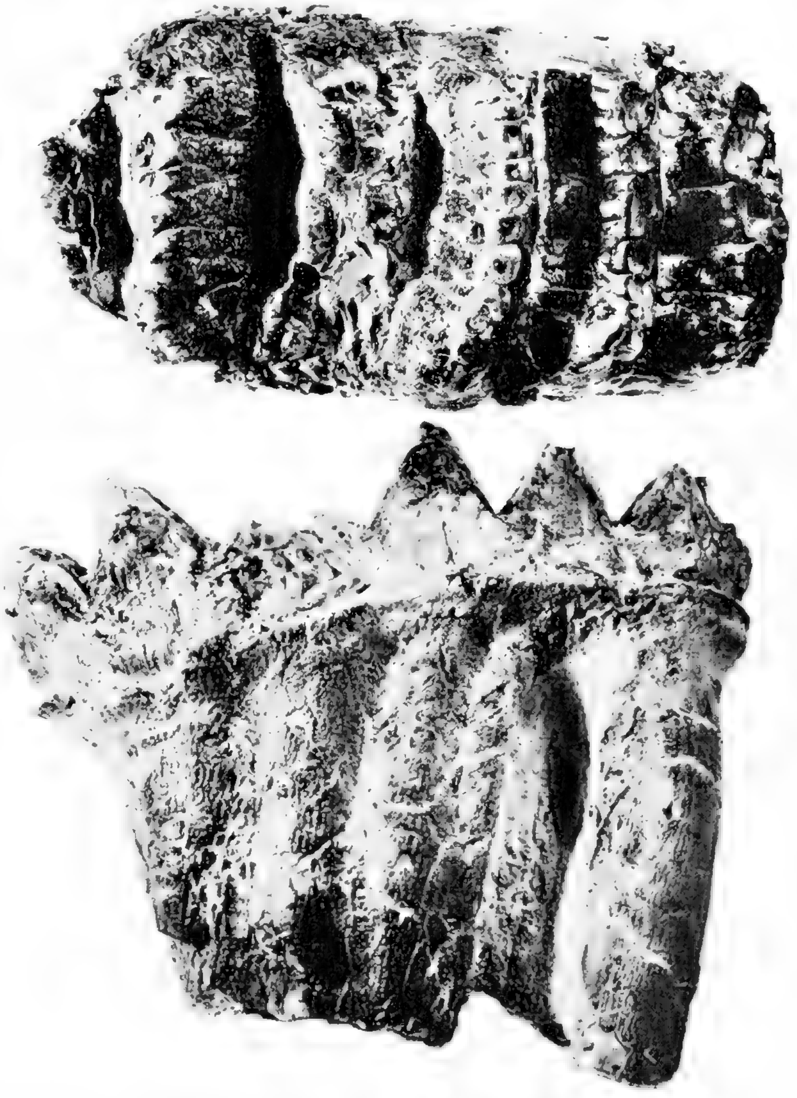

Fig. 785. Third superior molar of the left side, l.M^3, of *Stegodon yüshensis*, after Young, 1935, Pl. v, figs. 1, 1a, two-thirds natural size. From Yüshe, China. (Upper) Crown view. (Lower) External view.

Parastegodon? kwantoensis Tokunaga, 1934

Figure 784

Kakio, Kanagawa Prefecture, Japan. Upper Pliocene (*fide* Tokunaga).

[The description in Japanese by Professor Shigeyasu Tokunaga of his species *Parastegodon? kwantoensis*, 1934, was not reviewed by Professor Osborn. However, as the present author regarded *Parastegodon* as either a progressive *Stegodon* or a primitive *Archidiskodon*, his generic reference cannot be given in the present Memoir. The following résumé in English is by Mr. Ushinosuke Narahara of the American Museum of Natural History.—Editor.]

Parastegodon? kwantoensis Tokunaga, 1934. "Fossil Elephant teeth found at Yokohama and Kakio, Kanagawa Prefecture," Journ. Geog. (Tokyo), Vol. XLVI, No. 546, July, 1934, pp. 365–369. TYPE.—Portion of lower jaw with right second molar, r.M_2, *in situ*. HORIZON AND LOCALITY.—Kakio, Kanagawa Prefecture, Japan. Upper Pliocene (*fide* Tokunaga). TYPE FIGURE.—*Op. cit.*, Pl. IX, figs. 1–3.

DESCRIPTION.—Portion of a lower jaw with right second molar, r.M_2, *in situ*; eight and a half ridge-crests, probably ten if perfect; molar valleys deep, narrow, and filled with cement.

Length of jaw bone	253 mm.
Second molar, r.M_2	
Length	190
Breadth	76
Height (outside)	35
Height (inside)	31
5,4 ridge-crests in 100 mm.	

The specimen is primitive like *Parastegodon* [*Stegodon*] *auroræ* Matsumoto, but with certain differences, which he [Tokunaga] believes warrants its assignment to a new species, namely, *Parastegodon? kwantoensis*.

"With the exception of the first ridge which has three roots (external, internal, median) and of the last ridge, under which the roots build a continuous transversal lamella, each ridge has two distinct roots. The four posterior ones are laterally fused along the external side of the tooth, and the three posterior ones along the internal side."

"Dimensions:—[with some omissions]
Maximum length of the tooth . . . . 158 mm.
Breadth at the third ridge [maximum] . . . . 83 mm.
Height of the crown above the cingulum at the 3rd ridge . . . . 36 mm."

"Both *Stegodon officinalis* Hopw. and *zdanskyi* Hopw. are distinctly larger, and they have a higher number of ridges at the third molar. In size *Stegodon orientalis* Owen (1870) and *Stegodon orientalis grangeri* Osborn stand closer; but they also have one ridge more at M^3 and the cement of their teeth is more developed. *S. sinensis* Owen and *S.* aff. *bombifrons* are described from fragments only. The former one is hardly separable from *S. orientalis*: and the latter one is too large."

"We therefore have to deal with a new species, for which the name *Stegodon yüshensis* (sp. nov.) is proposed."

Stegodon officinalis Hopwood, 1935

Figures 786, 787

Said to have come from Szechuan(?), China. Horizon unknown.

Young in his memoir "Miscellaneous Mammalian Fossils from Shansi and Honan," 1935, p. 27, compares *Stegodon officinalis* Hopwood (ex MS.) with his new species *S. yüshensis.*

Fig. 786. Type of *Stegodon officinalis* Hopwood, consisting of the "first two ridges of an unworn lower molar" (cast Amer. Mus. 21878), one-half natural size. After Hopwood, 1935.1, Pl. VII, fig. 3.

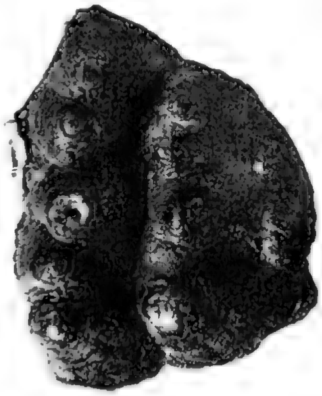

Fig. 787. "Last ridge and talon of an unworn upper(?) molar," referred by Hopwood to *Stegodon officinalis*, one-half natural size. Cast Amer. Mus. 21879. After Hopwood, 1935.1, Pl. VII, fig. 4.

Stegodon officinalis Hopwood, 1935. "Fossil Proboscidea from China." Pal. Sinica, (C), IX, Fasc. 3, 1935, pp. 73–75 (Hopwood, 1935.1). TYPE.—"The first two ridges of an unworn lower molar." Cast Amer. Mus. 21878. HORIZON AND LOCALITY.—"Bought in a medicine shop, Hanchow. Said to have come from Szechuan." Horizon unknown. TYPE FIGURE.—*Op. cit.*, 1935.1, Pl. VII, fig. 3.

MATERIAL.—(Hopwood, 1935.1, p. 73): "The unworn last ridge and talon of a third molar. Probably from the upper jaw." Cast Amer. Mus. 21879.

DESCRIPTION.—(Hopwood, 1935.1, pp. 73–75): "A *Stegodon* with the ridge-crests widely spaced, with four to five mamillæ on each ridge; first and second ridges of lower molar divided by a median cleft; conules of upper molars not united into ridges."

"The anterior ridge is divided into two cusps by a deep median cleft. The post-trite cusp has two large cones with a third, smaller one, between them. The tips of the cones of the pretrite cusps have, with one exception, been broken off. The second ridge is also divided by a median cleft, but this is not so prominent as in the first ridge. The pretrite cusp has three cones, and the post-trite has two. The ridges are much narrower at the top than at the base, this is especially true of the second hence the labial and lingual surfaces of the tooth slope inwards to a very marked extent. The anterior surface of the second ridge is nearly perpendicular, whereas the posterior surface slopes away at a fairly steep angle. This difference in the slope of the two surfaces gives the ridge the appearance of being tilted forwards, a sign of derivation from a lower tooth. . . . There are no lateral cingula, nor are there cingules at the entrances to the valleys. No cement is present."

"The second fragment consists of the last ridge and talon of a large tooth, which is doubtfully regarded as a third upper molar. The ridge consists of five cones which are not fused to one mass, but are separated by definite clefts. One cleft is deeper than the others; hence the cones are divided into two groups, one with three cones and the other with two. A large part of the talon is covered by cement, above which there rise the tips of four cones. . . The ridges are upright, with their anterior and posterior surfaces sloping at about the same angle; the valley between them is narrow, and partly filled with cement."

Discussion by Hopwood.—"There is no proof that these two specimens are correctly associated. At the same time it is evident from their preservation that they are both derived from the same deposit, which appears to have been of a lignitic, or peaty nature. They indicate the existence of a species which has hitherto been unknown and it is preferable to assume an unproven connexion, instead of making two 'species', one of which might have to be relegated to the synonymy at a later period."

"In placing the species with *Stegodon* rather than in *Stegolophodon,* I have had regard to the characters of the ridges of the holotype. One of the chief differences between the two genera is that whereas in *Stegodon* the cones are united into ridges, in *Stegolophodon* they remain discrete. Admittedly the cones in the fragment of an upper tooth are still divided by deep clefts, but they show the first stages of union, and the cones in each half of the ridge are more closely joined to each other than the two halves of the ridges."

"This species is the most primitive yet recorded from China. In the division of the lower ridges into two cusps, as well as in the division of the upper ridges and the slight displacement of the two halves, it retains characters which derive from a mastodont ancestry. Traces of this inheritance are never entirely lost among the Stegodontidæ and they persist with more or less regularity among the elephants. There are several species in a similar stage of evolution among the fauna of the Siwalik deposits of India, but they have not yet been described. So far as is at present known, the Indian species have blunter cones than the Chinese form, and their ridges are not so high."

"The trivial name refers to the chance that these specimens were purchased in the shop of a Chinese druggist."

Stegodon zdanskyi Hopwood, 1935

Figure 788

Horizon unknown.

The name *Stegodon zdanskyi* Hopwood first appeared (ex MS.) in Young's memoir on "Miscellaneous Mammalian Fossils from Shansi and Honan," 1935, pp. 27 and 28; to this species Young has referred "an upper left maxillary with M², M³ *in situ* and. . . an isolated right M³ evidently belonging to the same individual, both found in the Pontian sands of Yüshe. A fragment of molar and some milk teeth may also belong to the same species."

Stegodon zdanskyi Hopwood, 1935. "Fossil Proboscidea from China." Pal. Sinica, (C), IX, Fasc. 3, 1935, pp. 75, 76 (Hopwood, 1935.1). TYPE.—"The first four ridges of a right third lower molar." Cast Amer. Mus. 21872. HORIZON AND LOCALITY.—"Bought in a Medicine Shop, Shanghai." Horizon unknown. TYPE FIGURE.—*Op. cit.,* 1935.1, Pl. VII, fig. 5.

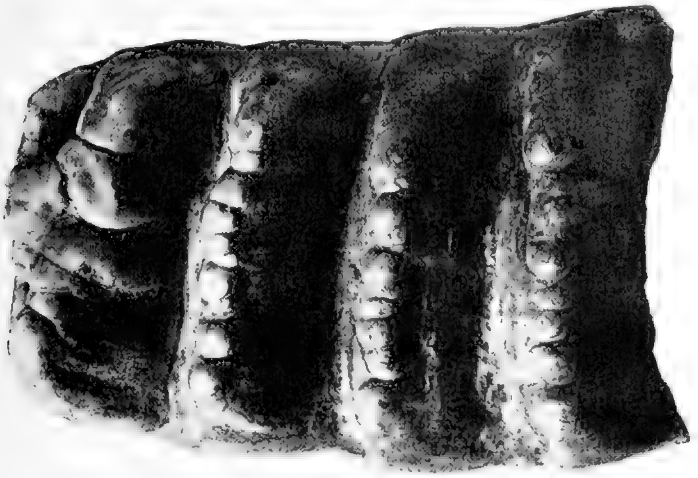

Fig. 788. Type of *Stegodon zdanskyi* Hopwood. "First four ridges of a right third lower molar" (cast Amer. Mus. 21872), after Hopwood, 1935.1, Pl. VII, fig. 5, one-half natural size.

DESCRIPTION.—(Hopwood, 1935.1, pp. 75, 76): "A *Stegodon* of very large size, with eight to ten mammillæ on each ridge-crest; anterior ridge still preserving the two cusps of the earlier mastodont ancestors, posterior ridges foreshadowing the structure of the plates found in the teeth of the Elephantidæ."

"The first ridge of this specimen is divided into two cusps by a prominent mesial cleft. Each cusp, especially the pretrite one, is divided into two cones by a cleft which is not so prominent as that which separates the cusps. The cones themselves are again divided at the summit into two or three mammillæ by grooves, which do not proceed very far down the anterior and posterior surfaces. None of the other ridges show this sub-division; they are all divided, but in a very different manner."

"Each of the posterior ridges has a large cone at either end, with one or two mammillæ at the summit. Between these cones is a long, roof-like portion with a mammillated crest. The number of mammillæ varies with the manner of counting. If the main eminences alone are reckoned, there are from four to six; if each tiny sub-division, or indication of one, is counted, this number is increased."

"The crown of the tooth is curved to the right, and, seen from the side, it is very slightly concave. The ridges have a forward pitch; that is to say, their anterior faces are steeper than the posterior. All these are marks of a right lower molar."

"Anteriorly there is a relatively slender cingulum, which receives a nodular buttress passing downwards and inwards from the inner cone of the pretrite cusp of the first ridge. There are no lateral cingules at the entrances of the valleys. A small quantity of cement is present."

Discussion by Hopwood.—"This species is the largest *Stegodon* yet recorded. Apparently it has nothing to do with the Indian species hitherto described; they are all smaller, have the ridges closer together, and more copious cement. An undescribed Indian species, in which the third upper molar is 243 mm long and 181 mm wide, is of about the same size, but its ridges are more of the type of *Stegolophodon stegodontoides* (Pilgrim), and it is probably referable to the same genus as that species."

"Apart from its size, the most interesting feature of *S. zdanskyi* is the curious mixture of elephantine and mastodontine features in its ridges. In its composition of two cusps, each made up of two cones, and in the relations between the pretrite cusp, anterior buttress, and the cingulum, the first ridge is, fundamentally, that of any mastodont of the bunolophodont, or primitive zygodont, type. All the other ridges are essentially elephantine in their structure. They each have a large cone at either end, and a long, mammillated, roof-like portion in the centre. If the two fissures which divide the tooth in this manner are deep enough, the partly worn tooth would show a tripartite enamel figure. This tripartite division is characteristic of the elephants, though it is also shown by some, at least of the *Stegodon* group (cf. Soergel, 1912 [1912.2], p. 8, fig. 2). In most cases it consists of two outer rings with an ellipse between them; exactly the type of figure which could arise during the wearing down of a lower tooth of *S. zdanskyi.*"

"All the other remains of *Stegodon* from China hitherto described (Owen, 1870 [1870.1]; Koken, 1885 [1885.1]; Schlosser, 1903 [1903.1]; *et alii*) belong to more advanced species, and, by a general consensus of opinion, the various writers, other than Owen, have referred them to such species as *S. bombifrons, S. ganesa,* or *S. insignis.*"

"The trivial name is given in honour of Dr. O. Zdansky of the Egyptian University, Cairo, who is well known for his valuable researches on the fossil mammals of China."

Parastegodon [Stegodon?] sugiyamai Tokunaga, 1935

Figure 789

At Iruhi, in Saida village, Shikoku, Japan. Upper Pliocene or Lower Pleistocene (*fide* Tokunaga).

Parastegodon sugiyamai Tokunaga, 1935. "A New Fossil Elephant Found in Shikoku, Japan." Proc. Imp. Acad. Tokyo, Vol. XI, p. 434. TYPE.—An upper molar of the left side, probably an M^2. HORIZON AND LOCALITY.—"Mr. T. Sugiyama recently sent the author [Tokunaga] a specimen of a molar-tooth, obtained during road construction at Iruhi in Saida village, Shikoku. The stratum from which it was obtained consists of an alternation of loose shale and coarse-grained quartz-sandstone, and probably referable to either the old Pleistocene or to the youngest Pliocene." TYPE FIGURE.—*Op. cit.*, p. 433, crown and inner side view of molar.

TYPE DESCRIPTION.—(*Op. cit.*, pp. 432–434): "Since mediaeval times numerous specimens of fossil bones and teeth of elephants have been scooped up from the sea-bottom by fishermen's nets along the eastern part of the Inland Sea of Japan. However, very seldom are specimens discovered from strata exposed on the land surface along that part of the sea. The author is aware of only several cases, namely, a few found in situ at Akashi on the north shore of the sea, and at Sue village, Ayauta-gun, and Saida village, Mitoyo-gun, Kagawa-ken, both in the south of the sea."

TYPE OF PARASTEGODON [STEGODON?] SUGIYAMAI

Fig. 789. Type molar, probably an LM^2, of *Parastegodon sugiyamai* Tokunaga, 1935, text figure, p. 433, one-half natural size. From Shikoku, Japan.

"The present specimen obviously belongs to *Stegodontinae* in having a low crown, and in other points, but in shape, size, number of ridges, and especially in the nature of its enamel plication the present fossil is referable to no known species from Japan. It closely resembles *Stegodon airâwana* Mart., and *Stegodon trigonocephalus* Mart. from Java; and is closest to the former. The following is the description of the specimen."

"In the crown view, one side of the tooth is nearly straight and the other slightly convex. The grinding surface is oval and slightly convex, and its base is also slightly convex antero-posteriorly, indicating that it is an upper left molar. The anterior part of the crown is broken off and there [are] preserved a posterior talon, seven ridges and a part of another; most probably the first ridge and the anterior talon are lost. The foremost, namely, second ridge has its anterior portion somewhat damaged and its outer portion broken off, and the next three ridges also lack their outermost portions. All the ridges are distinctly exposed, not covered by cement. The posterior talon was covered by cement and first showed itself by shaving off the cement; it is half as high as the adjoining ridge. The last ridge is just touched by wear and the other ridges were worn by grinding."

"The present specimens, when complete, probably had nine ridges, an anterior and a posterior talon."

"The length of the crown of the present specimen is 120 mm +20 mm, the latter term being the estimated length of the lost part. The width of the grinding surface is 60 mm at the sixth ridge (67 mm at its base). The height of the crest is 34 mm at the worn eighth and 38 mm at the unworn ninth. The eighth and ninth ridge-crests decline forwards and are a little curved in side view, while the seventh but slightly declines forwards and is flat and not curved in the same view; all the other ridges stand upright. In well worn stage each ridge-crest is narrowly rectangular, not strongly constricted, and has its enamel finely plicated; in a less advanced stage of wearing, it shows a large number of constrictions. In these features the present specimen resembles in general *S. airawana*; however, the detailed enamel plication of its crown-ridges is characteristic when compared with the specimens of the latter illustrated by Soergel, Janensch, Stehlin, Maarel and Koenigswald. The unworn last or ninth ridge of ours has seven mammillae on crest and the eighth has seven constrictions. In the seventh ridge the dentine area is expanded and there are still five constrictions, while in the sixth and all the others forwards there is no constriction. The enamel is finely and rather regularly plicated in the seventh and anterior ridges and never form rough irregular undulations exhibited on grinding surface by Maarel's Javan specimen, as his photograph shows, which is similar to our molar in the size of crown and grinding degree. The width of enamel measures 4 mm at the thickest portion in grinding surface."

"In this specimen all its ridges except the posterior talon rise higher above the cement and the last or ninth is the highest."

"The property of the enamel plication of each ridge-crest of the author's specimen agrees with no described Japanese species and differs in several points from the Javan species. Moreover it presents several features different from fossil elephants of other lands. The present specimen evidently needs a new name, and is named, *Parastegodon sugiyamai* in honor of the discoverer, Mr. Tsurukichi Sugiyama. The author is at present unable to affirm whether it represents the first or the second molar, but it evidently belongs to one of them."

APPENDIX TO CHAPTER XIV

MATSUMOTO ON THE PHYLOGENY AND CLASSIFICATION OF THE JAPANESE MASTODONTS, STEGODONTS, AND ELEPHANTS (1924, 1925, 1926, 1927)[1]

The numerous and diversified Proboscidea of Japan prove that this region from Miocene to early Pleistocene times had broad land connections with southern Asia, Burma, and India, with remote relations by migration to Europe and Africa.

Subsequent to and independently of the conclusions reached by Osborn on the classification and phylogeny of the mastodontine and elephantine Proboscidea, Hikoshichirô Matsumoto published the systematic and theoretic results of his important revision of the Japanese Proboscidea in six papers, as follows:

> "Preliminary Note on Fossil Elephants in Japan," Journal of the Geological Society of Tokyo, Vol. XXXI, No. 371, September 20, 1924 (1924.2).
>
> "Preliminary Notes on the Species of Stegodon in Japan," Journal of the Geological Society of Tokyo, Vol. XXXI, No. 373, November 20, 1924 (1924.3).
>
> "Preliminary Notes on Two New Species of Fossil Mastodon from Japan," Journal of the Geological Society of Tokyo, Vol. XXXI, No. 375, December 20, 1924 (1924.4).
>
> "On Two New Mastodonts and an Archetypal Stegodont of Japan," Science Reports of the Tôhoku Imperial University, Second Series (Geology), Vol. X, No. 1, 1926 (1926.1).
>
> "On the Archetypal Mammoths from the Province of Kazusa," Science Reports of the Tôhoku Imperial University, Second Series (Geology), Vol. X, No. 2, 1926 (1926.2).
>
> "On a New Fossil Race of the Asiatic Elephant in Japan," Science Reports of the Tôhoku Imperial University, Second Series (Geology), Vol. X, No. 3, 1927 (1927.1).

His results are summed up in his three phylogenetic diagrams reproduced herewith (Figs. 791, 792, 793) and in the following systematic summary or conspectus compiled from notes included in Doctor Matsumoto's letters of July 14 and November 20, 1924, and from his two more recent papers of 1926 and 1927. Matsumoto's valuable letters and notes, intercalated in the English text of his published report of 1926, give us a clear statement of his observations and opinions, as compared with those of the present Memoir indicated in square brackets.

Osborn (1927) adopts certain of Matsumoto's generic and specific terms (e.g., *Palæoloxodon* Mats., which antedates *Sivalikia* Osb.), but rejects others (e.g., *Hemimastodon* Pilgrim, *Prostegodon* and *Parastegodon* Matsumoto, which are antedated by genera of other authors). A full synopsis of Matsumoto's work (1924–1927)[1] is given herewith for monographic purposes, followed by Osborn's comments (p. 908 below).

1. Genus Hemimastodon Pilgrim [=Suina, Volume I, Chapter VIII]

Hemimastodon Pilgrim.

1. *Hemimastodon annectens* sp. nov., Journ. Geol. Soc. Tokyo, Vol. XXXI, 1924.4, pp. 401, 405. See present Memoir, Chapter X, p. 457. [=*Serridentinus annectens.*]

2. Genus Trilophodon Falconer [=Trilophodon of the Present Memoir, Chapter VIII]

Trilophodon Falconer.

2. *Trilophodon sendaicus* sp. nov., Journ. Geol. Soc. Tokyo, Vol. XXXI, 1924.4, pp. 402, 408. See present Memoir, Chapter VIII, p. 280. [=*Trilophodon sendaicus.*]

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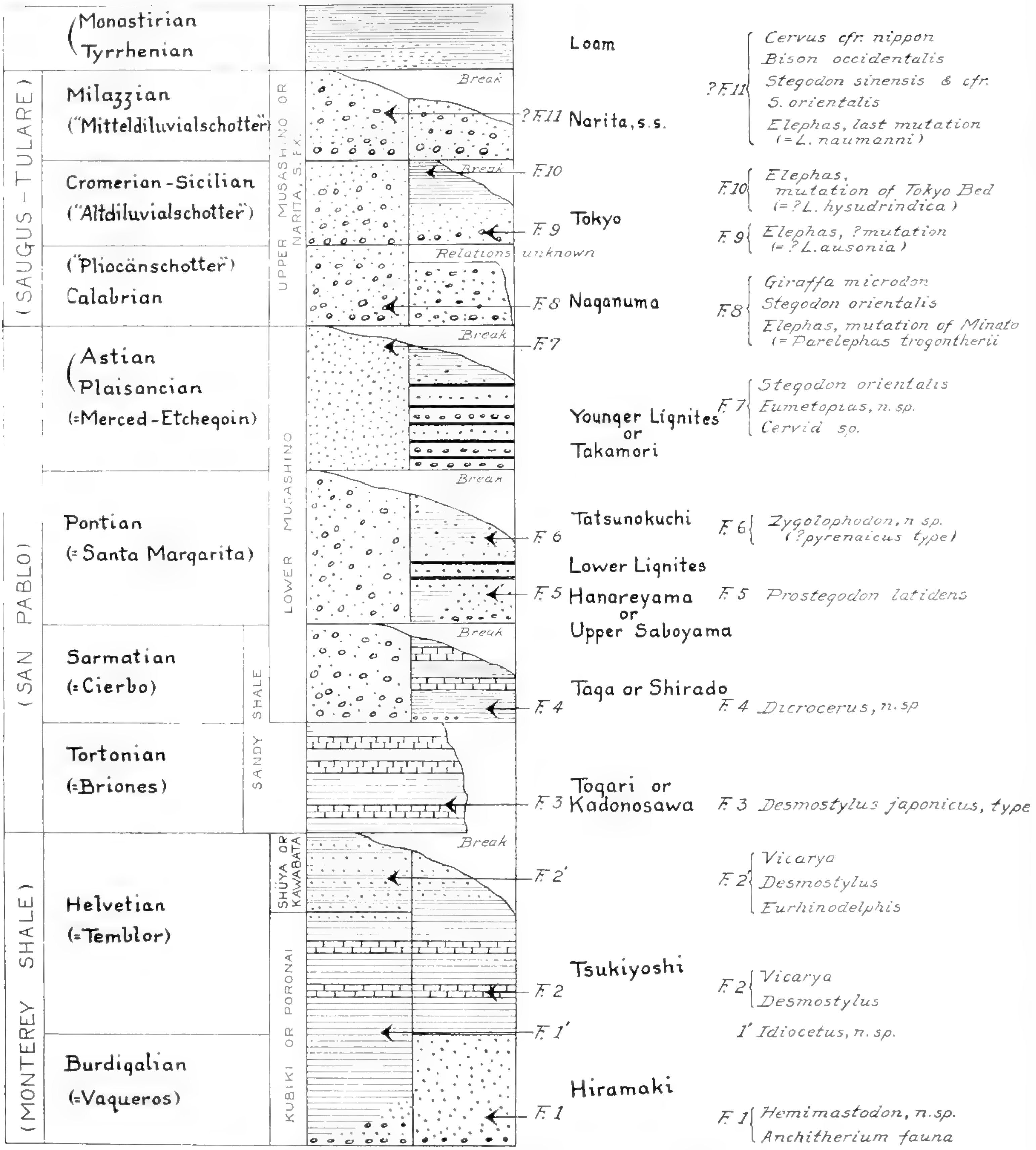
[1] [For a continuation of Matsumoto's observations and theories, up to and including 1929, see Chap. XIX, pp. 1289 to 1300 below.—Editor.]



THIRTEEN FOSSIL MAMMAL-BEARING FORMATIONS OF JAPAN. MATSUMOTO, 1924

Fig. 790. Correlation from the Lower Miocene Burdigalian to the summit of the Pleistocene Monastirian of the marine and freshwater beds of Japan with the marine and coastal stages of western Europe (Burdigalian to Monastirian) and with the epicontinental and coastal stages of the California coast of North America (Monterey shale, San Pablo, Saugus-Tulare, etc.). Reproduced with slight additions after pen drawing by Doctor Matsumoto (letter, July 14, 1924).

It will be observed that Matsumoto's summary of 1929 (see Chap. XIX, pp. 1290-1292) also Osborn's summary (p. 1292) alter both the above specific nomenclature and the geologic levels in the Japanese Tertiaries.

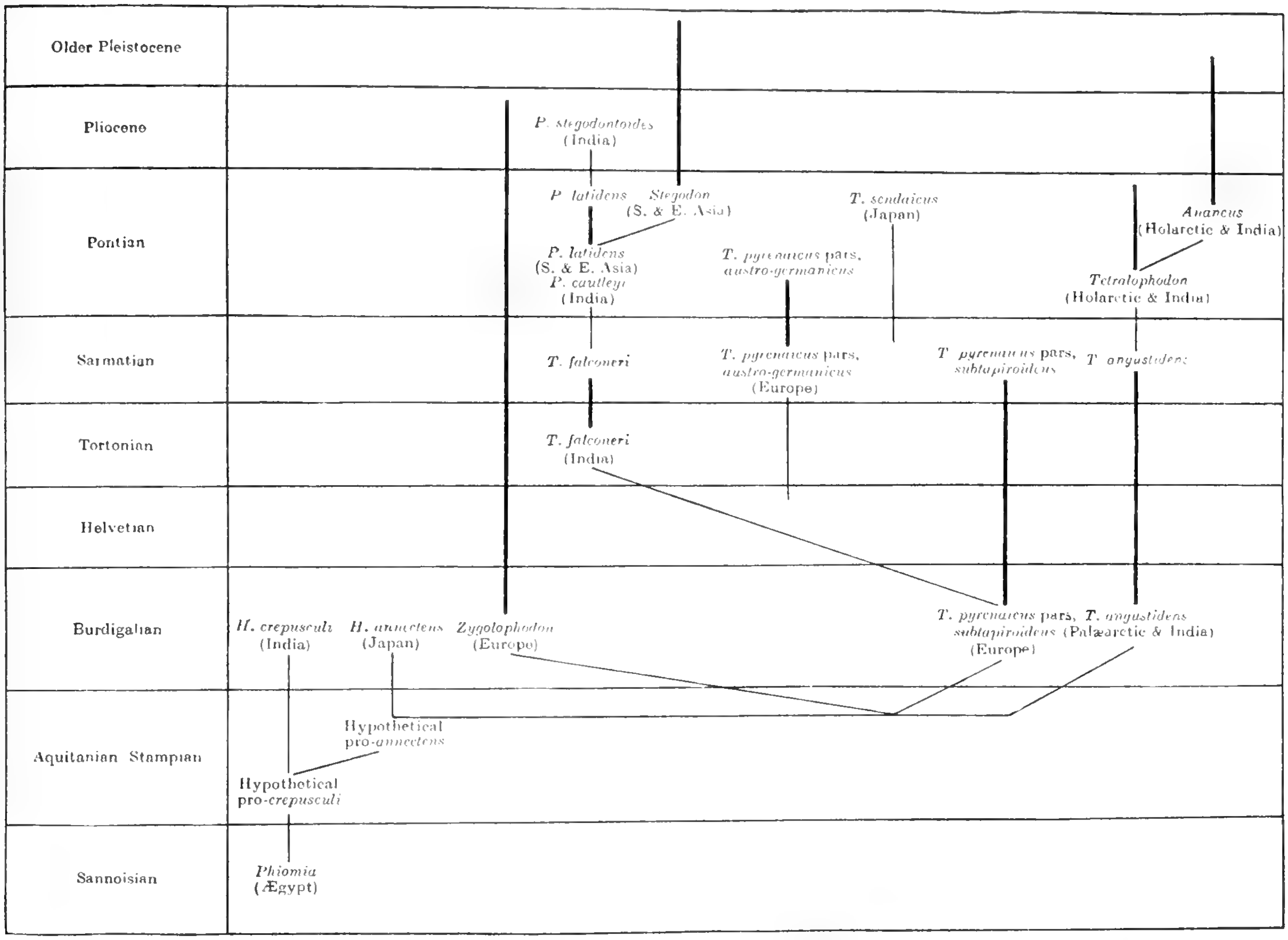


Fig. 791. Theoretic phylogeny of the Mastodontidæ (after Matsumoto, 1926.1, p. 3)

It is observed in this phylum that: (1) *Phiomia* gives rise to *Trilophodon* (pro-*annectens*, *Hemimastodon crepusculi* [=Suina], *H.* [=*Serridentinus*] *annectens*); that it extends into *Trilophodon angustidens* of the Burdigalian and Sarmatian (of Europe), also into *Tetralophodon* and *Anancus* (all unknown in Japan). (2) The second phylum includes: *Trilophodon* [=*Zygolophodon*] *pyrenaicus* theoretically giving rise to *T. falconeri*, *Parastegodon latidens*, *P. stegodontoides*, and *Stegodon*; the possible derivation of *Parastegodon* [=*Stegolophodon*] *latidens* from *Trilophodon* [=*Zygolophodon*] *pyrenaicus* is in accord with Schlosser and Osborn.

3. Genus Parastegodon Matsumoto, 1924 [may equal Archidiskodon Pohlig, 1885, 1888, of the Present Memoir, Chapter XVI, or a Progressive Stegodon, this Chapter][1]

Parastegodon gen. nov., Journ. Geol. Soc. Tokyo, Vol. XXXI, 1924, pp. 256, 257, 262(1924.2).

=*Stegodon mindanensis-Elephas auroræ* group of Matsumoto.

3. Genotype: *Elephas auroræ*.

S. mindanensis-auroræ group. Low crowned, hence *Stegodon*-like; ridges close set and valleys very narrow, very acute toward the base of crown (contrast to *Stegodon*, even to those with rather high and narrow ridges of the Pleistocene). No loxodont sinus.

Parastegodon [=*Stegodon*] *auroræ* Matsumoto, 1924, *op. cit.*, p. 262.

Mt. Tomuro, Province of Kaga—horizon unknown, possibly Pliocene.

Archidiskodon Pohlig, 1885, 1888, Matsumoto, 1924, pp. 256, 259 (1924.2).

=*Elephas planifrons-meridionalis* group. No known Japanese representative.

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[1] [See Matsumoto, 1929, "On Parastegodon Matsumoto and its bearing on the Descent of Earlier Elephants," Sci. Rept. Tôkoku Imp. Univ., (2), Geology, XIII, No. 1, pp. 13–15 (in English).—Editor.]

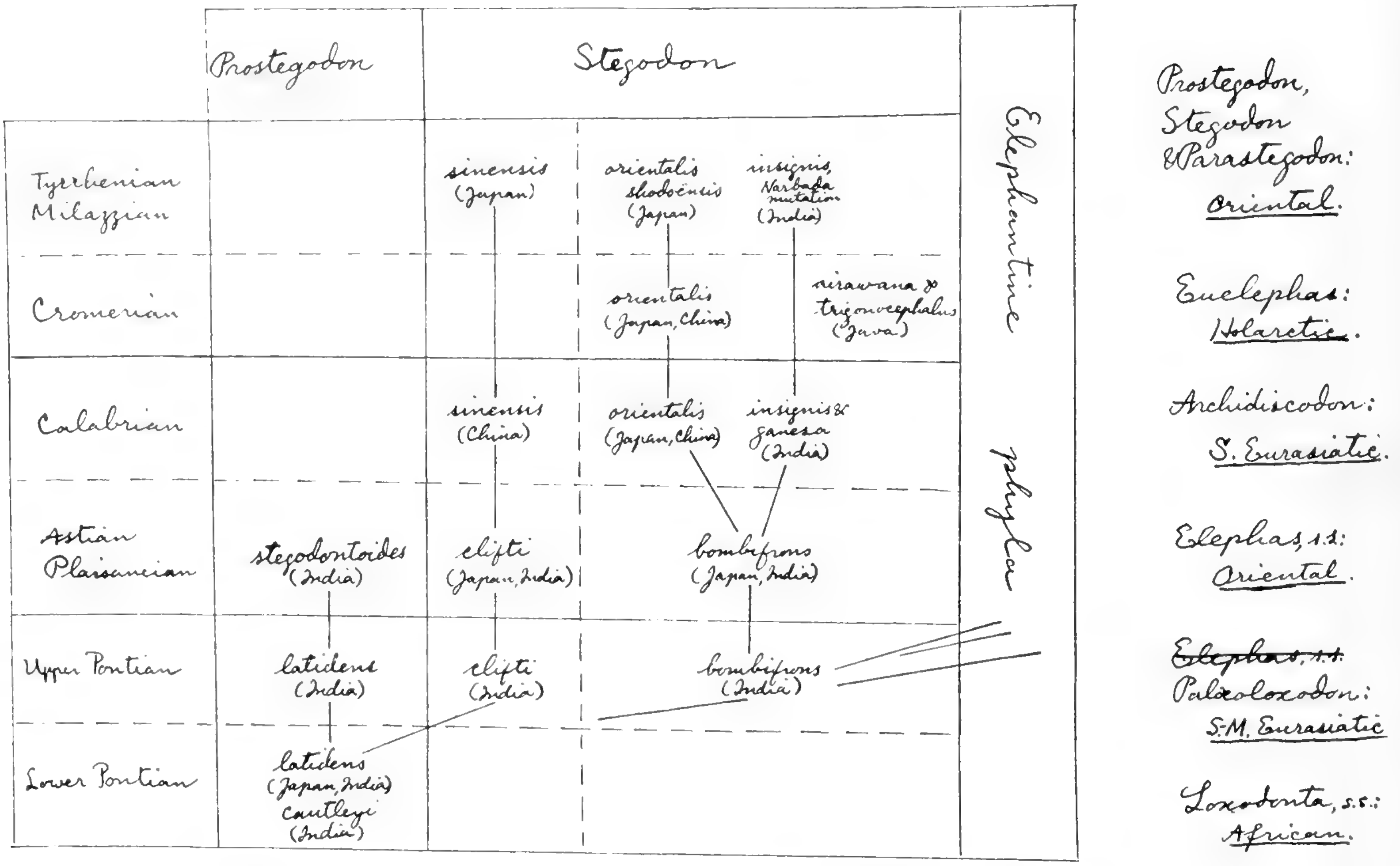

FIG. 792. THEORETIC PHYLOGENY OF THE STEGODONTS (AFTER MATSUMOTO, MS. OF NOVEMBER 20, 1924)

Observe that *Prostegodon* includes five phyla, namely: (1) The phylum of *latidens* and *stegodontoides* [=the *Stegolophodon of* Schlesinger]; that *Stegodon* includes (2) the phylum of *clifti* and *sinensis*, (3) the phylum of *bombifrons, orientalis,* and *orientalis shodoënsis*, (4) the phylum of *bombifrons, insignis,* and *ganesa*, and (5) the phylum of *airâwana* and *trigonocephalus*. This subdivision of the species of Stegodonts into several phyla, grouped under two genera, namely, (a) *Prostegodon* [=*Stegolophodon*] and (b) *Stegodon*, with their numerous branches, agrees substantially with the conclusions reached by Osborn. This diagram is reproduced in Matsumoto (1924.3, p. 339), with omission of text outside of black lines and with extension of diagonal line from *bombifrons* (India) into the *clifti* (India) column.

4. GENUS PROSTEGODON MATSUMOTO, 1923, 1924 [=STEGOLOPHODON SCHLESINGER, 1917, OF THE PRESENT MEMOIR, THIS CHAPTER]

Prostegodon gen. nov., Matsumoto in Osborn, Amer. Mus. Novitates, No. 99, 1923, p. 2 (Osborn, 1923.601); also Matsumoto, Journ. Geol. Soc. Tokyo, Vol. XXXI, p. 325 (1924.3).

4. Genotype: *Mastodon latidens* Clift. [This genus (*Prostegodon*=*Stegolophodon*[1]) includes also *Mastodon cautleyi* Lydekker and *M. stegodontoides* Pilgrim, etc.]

MATSUMOTO, 1926.1, P. 9.—"Skull and mandible only, imperfectly known, brevirostral. Lower incisor-tusks might be absent, or abortive if present at all. Intermediate molars four- or five-ridged, last molars five- or six-ridged. Grinders essentially lophodont, though their first and second ridges may show a slight tendency of bunodonty and of trefoil pattern of cusps; mesial longitudinal cleft evident; inner and outer cusps opposite, instead of being alternate; valleys widely open, free of cement. . . . As clearly pointed out by Lydekker and by Pilgrim, the group which now forms the present genus is very closely allied with the common Stegodonts, though more archetypal than the same. Notwithstanding that, it is perfectly distinct phyletically from the other two phyla of

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[1] [See page 839.—Editor.]

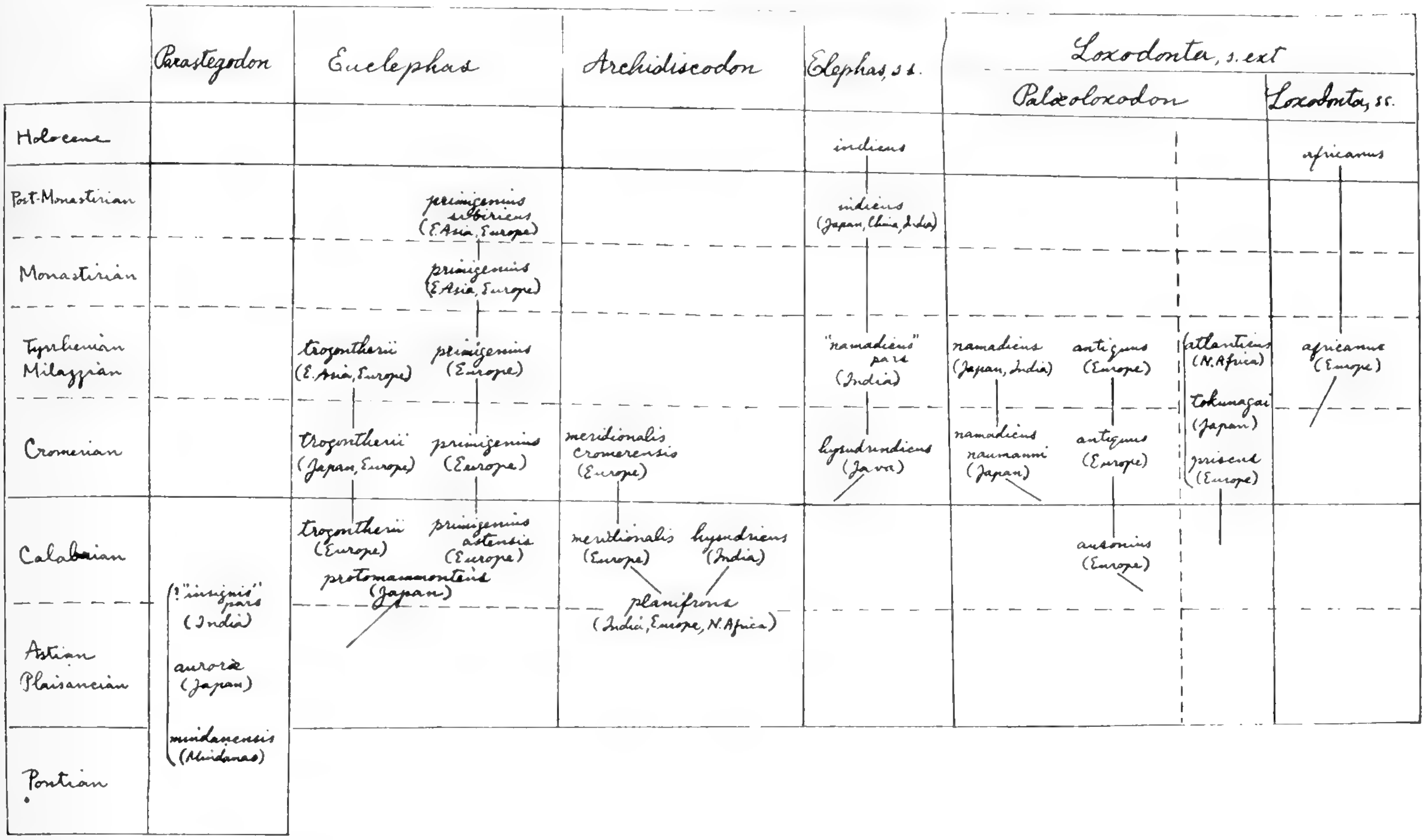

FIG. 793. THEORETIC PHYLOGENY OF THE ELEPHANTIDÆ OF ASIA AND EUROPE (AFTER MATSUMOTO, MS. OF NOVEMBER 20, 1924)

Observe that: (1) *Parastegodon* includes "*insignis*" (pars), *auroræ*, and *mindanensis*; (2) *Euelephas* includes the "*trogontherii*" phylum [=*Parelephas* of Osborn] and the "*primigenius*" phylum [=*Mammonteus* of Osborn], both derived from the species *protomammonteus* of Japan; (3) the *Archidiskodon* phylum includes the species *planifrons*, *cromerensis*, *meridionalis*, and *hysudricus*; (4) the *Elephas* phylum includes *hysudrindicus*, *namadicus* (in part), and the true *indicus* of Japan, China, and India; (5) the *Palæoloxodon* phylum includes three divisions (a) typical *Palæoloxodon namadicus* and *naumanni* [equivalent to the *Sivalikia* of Osborn], (b) the *antiquus* phylum of Europe, with *ausonius* and *antiquus*, (c) the narrow-toothed *priscus*, *tokunagai*, and *atlanticus* [=*Pilgrimia* of Osborn, made by Osborn in 1934 a synonym of *Palæoloxodon* Matsumoto], and (6) *Loxodonta* including *africanus*.

Tetralophodonts, viz., *Tetralophodon* (longirostral) and *Anancus* (=*Dibunodon*), being distinguished from the former by being brevirostral, by the more distinct lophodonty, and by the single and feeble, but not double and prominent, trefoil pattern of cusps of grinders, if distinct at all, and from the latter by the more distinct lophodonty, by the simpler and feebler trefoil pattern of cusps and by the opposite, but not alternate, halves of ridges of grinders. Further, it is distinguished from the common Stegodonts by the lower ridge-formula, by the rather less distinct lophodonty, by the ridges of grinders consisting of smaller number of mammillæ and by the entire absence of cement."

Prostegodon latidens Clift. Mt. Hanare, Kuji District, Province of Hitachi; Kitayama, northern precinct of Sendai. (Letter of Nov. 20, 1924.) Lower Pontian.

Prostegodon latidens Clift. Shiwogama, Miyagi District, Province of Rikuzen. Horizon: a bed of coarse-grained sandy tuff, probably to be referred to the Sawoyama Formation proper (Matsumoto, 1926.1, p. 10). Probably of typical Pontian age.

Note: In connection with a long description of this latter specimen, measurements are given of the tooth, a Dp^4 or an M^1.

5. GENUS STEGODON FALCONER AND CAUTLEY [=STEGODON OF THE PRESENT MEMOIR, THIS CHAPTER]

Stegodon Falconer and Cautley.

5. *Stegodon clifti* Falconer and Cautley, Journ. Geol. Soc. Tokyo, Vol. XXXI, 1924, p. 329 (1924.3).
   Akira-mura, Kage District, Province of Ise—possibly Plaisancian-Astian.

6. *Stegodon sinensis* Owen, *op. cit.*, 1924, p. 328 (1924.3).
   Island of Shôdo (Shôdo-shima or Shôzu-shima), Inland Sea—Milazzian-Tyrrhenian.

7. *Stegodon orientalis* Owen (*typicus*), *op. cit.*, 1924, p. 330 (1924.3). (Also as *S. bombifrons, op. cit.*, p. 329.)
   Nagahama, Minato Town, Kimitsu District, Province of Kazusa; *Euelephas protomammonteus* zone, i. e., Calabrian. Togane Town, same province—Calabrian. Ikadachi-mura (formerly Riuge-mura), Province of Omi: may possibly be Calabrian or Cromerian. (This locality has not yet yielded elephant remains. The specimen of '*E. namadicus*' mistakably said to have come from this locality, is really from Yokosuka.) Okimisone, Ube coal-field, Province of Suwô—probably Cromerian (Sicilian).

8. *Stegodon orientalis shodoënsis* subsp. nov., *op. cit.*, 1924, p. 333 (1924.3).
   Islands of Mitsugo (Mitsugo-shima) and Island of Shôdo, Inland Sea; off Nagasaki, Eastern Sea—Milazzian-Tyrrhenian. Kashiwazaki (town), Province of Echigo (?this form).

9. *Stegodon bombifrons* Falconer and Cautley, 1924.3, p. 336.
   Higashi-Kanamachi (town), Province of Kazusa. Upper part of Plaisancian-Astian.

6. GENUS EUELEPHAS FALCONER [=PARELEPHAS OSBORN (CHAP. XVII), MAMMONTEUS OSBORN (CHAP. XVIII), AND PALÆOLOXODON MATSUMOTO (CHAP. XIX), IN PART, OF THE PRESENT MEMOIR]

Euelephas Falconer.

=*E. trogontherii–primigenius* group. Matsumoto, 1924, pp. 256, 258 (1924.2).

The Upper Pliocene form of this phylum is *auroræ*-like in the shape of the basal parts of ridges and valleys. No loxodont sinus.

10. *Euelephas protomammonteus*, sp. n., *op. cit.*, p. 262, 265.

Nagahama, Minato Town, Kimitsu District, Province of Kazusa (type loc.); Seki-mura, same district; Uëhata, Akimoto-mura, same district; Kokubo, Ônuki-mura, same district; Ôtomi, Matsuoka-mura, same district.

Horizon: Sanuki Bed, which is the lowest one of the gravel bed series (Narita Series, s. ext.) of Calabrian-Pleistocene.

Smaller and more archetypal than *E. trogontherii*.

Newly recognized in the Japanese Upper Pliocene fauna. I mean the oldest *Elephas* from Minato. Molars small; crown low. Lower molars *E. trogontherii*-like, while the upper molars are *E. primigenius*-like. I became convinced, after examining a number of upper molars, that it is a mammoth but not a Loxodont.

Parelephas protomammonteus (Matsumoto) *typicus*, 1926.2, p. 43, Pl. XVIII, figs. 1–4 (holotype); Pl. XIX, figs. 1–3 (paratype); Pls. XX–XXIII, figs. 1, 2 (referred).

Nagahama, Town of Minato, Kimitsu District, Province of Kazusa (locality of type and paratype and one referred specimen); Seki-mura, same district; Uëhata, Akimoto-mura, same district; Sankawa Valley, Hosono, Matsuoka-mura, same district (referred specimens).

10*a*. *Parelephas protommamonteus proximus,* mut. nov., 1926, p. 48, Pl. XXIV, figs. 1, 2 (1926.2).

Isone, Kokubo, Ônuki-mura, Kimitsu District, Province of Kazusa. Horizon: Probably "from a certain lower part of the Narita Series." Age: May belong to Lower Calabrian.

11. *Euelephas trogontherii* (Pohlig), 1924.2, p. 265.

Lake Kasumiga-ura, Province of Hitachi; Hishiike, Hadsu District, Province of Mikawa (lost specimen).

Horizon: *Loxodonta* (*Palæoloxodon*) *namadicus naumanni* zone, which corresponds to the Tokyo Bed, as well as the middle bed of the Narita Series, s. ext., just mentioned.

Age: Cromerian (= Sicilian).

12. *Euelephas primigenius typicus.* Japan, Siberia, Eastern Mongolia (1924.2).

The precise locality of the Japanese specimen, which I examined, from the collection of the Kyoto Imperial University, subsequently will be determined by one of the professors of that University.

(*Euelephas primigenius sibiricus*). Siberia, Eastern Mongolia; but not yet in Japan.

7. GENUS ELEPHAS LINNÆUS [= ELEPHAS OF THE PRESENT MEMOIR, CHAPTER XX]

Elephas Linné, s. s. (1924.2, p. 256).

= *E. hysudrindicus-indicus* group.

Characterized by the total absence of loxodont sinus, and very fine, regular, and deep plication of enamel.

13. *Elephas indicus* Linné, *op. cit.*, 1924, p. 266 (1924.2).

Between Tokyo and Kanagawa (Leith Adams); Yedobashi, Tokyo; Ninohe District, Province of Mutsu; Sapporo, Hokkaidô; Province of Mino; Prefecture of Wakayama; besides several specimens from unknown localities—probably Post-Monastirian and Pre-Neolithic. This species lived also in China.

This true *Elephas* phylum was doubtless present in Japan, though so long confused with '*E. namadicus*.' E.g., Naumann's Yedobashi specimen; Busk-Lydekker's Kanagawa specimen; Province of Mino specimen and Prof. Tokunaga's photograph at your hand (this specimen was lost by the great disaster of last year of Japan). All the Japanese specimens are not at all or scarcely fossilized, occurring from loam-soil or surface deposits. May possibly be of Post-Monastirian warm period.

13*a*. *Elephas indicus Buski* subsp. nov., 1927, p. 57, Pls. XXVII, figs. 2 and 3 (type); Pl. XXVIII, figs. 1, 2 (referred).

Ninohe District, Province of Mutsu (type locality); precise locality of referred specimen unknown.

Age: May belong to a very late geological age, such as the Post-Monastirian.

8. GENUS LOXODONTA CUVIER [= PALÆOLOXODON MATSUMOTO OF THE PRESENT MEMOIR, CHAPTER XIX]

Loxodonta Cuv. s. ext., 1924, pp. 257, 260 (1924.2).

Subgenus *Palæoloxodon*, subg. n., *op. cit.*, pp. 257, 260 [antedates *Sivalikia* Osborn].

= *E. antiquus-namadicus* group.

Genotype: *E. namadicus naumanni* Makiyama. Almost similar to Cromerian stage of *E. antiquus.* Tokyo Bed, i.e., middle bed of Upper Musashino. Probably Cromerian.

Phylum A. *E. melitensis-atlanticus* phylum.

14. *Loxodonta* (*Palæoloxodon*) *tokunagai*, sp. n., 1924, p. 267 (1924.2).
Hira-mura, Higashi-Tonami District, Province of Etchû (type loc.).
Horizon and age unknown, may be either Calabrian or older Pleistocene.

Phylum B. *E. antiquus-namadicus* phylum.

15. *Loxodonta* (*Palæoloxodon*) *namadicus naumanni* (Makiyama), 1924, p. 264 (1924.2).

Yokosuka, Province of Sagami (Naumann); Tabata, Tokyo (Tokunaga); Sahamma, Province of Tôtômi (Makiyama); Kasumiga-ura (lake), Province of Hitachi; Imba-numa (lake), Province of Shimôsa; Hishiike, Hadzu District, Province of Mikawa; Nakao, Kiyokawa-mura, Kimitsu District, Province of Kazusa; Yamawaki, Tamaki-mura, same district; Miyata, Miura Penninsura, Province of Sagami.

Horizon: Tokyo Bed, as well as middle bed of the Narita Series, s. ext., above mentioned.
Age: Cromerian (=Sicilian).

16. *Loxodonta* (*Palæoloxodon*) *namadicus* (*typicus*) Falconer and Cautley, 1924, p. 269 (1924.2).

'*E. namadicus*,' younger type. Shôzu-shima; and also younger terrace deposits all over Japan including Hokkaidô. Probably Milazzian, or also ?Tyrrhenian. Inland Sea; Tsukiyoshi, Minami-Akita District, Province of Ugo (Matsumoto); Sagawa Town, Aki District, Province of Tosa. Hannosura, Province of Noto (Matsumoto); Sorachi, Province of Ishikari, Hokkaidô (Matsumoto); Itsukaichi, Province of Musashi.

This form in Japan consists of two types, the larger-molared type corresponds well to the Narbada type, while the smaller-molared type is commonest in Japan. Age: Milazzian-Tyrrhenian.

Few-ridged Palæarctic *Loxodonta* [*priscus-melitensis* group].

E. priscus-like form. M_3, ca.×13×; crown low; enamel thick. Hira-mura, Province of Etchû (horizon unknown); Shôzu-shima, probably Milazzian.

Subgenus *Loxodonta*, s.s., *op. cit.*, 1924, pp. 257, 261 (1924.2).
=*E. africanus* group. No known Japanese representative.

OSBORN COMMENTS (1929) ON MATSUMOTO'S PHYLOGENY AND CLASSIFICATION (1924–1927)

The very important but debatable result of Matsumoto's researches and observations above cited is the presence in Japan of the mastodontoid genus *Trilophodon* and of representatives of four[1] subfamilies, namely, the Stegodontinæ, Mammontinæ, Loxodontinæ, and Elephantinæ. Without monographic examination and comparison of these original materials and types of Asiatic and European species, it is difficult to form correct judgments as to the true phyletic and generic relationships of many of these species and subspecies.

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[1] [Actually five subfamilies, as Professor Osborn described a new subfamily, the Stegolophodontinæ, type *Stegolophodon*, in Volume I of the present Memoir.—Editor.]

PROBOSCIDEA DISCOVERED IN JAPAN, BURMA, INDIA, AND CHINA

REFERENCES BY MATSUMOTO (1924–1927)	REFERENCES BY OSBORN IN THE PRESENT MEMOIR	JAPAN	BURMA	INDIA	CHINA
Genus *Hemimastodon* Pilgrim	= SUINA				
1. *H. annectens* Matsumoto	= *Serridentinus annectens* Matsumoto	×			
Genus *Trilophodon* Falconer	= *Trilophodon* Falconer				
2. *T. sendaicus* Matsumoto	= *Trilophodon sendaicus* Matsumoto	×			
Genus *Parastegodon* Matsumoto	= *Archidiskodon* Pohlig or progressive *Stegodon*				
3. Genotypic species *Parastegodon auroræ* Matsumoto	= *Stegodon auroræ* Matsumoto	×			
Genus *Prostegodon* Matsumoto	= *Stegolophodon* Schlesinger				
4. Genotypic species *M. latidens* Clift	= *Stegolophodon latidens* Clift	×	×	×	
Genus *Stegodon* Falconer and Cautley	= *Stegodon* Falconer and Cautley				
5. *Stegodon cliftii* F. and C.	= *Stegodon elephantoides* (= *cliftii*) Falconer and Cautley	×	×	×	
6. *Stegodon sinensis* Owen	= *Stegodon sinensis* Owen	×			×
7. *Stegodon orientalis* Owen	= *Stegodon orientalis* Owen	×			×
8. *Stegodon orientalis shodoënsis* Matsumoto	= *Stegodon orientalis shodoënsis* Matsumoto	×			
9. *Stegodon bombifrons* Falconer and Cautley	= *Stegodon bombifrons* Falconer and Cautley	×		×	
Genus *Euelephas* Falconer	= *Parelephas* Osborn (in part), *Mammonteus* Osborn (in part), *Palæoloxodon* Matsumoto (in part)				
10. *Euelephas* (*Parelephas*) *protomammonteus* Matsumoto	= *Palæoloxodon protomammonteus* Matsumoto	×			
10a. *Parelephas protomammonteus proximus* Matsumoto	= *Palæoloxodon protomammonteus proximus* Matsumoto	×			
11. *Euelephas trogontherii* Pohlig		×			
12. *Euelephas primigenius*	= *Mammonteus primigenius* Blumenbach	×			
Genus *Elephas* Linnæus	= *Elephas* Linnæus				
13. *Elephas indicus* Linnæus	= *Elephas indicus Linnæus*	×		×	
13a. *Elephas indicus Buski* Matsumoto	= *Elephas* [*Palæoloxodon*?] *Buski* Matsumoto	×			
Genus *Loxodonta* Cuvier	= *Loxodonta* Cuvier				
Subgenus *Palæoloxodon* Matsumoto	= *Palæoloxodon* Matsumoto; *Sivalikia* Osborn, a synonym				
14. *Loxodonta* (*Palæoloxodon*) *tokunagai* Matsumoto	= *Palæoloxodon tokunagai* Matsumoto	×			
15. *Loxodonta* (*Palæoloxodon*) *namadica naumanni* Makiyama	= *Palæoloxodon namadicus naumanni* Makiyama	×			
16. *Loxodonta* (*Palæoloxodon*) *namadica* Falconer and Cautley	= *Palæoloxodon namadicus* Falconer and Cautley	×		×	

At present (1929) Osborn is disposed to review these Japanese proboscideans systematically (see pp. 1289–1301) in accordance with the nomenclature and in comparison with the types of species and genera illustrated in the present Memoir.

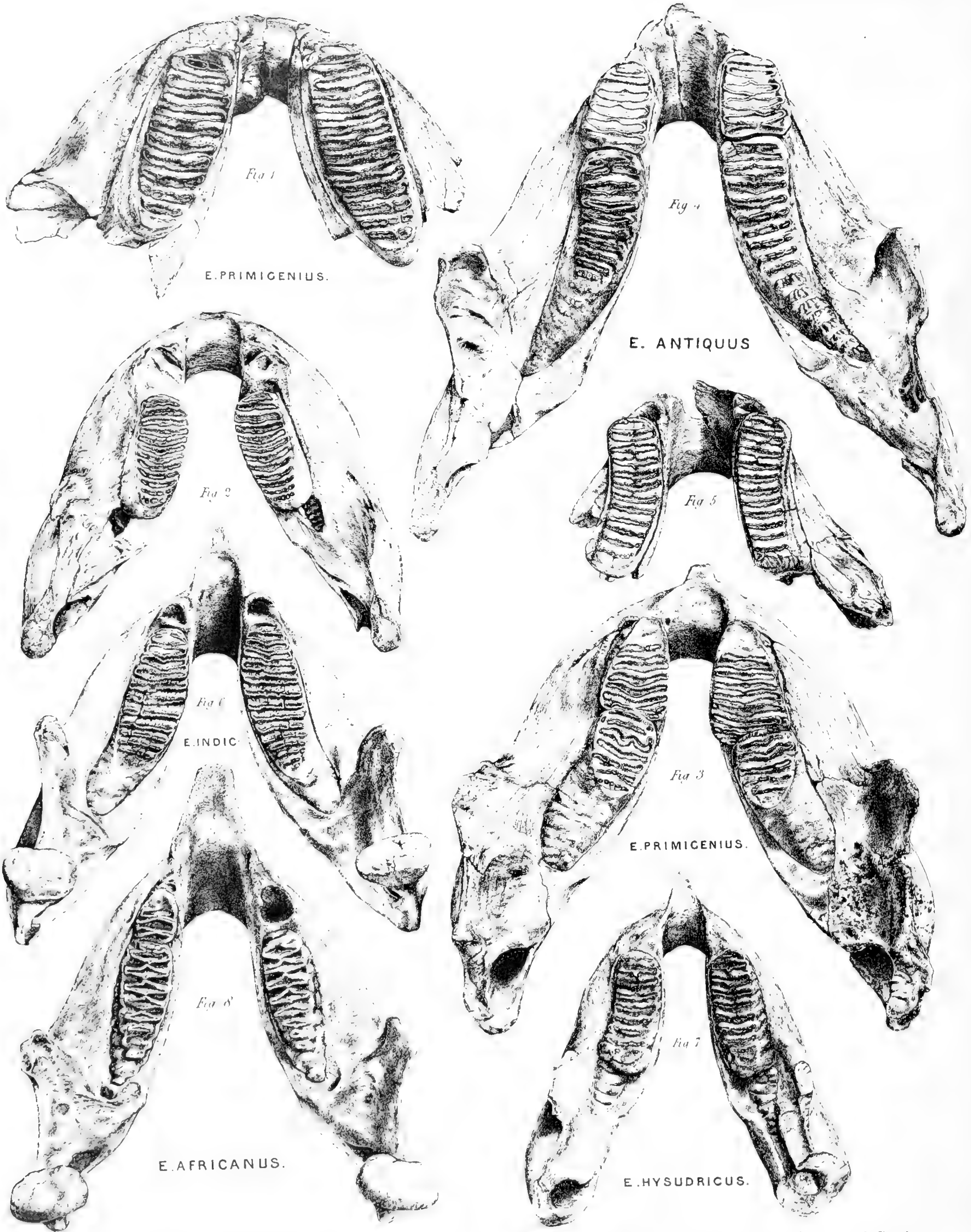

Fig. 794. Primitive, intermediate, and progressive mandibles and grinding teeth of the Elephantidæ. After Falconer and Cautley, 1846 [1847, Pl. XIII.A]. One-sixth natural size.

Fig. 8. *E. africanus* [=*Loxodonta africana*]. Least progressive, platycephalic mandible, with primitive ridge formula and elongate rostrum. = LOXODONTINÆ
Fig. 6. *Elephas indicus.* Slightly more progressive mandible, with somewhat more reduced rostrum. = ELEPHANTINÆ
Fig. 7. *Elephas hysudricus* [=*Hypselephas hysudricus*]. Still more abbreviated mandible, with reduced rostrum. = ELEPHANTINÆ
Fig. 3. *Elephas primigenius* [probably *Parelephas trogontherii*]. Very robust mandible, with vestigial rostrum. = MAMMONTINÆ
Figs. 4, 5. *Elephas antiquus* [=*Hesperoloxodon antiquus*]. Relatively elongate mandible, with reduced rostrum. Appears as *E. meridionalis* on plate; changed by Falconer on original plate in British Museum. = LOXODONTINÆ
Fig. 2. *Elephas primigenius* [=*Mammonteus primigenius*]. Juvenile individual, with second inferior molars *in situ*, greatly reduced rostrum. = MAMMONTINÆ
Fig. 1. *Elephas primigenius* [=*Mammonteus primigenius*]. Fully adult mandible, with broadly arched rostrum. Third inferior grinders well worn, indicating advanced age. The most progressive, hypsicephalic, brachycephalic, and bathycephalic type of mandible. = MAMMONTINÆ

Chapter XV

CLASSIFICATION OF THE ELEPHANTOIDEA BY THEIR DIVERGENT AND HARMONIC CRANIAL AND DENTAL CHARACTERS

Application of principles of phylogenetic classification. Distinction of parallel and convergent from divergent and adaptively radiating characters observable in cranial and dental mechanisms. Recapitulation of ancestral characters in course of development. Correlation of brachycephaly and hypsicephaly with feeding habits and habitat, with brachyodonty and hypsodonty. Three subfamily phyla: mammontinæ, loxodontinæ, and elephantinæ.

I. Introductory Section.
  1. Principles and methods of phylogenetic classification applied to the Elephantidæ.
    - Failure of previous dental classifications.
    - Classification by cranial and dental characters.
    - Cranial mechanics of *Elephas* (Weithofer, Osborn, Gregory).
    - Comparative cranial sections of elephant skulls.
    - Ontogenetic cranial changes in *Elephas indicus*.
    - Generic contrasts in cranial sections: *Loxodonta*, *Parelephas*, *Mammonteus*, *Elephas*, and *Archidiskodon*.

II. Dental and Cranial Adaptation to Prevailing Feeding Habits the Key to Phylogenetic Classification.
  1. Ridge-plate formulæ of primitive and progressive genera in adaptation to prevailing habits of feeding.
  2. Food of the Indian and African elephants and of the mammoth.
  3. Seasonal changes in food of the mammoth.
  4. Summary of progression from browsing to grazing dentition.

III. Vertebral Distinctions of Elephas, Loxodonta, Mammonteus, and Parelephas.
  1. Vertebral formulæ in the above genera.

IV. Synopsis of Subfamily Classification of the Elephantoidea.
  1. Subfamily Mammontinæ, originally browsing, progressive to extreme grazing type. Genera: *Archidiskodon*, *Parelephas*, *Mammonteus*.
  2. Subfamily Loxodontinæ, feeding habits chiefly browsing. Genera: *Loxodonta*, *Palæoloxodon*, *Hesperoloxodon*.
  3. Subfamily Elephantinæ, chiefly browsing, secondarily grazing. Genera: *Elephas*, *Hypselephas*, *Platelephas*.

V. Final Summary of Chapter.

I. INTRODUCTORY SECTION

In the years 1902–1903 the author, with the aid of his colleague William King Gregory, devoted many months of research to the ontogenetic development of the elephantine cranium, also to the method of analyzing the actual forms and proportions of the elephantine cranium by means of sections made with bent wire. Only by such means can the cranial proportions be effectively studied and illustrated. Gregory published part of the results of these ontogenetic studies in his paper of 1903, entitled, "Adaptive Significance of the Shortening of the Elephant's Skull," as quoted below. The complete results obtained by the wire sectional method, as illustrated in figures 801, 803 to 814, are here published for the first time.

1. PRINCIPLES AND METHODS OF PHYLOGENETIC CLASSIFICATION APPLIED TO THE ELEPHANTIDÆ

The secret of phylogenetic classification in the family Elephantidæ is to discover characters in which the different branches diverge from each other. Hitherto students of phylogeny have been deceived by the more numerous characters in which they converge, in other words, by their parallelism. In the present chapter it is shown that whereas all the Elephantidæ converge in their proboscis, in their tusks, and in certain progression in their grinding teeth (e.g., addition of ridge-plates), they also diverge in the *profound proportional changes* in the cranium, with which naturally the tusks and the grinding teeth are *harmonic*. *While outwardly similar, the crania in different subfamilies of elephants are inwardly profoundly divergent.* These divergences are in continuous adaptation to the prevailing habitat and feeding habits.

Step by step it has been observed by Osborn, in comparing the crania of the living and fossil elephants, that all the dental and cranial characters are harmonic, that there is a close adaptive correlation between the form and position of the grinding teeth and of the component parts of the cranium. Moreover, the lines of descent, which are apparently dissimilar in superficial dental structure, are really profoundly related both in dental and cranial harmony. From these comparative observations, which will now be described in detail, has arisen the present phylogentic classification of the Elephantidæ. After a review of the cranial and what is known of the vertebral characters, the three subfamilies and included genera will be fully defined in Section IV of the present chapter (cf. p. 932 below).

SUBORDER OR SUPERFAMILY: ELEPHANTOIDEA Osborn, 1921

(See Volume I of the present Memoir, pp. 22–33, figs. 3, 4, 5, 7, 8, and Pl. XI)

Original reference: "The Evolution, Phylogeny and Classification of the Proboscidea" (Osborn, 1921.515, pp. 2 and 4).

[The present chapter was written before Professor Osborn separated the Stegodontoidea from the Elephantoidea, as fully set forth in the introductory pages of the preceding chapter. Consequently in the following citations the reader should disregard the inclusion of the Stegodonts in the Elephantoidea, retaining only the subfamilies Mammontinæ (*Archidiskodon, Parelephas, Mammonteus*), Loxodontinæ (*Loxodonta, Palæoloxodon, Hesperoloxodon*), and Elephantinæ (*Elephas, Hypselephas, Platelephas*).

It was in January, 1921, in his article on "The Evolution, Phylogeny and Classification of the Proboscidea" that Professor Osborn first published the term Elephantoidea (Osborn, 1921.515, pp. 2 and 4 respectively):

> IV.—ELEPHANTOIDEA to include the Elephantinæ, Loxodontinæ, Stegodontinæ, and Mammontinæ. . . [p. 4] One prime distinction in this superfamily is the very early complete loss of the lower incisor teeth, accompanied by the early development of the upper incisors into horizontal or upturned tusks finally devoid of enamel except at the tips in the young stage. Vestigial enamel bands are recorded in early stages of the stegodonts. A second distinctive character is the absence of conule development into trefoils, so characteristic of the mastodontoids, and the early tendency to form evenly transverse, more or less mammillate, crests which become in the highest degree hypsodont and polylophodont in adaptation to chiefly grazing habits.

Subsequently on sectioning certain of the molars of the Stegodontoidea and the Elephantoidea it was found that the valleys separating the adjacent ridges were V-shaped in the former and U-shaped in the latter.

FAMILY: ELEPHANTIDÆ Gray, 1821

Original reference: Gray, "On the Natural Arrangement of Vertebrose Animals," London Medical Repository, 1821, XV, No. 88, p. 305.

Syn.: Elephasideæ Lesson, 1842, p. 156; Elephantidæ Bonaparte, 1838, p. 112, and 1850; Girard, 1852, p. 326; Zittel, 1891, p. 458.

While Gray in his classification of the Proboscidea (*op. cit.*, p. 305) assigned the terms Elephantidæ and Mastodonadæ respectively to the elephants and mastodonts, Girard (1852, p. 326) was the first to use the form Mastodontidæ.

> FAMILY DEFINITION (Gray, 1821, p. 305).—PROBOSCIDIÆ. . . . *Fam.* 1. ELEPHANTIDÆ.—Teeth, two grinders in each jaw, composed of transverse vertical laminæ, enveloped in enamel, and soldered together by a cortical substance.
>
> Elephant, Elephas Lin. E. Indicus Cuv.
>
> Osborn (1910.346, p. 558): FAM. Elephantidæ. Dinotheres, Mastodons, and Elephants.

> Osborn (1925.662, p. 28): FAMILY: ELEPHANTIDÆ, distinguished by plated grinding teeth developing out of the more or less closely compressed, serrated ridges of *Stegodon* into the broadly plated grinders of *Archidiskodon*, the lozenge-shaped grinders of *Loxodonta*, and the compressed, finely plated grinders of *Parelephas*, of *Mammonteus*, and of *Elephas* the type genus of the family.

It will be observed, however, by referring to page 25 of Volume I (1936) of the present Memoir, that Professor Osborn altered his opinion as to the development of the grinding teeth of the Elephantidæ (p. 942 below) "out of the more or less closely compressed, serrated ridges of *Stegodon*": "It has been assumed by practically all palæontologists that the Elephants were descended from the Stegodonts. This assumption now proves to be erroneous, for neither the *Stegodon* grinding tooth with enamel valleys closed at the bottom, nor the *Stegodon* cranium with its extremely short face, can give rise to the elephantoid molar or the face of the elephantoid cranium."—Editor.]

SUBFAMILY: MAMMONTINÆ Osborn, 1921

The Mammontinæ include the southern mammoth (*Archidiskodon*), the north temperate mammoth (*Parelephas*), the true northern mammoth (*Mammonteus*).[1]

Genus *Archidiskodon* = the Southern Mammoth.
including *Archidiskodon proplanifrons, subplanifrons, planifrons, A. meridionalis, A. imperator,* and other species, chiefly ranging in the south temperate zone.

Genus *Parelephas* = the North Temperate Mammoth.
including the species *Parelephas trogontherii, P. jeffersonii, P. trogontherioides, P. columbi,* usually intermediate in geographic range and climatic life zone between the southern mammoth and the northern mammoth.

Genus *Mammonteus*[1] = the Northern or Woolly Mammoth.
typified by *Mammonteus primigenius,* including also *M. primigenius americanus, M. primigenius alaskensis, M. primigenius compressus,* and other subspecies of the northern steppes and tundras.

SUBFAMILY: LOXODONTINÆ Osborn, 1918

The Loxodontinæ include the three genera *Loxodonta, Palæoloxodon,* and *Hesperoloxodon.*

Genus *Loxodonta*
including *Loxodonta africana,* and probably *L. zulu, L. prima, L. africana* var. *obliqua, L. subantiqua,* of Africa.

Genus *Palæoloxodon*
including especially *Palæoloxodon namadicus* of India; *P. melitensis, P. mnaidriensis, P. falconeri, P. cypriotes,* and *P. creticus* of the Mediterranean Islands, also the Palæoloxodonts of Africa, of Japan, and of Java.

Genus *Hesperoloxodon*
including *Hesperoloxodon antiquus, H. antiquus italicus, H. antiquus germanicus,* etc. of Europe.

SUBFAMILY ELEPHANTINÆ: Osborn, 1910

The Elephantinæ include the typical or true elephants of India, consisting of the three genera *Elephas, Hypselephas,* and *Platelephas.*

Genus *Elephas*
including the typical *Elephas indicus* and the geographical varieties of *E. indicus bengalensis* and *E. indicus ceylanicus,* also *E. sumatranus.*

Genus *Hypselephas*
including the extinct Pleistocene species *Elephas* [*Hypselephas*] *hysudricus* of India.

Genus *Platelephas*
including *Platelephas platycephalus* of the Upper Pliocene or Lower Pleistocene of India.

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[1] [The validity of the generic term *Mammonteus* is doubtful—see Chapter XXI, pp. 1365–1367, below, on the nomenclature of the Proboscidea.—Editor.]

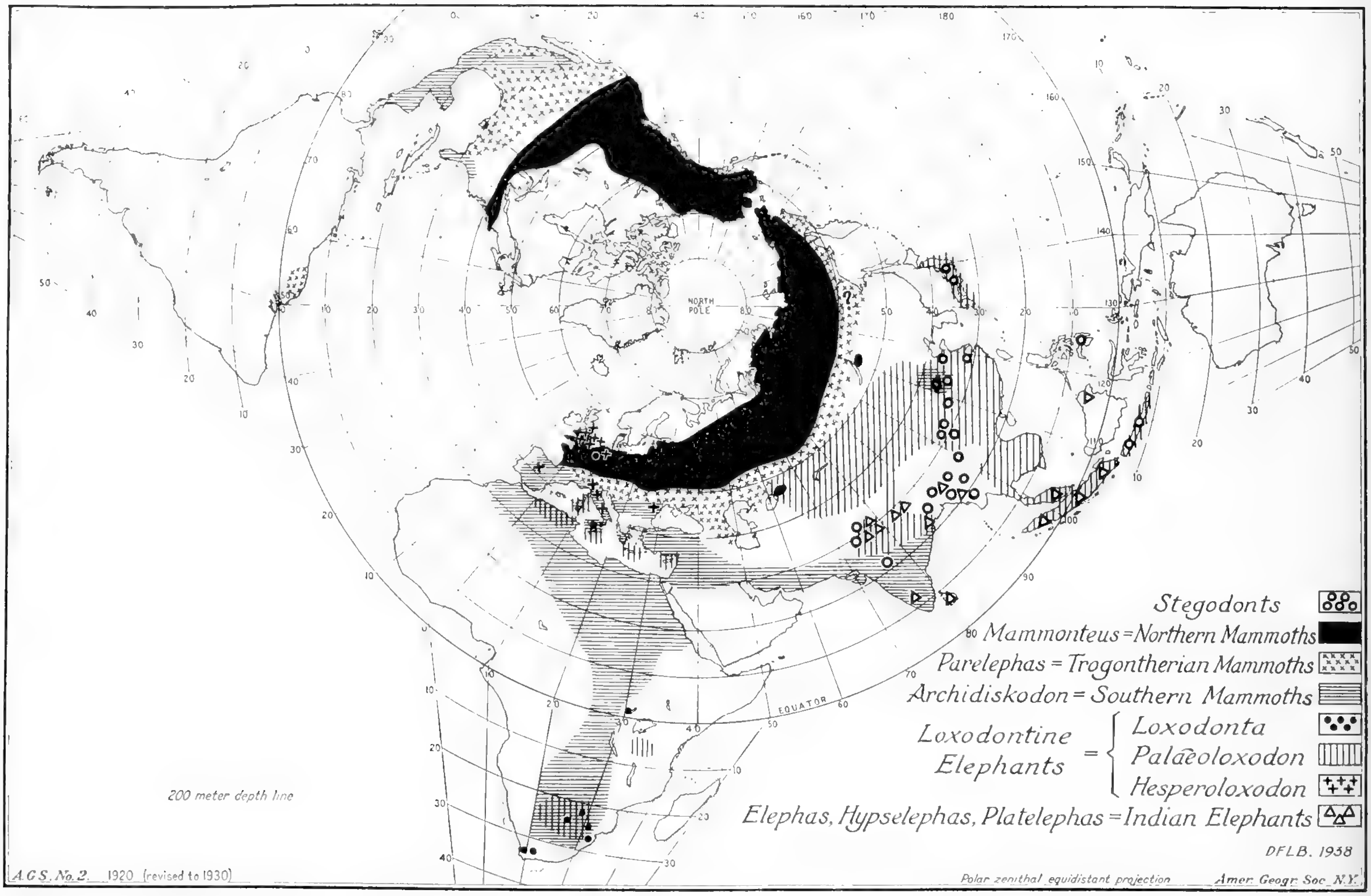

FIG. 795. GENERAL CLIMATIC DISTRIBUTION OF THE SUBFAMILIES OF THE ELEPHANTOIDEA AND STEGODONTOIDEA, INCLUDING THEORETIC MIGRATION LINES (1938)

NORTH POLAR PROJECTION PREPARED BY THE AMERICAN GEOGRAPHICAL SOCIETY IN 1924

1) THE STEGODONTS (*Stegodon*): Southern and Eastern Asia, Japan, and the East Indies.

2) THE SOUTHERN MAMMOTHS (*Archidiskodon*): Africa, Southern Europe, England, Southern Asia, the United States, and Mexico.

3) THE NORTHERN MAMMOTHS (*Mammonteus*): Circumpolar distribution extending southward to the 40th parallel in late Pleistocene times.

4) TROGONTHERIAN MAMMOTHS (*Parelephas*): Southern and Eastern Europe, the United States, Mexico, and South America; elsewhere theoretic (?) migration lines.

5) THE LOXODONTINE ELEPHANTS (*Loxodonta, Palæoloxodon, Hesperoloxodon*): Southern Europe, Asia, and the continent of Africa. See figure 1242 for living African elephants.

6) INDIAN ELEPHANTS (*Elephas, Hypselephas, Platelephas*), recent and fossil: Southern Asia and the East Indies. See also figure 1242.

FAILURE OF PREVIOUS DENTAL CLASSIFICATIONS

Falconer's classification (1857, p. 318, and 1868, Vol. I, p. 82 *et seq.*) into three subgenera was based chiefly on the grinding teeth: Subgen. 1. *Stegodon.* Subgen. 2. *Loxodon.* Subgen. 3. *Euelephas.* Pohlig's classification (1888, p. 138) was also based solely on the grinding teeth: *Polydiskodon, Archidiskodon,* and *Loxo(disko)don.* We find that classification of the Elephantidæ by dental characters alone cannot be phylogenetic.

CLASSIFICATION BY CRANIAL AND DENTAL CHARACTERS

The phylogenetic classification in this Memoir is based on the evolution of the cranium and jaws, harmonic with the grinding teeth, especially with the third superior and inferior molars, M^3-M_3, which proves to afford an absolute means of distinguishing generic phyla from each other.

CUVIER.—From the first distinction by Cuvier of the African from the Indian elephant and from *Elephas primigenius*,[1] all authors have given more or less attention to the external characters of the crania of the Elephantidæ, although they have not made the cranium the chief basis of classification.

CRANIAL MECHANICS OF ELEPHAS (WEITHOFER, OSBORN, GREGORY)

WEITHOFER.—In 1890 Weithofer made a detailed comparative and functional study of the elephant's skull, and concluded that the ontogenetic mechanical changes in the skull, observable during individual growth, as affecting phylogeny, such as the fore-and-aft compression and vertical heightening and deepening of the skull, the wide separation of the inner and outer tabulæ of the bones and the cancellous condition of the diploë, the forward shifting of the orbits from a point above the anterior grinders, etc., are *primarily correlated with the prodigious development of the tusks*—weapons and crowbars whose effectiveness increased with and reciprocally hastened the phyletic advance in body dimensions. Gregory (1903.1) did not accept Weithofer's conclusion that the tusks were the chief cause of fore-and-aft compression, but showed that the *proboscis* is another and perhaps the chief factor in the extraordinary process of fore-and-aft cranial compression, or cyrtocephaly.

OSBORN–GREGORY.—Studies of the elephant cranium as a whole were undertaken by Osborn (1902–1903) with the coöperation of William K. Gregory. Gregory (1903) in his "Adaptive Significance of the Shortening of the Elephant's Skull" attributed the fore-and-aft compression principle to the enlargement and backward shifting both of the *proboscis and of the tusks.* His principal conclusions and explanatory figures may be freely summarized, without quotations, as follows: (1) *First factor.* Lengthening of the proboscis correlated with shortening of cranium and of neck *pari passu* with lengthening of limbs and increased height; also with downward shifting and elongation of tusks (*vide* Weithofer). (2) *Second factor.* Backward shifting of weighty tusks and of proboscis diminished the anteroposterior space (i.e., brachycephaly) for grinding teeth (Dp 2–M 3). (3) *Third factor.* Rapidly heightening grinding teeth (i.e., hypsodonty), together with large backwardly and upwardly growing molar-alveolar pouch.

Harmonic with the enlargement and backward shifting of the tusks, the elongation of the proboscis, the fore-and-aft compression of the whole cranium, and the vertical elongation (hypsodonty) of the grinding teeth, are the following proportional changes in the cranium of *Elephas*: (a) Hard palate tilted obliquely upwards; (b) palatines reduced lateroposteriorly and widely divergent posteriorly; (c) posterior nares pushed very far back; (d) large vertical pterygoid wing of alisphenoid encircles and functionally replaces posterior molar-alveolar pouch; (e) foramen ovale of alisphenoid shifted backward and outward, becomes confluent with foramen lacerum medium; (f) presphenoid, basisphenoid, basioccipital thicken in median plane, so that basis cranii point sharply downward at an angle of 90°+ with occipital plane; (g) tympanic bullæ flatten and become closely appressed to the skull.

The following is cited from Gregory (1903.1, p. 391):

> . . . the obliquely placed external portion [Fig. 797] of the orbitosphenoid . . . has been squeezed into a long, thin process; internally [Figs. 798, 802] the anterior edges of the basisphenoid are directed outward and backward; both internally and externally the optic foramen, foramen lacerum anterius, and foramen rotundum, in the order named, are obliquely arranged on descending levels from within outward and from in front backward, the whole region having been thickened by the separation [diploë] of the inner and outer tabulæ of all the bones, and also sharing in the upward-and-backward tilting of the nasal region and in the general fore-and-aft squeezing [= cyrtocephaly] of the skull, the end result being that the foramina have been pulled out into long tunnels running obliquely forward, outward, and downward; especially internally the fore-and-aft extent of the alisphenoid proper is brief. Internally the skull has shortened up, one might almost say in bellows fashion, with the optic foramen on each side at the apex of the internal transverse folding [Figs. 798, 802], the ridge of the 'lesser wing' of the human sphenoid. As the skull has also expanded transversely [= brachycephaly], the general effect of the internal view of the skull is thus that of compression around the center (represented by the basisphenoid) and increasing expansion toward the periphery—somewhat recalling the conditions of the domelike human skull.

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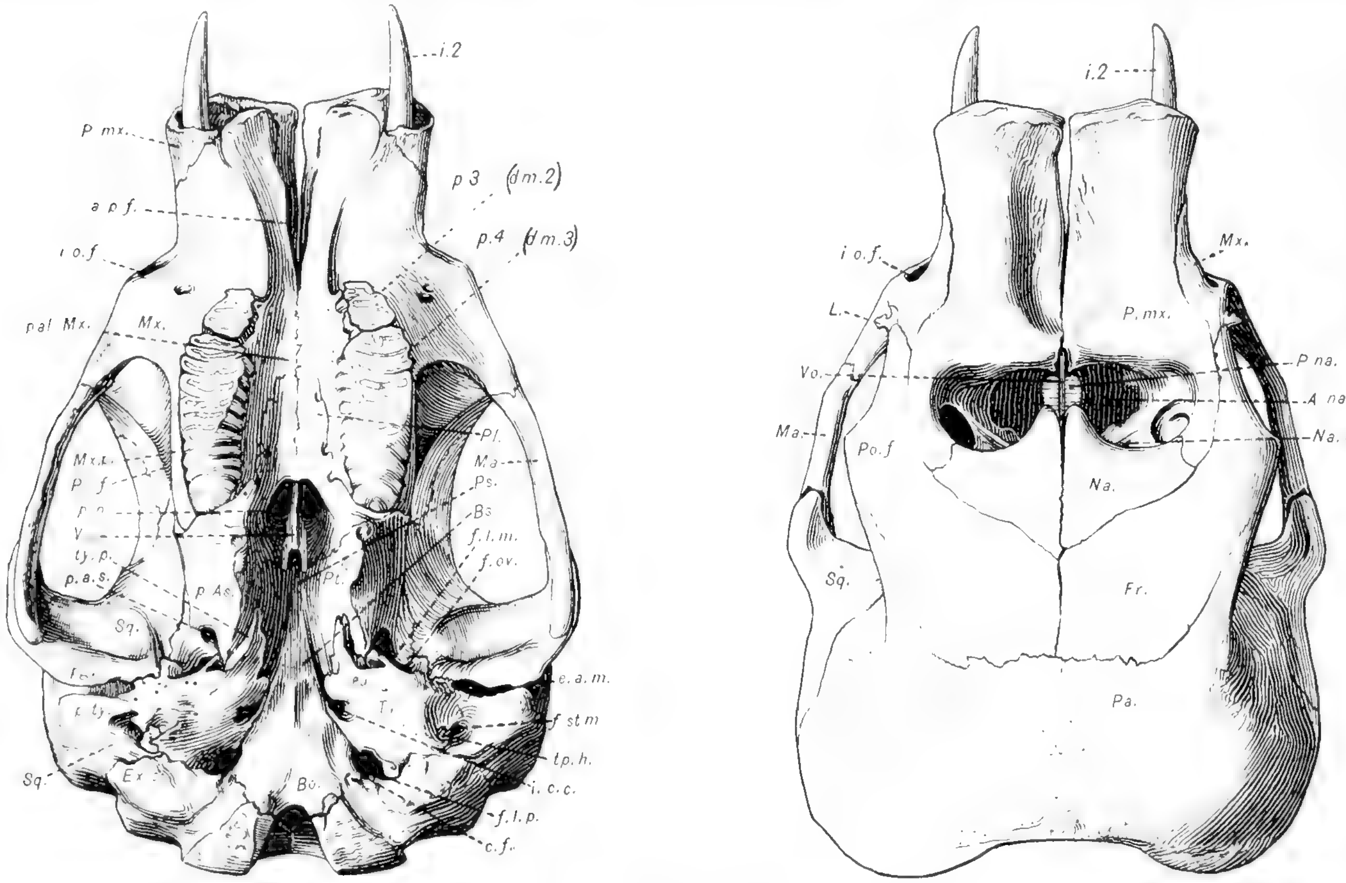
[1] Cuvier's keen perception of the cranial distinctions of *Elephas primigenius*, *E. africanus*, and *E. indicus* are shown clearly in his definitions of these three species in the first edition of his "Ossemens Fossiles" (1806.1, pp. 262–264), in which the three crania are figured side by side (cf. Fig. 992 of the present Memoir) in anterior and lateral aspects. See further comment in Chapter XVIII (*Mammonteus*) on Cuvier's treatment of *E. primigenius*.

The above principles of the ontogenetic and phylogenetic adaptations in the *Elephas indicus* cranium cover three chief cranio-mechanical factors in the order named:

(1) The lengthening of the proboscis or trunk of first importance as affecting alike males and females.

(2) The lengthening and increasing weight of the tusks, as affecting chiefly the male, and to a much less degree, the female cranium.

(3) The heightening of the molar crowns, especially of M^3-M_3, as affecting the male and female cranium alike.

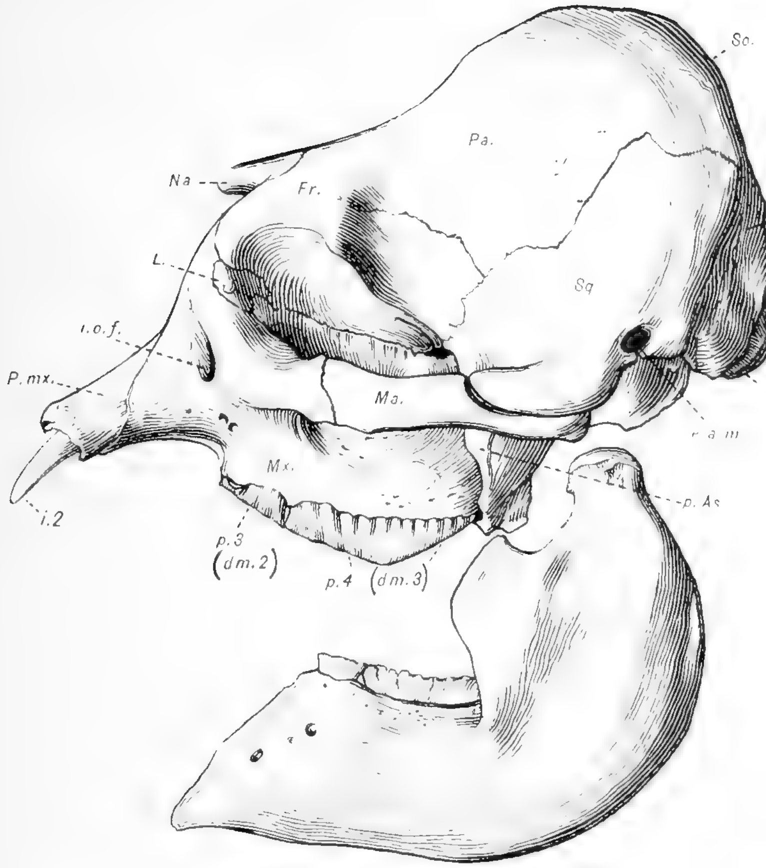


Juvenile Cranium of Asiatic Elephant

Fig. 796. Palatal view (left) of juvenile cranium of Asiatic elephant (*Elephas indicus*); superior view (right) of same cranium. After Osborn and Gregory (see Gregory, 1903.1, figs. 1 and 2, pp. 390 and 391).

P.mx.—Premaxillary.
Mx.—Maxillary.
Mx. p.—Maxillary pouch for molars.
Ma.—Malar.
Po.f.—Postorbital ridge of frontal.
pal. Mx.—Palatine ledge of maxillary.
Pl.—Palatine.
Vo.—Vomer.
Ps.—Presphenoid.
Bs.—Basisphenoid.
Bo.—Basioccipital.
p. As.—Pterygoid wing of alisphenoid.
Pt.—Pterygoid.
Sq.—Squamosal.
Ex. o.—Exoccipital.
pg.—Postglenoid ledge of squamosal.
p.ty.—Post-tympanic ledge of squamosal, which with *pg.* forms a secondary external auditory meatus.
Ty.—Tympanic bulla.
ty. p.—Anterior process of tympanic.
tp. h.—Tympanohyal.
eu.—Eustachian opening of tympanic.
a. p. f.—Anterior palatine foramina (canals).
i. o. f.—Infraorbital foramen.
p. n.—Posterior nares.
p. a. s.—Alisphenoid canal.
f. l. m.—Foramen lacerum medium.
f.ov.—Foramen ovale (confluent with *f. l. m.*).
i. c. c.—Canal for internal carotid artery.
f. st. m.—Stylomastoid foramen.
f. l. p.—Foramen lacerum posterius.
c. f.—Notch, a vestige of condylar foramen (?) (confluent with *f. l. p.*).
$i.^2$—Tusk.
p^3 (*dm* 2).—Third premolar (or second deciduous molar of authors).
p^4 (*dm* 3).—Fourth premolar (or third deciduous molar of authors).

Osborn (1904–1924), in comparative observations, is inclined to attribute equally great, if not greater cranio-mechanical influence to the vertical elongation (=hypsodonty+bathycephaly) of the posterior grinding teeth in relation to adaptive radiation in feeding habits, as shown in a comparison of (Fig. 806) the purely browsing African elephant (*Loxodonta*) with the browsing and grazing Indian elephant (*Elephas*) and with the chiefly grazing northern mammoth (*Mammonteus*).



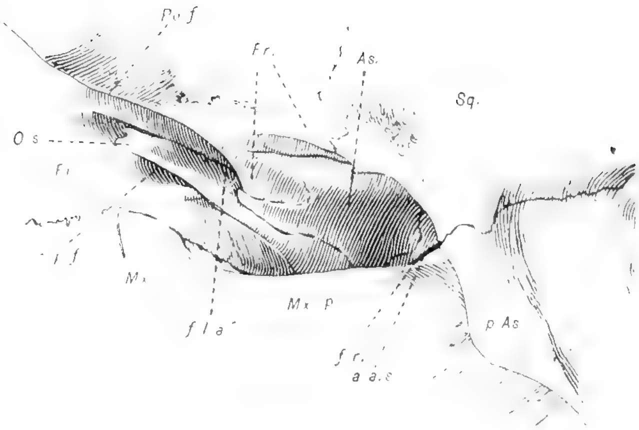
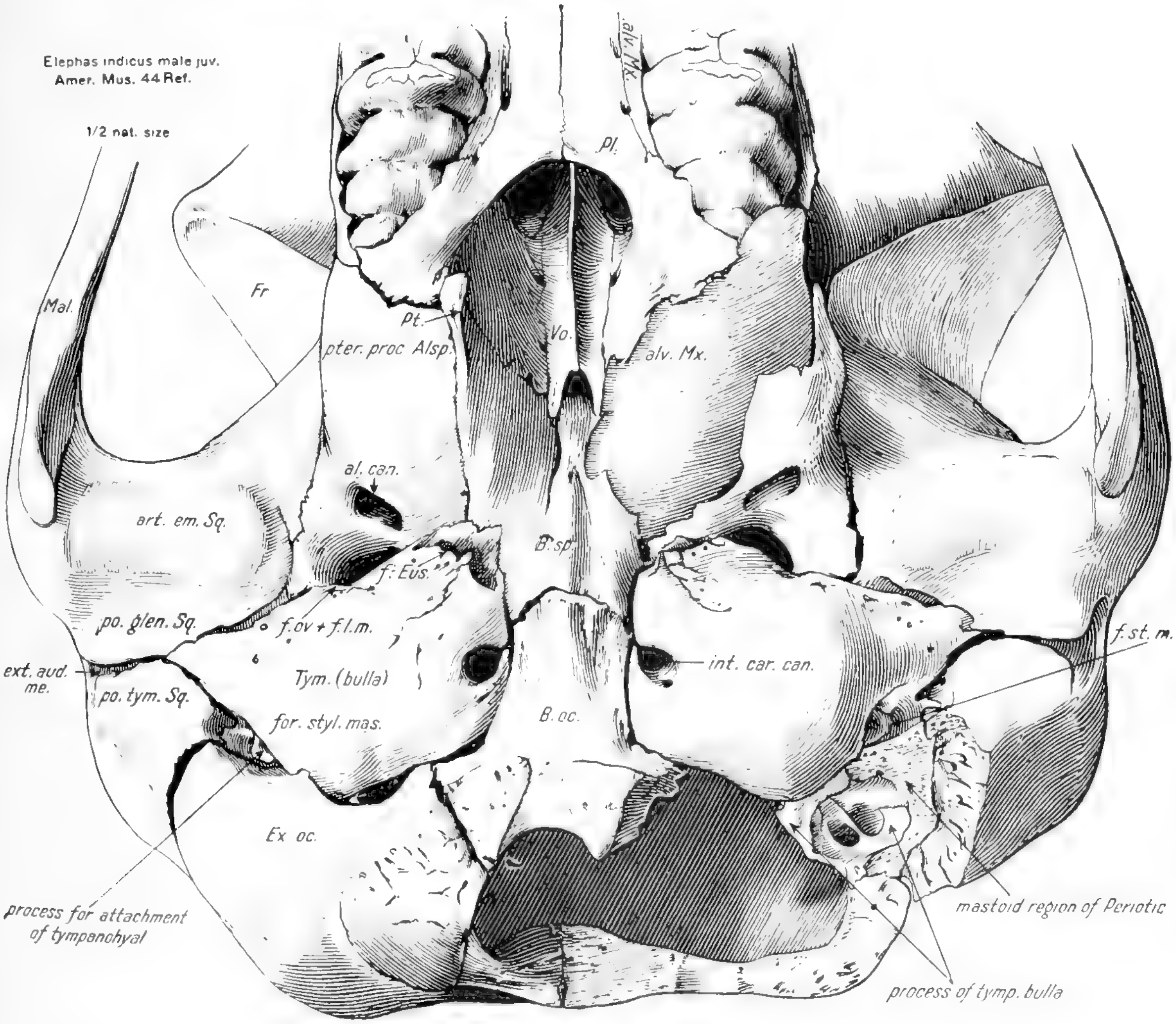


Fig. 797. (Right figure) Orbitosphenoidal region, left side. From Osborn and Gregory (see Gregory, 1903.1, p. 393, fig. 4). The view is obliquely from the side and from below the malar bone (cf. left figure—Fig. 3 of Gregory, 1903.1).

(Left figure) Juvenile cranium of Asiatic Elephant (see Gregory, 1903.1, p. 392, fig. 3). Compare figure 796.

Po. f.—Postorbital ridge of frontal.
Fr.—Frontal.
O. s.—External process of orbitosphenoid.
As.—Alisphenoid.
Sq.—Squamosal.
p. As.—Pterygoid wing of alisphenoid.
Mx. p.—Maxillary pouch for molars.
op. f.—Foramen opticum.
f. l. a.—Foramen lacerum anterius.
f. r. and *a. a. s.*—Arcade leading to foramen rotundum and anterior opening of the alisphenoid canal.

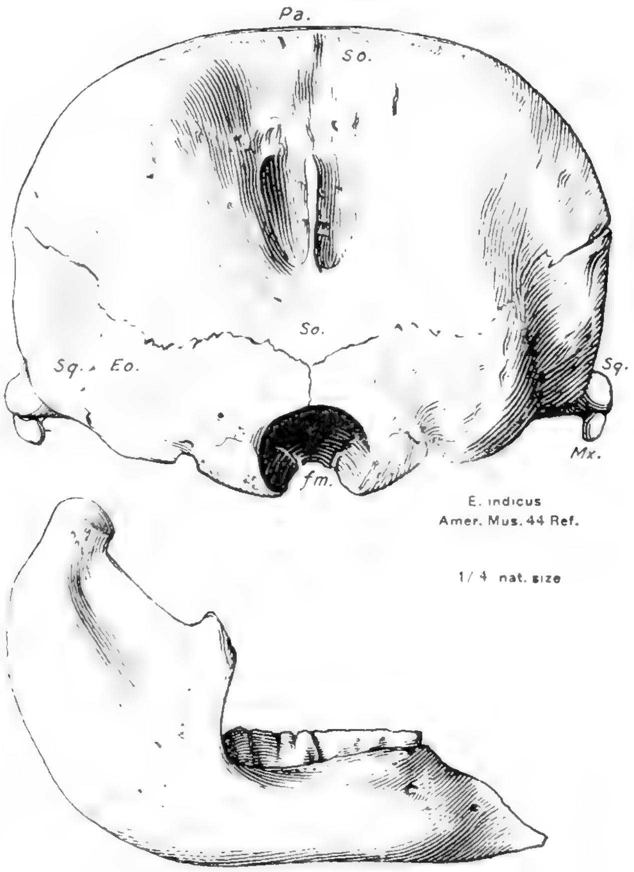


INFANTILE CRANIUM OF ASIATIC ELEPHANT

Fig. 798. Infantile basis cranii. Skull of *Elephas indicus* (Amer. Mus. Dept. Mam. 44); same individual as that represented in figure 799. One-half natural size. Observe identification of basicranial foramina by Gregory in 1903.

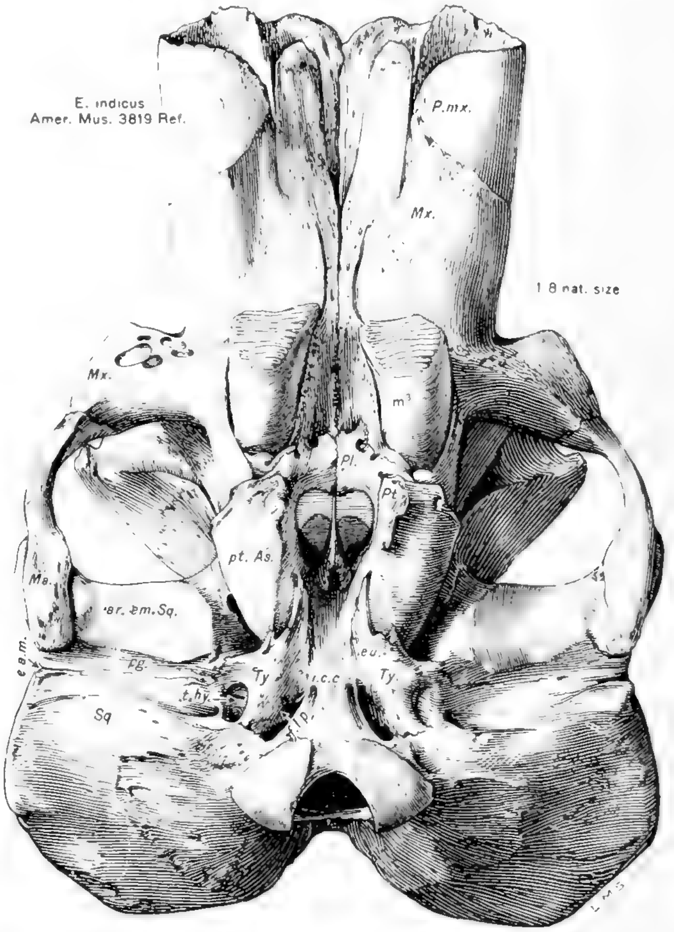
Compare infantile separation with the adult fore-and-aft compression and confluence, cyrtocephaly (Fig. 800), of the basicranial foramina.

Assigning, therefore, a proportional influence to the three great cranio-mechanical factors, (1) the proboscis, (2) the tusks, and (3) the grinders, *relative to the prevailing feeding habits*, whether purely browsing, browsing and grazing, or purely grazing, we shall come very near a complete mechanical interpretation of the cranium of the elephants in the five generic phyla which we shall presently examine.



INFANTILE CRANIUM OF ASIATIC ELEPHANT

Fig. 799. Referred infantile occiput and jaws of *Elephas indicus* (Amer. Mus. Dept. Mam. 44). This is a much younger specimen than that figured (Fig. 797) by Gregory in 1903, p. 392, fig. 3, which shows a long shallow jaw. One-fourth natural size.



ADULT CRANIUM OF ASIATIC ELEPHANT

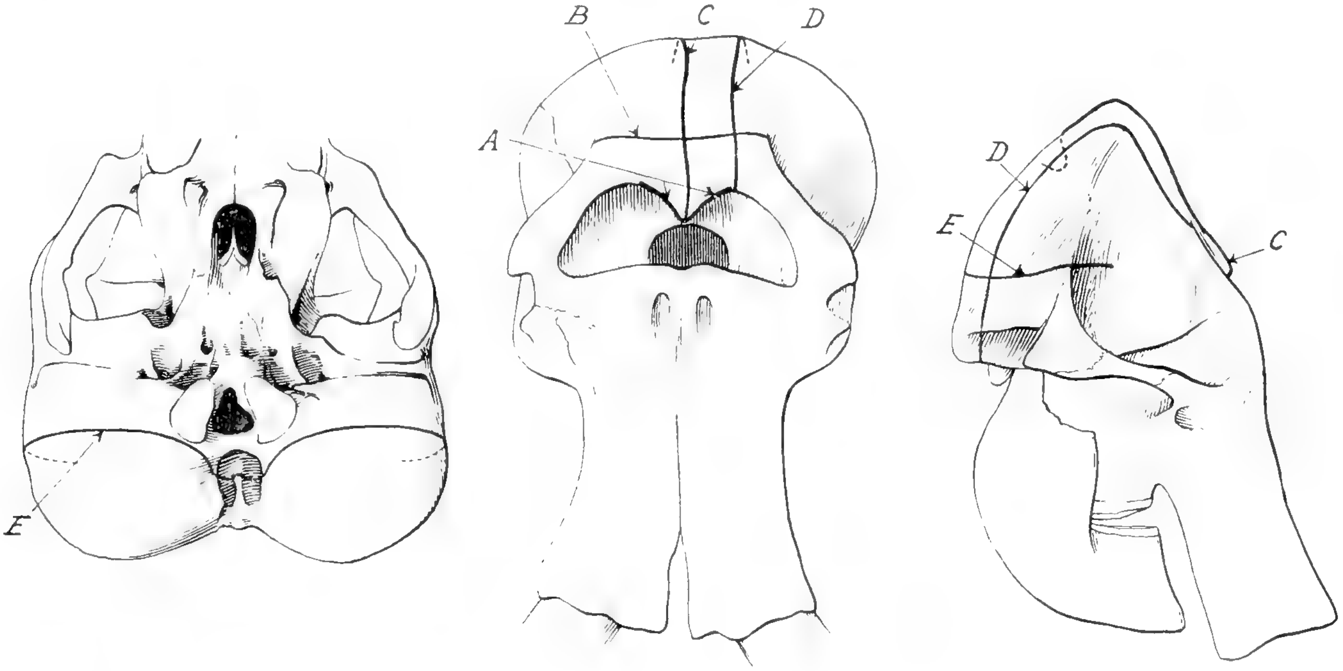
Fig. 800. Adult palate of Indian elephant (*Elephas indicus bengalensis*), Amer. Mus. Dept. Mam. 3819. This is a middle-aged specimen with superior molar, ?M^3, showing eleven to twelve worn plates. One-eighth natural size.

Compare the fore-and-aft compression and confluence (cyrtocephaly) of the basicranial foramina with the relatively primitive condition in the infantile cranium (Fig. 798).

COMPARATIVE CRANIAL SECTIONS OF ELEPHANT SKULLS

OSBORN.—In order to ascertain the more profound changes which have taken place in the evolution of the crania of the elephants, Osborn and Gregory, as stated above, employed in 1902–1903 a method of sectioning the skull (Fig. 801) in four different planes, by means of copper wires. A similar method had been used (Osborn-Gregory) in studying the cranial mechanics of the perissodactyl family of titanotheres.

These planes were established with reference to the *basicranial axes*, after the manner of Huxley, Flower, Lankester, and others in their studies on the cranial axes of other ungulates; also with reference to the horizontal grinding surfaces of the molar teeth.



THE FIVE WIRE SECTION LINES (A–E)

Fig. 801. Key to Sections. Young *Elephas indicus bengalensis* cranium apparently of the broad narial 'Dauntela' variety. The manner in which the cranial sections are recorded in the figures of this chapter is shown in the above key diagram to sections, also in diagrammatic figures 803–814.

C, Midvertical, sagittal, nasals to vertex of the occiput. *D*, Para-occipitofrontal, sagittal, longitudinal rim of anterior nares to occipital condyles. *A*, Horizontal nasal. *E*, Occipitohorizontal through back of occiput. *B*, Vertical transverse frontals, intertemporal.

The intensive application of this method by Osborn in 1924 revealed the following lines of phylogenetic divergence: (1) Progressive brachycephaly of the skull involves fore-and-aft shortening of the individual bones (=cyrtocephaly), also an expansion in the vertical planes (=hypsicephaly). (2) Shortening (=cyrtocephaly) and deepening (=bathycephaly) of the temporal fossæ and upward expansion of the grinders (=hypsodonty) and of the alveolar pouch profoundly alter the bones and foramina of the sphenoidal region. We may summarize these proportional changes as follows:

Cyrtocephaly:	Fore-and-aft faciocranial abbreviation.
Cyrtodonty:	Fore-and-aft molar-crown abbreviation.
Hypsicephaly:	Vertical heightening of the cranium and jaws.
Hypsodonty:	Vertical heightening of the molar crowns.
[Brachyodonty:	Vertically low molar crowns.]
Acrocephaly:	Vertical heightening of the occipitofrontal apex.
Bathycephaly:	Vertical deepening of the basicranium, molar alveoli, and jaws.
Brachycephaly:	Broadening of (a) the occiput, or of (b) the zygomatic arches.
Cyptocephaly:	Downward flexure of the facial to the basicranial axes.
[Orthocephaly:	Lack of inclination of the basifacial to the basicranial axis (cf. p. 924 below)].

ONTOGENETIC CRANIAL CHANGES IN ELEPHAS INDICUS

Applying the methods described above, it is desirable to examine the *ontogeny* of the *Elephas indicus* cranium, in accordance with the biogenetic law that *youthful crania and jaws in all phyla of the Elephantidæ more or less closely resemble each other*, whereas *adult crania and jaws very widely differ from each other.*

The chief ontogenetic or growth and age changes are clearly displayed in the accompanying series of figures (Figs. 801, 807, 809, 799, 798, 796, 797, 802) illustrating the transformation from the infantile to the adult condition in the cranium of *Elephas indicus*, which should be examined in connection with the comparative sections, also with the adult crania figured in the present and succeeding chapters on *Mammonteus*, *Loxodonta*, and *Elephas*.

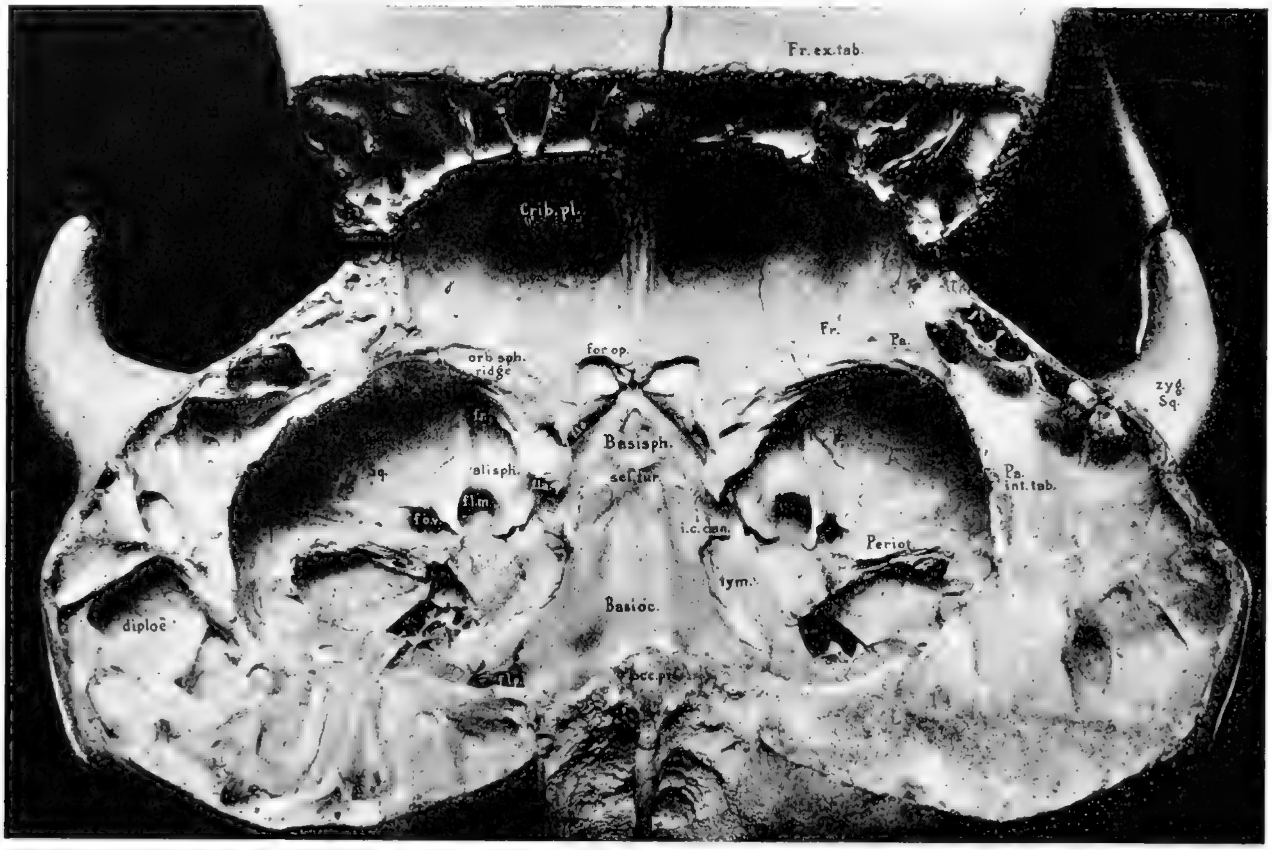


Fig. 802. Interior view of skull of young Asiatic Elephant, after Gregory, 1903, Pl. xxiii. Same skull as that represented in figures 796, 797.

Crib. pl.—Cribriform plate.
orb.sph.ridge—Orbitosphenoid ridge.
sel.tur.—Sella turcica.
Fr.—Frontal.
f.r.—Foramen rotundum.
f.l.a.—Foramen lacerum anterius.
f.l.m.—Foramen lacerum medium.
f.l.p.—Foramen lacerum posterius.
i.c.can.—Internal carotid canal.
tym.—Tympanic bulla.
Pa.int.tab.—Internal table of parietal.
Fr.ex.tab.—Outer table of frontal.
Basisph.—Basisphenoid.
Alisph.—Alisphenoid.

FRONTO-OCCIPITAL AND FRONTAL GROWTH CURVES (Figs. 803, 804).—As shown in midsection *D*, the frontal profile of the infantile cranium of *Elephas indicus* resembles that of the adult profile of *Loxodonta africana*. The juvenile profile displays the rounded and expanded fronto-occipital curve characteristic of *E. indicus*, in contrast to the angular occipitofrontal curve of *L. africana*. The adult fronto-occipital profile is a uniformly rounded dome. The old male profile exhibits an acrocephalic dome, which attains the same height as in the highest *Parelephas jeffersonii* (Fig. 810) and is distinguished by the rounded bulbous frontals.

The infantile frontals resemble those of *L. africana*. The juvenile frontal curve is elongate, convex superiorly, concave inferiorly or convexo-concave, in contrast to the uniformly convex frontals of *L. africana* (Fig. 811), or the uniformly concave frontals of *Parelephas* and *Mammonteus* in section (Figs. 805, 806, 810, 811).

Nasal Growth Stages (Fig. 807).—The nasal growth stages reflect the increasing abbreviation (cyrtocephaly) and broadening (brachycephaly) of the cranium. The infantile nasals are short, pointed, and narrow. The juvenile nasals are broader and uniformly arched. The adult nasals are broad and truncated. The old male nasals are extremely broad, truncated, and abbreviated.

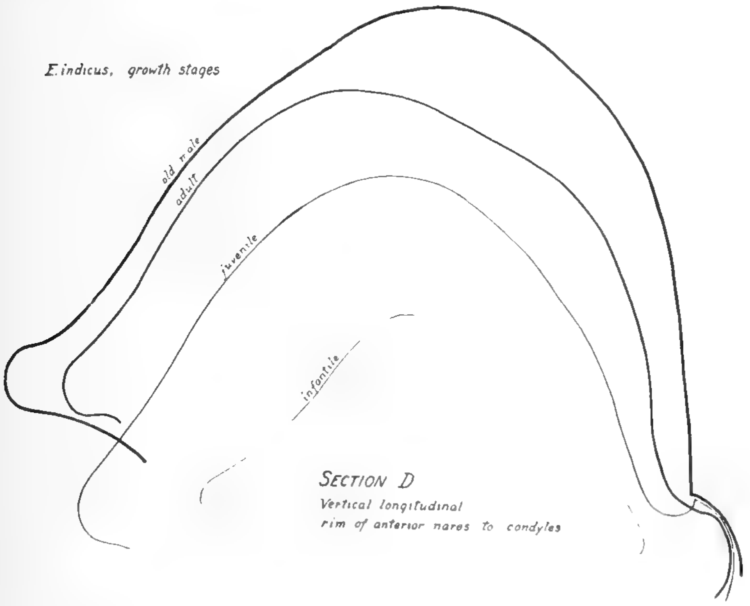


Fig. 803. Fronto-occipital growth curves of vertex. *Elephas indicus* cranium, one-sixth natural size. This Section *D* passes between the occipital convexities. The increasing occipital convexities are shown in the passage from the infantile to the old male stages of growth. The section is taken at the left of the medial line.

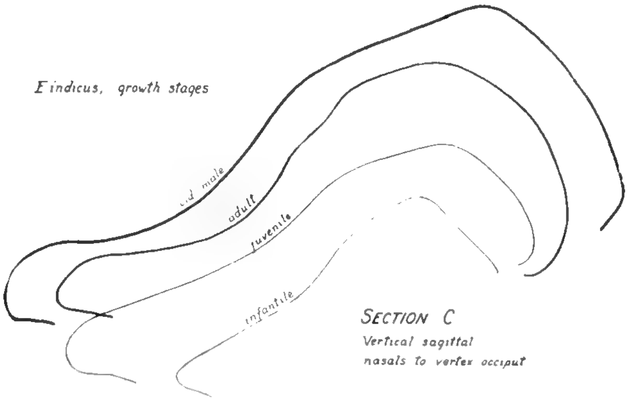


Fig. 804. Growth curves of vertex. Midfrontal vertical Section *C* of *Elephas indicus* skull, one-sixth natural size. The increasing concavity of the lower part, and convexity of the upper part, of the forehead in the passage from the infantile to the old male stages of growth are shown.

Fronto-intertemporal Growth Stages (Fig. 808).—Like the nasal growth, the fronto-intertemporal growth reflects increasing abbreviation (cyrtocephaly) and broadening (brachycephaly) of the cranium, as observed in the infantile, the juvenile, the adult, and the old male growth stages shown in Section *B*. As compared with the convex profile of *L. africana* (Fig. 813), the midfrontal profile of *E. indicus* is plane. The angle between the superior fronto- and laterotemporal surfaces of *E. indicus* (Figs. 808, 813) is sharply angular, whereas in *L. africana* (Fig. 813) and *Parelephas jeffersonii* (Fig. 813) the frontotemporal union is rounded or gently convex.

Occipitohorizontal Growth Stages (Fig. 809).—The extraordinary brachycephaly of the *E. indicus* cranium is most clearly displayed in the rapid lateral expansion of the occiput and deepening of the interoccipital space. As clearly displayed in figure 809, even the infantile cranium is relatively broad in horizontal section. In the juvenile stage the bulbous backward growth of the occiput begins with the deepening of the interoccipital space. In the adult the occipital expansion describes a uniformly convex rounded curve. In the old male the winglike lateral expansion results in an acute angle between the occipital and temporal faces. This shows that the extreme of brachycephaly is attained in the broadening of the occiput. In the comparative figure 814 it appears that this extreme occipital brachycephaly is much greater in the old male of *E. indicus* than in the adult *P. jeffersonii*; it also exceeds the occipital brachycephaly of the *L. africana* cranium.

Palatal Abbreviation (Figs. 796, 800).—The palate of the juvenile cranium (Fig. 796, left), as compared with the adult palate of *E. indicus bengalensis* (Fig. 800) and the adult palate of *L. africana* (Fig. 1061), proves that in the transition from the juvenile to the adult stage there is a very marked abbreviation (cyrtocephaly) and

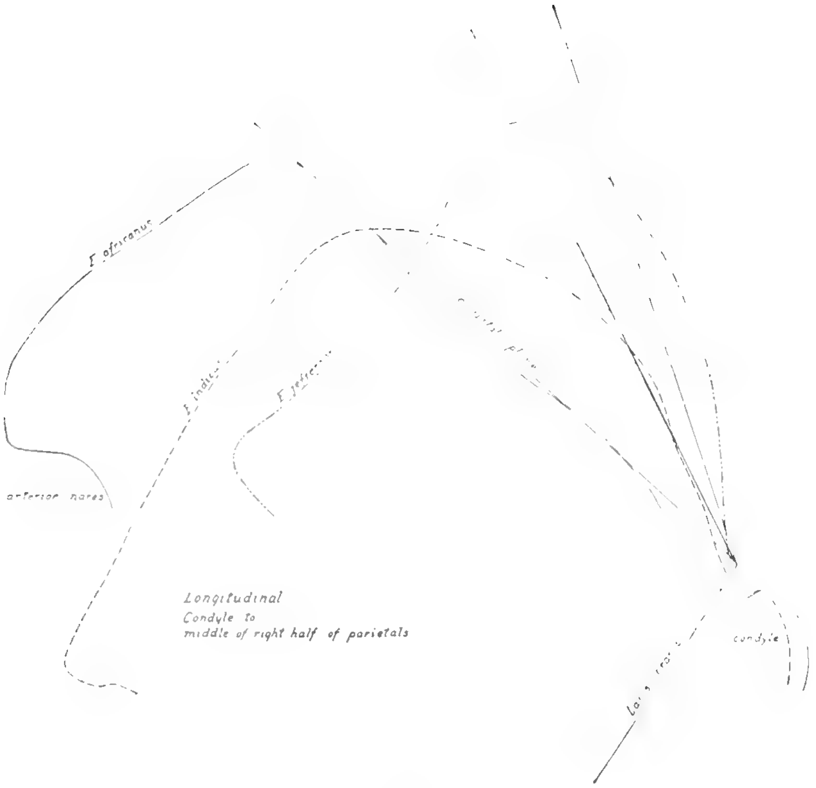


Fig. 805

PRELIMINARY STUDY OF FRONTO-OCCIPITAL-BASILAR PLANES

Fig. 805. Comparative para-occipitofrontal section *D* (Fig. 107). Section carried down through the *basis cranii* to show the widely different occipitofrontal planes of the skull in the three great subfamily divisions of the Elephantidæ. Reduced to one-sixth natural size. For *basis cranii* substitute basioccipital plane (see Fig. 1192 below).

ELEPHANTINÆ = *Elephas indicus*, Indian elephant contour. Para-occipitofrontal union a right angle, *rounded*.

LOXODONTINÆ = *Loxodonta africana*, African elephant contour. Occipitofrontal union *rectangular*.

MAMMONTINÆ = *Parelephas jeffersonii*,[1] Mammoth contour. Occipitofrontal union *acute*.

These three sections are made from adult skulls in the American Museum collection, namely, of *Elephas indicus*, of *Loxodonta africana*, and of a young male skull of *Parelephas jeffersonii* (Amer. Mus. 14475).[1] Compare sections in figure 806.

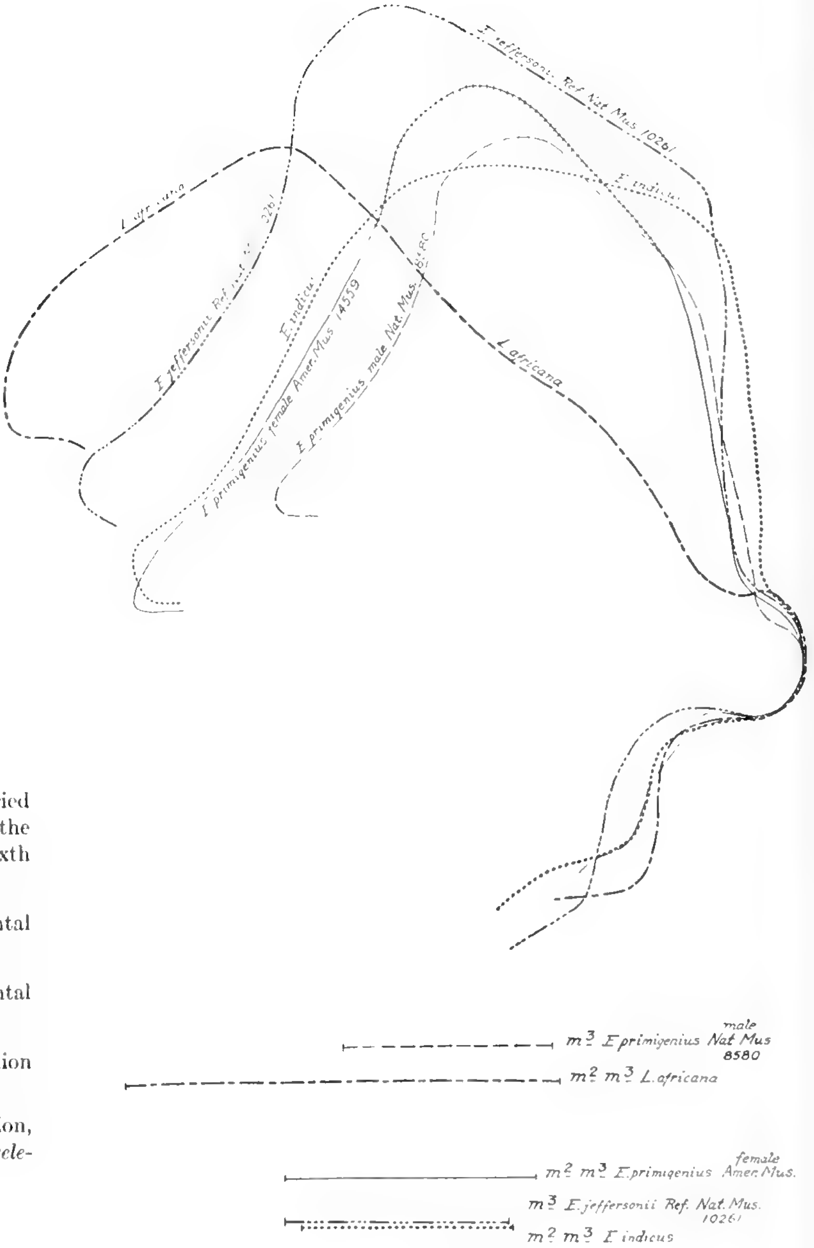


Fig. 806

LATER STUDY OF FRONTO-OCCIPITAL-MOLAR-3 PLANES

Fig. 806. Para-occipitofrontal section *D* (Fig. 801) of: Loxodontinæ (*Loxodonta africana*), Mammontinæ (*Parelephas jeffersonii, Mammonteus primigenius*), Elephantinæ (*Elephas indicus*). Each section (*D*) is taken as follows: (1) To the left of the median sagittal line; (2) the inferior surface of the grinding teeth (M^2-M^3) placed horizontally; (3) the occipital condyles superimposed. It will be observed that:

(1) LOXODONTINÆ. In *Loxodonta africana* the fronto-occipitocondylar angles and the molar teeth (M^2-M^3) are profoundly different from those in the Elephantinæ and in the Mammontinæ.

(2) MAMMONTINÆ. *Parelephas jeffersonii* agrees with *Mammonteus primigenius*, male and female[2], in the concave frontal profile; *P. jeffersonii* differs from *M. primigenius* in the greater anteroposterior extent, it is less compressed. *M. primigenius*, male and female, is the most strongly compressed, i.e., hypsicephalic, acrocephalic.

(3) ELEPHANTINÆ. The adult *Elephas indicus* skull differs widely from the loxodontine and mammontine types in the frontal convexity as well as in the more vertical position of the occipital plane. Compare sections in figure 805.

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[1] [Subsequently Amer. Mus. 14475 was provisionally referred by Professor Osborn to *Archidiskodon imperator*.—Editor.]

[2] Amer. Mus. 14559 was made the type of *Mammonteus primigenius compressus* by Osborn in 1924 (1924.633, p. 5).

a moderate lateral expansion (brachycephaly) of the *E. indicus* cranium. As noted above, the brachycephaly of the *E. indicus* cranium is most marked in the transverse occipital expansion at the very back of the skull, whereas in *L. africana* (Fig. 1061) the transverse zygomatic expansion of the temporal arcades exceeds the occipital expansion.

Growth of the Jaw (Figs. 799, 797, left).—The elongate infantile jaw of *E. indicus* (Fig. 799) resembles the adult jaw of the Upper Pliocene *Archidiskodon planifrons* (Fig. 849), also to a less degree the adult jaw of *L. africana*. In brief, the juvenile jaw of *E. indicus* is harmonic with the mesocephalic juvenile cranium (Fig. 797, left). The growth stages in the jaw are harmonic with the increasing cyrtocephaly, brachycephaly, and bathycephaly of the cranium. Consequently the proportions of the adult jaws of *E. indicus*, as well shown in figure 1204, are abbreviated (cyrtocephalic), deepened or depressed (bathycephalic), and broadened (brachycephalic). In the jaw evolution of every phylum of the Elephantidæ, these three contemporaneous adaptations occur to fit the jaw into its very confined space behind the vertically placed (cyptocephalic) maxillopremaxillary sockets of the tusks.

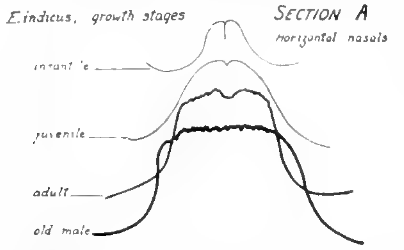

Fig. 807. Superior nasal growth stages. Section *A* horizontal, showing increasing breadth of the nasals in the passage from the infantile to the old male growth stages of *Elephas indicus*. One-sixth natural size.

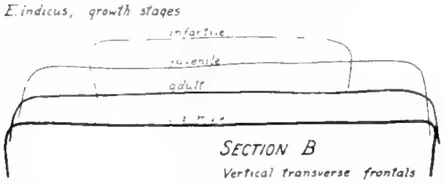

Fig. 808. Transfrontal growth stages. Section *B*. Expansion of the fronto-intertemporal space in infantile to old male growth stages in *Elephas indicus*. One-sixth natural size.

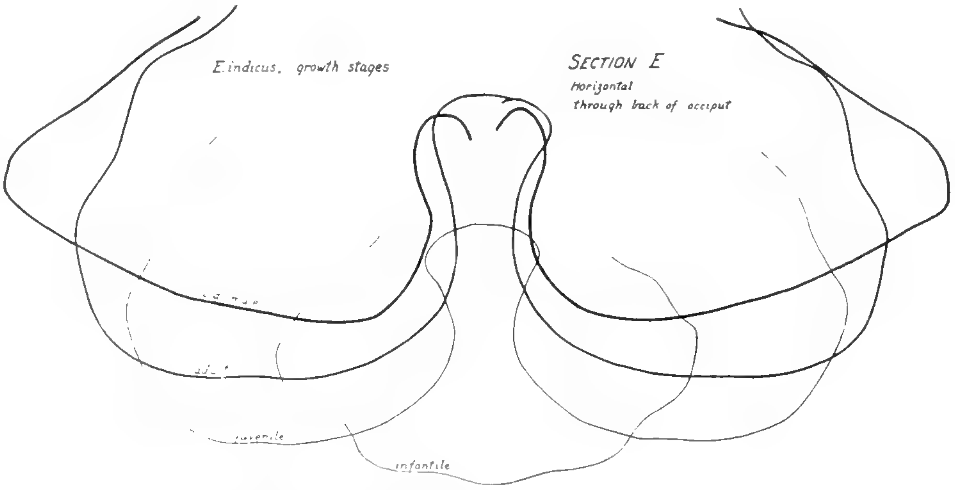

Fig. 809. Occipitohorizontal growth stages, Section *E*. Complete brachycephalic transformation of the horizontal contours of the back of the occiput of *Elephas indicus* in the passage from the infantile to the old male growth stages. One-sixth natural size.

Downward Flexure of Basis Cranii (Figs. 805, 806).—The ontogenetic *progressive downward flexure of the basis cranii* (cyptocephaly) is illustrated in the series of comparative figures (Figs. 805, 806, 1192) which demonstrate the transition between the relatively horizontal *L. africana* basis cranii (Fig. 1192) and the most sharply deflected basis cranii of *Parelephas* and of *Mammonteus* (Figs. 805, 806).

Downward Flexure of Dental Alveoli (Fig. 806).—As first observed by Leith Adams, and as again observed by Gregory and by Osborn, the downward growth of the dental alveoli is harmonic with the vertical extension (hypsodonty) and fore-and-aft compression (cyrtodonty) of the grinding teeth, especially of M^3-M_3. This ontogenetic bathycephaly is not shown in the ontogenetic figures but is clearly displayed in the comparative figure 806, in which it appears that the second and third molars of *E. indicus* are much more depressed or bathycephalic than the second and third molars of *L. africana*.

GENERIC CONTRASTS IN CRANIAL SECTIONS: LOXODONTA, PARELEPHAS, MAMMONTEUS, AND ELEPHAS

The sectional contours described above were plotted as in figure 805 and almost immediately revealed the profound differences between the three chief phyla of elephants.

Encouraged by this preliminary observation, which gives a new clue to the classification and phylogeny of the Elephantidæ, a series of sections were taken in all crania available to the author and it was found that the other cranial sections supported the inferences derived from the axial section, as shown in figures 805 and 806.

It is demonstrated that the crania exhibit three subfamily types, namely, loxodontine, elephantine, and mammontine.

(1) FLEXURE (CYRTOCEPHALY) OF FRONTO-OCCIPITAL-BASILAR PLANES (FIG. 805).—The midvertical section (*C*) combined with the para-occipitofrontal section (*D*) is the most important, because, as shown in figures 805, 806, and 816, it reveals the angular flexure (cyrtocephaly) which the entire upper part of the cranium bears to the *basis cranii* and especially the angle between the *occipital plane* and the basis cranii. It appears that in *Loxodonta africana* the angle of the basis cranii to the occipital plane (100°) approaches a right angle; this is because the cranium of the African elephant as compared with that of *Elephas indicus* is less brachycephalic, more orthocephalic, and less bathycephalic or vertically deepened. In *E. indicus* the occipital plane forms a more open angle of 121° with the basis cranii, expressive of its greater bathycephaly. A still wider angle (130°), however, is attained in the bathycephalic *Parelephas jeffersonii*, while in *Mammonteus primigenius* the angle rises to 136°.

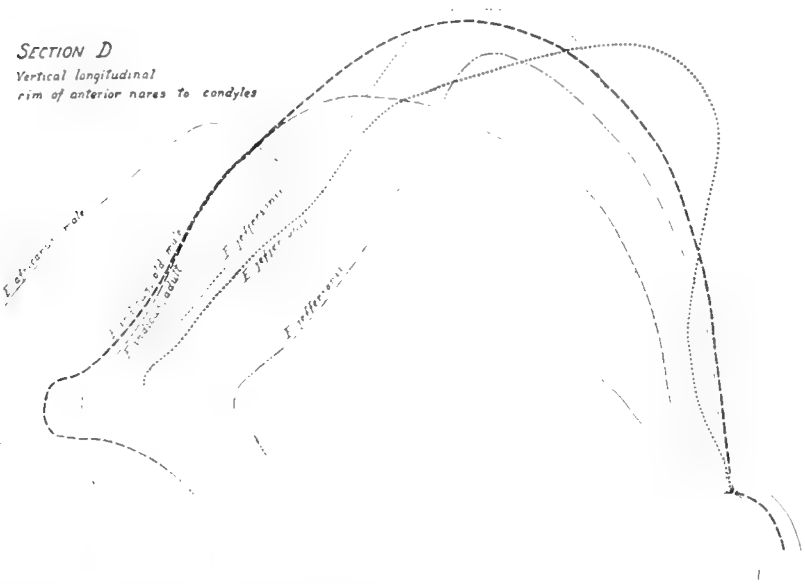

Fig. 810. Skull. Mid-occipitofrontal Section *D*, vertical longitudinal, from rim of anterior nares to occipital condyles, with the *basis cranii* in a uniform plane. Reduced to one-sixth natural size.

LOXODONTINE type (*Loxodonta africana*, male), fronto-occipital angulate, pitching forward.

ELEPHANTINE type (*Elephas indicus*, male, adult), fronto-occipital rounded, convex.

MAMMONTINE type (*Parelephas jeffersonii*, adult males, and a young male[1]), fronto-occipital angle concave or slightly convex.

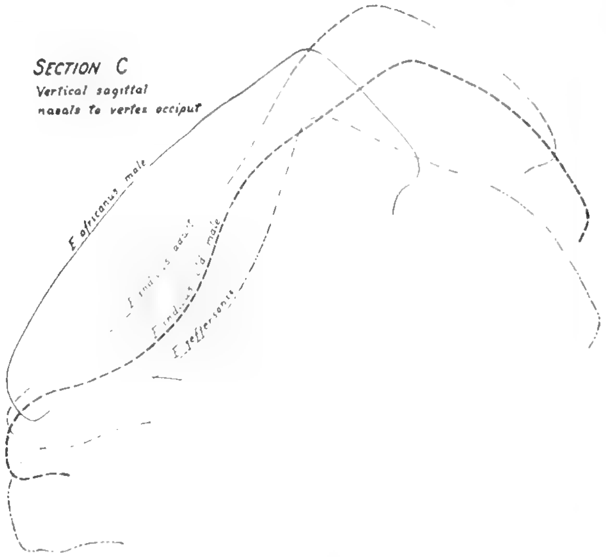

Fig. 811. Frontal sections. Comparative vertical section of the frontal bones and occiput of the three subfamily divisions of the elephant family (*C*), vertical sagittal, nasals to vertex of occiput. Reduced to one-sixth natural size.

LOXODONTINE type (*Loxodonta africana*, male), convex.

ELEPHANTINE type (*Elephas indicus*, adult), concave.

ELEPHANTINE type (*Elephas indicus*, old male), concavo-convex.

MAMMONTINE type (*Parelephas jeffersonii*,[1] young male), uniformly concave.

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[1] [Subsequently Amer. Mus. 14475 was provisionally referred by Professor Osborn to *Archidiskodon imperator*.—Editor.]

(2) Deepening (Bathycephaly) of the Molar—3 Plane (Fig. 806.)—The horizontal grinding surface of the superior molars below, compared with the cranial profiles above (Fig. 806), reveals bathycephaly as the most distinctive cranio-mechanical adaptation.

In the Loxodontinæ: (a) The bathycephaly is less extreme; (b) the occipitofrontal union is less elevated above the horizontal $M^{2\text{-}3}$ grinding surface; (c) the fronto-occipital plane is at an *oblique angle* with the molar–3 plane; consequently the *Loxodonta* skull is less hypsicephalic.

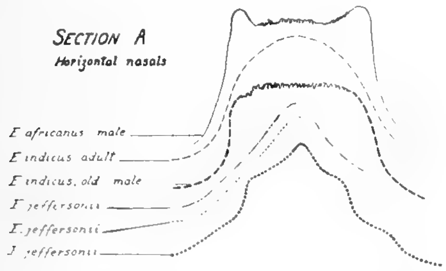

Fig. 812. Nasal contours. Comparative horizontal, Section *A*, of nasals showing the *broad* nasals of *Loxodonta africana* and of *Elephas indicus* as compared with the pointed *mammontine* nasals of *Parelephas jeffersonii*, male, of *P. jeffersonii*,[1] young male, and of *P. jeffersonii*, adult male—all in the American Museum collections. Reduced to one-sixth natural size.

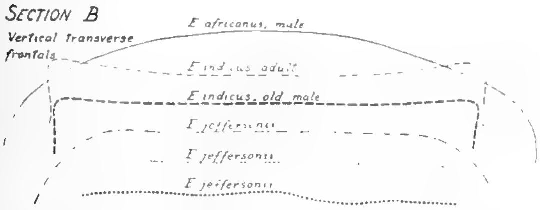

Fig. 813. Midfrontal or intertemporal forehead. Uniformly convex transfrontal, Section *B*, of *Loxodonta africana*, male, as compared with the slightly concave frontal section of an adult *Elephas indicus* and the planoconcave frontal sections of three skulls of the *mammontine* type of *Parelephas jeffersonii*—all in the American Museum collections. Reduced to one-sixth natural size.

Loxodontinæ = *Loxodonta africana*, uniformly convex.

Elephantinæ = *Elephas indicus*, planoconcave, borders angulate.

Mammontinæ = *Parelephas jeffersonii*, planoconcave, transfrontal borders rounded.

In the Mammontinæ it is observed (Fig. 806): (a) That the bathycephaly of *Mammonteus primigenius* and of *Parelephas jeffersonii* is practically the same as that of *Elephas indicus*, because the molar-2-3 plane descends to the same degree below the occipital condyle; (b) while the Mammontinæ agree with the Elephantinæ in bathycephaly, they differ widely in the fronto-occipital profiles, as shown in comparison of the line *E. indicus* with the line '*E.*' *jeffersonii*; (c) the Mammontinæ agree with each other in the fronto-occipital profiles, as shown in the lines '*E.*' *jeffersonii* '*E.*' *primigenius* female [= type of *Mammonteus primigenius compressus* Osborn, 1924], '*E.*' *primigenius* male; (d) in the Mammontinæ the *M. primigenius* male and female profiles seem to be relatively more hypsicephalic and acrocephalic than those of *P. jeffersonii*; consequently the *Mammonteus* cranium suffers even greater fore-and-aft compression than the *Parelephas* cranium.

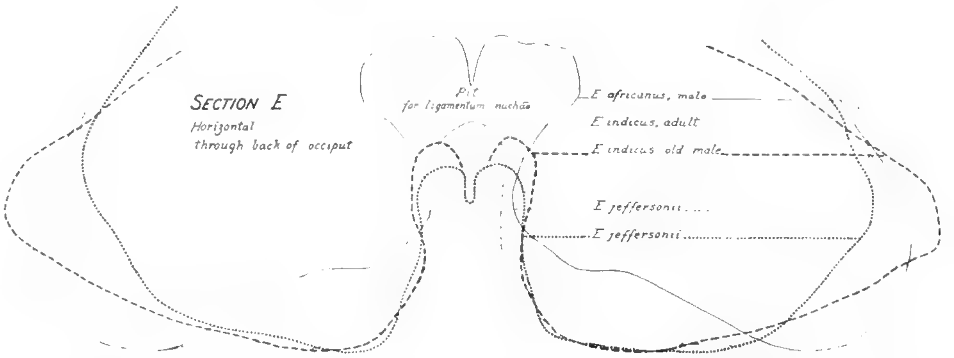

Fig. 814. Occipitohorizontal, Section *E*, through back of occiput at broadest portion in the three subfamily divisions of the elephant family. Reduced to one-sixth natural size.

Loxodontinæ = *Loxodonta africana*, broad convex flare of occiput; deep ligamentum nuchæ pit. Indicated by ——

Elephantinæ = *Elephas indicus*, very broad, acute flare of occiput; ligamentum nuchæ pit moderately deep. Indicated by – – –

Mammontinæ = *Parelephas jeffersonii*, convex flare of occiput, less expanded; ligamentum nuchæ pit moderately deep. Indicated by . . .

The Elephantinæ profile is followed in the dotted line *E. indicus*: (a) The bathycephaly indicated by the $M^{2\text{-}3}$ depression is the same as in *Parelephas jeffersonii*; (b) the fronto-occipital profile of *E. indicus* differs widely from that of *P. jeffersonii* and still more widely from that of *Mammonteus primigenius*; thus the *E. indicus* cranium is equally bathycephalic but it is less hypsicephalic and acrocephalic than either that of *Parelephas* or *Mammonteus*.

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[1] [See footnote on opposite page.—Editor.]

(3) HYPSICEPHALY AND ACROCEPHALY IN FRONTO-OCCIPITAL PROFILES (FIG. 810).—In the Loxodontines, as shown also in figures 805 and 806: (a) The angular fronto-occipital profile is totally different from that of either *Parelephas* or *Elephas*; (b) in *Elephas*, both in the adult and old male stages of *E. indicus*, there is a rounded dome-like fronto-occipital profile, which rises to a great height in the old male; (c) in the "*Parelephas jeffersonii*" crania, shown in the line '*E.*' *jeffersonii*, the cranium is equally hypsicephalic, but it is not acrocephalic, since it reaches an acute apex through the characteristically mammontine concavity of the frontals.

In the frontal sections of the forehead profile we readily distinguish between the uniformly *convex* profile of *Loxodonta africana*, the *concavo-convex* profile of *Elephas indicus*, and the *concave* profile of *Parelephas jeffersonii*. The concave frontal profile of *P. jeffersonii* relates this animal to *Mammonteus*.

(4) BRACHYCEPHALIC AND HYPSICEPHALIC NASAL CONTOURS (FIG. 812).—The broad nasals of *Loxodonta africana* male are harmonic with the brachycephaly of the cranium. In the *Elephas indicus* adult the nasals exhibit a rounded profile, but in the *E. indicus* old male the end of the nasals is truncated. In *Parelephas jeffersonii* the crania examined exhibit uniformly acute or pointed nasals clearly distinguishable from those of either *Elephas* or *Loxodonta*.

(5) CONVEX OR CONCAVE TRANSFRONTAL SECTIONS (FIGS. 806, 801, 805, 813).—In *Loxodonta* the forehead or frontal bone is convex in both planes, sagittal and transverse, as shown in figures 806, 805, and 813. In *Elephas indicus* the transfrontal section (Fig. 813) is seen to be plane with sharply angulate lateral borders defining the temporal fossæ. In *Parelephas jeffersonii* the transfrontal section is rounded but less convex than that of *L. africana*.

(6) RELATIVE BRACHYCEPHALY OF THE OCCIPITAL PLANES (FIG. 814).—Whereas the *Loxodonta africana* cranium, as shown in the plain line '*E.*' *africanus* male, is in general more brachycephalic than that of *Elephas indicus*, the greatest lateral expansion of the occipital region is attained in the *E. indicus* old male, in which the expansion far exceeds that of *Parelephas jeffersonii*, as indicated in the lines '*E.*' *jeffersonii*. The pit for the ligamentum nuchæ is similar in the *E. indicus* old male and in '*E.*' *jeffersonii*, whereas the pit in *Loxodonta africana* is very much deeper.

SUMMARY. In summing up the cranial and profile proportions of *Loxodonta*, of *Parelephas*, of *Mammonteus*, and of *Elephas* in respect to the six chief regions described above, we observe that *Loxodonta* differs profoundly in every character from *Elephas*, *Parelephas*, and *Mammonteus*; this is probably due to profound differences in feeding habits. The crania of *Parelephas* and of *Mammonteus* agree in their bathycephaly with the cranium of *Elephas*, but differ widely in their acrocephaly. There appear to be clear lines of demarcation into three subfamily groups which are summarized below (p. 932).

While the mechanical problem of the tusks and of the proboscis remains relatively the same in these three generic stages of cranial evolution, the mechanical problem of the grinding teeth changes, as follows: (1) The relatively low-crowned grinding teeth of *Loxodonta* are correlated with a relatively less brachycephalic or mesocephalic cranium; (2) in the opposite extreme the many plated, high-crowned, extremely hypsodont grinding teeth of *Mammonteus* are correlated with an extremely hypsicephalic and bathycephalic cranium; (3) extreme fore-and-aft compression of the cranium of *Mammonteus* (i.e., cyrtocephaly, bathycephaly) is coördinated with extreme shortening, heightening, and multiplication of the dental ridge-plates (i.e., cyrtodonty, hypsodonty, polydiskodonty).

II. DENTAL AND CRANIAL ADAPTATION TO PREVAILING FEEDING HABITS THE KEY TO PHYLOGENETIC CLASSIFICATION

As among other ungulates, the choicest elephantine diet *abundant in favorable seasons* of the year is that most frequently resorted to and most dominant in cranial and dental mechanics. Seasonal or climatic and secular changes may have enforced changes of prevailing diet. Persistence of dental type is favored by persistent climatic conditions and flora, as we believe was the case in the true *Stegodon,* which continued to browse through the Upper Tertiary and into early to Upper Pleistocene time in the tropical forests of India and the islands of the East Indies, eastward into China and Japan. Accordingly the grinding teeth of *Stegodon* multiply their ridge-crests but do not become sensibly hypsodont as in the elephants. The cranial evolution of the Stegodonts also appears to be distinctive.

1. RIDGE-PLATE FORMULÆ OF PRIMITIVE AND PROGRESSIVE GENERA IN ADAPTATION TO PREVAILING HABITS OF FEEDING

The *ridge-crests* of *Stegodon* are transformed into the *ridge-plates* of the Elephantoidea.[1]

Ridge-plate Formulæ.—Falconer (1868, Vol. II, p. 13) in defining his three subgenera of *Elephas* laid great stress on the number of ridge-plates in the intermediate molars, namely, Dp 4, M 1, M 2, as follows:

Subgen. *Stegodon,* hypisomeris, e. g., Dp 4 = 7, M 1 = 7, M 2 = 8.
" *Loxodon,* hypisomeris, e. g., Dp 4 = 7, M 1 = 7, M 2 = 8.
" *Euelephas,* anisomeris, e. g., Dp 4 = 12, M 1 = 14, M 2 = 18.

Throughout his masterly work "On the Species of Mastodon and Elephant Occurring in the Fossil State in Great Britain," 1863, Parts I and II, and "On the American Fossil Elephant of the Regions Bordering the Gulf of Mexico," Part III, Falconer makes a profound study of the ridge formulæ, describing the formulæ in various species with an accuracy which cannot be challenged today. This great section of Falconer (1868, Vol. II, pp. 1–291) is a masterpiece of accurate observation, including very appropriately a discussion of the unity or plurality of species (pp. 254–271) based on the vertebral formulæ, as cited below.

2. FOOD OF THE INDIAN AND AFRICAN ELEPHANTS AND OF THE MAMMOTH

Falconer concludes Section III of his "Palæontological Memoirs" of 1868, Vol. II, with a philosophical treatise (pp. 277–291) on the "Food of Living and Extinct Elephants," which he connects very closely with the comparative structure of the ridge-plates in *Elephas, Loxodonta,* and *Mammonteus.*

> Food of the Indian Elephant [Falconer, 1868, II, pp. 277–280].—The 'Sàl,' or 'Tarai' Forests, which stretch at the foot of the Himalayahs, from lat. 30°, where the Ganges and Jumna escape from the mountains, to the Brahmapootra, embracing a range of several hundred miles, are here selected to furnish the chief illustrations which I have to adduce. They everywhere abound with Elephants, southwards from lat. 30°, which may be regarded as the extreme northern limit of the habitat of the species at the present day. Forests presenting similar physical characters extend along the continuation of the same range, through Sylhet, Chittagong, Arracan, Pegu, and the Tenasserim provinces, to the point of the Malay Peninsula; they become more and more tropical in their vegetation, and, as a general rule, the Elephants improve in size, form, and vigour, according to their more southern habitat. . . . In fact, the range of his [Indian Elephant] arboreous selection is restricted within a narrow circle, and mainly to the foliage and branches of trees that abound in milky juice which is not acrid, belonging to the families of the *Moreæ, Artocarpeæ,* and *Sapotaceæ,* such as species of *Ficus, Batis, Artocarpus, Bassia,* and *Mimusops* [Footnote: 'Also *Mesua*

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[1] [It will be noted from the following quotation (see Volume I, p. 25, of the present Memoir) that Professor Osborn subsequently altered his opinion: "It has been assumed by practically all palæontologists that the Elephants were descended from the Stegodonts. This assumption now proves to be erroneous, for neither the *Stegodon* grinding tooth with enamel valleys closed at the bottom, nor the *Stegodon* cranium with its extremely short face, can give rise to the elephantoid molar or the face of the elephantoid cranium."—Editor.]

ferrea (Nat. Ord. *Clusiaceæ*), on the authority of Tennent's Nat. Hist. of Ceylon, p. 230.']. Of these, by far the greater part of his staple food is derived from the colossal fig-trees which abound in the forests of India; such as *Ficus Indica*, the 'Bur,' or Banyan-tree; *F. religiosa*, 'Peepul,' or 'Bodhi-drooma' (Tree of knowledge); *F. venosa*, 'Pilkhun'; *F. cordifolia*, 'Gujeena,' or 'Assoud'; *F. glomerata*, 'Goolur'; *F. Tsiela*, 'Kuth-bur'; and in Assam, *Ficus elastica*, or the 'India-rubber tree,' besides other more southern species of similar habit and properties. The strong partiality of the Elephant for these trees is so well known to the natives, that the *'Obees,'* or Pit-falls, for entrapping the animal are invariably constructed in their neighbourhood, and many of their old Sanscrit names connect them specially with the Elephant [Footnote: ' "Nagbhundoo," "Koonjurashun"; "Gujashun," and "Gujbhukshuk"; all being to the effect of "food of Elephants." (*Vide* Madden, Journ. Asiat. Soc. Beng., vol. xvii. p. 380.)']. He tears down their branches, and crunches the twigs and leaves, stripping off the lactiferous bark of the larger boughs. The Elephant of the 'Sàl' Forests also derives occasional food from the foliage and fruit of *Artocarpus Lackoocha*, 'Dhao'; . . . Of aliment derived from the roots of Dicotyledonous trees and shrubs, such as the African Elephant is said to affect, I know of but one form in the 'Sàl Forests' which the Indian species is known to touch, namely, the huge tuberous dilatation of the ligneous root of the Scandent, *Pueraria tuberosa*, 'Sural.' . . . Among the monocotyledonous families, a very large portion of his habitual fare is derived from the *Gramineæ*, and more sparingly from Palms; of the former, he luxuriates on the young shoots and tender foliage of various species of Bamboo, which occur in vast abundance, together with the fleshy albuminous fruit of *Beesha Rheedii*, found in the southern forests. The 'jhils,' or swamps, to which he resorts, are sheeted with the gigantic reeds of *Arundo kurka*, 'Nul,' the young culms of which, together with the stems and leaves of *Typha Elephantina*, 'Patela,' at certain seasons, constitute a favourite food of the Indian Elephant. The open glades and prairie lands are covered with species of *Saccharum*, forming what is called 'Grass Jungle,' composed chiefly of *S. spontaneum*, 'Kas,' interspersed with *S. fuscum*, 'Tat,' *S. Sara*, *'Surkura,'* or 'Moonj,' *S. exaltatum*, 'Suroo,' &c. Clumps of these grasses are twisted up by his trunk, in his journeys to and from the forests; they are beaten against his legs to free the roots from sand, and then subjected to mastication. The sand which still adheres to these grasses, together with the large quantity of silica contained in the leaves and culms of *Saccharum spontaneum*, the most characteristic species of the grass jungle, performs an important duty in the economy of wear of the Elephant's molar teeth [Footnote: 'The excessive abundance of silica in the culms and leaves of *S. spontaneum* is practically shown when it is attempted to mow it with an English scythe. After a few sweeps, the edge of the implement is rounded off, as I have repeatedly witnessed.'] . . . It is difficult to conceive of a mechanism better adapted to the duty which they have to perform than is presented by the molars of the Indian Elephant. Taking the three true molars, which serve during the adult stage of the animal, they are composed successively of 12, 16, and 24 ridges. Each ridge has the core formed of a high wedge-shaped plate of ivory; . . . A constant equilibrium is maintained, in the normal state, between the nature of the food, the waste of the crown-surface, the absorption of the fangs, the forward movement of the body of the tooth, and the replacement of the worn-out portion by a succession of fresh plates, protruded from behind.

Food of the African Elephant [Falconer, 1868, II, pp. 282–284].—Our knowledge of his food is, therefore, of a vague and general character, being derived from the cursory observation of travellers, whose attention was not specially directed to the subject. The molar teeth of the African Elephant are intermediate, in construction and triturating characters, between those of the *Euelephantes*, or Elephants proper, and the fossil *Stegodons*. They present, in the three intermediate and last molars for the ridge-formula, the successive ciphers 7: 7, 8, 10; while *E. antiquus* presents the ciphers 10: 10, 12, 16, and *E. primigenius* and *E. Indicus*, 12: 12, 16, 24. The aggregate of the series of ridges in the first amounts only to 32; in the second to 48; and in the two last to 64; involving a great difference in the triturating mechanism of the teeth. In the African form the molars are also shorter, narrower, and of less elevation, than in the Asiatic species. The discs of wear, instead of the narrow transverse bands seen in the latter, exhibit the well-known rhomboidal expansion characteristic of the species. Instead, therefore, of being adapted to contuse and triturate the branches and twigs of trees, they are better suited for squeezing and crushing leaves, and succulent stems or roots. The habits of the animal, as observed by travellers, are in accordance with these indications. Besides browsing on the foliage of the Mimosas and Acacias, which abound in Southern Africa, they tear up the trees of certain species of these genera by the roots, aided, according to Pringle, by their tusk, used as a crow-bar (?), and they devour the succulent parts of these roots in the inverted trees [Footnote: 'Cited in the "Library of Entertaining Knowledge." Menageries, vol. ii. p. 36.']. Burchell mentions a small species of *Prosopis*, *P. Elephantorhiza*, as yielding a favourite food to the Elephant [Footnote: '*Acacia Elephantina*, Burch. "Travels in South Africa," vol. i. p. 236. *Elephantorhiza Burchellii*, Benth.']; and the succulent 'Spekboom' *Portulacaria Afra*, or 'Tree Purslane,' is noticed by most travellers as yielding another. That the African Elephant, such as we now see it, formerly extended to the South of Europe, has been put beyond question—1st, by the researches of Lartet upon remains found in the neighbourhood of Madrid [Footnote: 'Comptes Rendus. 22 fév. 1858. Tom. xlvi.']; 2nd, by the remains discovered by Baron Anca in the cave of San Teodoro in Sicily [Footnote: 'Bullet. Soc. Géol. de France. 2e Sér. t. xvii. p. 684. Pl. xi. figs. 5 & 6.']; 3rd, by a molar from Grotta Santa, near Syracuse, described by the Canon Alessi [Footnote: 'Atti dell' Accad. di Scienz. Natur. tom. vii. p. 223.'], and identified by myself; and lastly, by a molar exhumed by M. Charles Gaudin, in 1858, in a cave near Palermo. . . . Of the more ancient European fossil species, *E. antiquus* is that which most resembles the African Elephant in the mesial expansion of the discs of its worn molars. But the character is shown in a much less degree, and the great difference in the ridge-formula of the two species places them in two distinct subgenera.

Food of the Mammoth [Falconer, 1868, II, p. 284].—In order to estimate the force and value of the arguments which have been raised on this head, it is necessary to institute a rigorous comparison between the mechanical conditions of the molar-crowns of the Indian Elephant and of the fossil species. The ridge-formula is the same in both, being for the four last teeth of the upper jaw 12: 12, 16, 24. The number of ridges in the three first of these is very constant; the last, as already stated, is variable within certain limits, twenty-two being the most common number. Taking the penultimate, as in the case of the Indian Elephant, the worn surface of the crown would show sixty-four alternations of unequally hard materials.

Falconer points out that the teeth of the mammoth are far less adapted to browsing and especially to crushing the woody fiber and bark of trees than the teeth of the Indian elephant, and he ingeniously argues *a priori* that the food of the mammoth was widely different from that of the Indian elephant. This argument, based on the structure of the molar crowns, is fully sustained by the discovery that, during certain seasons of the year at least, the food of the mammoth consisted chiefly of grasses, as quoted in full from Felix in his description of *Elephas primigenius* (see Felix, 1912, p. 1127 of this Memoir).

3. SEASONAL CHANGES IN FOOD OF THE MAMMOTH

It proves that the extremely hypsodont, finely plated teeth of the mammoth are principally adapted to the northern grasses which prevail on the tundras and Arctic prairies during the summer season. As recently described by Stefansson, the summer tundra flora closely imitates that of the grasslands which we know as 'prairies' in temperate latitudes. In this brief season the mammoth obtained its chief food supply for the year, and, like other northern Herbivora, stored up large reservoirs of fat which were drawn upon during the long Arctic winter season. In summer a grazer chiefly if not exclusively, in winter it became a browser, feeding upon twigs and the branches of conifers and woody substances which contained materials of far less nutritional value. Thus its habits directly reversed those of the African elephant (*Loxodonta*), which is chiefly a browser and incidentally, and for the sake of food variety, a grazer, or of the Indian elephant, which is both a browser and a grazer. Similar seasonal habits are doubtless characteristic of the northern types of horses with extremely hypsodont teeth, primarily adapted to grazing, secondarily to browsing.

Conclusion.—*The number, compression, and elevation of the ridge-plates increase in all generic phyla, as the primitive browsing habit develops into a grazing habit.*

4. SUMMARY OF PROGRESSION FROM BROWSING TO GRAZING DENTITION

(1) The proboscis, the tusks, and the grinding teeth of the Elephantidæ originate in the browsing and plant-uprooting habits of *Stegodon* with elongate tusks.[1]

(2) As in other ungulates, the Elephantidæ first passed through a purely browsing stage with brachyodont grinders, into a browsing stage with hypsodont grinders, typified by primitive species of *Archidiskodon* like *A. proplanifrons* and *A. planifrons.*

(3) There also arose the browsing and crushing stage with hypsodont and loxodont grinders, typified by *Loxodonta africana,* in which the teeth were adapted to browsing not only on leafage but on the stems, twigs, branches, and roots, in which the plant-uprooting functions of the tusks were useful. There is little or no record of grazing in this stage.

(4) Adaptation to seasonal habits of browsing on the more tender foliage and of grazing on the coarser weeds and grasses, as well as on tender shoots and buds, is typified in the still more hypsodont grinders of *Elephas indicus,* which closely parallel in the elongation and multiplication of the ridge laminæ species of the genus *Parelephas.*

(5) Finally there arose the extremely hypsodont, thin-plated, reatively smooth-crowned grinding teeth of *Mammonteus primigenius,* chiefly adapted to grazing, but during certain seasons of the year forced into use for browsing purposes.

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[1] [But see footnote on page 927 above.—Editor.]

The primary ridge formulæ and the primary cranial characters in the several subfamily and generic phyla of the Elephantidæ were probably similar. We have seen that the juvenile *Elephas indicus* cranium resembles in many respects the adult *Loxodonta africana* cranium; the only primitive true elephant cranium we know is that of *Archidiskodon planifrons*, which it would be interesting to section and compare with *Stegodon* on the one hand and with *Elephas indicus* on the other.

As clearly set forth in the introductory pages of this chapter, there is so much parallelism, and even *convergence*, in the grinding teeth characters of different phyla of elephants as they pass from the chiefly browsing into the browsing and grazing and into the chiefly grazing and browsing types, that it is only by the combined analysis of the tusks, of the grinding teeth, of the cranial axes, and of the cranial planes and profiles, that we can distinguish these great family and subfamily phyla from each other.

III. VERTEBRAL DISTINCTIONS OF ELEPHAS, LOXODONTA, MAMMONTEUS, AND PARELEPHAS

Divergence in vertebral and rib formulæ in the dorsal, lumbar, and caudal regions will undoubtedly aid us in distinguishing genera, species, and subspecies of the elephants. We have not at present accurate and final observations on the distinctive characters of the ribs and of the backbone, as shown in the following review.

1. VERTEBRAL FORMULÆ IN THE ABOVE GENERA

Falconer in his invaluable Memoir of 1863, as reprinted in full in the "Palæontological Memoirs" of 1868, Vol. II, pp. 212–291, gives an excellent review of the existing and extinct species of elephants, including his own observations (presented in more detail in Chap. XX, pp. 1312, 1313 of the present Memoir) on the vertebral as well as on the ridge-plate formulæ; he summarizes (p. 257) the conclusions of Schlegel, 1845–1867, and of Temminck, 1862 (see Sclater's translation, 1862.1, of Schlegel's paper on "The Sumatran Elephant") in the following table:

	African Elephant		Sumatran Elephant		Indian Elephant	
	In Temminck [1862]	Schlegel [1845–1867]	In Temminck [1862]	Schlegel [1845–1867]	In Temminck [1862]	Schlegel [1845–1867]
Cervical vertebræ.	7	7	7	7	7	7
Dorsal vertebræ.	21	21	20	20	19	19
Lumbar vertebræ.	3	3	3	3	3	3
Sacral vertebræ.	4	4	4	4	5	4
Caudal vertebræ.	26	26	34	33	34	33
True ribs[1].	6	5	6	5	6	5
False ribs.	15	16	14	15	13	14
Pairs of ribs.	21	21	20	20	19	19

According to this Schlegel-Temminck table, the continental *Elephas indicus* has only 19 dorsal vertebræ and 19 pairs of ribs, while the insular *Elephas sumatranus* has 20 dorsal vertebræ and 20 pairs of ribs, the African elephant, *Loxodonta africana*, having 21 dorsal vertebræ and 21 pairs of ribs. These differences, remarks Falconer, if they prove to be constant, would be of considerable systematic importance.

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[1] "Schlegel expressly states, 'that the number of true ribs is alike in all the species, that is only five;' but there is evidently a numerical slip in the ciphers which he immediately afterwards assigns to the false ribs, namely, 15, 14, and 13 respectively, in the three different species, which would give a total of 20, 19, and 18, instead of 21, 20, and 19, being the asserted aggregate of pairs corresponding with the assigned number of dorsal vertebræ in the different species. (Nat. Hist. Review, vol. ii, p. 75.)"

Falconer's own observations and records differ from those of Schlegel and Temminck and may be summed up as follows:

Elephas primigenius: In the mammoth there appear (Schlegel) to be 18 dorsal vertebræ and 18 ribs. According to Tilesius, in the mammoth skeleton (*E. primigenius*) in St. Petersburg there are 19 dorsal vertebræ and 19 ribs.

Loxodonta africana, African elephant:

- Congo (Cuvier, de Blainville, 1844, Laurillard, Daubenton) an imported elephant: 20 dorsal vertebræ and 20 pairs of ribs; total formula: 7 cervical, 20 dorsal, 3 lumbar, 3 sacral, 31 caudal vertebræ; 20 pairs of ribs.
- Cape of Good Hope: 7 cervical, 20 dorsal, 3 lumbar, 4 sacral, 26–30 caudal vertebræ; 20 pairs of ribs [typical *capensis*].
- Algoa Bay[1] (Flower-Falconer): 7 cervical, 21 dorsal, 3 sacral, 30 caudal vertebræ; 21 pairs of ribs.
- Sumatran elephant (Schlegel): 20 dorsal vertebræ and 20 pairs of ribs.

Indian Elephant:

- Ceylon (Camper, de Blainville, Cuvier): 20 dorsal vertebræ and 20 pairs of ribs.
- Bengal (Camper, de Blainville, Cuvier): 20 dorsal vertebræ and 20 pairs of ribs.
- Bengal (Falconer): 7 cervical, 20 dorsal, 3 lumbar, 4 sacral vertebræ, 20 pairs of ribs; 20th dorsal small and unsymmetrical.

Falconer concludes that the continental elephant of northern India varies in the number of its dorsal vertebræ from 19 to 20, as the African varies from 20 to 21.

VERTEBRAL FORMULÆ ACCORDING TO FALCONER'S SUMMARY

	African	Indian	Sumatran	[According to Eales (1929)[2] African Fœtus
Cervical vertebræ	7	7	7	7
Dorsal vertebræ	20–21	19–20	20	21
Pairs of ribs	20–21	19–20	20	21
Lumbar vertebræ	3	3	3	3
Sacral vertebræ	3 [–4]	3 [–4]	3 [–4]	6
Caudal vertebræ	26–31		26 [–34]	26]

VERTEBRAL FORMULÆ ACCORDING TO FLOWER'S AND OSBORN'S SUMMARY OF 1926[3]

	Loxodonta africana		*Elephas indicus*	*Mammonteus primigenius*		*Parelephas jeffersonii*
	Flower, 1885	"Jumbo" Amer. Mus. Dept. Mam. 3283	Flower, 1885	Falconer and Amer. Mus. 14559 (=*M. primigenius compressus* Type)	Felix, 1912 *M. primigenius*	Type Amer. Mus. 9950
Cervicals	7	7	7	7	7	7
Dorsals	19	20	19–20	18-19	19	19
Pairs of ribs				18–19	19	19
Lumbars	4	3	5-3	4-3	5	4
Sacrals	5	4	4	4 3	4	5
Caudals	24+	21	24–30+	21	21 (Salensky)[4]	12+

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[1] [Cited from letter, July 25, 1929, from Dr. Hubert Collar, Curator, The Museum, Saffron Walden, Essex: "I have verified the particulars you send relating to the skeleton of the African Elephant in this Museum and find them to be correct, except that a few of the caudal vertebræ are missing."

"The geographic locality is also correct according to our records, but I would point out that the term 'imported from Algoa Bay' does not necessarily mean that the animal was killed at that place. Actually, this specimen with many others was sent from Port Elizabeth in 1833, and so far as I know, there is no record showing exactly where it was obtained. It is a fair inference, however, from indirect evidence that the place was somewhere in the locality." —Editor.]

[2] Eales (1929, pp. 223, 224) observes as to the Congo elephant: "The number of fœtal vertebræ is: Cervical, 7; Thoracic, 21; Lumbar, 3; Sacral, 6; Caudal, 26. . . .Six sacral vertebræ bear facets for the ilium. There is, however, no fusion of vertebræ in this region in the fœtus. . . . The difference between the African and the Indian Elephant lies in the thoracic and sacral regions. The African Elephant has a larger number of ribs but fewer sacral vertebræ than the Indian Elephant (adult). In the fœtus, however, there are six vertebral attachments on the ilium, a number greater than any given for the Indian Elephant. . . .

Fœtus.—[In addition to the 21 dorsal vertebræ]: sternal ribs, 6; indirectly sternal ribs, 11; free, 4.
Adult African (Oxford Museum).—6, 10, 5, giving a total of 21 in each case.
Adult Indian.—Various figures, *e.g.* Camper, 8, 12; Perrault, 7, 13; Blair, 8, 11—the details of indirectly sternal and free ribs not being given."

[3] Compare a more recent summary (1929) in Chapter XIX, p. 1227.

[4] [See Zalensky, Vladimir Vladimirovich, in Bibliography of Volume I of the present Memoir.—Editor.]

SYNOPSIS OF THE THREE SUBFAMILIES OF THE ELEPHANTOIDEA DISTINGUISHED BY PROFOUND PROPORTIONAL RESEMBLANCES (COMPARE PAGES 924–926 ABOVE)

TYPICAL SPECIES	1. Subfamily MAMMONTINÆ, including the three generic phyla *Archidiskodon*, *Parelephas*, and *Mammonteus*, which exhibit three distinct modes of adaptation in the grinding teeth.	2. Subfamily LOXODONTINÆ, typified by *Loxodonta africana* with narrow-plated teeth, by *Palæoloxodon namadicus* and *Hesperoloxodon antiquus* with broad-plated teeth, also by *Hesperoloxodon antiquus ausonius* with extremely narrow-plated teeth.	3. Subfamily ELEPHANTINÆ, typified by *Elephas indicus*; convergent with *Parelephas* in ridge-plate multiplication and hypsodonty.
TUSKS	Tusks and tusk alveoli progressively vertical; tusks elongate, incurved, crossing in old males, not serving in feeding habits.	Tusks elongate, oblique, relatively straight or slightly incurved, continuously serving in browsing habits.	Tusks relatively straight, incurved, used in feeding and uprooting habits; sockets subvertical, as in the Mammontinæ.
GRINDERS	Grinding teeth subhypsodont to extremely hypsodont, typically broad and typically short vertically; progressively deepening ridge-plates; typical M 3 $\frac{10+}{11+}$ in *Archidiskodon planifrons*, multiplying to M 3 $\frac{27}{27}$ in *Mammonteus primigenius compressus*.	Grinding teeth subloxodont or simply plated, moderately hypsodont, typically elongate and narrow; progressively broadening ridge-plates; typical M 3 $\frac{10}{11}$ in *Loxodonta africana*, multiplying to M 3 $\frac{15}{16}$ in *Palæoloxodon namadicus*, to M 3 $\frac{16}{17}$ in *Hesperoloxodon antiquus*.	Ancestors unknown. Ridge-plates multiplying and elongating to M3$\frac{24}{24-27}$; not heightening to the extreme hypsodonty of *Archidiskodon* or *Mammonteus*.
CRANIUM	Cranium shortened (cyrtocephalic), deepened (bathycephalic), heightened (hypsicephalic), pointed (acrocephalic), reaching an extreme fore-and-aft abbreviation and elevation in *Mammonteus*.	Cranium relatively mesocephalic, brachycephalic, platycephalic. Grinding tooth plane slightly depressed or bathycephalic.	Cranium bathycephalic, cyrtocephalic, hypsicephalic, not *acrocephalic*. Cranial dome rounded, with expanding diploë.
HABITS	Habits varying in the three generic phyla. Originally browsing, progressive to extreme grazing type.	Feeding habits, crushing of coarse leafage, herbage, and wood fiber, progressing to chiefly browsing in *Palæoloxodon namadicus*, *Hesperoloxodon antiquus*.	Known habits chiefly browsing, secondary grazing.

MAMMONTINÆ

/ *Archidiskodon* tusks and cranium as above. Grinding teeth primitive, subloxodont, subhypsodont to hypsodont. Ridge-plates of M 3 $\frac{10+}{11+}$, progressively broad plated, laminate, hypsodont; ridge-plates progressive to M 3 $\frac{17-18}{18-20}$.

Chiefly browsing.

Parelephas tusk and cranial characters as above in other Mammontinæ. Convergent with the Elephantinæ in bathycephaly and multiplication of ridge-plates; progressively hypsodont multiplying from *P. trogontherii* (M 3 $\frac{15+}{16+}$), to *P. jeffersonii* (M 3 $\frac{25}{24}$), to *P. progressus* (M 3 $\frac{30}{26}$).

Browsing and grazing habits, adaptations similar to *Elephas indicus*.

Mammonteus, typified by *M. primigenius*. Cranial type as in the above Mammontinæ, but excessively acrocephalic, hypsicephalic, bathycephalic, and cyrtocephalic. Ridge-plates progressively deepening, broadening, and multiplying, from *M. astensis* (M 3 $\frac{19-20}{19-20}$), to *M. primigenius* (M 3 $\frac{24}{24}$), to *M. primigenius compressus* (M 3 $\frac{27}{27}$).

Habits chiefly grazing, browsing in unfavorable seasons.

IV. SYNOPSIS OF SUBFAMILY CLASSIFICATION OF THE ELEPHANTOIDEA

As shown in the three leading sections of the present chapter, the *cranium* affords the chief basis of subfamily classification, secondly the *tusks*, and thirdly the *grinding teeth*. The three genera *Archidiskodon*, *Parelephas*, and *Mammonteus* appear to show profound subfamily resemblances in the cranium and tusks, while they are widely divergent in the grinding teeth.

In the succeeding chapters distinctions between these profound subfamily resemblances in the cranium, tusks, and grinding teeth are pointed out in detail, in addition to the accompanying synopsis (p. 932).

V. FINAL SUMMARY OF CHAPTER

The present Chapter XV demonstrates that *profound cranial characteristics separate generic phyla which hitherto have been united by parallelism or convergence in characters of the grinding teeth.*

The principles of adaptive radiation and of phylogenetic classification as applied to the Elephantidæ, and developed chiefly through the researches of Falconer, Weithofer, and Osborn, yield a number of very surprising results and run counter to all previous systematic and phylogenetic conclusions. The systematic synopsis at the close of the present chapter (p. 932) summarizes the conclusions arrived at in this and the following chapters, resulting from the most intensive and difficult research incurred in the preparation of this entire Memoir.

The author hopes that the reader will suspend judgment as to this surprising divergence and polyphyly in the Elephantidæ until the succeeding chapters of this Memoir have been thoroughly examined, namely, Chapters XVI (*Archidiskodon*), XVII (*Parelephas*), XVIII (*Mammonteus*) included within the subfamily Mammontinæ; Chapter XIX (Loxodontinæ), and Chapter XX (Elephantinæ).

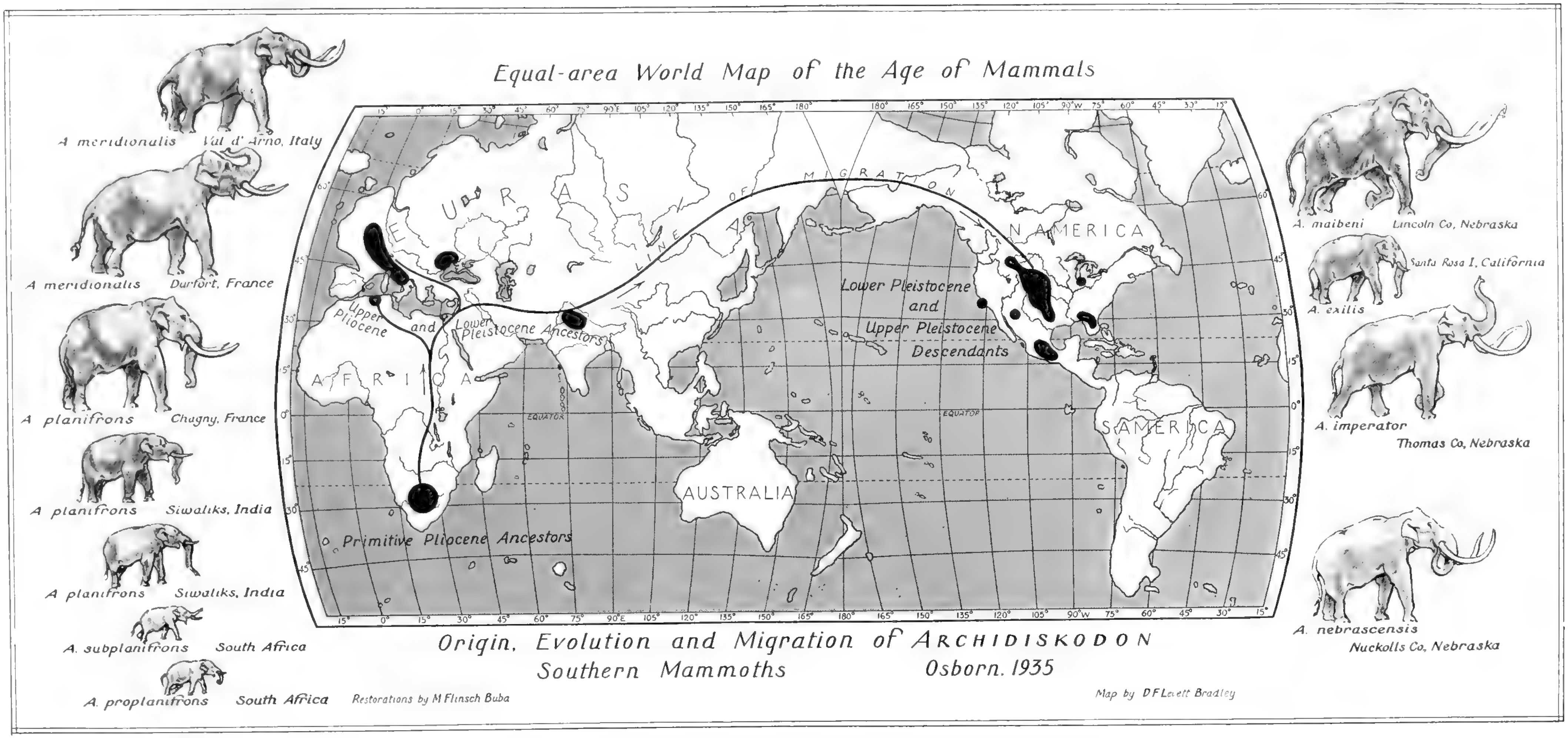

Fig. 815. Successive Habitats and World Migration Routes of the Archaic-toothed Mammoth Archidiskodon. World Map on the 100 Fathom Line
Restorations by Margret Flinsch Buba. Map by D. F. Levett Bradley. Compare Plate xxi.

Vaal River Gravels of South Africa, habitat of the recently discovered primitive Pliocene ancestors of *Archidiskodon.*

Siwalik Hills of Northern India, habitat of the Upper Pliocene-Lower Pleistocene successors (*Archidiskodon planifrons*) described by Falconer and Cautley in the year 1846 (1845).

Southwestern Eurasia, habitat of the Archidiskodonts intermediate between *Archidiskodon planifrons* of northern India, and the southern mammoth *Archidiskodon meridionalis* discovered in Italy and described by Nesti in the years 1808, 1825.

(During this era of Upper Pliocene and Lower Pleistocene time, *Archidiskodon* disappeared in western and southern Eurasia and migrated to the hospitable plains of North America.)

Nebraska to Mexico. Lower and Upper Pleistocene descendants of the *Archidiskodon meridionalis* of southern France (see Fig. 1239), evolving to the close of Third Interglacial time in the Pleistocene epoch into the gigantic *Archidiskodon imperator maibeni* of Nebraska.

CHAPTER XVI

THE GENUS ARCHIDISKODON (SUPERFAMILY ELEPHANTOIDEA), MOST PRIMITIVE MEMBER OF THE SUBFAMILY MAMMONTINÆ

ARCHIDISKODON, PARELEPHAS, AND MAMMONTEUS, UNITED IN THE SUBFAMILY MAMMONTINÆ BY SIMILAR PROFOUND CRANIAL CHARACTERS. WIDELY SEPARATED IN THE RIDGE-PLATE STRUCTURE OF THEIR GRINDING TEETH, ALSO IN THEIR HABITS AND GEOGRAPHIC DISTRIBUTION: ARCHIDISKODON IN SOUTHERN PARALLELS; PARELEPHAS IN TEMPERATE PARALLELS; MAMMONTEUS IN NORTHERN PARALLELS. SPECIES, PHYLOGENY, AND DISTRIBUTION OF ARCHIDISKODON.

I. HISTORICAL INTRODUCTION.
  1. History of the subfamily Mammontinæ.
  2. History of the genus *Archidiskodon*.
  3. Order of discovery and description of twenty-two species of Archidiskodonts.
  4. Archidiskodonts of Eurasia and America.
  5. New Archidiskodonts and Loxodonts of Africa.
  6. Approximate ascending phylogenetic order of succession of species of *Archidiskodon* and *Parelephas* (1928).

II. CHARACTERS OF ARCHIDISKODON AND METARCHIDISKODON AND INCLUDED SPECIES.
  1. Archidiskodonts of southern Eurasia.
  2. Archidiskodonts and Metarchidiskodonts of South Africa.
  3. Archidiskodonts of the United States and Mexico.

Review of successive discoveries in Nebraska, Kansas, Texas, California, Florida, South Carolina, Oklahoma, Indiana, and Mexico.

Archidiskodon imperator Leidy, type characters, distinctions from *Elephas* [*Parelephas*] *columbi*, and comparison with *A. meridionalis* and *A. planifrons*.

Type dental, cranial, and skeletal characters.

Observations on the characters and geographic distribution of *A. imperator* in the United States and Mexico.

Synopsis of *A. imperator* in the American, U. S. National, Nebraska State, City of Mexico, and other museums.

Cranial characters of *Archidiskodon* in comparison with all the known American crania.

Skeletal characters of *Archidiskodon* from a comparison of the various skeletal materials known.

I. HISTORICAL INTRODUCTION

SUBFAMILY CLASSIFICATION.—In its profound cranial characters, as shown in figures 805, 806, and 816, as well as in its cranial profile, we observe the surprising fact that *Archidiskodon* is far closer to *Mammonteus* and *Parelephas* than to either *Elephas* or *Loxodonta*. Consequently the subfamily Mammontinæ, as shown on page 932, appears to include three great branches, *Archidiskodon*, *Parelephas*, and *Mammonteus*, which exhibit three distinct modes of adaptation of the grinding teeth, independently developed. The author has been very slow in reaching this conclusion, for, as shown below, his subfamily Euelephantinæ [=Mammontinæ] at first included the northern mammoths only.

1. HISTORY OF THE SUBFAMILY MAMMONTINÆ

In December, 1917, Osborn (1918.468) presented before the Palæontological Society of America his polyphyletic theory of the Proboscidea, a theory more or less fully anticipated by previous authors but more radical in its inclusion of numerous branches. These branches of the Elephantidæ, as extended in successive years between 1910 and 1921, are as follows:

Elephantinæ Osborn, 1910, p. 558. The true elephants of Asia.
Stegodontinæ[1] Osborn, 1918, pp. 135, 136. Primitive elephants of southern Asia.
Loxodontinæ Osborn, 1918, pp. 135, 136. The African, Eurasiatic, and insular loxodonts.
Euelephantinæ[2] Osborn, 1918, p. 136. The mammoths of Eurasia and North America.
Mammontinæ Osborn, 1921, p. 1, established "because the genus *Euelephas* is invalid; the term *Mammontinæ* (i.e., *les mammonts*, the mammoths) may be substituted."

According to this fourfold subfamily classification of 1918–1921, the synoptic arrangement of these branches is as follows:

ELEPHANTOIDEA, elephant-like proboscideans.	Subfamily: Stegodontinæ,[1] including the Stegolophodonts[3] and true Stegodonts, from primitive members of which the elephant subfamilies may have branched off.
Elephantidæ, the elephant-like proboscideans and their ancestors, in which the ridge-crested grinders gradually transform into ridge-plated grinders, the lower incisive tusks abort, and the upper incisive tusks attain very great size.	Subfamily: Mammontinæ or mammoths, united by very distinctive cranial characters; separated by *several types of dental characters.* Subfamily: Loxodontinæ, typified by the African elephants (*Loxodonta africana* and the numerous living subspecies), by *Palæoloxodon antiquus*[4] and *P. namadicus*, of southern Asia, and by the dwarfed elephants of the Mediterranean islands. Subfamily: Elephantinæ, typified by *Elephas indicus* (*maximus*), such as the insular types of Ceylon and the continental types of southern Asia.

We may now recall the first conception by the present author of the diversities which prevail in the subfamily Mammontinæ, by quoting from the author's paper (1921.515) on the "Evolution, Phylogeny, and Classification of the Proboscidea," pages 14 and 15:

> The Mammontinæ. The Mammoths
>
> It is a striking fact that the oldest geologic appearance of a member of the true Elephantoidea is the *Elephas planifrons* occurring in the Pinjor horizon, Upper Siwaliks, Middle to Upper Pliocene, India. All the fauna of the great Siwalik deposits underlying this geologic level, according to Pilgrim, contain only Stegodonts, Longirostrines, and Brevirostrines. This is significant of a north Eurasiatic center of adaptive radiation of both the Mammontinæ and the Elephantinæ. The chief distinction between these two subfamilies lies in the flattened forehead of the Mammoths, to which the specific name *planifrons* refers, a forehead which becomes increasingly concave and compressed anteroposteriorly until it reaches the high, narrow peak of *E. imperator.*
>
> Again, the succession of species is probably polyphyletic, awaiting analysis. In descending order the main geologic succession is as follows:

	[Reference in Present Memoir
Elephas primigenius Blumenbach. Northern Eurasia and North America, Upper Pleistocene	= *Mammonteus primigenius*
" *columbi* Falconer. Middle Pleistocene, North America	= *Parelephas columbi*
" *imperator* Leidy. Lower Pleistocene, North America	= *Archidiskodon imperator*
" *trogontherii* Pohlig. Lower Pleistocene, Europe	= *Parelephas trogontherii*
" *hysudricus* [5] Falconer. Uppermost Pliocene, India	= *Hypselephas hysudricus*
" *meridionalis* Nesti. Upper Pliocene, Val d'Arno, Italy	= *Archidiskodon meridionalis*
" *planifrons* Falconer. Pinjor horizon, Middle to Upper Pliocene, India, also Austria and Bessarabia (Russia)	= *Archidiskodon planifrons*]

> The position of *E. hysudricus* [5] in this phylum is doubtful. The cranium referred to this species by Falconer is not of the mammontine type. In 1913 Pilgrim traced back *E. planifrons* to the Upper Miocene [Middle Pliocene] *Stegodon cautleyi*, but it would appear at present that none of the known Stegodonts gave rise to the Mammoths. Extreme cranial abbreviation, hyperbrachycephaly, and acrocephaly are great characteristics of all the phyla in this subfamily (excepting possibly that to which *E.*

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[1] [Removed by Professor Osborn, Vol. I, p. 22, of the present Memoir to his new superfamily Stegodontoidea.—Editor.]

[2] [Subfamily Mammontinæ substituted (see Osborn, 1921.515, p. 1).—Editor.]

[3] [Separated by Professor Osborn from the true Stegodonts under the new subfamily name Stegolophodontinæ and placed in the superfamily Mastodontoidea, family Mastodontidæ (see Vol. I, p. 700).—Editor.]

[4] [Members of the '*Elephas*' *antiquus* group subsequently regarded by Professor Osborn as belonging to his new genus *Hesperoloxodon* (see Osborn, 1931.846, p. 21).—Editor.]

[5] [Included in the subfamily Elephantinæ of the present Memoir.—Editor.]

hysudricus belongs). There is a wide range of divergence in the thickness and multiplication of the lamellæ of the grinders. *Elephas imperator* may be derived from the *E. meridionalis* type, with very few lamellæ, composed of thick enamel bands and with a great coating of cement, or from the *E. planifrons* Falconer type. The *E. primigenius* phylum presents the highest lamellar formula known, with relatively little cement; this phylum is also distinguished by the loss of a digit in the pes, becoming tetradactyl, a unique character among proboscideans. Very great shoulder height, estimated at thirteen feet, is attained by *E. imperator* in the favorable environment of the southern United States and Mexico, as compared with the height of nine feet six inches attained by *E. primigenius* in the frigid north.

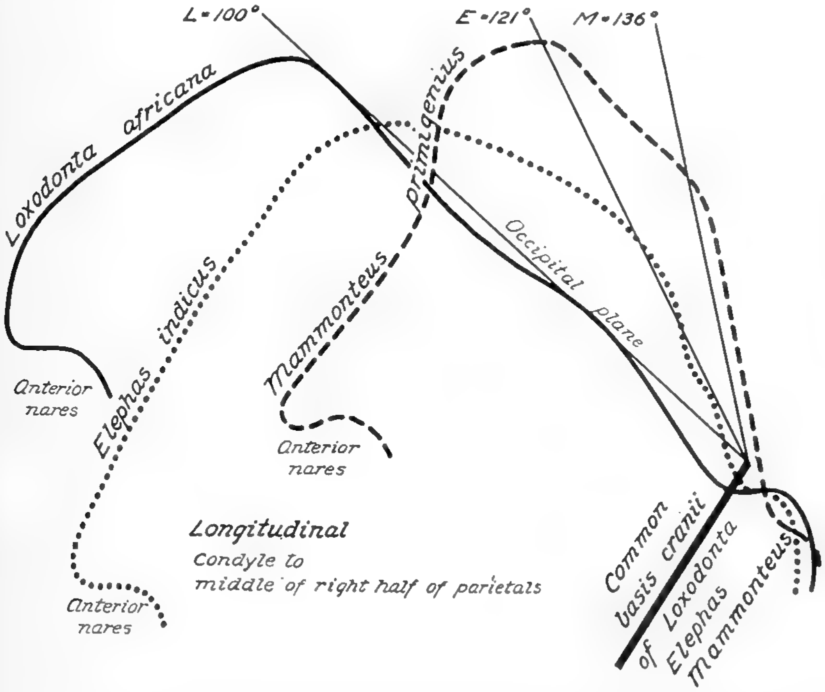
SUPERFAMILY: ELEPHANTOIDEA Osborn, 1921
FAMILY: ELEPHANTIDÆ Gray, 1821

SUBFAMILY: **MAMMONTINÆ** Osborn, 1921

Original reference: Amer. Mus. Novitates, No. 1, pp. 1 and 14 (Osborn, 1921.515).
Includes Archidiskodontinæ and Parelephantinæ of Dietrich, 1927, p. 313 (in part).

SUBFAMILY CHARACTERS.—United by the common cranial characters of *Archidiskodon, Parelephas,* and *Mammonteus,* namely, cyrtocephaly, bathycephaly, hypsicephaly, acrocephaly, attaining extreme cyrtocephaly and acrocephaly in *Mammonteus.* Incisive tusk alveoli vertical, tusks elongated, incurved, crossing each other in old males, not serving in feeding habits. Grinding teeth progressive from a primitive, subhypsodont stage (*Archidiskodon*) to an excessively progressive, hyperhypsodont stage (*Mammonteus*). Habits and geographic distribution varying widely in the three generic phyla.

The cranial unity of the Mammontinæ and the profound distinctions both from the *Loxodonta africana* and *Elephas indicus* types are fully discussed in Chapter XV and clearly set forth in the diagrams (Figs. 805, 806, and 816); figure 816 represents sagittal sections taken through the center of the right half of the cranium. The sections reveal a most surprising resemblance between the three genera of the Mammontinæ to each other and equally surprising contrasts between the mammontine and the Indian and African elephant crania. A summary of these characters, quoted from page 932 above, is as follows:



LOXODONTINE, ELEPHANTINE, AND MAMMONTINE MID-CRANIAL AXES
Compare with figures 805 and 806 of Chapter XV

Fig. 816. The horizontal plane of the worn surface of the superior grinders corresponds with the line from the mid-condyle to the anterior nares in *Elephas indicus.*

Loxodonta africana, the most primitive, occipital plane (L) 100°. =LOXODONTINÆ

Elephas indicus, intermediate, with rounded cranial section, occipital plane (E) 121°. =ELEPHANTINÆ

Mammonteus primigenius, the most progressive, hypsicephalic, acrocephalic, bathycephalic, occipital plane (M) 136°. =MAMMONTINÆ

(1) Subfamily MAMMONTINÆ, including the three generic phyla *Archidiskodon, Parelephas,* and *Mammonteus,* which exhibit three distinct modes of adaptation in the grinding teeth.

(2) Tusks and tusk alveoli progressively vertical; tusks elongate, incurved, crossing in old males, not serving in feeding habits.

(3) Grinding teeth subhypsodont to extremely hypsodont, typically broad and typically short vertically; progressively deepening ridge-plates; typical M 3 $\frac{10+}{11+}$ in *Archidiskodon planifrons*, multiplying to M 3 $\frac{27}{27}$ in *Mammonteus primigenius compressus*. [*Parelephas progressus* has the following ridge-plate count: M 3 $\frac{30}{26}$.—Editor.]

(4) Cranium shortened (cyrtocephalic), deepened (bathycephalic), heightened (hypsicephalic), pointed (acrocephalic), reaching an extreme fore-and-aft abbreviation and elevation in *Mammonteus*.

(5) Habits varying in the three generic phyla. Originally browsing, progressive to extreme grazing type.

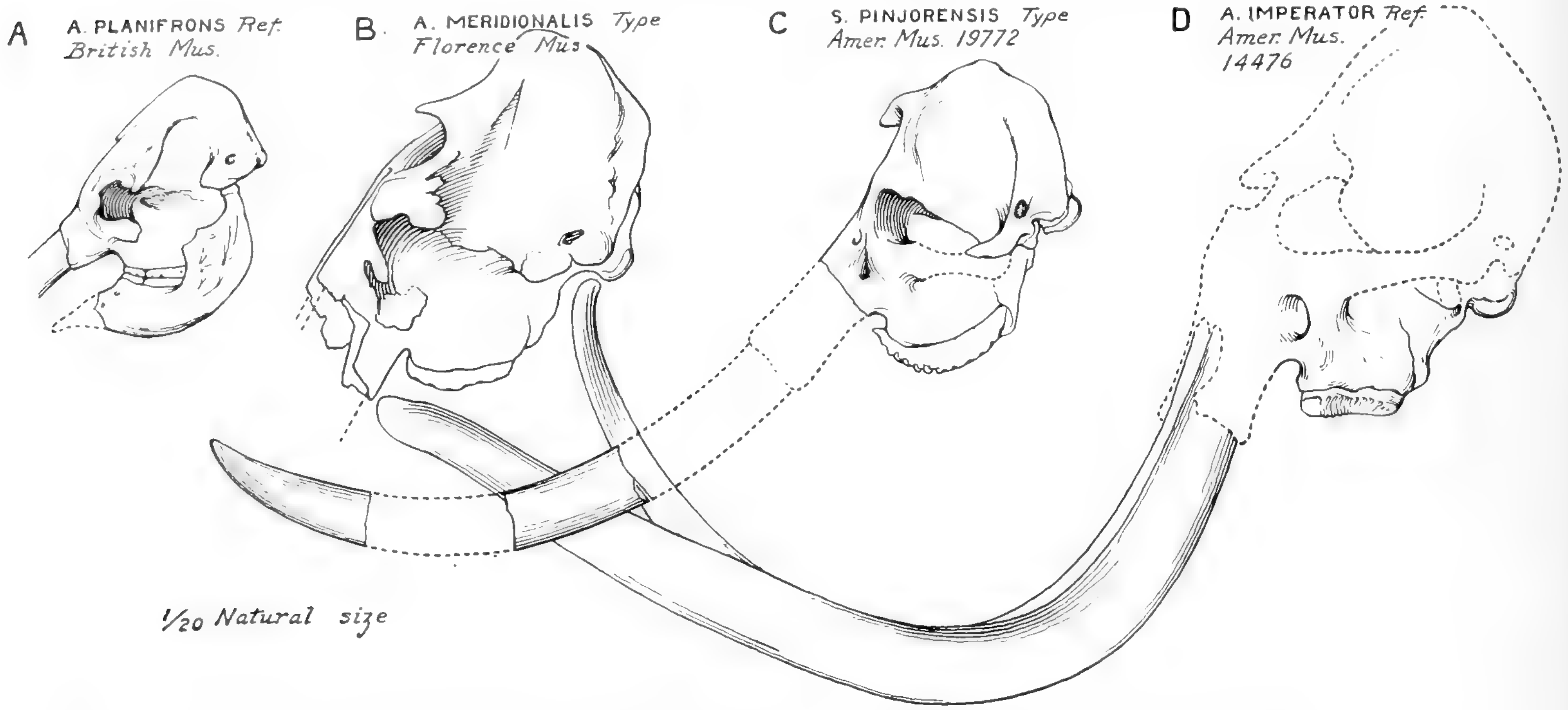


Fig. 817. Comparative profiles of crania of *Archidiskodon* (A, B, D) and cranium of *Stegodon* (C), all one-twentieth natural size.
A, *Archidiskodon planifrons* ref. (Brit. Mus. M.3060). C, *Stegodon pinjorensis* type (Amer. Mus. 19772).
B, *Archidiskodon meridionalis* type (Florence Mus.). D, *Archidiskodon imperator* ref. (Amer. Mus. 14476).
Observe in A, B, D the progressive increase in size, abbreviation, heightening, and deepening of the cranium, heightening of the occipital crest, and concavity of the lengthening forehead. Contrast with the still more abbreviated, hypsicephalic cranium of *Stegodon pinjorensis* (C).

While united by these profound cranial characters, the three genera, on the contrary, are widely distinguished by the specialization of their grinding teeth. It seems hazardous, therefore, to unite them in a single subfamily. The outstanding generic distinctions are as follows:

Archidiskodon Pohlig, typified by *Elephas meridionalis* and *E. planifrons*.	*Parelephas* Osborn, typified by *Elephas jeffersonii*.	*Mammonteus* Camper-Osborn, typified by *Elephas primigenius*.
Archidiskodon tusks and cranium as in other Mammontinæ. Primitive grinding teeth, subloxodont, subhypsodont to hypsodont. Ridge-plates extremely broad plated, laminate, slowly progressing in number from M 3 $\frac{10+}{11+}$ (*A. planifrons*) to $\frac{17-18}{18-20}$ (*A. imperator*). Enamel thick.	*Parelephas* tusk and cranial characters as in other Mammontinæ; cranium less cyrtocephalic than in *Archidiskodon* or *Mammonteus*. Convergent with the Elephantinæ in bathycephaly and multiplication of ridge-plates; grinders resembling those of *Elephas indicus*; ridge-plates relatively fine, progressively hypsodont, multiplying from *P. trogontherii* (M 3 $\frac{15+}{16+}$), to *P. jeffersonii* (M 3 $\frac{25}{24}$), to *Parelephas progressus* (M 3 $\frac{30}{26}$). Enamel medium.	*Mammonteus* crania as in other Mammontinæ, but excessively acrocephalic, hypsicephalic, bathycephalic, and cyrtocephalic. Grinders with extreme fore-and-aft compression; ridge-plates progressively deepening and broadening, the most elevated and attenuated known, multiplying from M 3 $\frac{19-20}{19-20}$ (*M. astensis*), to M 3 $\frac{24}{24}$ (*M. primigenius*), to M 3 $\frac{27}{27}$ (*M. primigenius compressus*). Enamel thin.
Mammoths of the south temperate regions; chiefly browsing.	Mammoths of the mid-temperate regions of Eurasia and North America; browsing and grazing habits, adaptations similar to *Elephas indicus*.	Mammoths of circumpolar regions; habits chiefly grazing, browsing in unfavorable seasons.
Progressive in size to the gigantic *Archidiskodon imperator maibeni*.	Intermediate in size, progressive to *Parelephas floridanus*.	Dwarfed in size, with digits in pes reduced to four.

2. HISTORY OF THE GENUS ARCHIDISKODON

Although long united with *Elephas*, the species which are grouped in this genus constitute a very distinct generic phylum for which Pohlig's name *Archidiskodon*, referring to the archaic molar ridge-plates, seems very appropriate. As shown in our "Classification of the Elephantoidea" (Chapter XV) above, also in figures 805, 806, 816, and 817, *Archidiskodon* is profoundly related in its cranial characters to *Mammonteus* and to *Parelephas*; consequently it belongs in the subfamily Mammontinæ, as defined on page 937 of this Memoir.

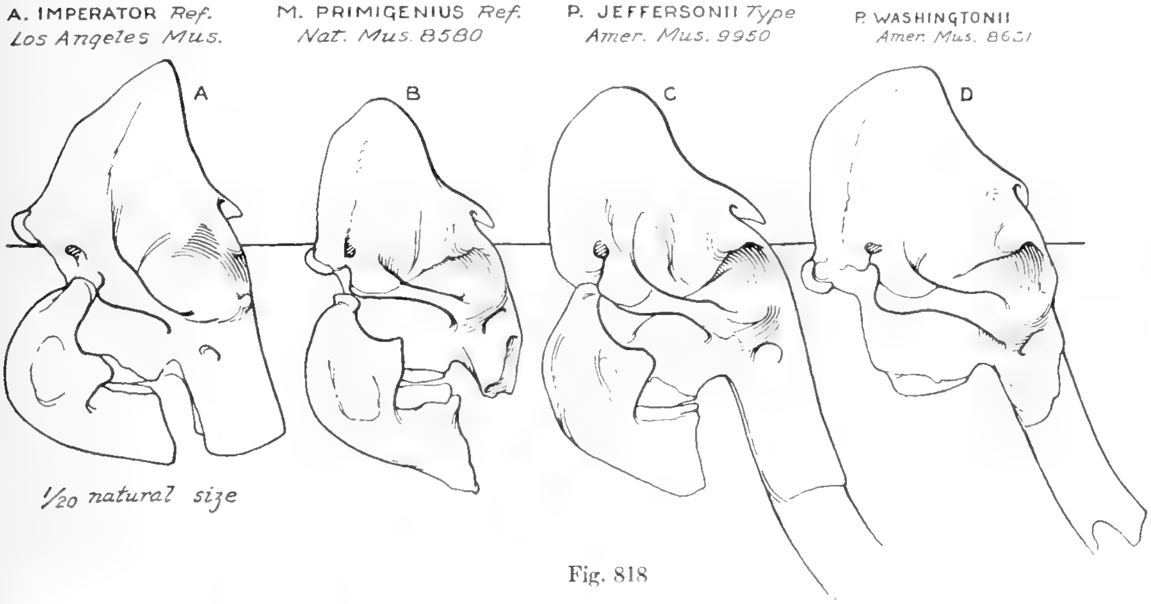


Fig. 818

Fig. 818. Hypsicephalic Crania of the Mammontinæ

A, *Archidiskodon imperator*, juvenile male cranium, from Rancho La Brea, California.
B, *Mammonteus primigenius*, young adult male cranium, from Siberia.
C, *Parelephas jeffersonii*, type cranium, aged male, from Indiana.
D, *Parelephas washingtonii*, adult male cranium, from the state of Washington.

Observe (1) the strong fore-and-aft cranial compression and vertical elevation of the occiput (hypsicephaly); (2) the slightly concave forehead; (3) the very deep depression of the mandibular rami (bathycephaly); (4) the sharp downward flexure of the basicranial axis (cyptocephaly); (5) the disparity in size of the *M. primigenius* skull and jaws.

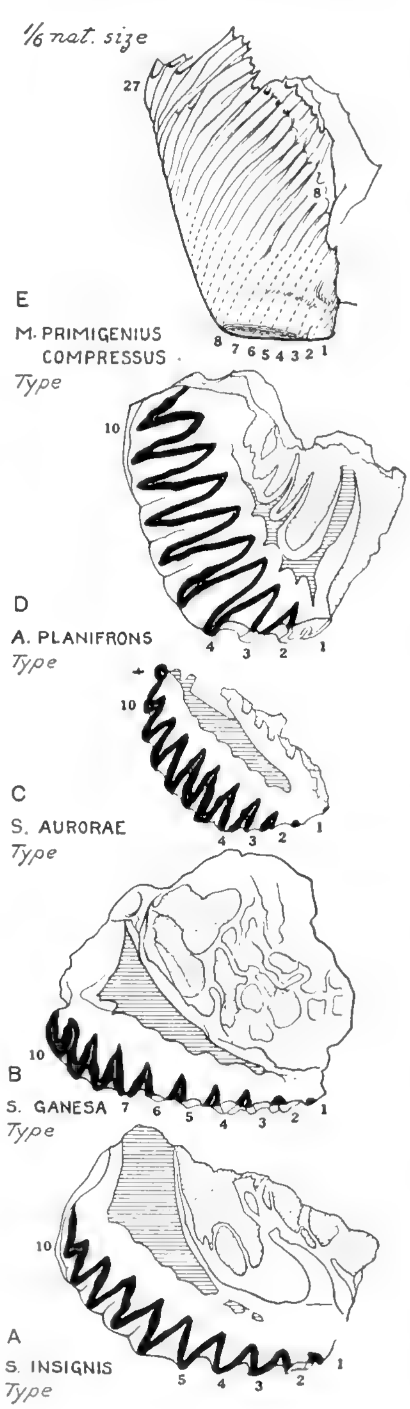


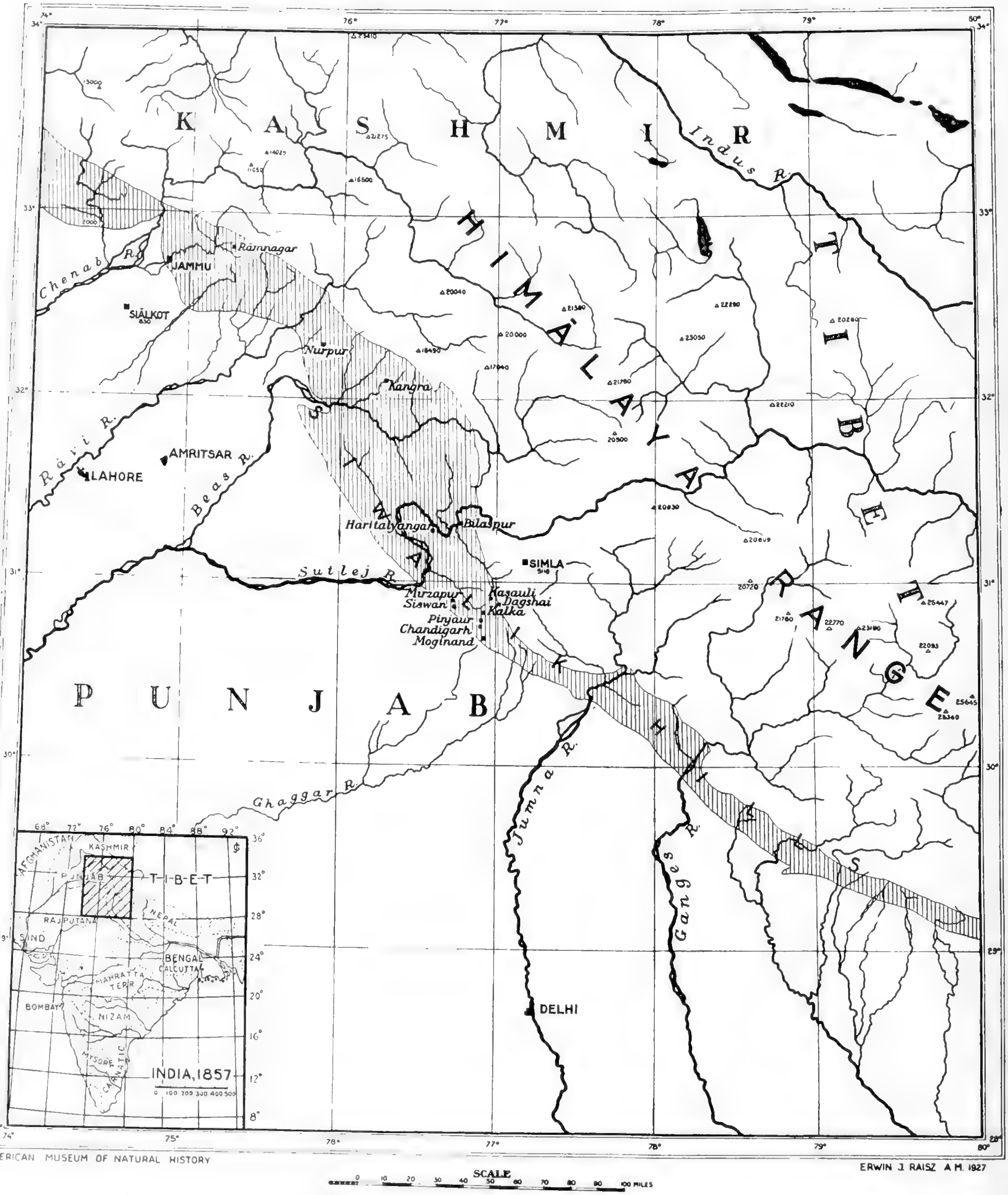
Fig. 819

Fig. 819. Comparative Series of Superior Molars showing evolution of the ridge in the Elephantoidea and Stegodontoidea. One-sixth natural size.

E, *Mammonteus primigenius compressus*, type M^3, showing extreme compression of 27 ridge-plates.
D, *Archidiskodon planifrons*, type M^2, with 9-10 ridge-plates.
C, *Stegodon auroræ*, type M^2, with 10+ ridge-crests (cf. *S. airâwana*, Fig. 764C).
B, *Stegodon ganesa*, type M^3, with 10+ ridge-crests.
A, *Stegodon insignis*, type M^3, with 10 ridge-crests.

Stegodon auroræ (cf. p. 892) "is either a highly progressive *Stegodon* or a primitive *Archidiskodon*, a point to be determined positively by the discovery of a cranium."

Pohlig, 1885, 1888.—To our knowledge Pohlig was the first to separate the elephants with archetypal ridge-plates as Archidiskodonten (1885, p. 1027): "8. Ich theile die Elephanten nach Kronenformen und Lamellenzahlen der Molaren ein in Archidiskodonten (*E. planifrons, E. meridionalis*), Loxodonten (*E. africanus, ?E. antiquus*) und Polydiskodonten (*E. primigenius, E. indicus* etc.), die Stegodonten mit Clift wieder zu *Mastodon* zählend." Three years later Pohlig (1888, p. 138) defined the genus as follows: "1. *Archidiskodonten.* Typus: *E. meridionalis.* Uebergang zu der folgenden Gruppe bildet *E. planifrons.* Tapinodiske, laticoronate, kurze und



Central Region (see black square) of the Siwalik Hills, 200 miles south and north of Simla, India

Fig. 820. A flanking Tertiary range, 800 miles in length, on the southwestern base of the Himalaya Mts., and northeast of the Punjab. Classic "Sewalik" exposures (vertical lines, now divided into Upper, Middle, and Lower Siwaliks) discovered by Lieut. Proby T. Cautley in 1827, explored by Dr. Hugh Falconer in 1831, and determined as of Tertiary age by the bones of crocodiles, tortoises, and other fossil vertebrates (cf. Fig. 729, after Falconer, Pl. xxv, map of India, and Fig. 826, detail of the Simla region).

pachyganale Molaren. Parsilamellat. (Meist nur 15 Lamellen an M. III.)" In the same Memoir (p. 252) he introduced the generic terms: 4^{a}. Archidiskodon 5. Polydiskodon 4^{b}. Loxo(-disko-)don. From these citations we have abstracted the above generic characters.

Schlesinger, 1912, 1916.—Schlesinger (1912, pp. 98, 99, footnote) confirmed this generic description and amplified Pohlig's definition as follows: "Ausdrücke halte ich für einen Missgriff und gebe ihre Erklärung: Tapinodisk = mit niedrigen Jochen (Gegensatz = hypselodisk), latikoronat = breitkronig (Gegensatz = angustikoronat), pachyganal = mit dickem Schmelzblech (Gegensatz = endioganal), parsilamellat = mit wenigen Lamellen (Gegensatz = densilamellat)." In a later paper (1916, pp. 102, 103) Schlesinger cites the term as a subgenus: "*Elephas* (*Archidiscodon*) *meridionalis* Nesti," and (*op. cit.*, pp. 112, 113)"*Elephas* (*Archidiscodon*) *planifrons* Falc." Schlesinger also in his "Studien über die Stammesgeschichte der Proboscidier" of 1912 recognized a resemblance to the broad-plated American species *Elephas columbi* and *E. imperator*, but failed to separate these species into a distinct generic phylum.

Osborn (1922.555) distinguished *Elephas columbi* from *E. imperator* (p. 3) as follows: "We thus find by the characters of the type and neotype specimens that the real *Elephas columbi* is not the animal we have been describing under this name; it is a dwarf form, perhaps a dwarf female, of the animal which we have been describing under the name *Elephas imperator*."[1]

He clearly defined (*op. cit.*, pp. 3 and 4) the characters of the grinding teeth of *E. imperator*, concluding (p. 5): "The cranial characters observed in three more or less complete skulls referred to *Elephas imperator* tend to support the direct descent of this animal from the *E. meridionalis* of the Val d'Arno, Upper Pliocene of Italy."

Fig. 821. Chief Lower and Upper Pleistocene localities of western Eurasia in which occur species of *Archidiskodon*, *Parelephas*, *Mammonteus*, *Loxodonta*, and *Palæoloxodon*. After Osborn, 1910.346, p. 391, fig. 176. See more detailed caption, figure 932, below.

PLEISTOCENE EUROPE.—**1** *Forest Bed of Cromer* (Norfolk). Sables de **2** *St. Prest* near Chartres (Eure-et-Loire). **3** *Malbattu* (Puy-de-Dôme). **4** *Peyrolles* (Bouches-du-Rhône). **5** *Solhilac* near Puy. Clay deposits of **6** *Durfort* (Gard). **7** *Cajarc* (Lot-et-Garonne). **8** *Val d'Arno* (Tuscany). **9** *Leffe* near Bergamo (Lombardy). **10** *Rixdorf* near Potsdam (Brandenburg). Gravels of **11** *Süssenborn* near Weimar. Sands of **12** *Mosbach* in northern Baden. Freshwater deposits of **13** *Clacton* (Essex). Sands of Mauer near **14** *Heidelberg* (western Germany). **15** *Chelles* on the Marne, near Paris. **16** *St. Acheul* (Somme). **17** *Ilford* and *Grays Thurrock* (Essex). Lignites of **18** *Dürnten* and of *Utznach*, near Zürich. **19** *Taubach* near Weimar. **20** *Wildkirchli cave* on *Mont Säntis* (eastern Switzerland). Tuffs of **21** the *Tiber Valley*, near Rome. Caves of **22** *Neandertal*, near Düsseldorf (western Germany), **23** *Spy*, near Amur (Belgium), **23a** *Krapina* (Croatia), **24** *Chapelle-aux-Saints* (Corrèze). Caves and alluvial deposits of **25** *Ternifine* (or *Palikao*) near Oran (Algeria), **26** *Pointe Pescade*, near Algiers (Algeria). **27** *Prince's Cave* (Monaco). Sandy clays of **28** *Vöklinshofen* (Alsace). **29** *Saalfeld* (Saxe-Meiningen). Travertines, etc., of **30** *Gera*, *Jena* (Saxe-Weimar). **31** *Leipzig* (Saxony). **32** *Solutré*, north of Lyons. Loess of **33** *Würzburg* (Bavaria). **34** *Thiede* near Braunschweig (Prussia). Cave of **35** *Montmaurin* (Haute-Garonne). **36** *Châteauneuf-sur-Charente* (Charente). Caves of **37** *Schweizersbild* near Schaffhausen, and *Kesslerloch* near Thayngen (northern Switzerland). Remains of lake dwellings at **38** *Wauwyl* (Lucerne), **39** *Robenhausen*, south of Lake Pfäffikon, **40** *Concise* on Lake Neuchâtel (Switzerland). Peatbogs of **41** *Hassleben*, near Weimar. Travertines of **42** *Langensalza* (Erfurt) in central Germany. Caves of the **43** *Island of Malta*, **44** *Island of Crete*, **45** *Island of Cyprus*.

Subsequently Osborn (1924.633, p. 2) confirmed Pohlig: "We therefore confirm Pohlig's separation of the southern mammoths *Elephas planifrons*, *E. meridionalis*, and *E. imperator* into the distinct generic phylum *Archidiskodon*," and in the year 1925 (Osborn, 1925.662) he placed *Archidiskodon* among the Mammontinæ, as shown in the diagram of that year (Vol. I, Fig. 7, of the present Memoir), concluding (p. 28) with a redefinition of the family Elephantidæ and Race XIII, as follows:

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[1] [Subsequently (see pp. 997, 1001)Professor Osborn separated *Elephas imperator* and *E. columbi*, assigning the former to the genus *Archidiskodon* Pohlig and the latter to *Parelephas* Osborn.—Editor.]

FAMILY: ELEPHANTIDÆ, distinguished by plated grinding teeth developing out of the more or less closely compressed, serrated ridges of *Stegodon*[1] into the broadly plated grinders of *Archidiskodon*, the lozenge-shaped grinders of *Loxodonta*, and the compressed, finely plated grinders of *Parelephas*, of *Mammonteus*, and of *Elephas* the type genus of the family. . . .

Race XIII. THE SOUTHERN MAMMOTHS, OR ARCHIDISKODONTS. Excessively broad-plated grinders with abundant cement; first known in India, migrating westward into southern Europe, eastward into America, where arriving in late Pliocene or early Pleistocene time they finally gave rise to the Imperial Mammoth, *Archidiskodon imperator*, the last of its race.

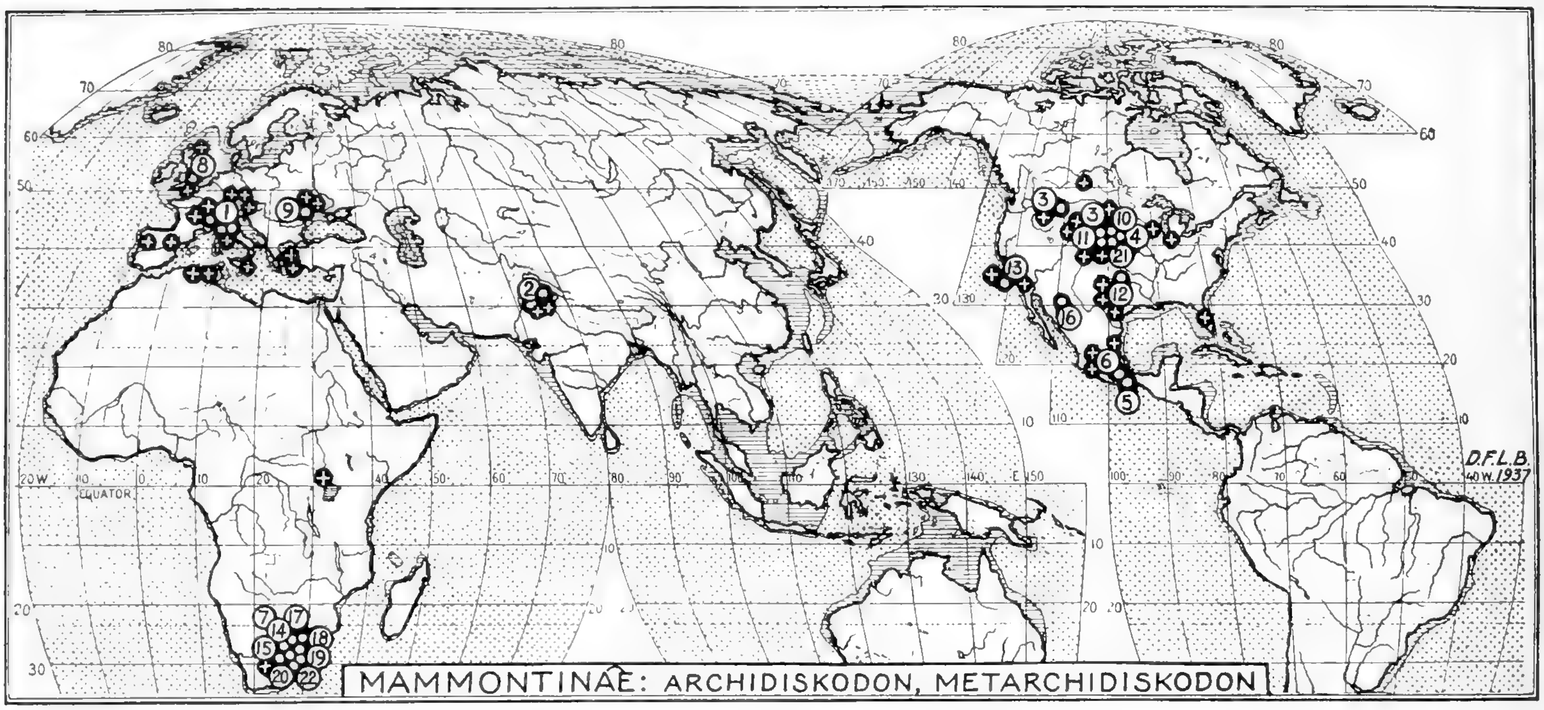

Fig. 822. Geographic distribution of the principal species of Archidiskodonts. The white dots within the black areas represent the approximate localities where the types of these twenty-two species were discovered; these dots each carry a number in a circle representing the chronologic sequence of type description. The white crosses represent some of the principal referred specimens mentioned in the present Memoir.

3. ORDER OF DISCOVERY AND DESCRIPTION OF TWENTY-TWO SPECIES OF ARCHIDISKODONTS

SEE FIGURE 822

			REFERENCE IN PRESENT MEMOIR
1.	1825	*Elephas meridionalis* Nesti, Val d'Arno, Italy	=*Archidiskodon meridionalis*
2.	1846 [1845]	*Elephas planifrons* Falconer and Cautley, Siwalik Hills, northern India	=*Archidiskodon planifrons*
1.	1855	*E. giganteus* Aymard (MS., also in Falconer, 1857, p. 321), France	Nomen nudum =*Archidiskodon meridionalis*(?)
	[1857–1868	*Elephas columbi* Falconer, Georgia	=*Parelephas columbi* (see Chap. XVII)]
3.	1858	*Elephas imperator* Leidy, ?Seneca, Thomas Co., Nebraska (*fide* Hay, 1924, p. 100)[2]	=*Archidiskodon imperator*
	[1859–1861	*Elephas texianus* Owen, 1859, Blake, 1861, Texas	=*Parelephas columbi* (see Chap. XVII)]
1.	1889–1890	*Elephas lyrodon* Weithofer, Val d'Arno, Italy	=*Archidiskodon meridionalis* (female?)
	[1890	*Elephas mindanensis* Naumann, Philippine Islands	=*Stegodon* (*Archidiskodon?*) *mindanensis* (see Chap. XIV)]
4.	1915	*Elephas hayi* Barbour, Crete, Saline Co., Nebraska	=*Archidiskodon hayi*
	[1922	*El.* [*Elephas*] *Columbi* var. *Felicis* Freudenberg, Mexico	=*Parelephas columbi felicis* (see Chap. XVII)]
5.	1922	*El.* [*Elephas*] *Columbi* var. *silvestris* Freudenberg, Ejutla, State of Oaxaca, Mexico	=*Archidiskodon imperator silvestris*

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[1] [See Chapter XIV, pp. 806, 807, where Professor Osborn's final views regarding the complete separation of the Stegodontoidea from the Elephantoidea are given.—Editor.]

[2] [Exact locality not cited. Lugn and Schultz (1934.1, p. 373) give Pawnee Loup Branch of Platte River = Middle Loup, probably Hooker County.—Editor.]

6.	1922	*El.* [*Elephas*] *Columbi* var. *Falconeri* Freudenberg, Tequixquiac, Valley of Mexico	=*Archidiskodon imperator falconeri*
7.	1922	*Loxodonta griqua* Haughton, Griqualand West, Transvaal, S. Africa	=*Metarchidiskodon griqua*
3.	1922	*Elephas Columbi* var. *imperator* Freudenberg, Spokam Bar, near Helena, Montana	=*Archidiskodon imperator*
8.	1923	*Elephas meridionalis*, mutation *cromerensis* Depéret and Mayet, Kessingland, Suffolk, England	=*Archidiskodon meridionalis cromerensis*
9.	1924	*Elephas antiquus rumanus* S. Stefănescu, Tulucesti (Covurlui), Rumania	=*Archidiskodon planifrons rumanus*
10.	1925	*Elephas scotti* Barbour, near Staplehurst, Seward Co., Nebraska	=*Archidiskodon imperator scotti* (or juvenile *A. imperator*)
11.	1925	*Elephas maibeni* Barbour, near Curtis, Lincoln Co., Nebraska	=*Archidiskodon imperator maibeni*
	[1927	*Archidiskodon transvaalensis* Dart, Lowest Terrace, Vaal River, S. Africa	=*Palæoloxodon transvaalensis* (see Chap. XIX)]
	[1927	*Archidiskodon sheppardi* Dart, Lowest Terrace, Vaal River, S. Africa	=*Palæoloxodon sheppardi* (see Chap. XIX)]
2.	1927	*Leith-Adamsia siwalikiensis* Matsumoto, Siwalik Hills, India	=*Archidiskodon planifrons*
12.	1928	*Elephas haroldcooki* Hay, Frederick, Oklahoma	=*Archidiskodon haroldcooki*
13.	1928	*Elephas exilis* Stock and Furlong, Santa Rosa Island, California	=*Archidiskodon exilis*
14.	1928	*Archidiskodon subplanifrons* Osborn, Sydney-on-Vaal, S. Africa	=*Archidiskodon subplanifrons*
15.	1928	*Archidiskodon broomi* Osborn, near Kimberley, S. Africa	=*Archidiskodon broomi*
16.	1929	*Archidiskodon sonoriensis* Osborn, near Arizpe, northern Sonora, Mexico	=*Archidiskodon sonoriensis*
	[1929	*Lox.* (*Pal.*) *Tokunagai junior* mut. Matsumoto	=*Palæoloxodon* (*Archidiskodon?*) *tokunagai* mut. *junior* (see Chap. XIX)]
17.	1929	*Archidiskodon vanalpheni* Dart, Sydney-on-Vaal, S. Africa	=*Archidiskodon vanalpheni*
18.	1929	*Archidiskodon milletti* Dart, Sydney-on-Vaal, S. Africa	=*Archidiskodon milletti*
19.	1929	*Archidiskodon loxodontoides* Dart, Sydney-on-Vaal, S. Africa	=*Archidiskodon loxodontoides*
20.	1929	*Archidiskodon yorki* Dart, near Christiana, S. Africa	=*Archidiskodon yorki*
	[1929	*Archidiskodon andrewsi* Dart, ?Middle Terrace, Vaal River, S. Africa	=*Palæoloxodon? andrewsi* (see Chap. XIX)]
	[1929	*Archidiskodon hanekomi* Dart, Vaal River, S. Africa	=*Palæoloxodon hanekomi* (see Chap. XIX)]
21.	1932	*Archidiskodon meridionalis nebrascensis* Osborn, Angus, Nuckolls Co., Nebraska	=*Archidiskodon meridionalis nebrascensis*
22.	1934	*Archidiskodon proplanifrons* Osborn, Gong-Gong, near the Vaal River, S. Africa	=*Archidiskodon proplanifrons*

4. ARCHIDISKODONTS OF EURASIA AND AMERICA

In the early part of the 19th century there was described by Nesti from northern Italy (1808) the first known species of this phylum, to which he later (1825) assigned the name *Elephas meridionalis*, or, as we may now call it, the 'Southern Mammoth,' in reference to its remote relationship to the 'Northern Mammoth.' In 1846 there was described from India a direct ancestor of *E. meridionalis*, namely, *Elephas planifrons*, the name alluding to its flattened forehead. In 1857 Falconer recognized as a remotely related species his *Elephas columbi* from Georgia, a species long confused with *Archidiskodon*. In 1858 Leidy described as a closely related species *Elephas imperator* from western Nebraska. The *Elephas texianus* of Owen and Blake, 1859, 1861, 1862, is a synonym of *Elephas* [*Parelephas*] *columbi*. The *Elephas lyrodon* of Weithofer, 1889, 1890, from northern Italy, is the female(?) form of *E. meridionalis*.

Then a long interval followed and a very primitive member of this phylum, namely, *Elephas hayi*, was discovered in western Nebraska and described (1915) by Barbour, indicating that these animals may have migrated into North America directly from India, because *E. hayi* appears to be almost as primitive in jaw structure as the *Elephas planifrons* of India.

In 1922 Freudenberg reviewed the elephants of Mexico and described four subspecies of *Elephas columbi*, namely, *El. Columbi* var. *Felicis, El. Columbi* var. *silvestris, El. Columbi* var. *Falconeri,* and *El. Columbi* var. *imperator*; the first (*El. Columbi* var. *Felicis*) we regard as more closely related to Falconer's species *Elephas columbi,* the remaining three to Leidy's species *Elephas imperator.*

In 1923 Depéret and Mayet devoted a volume to their thorough researches of the species of eastern Eurasia, *Elephas planifrons* and *E. meridionalis,* and added the Lower Pleistocene subspecies *Elephas meridionalis,* mutation *cromerensis,* of Kessingland, Suffolk, England.

The wide geographic distribution of *Archidiskodon* is indicated by Stefănescu's description in 1924 of *Elephas antiquus rumanus* of Rumania, by the discovery of two American species, *Elephas scotti* and *E. maibeni,* in Nebraska, described by Barbour in the year 1925, and finally by the most surprising and welcome discovery of all, the *Archidiskodon subplanifrons* and *A. broomi* in the Vaal River diggings of South Africa, described by the present author in 1928, as well as Dart's new species, *Archidiskodon transvaalensis* and *A. sheppardi* from the Vaal River gravel terraces, described in 1927.[1]

5. NEW ARCHIDISKODONTS AND LOXODONTS OF AFRICA

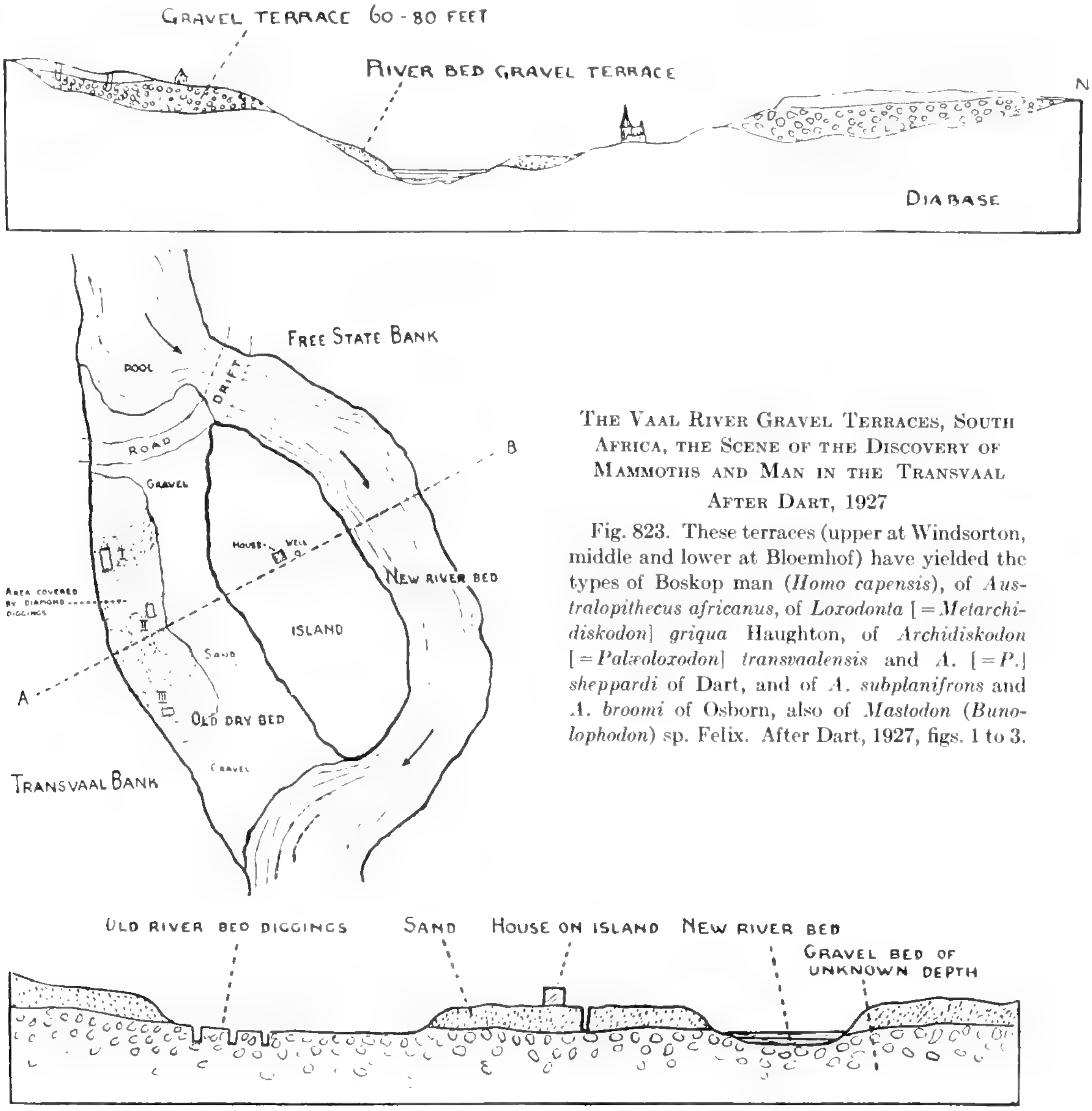
After the present author had described and figured, but not published,[2] the two names above (*Archidiskodon subplanifrons* and *A. broomi*), he received Prof. Raymond A. Dart's "Mammoths and Man in the Transvaal," Nature, December 10, 1927, with the welcome figures [Fig. 823 of the present Memoir] and description of the Vaal River terraces at Windsorton and Bloemhof, of which the following is an abstract:

> The Vaal River valley, near Bloemhof, in the southwestern Transvaal, belongs to a great watershed which has yielded *Australopithecus africanus* Dart, 1925 [from Taungs district, Bechuanaland], and the Boskop man, besides stone implements, rock engravings, and other evidences of primitive man. The watershed includes three gravel deposits of different geologic age (Du Toit, Ann. Rept. Geol. Comm., 1906) situated on a number of terraces.
>
> Upper.—The highest and presumably the oldest [Pliocene?] terrace has an altitude of some 200 to 300 feet above the river exposed at a distance of 3½ to 6 miles. *No fossils have hitherto been described from this most ancient terrace* (Dart, *op. cit.,* p. 1). [This is possibly the level at which *Archidiskodon subplanifrons* Osborn, a very primitive form, was found—Fig. 875 of the present Memoir.—Osborn.]
>
> Middle.—The middle or second [Pleistocene or Mastodon] gravel terrace is on a lower level at several points west of Barkly West; from this terrace numerous palæolithic implements have been described (Hodkinson, 1926); also (Beck, 1906) a fragmentary tooth of *Mastodon* (*Bunolophodon*) sp. Felix, at Waldeck's Plant, 60 to 80 feet above the river bed. Haughton described *Loxodonta griqua* [=*Metarchidiskodon*—see figure 882 of the present Memoir], also a new giraffe (*Griquatherium cingulatum*) from this 60 to 80 foot terrace. [Doctor Broom holds that the mammoth teeth are washed in from an older geologic deposit (see Nature, March 3, 1928, p. 324) and are not truly associated with the flint implements, in geologic age.]
>
> Lower.—A still lower gravel deposit [Pleistocene], near the level of the present river Vaal, contains *Equus* and *Hippopotamus amphibius* var. *robustus.* From this low river bed gravel, 1½ miles below The Bend on the Vaal River, Haughton determined as *Elephas* (cf. *antiquus*) a portion of a tooth recovered at a depth of 5 feet, but which Dart regarded (*op. cit.,* p. 42) as resembling *E. antiquus recki* Dietrich. [Apparently this same specimen is now described by Osborn as *Archidiskodon broomi,* the label of which bears the inscription, "3682 Mus. Kimb. The Bend. H. Else." Fig. 877 of the present Memoir.] From this level are recently recorded *Archidiskodon transvaalensis* Dart and *A. sheppardi* Dart.[1]

---

[1] [*Archidiskodon transvaalensis* and *A. sheppardi* prove to belong to the genus *Palæoloxodon* (see Osborn, 1934.925, pp. 2 and 14). Since this section of the Memoir was written, four species from South Africa have been described by Professor Dart (1929) and one by Professor Osborn (1934); also two species from North America have been described by Professor Osborn, one from Mexico (1929) and one from Nebraska (1932). A complete list of the species of *Archidiskodon* is given on pages 942 and 943 above.—Editor.]

[2] Subsequently published in Nature (Osborn, 1928.749, pp. 672, 673) under the title "Mammoths and Man in the Transvaal."



THE VAAL RIVER GRAVEL TERRACES, SOUTH AFRICA, THE SCENE OF THE DISCOVERY OF MAMMOTHS AND MAN IN THE TRANSVAAL

AFTER DART, 1927

Fig. 823. These terraces (upper at Windsorton, middle and lower at Bloemhof) have yielded the types of Boskop man (*Homo capensis*), of *Australopithecus africanus*, of *Loxodonta* [=*Metarchidiskodon*] *griqua* Haughton, of *Archidiskodon* [=*Palæoloxodon*] *transvaalensis* and *A.* [=*P.*] *sheppardi* of Dart, and of *A. subplanifrons* and *A. broomi* of Osborn, also of *Mastodon* (*Bunolophodon*) sp. Felix. After Dart, 1927, figs. 1 to 3.

Consequently a summary of the discoveries and descriptions of South African specimens (1928) is as follows:

ORIGINAL DESCRIPTION	REFERENCE IN PRESENT MEMOIR
Loxodonta griqua Haughton, 1922, type, Griqualand West, Transvaal	=*Metarchidiskodon griqua*
Elephas (*Loxodon*) *zulu* Scott, 1907, type, Zululand	=*Loxodonta zulu*
Elephas zulu, referred by Hopwood, 1926, Kaiso Bone-beds, near Lake Albert	=*Loxodonta zulu*
Elephas antiquus Recki Dietrich, 1916, type, Tanganyika Territory	=*Palæoloxodon recki*
Elephas aff. *meridionalis* Nesti, 1825, referred by Hopwood, 1926, from Kaiso Bone-beds, near Lake Albert	=*Metarchidiskodon griqua* (*or A. planifrons?*)
Archidiskodon transvaalensis Dart, 1927, type, middle Vaal River gravel terrace	=*Palæoloxodon transvaalensis*
Archidiskodon sheppardi Dart, 1927, type, lowest Vaal River gravel terrace	=*Palæoloxodon sheppardi*
Archidiskodon subplanifrons Osborn, 1928, type, middle(?) Vaal River gravel terrace	=*Archidiskodon subplanifrons*
Archidiskodon broomi Osborn, 1928, type, middle(?) Vaal River gravel terrace	=*Archidiskodon broomi*
Mastodon (*Bunolophodon*) sp. Felix, referred by Beck, 1906, Waldeck's Plant	=*Trilophodon*(?) sp. indet.

The above species of *Archidiskodon* from Africa are fully described below, following the description of the Eurasiatic Archidiskodonts.

6. APPROXIMATE ASCENDING PHYLOGENETIC ORDER OF SUCCESSION OF SPECIES OF ARCHIDISKODON AND PARELEPHAS (1928)

Only an approximate phylogenetic order of succession of the species of *Archidiskodon* may be given at the present time. In this phylogenetic list we may include with some certainty fifteen of the better-known species of *Archidiskodon* and *Parelephas*, placed in ascending order as follows:

ARCHIDISKODON AND PARELEPHAS OF NORTH AMERICA AND EURASIA

Pleistocene? level	1857–1868	Southern United States and Mexico	*Parelephas columbi* Falconer, originally described by Falconer as *Elephas columbi*, 1857
	1859–1861	Texas	*Parelephas columbi* Falconer, originally described as *Elephas texianus* by Owen, 1859, by Blake, 1861
	1922	Mexico	*Parelephas columbi felicis* Freudenberg, originally described by Freudenberg as *Elephas Columbi* var. *Felicis*, 1922
	1922	Mexico	*Archidiskodon imperator silvestris* Freudenberg, originally described by Freudenberg as *Elephas Columbi* var. *silvestris*, 1922
	1922	Mexico	*Archidiskodon imperator falconeri* Freudenberg, originally described by Freudenberg as *Elephas Columbi* var. *Falconeri*, 1922
Lower Pleistocene ?Aftonian (*fide* Osborn) Iowan or Late Pleistocene (*fide* Lugn and Schultz, 1934)[1]	1925	Nebraska	*Archidiskodon imperator maibeni* Barbour, originally described by Barbour (1925) as *Elephas maibeni*, subsequently (1926) as *Archidiskodon maibeni*
Lower Pleistocene	1925	Nebraska	*Archidiskodon imperator scotti* Barbour, originally described by Barbour as *Elephas scotti*, 1925
Pleistocene	1928	California	*Archidiskodon exilis* Stock and Furlong, originally described by Stock and Furlong as *Elephas exilis*, 1928
Pleistocene	1858	Nebraska	*Archidiskodon imperator* Leidy, originally described by Leidy as *Elephas imperator*, 1858
Lower Pleistocene or Upper Pliocene (?)[2]	1915	Nebraska	*Archidiskodon hayi* Barbour, originally described by Barbour as *Elephas hayi*, 1915
Lower Pleistocene	1923	England, Forest Bed	*Archidiskodon meridionalis cromerensis* Depéret and Mayet, originally described by Depéret and Mayet as *Elephas meridionalis*, mutation *cromerensis*, 1923
Upper Pliocene	1825	Italy	*Archidiskodon meridionalis* Nesti, originally described by Nesti as *Elephas meridionalis*, 1825
	1846 [1845]	India and southern Europe	*Archidiskodon planifrons* Falconer and Cautley, originally described by Falconer and Cautley as *Elephas planifrons*, 1845, 1846

ARCHIDISKODONTS OF AFRICA

Pleistocene	1927	South Africa	*Archidiskodon* [=*Palæoloxodon*] *transvaalensis*
	1927	South Africa	*Archidiskodon* [=*Palæoloxodon*] *sheppardi*
Lower Pleistocene(?)[3]	1928	South Africa	*Archidiskodon broomi* Osborn
Pleistocene	1922	South Africa	*Metarchidiskodon griqua* Haughton, originally described by Haughton as *Loxodonta griqua*, 1922
Upper (?) Pliocene[2]	1928	South Africa	*Archidiskodon subplanifrons* Osborn

According to the above phylogenetic arrangement, the four species *Archidiskodon subplanifrons*[3], *A planifrons*, *A meridionalis*, and *A*. *hayi*[2] are the only known [1928] Upper Pliocene representatives of this great phylum.

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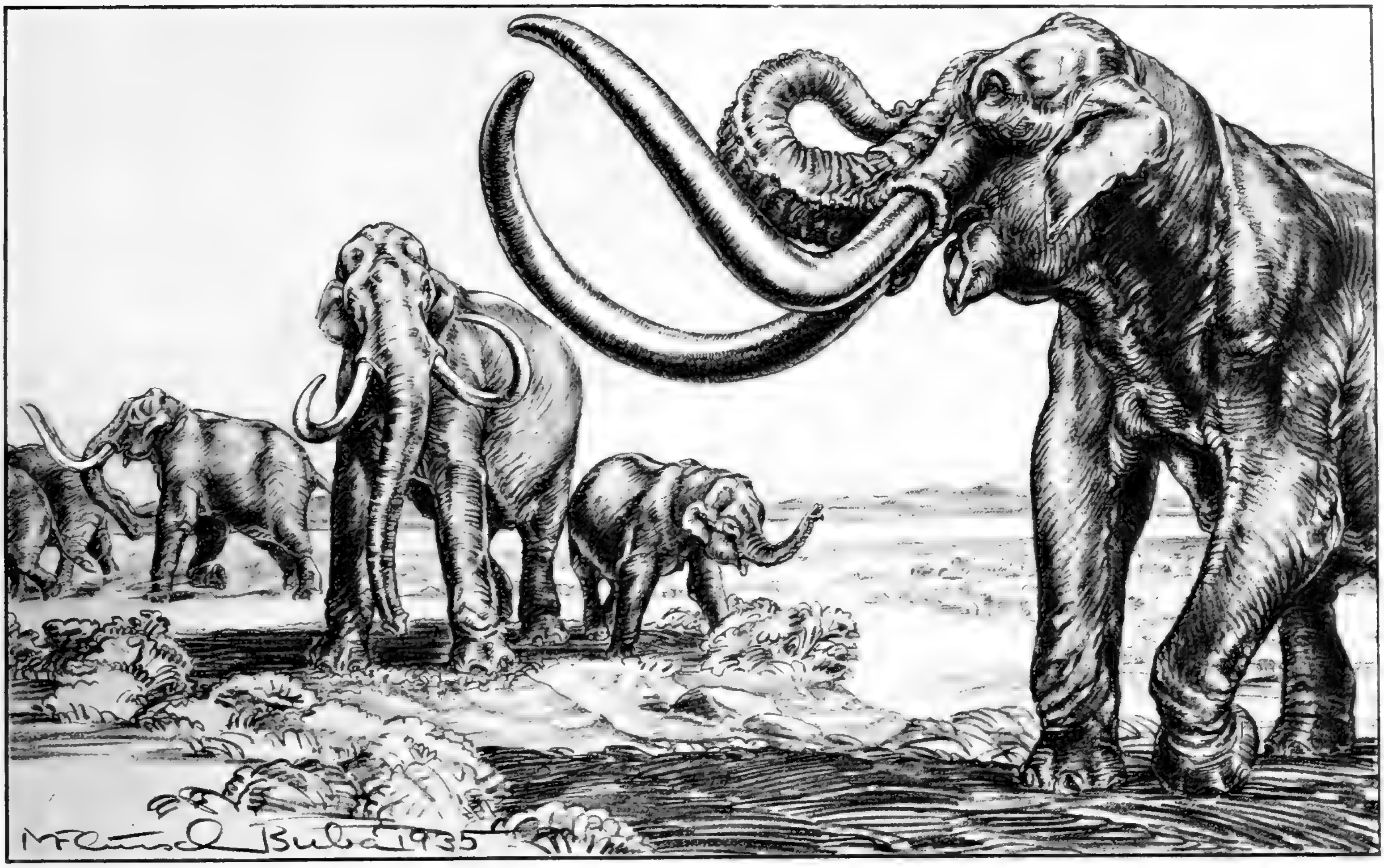
[1] [See page 1028 below for the present author's final determination.—Editor.]

[2] [Lugn and Schultz (1934.1, table opp. p. 358) regard *Archidiskodon hayi* as of Kansan (Grand Island) age, equivalent to the Lower Pleistocene.—Editor.]

[3] [Dr. C. van Riet Lowe places *Archidiskodon subplanifrons* in the early Pleistocene and *A. broomi* in the late Pleistocene (see van Riet Lowe, 1929.1, table opp. p. 682).—Editor.]



Family Group of Archidiskodon imperator maibeni along the Platte River, Nebraska

Restoration by Margret Flinsch Buba in 1935, under the direction of Henry Fairfield Osborn

Bull in foreground 1/40th natural size and bull at extreme left 1/140th natural size. Cow and calf in middle foreground 1/60th natural size

Fig. 824. The bull in the foreground and the one in the distance at the extreme left were based on measurements of the skeleton of *Archidiskodon imperator maibeni* in the Nebraska State Museum (Neb. Mus. 5-9-22), from Lincoln County, Nebraska (see Figs. 910–912, 918 of the present Memoir), supplemented by a fine skull of *A. imperator* in the Geological Institute of Mexico (No. 212) from Tepexpan (see Fig. 902) and of a giant tusk of the same species (*A. imperator*) in the American Museum (Amer. Mus. 22481), from Post, Texas (see Fig. 894). The height at the withers (top of shoulder blade) is 3826 mm.; adding the usual $6\frac{1}{3}\%$ gives a height in the flesh of 4068 mm. or 13 ft. $4\frac{1}{4}$ in.

II. CHARACTERS OF ARCHIDISKODON AND METARCHIDISKODON AND INCLUDED SPECIES

Superfamily: ELEPHANTOIDEA Osborn, 1921

Family: ELEPHANTIDÆ Gray, 1821

Subfamily: Mammontinæ Osborn, 1921

Genus: **ARCHIDISKODON** Pohlig, 1885, 1888

Original reference: Zeitschr. deutsch. geol. Ges., XXXVII, Heft IV, p. 1027 (Pohlig, 1885.1); Nova Acta Leop. Carol., LIII, No. 1, pp. 138, 252 (Pohlig, 1888).

Genotypic species: *Elephas meridionalis* and *E. planifrons.*

Syn.: *Parastegodon* Matsumoto, 1924 (in part); genotype, *Elephas auroræ* Matsumoto, 1924. *Leith-Adamsia* Matsumoto, 1927; genotype, *Leith-Adamsia Siwalikiensis* Matsumoto, 1927.

Generic Characters (translation after Pohlig, 1888, p. 138).—Genotypes *E. meridionalis, E. planifrons*; transitional to higher groups. Molars with few ridge-plates, not exceeding fifteen [?] lamellæ; crowns broad, short, and with thick enamel (i.e., "laticoronate, kurze und pachyganale Molaren"); ridge-plates tapering to summit in sections.

GENERIC CHARACTERS (OSBORN, 1928).—Superior tusks large, incurved, crossing in old males as in other Mammontinæ. Cranium extremely heightened (hypsicephalic), foreshortened and broadened (brachycephalic), deepened (bathycephalic). Molar ridge-plates extremely broad, enamel border thickened, cement usually very thick. Ridge-plate formula slowly progressing from minimum, M 3 $\frac{10+}{11+}$ (*A. planifrons*), to maximum, M 3 $\frac{17\text{-}18}{18\text{-}20}$ (*A. imperator*). Finally attaining gigantic size.

This genus is given first consideration in the history of the subfamily Mammontinæ for the reason that *Elephas* [= *Archidiskodon*] *planifrons* of the Upper Pliocene of India is geologically the earliest of the Elephantidæ at present known. It is a very striking circumstance that until we reach the Upper Pliocene, Pinjor horizon, of India we discover Mastodonts and Stegodonts only, there being no trace of the Elephantidæ; consequently *Archidiskodon planifrons* appears to be a new arrival in southern Eurasia in Upper Pliocene time, probably a descendant of ancestors coming from some region of southern Africa, such as *Archidiskodon subplanifrons*.[1]

Osborn, 1929: Comparing Falconer's measurements of thirty-nine Siwalik specimens (Table VI, opposite page) with Barnum Brown's measurements of twenty-seven Siwalik specimens (p. 954 below), we find a closely similar range of 'ascending mutations' rising from the most primitive ridge formula, M 3 $\frac{9\frac{1}{2}}{8\frac{1}{2}\text{-}9}$, through intermediate mutations, M 3 $\frac{10}{10\frac{1}{2}}$, to the most progressive mutations, M 3 $\frac{\frac{1}{2}\text{-}12\text{-}\frac{1}{2}}{13\frac{1}{2}\text{-}14\frac{1}{2}}$. Thus in sixty-six specimens collected in the Pinjor horizon, of the Siwaliks, India, we observe gradual ascending mutations of the *Archidiskodon planifrons* stage toward the *A. meridionalis* stage. The ridge-plates throughout in M_3 are more numerous than those in M^3.

SUMMARY.—The *ascending mutations* in the thirty-nine specimens referred by Falconer (1868) to '*Elephas planifrons*' are seen to compare very closely with those in the twenty-seven specimens of the collection made by Barnum Brown and referred by Osborn to *Archidiskodon planifrons*. This renders it probable that the Falconer collection and the Brown collection were from the same geologic horizon. The extremes in both collections are seen in the maximum and minimum heights of the ridge-plates:

UPPER PLIOCENE ARCHIDISKODON PLANIFRONS

MEASUREMENTS OF RIDGE-PLATES IN MILLIMETERS

	Falconer (1868)		Brown (1922)	
	Max.	Min.	Max.	Min.
Third superior molars, M^3				
Height	123	64	102	88e
Length	279	247	254	201
Third inferior molars, M_3				
Height	115	77	135	53
Length	323	224	313	203

Allowing for individual differences in size due to sex and geologic level, and for probable differences in mode of measurement, especially of the height of the ridge-plates, it appears probable that in both collections we have to do with a *series of ascending mutations some of which attain the size and ridge-plate height of Archidiskodon meridionalis*. It is noteworthy that in the *A. planifrons* r.M^2, the length (221 mm.) and the height of the 7th ridge-plate (71e mm.) agree closely with the 7th ridge-plate height of M^2 of *A. planifrons* from the Piltdown gravels of Sussex, England (see Figs. 852, 853, 854).

Falconer observes that while the ridge-plates in *A. meridionalis* increase in number they do not increase correspondingly in *height*. In two of his figures reproduced in the present Memoir (Fig. 862) the measurements are:

PRIMITIVE ARCHIDISKODON MERIDIONALIS [OR A. PLANIFRONS]

	Length	Breadth	Height
Val d'Arno, r.M_3	10 in. [=255 mm.]	3.4 in. [=87 mm.]	5 in. [=126 mm.]
Norwich Crag, r.M_3	11.25 [=287 mm.]	3.8 [=97 mm.]	4.8 [=123 mm.]

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[1] [Or *Archidiskodon proplanifrons*, an equally primitive species subsequently described by Professor Osborn from Gong-Gong, Vaal River (Osborn, 1934.925, p. 10).—Editor.]

UPPER SIWALIKS MUTATIONS

TYPICAL ARCHIDISKODON PLANIFRONS: M 3 $\frac{10+}{11+}$, ASCENDING TO TYPICAL A. MERIDIONALIS: M 3 $\frac{13-14}{11-14}$

Table VI. Summary of Measurements of Thirty-nine Specimens referred by Falconer, 1868, to Elephas [=Archidiskodon] planifrons

Superior	Plate	Figure	Molar	Length in. mm.	Breadth in. mm.	Index	Height in. mm.	Ridge-plates
Third Molars	XII	Footnote, p. 433. Unfig.	M^3	11 =279	3.7–4.8=95–123	34	8th 4.8=123	½-12-½
	XI	1	l.M^3	11 =279	4.5=114			
		4	[1]r.M^3	5.4=135	2.5= 63			8+
	XIV	8	[2]r.M^3	10 =255	3.5= 89		10th? 2.5= 63	8-9-½
			r.M^3	9.7=247			4 =102	
	X		r.M^3	9.7=247	3.5= 89		4 =102	
Second Molars	II	5*a* Type	r.M^2	8.7=221			[7th = 71c]	9
	XII	5	r.M^2	8 =204	3 = 77	37		½-8
		5*a*	l.M^2	7.5=191	3.2= 81	42		½-8-½
		6, 6*a*	r.M^2					8
First Molars	VI	Footnote, p. 427	M^1	6.5=165	3.4= 87	52	4th 3.5= 89	½-7-½
		6	M^1	5.5=140	2.7= 69	49	4th 3 = 77	½-7-½
	XII	4, 4*a*	.M^1	5.2=132	2.8= 71	55		7?
Fourth Deciduous	VI	5	Dp^4	4 =102	2.4= 61	60		½-6-½
Third Deciduous	XII	2	Dp^3	3.8= 97	2.3= 59	60		½-6-½
Second Deciduous		1, 1*a*	Dp^2					4
True Premolars	VI	4	l.P	1.2= 30	1.1= 28	96	.8= 21	3 with indistinct front and back ridges
Inferior								
Third Molars	XII	Footnote, p. 433. Unfig.	r.M_3	11.8=300	3.9=100	33	11th 4.6=115	14-½
			l.M_3	11 =279	3.3= 84	30	8th 3 = 77	13-½
		13	l.M_3	12.7=323	3.6= 91	28	10th 4.5=114	13-½+
	XI	8	M_2 [M_3]	12.1=308	3.8= 97	32		11-½
		2	r.M_3	11.8=300	3 = 77	25		½-13-½
		5	r.M_3	10.5=267	4.2=105	39	9th 3.5= 89	9+
	II	5*b* Paratype	l.M_3					9+
	XI	7	l.M_3	10.2=259	4 =102	44		
	XVIII.A	1, 1*a*	l.M_3	10.4=265	4.1=104		3.2= 81	8
	XI	3	l.M_3	10 =255	3.6= 91	36		7+
	XII	12, 12*a*	?r.M_3	10 =255	3.5= 89		7th 4 =102	½-10-½
	VIII	2, 2*a*	r.M_3	8.8=224	3.8= 97	43		9-11
	XIV	9	r.M_3	9.5=241	3.5= 89		6th 3 = 77	8½
	XI	10	l.M_3		3.7= 95		5th 3.8= 97	
Second Molars		6	l.M_2	8 =204	2.8= 71			9-½
		10	l.M_2	7 =178	3.7= 95			8-½
First Molars		6	l.M_1	6 =153	2.8= 71			6+
	XII	10, 10*a*	l.M_1	6.7=171	2.6= 66			½-7
Fourth Deciduous		8, 8*a*	l.Dp_4	4.4=113	2.4= 61			¾-7-½
Third Deciduous		7, 7*a*	r.Dp_3	2.4= 61	1.4= 36			6-½
True Premolars		10, 10*a*	l.P (frag.)	1 = 26	1 = 26		1.5= 38	Does not show ridges
		8, 8*a*	l.P	1 = 26	.8= 21			

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[1] [One of the genotypes of *Leith-Adamsia* Matsumoto.—Editor.]

[2] Valuable because found with r.M_3 (Pl. xiv, fig. 9). [Pl. xiv, fig. 8, represents one of the genotypes of *Leith-Adamsia* Matsumoto.—Editor.]

1. ARCHIDISKODONTS OF SOUTHERN EURASIA

From our present knowledge it appears probable that *Archidiskodon* originated in Africa, because seven stages in the specific evolution of this genus have been discovered on that continent. In India *Archidiskodon planifrons* suddenly appears in the Upper Pliocene, Pinjor horizon,[1] while *A. meridionalis* appears in the uppermost Pliocene and Lower Pleistocene of western Europe. The subspecific name *Elephas* [=*Archidiskodon*] *meridionalis cromerensis* has been applied by Depéret and Mayet to rather primitive archidiskodont molars found in the Forest Bed of East Anglia.

SYSTEMATIC DESCRIPTION OF SPECIES

Archidiskodon planifrons Falconer and Cautley, 1846 [1845]

Figures 815, 817, 819, 825, 827–850, 852–856, 865, 871, 876, 914, 1208, 1231, 1239, Pl. xxi

'Sewalik Hills' of Falconer, northern India; Pinjor horizon, Upper Pliocene, Upper Siwaliks (Pilgrim)[1]; Upper Siwaliks, below Boulder Conglomerate, Lower Pleistocene (Brown).

Syn.: *Leith-Adamsia Siwalikiensis* Matsumoto, 1927.

Specific Characters (Falconer, 1846, 1863, 1868; Osborn, 1928).—Species distinguished from *Elephas* [=*Stegodon*] *auroræ* by the more elevated or hypsodont ridge-plates; distinguished from *Elephas* [=*Archidiskodon*] *meridionalis* by the much less elevated ridge-plates; by the flattened forehead to which the specific name *planifrons* refers in distinction from the concave forehead of *A. meridionalis*; also by the more primitive ridge-plate formula, M 3 $\frac{10+}{11+}$, and by the succession of premolars, this being the last species of the Elephantidæ in which the true premolars, P 3 and P 4, are erupted. Rostrum of jaw elongated and depressed (see Fig. 849).

Materials.—The above comparison of measurements of thirty-nine specimens in the Falconer and Cautley collection (1830–1840) and of twenty-seven or more specimens in the American Museum collection of 1922 made by Barnum Brown (see Summary of Measurements, Tables VI and VII, pp. 949 and 954) renders it probable that both collections, totaling sixty-six or more specimens, came from the same general locality and represent ascending mutations, from the more primitive typical *Archidiskodon planifrons*, M 3 $\frac{10+}{11+}$, toward the more progressive *A. meridionalis* stage, M 3$\frac{13-14}{11-14}$. We have to do, therefore, with *ascending mutations.*

Geologic Locality and Levels.—All the chief specimens (numbering 39 in Table VI above) listed, described, or figured by Falconer and Cautley as '*Elephas planifrons*' are recorded as simply from the Siwalik Hills, since they did not distinguish between 'upper,' 'middle,' and 'lower' Siwaliks.

Pilgrim (1913) attributes this species only to the 'Upper Siwaliks,' Pinjor horizon, summit of the Pliocene; he writes (1913, p. 294): "There is absolutely no trace of *Elephas* either in the Middle Siwalik or in the Tatrot zone of the Upper Siwalik. It first appears as the species *Elephas planifrons* some 2,000 feet above the base of the Tatrot zone."

In the collection of 1922 made by Barnum Brown, twenty-seven or more specimens are now recorded as, or referred to, *Archidiskodon planifrons*; this collection (see map, Fig. 826) is recorded by Brown especially from near the towns of Kalka, Charnian, Siswan, Chandigarh, and Mirzapur, as shown in the complete list on page 955 below.

None of the twenty-seven or more specimens of the Brown collection was actually found embedded in the rock; all of them were loosely embedded in sand, occurring in gullies or depressions. Consequently the exact geologic age and horizon levels are indeterminable; yet they may all be safely classed as Upper Pliocene.[1]

History.—Falconer and Cautley first published in the "Fauna Antiqua Sivalensis" the name *Elephas planifrons* in the legend of Plate ii, figs. 5*a*, 5*b*, of date 1845. In 1846, p. 38, Falconer wrote: "The next serial modification in the disposition of the three dental substances, and in the consequent form of the teeth, is exhibited in fig. 5*a* of the same plate, which represents a section of the penultimate upper molar of another Indian fossil species which we have named *E. planifrons.*" As usual in his descriptions the locality is given simply Siwalik Hills, but we know from Pilgrim (1913, p. 294), as quoted above, that this phylum first appears as the species *E. planifrons* in the Pinjor horizon, Upper Pliocene,[1] some 2,000 feet above the base of the Tatrot horizon. It also occurs in Austria and Bessarabia.

As early as 1863 Falconer remarked (p. 80): "The nearest affinity, and that a very close one, of the European *E. meridionalis* is with the Miocene *E.* (*Loxod.*) *planifrons* of India." Falconer thus led the way for our present knowledge, namely, that *Archidiskodon planifrons* is directly ancestral to *A. meridionalis.*

E. [*Elephas*] *planifrons* Falconer and Cautley, 1846 [1845]. "Fauna Antiqua Sivalensis," 1846, p. 38 [1845, Pl. ii, figs. 5*a*, 5*b*]. Lectotype.—A second superior molar with nine ridges, the three anterior ridges being in use (Brit. Mus. M.3068). Cotype.—Broken third molar of lower jaw, l.M_3, with nine ridges remaining. Brit. Mus. M.2010. Horizon and Locality.—Siwalik Hills, India, Upper Siwaliks, Pinjor horizon, Upper Pliocene.[1] Lectotype and Cotype Figures.—Falconer and Cautley, 1846 [1845, Pl. ii, figs. 5*a*, 5*b*].

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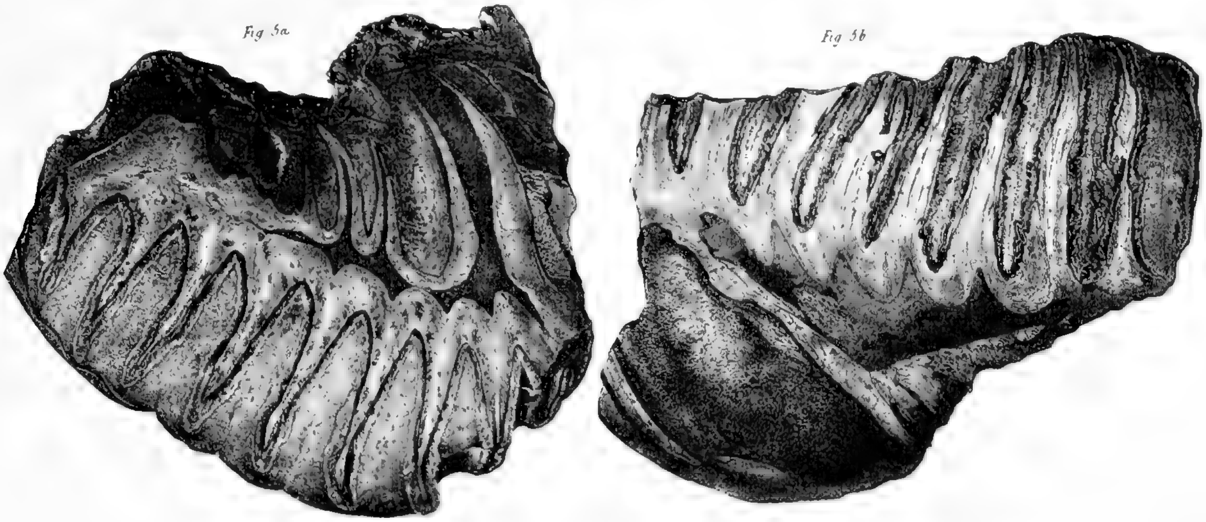
[1] [Recent field studies in northern India by Dr. Hellmut de Terra and Père Teilhard de Chardin have offered strong evidence to support the conclusion that the Tatrot and Pinjor horizons are equivalent and are entirely of Lower Pleistocene age. The Boulder Conglomerate ranges up to the Middle Pleistocene (see Chap. XXII below on the Geologic Succession of the Proboscidea for more detailed discussion). This note was prepared by Dr. E. H. Colbert, January, 1937.—Editor.]

Description.—(Falconer and Cautley, 1846.1, p. 38): "The next serial modification in the disposition of the three dental substances, and in the consequent form of the teeth, is exhibited in fig. 5*a* of the same plate, which represents a section of the penultimate upper molar of another Indian fossil species which we have named *E. planifrons*. This tooth shows nine ridges, the three anterior of which alone have been in use, the two first being worn down to a single disc of ivory. The common nucleus of this substance is of less thickness than in the corresponding tooth of *E. insignis*, and the divisions which are continued upwards from it into the centre of the ridges are more elongated, with a narrower base, forming irregular-shaped wedges. The layer of enamel is diminished in thickness and is less uniform in outline, and the surface in contact with the cement shows a feathered or ragged edge, indicating superficial inequalities for the firmer cohesion of this latter substance. The enamel is reflected over the ridges of ivory, and down into the hollows zig-zag wise, exactly as in fig. 6*a*, the principal difference being that the ridges are narrower, with a greater vertical height. The cement substance attains its maximum of development in this species, completely filling up the wide interspaces of the ridges, over which it is continued in a thick mass. This tooth measures 8.7 inches in length."



Lectotype (R.M^2) and Cotype (L.M_3) of Archidiskodon planifrons

Fig. 825. Lectotype and cotype of *Elephas planifrons* Falconer and Cautley, 1846 [1845, Pl. ii, figs. 5*a*, 5*b*]. From the Siwalik Hills, India, Upper Siwaliks, Pinjor horizon, Upper Pliocene.[1] One-third natural size. See "Description of the Plates in the Fauna Antiqua Sivalensis" (Falconer, 1867, p. 3; also Falconer [Murchison], 1868, Vol. I, p. 423):

"Fig. 5*a*.—. . . Vertical section of penultimate upper molar [r.M^2], with nine ridges, the three anterior of which alone have been in use, the two first being worn down to a single disc of ivory." Brit. Mus. M.3068. Molar inverted to show natural position.

"Fig. 5*b*.—"[Cotype.] Vertical section of portion of last molar of lower jaw [l.M_3], with nine ridges." Brit. Mus. M.2010. Osborn (1924): The cotype M_3 is a broken tooth which typically presents ten ridges, sometimes eleven.

Observe in comparing the original figure (5*a*) with the new figure (Fig. 827) that Falconer omitted the seven ridge-plated r.M^1. See also figure 828 after Lydekker. M^2, ridge-plates pre-concave, post-convex. M_3, ridge-plates pre-convex, post-concave.

"Fig. 5*b*, represents a corresponding section of a portion of the last molar of the lower jaw of the same species, comprising nine ridges. This tooth had been longer in use than that of the upper jaw, and all the ridges are more or less worn except the two last. It presents the same general characters exhibited by fig. 5*a*, in the elongated cuneiform ivory ridges, unequal enamel, and abundant cement, the differences being merely such as constantly hold between molars of the upper and lower jaws, and of different ages in the same species."

FALCONER'S NOTES OF 1868 ON TYPE AND REFERRED SPECIMENS OF ELEPHAS PLANIFRONS

Falconer, "Palæontological Memoirs," Vol. I, 1868, pp. 423–442, Plates ii, vi, viii, xi, xii, and xiv of the "Fauna Antiqua Sivalensis."

Falconer's observations on this species are to be found in his successive publications of 1845 (Plates), 1846 (Letterpress), 1857, 1863, 1865, and 1868. In the latter year ("Palæontological Memoirs" of 1868) a summary of all his observations was published by Murchison, covering in detail thirty-nine or more specimens referred to *Elephas planifrons*, all presumably collected from the Pinjor horizon, Upper Pliocene.[1]

Elephas planifrons: [Lectotype (Brit. Mus. M.3068) and Cotype (Brit. Mus. M.2010)].—Plate ii, fig. 5*a*, M^2 with 9 ridges, cement filling valleys, enamel folds thick, length 8.7 in. = 221 mm.; fig. 5*b*, M_3, vertical section, with 9 ridges.

Ridge Formulæ in Upper and Lower Grinding Teeth

Upper Jaws.—Plate vi, figs. 4, 5, 6. Skull with premolar, ?Pm, Dp^4, M^1. Left Pm with 3 ridges and 2 half-ridges. Dp^4 with 6 ridges also a heel and front ridge, enamel thick. (Footnote, p. 427): Palate with M^1, 7 ridges and 2 half-ridges; length 6.5 in. = 165 mm., width 3.4 in. = 87 mm., height at 4th ridge 3.5 in. = 89 mm., fifth and sixth ridges with 6 conelets each. Plate xi, fig. 1, aged palate with r. and l.M^3, 10 ridges including posterior half-ridge, enamel very thick; fig. 4, M^3, right side, remarkable fragment, 6¼ ridge-plates, length of fragment 5.4 in. = 135 mm., width 2.5 in. = 63 mm. Plate xii, figs. 1, 1*a*, Dp^2 with 4 ridges;

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[1] [See footnote on previous page.—Editor.]

fig. 2, section of r.Dp^3, with 6 main ridges, a back talon and front heel, total 6 and 2 half-ridges, length 3.8 in. = 97 mm., width 2.3 in. = 59 mm.; figs. 4, 4*a*, M^1 with 5 ridges and heel remaining, two gone, 7 probable total, length 5.2 in. = 132 mm., width 2.8 in. = 71 mm.; fig. 5, M^1 [same as fig. 4, this plate], M^2, the latter with 8 ridges and front heel, length of M^2 8 in. = 204 mm., width 3 in. = 77 mm.; fig. 5*a*, palate with r. and l.M^2, 8 distinct ridges and front and back heel, total of 8 ridges and 2 half-ridges, conelets few and large, enamel thick, length of l.M^2 7.5 in. = 191 mm., width 3.2 in. = 81 mm., fig. 6, M^2 with 8 main ridges. Plate XIV, fig. 8, r.M^3, showing 8 or 9 ridges and a heel, enamel thick, length 10 in. = 255 mm., width 3.5 in. = 89 mm.

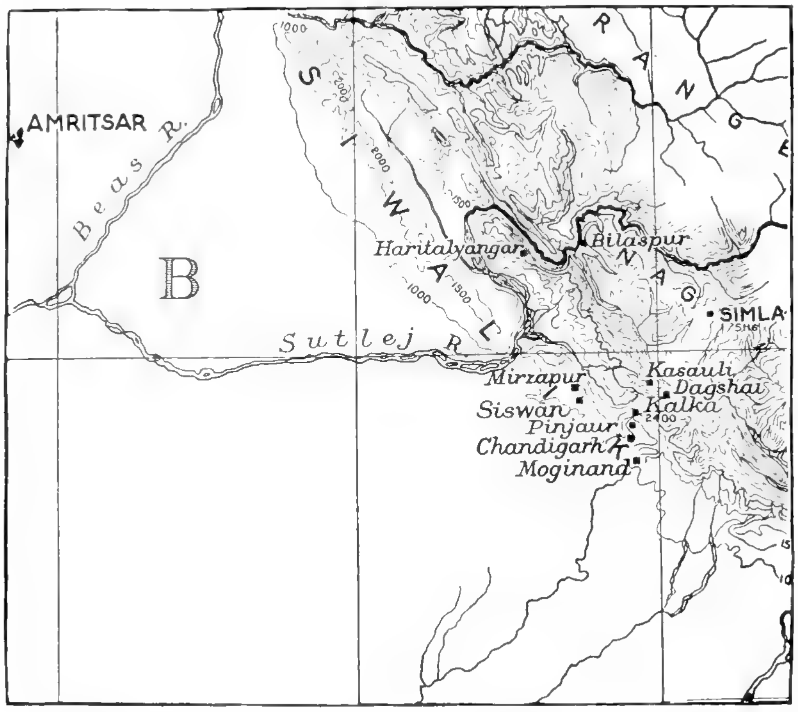
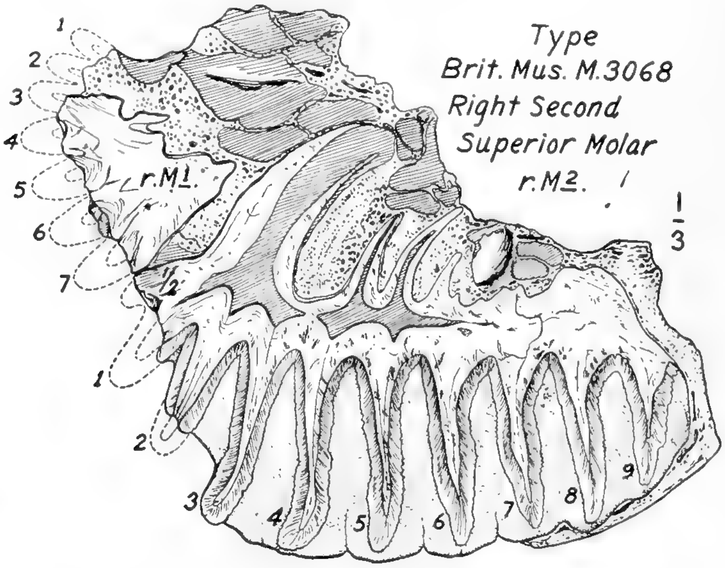


Fig. 826. Favorable exposures, southwest of Simla, of the *Archidiskodon planifrons* life zone, Upper Siwaliks, India, chiefly Pinjor horizon, from which were collected by Barnum Brown in 1922 twenty-seven or more specimens referable to this species, especially from Kalka, Charnian, Siswan, Chandigarh, and Mirzapur, also transitions to *A. meridionalis*. Compare figures 820, and 729, Pl. XXV.

LOWER JAWS.—Plate VIII, figs. 2, 2*a*, perfect lower jaw, M$_3$ with a total of 9-11 ridges, enamel very thick, length of M$_3$ 8.8 in. = 224 mm., width 3.8 in. = 97 mm. Plate XI, fig. 2, superb lower jaw, two mental foramina, r. and l.M$_3$ with 13 ridges and front and back half-ridges, enamel very thick, length of r.M$_3$ 11.8 in. = 300 mm., width 3 in. = 77 mm.; fig. 3, superb left half jaw, only 7 remaining ridges in M$_3$, enamel thick, cement abundant, "Proved to be *E. planifrons* by the distance between the plates, the very low crown, thick enamel, and two mental foramina," extreme length of jaw 24.2 in. = 614 mm., length of M$_3$ 10 in. = 255 mm., width of M$_3$ 3.6 in. = 91 mm.; fig. 5, r.M$_3$, enormous tooth fragment, very thick enamel, low ridges, and mesial expansion, 9 ridges remaining, length of M$_3$ 10.5 in. = 267 mm., width 4.2 in. = 105 mm., height of 9th ridge 3.5 in. = 89 mm.; fig. 6, left jaw with l.M$_1$, ridge-plates 6+, M$_2$, ridge-plates 9 and small heel, 5 conelets on 4th ridge, length of M$_1$ 6 in. = 153 mm., width 2.8 in. = 71 mm., length of M$_2$ 8 in. = 204 mm., width 2.8 in. = 71 mm.; fig. 7, left lower jaw, M$_3$ very aged, length of molar 10.2 in. = 259 mm., width 4 in. = 102 mm., three mental foramina; fig. 8, fine lower jaw fragment, M$_2$ [M$_3$, Osborn] complete, with 11½ ridges, enamel very thick, plates wide apart, much cement, few conelets, three mental foramina, length of M$_2$ [M$_3$, Osborn] 12.1 in. = 308 mm., width 3.8 in. = 97 mm.; fig. 9, fragment of l.M$_3$ much worn; fig. 10, lower jaw, M$_2$ with 8½ ridges, cement abundant, enamel thick, no crimping, and no mesial expansion, length of M$_2$ 7 in. = 178 mm., width 3.7 in. = 95 mm., l.M$_3$ height of 5th unworn ridge 3.8 in. = 97 mm. Plate XII, fig. 7, right lower jaw, with Dp$_3$ with 6 main ridges and small half-ridge (same formula as in *Loxodonta africana*); fig. 8, left lower jaw, with small vertically succeeding premolar (c), above it Dp$_3$, also Dp$_4$ with 7 main ridges, double front heel and small half-ridge behind; figs. 10, 10*a*, first left true molar, l.M$_1$, with 7 main ridges, a small ridge in front, no heel behind, length of M$_1$ 6.7 in. = 171 mm., width 2.3 to 2.6 in. = 59 to 66 mm.; figs. 12, 12*a*, ?r.M$_3$, "apparently of a small sized individual," length 10 in. = 255 mm., width in front 3.5 in. = 89 mm., height of crown at 7th plate 4 in. = 102 mm., ten main plates and a front plate and heel; fig. 13, left lower jaw, l.M$_3$ entire, with about 13 ridges and a heel, or possibly 14, length of M$_3$ 12.7 in. = 323 mm., width 3.6 in. = 91 mm., height at 10th ridge 4.5 in. = 114 mm. Plate XIV, fig. 9, last lower molar, right side, r.M$_3$, length 9.5 in. = 241 mm., width 3.5 in. = 89 mm., height at 6th ridge 3 in. = 77 mm., shows 8 ridges and a heel. Plate XVIII.A, figs. 1, 1*a*, an l.M$_3$, an enormous specimen; 8 plates, length 10.4 in. = 265 mm., width 4.1 in. = 104 mm., height 3.2 in. = 81 mm.



NEW LECTOTYPE FIGURE OF ARCHIDISKODON PLANIFRONS, R.M^2

Fig. 827. New lectotype figure of *Elephas planifrons* Falconer (Brit. Mus. M.3068), 9+ ridge-plated second superior molar, of the right side, r.M^2, with worn crown of a ?7½ ridge-plated first superior molar of the right side, r.M^1. Redrawn by Miss G. M. Woodward for this Memoir; one-third natural size. Compare figure 825.

Observe in comparing this figure with figure 854 of the same molar, that the ridge-plates agree in size with those of Piltdown, England (Fig. 853).

Collective Ridge Formula (Falconer, 1868).—(1) The permanent fourth premolar, P 4, persists, with 3 ridges. (2) From the specimens of *Elephas planifrons*, as described by Falconer (39 of which appear in Table VI "Summary of Measurements" above), from the Upper Siwaliks, we deduce the collective ridge formula below; (3) the minimum numbers represent partly worn or partly developed teeth, while the maximum numbers represent fully worn and fully developed teeth; (4) half-ridges develop both in front and behind the main ridges; (5) the collective formula below indicates the half-ridges as well as the main ridges.

Elephas planifrons.—Vertical and longitudinal section of the second upper true molar; from the Pliocene of the Siwalik Hills. $\frac{1}{3}$.

Fig. 828. Lectotype nine and a third ridged upper molar, r.M^2, of *Elephas* [*Archidiskodon*] *planifrons*. Reproduced from a wood engraving by Lydekker (1886.2, p.102, fig. 24). Brit. Mus. M.3068. One-third natural size. Inverted to show natural position of molar.

a, cement; *b*, enamel; *c*, dentine.

We observe that the cement (*a*) completely fills the valleys. The enamel (*b*) is extremely thick, since the sides of the enamel ridge-plates diverge towards the apex and converge towards the base; the cement interspaces between the ridge-plates become constantly narrower as the crown wears down, while the dentine within the enamel becomes constantly broader, as shown in the figure opposite.

Maximum and minimum collective ridge formula [of ascending mutations] of *Elephas planifrons*:

$$\text{Dp } 2\frac{4}{} \text{ Dp } 3\,\frac{\frac{1}{2}\text{-}6\text{-}\frac{1}{2}}{6\text{-}\frac{1}{2}}\;(\text{P } 4\,\frac{\frac{1}{2}\text{-}3\text{-}\frac{1}{2}}{})\;\text{Dp } 4\,\frac{\frac{1}{2}\text{-}6\text{-}\frac{1}{2}}{\frac{3}{4}\text{-}7\text{-}\frac{1}{2}}\;\text{M } 1\,\frac{\frac{1}{2}\text{-}7\text{-}\frac{1}{2}}{\frac{1}{2}\text{-}7}\;\text{M } 2\,\frac{\frac{1}{2}\text{-}8\text{-}\frac{1}{2}\text{-}9}{8\text{-}\frac{1}{2}\text{-}9\text{-}\frac{1}{2}}$$

$$\text{M } 3\,\frac{8\text{-}9\text{-}\frac{1}{2}\text{-}\frac{1}{2}\text{-}12\text{-}\frac{1}{2}}{8\text{-}9\text{-}\frac{1}{2}\text{-}10\text{-}\frac{1}{2}\text{-}\frac{1}{2}\text{-}12\text{-}\frac{1}{2}\text{-}14\text{-}\frac{1}{2}}$$

(6) It is interesting to observe the half-ridges arising both in front and behind the main ridges, which seems to be a characteristic feature of this species, as compared with *Elephas hysudricus*. (7) A primitive or simplified formula from Falconer of the minimum ridges in *E. planifrons* from the Upper Siwaliks of India would be:

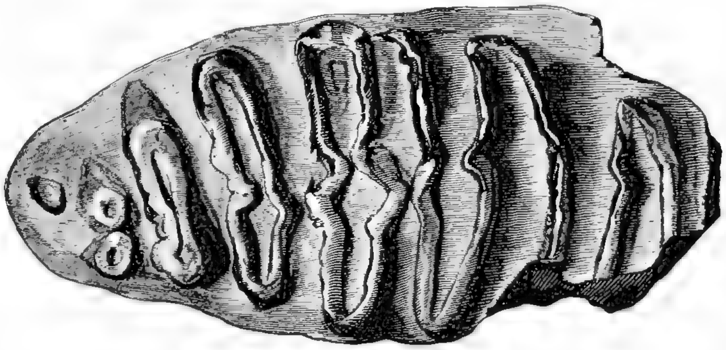
$$\text{Dp } 2\frac{4}{} \text{ Dp } 3\,\frac{6+}{6+}\;(\text{P } 4\,\frac{+3+}{})\;\text{Dp } 4\,\frac{6+}{7+}\;\text{M } 1\,\frac{7+}{7+}\;\text{M } 2\,\frac{8}{9}\;\text{M } 3\,\frac{10+}{11+}.$$

SPECIFIC CHARACTERS OF ARCHIDISKODON PLANIFRONS (LYDEKKER, 1886; OSBORN, 1924)

The next review of *Archidiskodon planifrons* is that of Lydekker (1886.2, pp. 98–107) in which the cranium (Brit. Mus. M. 3060—our Fig. 830) was selected as the type; in the present Memoir the specimen first described and figured by Falconer and Cautley is regarded as the *type* [lectotype] (see Fig. 825). From Lydekker's descriptions the following characters may be summarized:

(1) Both the third and fourth milk molars were vertically succeeded by premolars, thus the dental formula is: Dp$^{2-4}$ Dp$_{2-4}$, P$^{3-4}$ P$_{3-4}$, M$^{1-3}$ M$_{1-3}$. This succession is an important character which must be looked for in the *ancestors* of this species; it does not occur in any other species of the Elephantidæ thus far known; nor is it found in *Stegodon bombifrons*. (2) The correct collective ridge formula is that deduced from Falconer as his maximum-minimum or typical, as given above. The ridge formula of Lydekker (1886.2, p. 99) is incorrect. (3) Crowns of molars broad; cement in the interspaces frequently very great; enamel usually thick, frequently devoid of plication in the middle and near the root of the crown; plication near the summit of the crown relatively coarse. (4) Ridge-plates subellipsoidal, frequently with a mid-

Fig. 25.



Elephas planifrons.—The hinder half of the third right upper true molar from the Pliocene of the Siwalik Hills. $\frac{2}{3}$. The lower border of the figure is the inner border of the specimen.

Fig. 829. Referred right M^3 of *Elephas* [=*Archidiskodon*] *planifrons*. After Lydekker, 1886.2, p. 102, fig. 25. Brit. Mus. M.3070. Two-thirds natural size. Figured by Falconer and Cautley, 1846 [1845, Pl. xi, fig. 4], and made one of the genotypes of *Leith-Adamsia* Matsumoto, 1927, but regarded by the present author as a synonym of *Archidiskodon planifrons*. (See Fig. 847 below.)

As compared with figure 828 this is a crown view of a much worn third superior molar in which the enamel loops in the middle of the crown are contiguous, the dental areas are expanded, the cement areas are contracted. The cement extends beyond the outer borders of the plates, a highly characteristic feature of *Archidiskodon*.

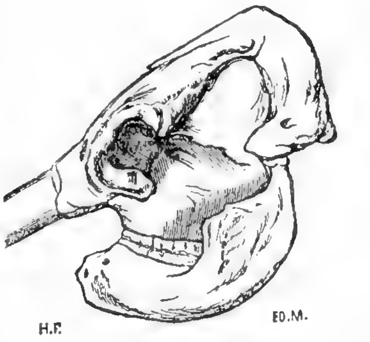


Fig. 830. Skull of *Elephas* [=*Archidiskodon*] *planifrons* from the Siwalik Hills, India, reproduced from Gaudry, 1878, p. 185, fig. 246, after Falconer 1846 [1845, Pl. x]. One-sixteenth natural size. This skull (Brit. Mus. M. 3060) was erroneously selected by Lydekker as the type of *Elephas planifrons*, and is figured in his "Catalogue of the Fossil Mammalia in the British Museum (Natural History)" of 1886 (1886.2, woodcut fig. 23, p. 100). Compare figures 848 and 817 of the same cranium.

Depéret and Mayet regard this cranium as that of a female, which, if true, partly accounts for its small size (see p. 962 of the present Memoir).

expansion, sometimes imperfectly lozenge shaped, in slightly worn teeth the middle portion of each ridge frequently forms an isolated disk. (5) Cranium characterized by flatness of the fronto-parietal region, by a small incision of the temporal fossæ on the frontals, by a comparatively slight elevation of the vertex (hypsicephaly), by smallness of the nasal aperture, by wide divergence of the incisive alveoli, as in *A. meridionalis*; vertex of skull flattened almost at right angles to occiput, occiput pitching forward 55° when the grinding teeth are horizontal; tusks very stout and incurved.

REVISION OF ARCHIDISKODON PLANIFRONS BY OSBORN (1927 1928), BASED ON THE SIWALIK COLLECTION MADE BY BARNUM BROWN IN 1922

The twenty-seven specimens referable to *Archidiskodon planifrons* and its ascending mutations were found in the 'Upper Siwaliks,' below the Boulder Conglomerate formation, and recorded as follows:

TABLE VII. MEASUREMENTS OF TWENTY-SEVEN SPECIMENS COLLECTED BY BROWN AND REFERRED BY OSBORN TO ARCHIDISKODON PLANIFRONS, ASCENDING TO A. MERIDIONALIS

All recorded by Barnum Brown from near Kalka, Charnian, Siswan, Chandigarh and Mirzapur (see Figs. 820, 826)

SUPERIOR	Figure	Amer. Mus.	Molar	Length mm.	Breadth mm.	Index est.	Height mm.	Ridge-plates act. or est.	Ridge-plates in 10 cm.
Third Molars		19882	r. M^2	254	96	38	9th = 102	12+	5½–6
	834	19950	l. M^3	219	100	46	7th = 88e	9–½–⅓–¼ = 12	4+
		19880	l. M^3	201	88	44	9th = 95	11+	5½
First or Second Molars	**833** **855**	19821	l. M^2	217	94	43	7th = 66e	8–½–⅓ = 10	3½–4
	832	19955	r. M^1	172	76	44	6th = 70	½–7–¼ = 9	4–4½
		19955	l. M^1	162	80	49	5th = 65	½–6–¾ = 8+	4–4½
	831	19881	l. M^1	165	90	54	3d = 67	½–6 = 7+	3½–4
		19916	?r. M^1	138	80	58	5th = 107	½–6	3½–4
INFERIOR									
Third Molars	**842** **845** **855**	19951	r. M_3	313	101	32	7th = 124	11⅓ = 12	3½–4½
	841	19861	l. M_3	250	79	32	9th = 88e	11½ = 12	5
	846	19879	l. M_3	190+	105+	55	8th = 135	10+	5–5½
	844	19819	l. M_3	292+	95	32	7th = 88e	10½ = 11+	4
	855	19798	r. M_3	203	80	39	7th = 53	11+	6½
		19870	l. M_3				2d = 85		
	843	19968	l. M_3	213e	95	45	7th = 66e	9+	5
	840	19965	r. M_3	180 (inc.)	86	48	7th = 55e	9	4–4½
	839	19864	r. M_3	194+	78	40	3d = 45	½–8–⅓ = 10+	5
	835	19952	l. M_3	233e	109	47	6th = 114	8½e = 9+	3½–4
Second Molars	**836**	19778	r. M_2	140+ (inc.)	90+	64	5th = 72	½–5+ = 6+	
		19871	l. M_2	167+	87	52	8th = 99	8+	
		19870	l. M_2				10th = 82		
First Molars	**838**	19862	?l. M_1	160e	80	50e	3rd = 45	½–8 = 9+	5
		19917	r. M_1	190+	78	41	5th = 91+	+7½	5
		19961	?l. M_1	189	90	48	7th = 73	7	4
		19871	l. M_1	127	85	67		½–6–½	
	836	19778	r. M_1	103	70	68		3+	
Fourth Deciduous	**837**	19873	r. Dp_4	121	63	52	7th = 44	½–7–½ = 9	7

As remarked above, the large American Museum collection of *Archidiskodon planifrons*, including examples of the entire dentition, but lacking a skull, renders it highly probable that the Falconer and Cautley collection of *A. planifrons*, figured and listed in detail, as above described, came from the same geologic localities of the Pinjor horizon level, namely, from deposits around Kalka (see Figs. 826, 820). The following 29 specimens, belonging to 24 individuals, are given with measurements above (Table VII); they are also illustrated in great detail in the accompanying figures (Figs. 831–844).

Near Kalka	9 miles west	Amer. Mus. 19778	Fragment of right jaw with M_1 and M_2 *in situ* (Fig. 836 for M_1).
	6 miles west	Amer. Mus. 19798	Fragment of jaw with r.M_3 *in situ* (Fig. 855 FOR r.M_3).
Near Charnian	2 miles south	Amer. Mus. 19819	Fragment of left jaw with l.M_3 *in situ* (Fig. 844).
Near Siswan		Amer. Mus. 19821	Fragment of maxilla with l.M^2 *in situ* (Fig. 833).
		Amer. Mus. 19870	Fragment of jaw with l.M_2 and l.M_3 *in situ*, M_2 incomplete, M_3 partly erupted (not figured in present Memoir).
		Amer. Mus. 19879	Fragment of jaw with l.M_3 *in situ* (Fig. 846).
		Amer. Mus. 19880	Left M^3 (not figured in present Memoir).
		Amer. Mus. 19881	Left M^1 (Fig. 831).
		Amer. Mus. 19882	Fragment of maxilla with r.M^3 (not figured in present Memoir).
	3 miles north	Amer. Mus. 19871	Fragment of jaw with l.M_1 and M_2 *in situ* (not figured in present Memoir).
	3 miles north	Amer. Mus. 19873	Fragment of jaw with r.Dp_4 *in situ* (Fig. 837).
	3 miles north	Amer. Mus. 19968	Fragment of jaw with l.M_3 *in situ* (Fig. 843).
		Amer. Mus. 19965	Fragment of jaw with r.M_3 *in situ* (Fig. 840).
		Amer. Mus. 19862	Fragment of jaw with l.Dp_4 and l.M_1 (Fig. 838).
Near Chandigarh	3 miles west	Amer. Mus. 19861	Fragment of jaw with l.M_3 *in situ* (Fig. 841).
	3 miles west	Amer. Mus. 19916	?Right M^1 (not figured in present Memoir).
	3 miles west	Amer. Mus. 19950	Fragment of maxilla with l.M^3 *in situ* (Fig. 834).
	1 mile west	Amer. Mus. 19951	Right M_3 (Fig. 842).
	1 mile west	Amer. Mus. 19952	Left M_3 (Fig. 835).
	3 miles west	Amer. Mus. 19955	Right M^1 and left M^1 (Fig. 832).
	1 mile west	Amer. Mus. 19961	?Left M_1 (not figured in present Memoir).
	3 miles west	Amer. Mus. 19917	Right M_1 (not figured in present Memoir).
Probably near Chandigarh, record incomplete		Amer. Mus. 19967	Lower jaw, left ramus.
Near Mirzapur	3 miles north-east	Amer. Mus. 19864	Fragment of jaw with r.M_3 *in situ* (Fig. 839).

SUMMARY OF DENTAL MEASUREMENTS OF THE AMERICAN MUSEUM COLLECTION MADE BY BARNUM BROWN IN 1922

These measurements accord in general with those of the Falconer and Cautley Collection in Table VI above and exhibit variations in size, length, breadth, and proportions, partly attributable to male or female sex, partly to progressive ascending mutations. The increase in *number* of the ridge-plates and half ridge-plates is probably attributable to progressive evolution or to ascending mutations ranging into higher geologic levels. In general, the smaller animals, with fewer ridge-plates, probably occurred in lower geologic levels than the larger animals, with more numerous ridge-plates and other progressive characters.

Third Superior Molar, M^3	Minimum	Maximum
Length	201	254
Breadth	88	109
Breadth-length index	38	47
Height	66e	102
Ridge-plates	9+	12
Second Superior Molar, M^2		
(Only specimen available in Amer. Mus. Coll., No.19821)		
Length	217	
Breadth	94	
Breadth-length index	43	
Height	66e	
Ridge-plates	10	

First Superior Molar, M^1	Minimum	Maximum
Length	138	172
Breadth	76	90
Breadth-length index	44	58
Height	65	107
Ridge-plates	7	9
Third Inferior Molar, M_3		
Length	190+	313
Breadth	78	105
Breadth-length index	32	55
Height	45	135
Ridge-plates	9+	12
Second Inferior Molar, M_2		
Length	140+	167+
Breadth	87	90+
Breadth-length index	52	64
Height	72	99
Ridge-plates	8+	8+
First Inferior Molar M_1		
Length	127	190+
Breadth	85	78
Breadth-length index	67	41
Height	. . .	91+
Ridge-plates	½–6–½	+7½

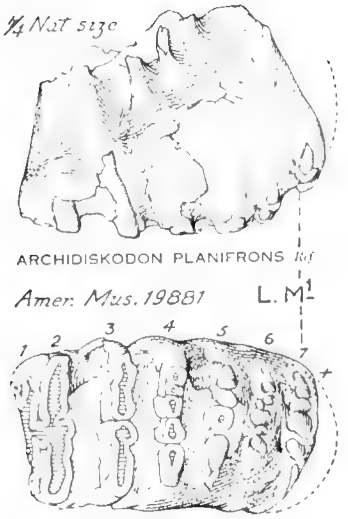


Fig. 831

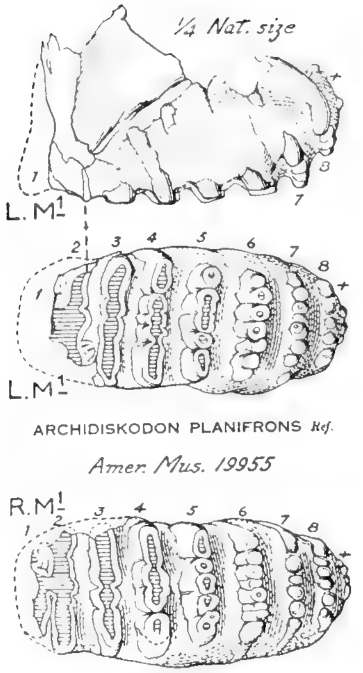


Fig. 832

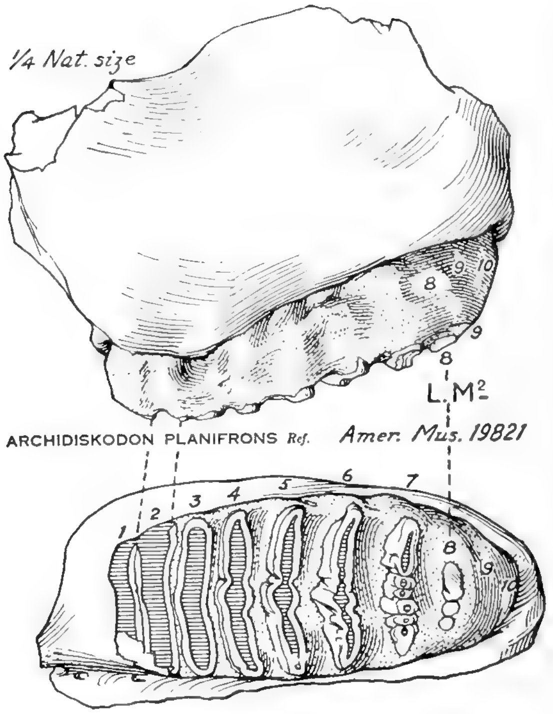


Fig. 833

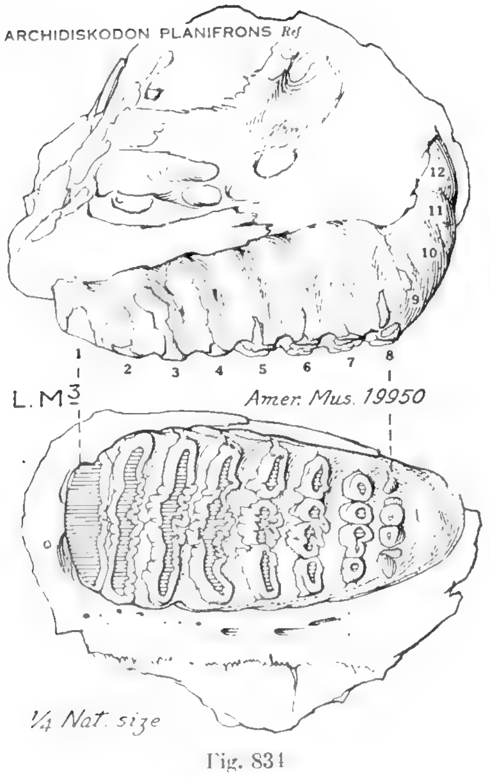


Fig. 834

American Museum Collection
Upper Pliocene Archidiskodon planifrons of the Pinjor Horizon

(see Fig. 826)

Figs. 831–835. *Archidiskodon planifrons*, referred superior and inferior grinding teeth of the Barnum Brown Siwalik Collection, listed with measurements in Table VII. All figures drawn to the same one-fourth scale. Cement (dotted), dentine (horizontal lining). Compare Falconer's measurements in Table VI.

Figures: (831) First left superior molar, l.M^1. (832) First left and right superior molars, l.M^1, r.M^1.

(833) Second left superior molar, l.M^2; a primitive stage as shown in midsection (Fig. 855); this M^2 agrees closely with that of Piltdown, Sussex (Fig. 853). (834) Third left superior molar, l.M^3, 12 plated.

(835) Third left inferior molar, l.M$_3$.

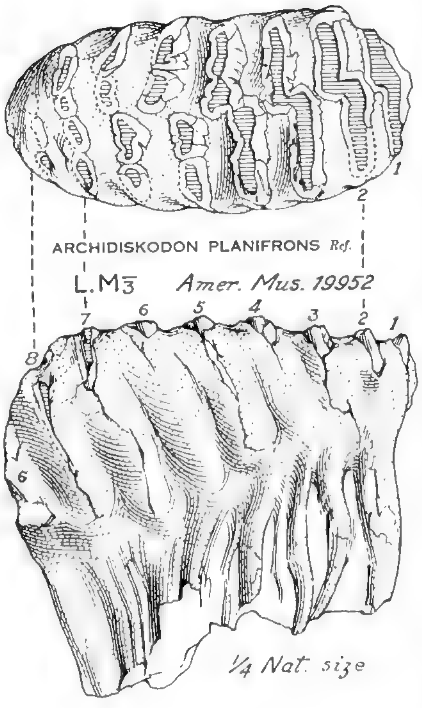


Fig. 835

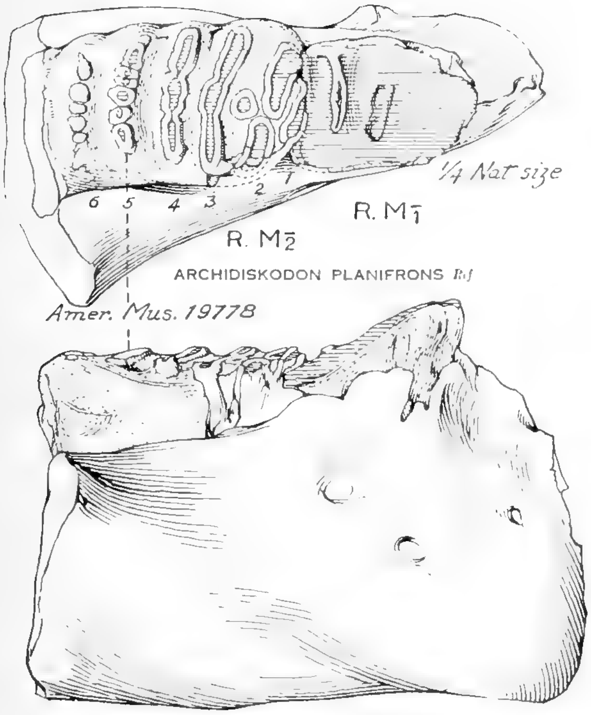


Fig. 836

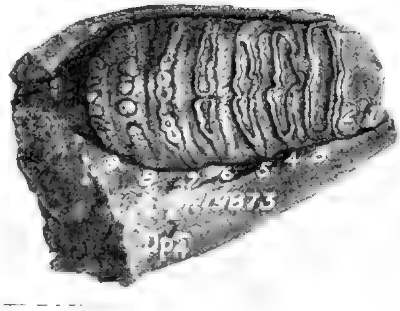


Fig. 837

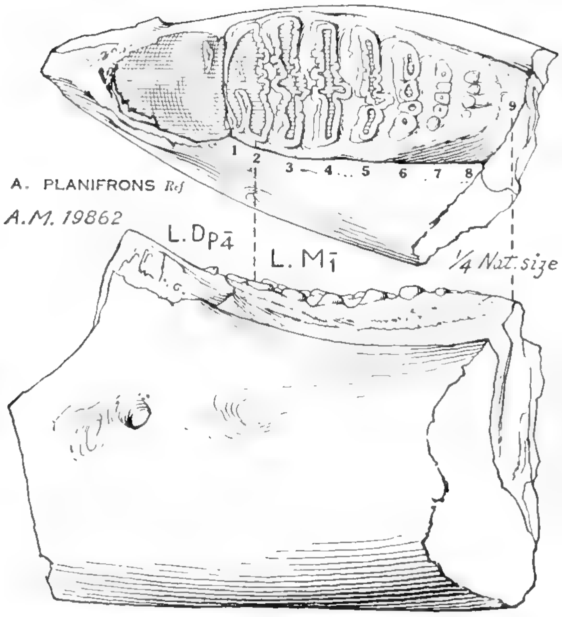


Fig. 838

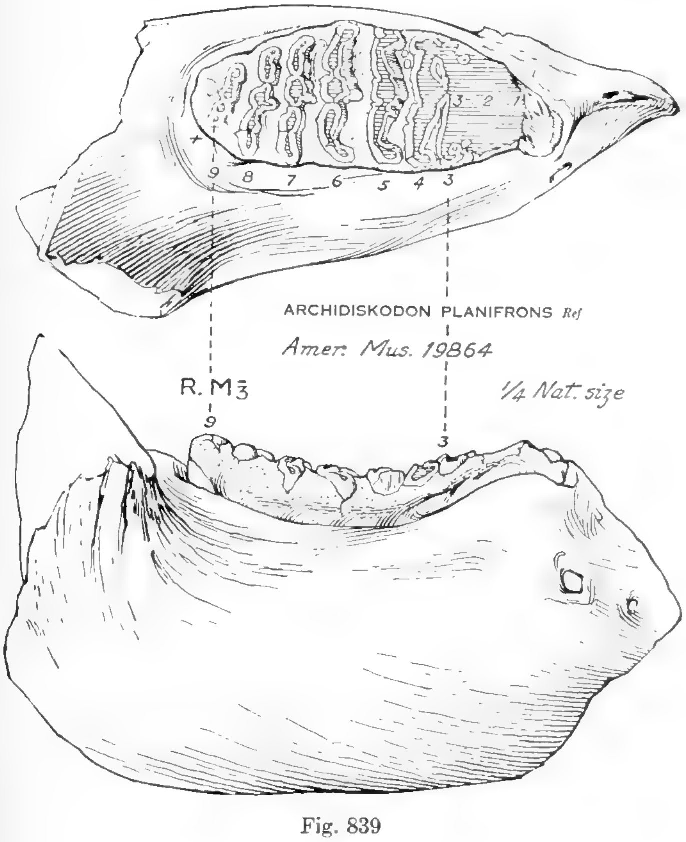


Fig. 839

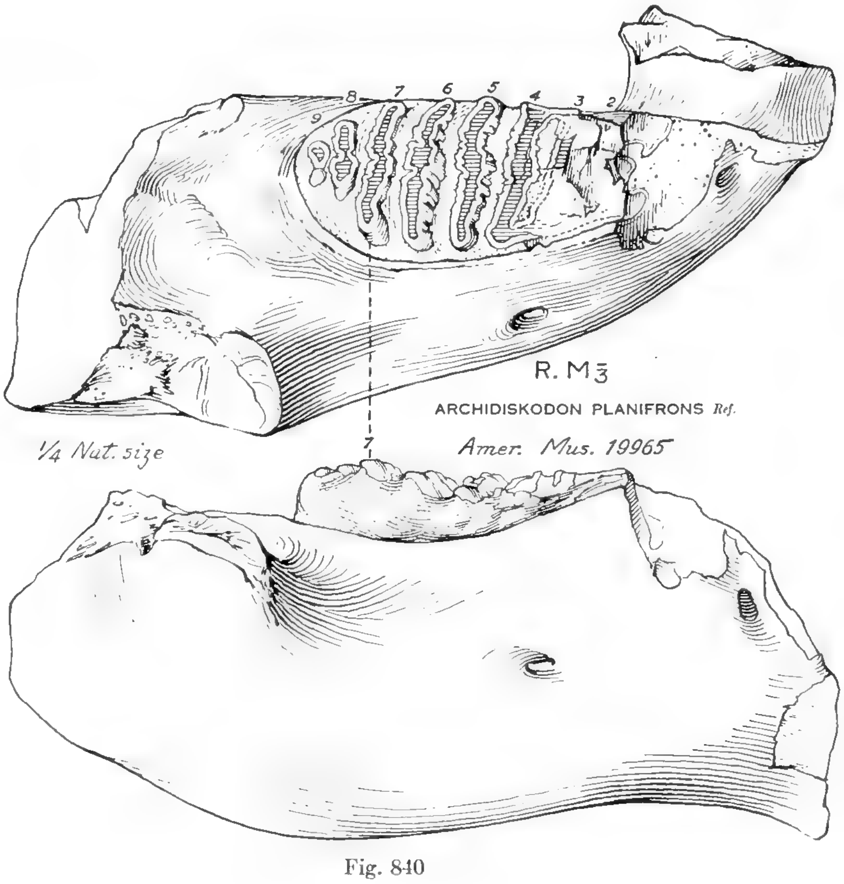


Fig. 840

AMERICAN MUSEUM. UPPER PLIOCENE ARCHIDISKODON PLANIFRONS OF THE PINJOR HORIZON (SEE FIG. 826)

Figs. 836–840. Inferior grinders of *Archidiskodon planifrons* (Figs. 836–840), in the Barnum Brown Siwalik Collection, fully listed with measurements in Table VII. All figures one-fourth natural size, excepting 837 which is one-third natural size. Cement (dotted), dentine (horizontal lining). Compare Falconer's measurements, Table VI.

Figures: (836) Portion of first and second right molars, r.M$_1$, r.M$_2$. (837) Fourth deciduous premolar, Dp$_4$, with 9 ridge-plates. (838) Worn crown of left fourth premolar, l.Dp$_4$, and first molar, l.M$_1$. (839) Portion of lower jaw with third right molar, r.M$_3$. (840) Portion of lower jaw with third right molar, r.M$_3$.

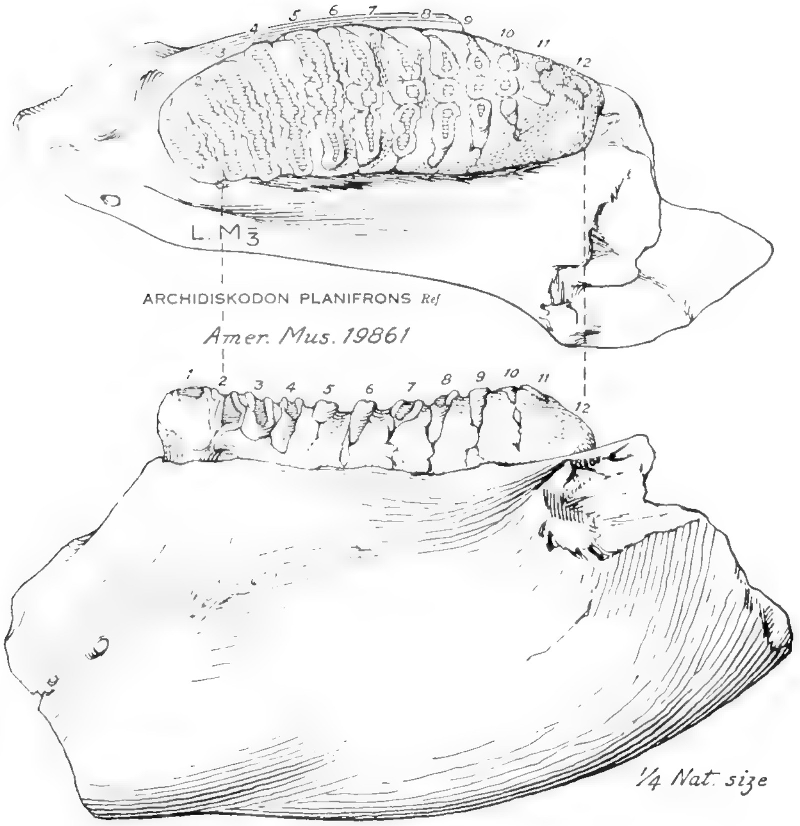


Fig. 841

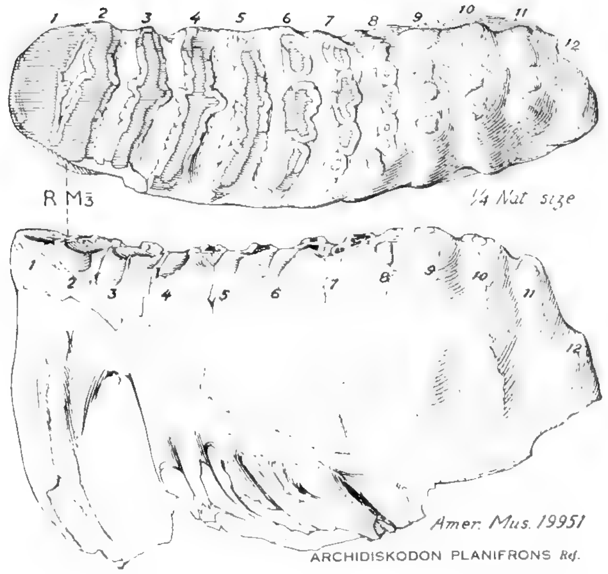


Fig. 842

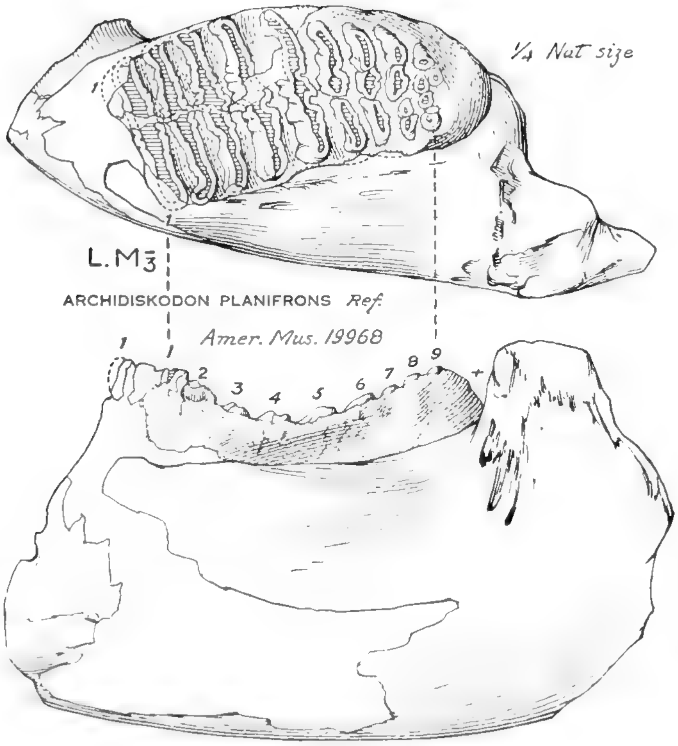


Fig. 843

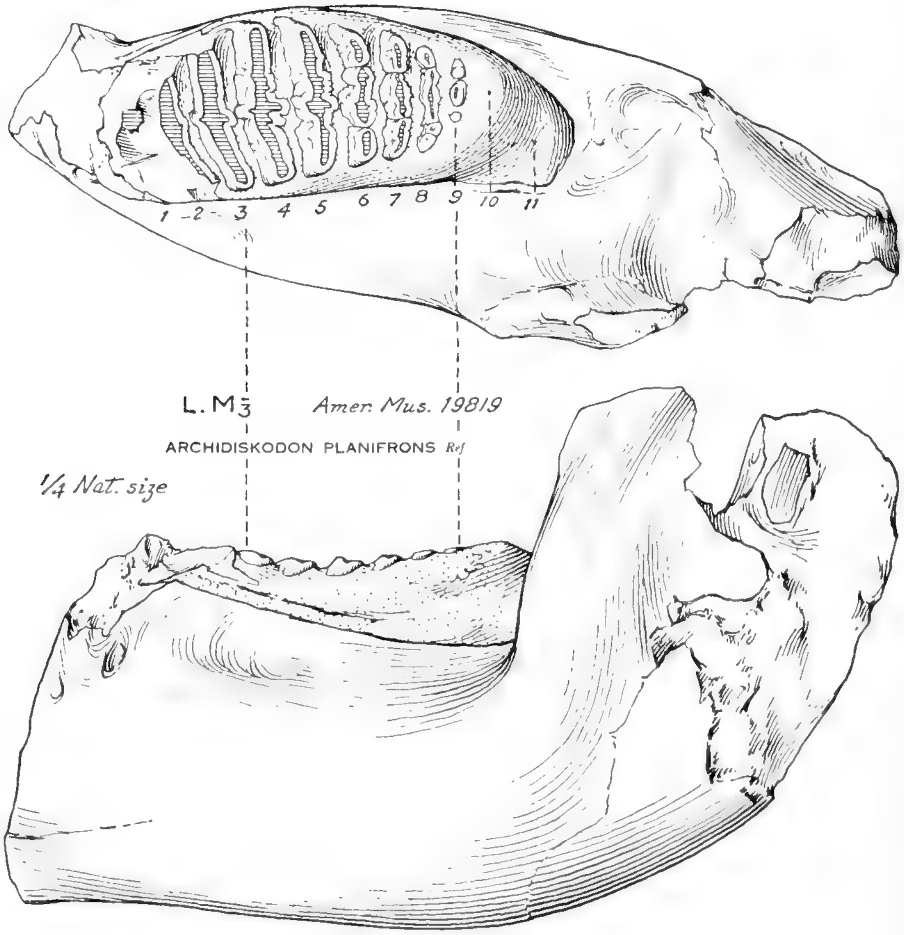
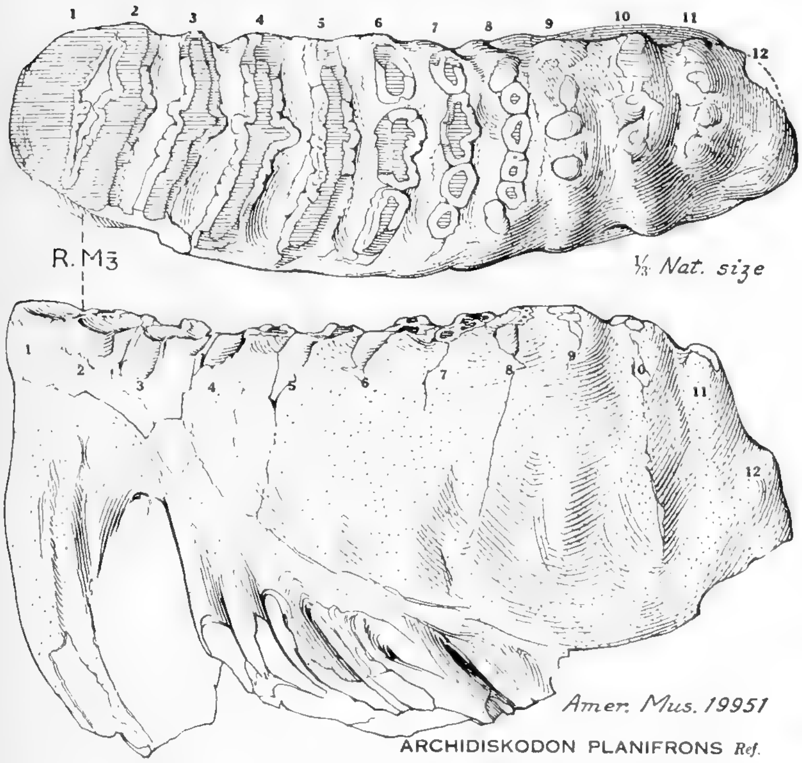


Fig. 844

American Museum Archidiskodon planifrons of the Pinjor Horizon (see Fig. 826). Inferior Molars

Figs. 841–844. *Archidiskodon planifrons* referred inferior grinding teeth and jaws in the Siwalik Collection of the American Museum made by Barnum Brown, as fully listed with measurements in Table VII. All figures one-fourth natural size. Cement (dotted), dentine (horizontal lining). Compare Falconer's measurements, Table VI.

Figures: (841) 12 plated left third molar, l.M$_3$. (842) 12 plated right third molar, r.M$_3$, of a slightly older individual; a progressive stage as shown in midsection (Fig. 855B). (843) 9+ plated left third molar, l.M$_3$, imperfect anteriorly. (844) 11 plated left third molar, l.M$_3$.



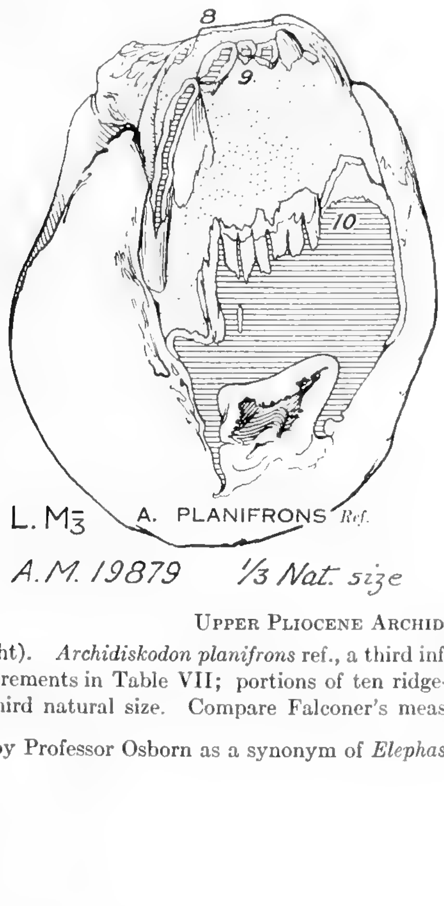
Upper Pliocene Archidiskodon planifrons of the Pinjor Horizon (see Figs. 826, 820)

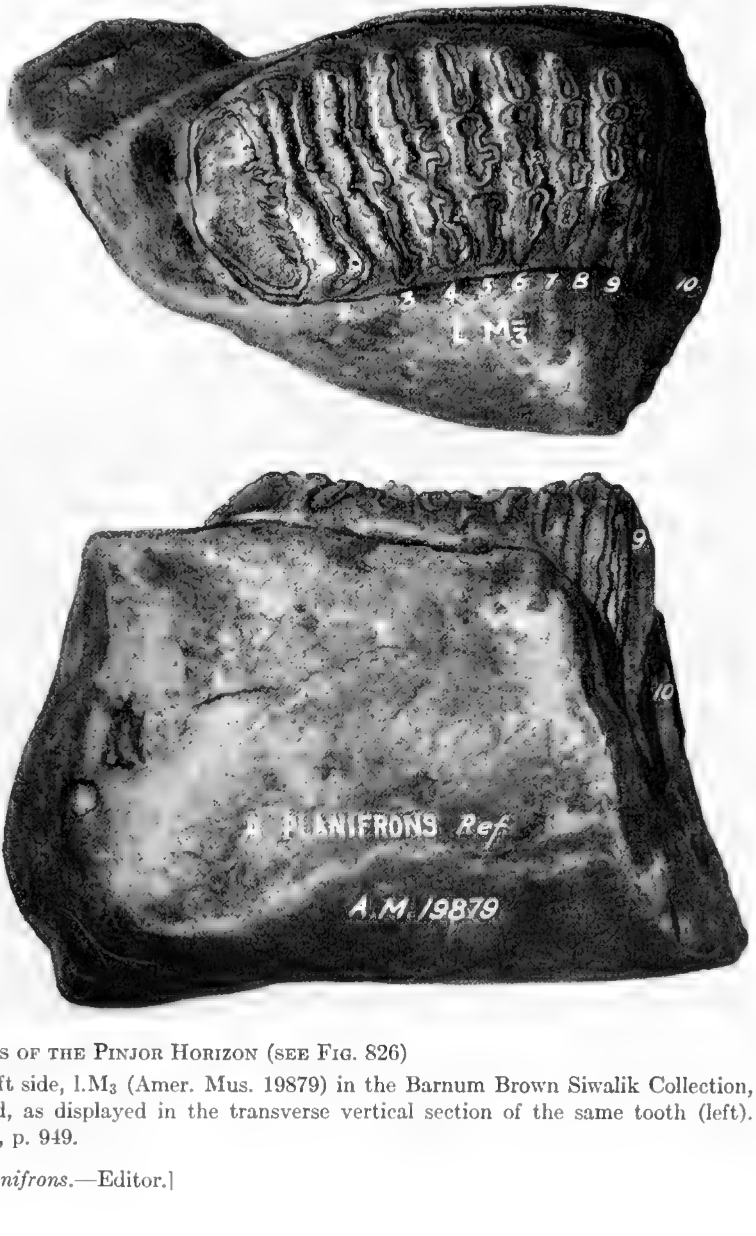
Fig. 845. *Archidiskodon planifrons* ref., third right inferior molar, r.M_3 (Amer. Mus. 19951), in the Barnum Brown Siwalik Collection, one-third natural size. Compared with the collective figures above, this specimen is very close to the typical ridge formula of *Archidiskodon planifrons*, namely, $M\ 3_{\overline{11\frac{1}{2}}}$ ridge-plates. Length 313 mm., width 101 mm., height of seventh ridge-plate 124 mm. (see Table VII, p. 954).

LEITH-ADAMSIA SIWALIKIENSIS

Figure 847

Leith-Adamsia siwalikiensis[1] Matsumoto, 1927.—"On Leith-Adamsia siwalikiensis, a New Generic and Specific Name of Archetypal Elephants." Japanese Journ. Geol. and Geog., V, No. 4, Art. 12, 1 page. Type.—Two superior molars, both of the right side, r.M^3, in the collections of the British Museum (Brit. Mus. M.3070 and 36695). From India. Type Figure.—Falconer, "Fauna Antiqua Sivalensis," Pls. xi, fig. 4, and xiv, fig. 8. Type Description.—(Matsumoto, 1927.2): "In the course of a study of fossil Elephants, the writer has come to be faced with the serious need for a proper name for a certain type of archetypal Elephants of India. He means the small and narrow-molared form recorded under the name of *Elephas planifrons*. This form appears, in all likelihood, to stand at the starting point of the entire phylum of the Loxodontine Elephants. As it would appear to occupy too important a position among the Elephantidæ to be left unnamed, the writer proposes here to call





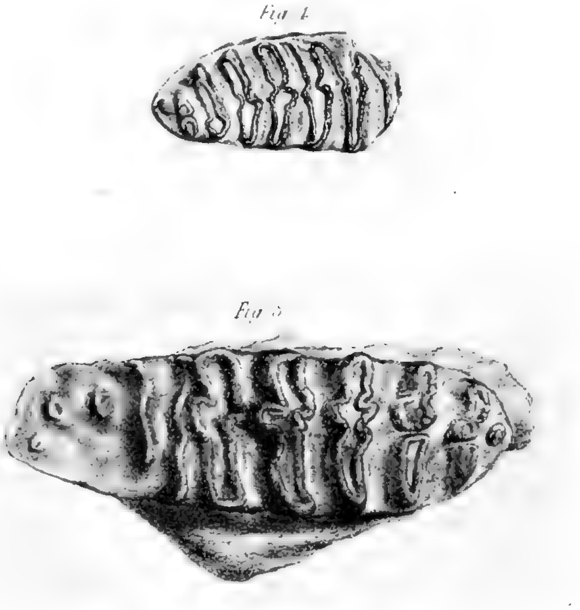
Upper Pliocene Archidiskodon planifrons of the Pinjor Horizon (see Fig. 826)

Fig. 846 (right). *Archidiskodon planifrons* ref., a third inferior molar of the left side, l.M_3 (Amer. Mus. 19879) in the Barnum Brown Siwalik Collection, listed with measurements in Table VII; portions of ten ridge-plates are preserved, as displayed in the transverse vertical section of the same tooth (left). All figures one-third natural size. Compare Falconer's measurements Table VI, p. 949.

[1] [Regarded by Professor Osborn as a synonym of *Elephas* [*Archidiskodon*] *planifrons*.—Editor.]

it by a generic name as follows, in honour of the late Professor Doctor Leith Adams, the eminent palæontologist and specialist on fossil Elephants."

"*Leith-Adamsia*, gen. nov. A genus of archetypal Elephants. Cheek-teeth subhypsodont, narrow-crowned, with a low ridge-formula; loxodont sinus present, and of an obtuse type; disks of well-worn ridges may be more or less lozenge-shaped."



Referred Archidiskodon planifrons

Fig. 847. Type molars of *Leith-Adamsia siwalikiensis* Matsumoto, 1927. After Falconer and Cautley, 1846 [1847, Pl. XI, fig. 4, and Pl. XIV, fig. 8], one-third natural size, reduced to one-fourth natural size.

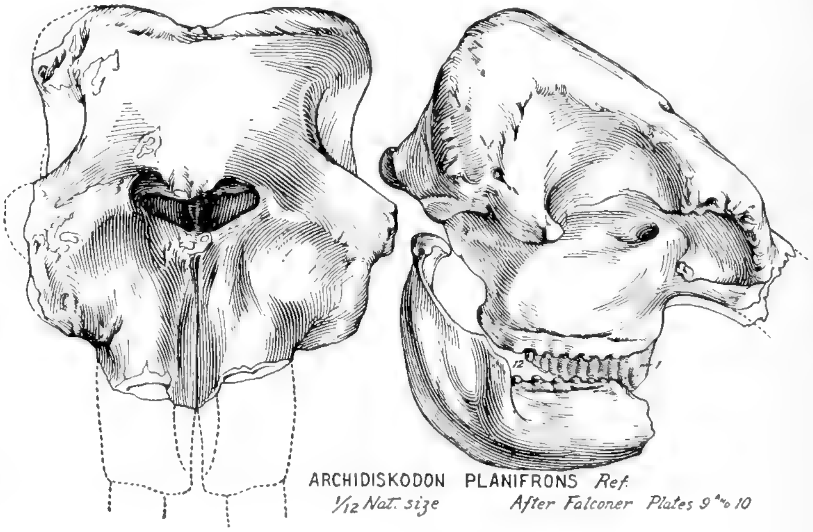
(Pl. XI, fig. 4) Brit. Mus. M.3070. An r.M^3, posterior half of crown, exhibiting 6¼ ridge-plates (same molar as in Fig. 829, above).

(Pl. XIV, fig. 8) Brit. Mus. 36695. An r.M^3, with 6¼ posterior ridge-plates preserved of a probable total of 10 ridge-plates.

CRANIAL CHARACTERS OF ARCHIDISKODON PLANIFRONS

The single cranium known in the British Museum collection (Brit. Mus. M.3060—see Figs. 830, 848, and 817) is extremely primitive, somewhat resembling that of certain species of *Stegodon*, for example, *Stegodon pinjorensis* type (Amer. Mus. 19772—see Figs. 711, 765, and 817C), except that *Archidiskodon planifrons* is much less elevated (acrocephalic) than *S. pinjorensis*, as clearly shown in the comparative profiles (Fig. 817). This is in adaptation to the relatively abbreviate 10+ ridge-plated crown of M^3 in *A. planifrons*, as compared with the extremely elongate 15 ridge-plated crown of M^3 in *S. pinjorensis*. Also compare the flattened forehead of *A. planifrons* with the abbreviated and extremely elevated forehead of *S. pinjorensis*.

This flat-faced condition, to which Falconer assigned the specific name *planifrons*, develops into the concave-forehead profile of *A. meridionalis* (Fig. 817). Meanwhile the cranium heightens (hypsicephaly) and deepens (bathycephaly), in adaptation to the enlarging and deepening of the third superior molars, also, as fully explained in Chapter XV, p. 915, on the mechanics of the proboscidean cranium, the heightening of the occipital crest (acrocephaly) is in adaptation to the elongating tusks and the strengthening of the cervical ligaments and muscles which sway the great tusks and proboscis. Nothing is known of the limb skeleton of *A. planifrons*, but it is inferred that the animal was greatly inferior in shoulder height, in length, and in proboscis development to its giant successors *A. meridionalis* and *A. imperator*. The completely preserved tusks in members of this species discovered in southern France (Fig. 850) lack the strong outward curvature and incurvature characteristic of *A. meridionalis* (*lyrodon*), see figure 864, reaching a supreme stage in *A. imperator*.



Supposed Female Cranium

Fig. 848. Cranium of *Archidiskodon planifrons* in the British Museum (Brit. Mus. M.3060) redrawn after Falconer and Cautley, 1846 [1845, Pl. IX, front view of skull, Pl. X, side view of skull]. Five views of this unique cranium are shown in Falconer and Cautley's plates IX and X; a brief description in the "Palæontological Memoirs" of 1868, Vol. I, p. 430, is as follows:

> "Plate IX. *Elephas planifrons* (Falc. and Caut.), from the Sewalik Hills. Front view of skull, one-third of natural size. The forehead of this species is very flat; the naso-maxillary opening very small, and the occipital fissure very low. . . . Plate X. . . . The last true molar is seen in germ and intact on the right side, and well worn on the other, so that the corresponding tooth on the right side of the lower jaw had probably been wanting. It has eleven ridges and a heel. The pterygoids are very low."

The principal measurements given by Falconer (cf. *op. cit.*, 1868, p. 430) are the following:

Extreme length from occiput to incisive alveoli	25 in.	=635 mm.
Extreme width of occiput	21.7	=551
Height of occiput	13.7	=348
Occiput to anterior border of orbits	20.7	=526
Length of right M^3	9.7	=247
Width of crown	3.5	= 89
Height of crown plates	4.0	=102

ARCHIDISKODON PLANIFRONS IN WESTERN EURASIA, AUSTRIA, RUMANIA, AND RUSSIA

The species of southern mammoth known as *Archidiskodon meridionalis* has long been known in western Eurasia. The discovery of the more primitive ancestral *A. planifrons* in Austria, Bessarabia (southern Russia), southern France, and England, is relatively recent, dating from Schlesinger's announcement of the discovery of '*Elephas*' *planifrons* in Lower Austria in 1912.

Austria.—Schlesinger in his "Studien über die Stammesgeschichte der Proboscidier," of 1912, p. 89, announced the evidence of *Elephas planifrons* in Lower Austria: "Um so überraschender war es, als dem niederösterreichischen Landesmuseum in Wien ein Elefantenmahlzahn von ungemein primitivem Charakter zukam. Es war sehr naheliegend, das Stück mit einer der beiden im Jungtertiär Europas nicht seltenen Arten zu identifizieren. Ein nur oberflächlicher Vergleich rückte den Urelefanten (*E. antiquus Falc.*) gänzlich ausser Betracht, eingehende Studien aber sprachen zufolge eben der Merkmale gegen eine Bestimmung als *E. meridionalis Nesti*, welche den Zahn dem *E. planifrons Falc.*, einer typischen Form der indischen Sewalik-Hills [Footnote: 'Ich bemerke, dass dies der von H. Falconer und P. Cautley (Palaeontological Memoirs Vol. I, pag. 31) zum erstenmal gebrauchte richtige Name für die dem Himalaya südlich vorgelagerte Hügelkette ist.'] nahe brachten.

Die Annahme des Vorkommens einer so ausschliesslich sewalischen Art in unserem Gebiete mag vorerst befremdend und gewagt erscheinen. Doch schwinden derartige Zweifel alsbald, wenn wir bedenken, dass sich die Verbreitung der Rüsseltiere, wie die etlicher Säugerstämme, ohne die Annahme ausgedehnter Wanderungen nicht begreifen lässt [Footnote: 'Vgl. Ch. Depéret, Die Umbildung der Tierwelt (deutsch von R. N. Wegner), pag. 260 ff., Stuttgart 1909.']."

This specific determination as well as the geologic age of the specimen very carefully described in great detail by Schlesinger (*op. cit.*, pp. 94–111) were challenged by Soergel in articles entitled "Die Stammesgeschichte der Elephanten," 1915, and "Die Planifrons-Frage," 1921, with the following conclusion, namely, that the teeth from Dobermannsdorf, Krems, and Laaerberg are actually referable to *Elephas meridionalis* and that the geologic age is not Middle Pliocene but of much more recent date. Schlesinger replied in great detail in his "Meine Antwort in der Planifronsfrage" of 1916.

The molar referred to *A. planifrons* from Laaerberg, said to be a third inferior molar of the left side (see Schlesinger, 1916.2, p. 119, figs. 6, 7) does not in Osborn's opinion sustain the specific reference of this specimen to "*Elephas* (*Archidiscodon*) *planifrons*"; it is too high and narrow, the ridge formula (10½–11), length (280 mm.), width (87 mm.), index (31), and height of the 4th ridge-plate (106 mm.) seem to rule out this third inferior molar from *A. planifrons* and to relate it to *Palæoloxodon* [*Hesperoloxodon*] *antiquus*.

Bessarabia, Russia.—In the valuable Memoir by Marie Pavlow, "Les Éléphants fossiles de la Russie" (1910), cited by Mayet, she fully discusses in her description of the elephants of Tiraspol (p. 4) the milk and permanent dentition of *Elephas planifrons* and on page 27 she describes "*El.* af. *planifrons* Falc., Pl. I, fig. 23," discovered in ferruginous sands near the village of Farladani (Bessarabia), a locality which had previously yielded remains of *Mastodon* (*Zygolophodon*) *borsoni*, and thus regarded as of Upper Pliocene age. Madam Pavlow concludes (p. 27): "C'est une dent (m^6?) très massive (fig. 23), surtout dans sa partie supérieure. Elle est très jeune, à peine usée, sur une surface de 15 cm., elle n'a que 5 lames aux contours très irréguliers, à l'émail très épais et avec de larges espaces de cément. Les quatre premières lames sont usées, la 5-e très peu; la 6-e presque intacte, ce ne sont que des rondelettes liées entre elles. Par derrière se trouvent encore 9 plaques intactes; elles sont toutes très robustes et mesurent sur le côté 2 cm. entre les enfoncements qui les bornent. Je n'ai pu trouver aucune forme en Europe qui pourrait correspondre avec cette dent par le dessin de l'émail, ainsi que par le nombre des lames, et c'est parmi des figures donnée par Falconer pour l'*El. planifrons* que j'ai trouvé ses semblables. T. XI, f. 57. T. XVIII, f. 12. T. XIV, f. 8, 9 (Fauna Antiq. Sivalensis)."

Summary.—Mayet (1920, p. 310) remarks: "Une révision des Éléphants pliocènes d'Europe devient nécessaire, à la suite de laquelle une partie des molaires regardées comme appartenant à des formes archaïques d'*E. meridionalis* seront vraisemblablement considérées comme provenant de *E. planifrons*. La nécessité de cette révision a eté entrevue par d'éminents paléontologistes. La mise au jour dans les sables de Chagny d'un *E. planifrons* l'impose. Déjà M^{me} Pavlow [Footnote: 'Marie Pavlow, Les Eléphants fossiles de la Russie (Nouveaux Mémoires de la Société impériale des Naturalistes de Moscou, t. 17, p. 2.')] a signalé son existence dans le Pliocène récent de la Bessarabie et le Dr. Schlesinger [Footnote: 'Günther Schlesinger, Studien über die Stammesgeschichte der Proboscidier (Jahrbuch der k. k. Geolog. Reichsanstalt, Vienne, 1912, p. 87).'] dans celui de la Basse-Autriche, à Dobermannsdorf."

ARCHIDISKODON PLANIFRONS IN FRANCE

An indubitable discovery of *Elephas planifrons* Falc.[1] is that recorded by Mayet in his "Découverte d'un squelette d'*Elephas planifrons* Falconer dans les sables de Chagny, à Bellecroix près Chagny (Saône-et-Loire)," 1920, in the Comptes Rendus (Paris), pp. 308–311.

Geologic Age.—(Mayet, 1920, p. 308): "Une faune abondante les date parfaitement: les sables de Chagny se parallélisent avec les sables à Mastodontes de la région du Puy, avec les alluvions de Perrier et probablement avec le Crag de Norwich. Ils sont de l'extrême début du Pliocène supérieur. Les depôts marécageux du cirque de Senèze sont plus récents; les gisements classiques du Val d'Arno supérieur, du bassin de Florence, des niveaux fluviolacustres de l'Astesan, sont du même âge. Cet ensemble diffère de celui des gisements plus récents qui appartiennent au Saint-Prestien: sables à *E. meridionalis* de Saint-Prest, tufs volcaniques de Saint-Martial (Hérault), limons de Durfort, etc. Dans ces graviers de Chagny-Bellecroix, fin mai dernier, a été découvert un squelette incomplete d'éléphant: base du crâne (celui-ci très fragmenté, dépourvu de sa moitié antéro-supérieure) avec deux

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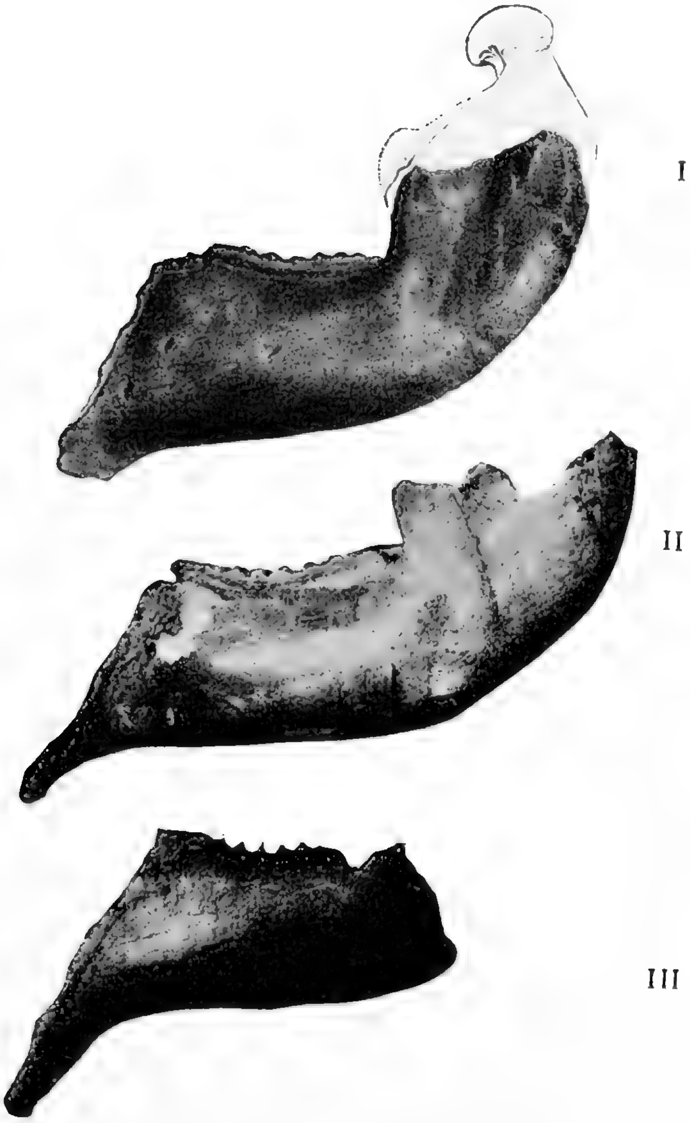
[1] [Professor Osborn regarded this specimen as a Lower Pleistocene form (see Fig. 1239 of present Memoir) and intended to make it the type of a new species of *Archidiskodon*. The description, however, was never written. For restoration, see figure 815.—Editor.]



Primitive Lower Jaws of Archidiskodon

Fig. 849. Superposition of three mandibles of *Elephas planifrons*, India and France, reduced to approximately the same one-tenth scale, after Mayet and Roman, 1923, p. 81, fig. 13. See figure 914 below.

I, *Elephas planifrons* of the Siwaliks. After Falconer.

II, *Elephas planifrons*[1] of Chagny-Bellecroix, France. See also figure 850.

III, *Elephas planifrons* of Senèze, France.

We observe the uniform prolongation and beaklike depression of the symphysis. In describing these jaws Mayet and Roman remark (*op. cit.*, p. 79): "Mandibule (pl. I, fig. 1 et 2). Courte, à branches horizontales basses, épaisses, la mandibule donne l'impression d'être massive en arrière, amincie, effilée dans sa partie antérieure a comme projetée en avant. Cette impression tient à la direction de la symphyse et, pour une grande partie, à l'existence d'un 'bec', d'une sorte d'apophyse mentonnière, qui plonge obliquement. Déjà, en 1825, Nesti disait que l'*E. meridionalis* était un Eléphant à bec et, dans *Fauna antiqua sivalensis*, Falconer insiste sur le bec d'*E. planifrons*. Il faut toutefois remarquer, dès maintenant (voir aussi 2^e partie), que le bec de l'*E. meridionalis* se dirige en avant presque horizontalement et que celui d'*E. planifrons* plonge vers le bas en tendant à se rapprocher de la verticale. Ce caractère est particulièrement net sur une mandibule de Senèze (v. pl. II)."

molaires, M^3; mandibule avec deux molaires en place, M_3, et une apophyse mentonnière bien développée, deux défenses, atlas, omoplate, fémurs, côtes, etc. Ces ossements ne justifieraient qu'imparfaitement la présente Note s'ils ne se rapportaient à une espèce non encore identifiée parmi les éléphants pliocènes de l'Europe occidentale: *Elephas planifrons* Falconer."

In the original and subsequent papers the authors compare this important specimen both with the typical *Elephas planifrons* of the Pinjor horizon and with *Elephas meridionalis*. Mayet and Roman (1923) devote to this subject an exhaustive review in their "Les Éléphants Pliocènes" (Première Partie), in which by far the most profound study is made of the dentition of the Upper Pliocene Proboscidea of France, and Depéret and Mayet (*op. cit.*, Deuxième Partie) of the chief specimens referable to this species from the Siwaliks (pp. 95–97), from Bessarabia (pp. 101, 102), from Austria (the Schlesinger discoveries, pp. 102–104), as well as specimens possibly referable to this species from England (p. 104), from other parts of France, including especially Chagny (pp. 106–110), from Italy (pp. 110–120), and possibly also from Africa (p. 120). From all these materials the following specific characters are deduced.

Charactères Spécifiques de L'Elephas planifrons (Depéret and Mayet, 1923, pp. 121–123).—"[1] Le *crâne* mâle adulte est encore inconnu. Le seul crâne qui ait été découvert est le crâne des Siwaliks figuré par Falconer (pl. IX et X), et reproduit dans tous les ouvrages. C'est un crâne femelle de taille relativement faible, au vertex peu élevé, au front plat et non excavé, peu échancré sur le côté par la fosse temporale; le plan fronto-nasal est oblique en avant, très peu redressé. Ce sont là des caractères qui se retrouvent dans les crânes jeunes et dans les crânes femelles des autres espèces d'éléphants vivants et fossiles. [2] Les *défenses*, bien conservées dans le sujet de Chagny (1re partie, p. 77), sont très rapprochées l'une de l'autre à la base, peu divergentes; elles sont longues (plus de trois mètres), mais surtout très épaisses (grand diamètre, maximum 22 centimètres); leur incurvation est faible vers le haut et un peu en dehors, avec à peine une tendance spiralée. [3] La *mandibule* bien conservée des pièces de Chagny et de Senèze présente un *caractère distinctif important*: la symphyse se prolonge en avant par une sorte de *bec allongé et recourbé en bas*. Ce caractère existe également dans la mandibule des Siwaliks figurée par Falconer (pl. VIII, fig. 2) sous le nom erroné d'*E. hysudricus*. On voit également ce bec un peu brisé au bout dans la mandibule du Serre, près Peccioli (Musée géologique Florence). [4] La *dentition* est complète: 3 molaires de lait et 3 arrière-molaires. On a observé dans les pièces de l'Inde la présence de deux *prémolaires inférieures de seconde dentition* (fig. 15, p. 122), caractère unique dans tout le groupe des Eléphants. Ces prémolaires n'ont pas encore été observées dans les sujets d'Europe et c'est la seule objection qui puisse subsister sur leur assimilation spécifique avec l'espèce des Siwaliks. Nous pensons qu'on observera ces prémolaires lorsqu'on aura des mandibules à l'état d'évolution individuelle convenable. [5] Parmi les *molaires*, les MIII sont les plus caractéristiques: la formule dentaire est de 9 à 10 lames en haut, et de 10 à 11 en bas, chiffres un peu inférieurs à ceux de l'*E. meridionalis*. La *fréquence laminaire* est de 3, 5, à 4 pour 10 centimètres de longueur de couronne, chiffre toujours inférieur à celui de l'*E. meridionalis* (4, 5, à 5). La couronne est notablement plus basse que dans cette dernière espèce; elle est

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[1] [See footnote on previous page.—Editor.]

d'un type remarquablement brachyodonte. Les lames sont larges, l'émail épais et généralement peu festonné, la plicature n'intéressant qu'exceptionnellement la totalité du cordon d'émail. On observe un *sinus loxodonte* inconstant, plus fréquent sur le côté postérieur des lames, mais existant parfois des deux côtés. [6] La taille de l'*E. planifrons* est considérable: la hauteur du sujet de Chagny au garrot devait être d'environ 3 m. 85 mètres: c'est une dimension à peine un peu inférieure à celle d'*E. meridionalis.*"

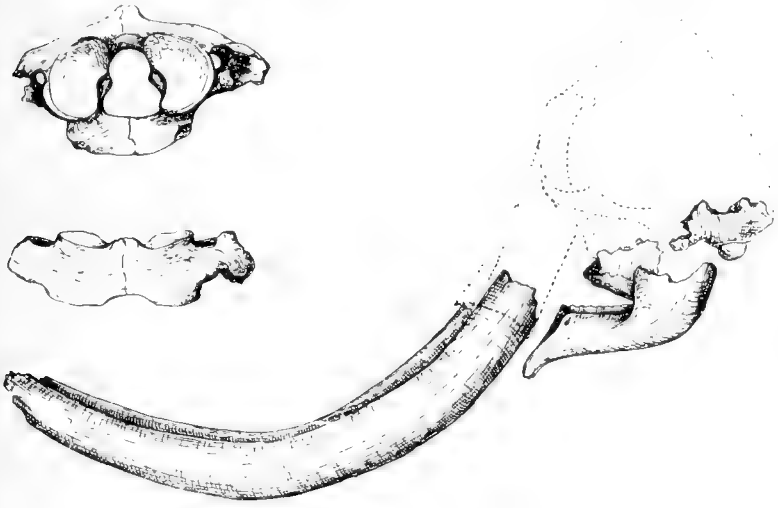

Fig. 12. — *Elephas planifrons* de Bellecroix-Chagny.

Primitive Tusks and Jaws of Archidiskodon of Chagny

Fig. 850. Tusks, maxillæ, condyle, and atlas of *Elephas planifrons* of Chagny. After Mayet and Roman, 1923, p. 77, fig. 12. From the *sables de Chagny* at Bellecroix near Chagny, France. Upper Pliocene. About one-thirtieth natural size. This specimen is carefully described (*op. cit.*, 1923, pp. 75–80). The tusks are massive, nearly straight when viewed from above, with a very feeble torsion from within outwards. The tusks measure: right 2.15 m., left 2.18 m. The third superior molar measures: ap. 264 mm., tr. 117 mm.; length of median lamina 26 mm. The lower molars measure: ap. 305 mm., tr. 108 mm., height 44 mm.; laminar formula 10+; superior molars 9+, inferior molars 10+. For restoration, see figure 815 above.

Description of Chagny Specimen.—An animal from the Upper Pliocene[1] of Chagny, France, is characterized by Mayet (1920, pp. 309, 310) as follows: "Nous pouvons rapprocher notre éléphant de Bellecroix de *Elephas planifrons* du Pliocène moyen et supérieur de l'Inde (Pinjor horizon, Siwalik-Hills): même formule $\frac{x-10-x}{x-10-x}$ même couronne très basse, même caractère de l'émail, même aspect *mastodontoïde* de la mandibule, du menton, des défenses, il y a identité des caractères spécifiques."

"Espèces.	Rapport$\frac{\text{L}}{\text{L}}$.	Fréquence laminaire.	Formule dentaire.
E. planifrons, Chagny	2,28	4	$\frac{x-10-x}{x-10-x}$
E. planifrons, Siwalik-Hills	2 à 2, 5	4	$\frac{x-10-x}{x-10-11-x}$"

The number of plates in 10 cm. ("fréquence laminaire") is *four* as compared with five to six in *E. meridionalis.* The x of Mayet's description refers to the rudimentary plates at the front and back of the crown. It would appear that the ridge formula of *E. planifrons* in comparison with the Chagny specimen may be written:

$$\text{M}\ 2\tfrac{8}{9}\ \ \text{M}\ 3\tfrac{10+}{11+}$$

ARCHIDISKODON MERIDIONALIS [AND ?PLANIFRONS] IN THE PLIOCENE RED CRAG AND NORWICH CRAG OF SUFFOLK AND NORFOLK, ENGLAND

Compare page 972; see figure 871 G, H

The Red Crag is of greater antiquity as a whole than the Norwich Crag (Judd, 1911, p. 185; Osborn, 1922.563, p. 436); in it are recorded both *Archidiskodon* (?)*planifrons* and *A. meridionalis.* The less richly mammaliferous Norwich Crag is partly more recent and yields *A. meridionalis* (Osborn, *op. cit.*, p. 437). Together these horizons represent a very long period of closing Pliocene time, in which *A. planifrons* may have evolved into *A. meridionalis.* Compare similar *ascending mutations* in Europe (Depéret) and in India (Osborn).

Possibly belonging to *Archidiskodon planifrons* are the Red Crag teeth, 'broad plated with very thick enamel,' and the femur, referred to "*E. antiquus*" and "*E. meridionalis*" by Leith Adams (1877–1881, Pl. xxvi, figs. 2, 3, 4).

In the Ipswich Museum (Osborn, 1922.563) is to be found a typical Upper Pliocene collection recorded from the Red Crag horizon; it contains specimens referred to *Castor* (*Trogontherium*), *Orca* (*Trichecodon*) *huxleyi*, *Hyænarctos*, *Felis pardoides*, *Ursus arvernensis*, *Mastodon* [*Anancus*] *arvernensis* (27 specimens), *Mastodon* [*Zygolophodon*] *borsoni* (20 specimens), also two 10–11 ridge-plated molars (?)erroneously referred to *E.* [=*Hesperoloxodon*] *antiquus* and *E.* [=*Archidiskodon*] *meridionalis.* Compare figure 871 G, H, *Archidiskodon* (?)*planifrons.*

In three British collections and in several faunal lists (Osborn, 1922.563, pp. 436, 437) six grinding teeth *referred* to '*Elephas meridionalis*' are attributed to the Red Crag or to the Norwich Crag of East Anglia, an Upper Pliocene stage; it is possible that certain of these grinders are referable rather to the more primitive *Archidiskodon planifrons.* See Falconer's notes (1868, Vol. II, pp. 130–132, and Pl. viii, figs. 1 and 4) on "*Elephas* (*Loxodon*) *meridionalis.*" Falconer repeatedly compares these teeth to those of "*E.* (*Loxodon*) *planifrons*"; see full abstract below (pp. 972–974) of Falconer's notes of 1868.

The finely preserved 10–11 ridge-plated molar in the Ipswich Museum (Fig. 871 G below) from the 'Norfolk Bone Bed,' referred to '*Elephas meridionalis,*' appears to Osborn to resemble *Archidiskodon planifrons*, as indicated in the figure; the approximate measurements are, length 190 mm., breadth 77 mm., index 41; it exhibits ten to eleven ridge-plates only (cf. Amer. Mus. 19864—Fig. 839); it is greatly inferior in breadth to the more recent Forest Bed molar (Fig. 871 F) attributed to *A. meridionalis* (Savin Mus., Cromer, No. 197), to be described below under *Archidiskodon meridionalis cromerensis*, also to the Forest Bed molar (Fig. 871 E). The measurements and other characters of these molars resemble very closely those of the molars described by Depéret and Mayet in their Memoir of 1923 and figured in Pl. ix.

Lydekker (1886.2, p. 113) provisionally refers to *Archidiskodon meridionalis* a mandibular symphysis from the Norwich Crag of Thorpe (Brit. Mus. M.2009); four ridges of a true molar, transversely cut and polished, from the Red Crag of Felixstowe, Suffolk (Brit. Mus. 44895); also fragment of a molar, vertically and longitudinally cut and polished, from the Red Crag of Fakenham,

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[1] [See footnote on page 961 above.—Editor.]

Suffolk (Brit. Mus. 44140). These specimens are probably attributable to *A. planifrons.*

Osborn, 1929: Certain of the 'Norfolk Bone Bed' or Red Crag molars agree precisely in measurement (length, breadth, index) and in the number of ridge-plates with certain of the *Archidiskodon planifrons* molars of the American Museum collection made by Barnum Brown, e.g., figure 839, found three miles northeast of Mirzapur, Pinjor horizon, India, indicating a common eastward to westward range of *A. planifrons* from the Siwalik Hills to East Anglia in Upper Pliocene time.

GEOGRAPHIC DISTRIBUTION OF ARCHIDISKODON PLANIFRONS (COMPARE SCHLESINGER, 1911, 1912, 1913, DEPERET AND MAYET, 1923, SABBA STEFANESCU, 1927, HOPWOOD, 1935)

The migration area of *Archidiskodon planifrons* extends from India to western Europe, passing through southern Russia (the Caucasus, Crimea, Bessarabia) the basin of the Danube, near Vienna, Italy (Astésan, the superior and inferior Val d'Arno), France (Chagny, Senèze, le Puy, Randan) to England (Crag of Suffolk and Norfolk, Piltdown gravels of Sussex), finally in northern Africa (Algeria). In many of these localities the geologic and stratigraphic level is difficult to determine precisely. The type horizon of the Pinjor, Siwaliks, is regarded as between Middle and Upper Pliocene.[1] In Russia and Austria the formations containing *A. planifrons* are Pliocene, but it is difficult to exactly determine the level. In France and Italy it is possible to determine with great precision the horizon of Puy, of Senèze, and of Chagny, which are the exact equivalents of the classic horizon of Perrier (Auvergne) and constitute the most ancient phase of recent Pliocene time (Calabrian = Villafranchian) at the limit of the 'Pliocène ancien' (Astian). We may therefore consider that *A. planifrons* characterizes the horizon bounded by the 'Pliocène ancien' and the 'Pliocène récent,' a horizon somewhat in advance of that which contains *A. meridionalis, a species to which A. planifrons is related by a continual series of intermediate mutations.*

[A third superior molar found in the Lower Pleistocene of Shansi, China, has been compared by Dr. A. Tindell Hopwood (1935.1, p. 88, Pl. VIII) to *Archidiskodon planifrons.*—Editor.]

Ascending Mutations of A. planifrons in India and in Western Eurasia (Osborn, 1928).—The above conclusion of Depéret and Mayet that *Archidiskodon planifrons* passes by a continuous series of *ascending mutations* into *A. meridionalis* agrees entirely with that independently reached above by Osborn in the measurement and analysis (Tables VI and VII) of the sixty-six specimens in the Falconer and Cautley and Barnum Brown collections of the Pinjor horizon, Upper Siwaliks, India. The *A. planifrons* ridge formulæ of the specimens of Chagny, France, agree closely with the typical *A. planifrons* ridge formulæ of the specimens from the Pinjor horizon, India. This was undoubtedly a case of independent contemporaneous progression in India and in France.

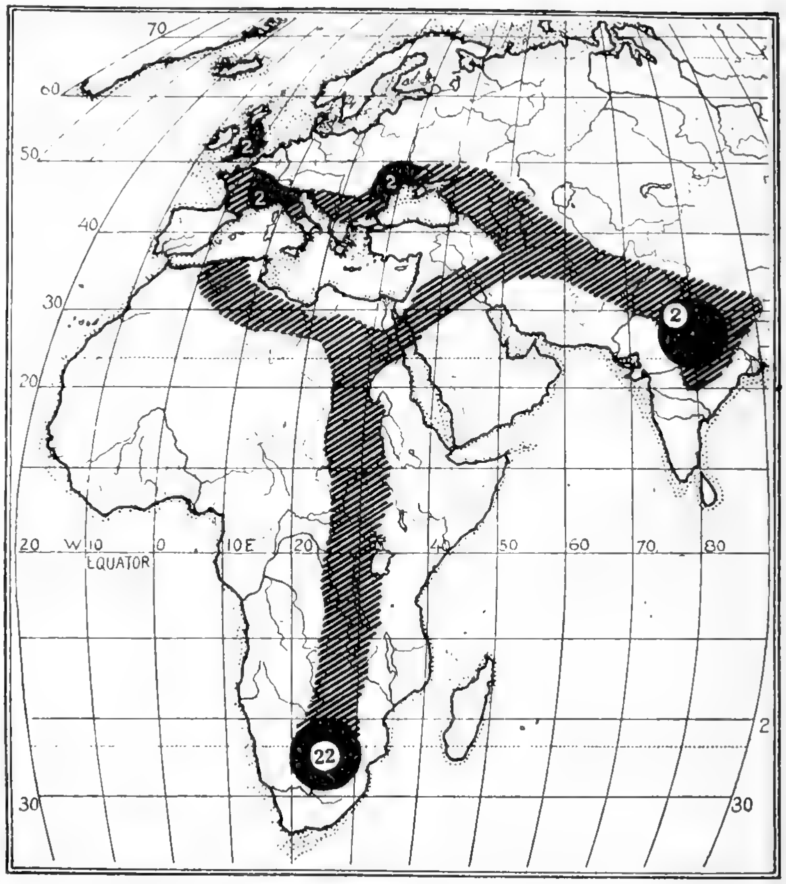

Fig. 851. Type localities of *Archidiskodon proplanifrons* (22) and of *A. planifrons* (2) in circles. In solid black (2), Upper Pliocene[1] localities of *A. planifrons* referred specimens. In oblique lines, theoretic range from the supposed African center (22) northward to France and Britain, eastward to India. Compare Depéret and Mayet (1923) who give the route of migration in the opposite direction.

ARCHIDISKODON PLANIFRONS OF THE PILTDOWN GRAVELS

(Figs. 852 and 853)

The teeth figured (Fig. 852) and determined by Smith Woodward as *"Stegodon,"* as pointed out by Freudenberg (1915) and Matsumoto (1918), probably belong to *Elephas* [= *Archidiskodon*] *planifrons.* These and other fossil mammal remains in the Piltdown gravels may be divided geologically as follows:

Pleistocene(?)	*Cervus elaphus* ref.
	Castor (?) fiber ref.
	Hippopotamus amphibius (?) ref.
Pliocene(?)	*Eoanthropus dawsoni* type.
	Archidiskodon planifrons ref., "*Stegodon* sp." of Smith Woodward.
	Anancus arvernensis ref., "*Mastodon*" of Smith Woodward.
	Equus stenonis (?) ref.
	Rhinoceros etruscus ref.

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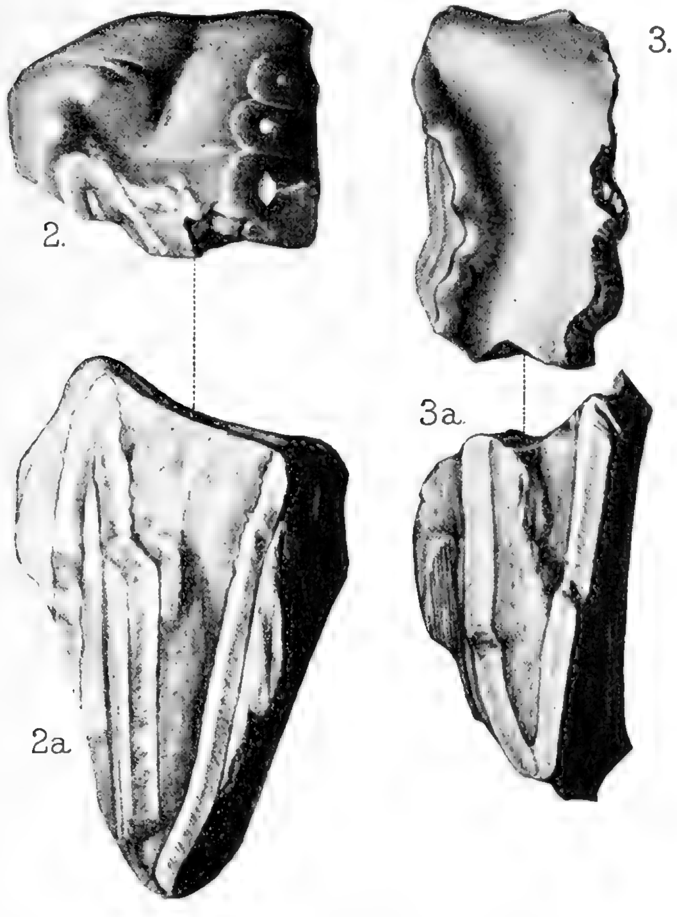
[1] [Upper Pliocene to Lower Pleistocene (see Vol. I, fig. 413). See also footnote on p. 950 above.—Editor.]

Authorities differ as to whether the Piltdown gravels, containing *Eoanthropus dawsoni*, are of Upper Pliocene or of Pleistocene age, as shown in the following citations from Smith Woodward and Freudenberg:

SMITH WOODWARD (1913, P. 123).—"It is clear that this stratified gravel at Piltdown is of Pleistocene age, but that it contains, in its lowest stratum, animal remains derived from some destroyed Pliocene deposit probably situated not far away, and consisting of worn and broken fragments. These were mixed with fragments of early Pleistocene mammalia in a better state of preservation, and both forms were associated with the human skull and mandible, which show no more wear and tear than they might have received *in situ*."



ARCHIDISKODON PLANIFRONS OF PILTDOWN (SUSSEX)

Fig. 852. Fragments of a molar tooth probably referable to *Archidiskodon planifrons*. After Smith Woodward, 1913, Pl. XXI, figs. 2, 2a and 3, 3a, natural size. Found with the remains of *Eoanthropus dawsoni* in the Piltdown gravels, Piltdown Common, Fletching (Sussex), England.

Vertical section of supposed portion of molar representing the valleys between the superior (2, 2a) sixth and seventh or seventh and eight ridge-plates and inferior (3, 3a) third and fourth ridge-plates (see Figs. 853 to 855 C).

FREUDENBERG (1915, P. 420).—"An der Basis fanden sich Schädel und Unterkiefer von *Eoanthropus Dawsoni* in unzusammenhängenden Fragmenten. Im selben Lager zwei Zahnfragmente eines etwas gerollten Molaren von *Elephas* cf. *planifrons* (wohl nicht *Stegodon*!), wie solche schon früher aus Red Crag von Leith Adams in A monograph on the British fossil Elephants, Pl. 26, Fig. 3 und 4, kürzlich aus dem Belvedereschotter von Wien durch Schlesinger abgebildet wurden. Ferner fanden sich mehrere Zähne von *Castor fiber*, der nach Newton (The Vertebrata of the Pliocene deposits of Britain, Pl. v fig. 16) gleichfalls im Red Crag vorkommt. Ferner ein Fragment von *Mastodon arvernensis?*, von *Hippopotamus major* und von *Rhinoceros etruscus?*"

HISTORY.—(1) Freudenberg (1915, p. 420) pointed out that the molar crest fragments (Fig. 852) found in the Piltdown gravels with the type of *Eoanthropus dawsoni* resemble *Archidiskodon planifrons* rather than the "*Stegodon* sp." to which Smith Woodward referred them (Woodward, 1913, pp. 139, 142, 144, Pl. XXI, figs. 2, 2*a*, 3, 3*a*). (2) Matsumoto observed (1918, p. 55): "But, judging from his [Woodward's] figures, the real reference of his '*Stegodon* sp.' appears to the present writer, as well as to Freudenberg [Footnote: 'Neu. Jahrb. f. Min. Geol. u. Pal., Bd. I., Heft 3, 1915:—Freudenberg, referating Woodward's papers on *Eoanthropus dawsoni*, has pointed out that, Woodward's '*Stegodon* sp.' is not referred to genuine *Stegodon* but to *Elephas* cf. *planifrons*.'], to be otherwise than that stated by Woodward. Woodward's material consists of several fragments of molars, of which the ridges appear to be too high and too narrow and the valleys too deep and too narrow to be referred to the Stegodonts. Woodward has compared it with molars of *E. meridionalis* but not of *E. planifrons*. The present writer suspects that, if one compare Woodward's material with molars of *E. planifrons* and of the Stegodonts, one may easily recognise its closer resemblance to the former rather than to the latter." (3) As remarked by Matsumoto (*op. cit.*, 1918, p. 56): "As to Woodward, his *Mastodon* sp. and '*Stegodon* sp.,' of which association with these human remains may perhaps be secondary, have very probably been due to earlier—Tertiary—strata; and the former species is probably to be referred to *M. arvernensis*. Now, the age of European *E.* cf. *planifrons* is included in that of *M. arvernensis*; so that it is highly possible, that these two species are found from one and the same deposit either primary or secondary." (4) This determination by Freudenberg and Matsumoto is in accord with the discovery of Reid Moir that the flint implements found in the Upper Pliocene Red Crag of Foxhall are similar to those found in the Piltdown gravels.

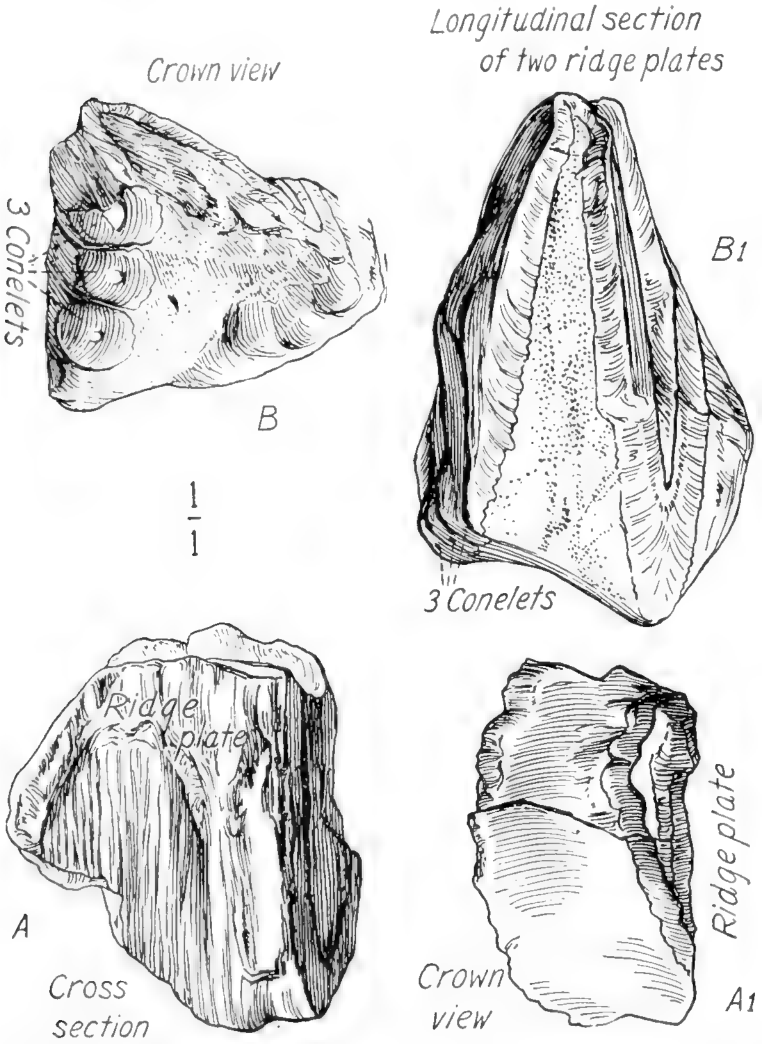
CONCLUSIONS AS TO GEOLOGIC AGE (OSBORN, JUNE, 1928).—Smith Woodward and other high English authorities (1913) regarded the two probable Pliocene species, *Archidiskodon planifrons* ref. and *Anancus arvernensis* ref., as washed in from an older Pliocene deposit; whereas the Piltdown skull, *Eoanthropus dawsoni*, was regarded as of the same geologic age as the Piltdown gravels, an age which has not yet been positively determined, and which may also include *Castor fiber* ref., *Hippopotamus amphibius* ref., and *Cervus elaphus* ref., properly belonging in the Pleistocene. Osborn observes:

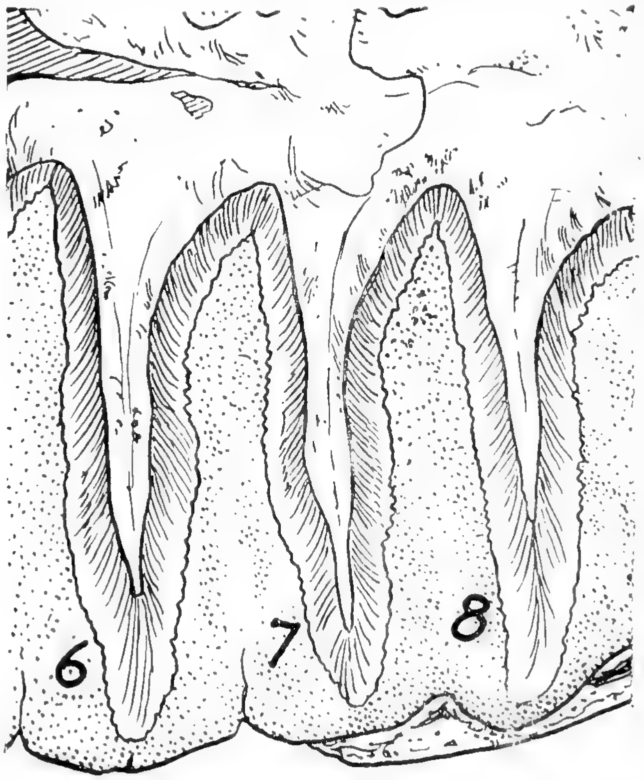
(1) The dark-colored skull fragments of *Eoanthropus dawsoni* are of Pliocene age, if washed in from the same geologic stratum as *Archidiskodon planifrons* and *A. arvernensis*. (2) On the other hand, these skull fragments are of Pleistocene age, if washed in from the same stratum as *Hippopotamus amphibius* and other Pleistocene fossils. On this point Hopwood inclines to Pliocene age; he writes (letter, June 4, 1928):

"Secondly, I am inclined to put the skull with the older fauna, and the Eolithic culture. To put the skull with the older objects presents some difficulties, but I think that there is much to be said in favour of such a step. First, the remains are of the same dark chocolate colour[1] as the other fossils in the same group, whereas the younger fauna is represented by fragments of a light ochraceous colour. This is not very strong evidence I admit, but it would be strange to find one dark specimen where all the others are light. . . . The find of the nasal-bones and turbinals presents the most serious difficulty to be met. They were found lying together in the same spot. My own idea is that the skull had been rolling along the stream entire, and that for some reason or other the facial skeleton became detached. The brain-case was lying apart from the face and the whole lot was smashed [by the workmen] when the gravel was being dug. It is noteworthy that the nasals were found in the disturbed gravel, and this would account for the fact that the maxillæ and other facial bones were missing. I do not pretend that this is the whole story, but it seems to me that these are little circumstantial details which help to strengthen the case for putting the skull with the older set of fossils."

[The foregoing text on *Archidiskodon planifrons* of the Piltdown gravels was written by Professor Osborn in June of 1928.

In the autumn of 1933, at the request of Prof. Dr. Henri Delsol, Secrétaire, Jubilé du Professeur Begouen, Professor Osborn prepared an article for the volume in celebration of the 70th birthday of Comte Henri Begouen entitled "The Geologic Age of the Piltdown (*Eoanthropus*) and of the Trinil (*Pithecanthropus*) Man," (?published)[2] in which he advanced certain evidence in support of the new hypothesis that *Eoanthropus* is of closing





ARCHIDISKODON PLANIFRONS OF PILTOWN, ENGLAND, AND OF THE PINJOR HORIZON, INDIA, EXHIBITING APPROXIMATELY THE SAME ENAMEL RIDGE-PLATE HEIGHT, NAMELY, 71 MM. NATURAL SIZE.

Fig. 853. England. Rolled fragments of *Archidiskodon* molars (Brit. Mus. E595 lower, E622 upper), presumably portions of molar representing the valleys between the superior (B, B1) sixth and seventh or seventh and eighth ridge-plates and inferior (A, A1) third and fourth ridge-plates, from the Piltdown gravels, Sussex. Redrawn natural size by Miss G. M. Woodward, July, 1928. Longitudinal and cross-sections; crown views. Compare figures 852 and 855.

Fig. 854. India. Sixth, seventh, and eighth superior ridge-plates of the Siwalik lectotype of *Elephas* [=*Archidiskodon*] *planifrons* reproduced natural size from drawing by Miss G. M. Woodward (Fig. 855D), for direct comparison with the corresponding ridge-plates (Fig. 853) of *A. planifrons* from the Piltdown gravels.

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[1] [Doctor Hopwood in a later paper ("Fossil Elephants and Man," Proc. Geol. Assoc., XLVI, Pt. 1, 1935, p. 48) makes the following statement: "Concerning the colour, reference should here be made to a recent paper by Sir Arthur Smith Woodward (1933) in which he states that Mr. Dawson soaked the first pieces in a solution of bichromate of potash to harden them! The remaining pieces were not so treated and retain their original colour. This explains the very dark chocolate tone of parts of the brain-case in contrast with the lighter, slightly more greyish colour of the remainder, but it does not affect the statement that the colour of the human remains as a whole agrees with that of the fossils in Group A rather than with those in Group B. The fragments of Piltdown II. confirm this statement."—Editor.]

[2] [See Bibliography under Osborn (1936.951), at close of this Volume.—Editor.]

Tertiary age, while *Pithecanthropus* is of middle Quaternary age—evidence based chiefly on the ridge-plate and ganometric method, which consists of counting the number of ridge-plates and estimating the enamel length of proboscidean molars. While Dr. Eugen Dubois adhered to his original opinion that *Pithecanthropus* is of Upper Pliocene or Lower Pleistocene age, Dr. W. O. Dietrich and Professor Osborn independently reached the conclusion that there is strong evidence for assigning to *Pithecanthropus* a more recent geologic age, namely, Middle Pleistocene, owing partly to the associated remains of *Stegodon airâwana* and *Elephas* [*Palæoloxodon*] *hysudrindicus* in the Trinil beds. As to the Piltdown fossils and flints, Professor Osborn regarded these remaniés, or worked over specimens, as having been washed in from older horizons, belonging in two groups, as clearly shown in the coloring of the very fragmentary fossils.

The following is a citation from Professor Osborn's article (forwarded to Dr. Delsol in October, 1933), which, to the best of our knowledge, gives his final opinion on the subject in question:

"The conclusions which may now be drawn from the ridge plate and ganometric and from other palæontological methods of comparison are as follows:

"*First*, *Pithecanthropus erectus*, by association with *Stegodon airâwana* with a ganometric measure of 482 mm., also with an

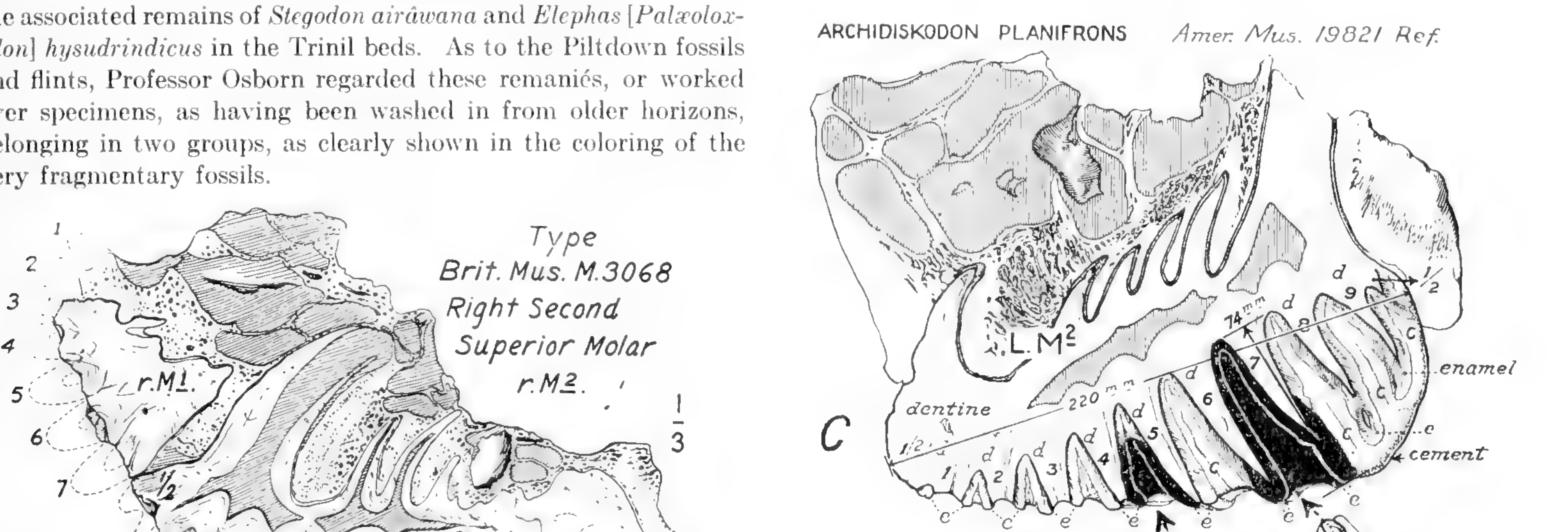

Fig. 855. Comparative sections of the lectotype and referred *Archidiskodon planifrons* molars, with the *A. planifrons* molar fragments of Piltdown (solid black). Reduced to a uniform one-third scale for comparison with Falconer's figure (Fig. 825).

A, Referred eleven ridge-plated r.M_3 (Amer. Mus. 19798), 203 mm. in length, maximum 10th ridge-plate height 61 mm., a small and very primitive molar.

B, Referred third right inferior molar, r.M_3 (Amer. Mus. 19951), 313 mm. in length, maximum 9th ridge-plate height 113 mm., consequently a large and progressive lower molar stage. Exterior of the same tooth (Fig. 845).

C, Second left superior molar, l.M^2 (Amer. Mus. 19821), 220 mm. in length, maximum 7th ridge-plate height 74 mm., somewhat exceeding the 71 mm. ridge-plate height in the Piltdown specimen.

D, Falconer's type of *Elephas* [*Archidiskodon*] *planifrons* (Brit. Mus. M.3068), an r.M^2, 221 mm. in length, maximum 7th ridge-plate height 71 mm. Redrawn by Miss G. M. Woodward for this Memoir (cf. Figs. 828 and 825).

Elephas hysudrindicus grinder of an estimated measure of 5459 mm., proves to be of Middle Pleistocene age."

"*Second,* by association with *Archidiskodon planifrons* with eleven ridge plates and an enamel length of 1113 mm., *Eoanthropus dawsoni* of the Piltdown gravels may prove to be of Upper Pliocene age."

"*Third,* thus, by the application of this ridge plate and ganometric method these two famous fossil men change places, as follows:

"*The supposed oldest fossil man, Pithecanthropus, is dethroned and becomes a survival; Eoanthropus is enthroned as the oldest fossil man known up to the present time.*"—Editor.]

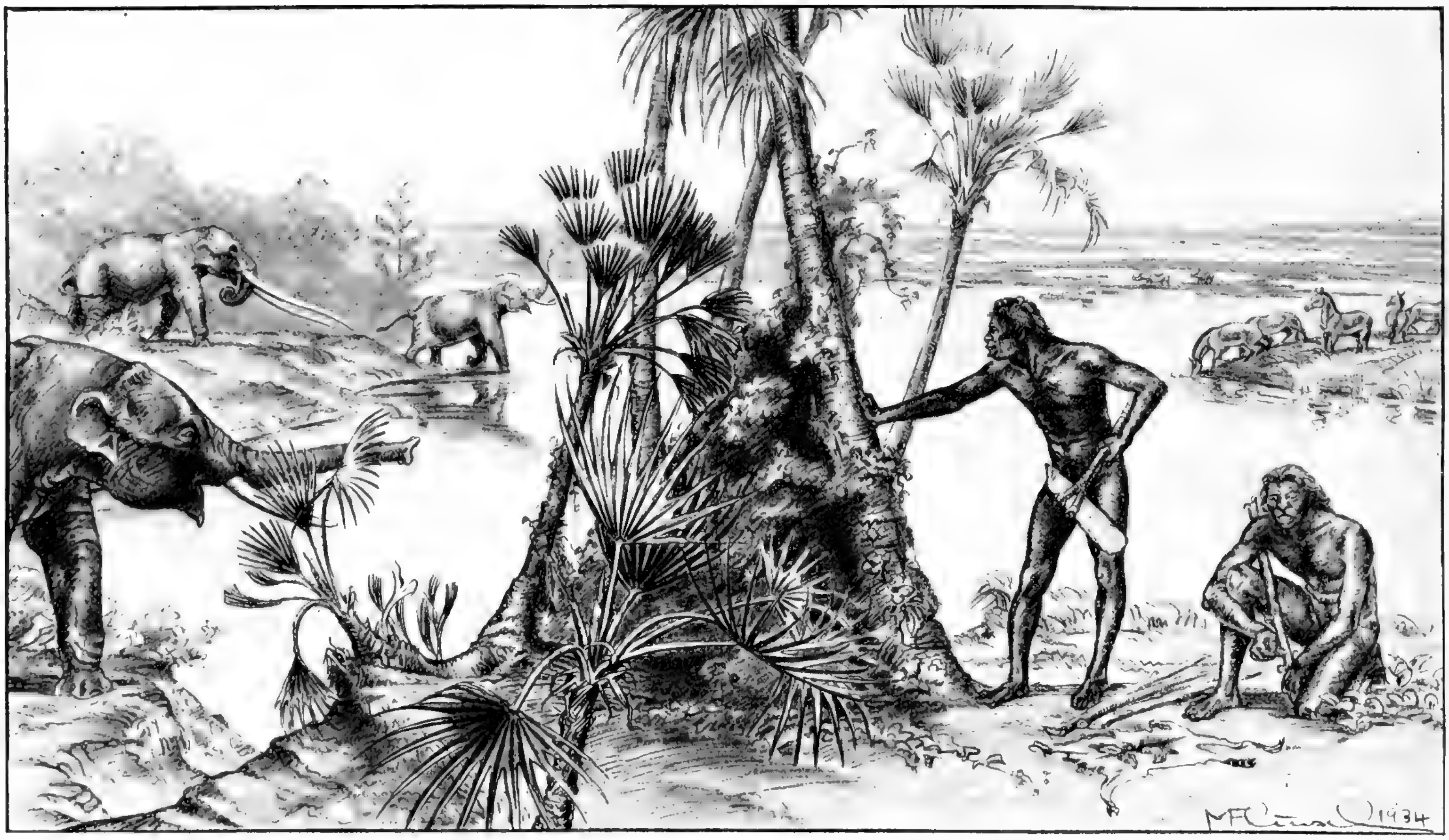

Fig. 856. Scene on the Ancient River Ouse Illustrating the Osborn Theory of the Upper Pliocene Age of Eoanthropus dawsoni

Restoration by Margret Flinsch in 1934, under the direction of Henry Fairfield Osborn

Eoanthropus dawsoni Woodward, as restored from the cranium and jaw discovered in the Piltdown gravels deposited in the channel of the ancient river Ouse. Bodily proportions and outlines from a Bushman hunter (5 feet) of the Kalahari Desert, West Africa, reduced in present restoration to a scale of 1/30th natural size. The erect figure is holding the sharpened femur of *Anancus* or of *Archidiskodon* discovered in the Piltdown gravels. Osborn does not agree with his friend Henri Breuil that this sharpened bone is the work of a rodent.

The mammals are (left foreground) *Archidiskodon planifrons*, 1/39th natural size, (left rear across the river) the straight-tusked mastodon, *Ancus arvernensis*, and *Archidiskodon planifrons*, 1/160th natural size, (right bank) herd of *Equus stenonis*, 1/160th natural size.

ARCHIDISKODON PLANIFRONS OF RUMANIA

Archidiskodon planifrons rumanus S. Stefănescu, 1924

Figure 857

From Tulucesti (Covurlui), Rumania. Upper Pliocene.

Elephas antiquus rumanus Stefănescu, 1924. "Sur la présence de l'*Elephas planifrons* et de trois mutations de l'*Elephas antiquus* dans les couches géologiques de Roumanie." Compt. Rend. Acad. Sci., Paris, Tome 179, p. 1418, December 15, 1924. Type.—Fragment of a third inferior molar of the left side, l.M_3, in the Laboratory of Geology, University of Bucharest. Horizon and Locality.—Upper Pliocene. Tulucesti (Covurlui), Rumania. Type Figure.—Sabba Stefănescu, 1927; originally figured by Sava Athanasiu in 1912 [1915], Pl. xvii, fig. 4, as *Elephas* cfr. *meridionalis.*

Type Description.—(S. Stefănescu, 1924, p. 1418, and 1927): "A l'exception de Maria Pavlow . . qui a rapporté a l'*Elephas* af. *planifrons* une molaire qu'elle a reçue de Ferladany (Fârladeni) en Bessarabie, personne a ma connaissance n'a indiqué jusqu'a présent cette espéce dans les couches géologiques de Roumanie. Or plusieurs molaires et quelques moitiés de mandibules d'éléphants de ma collection présentent des caractères qui rappellent de très prés ceux de l'*Elephas planifrons.* Par conséquent, je puis affirmer que cette espèce est non seulement représentée mais qu'elle est l'une des plus répandues dans les couches pliocènes et pléistocènes de notre pays. Mais n'ayant pas recueilli moi-même ces fossiles, il me paraît hasardeux de préciser leur âge géologique. . . . D'autre part, vu la grande variabilité des caractères spécifiques de l'*Elephas planifrons,* il est absolument nécessaire de reviser ces caractères afin de conclure, s'il y a lieu, à l'existence d'une seule ou de plusieurs mutations, ou même à l'existence d'une seule ou de plusieurs espèces, confondus ensemble par les paléontologistes qui m'ont précédé. Dans ce but je pratiquerai *ma méthode de recherches basée sur l'organisation des lames isolées des molaires,* méthode naturelle qui tout récemment m'a permis de reconnaître que la molaire provenant de Tulucesti (Covurlui) et rapportée par Sava Athanasiu [Footnote: '*Mamifere pliocene de la Tulucesti, districtul Covurlui, 1915.*'] à l'*Elephas* cf. *meridionalis,* doit être attribuée à une mutation ancestrale de l'*Elephas antiquus,* que j'ai dénommée *rumanus.*"

"Je n'insiste pas pour le moment sur les caractères de cette mutation qui, à mon avis, est la plus rapprochée de l'origine mastodontide de l'espèce *antiquus.* J'ajoute seulement que la mutation *ausonius* de l'Italie lui succéde et que la mutation de Weimar et Taubach (Allemagne), que je désigne sous le nom *germanicus,* est la plus récente."

"Toutes ces trois mutations ont été trouvées en Roumanie: *rumanus* à Tulucesti (Covurlui), *ausonius* à Colintina (Ilfov), *germanicus* à Tânganu (Ilfov)."

Type and Referred Inferior Molars of Archidiskodon planifrons rumanus

Fig. 857. (Left) Type third left inferior molar, l.M_3, of *Elephas antiquus rumanus* S. Stefănescu, 1924; originally figured by Sava Athanasiu, in 1912 [1915], Pl. xvii, fig. 4, as "*Elephas* cfr. *meridionalis*"; refigured by Stefănescu in 1927 as *Elephas antiquus rumanus.* Original in the Laboratory of Geology, University of Bucharest. (Right) Last two ridge-plates and talon of a referred third right inferior molar, r.M_3, stripped of its very thick cement (Coll. of the Laboratory of Palæontology, University of Bucharest). After Stefănescu, 1927.

The present author considers that this type is more closely related to *Archidiskodon* owing to the comparatively low ridge-plates and the excessively wide cement areas between them. Stefănescu rightly attributes this specimen to *Elephas* [=*Archidiskodon*] *planifrons.* He states (1924, p. 1418): "Or plusieurs molaires et quelques moitiés de mandibules d'éléphants de ma collection présentent des caractères qui rappellent de très prés ceux de l'*Elephas planifrons.* Par conséquent, je puis affirmer que cette espèce est non seulement représentée mais qu'elle est l'une des plus répandues dans les couches pliocènes et pléistocènes de notre pays."

ARCHIDISKODON MERIDIONALIS AND A. MERIDIONALIS CROMERENSIS

Archidiskodon meridionalis Nesti, 1825

Figures 815, 817, 858–869, 925–928, 1239, Pl. xxi

Upper Pliocene[1] to Lower Pleistocene of Val d'Arno supérieure, northern Italy, of Saint-Prest, France, and of England (Forest Bed).

Syn.: *Elephas giganteus* Aymard (MS. in Lartet, 1857); *Elephas lyrodon* Weithofer, 1890, based on a female type skull.

Early Discoveries of Elephas meridionalis by Tozzetti in the Val d'Arno.—Giovanni Targioni Tozzetti, who in 1725–1745 traveled through the greater part of Tuscany, described especially the geology of the valley of the Arno, making a sharp distinction between the Lower (Val d'Arno inférieure) and the Upper (Val d'Arno supérieure). The 'Val d'Arno inférieure' he regarded as a sea-water deposit, which formed the hills and filled them with marine fossils; these fossils occur in abundance from Capraja to the sea. The 'Val d'Arno supérieure,' with its hills of chalk and ochreous clay, weathered by sand and ice, shows no trace of marine animals; these deposits, Tozzetti believes, were attributable to the fluviatile waters of the Arno, which at some ancient period poured forth from natural cataracts having their source in the mountains between Incisa and Rignano. If it is true, however, that ribs of Fiseter [*Physeter*] were found two miles from Arezzo, then there is reason to believe that the deposits of the Val d'Arno supérieure were not of fluviatile origin.

Falconer in the "Palæontological Memoirs" of 1868, Vol. II, p. 104, remarks that "The 'Val d'Arno Superiore' has, from remote ages, been celebrated for the vast abundance of fossil remains found there. Huge bones and teeth of Elephants were especially numerous. A large collection of these was formed by Targioni Toretti [Tozzetti], which ultimately found its way into the Grand Ducal Museum at Florence; and numerous additions were made by Nesti, who, in 1808, soon after the publication of Cuvier's 'Memoir of the Mammoth' (Annales du Muséum, tom. viii.), examined the Tuscan Elephantine remains, and was so satisfied of their difference from those of the Mammoth, that he proposed for

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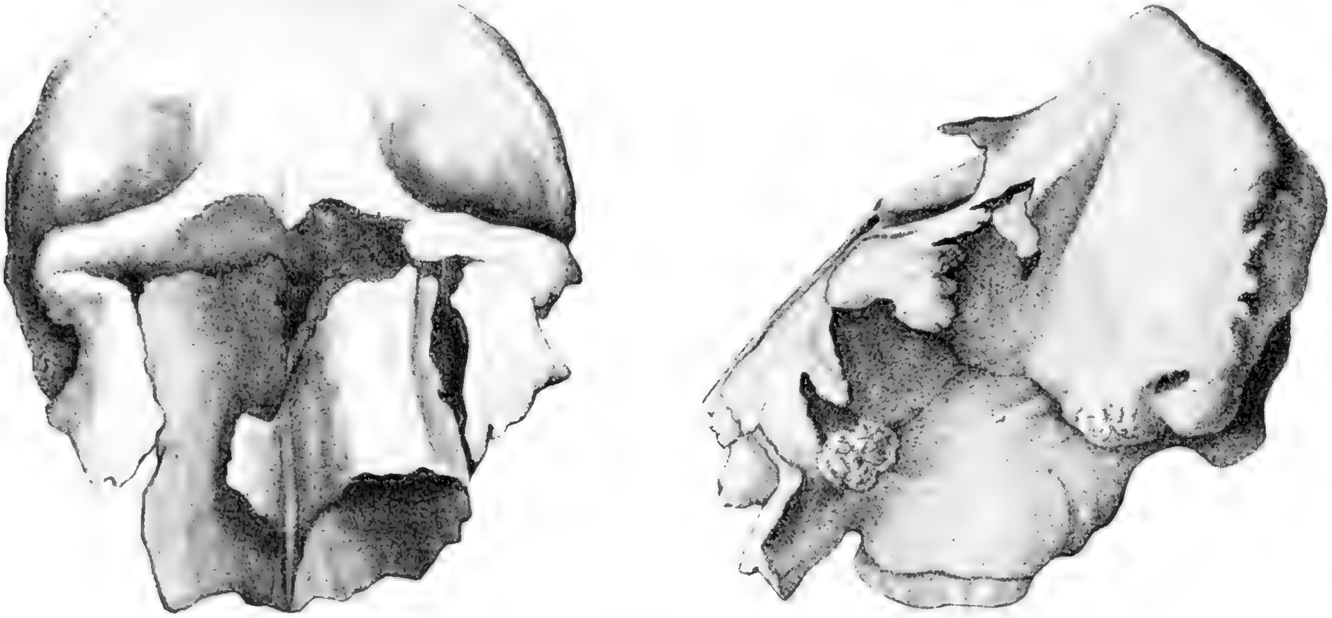
[1] Possibly Lower Pleistocene (see footnote on p. 1049).—Editor.

them two specific designations, namely, *Elephas meridionalis* and *E. minutus* [or *minimus*].[1] Influenced by the fact that Cuvier had laid so much stress upon the peculiar form of the lower jaw, and guttered beak of the symphysis, as distinctive marks of *E. primigenius*, Nesti (not a professed anatomist) was naturally led to direct his attention, in the first instance, chiefly to the same parts in the Val d'Arno remains. Unluckily the specimen that presented the most pronounced beak had lost its molar teeth [Nesti, 1808, Tav. I, figs. I and II]; Nesti assumed it to be of an Elephant. But this selected 'pièce justificative' for his *Elephas meridionalis* was proved by Cuvier to be the lower jaw of *Mastodon Arvernensis*, . . . and *E. minutus* to be merely a young Elephant."

of specific distinction. . . . This singular conclusion is, in some measure, explained by the fact that hardly a specimen of a molar of the true Mammoth exists in the Florentine Museum for comparison. It is, perhaps, still more remarkable that the experienced eye of Cuvier should have glanced over the multifarious evidence supplied by the Tuscan collections, without being convinced that *E. meridionalis* was a well-founded species, considering the rapidity with which he seized, and the logical precision with which he characterized, the distinctive marks of the Mammoth from the existing Indian Elephant."

"Failing the teeth, Nesti drew his specific distinctions from the form of the cranium and lower jaw. Ample evidence is afforded by them for establishing *E. meridionalis* as an independent form."



LECTOTYPE CRANIUM (C) OF ARCHIDISKODON MERIDIONALIS, MUSEUM OF FLORENCE

Fig. 858. Lectotype figure after Nesti of the first described and figured cranium (Cranium C) of *Elephas meridionalis* Nesti, 1825, Tav. I, figs. 1 and 2; cited by Falconer (1868, Vol. II, p. 122) and selected as the *type* by Depéret and Mayet (1923, p. 126). One-twelfth natural size. Compare figure 861 of the present Memoir, also figure 865 (13).

"After a long interval, during which Cuvier had visited the Tuscan collections, Nesti brought out another memoir upon the subject [1825], in which, upon greatly extended observations on specimens of all ages, from the fœtus upwards, including crania, lower jaws, molars, tusks, and bones of the extremities, he upheld the soundness of his first inference in regard to the distinctness of *E. meridionalis*, while he admits tacitly the force of Cuvier's criticism upon his second species, *E. minutus*. . . . Another circumstance, which materially damaged the authority of Nesti upon a question of such difficulty and importance, is that he states that, after examining a vast number of molars of all ages, he had found them to vary so much—some having thick plates, others thin, and the same tooth presenting such different patterns, according to its age and degree of wear—that he had abandoned the characters yielded by the molar teeth as worthless (!) for any reliable marks

"The Abbé Croizet, to whom palæontology is indebted for so much valuable research on the fossil fauna of Velay, was the first who had the courage to question the decision of Cuvier against *E. meridionalis*. In his work upon Puy-de-Dôme, he has figured and described a fragment of an upper (?) molar (lower left of Croizet and Jobert) discovered at Malbattu. . . . He refers to Nesti's researches, and sums up by inferring that, as there are two living Elephants, so there were two fossil species—the one with attenuated plates, being the Mammoth of Siberia, the other with thick plates, as seen in specimens from . . . the Val d'Arno. He considered the facts sufficient, but assigned no other name to the second species than that of 'Éléphant de Malbattu.'"

GEOLOGIC LEVEL, FOREST BED OR CROMERIAN (COMPARE OSBORN, 1922.563, PP. 439, 440.—(1) The survival in the Forest

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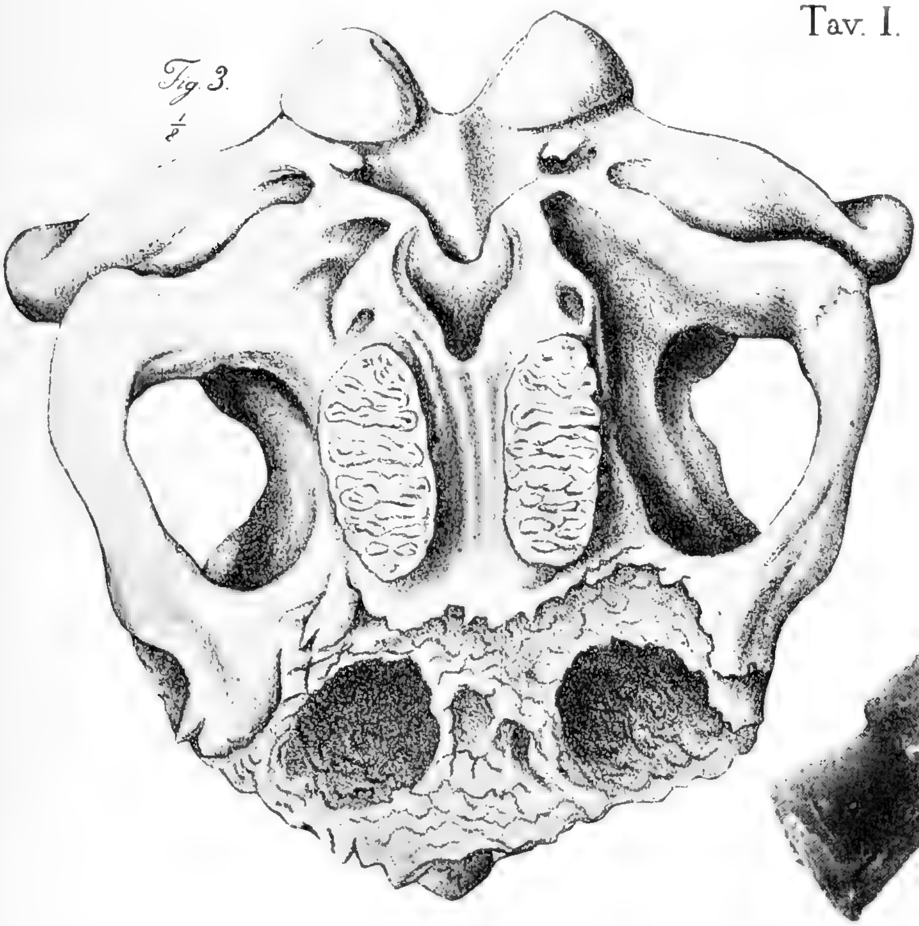
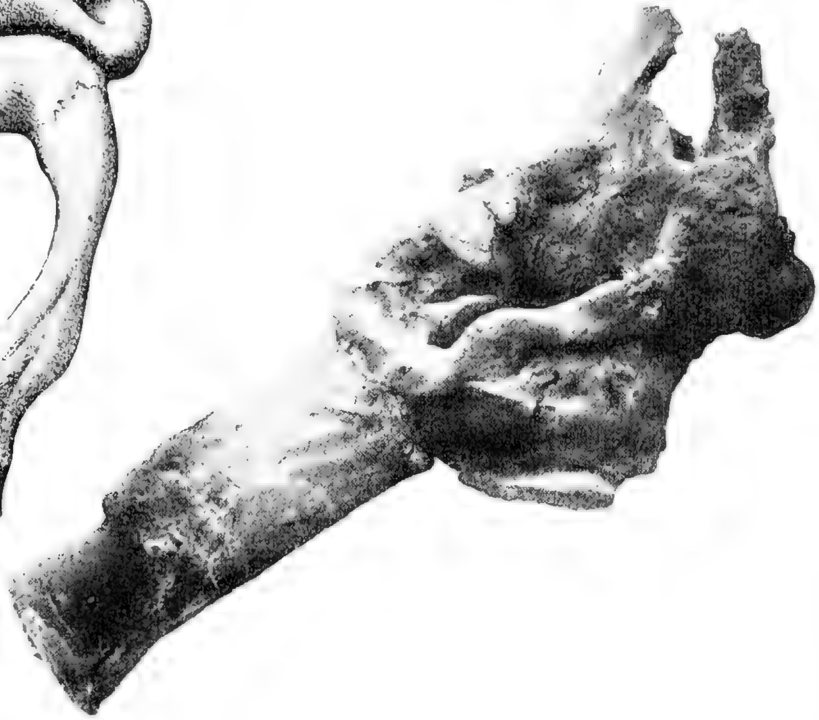
[1] [Researches of the present author failed to substantiate the assignment by Nesti of the names *Elephas minutus* or *E. minimus* in either of his articles of 1808 or 1825. Weithofer (1890.1, p. 134) attributes both these names to Falconer, i.e., *Elephas minutus* (Pal. Mem., 1868, Vol. II, p. 104) and *E. minimus* (1846, letterpress, "Fauna Antiqua Sivalensis," p. 13).—Editor.]

Bed of East Anglia, above the Red and Norwich Crags (*Archidiskodon planifrons* level) of warm temperate types, such as specimens referred to *Archidiskodon meridionalis*, *Palæoloxodon* [*Hesperoloxodon*] *antiquus*, *Hyæna striata*, *Dicerorhinus etruscus*, *Equus stenonis*, *Machærodus*, is exactly paralleled by the same genera and species occurring in southern France and northern Italy (Val d'Arno) during the long warm *1st Interglacial* period. (2) During this period there also appear for the first time in Great Britain certain African types, like the *Hippopotamus*, and there became more abundant in Great Britain the loxodontine type, *Palæoloxodon* [*Hesperoloxodon*] *antiquus*, as well as the *Hyæna*. (3) The Forest Bed arrival of tundra and northern forest types, such as *Mammonteus primigenius*, *Ovibos moschatus*, *Alces latifrons*, is a distinctive feature of the northern latitude and cold climate of East Anglia during the period of the first Scandinavian glaciation, which has no parallel in southern France or in northern Italy.

Specific Characters of Archidiskodon meridionalis.—As compared with *Elephas* [=*Archidiskodon*] *planifrons*, cranium of *Archidiskodon meridionalis* larger, more lofty or acrocephalic; frontonasal contour typically concave instead of plane (Fig. 861); fronto-occipital crest broadly truncated (Fig. 865) not rising to an acute apex as in *A. imperator*. Maximum ridge-plate formula: Dp $4\frac{8}{8}$ M $1\frac{8}{8+}$ M $2\frac{8\text{-}9}{8\text{-}9}$ M $3\frac{13}{13\text{-}15}$ as compared (p. 953) with the typical ridge-plate formula of *A. planifrons* (after Falconer) of Dp $3\frac{6+}{6+}$ Dp $4\frac{6+}{7+}$ M $1\frac{7+}{7+}$ M $2\frac{8}{9}$ M $3\frac{10+}{11+}$. Grinding teeth broad, heavily plated with cement; superior incisive tusks large and lyrate. Another progressive character in *A. meridionalis* is the loss of true premolar (P 3–4) eruption. In brief, the typical *A. meridionalis* of the Upper Pliocene, lowermost Pleistocene, and Lower Pleistocene is much more progressive than the typical *A. planifrons.*

This is the great 'southern mammoth,' well named *E. meridionalis* by Nesti in 1825. It is connected with *Elephas planifrons* by a series of ascending mutations, completely confirming Falconer's observations of 1863, p. 80: "The nearest affinity, and that a very close one, of the European *Elephas meridionalis* is with the Miocene *E.* (*Loxod.*) *planifrons* of India." Nesti's type is a fine skull still preserved in the Florence Museum.





Young Male Cotype Cranium (A) of Archidiskodon meridionalis Nesti, Museum of Florence

Fig. 859. Cranium A of Nesti, cotype of *Elephas meridionalis* Nesti, 1825, Tav. I, fig. 3, one-eighth natural size. Figure reproduced from a plate which also gives the profile (fig. 2) and front view (fig. 1) of the lectotype specimen (Cranium C).

After this cranium (A) was figured, as above, the incisive alveoli were added, as shown in figure 860 opposite. Falconer (1868, Vol. II, p. 122) observed that enormous tusks have also been added, yielding a diameter of 0.26 m. or 10.2 inches.

Fig. 860. Side view of the restored cotype skull of *Elephas meridionalis* in the Florence Museum. After Weithofer, 1890, Taf. I, fig. 2: "*Elephas meridionalis* Nesti; Cranium *A*; oberes Arnothal; von links." Reproduced about one-tenth natural size, for direct comparison with figure 859, which is one-eighth natural size, showing that the peak or apex of the cranium is greatly elevated. Consequently the frontoparietal plane is much more elongate than that in *E. planifrons.*

El. [*Elephas*] *meridionalis* Nesti, 1808, 1825. "Di Alcune Ossa Fossili di Mammiferi che s'incontrano nel Valdarno," Ann. Mus. Imp. di Fisica e Storia Nat. Firenze, 1808, I (description without name); "Sulla nuova specie di elefante fossile del Valdarno" (letter from Nesti to Dott. Prof. Ottaviano Targioni Tozzetti). Nuov. Giorn. Lett., 1825, XI, No. 24, p. 211. Lectotype.—Cranium with third superior grinding teeth, the rostrum and tusks being broken away (=Cranium C of Nesti). Cotype (=Cranium A of Nesti). Horizon and Locality.—Superior Val d'Arno, Upper Pliocene, northern Italy. Lectotype Figure.—*Op. cit.*, 1825, Tav. i, figs. 1 and 2. Cotype, Tav. i, fig. 3.

Description.—In his description of 1825 Nesti compares the skull with that of "Mastodonte" and of "*primigenia*," concluding (p. 211): "Potrebbe a questa Specie imporsi il nome di *Elephans Valdarnensis*, o *Etruscus*, o anco *Italicus*, ma poichè le regioni, nelle quali questo animale viveva, non sono note, e d'altronde pare che fosse destinato a climi più temperati e meridionali della Specie primigenia, preferisco di appellarlo *El. meridionalis*." There is an earlier reference to this fossil which does not include the name. It is to be found in the Annali del Museo Imperiale di Fisica e Storia Naturale, Firenze, Tome I, 1808, mentioned above with title of the article.

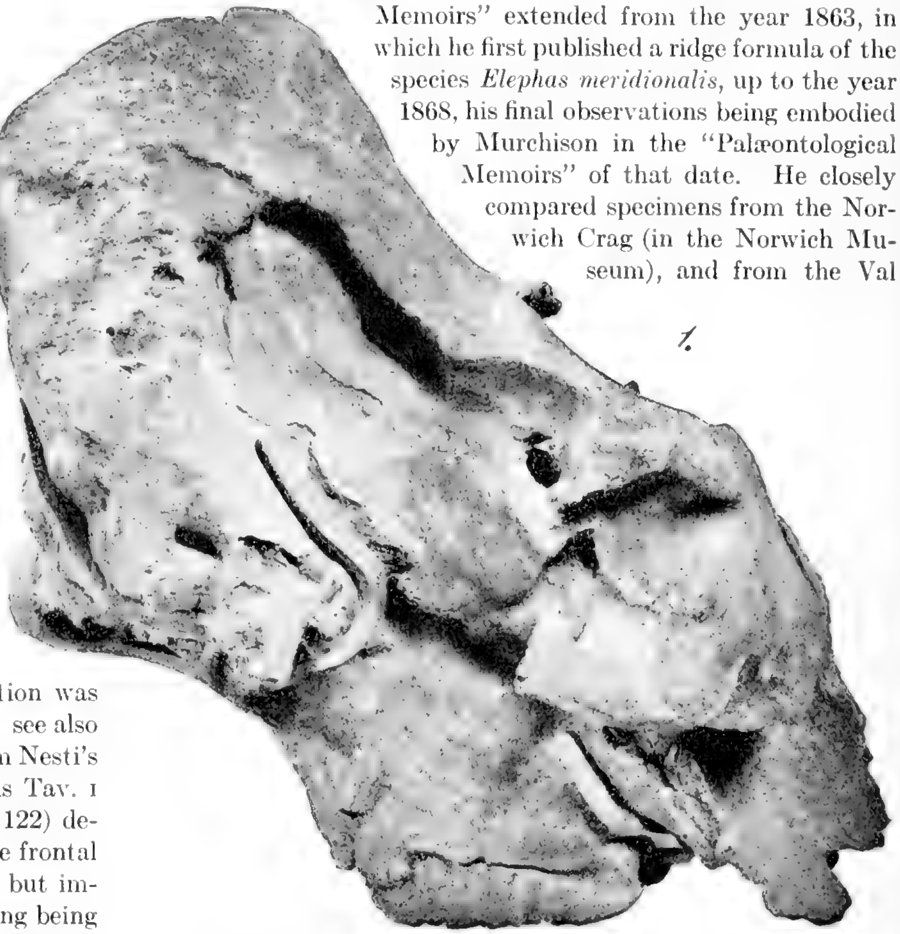
Lectotype Skull.—Cranium C of Nesti's description was selected by Depéret and Mayet (1923, p. 126) as the *type*; see also Falconer (1868, Vol. II, p. 122). It is here reproduced from Nesti's original figures, front and side views, figs. 1 and 2 of his Tav. i (Fig. 858 of the present Memoir). Falconer (*op. cit.*, p. 122) described Cranium C as follows: "It is nearly perfect in the frontal and occipital regions, condyles, maxillaries, and molars, but imperfect in the facial portion, the border of the nasal opening being broken, together with the terminal portion of the incisive alveoli and the zygomatic arches. Since Nesti's figures were taken, this specimen has suffered considerable damage, the upper lamina of the right incisive alveolus having disappeared, together with the salient tip of the nasals and the lateral margin including the left orbit. The last molar is present on either side, far advanced in wear. (See Pl. i. fig. 11, and Pl. ii. fig. 16.)"

Cotype Skull.—Falconer also described the cotype Cranium A as follows (*op. cit.*, p. 122): "4. The cranium A of Nesti's references, fig. 3, comprising the palatine, maxillary, and temporal regions, the inferior part of the occiput, and the zygomatic arches, the only deficiency being in the facial region. The specimen, which is highly ferruginous, has now joined on to it the entire incisive sheaths (not represented in Nesti's figure) and two enormous tusks, which are spread out horizontally in the *Theristocaulodon*-manner above noticed. Nesti, in his memoir, cites the tusks of this specimen as yielding a diameter of 0.26^{m}, or 10.2 inches. The last molar, much worn, is present on either side."

FALCONER'S NOTES OF 1868 ON TYPE AND REFERRED SPECIMENS OF ELEPHAS [ARCHIDISKODON] MERIDIONALIS [AND ?PLANIFRONS] OF THE NORWICH CRAG AND VAL D'ARNO

Falconer, "Palæontological Memoirs," Vol. I, 1868, pp. 443–447, Plate xiv.b[1] of the "Fauna Antiqua Sivalensis"

Falconer's observations collected in his "Palæontological Memoirs" extended from the year 1863, in which he first published a ridge formula of the species *Elephas meridionalis*, up to the year 1868, his final observations being embodied by Murchison in the "Palæontological Memoirs" of that date. He closely compared specimens from the Norwich Crag (in the Norwich Museum), and from the Val d'Arno (in the Museum of Florence). In his ridge formula he undoubtedly confused ascending mutations of specimens belonging to *Archidiskodon planifrons* with specimens truly representative of primitive *Archidiskodon meridionalis*.



Aged Male. Lectotype Skull (C) of Archidiskodon meridionalis Nesti, Museum of Florence

Fig. 861. Lectotype skull of *Elephas meridionalis* Nesti, as refigured by Weithofer in 1890, Taf. ii, fig. 1: "*Elephas meridionalis* Nesti; Cranium C; oberes Arnothal; von rechts." One-seventh natural size. Compare figures 858 and 865 (7, 13, 14) of the present Memoir.

An outline of the same skull, after Falconer's plate of 1847, appears in figure 865 of the present Memoir. All these figures agree in the peculiarly flattened appearance of the summit of the aged occiput, which is quite unlike the *acrocephalic occiput* of the juvenile *Archidiskodon imperator.*

Compare above with the ridge formulæ and measurements of *Archidiskodon planifrons*. The ridge formulæ below given by Falconer and others embrace the *A. planifrons* stage as well as the *A. meridionalis* stage.

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[1] [A footnote by the Editor of the Palæontological Memoirs on pp. 443, 444 of Volume 1, states that according to the corrected copy by Falconer in the British Museum, all the figures in Pl. xiv.b, except 10, 17, and 18, should belong to *E. antiquus*; that the correction, however, is incompatible with the description and identification of every figure in pl. xiv.b, given in a subsequent part of the same memoir, according to which every figure in the plate, with the exception of 16, belongs to *E. meridionalis*.—Editor.]

Elephas meridionalis Nesti, 1825. LECTOTYPE.—Cranium C, Tav. I, figs. 1 and 2. COTYPE.—Cranium A, Tav. I, fig. 3.

UPPER JAWS.—Plate XIV.B, figs. 1, 1*a*, Dp^3, ridge-plates ½-6-½, "the crown is composed of six principal ridges, besides front and back talons. . . . compared with the corresponding tooth of *E.* (*Loxodon*) *planifrons*, which it resembles very closely, . . . it has a broader crown"; figs. 2, 2*a*, r. Dp^3, ridge-plates 6, Norwich Crag.

LOWER JAWS.—Plate XIV.B,[1] figs. 3, 3*a*, lower jaw, r.Dp_3, ridge-plates ½-6-½, very broad in the crown relative to the length, discs of ridges very wide as in Italian specimens, Norwich Museum; figs. 4, 4*a*, lower jaw, l.Dp_4, 8 ridge-plates, Norwich Museum, the ridge formula in these specimens agrees with the Italian, also the broad crown, the low ridges, and thick plates of enamel; figs. 5, 5*a*, lower jaw, l.M_1, ridge-plates ½-8-½, eight principal ridges, with front and back talons, discs of first three wide and open, tendency to mesial expansion, crown low in reference to breadth; figs. 6, 6*a*, lower jaw, l.M_1, ridge-plates ½-8, the crown presents a front talon and eight ridges, all of them worn, discs wide and open, Norwich Museum; figs. 7, 7*a*, lower jaw, r.M_2, ridge-plates 7+, Norwich Museum; figs. 10, 10*a*, lower jaw from Val d'Arno, demonstrating how exactly the English specimens agree with the Italian, long symphysis, gradual inclination into a beak; figs. 17, 17*a*, r.M_3, from Val d'Arno, showing 13 ridge-plates, length 10 in. = 255 mm., width 3.4 in. = 87 mm.; figs. 18, 18*a*, Norwich, lower jaw, r.M_3, ridge-plates ½-11-½, "showing eleven principal ridges, an anterior talon, and [?] a back talon," cement decomposed or denuded, 4 thick denticles on 6th to 8th ridges, length 11.25 in. = 287 mm.

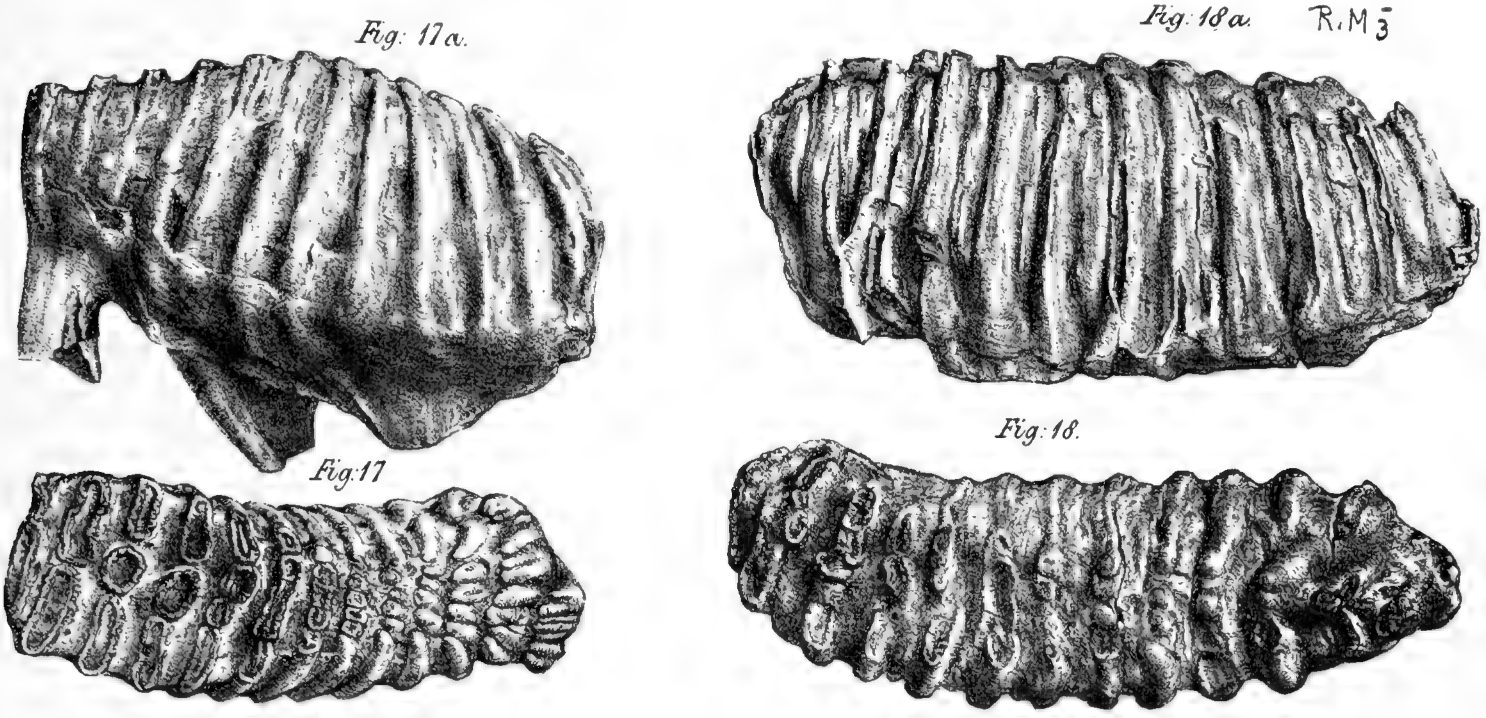

Fig. 862. MOLARS FROM THE VAL D'ARNO (LEFT) AND THE NORWICH CRAG (RIGHT) REFERRED TO 'ELEPHAS' [ARCHIDISKODON] MERIDIONALIS BY FALCONER

"Fauna Antiqua Sivalensis," Plate XIV.B, figs. 17, 17*a*, 18, 18*a*, one-third natural size
Compare "Palæontological Memoirs," Vol. I, 1868, pp. 443, 444, 447, 448

Figs. 17, 17*a*. Third inferior molar of the right side, r.M_3, Val d'Arno. Original in Oxford Museum, one-third natural size.

(*Op. cit.*, p. 447): "Figs. 17 and 17*a*.—*Elephas meridionalis.* A Val d'Arno lower molar of the same age, from Dr. Buckland's collection in the Oxford Museum, crown side. (Reproduced in Plate VIII of vol. ii.) Length of crown, 10. in. Width of crown, 3.4 in. Height of crown, 5. in."

NOTE I.—Falconer (as explained in the "Palæontological Memoirs," 1868, Vol. I, pp. 443, 444), in lettering the plates of the "Fauna Antiqua Sivalensis," became satisfied at the time the plates were lettered that he had interchanged *Elephas meridionalis* and *E. antiquus.* In his Memoir of 1857 (not published until after his death) he concluded [Pt. II of his Memoir published in 1865, p. 281]: "I beg leave to explain now, that all the plates bearing the name of *E. meridionalis* in the 'Fauna Antiqua Sivalensis,' including the outline-figures of crania in plate 42, belong to *E. antiquus*, while those that bear the latter name belong to *E.* (*Loxodon*) *meridionalis.* In the descriptions which follow, they will be cited as such."

Figs. 18, 18*a*. Third inferior molar of the right side, r.M_3, "Mammaliferous Crag" (Norwich). Norwich Museum 1570, one-third natural size.

(*Op. cit.*, p. 447): "Figs. 18 and 18*a*.—*Elephas meridionalis.* The finest detached molar of this species that has come under my observation is a specimen which was discovered in the 'Mammaliferous Crag' on the Thorpe Road, near Norwich, by Mr. Prestwich. . . . It is now lodged in the Museum at Norwich, and is the specimen which first convinced me many years ago that the 'Crag' yielded a species of Elephant entirely distinct from the Mammoth and from *E. antiquus.* . . . Extreme length of crown, 11.25 in. Width of crown in front, 3.3 in. Width at fifth ridge, where the crown is broadest, 3.8 in. Extreme height of ridge, 4.8 in. Width of ninth ridge, 3.5 in. Height of ninth ridge, 4.6 in." Reproduced in the 'Palæontological Memoirs,' Vol. II, Pl. VIII.

NOTE II.—Compare these primitive *A.* [*planifrons*] *meridionalis* molars of Italy and England with the more progressive *A. planifrons* molars of the Siwaliks, India.

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[1] [See footnote on opposite page.—Editor.]

Falconer, 1868, E. meridionalis: Dp $3\frac{6-\frac{1}{2}-6-\frac{1}{2}}{\frac{1}{2}-6-\frac{1}{2}}$ Dp $4\frac{}{8}$ M $1\frac{}{\frac{1}{2}-8-\frac{1}{2}}$ M $2\frac{}{7+-9}$ M $3\frac{}{\frac{1}{2}-11-\frac{1}{2}}$.

The above ridge formula is too low, obviously because Falconer included within his *'Elephas' meridionalis* grinding teeth belonging to *Archidiskodon planifrons.* More distinctive of the species *A. meridionalis,* in Osborn's opinion, is the ridge formula which we may deduce from Falconer's own observations (1868, Vol. II, p. 118) on nine Italian crania in the Florence Museum:

Falconer (Italy), E. meridionalis: Dp $2\frac{3}{3}$ Dp $3\frac{6}{6}$ Dp $4\frac{8}{8}$ M $1\frac{8}{8+}$ M $2\frac{8-9}{8-9}$ M $3\frac{13}{13-15}$.

Weithofer (1890, p. 173) observes that Falconer's high figure, M $3\frac{}{15}$, rests on a single individual.

Leith Adams, 1877–1881

Formula.—Leith Adams reviewed this important species in his "British Fossil Elephants," 1877–1881, and while in general confirming Falconer's observations by excluding *E. planifrons,* he reached a much more accurate dental formula which became the standard:

Leith Adams, 1877–1881, E. meridionalis: Dp $2\frac{3}{3}$ Dp $3\frac{6}{6}$ Dp $4\frac{8}{8}$ M $1\frac{8-9}{7-9}$ M $2\frac{9-11}{9-11}$ M $3\frac{13-14}{11-14}$.

This formula of 1877–1881, together with Leith Adams' summary of the points distinguishing the molars of *Elephas meridionalis* from those of the narrow-toothed *Elephas antiquus* (p. 232), are to be found in his important Memoir (p. 208). He assigns the following characters to *Elephas meridionalis.*

Characters.—(Cf. *op. cit.,* p. 30): M^2 in *E. meridionalis,* ridges nearly as broad as they are long, thick plates, grosser masses of intervening cement, machærides uncrimped, × 10 ×. (Cf. p. 44): M^3 massive, enamel and plates very thick, machærides scarcely plaited, great breadth and low ridge formula, which rarely if ever exceeds that of M^2 of *E. antiquus.* (Cf. p. 48): In M^3 the highest ridge formula of *E. meridionalis* equals lowest of *E. antiquus;* so that in number of ridges we find *E. primigenius, E. antiquus, E. meridionalis,* and *E. namadicus* meeting at their extremes. Leith Adams (cf. pp. 129 to 144) compares the cranium of *E. meridionalis* in great detail with that of *E. planifrons, E. hysudricus, E. bombifrons, E. africanus,* etc., concluding that the skull and dentition of *E. planifrons* make the nearest approach to *E. meridionalis* (see pp. 186, 208–210, 239, 244).

Error.—Originally Leith Adams also made the error of including the low ridge-plate formula (M $3\frac{10+}{11+}$) of *E. planifrons* with the high ridge-plate formula (M $3\frac{13-14}{11-14}$) of *E. meridionalis,* in describing the range of evolution and variation in the ridge formula of the British specimens of *E. meridionalis.*

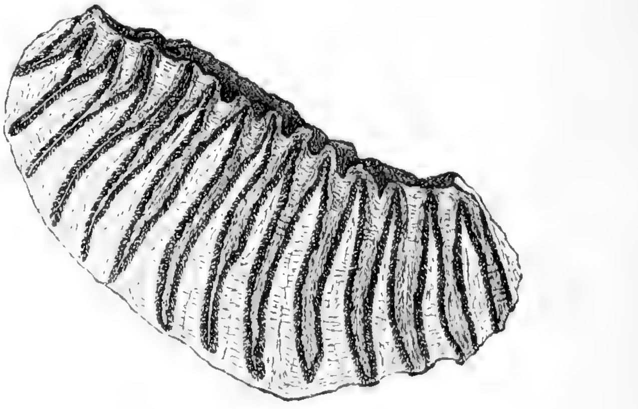
Weithofer, 1890, Lydekker, 1886

Collective Ridge Formula.—The collective ridge-plate formula [of *A. planifrons* and *A. meridionalis*] may also be cited from Weithofer (1890, p. 172): "Als Gesammtformel für die Zähne des *El. meridionalis,* soweit sie hauptsächlich aus dem Material des Museums zu Florenz resultirt, ergäbe sich demnach":

Weithofer, 1890, E. meridionalis: Dp $2\frac{3}{2-3}$ Dp $3\frac{5-6}{5-6}$ Dp $4\frac{7}{7-8}$ M $1\frac{8-9}{8-9}$ M $2\frac{8-10}{9-11}$ M $3\frac{10-13}{11-12}$.

Weithofer in his collective formula, like Falconer (1868), undoubtedly erred by including specimens having the typical *Archidiskodon planifrons* ridge formula with those of *A. meridionalis;* thus this collective formula ranges from the formulæ of *Archidiskodon planifrons,* e.g., M $3\frac{10}{11}$, to *A. meridionalis,* e.g., M $3\frac{13}{12}$.

Lydekker, 1886.—Lydekker in his "Catalogue of the Fossil Mammalia in the British Museum (Natural History)," 1886.2, p. 107, adopts the Leith Adams formula of 1877–1881 as follows: (1) The molars of *E. meridionalis* so closely resemble those of *E. planifrons,* that if they both occurred in the same area it is more than doubtful if they could be specifically distinguished; (2) both frequently exhibit partial denudation of the enamel ridges; (3) there is variation in the thickness of the enamel and in the breadth of the ridges, in some molars the enamel being relatively thin and considerably plicated; (4) the cranium is characterized by large, slightly curved tusks and widely diverging alveoli; (5) in general contour it is intermediate between the cranium of *E. planifrons* and *E. hysudricus,* although nearer the latter; (6) it agrees with the cranium of *E. planifrons* in the relative distance between the nasals and the vertex, but has the vertex more vaulted, the frontal profile concave, the temporal fossæ intruding largely on the frontal aspect; (7) the species attained an enormous size, the height of some individuals being estimated at upwards of fifteen feet.



Archidiskodon meridionalis Ref.

Fig. 863. Referred *Elephas meridionalis* of Chagny (Côte-d'Or), one-fourth natural size, after Gaudry, 1878, p. 178, fig. 237. This fourteen ridged third superior molar, M^3, of Chagny, is to be compared with the thirteen ridged molar stage of *Elephas meridionalis* of the Val d'Arno, i.e., M $3\frac{13}{13-15}$, as deduced by Falconer (see Falconer, 1868, Vol. II, p. 118). Observe superior ridge-plates pre-concave, post-convex (cf. Fig. 827, *A. planifrons*).

Cranial and Dental Characters.—Weithofer (1890, pp. 136, 137) refigures Nesti's type skull (Fig. 861 of the present Memoir) showing the right side (Taf. ii, fig. 1): "*Elephas meridionalis* Nesti; Cranium C; oberes Arnothal; von rechts." Falconer also refigures this skull (1846 [1847, figs. xix of Pls. xlii and xliv]), as well as Depéret and Mayet (1923, p. 128, fig. 16). The three skulls in the Florence Museum exhibit the following characters: (1) Pointed nasals, (2) concave frontals, (3) high occipital crest flattened anteroposteriorly, (4) extreme brachycephalic cranium shortened anteroposteriorly, (5) broad narial openings, (6) parallel sides of the premaxillary sockets of the tusks, as contrasted with the broadly flaring sides of the sockets similar to those in the contemporary *Hesperoloxodon antiquus.* All these characters point to the cranial relationship of the Italian *Archidiskodon meridionalis* and its ancestor *A. planifrons.*

Weithofer's Type Skull of Elephas lyrodon = Archidiskodon meridionalis Female

Fig. 864. Types of two individuals of *Elephas lyrodon* Weithofer, Florence Museum, upper Val d'Arno deposits (Weithofer, 1889, pp. 79 and 80): "Hier sei bezüglich der zum erstenmal genannten Species *Elephas lyrodon* nov. sp. nur bemerkt, dass sie auf zwei vollständige Schädel sammt Stosszähnen, sowie Schädelfragmenten mit Stosszähnen und mehreren Unterkiefern und isolirten Stoss- und Backenzähnen des Museums von Florenz basirt ist." After Weithofer, 1890, Taf. iii, fig. 2 (right); iv, fig. 2, Schädel *a* (left); v, fig. 1, Schädel *a* (middle). All one-twentieth natural size. Compare figure 865 (11, 11*a*).

MS. Elephas giganteus Aymard (in Falconer, 1857, p. 321).—(Lucien Mayet, letter, December 11, 1922): "*Elephas giganteus* Aymard n'est qu'une désignation portée sur des étiquettes de sa collection par ce paléontologiste. Il y aurait lieu de retrouver les pièces et de les déterminer; ce serait peut-être *E. meridionalis*(?) ou *E. trogontherii*(?) ou *E. antiquus*(?). Il s'agit très probablement là—comme pour beaucoup des ossements recueillis par Aymard dans le Pliocène supérieur et le Pleistocène du bassin du Puy—de désignation inscrite sur des étiquettes, sans que les pièces correspondantes aient jamais été déterminées ou aient fait l'objet d'une révision ultérieure. C'est un nom—celui d'*Elephas giganteus*—a faire disparaître purement et simplement."

SKULLS AND SKELETONS OF ARCHIDISKODON MERIDIONALIS

In figure 865 are displayed outlines of the lectotype (Nos. 7, 13, 14), cotype (Nos. 8, 9, 11, 11a, 15), and other skulls of *Archidiskodon meridionalis,* male and female, of which we have been able to find figures in the literature.

They include the following:

1) Male skull figured in error by Falconer and Cautley in 1847 as *Elephas antiquus*: front view, Pl. xlii, fig. xix; side view, Pl. xliv, fig. xix. Cranium C of Nesti [lectotype of *Elephas meridionalis* Nesti, 1825, Tav. i, figs. 1, 2].

2) Cranium of *Elephas meridionalis,* side view, after Weithofer. Cranium C of Nesti.

3) Cranium A of Nesti [cotype], palatal view after Nesti, 1825, Tav. i, fig. 3; front and side views after Weithofer, 1890, Taf. i, figs. 1, 2.

4) Front and side views of female cranium, type of *Elephas lyrodon* Weithofer, 1890, Taf. v, fig. 1, Taf. iv, fig. 2.

Characters (Osborn, 1924).—These crania agree in the following points: (1) Extremely broad and vertically shallow anterior narial openings, a feature shared by *Archidiskodon imperator* (Fig. 896); (2) extreme cranial abbreviation (hyper-brachycephaly) and depth (bathycephaly) resulting in *hypsicephaly* and *acrocephaly*; (3) concave forehead or frontoparietal profile; (4) parieto-occipital crest rising high in profile (cf. Weithofer, 1890, Taf. i, fig. 2, *E. meridionalis* cotype, with *E. imperator* ref., Los Angeles, Calif.); (5) through hypsicephaly, orbits and occipital condyles approximated, vertical diameters greatly exceeding anteroposterior diameters; there seems to be little doubt of the phylogenetic kinship of the *Archidiskodon meridionalis* with the *A. imperator* crania; (6) cranial profiles of *A. meridionalis* and *A. imperator* analogous to the hypsicephalic and acrocephalic profile of *Mammonteus primigenius*; (7) in comparison with the more primitive, more platycephalic *A. planifrons,* with smaller narial openings (Fig. 848), the known crania of *A. meridionalis* are much larger and more progressive than the known crania of *A. planifrons.*

CRANIA IN THE FLORENCE MUSEUM

(W. D. Matthew, September, 1920).—Here are found besides the type skull of *Elephas meridionalis* Nesti [Cranium C] several more or less incomplete skulls, many jaws and teeth, including those from the Upper Pliocene near Magello. A fine series of *E. meridionalis* crania published by Weithofer (1890) includes the type of *Elephas lyrodon* Weithofer, which is obviously a female of *Elephas* [= *Archidiskodon*] *meridionalis* in which the tusks are of a lyrate arrangement drawn together at the points, more after the manner of *Hesperoloxodon antiquus* but more slender. In the same beds with these crania of *E.* [*A.*] *meridionalis* was found part of a cranium of the straight-tusked elephant *H. antiquus,* which exhibits a wide spreading of the tusks at the base, a broadened rostrum not less than 2½ feet apart at the rim of the socket. Contemporary with the above *Archidiskodon* and *Hesperoloxodon* are numerous remains of *Anancus arvernensis,* including a fairly preserved skull with tusks found in the environs of Florence, one tusk broken off and repointed during life.

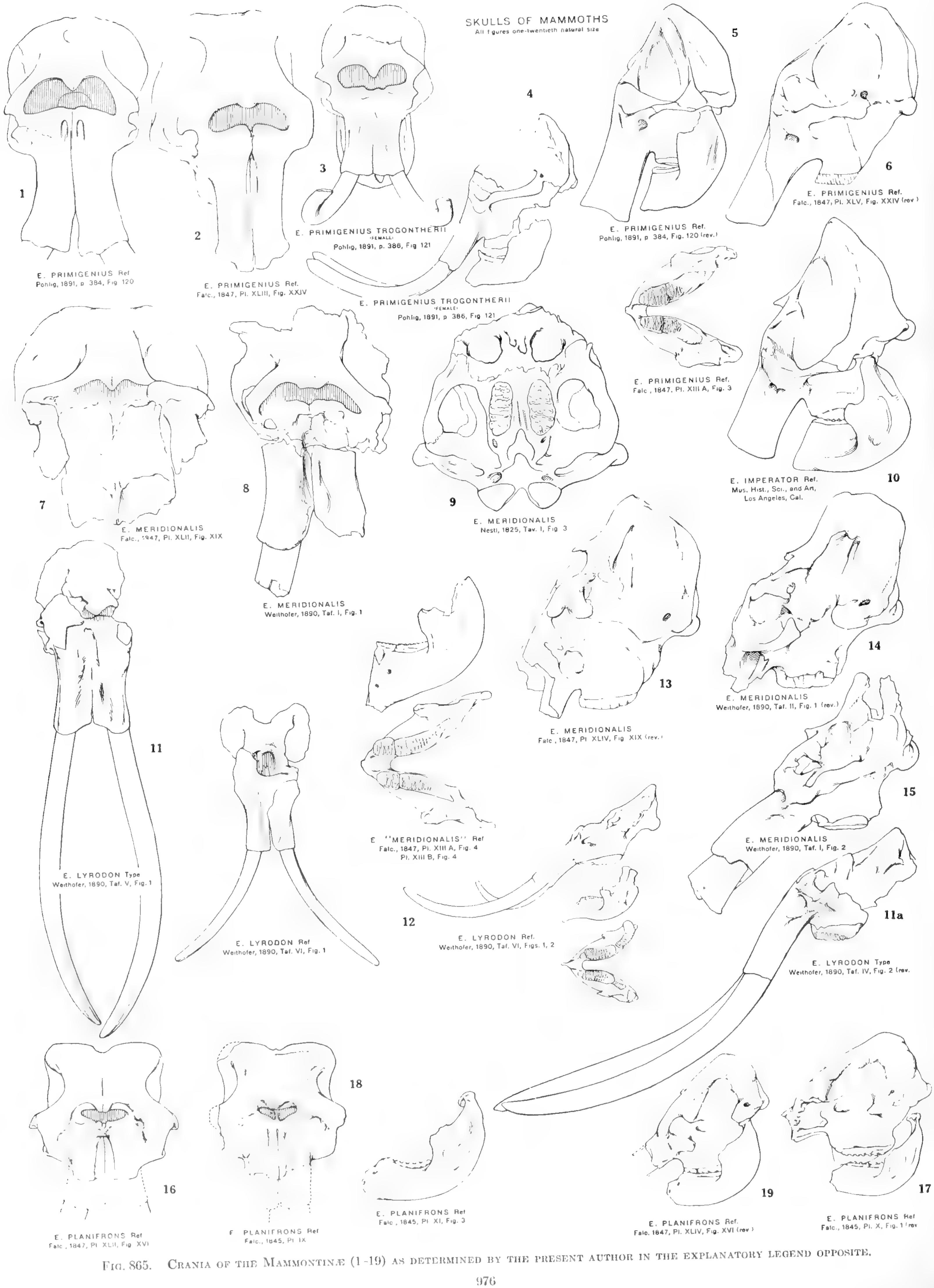


FIG. 865. CRANIA OF THE MAMMONTINÆ (1-19) AS DETERMINED BY THE PRESENT AUTHOR IN THE EXPLANATORY LEGEND OPPOSITE.

Elephas lyrodon Weithofer, 1889, 1890.—(Weithofer, 1890, p. 173): "Hier in Florenz befindet sich ein völlig ausgewachsener, leider aber nicht besonders gut erhaltener Schädel sammt den beiden Incisiven in situ (Falconer's Nr. 6), ein gleichfalls sehr altes Prämaxillarfragment mit dem rechten Stosszahn vollständig, dem linken zum grössten Theil erhalten (Falconer's Nr. 9), ferner ein jüngerer Schädel sammt beiden Stosszähnen und dem Unterkiefer, womit weiter auch die Wirbel, Rippen, Schulterblatt und Becken im Zusammenhang gefunden worden waren (Falconer's Nr. 8), ein Oberkieferfragment mit dem linken Stosszahn und jederseits zwei Backenzähnen in situ, endlich mehrere mehr oder weniger vollständige Unterkiefer oder Unterkieferhälften; einige Stosszähne, sowie offenbar auch einige der isolirten Backenzähne werden hieher gezählt werden können." Weithofer (*op. cit.*, pp. 191, 192)observes very close kinship to *E. meridionalis* in the dentition and ridge formula: M 3 $\frac{10\text{-}12}{11\text{-}13}$. He points out numerous differences in the structure of the skull and skeleton, and then concludes (p. 193): "Ich glaubte daher, durch die angeführten Umstände gezwungen, diese neue Form als eine distincte Species betrachten zu mussen, die ich nach der so überaus charakteristischen Form ihrer Stosszähne *Elephas lyrodon* nov. spec. benannte."

Matthew, 1920, Osborn, 1924: The type cranium of *Elephas lyrodon* may be regarded, from the very slender character of the tusks, as a female of *Archidiskodon meridionalis.*

SKELETON OF ARCHIDISKODON MERIDIONALIS IN THE PARIS MUSEUM

The affinity of *Archidiskodon meridionalis* to *A. imperator* is clearly displayed in a comparison of figures 866 (*A. meridionalis*) and 896 (*A. imperator*). The superb skeleton discovered in 1869 near the village of Durfort, Gard, is shown herewith (Fig. 866) through a photograph kindly furnished by Dr. Marcellin Boule and retouched by our own artist.

Skeletal Characters.—Gaudry (1893, p. 12) observes of this specimen: "L'Éléphant de Durfort n'appartient pas à la race primitive de l'*Elephas meridionalis,* où les molaires ont un petit nombre de collines basses, enduites d'un émail épais, mais à la race modifiée de cette espèce, c'est-à-dire au type du Val d'Arno [Footnote: 'Il y a des dents du Val d'Arno qui, par leur allongement et leurs lames nombreuses, étroites, à émail mince, ressem-

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Explanatory Legend of Mammonteus, Parelephas, and Archidiskodon Crania

Key to Osborn's determinations in the present Memoir of the crania
illustrated in figure 865.

Fig. 865. The inscriptions on this figure were written before the phylogenetic relationships of these crania were fully understood and before *Elephas trogontherii* was clearly separated from *E. primigenius.* The outline figures taken from various authors are arranged in three sections: Upper, including *Elephas primigenius* and *E. trogontherii*; middle, including *E. meridionalis,* and lower, including *E. planifrons.*

(A) Skulls of True Mammonteus primigenius (*a*); of Parelephas trogontherii (*b*)

2. Typical *Mammonteus primigenius.* *E. primigenius* ref., after Falconer, 1846 [1847, Pl. xliii, fig. xxiv].
(*a*) 1. *Mammonteus primigenius.* *E. primigenius* ref., after Pohlig, 1891, p. 384, fig. 120.
5. " " *E. primigenius* ref., after Pohlig, 1891, p. 384, fig. 120 (rev.).

3. Typical *Parelephas trogontherii.* *E. primigenius trogontherii* (female), after Pohlig, 1891, p. 386, fig. 121.
(*b*) 4. " " " Side view of same cranium as above.
6. " " " *E. primigenius* ref., after Falconer, 1846 [1847, Pl. xlv, fig. xxiv (rev.)].

(B) Skulls of Archidiskodon meridionalis; (C) Skull of A. imperator

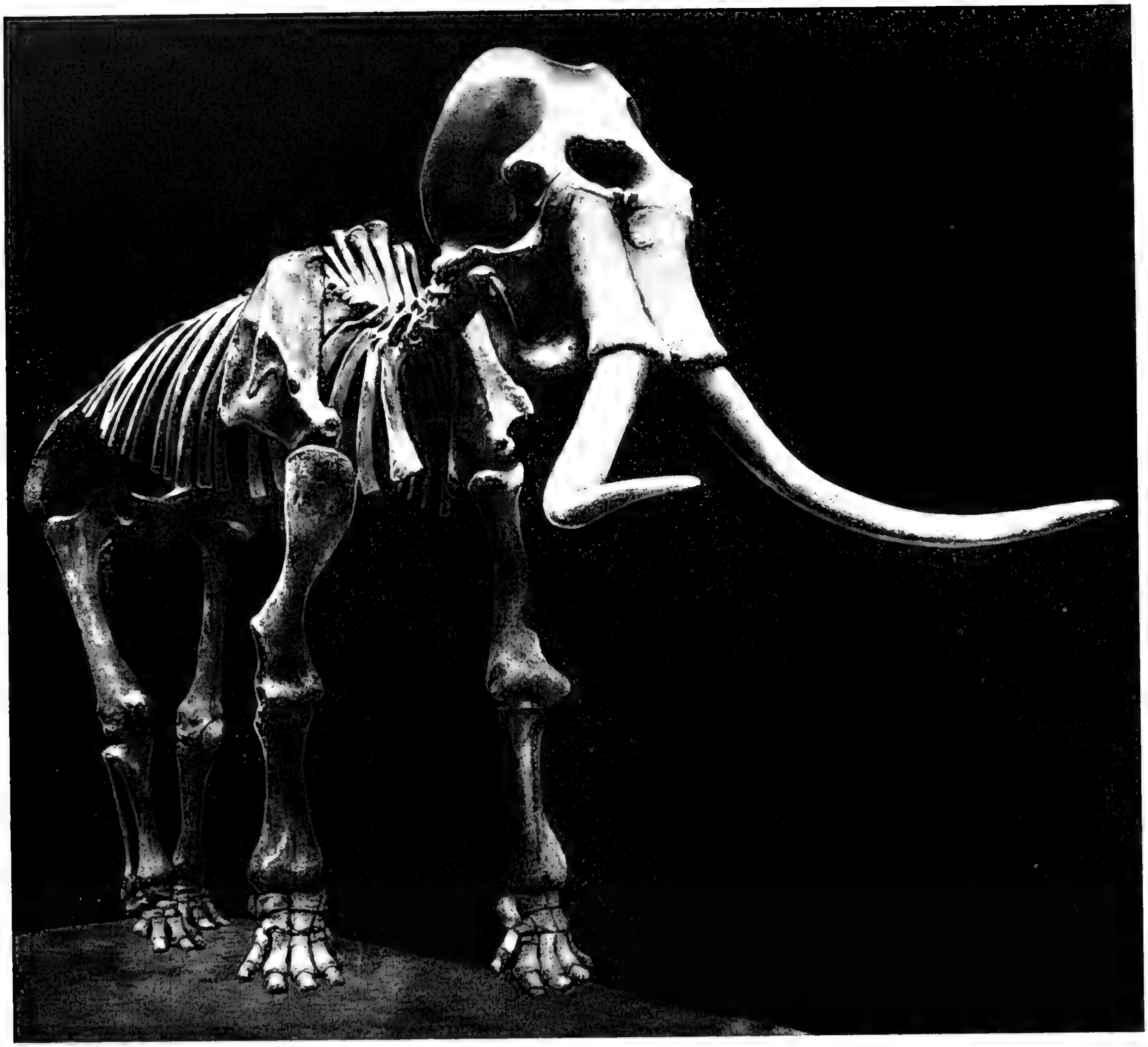
7. *Archidiskodon meridionalis.* *E. meridionalis* lectotype, after Falconer, 1846 [1847, Pl. xlii, fig. xix], Val d'Arno, Italy = Cranium C of Nesti.
13. " " *E. meridionalis* lectotype, after Falconer, 1846 [1847, Pl. xliv, fig. xix (rev.)]. Side view of same skull as above.
9. " " *E. meridionalis* Nesti, cotype, 1825, Tav. i, fig. 3, Val d'Arno, Italy = Cranium A of Nesti.
8. " " *E. meridionalis* cotype, after Weithofer, 1890, Taf. i, fig. 1 = Cranium A of Nesti, Florence Museum.
15. " " *E. meridionalis* cotype, after Weithofer, 1890, Taf. i, fig. 2 = Cranium A of Nesti, Florence Museum.
14. " " *E. meridionalis* lectotype, after Weithofer, 1890, Taf. ii, fig. 1 (rev.), Val d'Arno, Italy = Cranium C of Nesti. Side view of same skull as that figured by Falconer above.
11, 11*a*. ?Female of *Archidiskodon meridionalis.* *E. lyrodon* Weithofer, type, 1890, Taf. v, fig. 1, Taf. iv, fig. 2 (rev.).
12. ?Female of *Archidiskodon meridionalis.* *E. lyrodon* ref., after Weithofer, 1890, Taf. vi, figs. 1, 2.

(C) 10. *Archidiskodon imperator.* *E. imperator* ref., Museum of History, Science and Art, Los Angeles, Calif. From Rancho La Brea.

(D) Skulls of Archidiskodon planifrons, Upper Pliocene of India

16. *Archidiskodon planifrons.* *E. planifrons* ref., after Falconer, 1846 [1847, Pl. xlii, fig. xvi], Pinjor horizon, India.
17. " " *E. planifrons* ref., after Falconer, 1846 [1845, Pl. x, fig. 1 (rev.)].
18. " " *E. planifrons* ref., after Falconer, 1846 [1845, Pl. ix (skull); Pl. xi, fig. 3 (jaw)].
19. " " *E. planifrons* ref., after Falconer, 1846 [1847, Pl. xliv, fig. xvi (rev.)].

We observe that in its front and side cranial aspects *Archidiskodon planifrons* is very primitive. In the two crania of *A. meridionalis* shown in side view, we observe a transition from the *A. planifrons* type to the more typical *A. meridionalis,* namely, *E. meridionalis* Weithofer, 1890, Taf. i, fig. 2; this skull is decidedly *hypsicephalic*; it strongly resembles in this feature the skull of *A. imperator,* also the skull of the typical *Mammonteus primigenius*; it differs profoundly from the skull of *Parelephas trogontherii* which has a profile more like that of *Elephas indicus.*



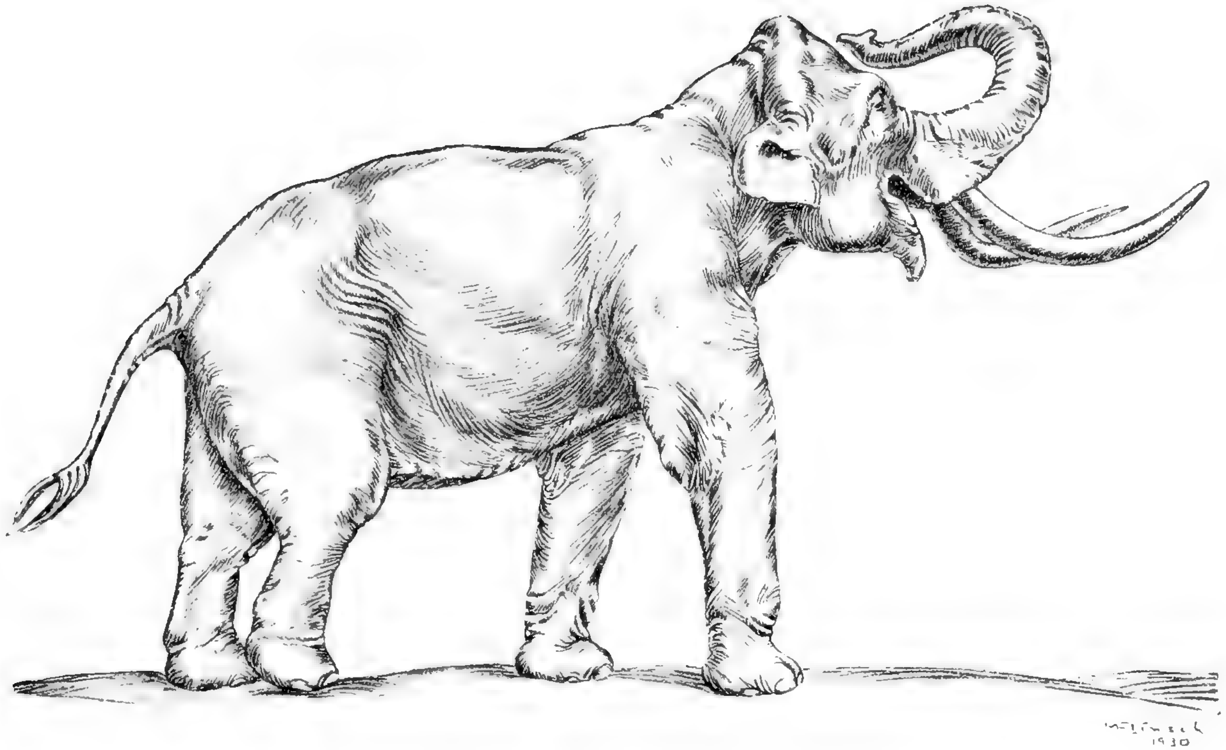
ARCHIDISKODON MERIDIONALIS OF DURFORT, OF CROMERIAN OR NORFOLKIAN, LOWER PLEISTOCENE, AGE

Fig. 866. Skeleton (largely restored) of *Elephas* [= *Archidiskodon*] *meridionalis*, known as "l'Éléphant de Durfort," as restored and mounted in the Galerie de Paléontologie, Muséum d'Histoire Naturelle, Paris (Gaudry, 1893); discovered in 1869 near the village of Durfort, Gard, between Nîmes and Vigan; excavation completed June 21, 1873; restored under the direction of Gervais; installed in 1885; fully compared, measured, and figured by Gaudry in 1893. One-thirtieth natural size. Photograph by courtesy of Dr. Marcellin Boule.

Doctor Boule writes as to the parts restored, or "artificiels," in this Durfort skeleton (letter of December 12, 1921): "Je n'ai pas voulu détériorer cette photographie en marquant sur elle les parties restaurées, mais voici la nomenclature des principaux éléments de squelette qu'un examen assez sommaire et superficiel, le seul qu'on puisse faire en cette saison sans avoir recours à des échafaudages, nous a montré être *artificiels*: *Crâne*. Parties supérieure et postérieure. Alvéoles des défenses, en partie. Extrémité antérieure de la défense droite. *Mandibule* droite.—Branches montantes, extrémité de la symphyse. *Colonne* vertébrale. Quelques vertèbres cervicales, lombaires et caudales. *Côtes.* –La plupart sont restaurées ou en plâtre. *Membres* antérieurs.—Un scaphoïde et 3 ou 4 phalanges. *Membres* postérieurs. Tête supérieure du tibia droit et péroné droit."

Compare figure 868, lateral view of the same skeleton, modified after Gaudry, 1893, Plate.

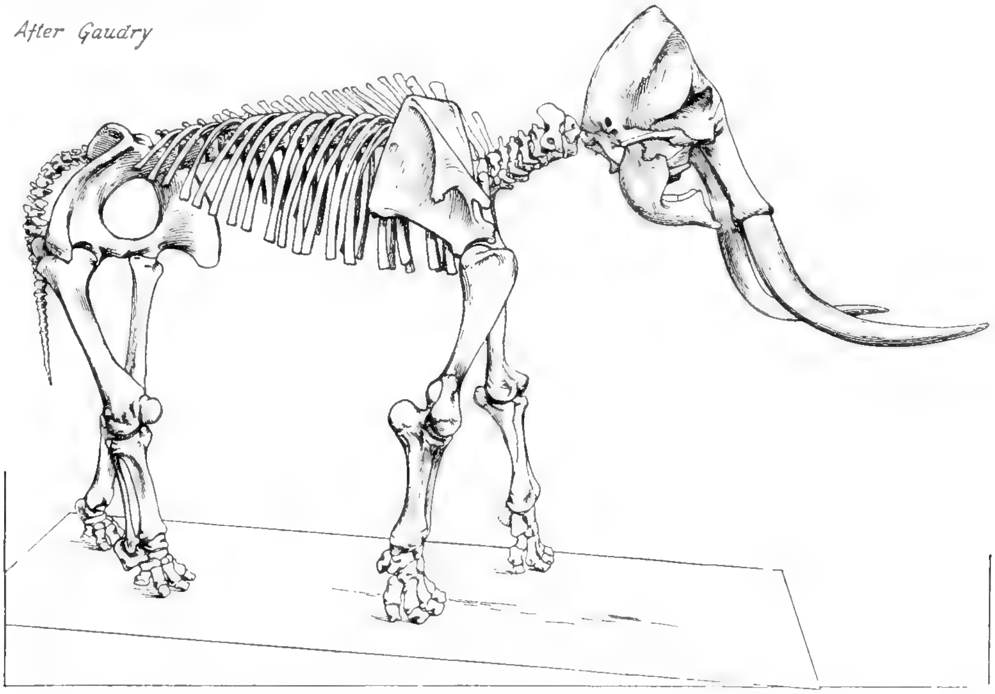
Ridge-plates (Gaudry, 1893, p. 13): "Les molaires de l'Éléphant de Durfort ont des lames plus nombreuses et plus minces que celles de Semur, de Chagny, de Pérols, près de Montpellier, de Randan (Allier), du Monte Verde, près de Rome, que nous possédons au Muséum. . . Elles ressemblent presque autant aux dents de l'*Elephas antiquus* appelées *intermedius* qu'aux dents de l'*E. meridionalis.*" Referred by Gaudry to a progressive stage of *Elephas* [= *Archidiskodon*] *meridionalis.*



Archidiskodon meridionalis of Durfort, France

Restoration by Margret Flinsch Buba, May 23, 1930, one-fiftieth natural size

Fig. 867. Primitive stage, drawn directly from skeleton in Paris Museum, representing an animal of young adult age. Observe the half-grown tusks, the proboscis elevated in order to expose the long slender rostrum of the lower jaw characteristic of this species. Ear drawn small, of somewhat primitive contour. Rather drooping posterior quarters, drawn from supposed mammontine affinities. Digits 5 in the manus and 4 in the pes, ungues 5 and 4.



Durfort Skeleton of Archidiskodon meridionalis. Lower Pleistocene Age. About one-fiftieth natural size. Compare Figure 866

Fig. 868. Lateral view of "l'Éléphant de Durfort" in the Galerie de Paléontologie, Muséum d'Histoire Naturelle, Paris (Gaudry, 1893); for details see legend of figure 866, for description see pages 977, 980 of the present Memoir.

This classic skeleton, redrawn after photographic plate in Gaudry (1893), exhibits the right *lateral* view as compared with the oblique anterior view introduced in figure 866 above, and enables us to estimate clearly the height of this animal in the restoration (Fig. 867).

According to Gaudry's measurements, the skeletal shoulder height from the ground to the top of the anterior dorsal spine is 3830 mm. (12 ft. 6¾ in.); summit of occiput to the ground 4150 mm. (13 ft. 7⅓ in.), as mounted.

According to Osborn's measurements, the skeletal shoulder height is 3499 mm. (11 ft. 5⅔ in.).

The method of the present author of estimating the skeletal shoulder height is to take the standing height of the forelimb to the top of the scapula. This measurement was arrived at through the observation of the author, when sitting upon a living elephant, that by placing his thumbs together on the tallest spine between the scapulæ with the extended small fingers resting on the top of each scapula, the spines were found to be on a level with the scapulæ, the latter rising and lowering a few inches above and below the spines in the process of walking. This accounts (in the present instance) for the smaller measurement given by Osborn (3499 mm.) in the skeleton and, after adding the usual 6⅓ per cent, of 3721 mm. or 12 ft. 2½ in. in the flesh (see restoration to the same one-fiftieth scale, Fig. 867).

blent plus à celles de l'*Elephas antiquus* qu'à certaines dents d'*Elephas meridionalis*.'] et du Forest-bed où les collines commencent à se multiplier, à diminuer d'épaisseur, à augmenter de hauteur. Elles ressemblent presque autant aux dents de l'*Elephas antiquus* appelées *intermedius* qu'aux dents de l'*E. meridionalis*. Il me semble en outre que les défenses sont plus courbées et que les os des pattes sont moins épais que dans les *E. meridionalis* les plus anciens; en cela l'animal de Durfort marque encore une tendance vers les Éléphants quaternaires. Les molaires de l'Éléphant de Durfort ont des lames plus nombreuses et plus minces que celles de Semur, de Chagny, de Pérols, près de Montpellier, de Randan (Allier), du Monte Verde, près de Rome, que nous possédons au Muséum."

"J'ai dernièrement, avec M. Marcellin Boule, travaillé à dégager un énorme *Elephas meridionalis* qui a été découvert dans les sables volcaniques de Senèze, près de Brioude, par un savant archéologue, M. Le Blanc. Ses dents contrastent singulièrement avec celles de l'*Elephas meridionalis* de Durfort par leurs collines basses, très grosses, à émail épais. Elles annoncent un animal encore plus gigantesque."

The dimensions given by Gaudry (p. 19) are as follows:

"Hauteur du squelette, à la tête	$4^{m}15$
du squelette, au garrot	3 83
Longueur du squelette avec les défenses, la queue n'étant pas allongée et étant placée dans sa position naturelle	6 80"

The associated *fauna* is described by Gaudry (*op. cit.*, p. 14) as follows: "En réalité, tous les os de mammifères de Durfort que nous avons dans le Muséum se rapportent seulement à 4 Éléphants, 4 Hippopotames, 5 Bisons, 4 Cerfs, 1 Rhinocéros, 1 Cheval." The associated *flora* is rich in oak trees (*op. cit.*, p. 17): ". . . il y a eu là une véritable forêt de ces arbres, comprenant au moins quatre espèces." There were also beeches.

Archidiskodon meridionalis cromerensis

Depéret and Mayet, 1923

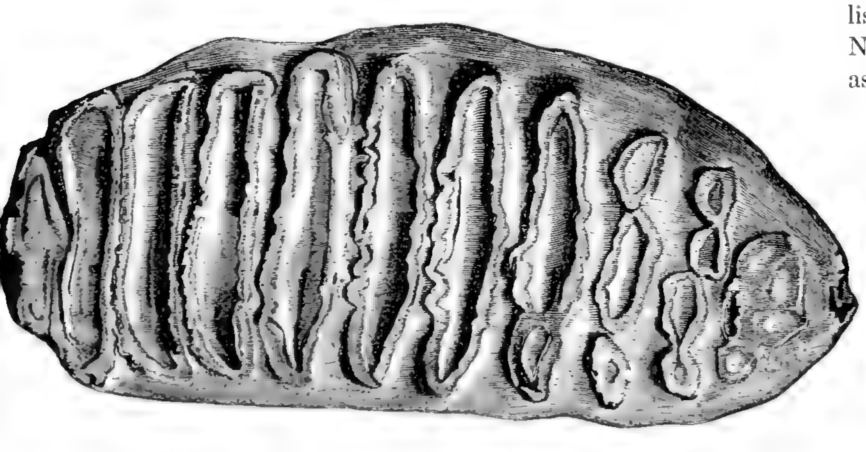
Figures 870, 871F

Kessingland, Suffolk, England. Age: Cromer Forest Bed of Norfolk East Anglia = Cromerian or Norfolkian stage, *1st Interglacial* of authors. See geologic note above on the Forest Bed or Cromerian (p. 970). Lower Pleistocene.

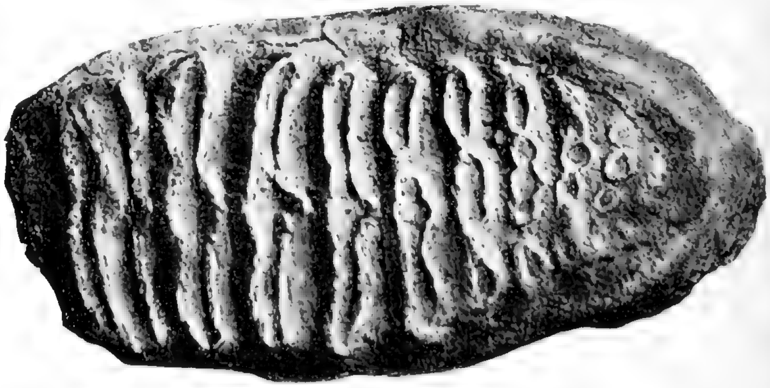
Specific Characters (compare Depéret and Mayet, 1923, p. 153).—M^3 with $+10\frac{1}{2}$ (i.e., 13?) ridge-plates; very broad, diameters 180 mm. × 80 mm.; laminar frequency 6–5 in 10 cm., greatly exceeding the typical *E. meridionalis* (5); enamel of moderate thickness, much plicated, with salient loxodont sinus on posterior border.

According to Depéret and Mayet this subspecies is regarded as a final phase of the Lower Pleistocene Forest Bed age of England, a horizon which Osborn (1922.570) regards as corresponding with the *1st Interglacial* period, the period at which the true *Archidiskodon meridionalis* makes its last appearance in southern Europe.

Giant grinders of the southern mammoth, *Archidiskodon meridionalis*, occur in the Forest Bed fauna (Osborn, 1922.563, p. 440, list of vertebrata, etc.). The 12+ ridge-plated tooth (Savin Mus. No. 197—Fig. 871 F of the present Memoir) is 109 mm. in breadth, as compared with 80 mm. in Depéret and Mayet's type (see Fig.



Elephas antiquus.—The first left upper true molar; from the Pleistocene of Grays, Essex. ¾. The lower border of the figure is the inner border of the specimen.



Referred Archidiskodon meridionalis from the Lower Pleistocene of Essex (Left), and Type of Archidiskodon meridionalis cromerensis of Norfolk (Right)

Fig. 869. Eleven plated grinder, ?l.M^3, of *Archidiskodon meridionalis* illustrated and erroneously referred by Lydekker to "*Elephas antiquus.*" After Lydekker, 1886.2, p. 125, fig. 26 (Brit. Mus. M.2004). Three-fourths natural size.

Lydekker described (p. 126) this tooth as follows: "The first left upper true molar in a half-worn condition; probably from Grays. This specimen (woodcut, fig. 26) agrees very closely in general characters with the Japanese molar of *E. namadicus* figured on page 168 [Fig. 1189 of present Memoir]; it is noticed by Leith-Adams, *op. cit.* [1877–1881], p. 22. *No history.*" Compare figure 870 opposite, type of the *Elephas meridionalis cromerensis* of Depéret and Mayet.

Fig. 870. Type l.M^3 of *Elephas meridionalis cromerensis* Depóret and Mayet, 1923, Pl. ix, fig. 1, p. 220, about one-half natural size:

"Fig. 1.—*Elephas meridionalis* mutation *cromerensis*, du Forest-Bed, à Kessingland. M^3 gauche avec fossilisation et patine caractéristiques (Iron-pan). (Voir, p. 152.) Ce très beau document paléontologique qui ressemble de façon frappante à la dent n° 33,334 du British Museum—fait partie de la collection du Dr. Pontier. Photographie obligeamment communiquée par notre savant confrère."

(Osborn) Brit. Mus. 33,334 from the Forest Bed of the Norfolk coast (see Leith Adams, 1877–1881, Pl. xxiv, fig. 2, p. 198) agrees closely with the above Depéret and Mayet type.

871 as compared with Fig. 870, Depéret and Mayet's type). Also very numerous *A. meridionalis* grinders in the British Museum are catalogued by Lydekker (1886.2, pp. 108–113), mostly entered as "dredged off Happisburgh" or from the Forest Bed of Cromer, Norfolk. Two grinders (cf. Fig. 862) figured by Falconer agree in width with the measurements of Depéret and Mayet's type (80 mm.). The superior grinders of *A. planifrons* from the Siwaliks vary in width from 88 to 100 mm.; the inferior grinders vary in width from 78 to 109 mm. (see Table VII above). There is therefore no appreciable change in the breadth of the grinding teeth between *A. planifrons* and these specimens of *A. meridionalis* (see Osborn's remarks above, page 970, on the Forest Bed fauna).

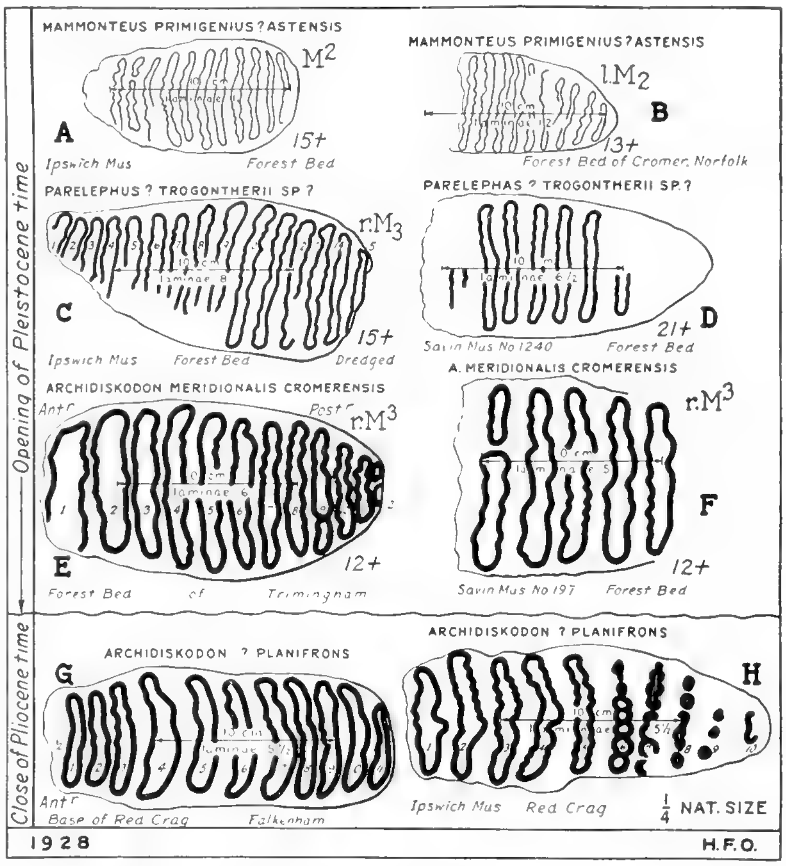
Elephas meridionalis, mutation *cromerensis* Depéret and Mayet, 1923. "Monographie des Éléphants Pliocènes d'Europe et de l'Afrique du Nord," Deuxième Partie of "Les Éléphants Pliocènes." Ann. Univ. de Lyon, Nouvelle Série, I.—Sciences, Médecine. Fasc. 43, pp. 150, 152, 157. TYPE.—A third superior molar of the left side, l.M^3. HORIZON AND LOCALITY.—Forest Bed at Kessingland, England, Lower Pleistocene. TYPE FIGURE.—*Op. cit.*, Pl. IX, fig. 1.

TYPE DESCRIPTION.—(*Op. cit.*, p. 153): "Cette dernière pièce (pl. IX, fig. 1) est une M^3 très usée en avant où manquent sans doute plusieurs lames. La couronne est large (80 mm.) pour une longueur conservée de 180 millimètres. On n'observe plus que 10 lames plus le talon postérieur. L'émail est peu épais et très plissé sur toute l'épaisseur des bandelettes; il existe de sinus loxodontes assez saillants du côté postérieur. La fréquence laminaire atteint 6, 5 pour 10 centimètres, chiffre très supérieur à celui de l'*E. meridionalis* type (5) et même à celui de l'animal de Saint-Prest (5, 5). C 'est le caractère essentiel qui permettra toujours de reconnaître la mutation *cromerensis* de l'horizon du Forest-bed."

ASCENDING MUTATIONS OF ARCHIDISKODON MERIDIONALIS

Revision by Depéret and Mayet (1923)

Depéret and Mayet give a detailed description (*op. cit.*, pp. 125–160) of all the principal known remains referable to this great species, showing that the archaic forms of skull, jaw, and molar



PRIMITIVE GRINDING TEETH OF THE MAMMONTINÆ: ARCHIDISKODON, PARELEPHAS, MAMMONTEUS

Fig. 871. Molar ridge-plate structure and laminar frequency in the Forest Bed (Lower Pleistocene) and Red Crag (Upper Pliocene) elephants, after pencil sketches by the author in 1926 of specimens in the Ipswich and Savin (Cromer) Museums. All figures reproduced one-fourth natural size. Compare Depéret and Mayet, 1923, Pls. IX and XI.

PLEISTOCENE	A, Cromer Forest Bed (Ipswich Mus.)	*Mammonteus primigenius*(?) *astensis* Depéret and Mayet, M^2 (?), 11 ridge-plates or laminæ in 10 cm.; total of 15+ ridge-plates.
	B, Cromer Forest Bed	*Mammonteus primigenius*(?) *astensis*(?) Depéret and Mayet, l.M$_2$, 12 ridge-plates or laminæ in 10 cm.; total of 13+ ridge-plates.
	C, Cromer Forest Bed (Ipswich Mus., dredged)	*Parelephas* (?) *trogontherii* Pohlig, sp.(?),r.M$_3$, 8 ridge-plates or laminæ in 10 cm.; total of 15+ ridge-plates.
	D, Cromer Forest Bed (Savin Mus. 1240)	*Parelephas* (?) *trogontherii* Pohlig. sp.(?),[1] 6½ ridge-plates or laminæ in 10 cm.; total of 21+ ridge-plates. The determination of *Parelephas* (?) (C, D), corresponding to *P. trogontherii*, is somewhat doubtful. In the Savin Museum also occurs the typical *Hesperoloxodon antiquus ausonius* (?) with 12 ridge-plates.
	E, Cromer Forest Bed (Trimingham)	*Archidiskodon meridionalis cromerensis* Depéret and Mayet, r.M^3, 6 ridge-plates or laminæ in 10 cm.; total of 12+ ridge-plates.
	F, Cromer Forest Bed (Savin Mus. 197)	*Archidiskodon meridionalis cromerensis* Depéret and Mayet, r.M^3, only 5 ridge-plates or laminæ in 10 cm.; total of 12+ ridge-plates.
PLIOCENE	G, Red Crag (Falkenham)	*Archidiskodon planifrons* (?) Falconer and Cautley, or *E.* [*Hesperoloxodon*] *antiquus*, M$_3$, 5½ ridge-plates or laminæ in 10 cm.; total of +11 ridge-plates.
	H, Red Crag (Ipswich Mus.)	*Archidiskodon planifrons* (?) Falconer and Cautley, or *E.* [*Hesperoloxodon*] *antiquus*, 5½ ridge-plates or laminæ in 10 cm.; total of 10+ ridge-plates.

Observe that *Mammonteus* has very compact ridge-plates and fine enamel, that in the *Parelephas*(?) ridge-plates the enamel is somewhat thicker, that *Archidiskodon* has extremely broad and widely separated ridge-plates of coarse enamel. Compare Depéret and Mayet (1923, "Les Éléphants Pliocènes," Deuxième Partie, pp. 98–160) for molar diagrams of *A. planifrons* and *A. meridionalis, type ancien*, which correspond very closely with the present diagram (E, F, G, H).

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[1] Teeth similar to those of *Parelephas trogontherii* were selected by Pohlig, 1891 (1892), pp. 303, 304, as the cotypes of his *Elephas antiquus Nestii*, as shown in figure 941 below (Chap. XVII); referred by the present author to *Parelephas*(?) *trogontherii nestii*.

teeth approach *A. planifrons*, while the highly progressive forms (*op. cit.*, p. 153) approach the Lower Pleistocene stage of *Archidiskodon meridionalis cromerensis.*

History.—The southern mammoth is represented by superb specimens in the museums of France, which have recently been monographed by Depéret and Mayet (1923), reciting the studies of Nesti (1808, 1825), of Falconer (1868), of Weithofer (1890), of Cuvier, of de Blainville, of Owen, and of Gervais. The southern mammoth (*Elephas meridionalis*) was long confused with the northern mammoth (*Elephas primigenius*). Depéret and Mayet remark (*op. cit.*, p. 125): "C'est seulement après les voyages de Falconer en Italie et la publication des observations de ce savant en 1868 que les caractères l'*E. meridionalis* furent enfin reconnus et l'espèce définitivement admise par les paléontologistes."

Distribution.—As to geographic distribution, Depéret and Mayet conclude (*op. cit.*, p. 144): "L'*Elephas meridionalis*, dont le centre de dispersion principal est l'Italie, s'est répandu sur presque toute la surface de l'Europe tempérée: Russie du Sud, bassin du Danube, Allemagne du Sud, France, Angleterre, péninsule Ibérique, et enfin dans l'Afrique du Nord. Les gisements sont très nombreux; aussi notre étude descriptive se limitera-t-elle aux pièces les plus importantes, notamment les Miii, et surtout à celles dont nous avons pu obtenir des photographies directes, grâce à l'obligeance de divers de nos confrères, que nous citerons au cours de cet exposé. Comme en Italie, nous pourrons y reconnaître trois mutations successives de l'espèce: A. *Forme archaïque.* B. *Forme type.* C. *Forme évoluée ou récente.*"

Mutations.—The chronological mutations close as follows (*op. cit.*, p. 150):

"2° *Mutation* de l'étage Cromérien (Sicilien) qui représente le début du Quaternaire et que nous désignerons sous le nom de *mutation cromerensis.*"

"1° *Mutation* de l'étage Saint-Prestien, que nous rapportons à l'extrême fin du Pliocène."

Ascending Series of Stratigraphic Mutations of A. meridionalis, Beginning of Extinction of the Phylum in Europe (Depéret and Mayet, 1923, p. 157)

"I. *Elephas planifrons.* Couronne très basse (hauteur d'une lame médiane moyennement usée, 50 à 60 millimètres) et large; lames transverses peu nombreuses (10 chez M^3 et 10–11 chez M_3); grand écartement des lames (fréquence laminaire 3, 5 à 4 lames par 10 centimètres de longueur de la couronne); émail très épais, à larges ondulations limitées à la paroi externe des bandelettes; sinus loxodontes très saillants et assez réguliers, surtout en avant."

"II. *Elephas meridionalis, mutation archaïque.* Couronne large et basse (H = 60 à 75 millimètres); fréquence laminaire 4, 5; émail épais à larges plis peu profonds; sinus loxodontes plus irréguliers."

"III. *Elephas meridionalis, mutation type.* Couronne large et un peu moins basse (H = 75 à 90 millimètres); M^3 avec 11 à 13 lames, M_3 avec 11 à 14; fréquence laminaire 5. Email moins épais et à plis plus serrés qui intéressent presque toute l'épaisseur des bandelettes; sinus loxodontes peu accusés et irréguliers."

"IV. *Elephas meridionalis, mutation du Saint-Prestien* (fin du Pliocène). Couronne large et moins basse (H = 90 à 95 millimètres); 1 ou 2 lames de plus aux Miii; fréquence laminaire 5, 5; émail plus mince à plis serrés affectant toute l'épaisseur de la bandelette sinus loxodontes faibles et irréguliers."

"V. *Elephas meridionalis, mutation cromerensis* (forme quaternaire du Forest-bed). Couronne moins large et plus haute (H = 90 à 95 millimètres); 12 à 15 lames aux M^3, de 12 à 16 aux M_3 sur les molaires entières. Fréquence laminaire 6 à 6, 5; émail beaucoup plus mince, à plis nombreux et serrés affectant toute l'épaisseur de la bandelette; sinus loxodontes peu accusés et très irréguliers."

"Extinction du rameau."

Specific Characters of Archidiskodon meridionalis (Depéret and Mayet, 1923, p. 156).—"1° *Crâne.*—Le crâne connu surtout par les belles pièces de Florence, est caractérisé par: une boîte cérébrale arrondie très large en haut et à bords presque parallèles; un vertex peu élevé arrondi, mais non prolongé en dôme; une région fronto-pariétale excavée chez l'adulte une ouverture nasale reculée très en arrière, étroite et très étendue en travers, surmontée d'une épine nasale saillante; des arcades zygomatiques déjetées vers le bas; des alvéoles des défenses rapprochés et subparallèles."

"2° *Mandibule.*—La mandibule offre des particularités intéressantes: chez le jeune et la femelle, la symphyse se prolonge par un bec presque horizontal qui continue le bord inférieur de l'os. Chez le mâle adulte, au contraire, la mandibule est dépourvue de bec et présente une terminaison mousse et obtuse, avec parfois une toute petite pointe médiane insignifiante (squelette de Durfort). On a déjà dit que l'*E. planifrons* possède dans les deux sexes un bec mandibulaire beaucoup plus fort et déjeté presque verticalement vers le bas."

"3° *Défenses.*—Les défenses sont, chez le jeune et la femelle, divergentes dès la base et assez fortement spiralées. Chez le mâle adulte, elles sont presque parallèles à leur base, se dirigent en bas et en dehors, décrivant ensuite une légère spirale dont les pointes reviennent un peu en dedans. Chez l'*E. planifrons*, les défenses sont encore plus parallèles et ont une courbure concave moins prononcée."

"4° *Molaires.*—Les molaires de l'*E. meridionalis* sont de même type général que celles de l'*E. planifrons*: couronne large et basse, lames transverses peu nombreuses, émail épais et généralement peu plissé; sinus loxodontes assez accusés mais inconstants."

THE ARCHIDISKODON MERIDIONALIS PHYLUM MIGRATES TO AMERICA

Osborn (1924) welcomes this splendid résumé by his friends Depéret and Mayet of specific characters and mutations of *A. planifrons* and *A. meridionalis*, but does not agree that there is adequate evidence that this phylum became extinct, for it appears quite certain that the *Archidiskodon meridionalis* type migrated from Asia into North America and became ancestral to *Archidiskodon imperator* of Nebraska. Nor does Osborn believe that the *meridionalis* of Italy and France is in any way related to the

Elephas hysudricus of the Upper Siwaliks treated in Chapter XX. The cranial types in these two animals are fundamentally distinct.

If Africa should prove to be the home of *Archidiskodon*, as appears probable through the discovery of two new primitive species in southern Africa, namely, *A. subplanifrons* and *A. broomi*, it may indicate that members of the generic phylum *Archidiskodon* originated in Africa and migrated northward into Europe and eastward into southern Asia rather than having followed the generally accepted reverse line of migration from southern Asia westward into Europe and Africa.

[It will be observed that Professor Osborn wrote this portion of the Memoir in 1924. From that time onward he constantly sought new evidence to test his hypothesis of an African center of dispersal of the Proboscidea (see Fig. 815). A decade of study (1924–1934) only confirmed him in his belief and in 1934 he wrote an article in American Museum Novitates (Osborn, 1934.925) entitled "Primitive *Archidiskodon* and *Palaeoloxodon* of South Africa," on the basis of which the following section has been revised but in no sense have the views of the author been changed otherwise than appear in his own writings.—Editor.]

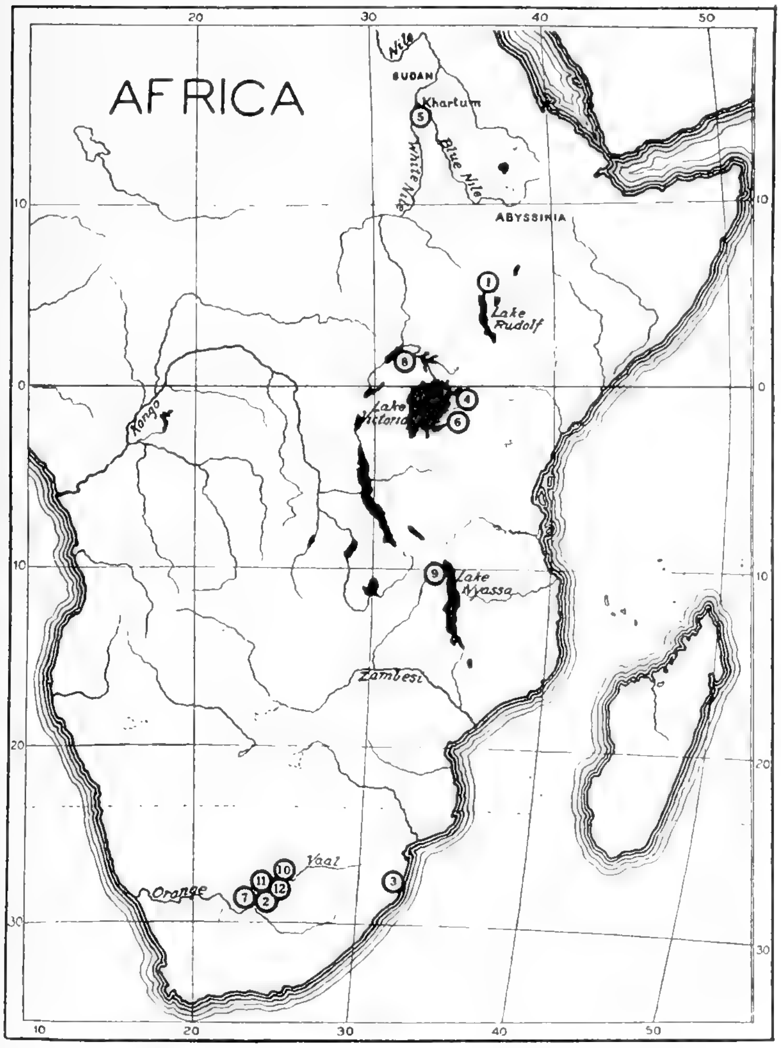

FIG. 872. FOSSIL PROBOSCIDEA ROUTE FROM SOUTHERN EQUATORIAL AFRICA

Compare Andrews (1911), Dietrich (1916), Haughton (1922), Hopwood (1926), Dart (1927), and Broom (1928). [Since 1928 other species have been described (see pp. 986–993 below).—Editor.]

(2) *Archidiskodon subplanifrons*, Sydney-on-Vaal, Vaal River diggings, near Kimberley.

(7) *Metarchidiskodon griqua*, Vaal River diggings, Griqualand West.

(10) *Archidiskodon broomi*, The Bend, Vaal River, near Kimberley.

(11) *Palæoloxodon transvaalensis*, Bloemhof, southwestern Transvaal.

(12) *Palæoloxodon sheppardi*, Bloemhof, southwestern Transvaal.

(3) *Loxodonta zulu*, Zululand.

(9) *Mastodon* sp. (?), northwest of Lake Nyassa, near Uraha Hill.

(4) *Deinotherium hobleyi*, Karungu, near Victoria Nyanza, Tanganyika Territory.

(6) *Palæoloxodon recki*, near Oldoway, Serrengetisteppe, northern Tanganyika Territory.

(8) *Metarchidiskodon griqua*, Kaiso Bone-beds, near Albert Nyanza.

(5) *Mastodon* sp. (?), near Khartum, Sudan.

(1) *Deinotherium* ref., *Elephas* ref., Lake Rudolf.

2. ARCHIDISKODONTS AND METARCHIDISKODONTS OF SOUTH AFRICA

(Osborn, 1934.925, pp. 1—10): "Every year brings fresh proof that Africa was the center of the origin and adaptive radiation of the Proboscidea. Since 1907 numerous more or less primitive superior and inferior grinding teeth have been discovered from the Vaal River terraces and other localities of the Transvaal, South Africa. The geologic level and localities are chiefly on the (1) higher and most ancient terrace (200–300 feet) of the Vaal River; (2) middle terrace (60–80 feet) of the Vaal River; (3) lowest and most recent terrace (40 feet) of the Vaal River.

Theoretically the lowest terrace may be as old as the lower levels of the middle terrace. Flint implements occur in the middle and lower terraces only (Dart, 1929). In Osborn's opinion the *Archidiskodon subplanifrons*, and *Archidiskodon proplanifrons*, . . . types found in the middle terrace were washed in from an older Pliocene horizon."

"Certain of the Transvaal grinding teeth surely belong to very primitive stages of *Archidiskodon*; others probably belong to primitive stages of *Palaeoloxodon* and were originally referred to *Loxodonta*, to *Archidiskodon* and to *Pilgrimia*.[1] Only by careful comparison and analysis is it possible to separate the species belonging to these several genera from each other."

"Up to the present time [1934[2]] the nineteen species described by W. B. Scott (1907), Raymond A. Dart (1927, 1929), S. H. Haughton (1922, 1932) and H. F. Osborn (1928) are provisionally referred as follows:

LOCALITY	ORIGINAL REFERENCE	PRESENT GENERIC REFERENCE
Zululand	*Loxodon zulu* Scott, 1907	= *Loxodonta*
?Middle terrace, Vaal River	*Loxodonta griqua* Haughton, 1922	= *Metarchidiskodon*, n.g.
Lowest terrace, Vaal River	*Archidiskodon transvaalensis* Dart, 1927	= *Palaeoloxodon*
Lowest terrace, Vaal River	*Archidiskodon sheppardi* Dart, 1927	= *Palaeoloxodon*
?Middle terrace (lower), Vaal River	*Archidiskodon subplanifrons* Osborn, 1928	= *Archidiskodon*
Lowest terrace, Vaal River	*Archidiskodon broomi* Osborn, 1928	= *Archidiskodon*
Middle terrace (lower), Sydney-on-Vaal	*Archidiskodon vanalpheni* Dart, 1929	= *Archidiskodon*
Middle terrace (lower), Sydney-on-Vaal	*Archidiskodon loxodontoides* Dart, 1929	= *Archidiskodon*
Middle terrace (lower), Sydney-on-Vaal	*Archidiskodon milletti* Dart, 1929	= *Archidiskodon*
?Middle terrace, Vaal River	*Archidiskodon andrewsi* Dart, 1929	= *?Palaeoloxodon*
Lowest terrace, Vaal River	*Archidiskodon hanekomi* Dart, 1929	= *Palaeoloxodon*
Middle terrace, Vaal River	*Archidiskodon yorki* Dart, 1929	= *Archidiskodon*
Lowest terrace, Vaal River	*Pilgrimia yorki* Dart, 1929	= *Palaeoloxodon*
Lowest terrace, Vaal River	*Pilgrimia wilmani* Dart, 1929	= *Palaeoloxodon*
Pniel Estate, ? River	*Pilgrimia kuhni* Dart, 1929	= *Palaeoloxodon*
?Recent, Limpopo River	*Loxodonta prima* Dart, 1929	= *Loxodonta*
?Recent, Steelpoort River	*Loxodonta africana* var. *obliqua* Dart, 1932 [1929]	= *Loxodonta*
?Middle Terrace, Vaal River	*Pilgrimia archidiskodontoides* Haughton, 1932	= *Palaeoloxodon*
Higher terrace, Vaal River	*Pilgrimia subantiqua* Haughton, 1932	= *Loxodonta*"

"Summing up these species, the ascending geologic level records (Dart, Haughton) are as follows" [Table VIII of the present Memoir]:

TABLE VIII.—"FAUNAL DISTRIBUTION ON THE RIVER TERRACES OF THE TRANSVAAL"

"Middle Terrace	Middle terrace, 60-80 feet. Sydney-on-Vaal. ?Lower Pleistocene	Lowest terrace, 40 feet. With flint implements. ?Middle Pleistocene. Bloemhof	Recent—4 feet. Pleistocene
	Upper levels:	Upper levels:	Levels unknown:
*?A. subplanifrons**	*A. yorki*	*Bubalis baini*	*?P. hanekomi*
*?A. proplanifrons***	*A. broomi*	*Equus capensis*	*?L. subantiqua*
Older than the Upper Pliocene *A. planifrons* of the Siwaliks, India	*M. griqua*		*?P. archidiskodontoides*
	Lower levels:	Lowest levels:	Recent:
*actually recorded from a depth of 50-60 feet, middle terrace (60-80 ft.)	*P. andrewsi*	*P. transvaalensis*	*L. prima*
	A. vanalpheni	*P. sheppardi*	*L. africana* var. *obliqua*"
	A. milletti	*P. yorki*	
**at a depth of 56 feet, middle terrace, Vaal River	*A. loxodontoides*	*P. wilmani*	
	Bunolophodon ?gen. ?sp.	*P. kuhni*	

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[1] *Pilgrimia* Osborn (December 20, 1924) is antedated by *Palaeoloxodon* Matsumoto (September 20, 1924).

[2] [To these might be added *Archidiskodon proplanifrons* described in this article (Osborn, 1934.925, p. 10), see page 986, figure 873, below.—Editor.]

"By their outstanding characters these species divide into four groups as follows" [Table IX of the present Memoir]:

TABLE IX. "PROVISIONAL GROUPING OF SPECIES REFERRED TO FOUR TRANSVAAL GENERA"

"*A. subplanifrons* group	*M. griqua* group	*P. transvaalensis* group	*Loxodonta prima* group
Crowns very broad, 101 to 114 mm. Enamel very thick. Transverse conelets 4–6 (*A. proplanifrons*) to 22–24 (*A. broomi*). Cement enveloping crown. V-shaped cemented valleys at summits broader than dentinal areas. Loxodont sinus foldings double, less prominent, irregular. The mass of cement exceeds the mass of dentine.	Crowns relatively narrow, 86–94 mm. Enamel thick. Transverse crests 6–8. Cement areas narrower, not enveloping crown. Valleys U-shaped (*M. griqua*). Postsinus fold very prominent. Total enamel length unknown. The mass of cement exceeds the mass of dentine.	Crowns of M^3 relatively narrow, 70 mm. (*P. wilmani*) to 110 mm. (*P. transvaalensis*). Indices = 41 to 51. Enamel relatively thin; conelets finely crimped, i.e. numerous. Cement areas progressively narrower than dentinal areas. Cemented valleys greatly reduced. Ridge plates narrow and increasingly lofty, 128 mm. (*P. wilmani*), 259 mm. (*P. hanekomi*). Ridge plates per 100 mm. 4–6. Sinus foldings extremely reduced or progressively wanting. Valleys V-shaped (*P. andrewsi*).	Crowns relatively narrow, 74 mm. (*L. prima*) to 92 mm. (*L. subantiqua*). Enamel relatively thin, coarsely crimped; conelets numerous. Cement thin in middle, thick at edge. Ridge plates per 100 mm. = 4 (*L. africana obliqua*) to 5½ (*L. subantiqua*). Broad typical loxodont sinus expansion, double sinus foldings in contact. Total ridge plates 9 (*L. prima*) to 12–13 (*L. zulu*).
Cf. paratype of *A. meridionalis* Nesti of Val d'Arno, also Brit. Mus. M12641, M12642.	Cf. *A. planifrons rumanus* Stefanescu.		
In this group are the following species:	In this group may be the following species:	In this group are the following:	In this group are the following:
A. proplanifrons, A. subplanifrons, A. milletti, A. yorki, A. vanalpheni, A. broomi.	*M. griqua, P. andrewsi, A. loxodontoides.*	*P.* [=*Pilg.*] *kuhni, P.* [=*Pilg.*] *yorki, P.* [=*Pilg.*] *wilmani, P. archidiskodontoides, P. sheppardi, P. transvaalensis* and *P. hanekomi.* Also possibly *?P. andrewsi.* These seven or eight types are much more uniform in character than members of the *M. griqua* group, *P. sheppardi* and *P. transvaalensis* formerly being referred by Dart to *Archidiskodon. P. kuhni, P. yorki* and *P. wilmani* were referred by Dart to *Pilgrimia*; the prevailing characters relate them more closely to *Palaeoloxodon.*	*L. zulu, L.* [=*Pilg.*] *subantiqua, L. africana obliqua, L. prima.*
The ridge plate height increases from 55 in *A. proplanifrons* to 62e. in *A. subplanifrons,* to 118 in *A. milletti,* to 129 in *A. vanalpheni* and 110+ in *A. broomi.* Meanwhile the number of ridge plates in 100 mm. remains constant, namely, 3 in *A. proplanifrons,* 4½ in *A. planifrons* of India and 3 in *A. broomi.*	The generic relationships of this group are doubtful; the narrow crowns separate the types of *M. griqua* and of *P. andrewsi* from the broad crowns of the typical *Archidiskodon.* The U-shaped valley of *M. griqua* of Fig. 3 is quite distinct from the V-shaped valley of *P. andrewsi*; similar teeth have been discovered in Europe. It is probable that these teeth represent a genus distinct either from *Archidiskodon* or *Palaeoloxodon,* namely *Metarchidiskodon.*		These occur only on the more recent levels and are clearly related to the existing African elephant, distinguished by the above characters."

"The above phylogenetic arrangement is provisional. Only by the longitudinal sectioning method of Falconer is it possible to ascertain the true structural relationships of these Proboscidean molars. This is illustrated in the wide difference between sections of *M. griqua* (Fig. 3 [=Fig. 882]) and *P. andrewsi* (Fig. 5 [=Fig. 1139]), also in the wide difference between the sections of *A. subplanifrons* (Fig. 1 [=Fig. 875] and *A. proplanifrons* (Fig. 2 [=Fig.

873]). A very interesting comparison is that of the *planifrons* series of Africa and the Siwaliks of India analysed as follows" [Table X of the present Memoir]:

TABLE X.—"COMPARATIVE MEASUREMENTS OF THE PRIMITIVE SPECIES OF ARCHIDISKODON FROM THE TRANSVAAL AND FROM THE UPPER SIWALIKS OF INDIA"

	Tooth	Ridge plate height	Number of ridge plates	Ridge plates per 100 mm.	Enamel thickness	Loxodont sinus and folds	Conelets and crimping	Length	Breadth	Index	Enamel length
A. proplanifrons	RM^3	55	5½–6	3	5	Pre- and post sinus folds	Conelets = 4–6. Foldings	179	104	58	690
A. subplanifrons	RM$_3$	62e.	6	4	4	Pre- and post sinus folds.	Conelets = 6–8.	153	101	66	650
*A. planifrons**	RM$_3$	55	8e.	4½	3½	Pre- and post sinus folds, greatly reduced.	Conelets = 16 e. in ridge plate 4.	179	86	48	810e."

SYSTEMATIC DESCRIPTION OF SPECIES

Archidiskodon proplanifrons Osborn, 1934

Figures 873, 1239, Pl. XXI

Recorded from Gong-Gong near the Vaal River, South Africa. [Middle (?) Pliocene—see Fig. 1239.]

Archidiskodon proplanifrons Osborn, 1934. "Primitive *Archidiskodon* and *Palaeoloxodon* of South Africa." Amer. Mus. Novitates, No. 741, August 24, 1934, pp. 10–12 (Osborn, 1934.925).

TYPE.—"Third superior molar of the right side with six complete ridge plates, McGregor Museum 4334, cast Amer. Mus. 26969." HORIZON AND LOCALITY.—Recorded from Gong-Gong 'at a depth of 56 feet in the "Middle Terrace," under a boulder, at a distance of 450 yards from the Vaal River, thus occurring at a depth of from 10–15 feet below the level of the present river bed' "[1]. "Probably washed from older Pliocene deposits into the Pleistocene terrace gravels." [Middle Pliocene—see fig. 1239 below.—Editor.] TYPE FIGURE.—*Op. cit.*, p. 5, fig. 2.

TYPE DESCRIPTION.—(Osborn, 1934.925, p. 10): "Third superior molar of the right side with six complete ridge plates. McGregor Museum 4334, cast Amer. Mus. 26969. . . . Length = 179 mm., breadth = 104 mm., index = 58. Height of 5th ridge plate = 55 mm. Enamel length, restored = 690 mm. Average enamel thickness = 5 mm. Ridge plate, number = 5½–6. Postconcave, preconvex, with 4–5 rounded conelets in the posterior plates and 6–6+ conelets in the anterior plates, slight median foldings in each transverse plate."

"According to these measurements by Osborn, 1934, and those of Haughton, 1932, this type third right superior molar is the most primitive elephant tooth thus far discovered, even more primitive than *Archidiskodon subplanifrons*; it is indubitably an ancestral *Archidiskodon* with widely open valleys, summits of ridge plates much more widely separate than in *A. subplanifrons*, cement bathing the entire surface of the crown, median pair of conelets entirely distinct and undivided, total number of conelets estimated in the crown 26, as compared with total estimated number 34 in *A. subplanifrons*."

"The . . . species, *Archidiskodon subplanifrons* Osborn, 1928, and the new species *Archidiskodon proplanifrons*, as tested by these thickly enameled, deeply cemented, low and spreading ridge plated, relatively broadened, third superior and inferior grinding teeth, are totally distinct from certain of the relatively thin enameled, high ridge plated, less deeply cemented, relatively narrow molar types which have been erroneously referred by Haughton, Dart and Osborn to *Archidiskodon*, but more properly belong to *Palaeoloxodon* including its synonym *Pilgrimia*."

"*This is No. 19965, American Museum Brown Collection (Fig. 4 [Fig. 876]) from near Siswan, India. This is the most primitive stage found in the large series of the *Archidiskodon planifrons* molars collected by Barnum Brown in the Upper Pliocene Pinjor horizon of the Siwaliks, India."

[1] "Haughton, 1932, page 2."

Archidiskodon subplanifrons Osborn, 1928

Figures 815, 874, 875, 1235, 1239, Pl. xxi

Upper (?) Pliocene. Sydney-on-Vaal, Vaal River diggings, South Africa, on the banks of the river, at a depth of from 50 to 60 feet [Middle Pliocene—see Fig. 1239].

History.—The type tooth was discovered by Mr. W. Millett in the Vaal River diggings at Sydney-on-Vaal, South Africa, on the banks of the river, at a depth of from 50 to 60 feet; the geologic age is probably Upper Pliocene. Through the courtesy of Miss Wilman, Curator of the McGregor Museum at Kimberley, and of our correspondent Dr. R. Broom, the molar was forwarded January 20, 1927, to the American Museum for comparison and type description; in return for this courtesy, a number of facsimile casts were made, so that each specimen bears the inscription: *Archidiskodon subplanifrons*, McGregor Mus. 3920, type, cast A. M. 21924. This species was finally described and figured by Osborn in "Nature," April 28, 1928, pp. 672, 673, in comparison with *A. broomi*.

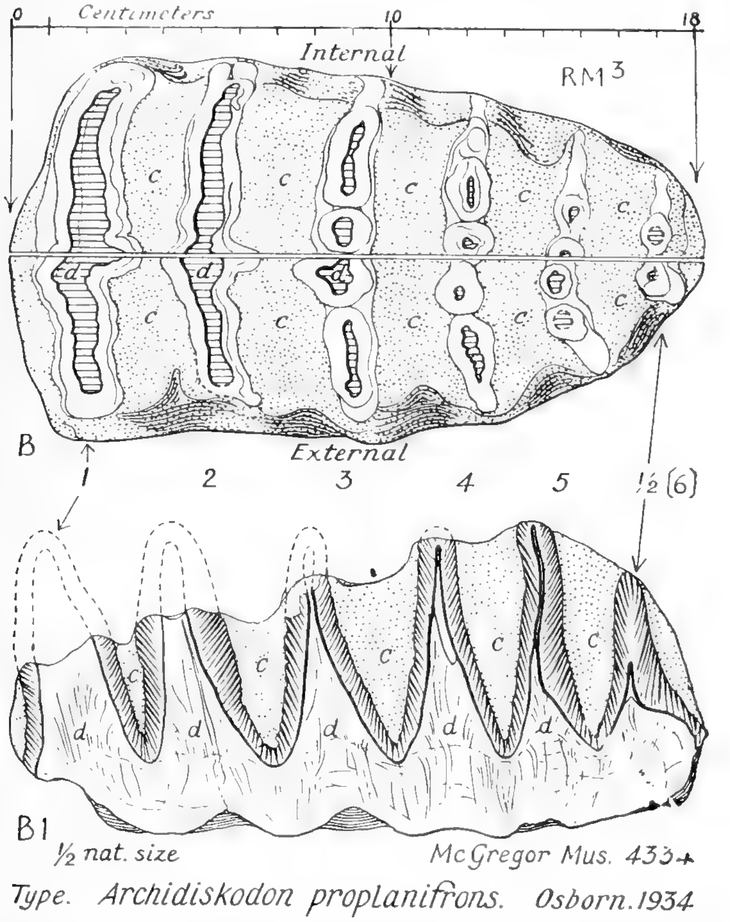


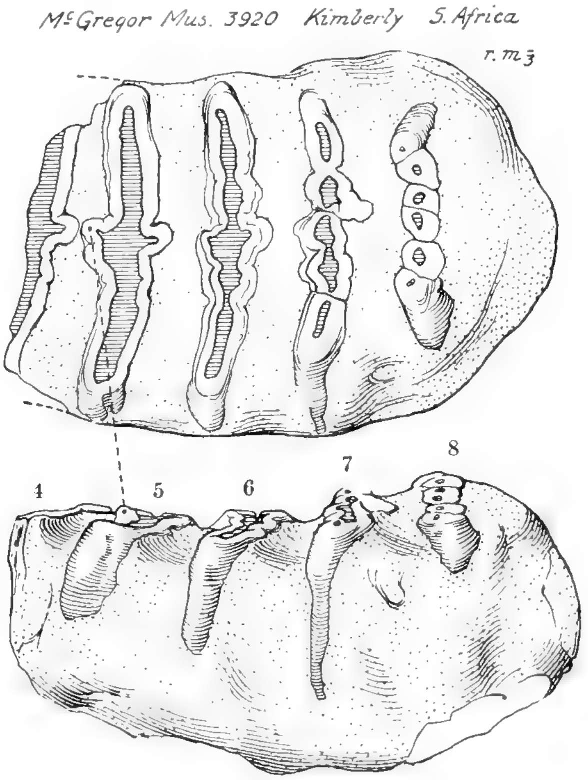
Fig. 873. Type, right third superior molar, r.M^3, of *Archidiskodon proplanifrons*, after original. McGregor Museum 4334, Kimberley, South Africa; cast Amer. Mus. 26969. One-half natural size. Originally referred by Haughton (1932.1, p. 2) to *Archidiskodon subplanifrons*.

B, Crown view showing 5½ ridge-plates, very broad cement areas—*c, c, c;* sixth plate represented by two conelets. B1, section of the same showing cement-filled ridge-plates more widely open than in *A. subplanifrons*.

Type Description.—The original description by Osborn is as follows (Osborn, 1928.749, p. 672): "The first type (represented in Fig. 1 [= Fig. 874 of the present Memoir]) I name *Archidiskodon subplanifrons*; it is a low-crowned, broad-plated, heavily cemented tooth, apparently a third inferior molar of the right side (McGregor Mus. 3920). The specific name *subplanifrons* refers to the fact that the crown height—from 2 to 2½ inches—is about equal to that of the low-crowned types of *Elephas planifrons* Falconer of the Siwalik Hills, India; in some of Falconer's Upper Siwalik specimens the crown rises from 3½ to 4½ inches. The present specimen accordingly is believed to be of Upper Pliocene age."

Archidiskodon subplanifrons Osborn, 1928. "Mammoths and Man in the Transvaal." Nature, Vol. CXXI, No. 3052, April 28, 1928, pp. 672, 673. Supplementary description: "Primitive *Archidiskodon* and *Palaeoloxodon* of South Africa" (Osborn, 1934.925, p. 10, fig. 1 = Fig. 875 of the present Memoir). Horizon and Locality.—Upper(?) Pliocene. [Middle Pliocene—See Fig. 1239 below.—Editor.] Sydney-on-Vaal, Vaal River diggings, on the banks of the river, at a depth of from 50 to 60 feet [?Middle Terrace], South Africa. Type Figure.—*Op. cit.*, p. 672, fig. 1

Type.—Posterior half of a third right inferior molar, r.M_3 (McGregor Mus. 3920, cast Amer. Mus. 21924), exhibiting four complete posterior ridge-plates and half of another ridge-plate, deeply surrounded with cement on crown and sides, also buried in cement is a rudimentary plate; extremely low crowned with broad,



ORIGINAL TYPE FIGURE OF ARCHIDISKODON SUBPLANIFRONS

Fig. 874. Type of *Archidiskodon subplanifrons* Osborn, 1928, from the Upper (?) Pliocene [Middle Pliocene—see Fig. 1239], Sydney-on-Vaal, South Africa, one-half natural size. Third inferior molar of the right side, r.M_3 (McGregor Mus. 3920, Kimberley, South Africa; cast Amer. Mus. 21924). After original type specimen kindly loaned to the American Museum for figuring and description (cf. Osborn, 1928.749, fig. 1, p. 672). Compare figures 840, 876, also an r.M_3 (Amer. Mus. 19965) of *A. planifrons* from the Siwalik Hills.

heavy enamel, ridge-plates set wide apart, two of the anterior ridge-plates expanding into a 'loxodont sinus' (4th and 5th); strongly resembling the *Archidiskodon planifrons* type (Figs. 828, 829), hence the specific name *Archidiskodon subplanifrons.*

Specific Characters.—The concavely worn superior surface (Fig. 874, lower) enables us to determine this as an inferior tooth of the right side, apparently an r.M$_3$, in view of the posterior convexity (Fig. 874, upper) which forbids its reference to an r.M$_2$. The crown is excessively broad and short, with convex cement-covered sides and ridge-plates which gradually increase in height posteriorly, as follows (reading backwards): 4th, imperfect, with central loxodont sinus; 5th, tr. 92 mm., height 53e mm., with anterior and posterior loxodont sinus; 6th, with cement, tr. 97 mm., height 53e mm., loxodont sinus less prominent; 7th, tr. 101 mm., height 63 mm., loxodont sinus less prominent, five to six conelets; 8th, with cement, tr. 95 mm., height 61 mm., summit of ridge-plate narrow with six conelets; after this a rudimentary plate buried in cement. The thick, non-crenulated enamel of the ridge-plates strongly reminds the observer of the ridge-plates of *A. planifrons* (Fig. 829). Without the aid of a section it is difficult to determine whether the ridge-plates are lofty as in Falconer's type of *A. planifrons* (Falconer and Cautley, "Fauna Antiqua Sivalensis," 1846 [1845, Pl. II, fig. 5*a*]—Figs. 825, 828 of present Memoir); in external aspect the ridge-plates are less elevated. Length of type molar 153 mm., breadth 101 mm., index 66; enamel length, restored, 650 mm., enamel area 2,600 sq. mm.; average enamel thickness 4 mm. Ridge-plates (6) postconvex, preconcave, 5–6 suboval to round conelets with double central folds in the ridge-plate; ridge-plates per 100 mm. = 4.

Specific Comparison with Archidiskodon planifrons in the Brown Siwalik Collection.—The South African type of *Archidiskodon subplanifrons* (Figs. 874, 875) is very similar to

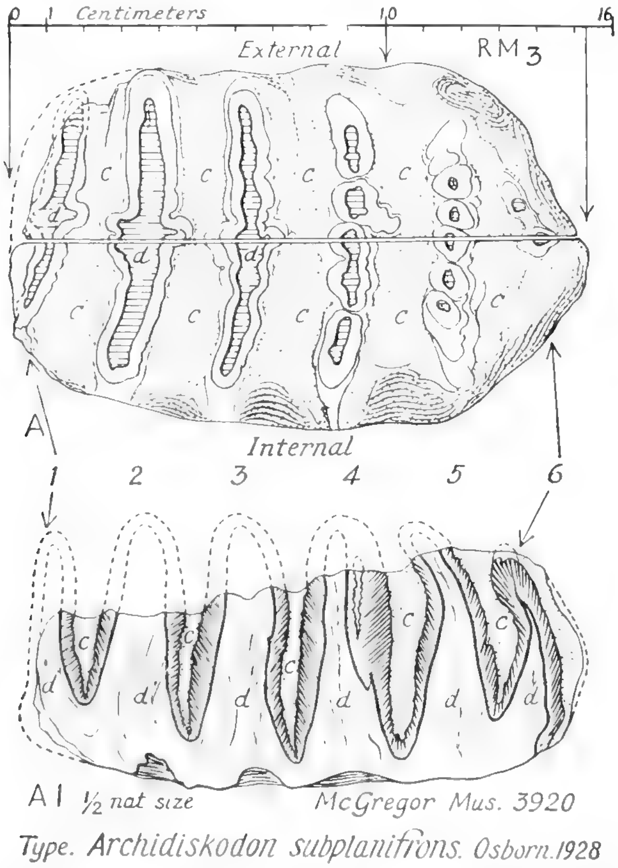


Fig. 875. New figure of type right third inferior molar, r.M$_3$, of *Archidiskodon subplanifrons* Osborn, 1928, from the middle terrace, Sydney-on-Vaal, South Africa. McGregor Museum 3920, Kimberley, South Africa; cast Amer. Mus. 21924. One-half natural size.

A, crown view. *c*—cement. *d*—dentine. Line of midsection. A1, the same in midsection, exhibiting six ridge-plates.

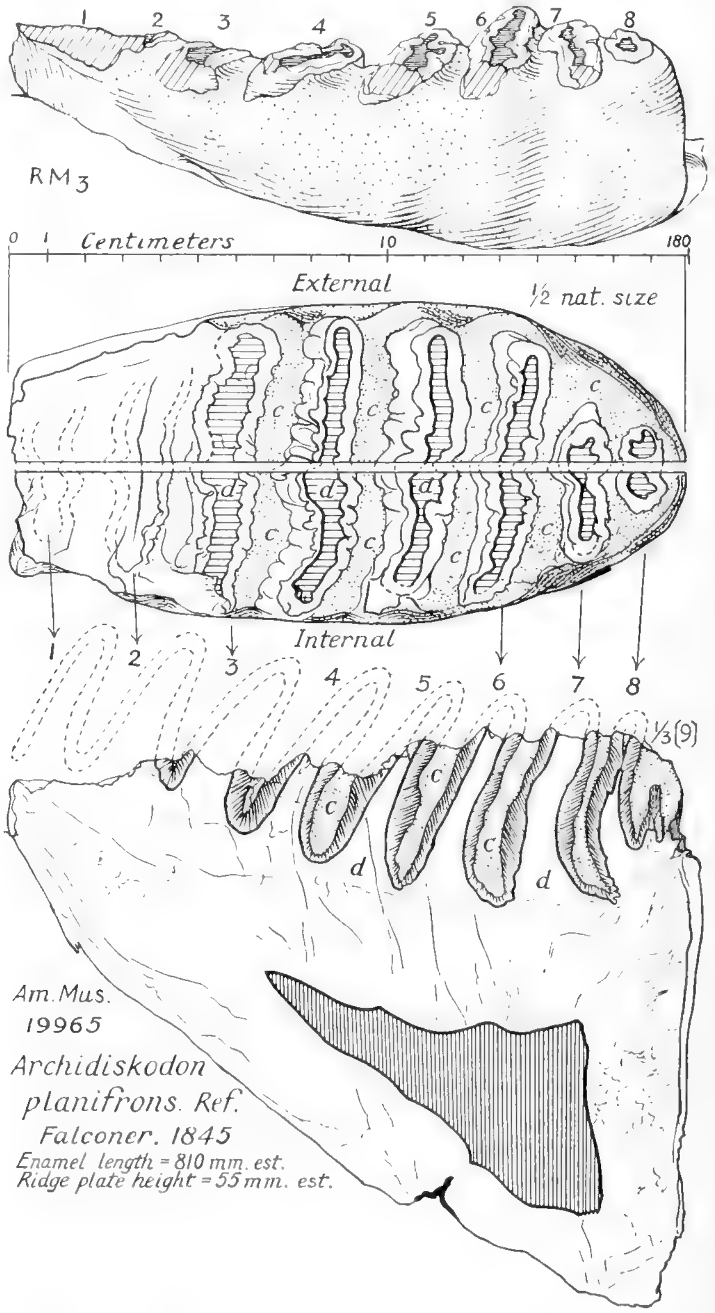


Fig. 876. Referred third right inferior molar, r.M$_3$, of *Archidiskodon planifrons* Falconer, 1845, from three miles north of Siswan, India. $8\frac{1}{3}$ [9] ridge-plates. Internal aspect (below), exhibiting the gently folded section of the entire molar with relatively low enamel ridge-plates and estimated total enamel length of 810 mm. One-half natural size.

Compare this molar of *Archidiskodon planifrons* from India with type molar of *A. subplanifrons* (Fig. 874) from South Africa.

a referred specimen of *A. planifrons* (Amer. Mus. 19965) from the Upper Pliocene Pinjor horizon, Upper Siwaliks, India. For comparison both teeth are carefully figured to a uniform scale (Figs. 875, 876). Observe in these teeth: (1) The similar height of the ridge-plates, e.g., *A. planifrons* 55e mm., *A. subplanifrons* 53e mm.; (2) *A. planifrons* with 8⅓ [9] ridge-plates, *A. subplanifrons* with 8½e ridge-plates; (3) similar constitution of the enamel and cement; (4) similar oblique, outwardly facing, slightly concave ridge-plates; (5) the median loops, 'loxodont sinus,' are somewhat more prominent in *A. subplanifrons* than in *A. planifrons.*

Archidiskodon broomi Osborn, 1928

Figure 877

Lower or Middle Pleistocene. Discovered in 1920 at The Bend, on the Vaal River, near Kimberley, South Africa.

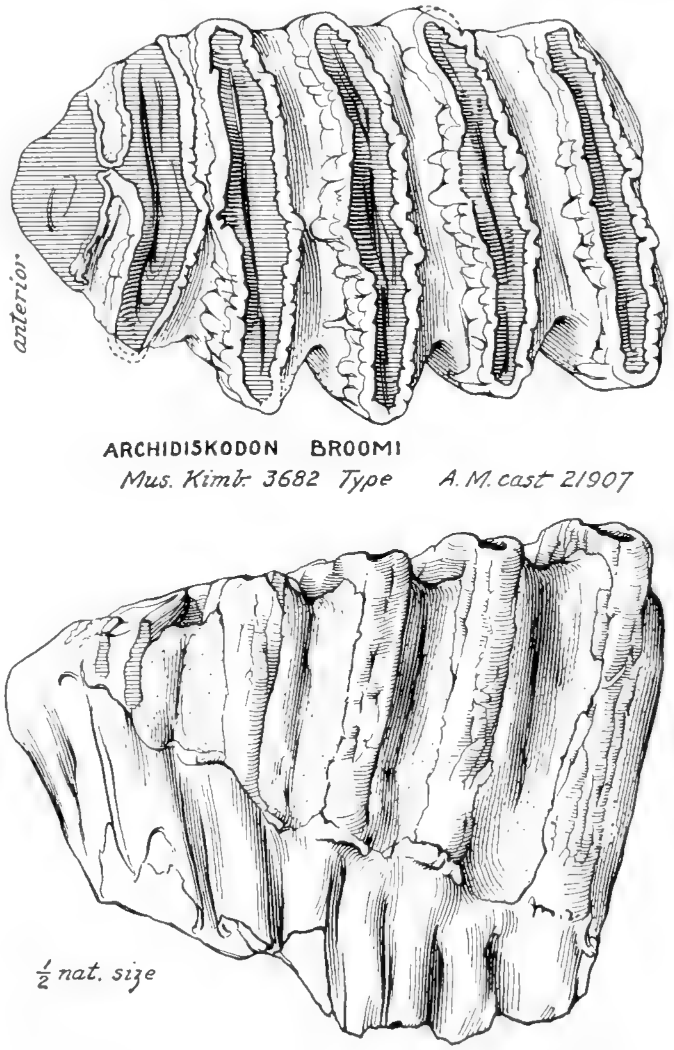
History.—Aside from the uncertainty as to the exact location in the jaw of this most interesting type molar of *Archidiskodon broomi,* there is no doubt as to its relationship to the gigantic, broad-plated genus *Archidiskodon* and as to its affinity to *A. meridionalis,* the southern mammoth of Europe, as well as to its American relative *A. imperator,* the imperial mammoth of the southern United States and of Mexico. Consequently this is a most important and interesting case of geographic distribution and of independent parallel evolution of species of *Archidiskodon* in South Africa and southern Europe and in the southern United States.

Archidiskodon broomi Osborn, 1928. "Mammoths and Man in the Transvaal." Nature, Vol. CXXI, No. 3052, April 28, 1928, pp. 672, 673. Horizon and Locality.—Lower or Middle Pleistocene. The Bend, on the Vaal River, near Kimberley, South Africa. Type Figure.—*Op. cit.,* fig. 2, p. 672.

Original Type Description of Archidiskodon broomi (Osborn, 1928.749, p. 672).—"In the second type (Fig. 2 [=Fig. 877 of the present Memoir]), the anterior half of a third superior [inferior] molar, probably of Pleistocene age, we observe a far more progressive stage, with lofty ridge-plates, the sixth attaining a height of 5 inches, equal to that of certain specimens of *Archidiskodon meridionalis* in which the ridge-plates equal or exceed 5 inches. This relatively high-crowned type (McGregor Mus., 3682) I name *Archidiskodon broomi,* in honour of Dr. Robert Broom, who, after the specimen was named in MS. and figured by myself, requested that one of these molars should be named after Mr. W. Millett, who discovered the type of *A. subplanifrons* at a depth of from 50 to 60 feet in the Vaal River diggings near Sydney-on-Vaal."

Type.—Seven-plated anterior portion of an imperfect third inferior molar of the right side, bearing the inscription: "3682 Mus. Kimb. The Bend. H. Else." Cast Amer. Mus. 21907. Reproduced from original specimen (Fig. 877 of the present Memoir). By comparison with the superior and inferior molars (Amer. Mus. 14476, 14558) referred to *Archidiskodon imperator* (as illustrated in Fig. 889 B, A, of the present Memoir), this type grinding tooth of *Archidiskodon broomi* agrees approximately in size with *A. imperator* in the maximum width of the fifth ridge-plate, namely, 107 mm. The ridge-plates of *A. broomi* also agree exactly in width (107 mm.) with those of M^3 in Brit. Mus. 7436 (see Falconer and Cautley, "Fauna Antiqua Sivalensis," 1846 [1847, Pl. xiv.b, fig. 13*a*]), a true *Elephas* [=*Hesperoloxodon*] *antiquus* molar.

Specific Characters.—(1) The ridge-plates present an anterior concavity and a posterior convexity as in *A. imperator* (Fig. 889A); (2) the ridge-plates converge towards each other on the external side and are somewhat farther apart on the internal side, consequently we are inclined to consider this molar as an r.M_2 by comparison with *Archidiskodon imperator* (Amer. Mus. 14558—Fig. 889A), but the exact placing of this tooth is uncertain; (3) the fact that the fifth ridge-plate preserved is broader (tr. 107 mm.) than the sixth and seventh ridge-plates preserved (tr. 105 mm.) favors the determination of this tooth as a ten or eleven plated r.M_2 rather than a twelve to fourteen plated r.M_3; (4) the maximum width of the fifth ridge-plate or pentalophid is 107 mm., practically the same as that of the corresponding penta-



Osborn's Original Type Figure of Archidiskodon broomi

Fig. 877. Type of *Archidiskodon broomi* Osborn, 1928. Original in the McGregor Museum, Kimberley, South Africa (No. 3682), cast Amer. Mus. 21907. Third inferior molar of the right side, r.M_3. From The Bend, Vaal River, near Kimberley, South Africa. After original specimen kindly loaned to the American Museum for figuring and description. Compare Osborn, 1928.749, p. 672, fig. 2.

Seven ridge-plates partly preserved, broadest portion of the crown at fifth ridge-plate, indicating that three or four posterior ridge-plates are missing and that this may represent a ten or eleven plated second molar, r.M_2, according to the formulæ of Leith Adams (1877–1881) and of Weithofer (1890), in which *Archidiskodon meridionalis* is clearly distinguished from *A. planifrons.*

lophid in *A. imperator* (tr. 108 mm.) and the corresponding pentaloph in *A. meridionalis* (M^3); (5) in *A. imperator* (Amer. Mus. 14476—Fig. 889B) the convexity of the ridge-plates is anterior, the concavity is posterior—therefore, by comparison, the *A. broomi* type is an inferior molar; (6) against this interpretation, however, is the fact that in profile (Fig. 877, lower) the wearing surface of the ridge-plates is slightly convex (as in superior molars generally), whereas, according to rule, the profile of the inferior molars in *Archidiskodon* should be slightly concave (Amer. Mus. 10598 and 14558—Fig. 892 B, A).

The detailed specific and generic characters and measurements are as follows: (1) First and second ridge-plates narrow and completely worn into confluence, third ridge-plate (tr. 86e mm.), fourth ridge-plate (tr. 102 mm.), fifth ridge-plate (tr. 107 mm.), sixth ridge-plate (tr. 105 mm.), seventh ridge-plate (tr. 105 mm.), height of seventh ridge-plate (110 mm.); (2) enamel borders of each ridge-plate folded or ptychoid, slightly expanded in the fourth ridge-plate on wear into a faint 'loxodont sinus'; (3) the ptychoid enamel borders distinguish the sides of the ridge-plates (Fig. 877, lower); (4) broad cement deposit between the ridge-plates, not, however, covering the plates at the sides as in *A. imperator*.

Archidiskodon vanalpheni Dart, 1929

Figure 878

From Sydney-on-Vaal, South Africa. Middle terrace (lower levels). ?Lower Pleistocene.

Archidiskodon vanalpheni Dart, 1929. "Mammoths and Other Fossil Elephants of the Vaal and Limpopo Watersheds." So. Afr. Journ. Sci., XXVI, p. 704. Type.—Third superior molar of the left side, l.M^3. McGregor Museum (Kimberley) 4086 (cast Amer. Mus. 22723). Horizon and Locality.—"Middle terrace at a depth of 80 feet at Sydney-on-Vaal," South Africa. ?Pliocene [?Lower Pleistocene (*fide* Osborn, 1934.925, pp. 2, 3)]. Type Figure.—Dart, *op. cit.*, p. 704, figs. 8 and 9.

Type Description.—(Dart, 1929.1, pp. 704–706): "This tooth (greatest length 234 mm., greatest width 112 mm., greatest height 129 mm.) has 8 plates and is incomplete posteriorly, there having been originally probably 9 plates present (see Figs. 8 and 9 [Fig. 878 of present Memoir])."

"The tooth in *A. vanalpheni* presents a characteristically rugged appearance, the massive plates being separated laterally by great valleculae approaching an inch in depth. These huge furrows are continued across the grinding surface of the tooth to a depth of ½ inch or more (save in the case of the space between the 3rd and 4th plates only) and give to the organ an appearance simulating that characteristic of the Stegodonts. Owing to the fragility of the specimen, the fangs of the tooth are absent, as also are most of the mammillated processes of the posterior four plates. The first or anterior plate is talon-like in appearance, being aborted and only half the height of the succeeding one, to which it is firmly adherent, with the interposition between them of very little cementum."

"The massive plates are markedly cuneiform, as opposed to the chevron-patterned plates of Stegodonts on the one hand, and the pectinated arrangement exhibited by more advanced elephants on the other hand, their antero-posterior width tapering from 1⅛ inches at their base to ⅜–½ inch at the grinding edge. The contraction of the plates is not less marked in their transverse length which at the base is in the region of 4 inches, but at the grinding edge is not more than 2½ inches or 63 mm. These features lend to the tooth as a whole a pyramidal appearance which is in sharp contrast to the squat semicuboidal form and exuberant cementum found in *A. subplanifrons*. The enamel in thickness (3–4 mm.) is comparable with that of *A. subplanifrons* but is somewhat more folded than in that form, definite longitudinal depressions running even along the exposed lateral and medial sides of the plates. It is these enamel foldings which more particularly give the tooth its rugged character."

"Owing to the early age of the tooth, not more than three plates (excluding the most anterior talon) being in wear, a clear picture of the grinding surface in full wear is not available. In the fourth plate, 6 mammillated points are in slight wear, in the third there are 2 islets and 3 mammillated processes—indicating in all apparently 7 mammillated processes to each plate, a number which appears to be ratified in the posterior plates which have lost their processes by fracture—while the second plate shows four islets. A tendency is demonstrated especially by the anterior talon and the second and third plates towards their centre to throw out a posterior buttress. There is no evidence whatever of an anterior buttress."

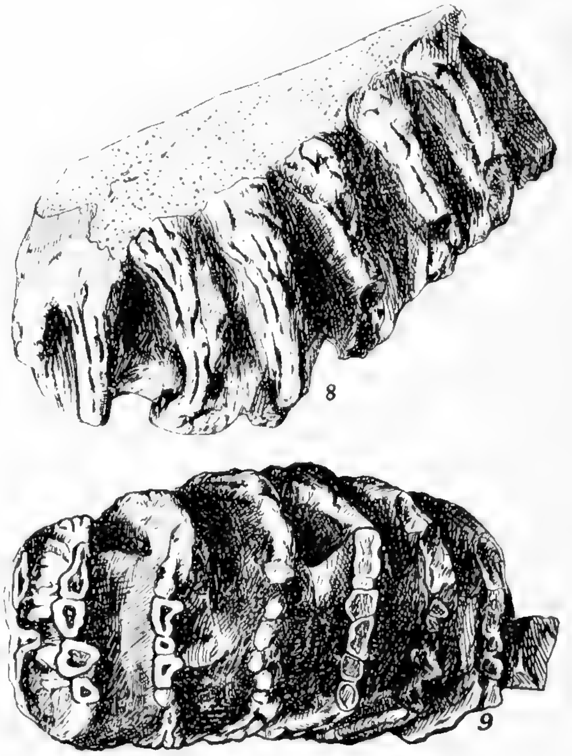


Fig. 878. Type left third superior molar, l.M^3 (McGregor Mus. 4086, cast Amer. Mus. 22723), of *Archidiskodon vanalpheni* Dart, 1929, figs. 8 and 9, p. 704, one-third natural size. From Sydney-on-Vaal, South Africa.

"The tooth is distinguished also by the great degree of separation between the plates owing to the presence of great wedges of interlamellar cementum despite their valleculisation. This separation, which in *A. subplanifrons* does not exceed ½–⅝ in., is

¾–1¼ in. in *A. vanalpheni*. There can be little doubt that we possess here another very ancient Archidiskodont species, which despite its greater number of ridge plates (*A. subplanifrons* shows only 5 plates but may have had more) illustrates in its cement characters and the ridge plate form an exceedingly primitive type. I have named it after Mr. van Alphen who was responsible for securing it for scientific investigation."

Archidiskodon milletti Dart, 1929

Figure 879

From Sydney-on-Vaal, South Africa. Middle terrace (lower levels). ?Lower Pleistocene.

Archidiskodon milletti Dart, 1929. "Mammoths and Other Fossil Elephants of the Vaal and Limpopo Watersheds." So. Afr. Journ. Sci., XXVI, p. 706. TYPE.—Third superior molar of the left side, l.M^3. McGregor Museum 4085; cast Amer. Mus. 22722. HORIZON AND LOCALITY.—"Middle terrace at a depth of 80 feet at Sydney-on-Vaal," South Africa. ?Pliocene [?Lower Pleistocene (*fide* Osborn, 1934.925, p. 3)]. TYPE FIGURE.—Dart, *op. cit.*, p. 706, figs. 10 and 11.

TYPE DESCRIPTION.—(Dart, 1929.1, pp. 707–708): "In general measurements (greatest length 222 mm., greatest width 108 mm., greatest height 118 mm.) it corresponds fairly closely [with *A. vanalpheni*] being, however, considerably shorter, wider and lower than the foregoing. These measurements are fairly comparable with those given for *A. vanalpheni*, seeing that here, too, the fangs are absent; here, too, eight plates are present including a similar anterior talon, which in this case, however, more closely approximates in height that of the second plate, and is actually in wear. Here also one or more posterior plates are absent by loss. (Figs. 10, 11 [Fig. 879 of present Memoir])."

"But it is on still closer examination that distinctions are to be drawn between the teeth. While in this tooth, too, the individual plates are cuneiform, the disparity between their thickness at base and edge is not so great, in that the plates are not more than ⅞ inch thick at their bases and are ⅜-½ inch thick at their edges. The degree of contraction in transverse length of plates from base to edge, is, however, virtually identical with that in *A. vanalpheni*."

"The enamel is just as thick as that of *A. vanalpheni* and while it displays some crimping is not nearly so rugged in appearance as that of *A. vanalpheni*, while on the exposed sides of the plates there is no trace whatever of longitudinal grooving. Owing to the early age of this tooth also, which is practically identical in this respect with that of the preceding, there is no clear picture of its surface in wear. The anterior talon is in wear and shows a median posterior buttress as also do the second, third and fourth plates. The fifth, seventh and eighth plates show five digitations, the sixth plate six, the fourth plate six digitations and a posterior buttress digitation, the third plate seven worn digitations and a posterior buttress digitation, and the second plate two islets, the posterior buttress protruding from the medial one of the two islets. There is no evidence of any anterior buttress in any of the plates."

"The degree of separation between the second and third plates, ⅞–1¼ in., is identical with what is typical for *A. vanalpheni*, but the other plates are not nearly so widely separated being generally only ¾ inch apart, so that in *A. milletti* a length of 5½ inches includes 5 plates while in *A. vanalpheni* it includes but 4 plates."

"When in addition it is pointed out that, while there is here, too, an appreciable valleculisation of the interlamellar cementum—which is continued across the tooth between the posterior plates—there is, nevertheless, in *A. milletti* a far greater relative bulk of cementum and a far greater tendency towards the reduction of the valleys, it is clear that we are confronted with an advancing and specifically distinct though closely related form of Archidiskodont. I have named it after Mr. Millett who has been responsible for the finding of the three mammoth teeth recovered at Sydney-on-Vaal."

"There remains, of course, the possibility that one of these forms with a well-marked posterior buttress is closely related to, if not identical with, *A. griqua* of Haughton. I have had the privilege personally of examining that well-worn and fragmentary specimen, and, with a view to making our knowledge of the South African mammoths as complete as possible, have taken the liberty of making some additional remarks upon the material."

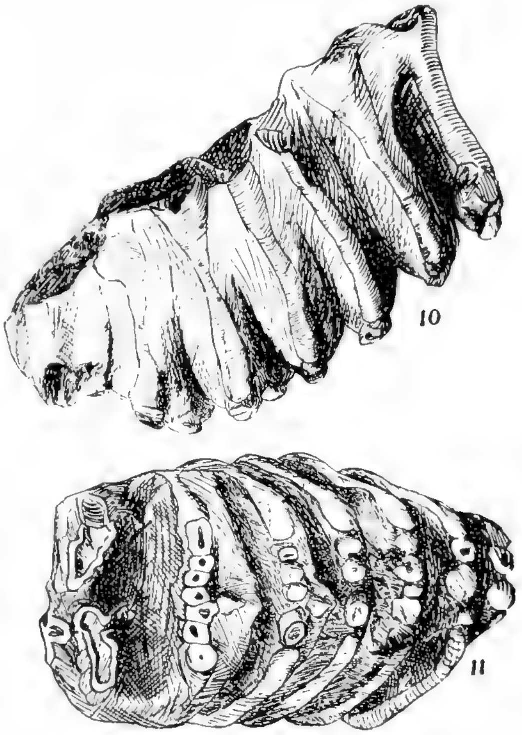


Fig. 879. Type left third superior molar, l.M^3 (McGregor Mus. 4085, cast Amer. Mus. 22722), of *Archidiskodon milletti* Dart, 1929, figs. 10 and 11, p. 706, one-third natural size. From Sydney-on-Vaal, South Africa.

Archidiskodon loxodontoides Dart, 1929

Figure 880

From Sydney-on-Vaal, South Africa. Middle terrace (lower levels). ?Lower Pleistocene.

Archidiskodon loxodontoides Dart, 1929. "Mammoths and Other Fossil Elephants of the Vaal and Limpopo Watersheds." So. Afr. Journ. Sci., XXVI, p. 709. TYPE.—Third superior molar of the left side, l.M^3. McGregor Museum (Kimberley)

4087; cast Amer. Mus. 22724. Horizon and Locality.—"Middle terrace at a depth of 80 feet(?) at Sydney-on-Vaal," South Africa. ?Pliocene [?Lower Pleistocene, *fide* Osborn, 1934.925, p. 3]. Type Figure.—Dart, *op. cit.*, p. 709, fig. 13.

Type Description.—(Dart, 1929.1, pp. 709–711): "This tooth, also apparently a third upper molar (greatest length 149 mm., greatest width 94 mm., greatest height 112 mm.), is less complete than the previous two new types described, presenting only 4¾ in. plates and lacking in addition one or more plates both anteriorly and posteriorly. It is impossible to state whether it possessed originally a ridge plate number as great as that of the two preceding—it probably did not. All the plates present were in wear and the specimen was probably from an old adult. For an upper molar in early wear it is not higher than one would expect in *A. subplanifrons*, but it is narrower than that specimen and, indeed, than all the aforementioned forms. Here also the fangs are absent and the measurements of height consequently comparable (see Fig. 13 [Fig. 880 of present Memoir])."

Fig. 880. Type left third superior molar, l.M^3 (McGregor Mus. 4087, cast Amer. Mus. 22724), of *Archidiskodon loxodontoides* Dart, 1929, fig. 13, p. 709, one-third natural size. From Sydney-on-Vaal, South Africa.

"The plates are not so distinctively cuneiform as in the two previously described forms, nor do they present so distinct a degree of contraction in length toward the grinding surface where they show a transverse length of 80 mm. The enamel is thick (3–4 mm.) and is very markedly plicated or crenated, despite its thickness. Longitudinal grooving of the medial and lateral aspects of the ridge plates is also strongly in evidence. Owing to the well worn nature of the tooth the pattern produced on the grinding surface is very clear. The most posterior or fifth plate shows 7 mammillated processes which have all been broken off, the fourth shows eight pedunculated processes in wear, the third and fourth from the medial side having fused to form a small islet. In the third plate there are three islets, one formed by the fusion of the medial two mamillae and one islet by the lateral two. The four central mamillae are fused to form a large central islet and in the region corresponding to the medial two of the four central mamillae a pronounced anterior and posterior dilatation is evident, due to the presence of distinct buttresses here on both the anterior and posterior aspects of the plate. In the second and first plates the islets have completely disappeared, and in the second plate especially there is shown a virtually median widening out with the full development of the buttresses."

"The plates, which are roughly 19 mm. wide in their more or less parallel portions, expand to 31 mm. in the regions of the buttresses with the result that the buttresses of adjacent plates are in direct contact with one another and together separate the interlamellar stratum of cementum, 10–17 mm. wide, on one side from that on the other side of adjacent buttresses, as occurs in the true Loxodonts, a condition not previously encountered to my knowledge in any Archidiskodont, and justifying the name given to this peculiar species."

"The cementum is abundant and almost encases the ridges completely on the medial aspect of the tooth. Laterally, however, there are distinct and deep trenches ¼–¾ inches in depth between adjacent plates, indicating the probable origin of this species from a form comparable with those previously described, especially *A. vanalpheni*. Indeed, if it were not for the greatly reduced width of the tooth and reduced width of interlamellar cementum as well as the presence of the anterior buttress in *A. loxodontoides*, I should have been considerably more reluctant to separate it specifically from *A. vanalpheni*. It must be closely related to that species and the recovery of further remains of both types, especially a well worn molar of *A. vanalpheni*, will be awaited with great interest in this connection. It may be repeated, however, that there is no evidence of such an unusual anterior buttress in *A. vanalpheni* and the resultant loxodontoid form of plate in surface wear as exists in *A. loxodontoides*. The same feature serves to distinguish it equally from the *A. griqua* of Haughton."

Archidiskodon yorki Dart, 1929

Figure 881

Vanasswegenshoek-Bloemheuvel, near Christiana, South Africa. Middle terrace (upper levels), ?Lower Pleistocene.

Archidiskodon yorki Dart, 1929. "Mammoths and Other Fossil Elephants of the Vaal and Limpopo Watersheds." So. Afr. Journ. Sci., XXVI, p. 717. Type.—". . . two very fragmented enamel plates of an Archidiskodont mammoth" (*op. cit.*, p. 715). McGregor Museum (Kimberley) 4073. Horizon and Locality.—"Middle gravel stratum of river bed gravels at Vanasswegenshoek-Bloemheuvel, near Christiana," South Africa. ?Middle Pleistocene [?Lower Pleistocene, *fide* Osborn, 1934.925, p. 3]. Type Figure.—Dart, *op. cit.*, p. 717, fig. 19.

Type Description.—(Dart, 1929.1, pp. 717, 718): "The plates of this tooth are of great size (fragment is 114 mm. broad and 193 mm. high, but the widest diameter of the tooth was at least 120 mm. and the height at least 200 mm.). In all their measurements these plates (see Fig. 19 [Fig. 881 of present Memoir]) exceed considerably those of *A. broomi* . . . The enamel plates measure 16–23 mm. across, that is, slightly narrower than in *A. broomi*, and approach closely in form the type presented by *A. broomi*. Laterally viewed, however, there is a distance from mid-point to mid-point of succeeding enamel ridge plates in *A. broomi* of at least 32 mm. whereas in this specimen the same measurement does not exceed 24 mm. thus demonstrating the relatively decreased amount in it of the interlamellar cementum. We are, therefore, dealing here with a broader and higher tooth than in the type of *A. broomi* and one with slightly narrower enamel plates and decreased interlamellar cementum. It must be specifically different but closely related thereto and I will name it, despite the paucity of the remains, *Archidiskodon yorki* in honour of its discoverer."

"The finding of *A. broomi* and *A. yorki*, which are advanced Archidiskodont types in gravel strata which appear to be directly capable of correlation with the advanced Archidiskodont gravel at Bloemhof, is of great interest and importance. Both of these mammoths are admittedly more primitive than the Bloemhof mammoths, although more advanced than *A. subplanifrons*, which came from the 50–60 feet depth at Sydney-on-Vaal."

"There is no question in my mind, from the state of fossilisation of *A. yorki*, from its fragmentation and from its unnatural stratigraphical position as compared with the Bloemhof mammoths, that it belongs to the more superficial part of the middle terrace, as I have already suggested is true also of *A. broomi*."

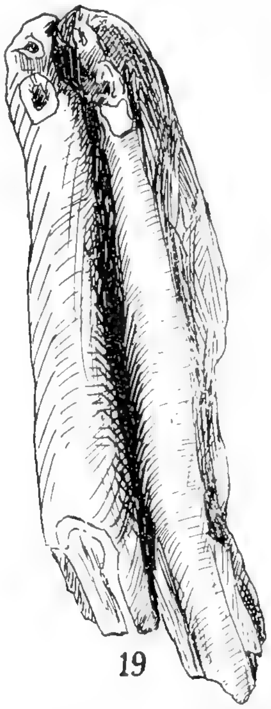


Fig. 881. Type molar fragment of *Archidiskodon yorki* Dart, 1929, fig. 19 (McGregor Mus. 4073), found in river bed gravels at Vanasswegenshoek-Bloemheuvel, near Christiana, South Africa. One-half natural size.

SPECIES PROVISIONALLY REFERRED BY THE PRESENT AUTHOR TO THE GENUS PALÆOLOXODON

Archidiskodon transvaalensis Dart, 1927

From Bloemhof, Vaal River, South Africa. Pleistocene.

A third superior molar, r.M³, described by Doctor Dart in 1927 as *Archidiskodon transvaalensis*, was removed by Professor Osborn to the genus *Palæoloxodon* (see Osborn, 1934.925, pp. 2 and 14). This species is treated fully in Chapter XIX, p. 1284, below (the Loxodontinæ).

Archidiskodon sheppardi Dart, 1927

From Bloemhof, Vaal River, South Africa. Pleistocene.

The species *Archidiskodon sheppardi*, type an l.M³, also described by Doctor Dart at the same time as his species *A. transvaalensis*, was regarded by Professor Osborn as belonging to the genus *Palæoloxodon* and as a consequence is treated in full in Chapter XIX, p. 1278 below (the Loxodontinæ).

Archidiskodon andrewsi Dart, 1929

From Gong-Gong, ?Middle terrace (lower levels), Vaal River, South Africa. ?Lower Pleistocene.

The type of *Archidiskodon andrewsi* Dart is a fragmentary third lower molar of the left side, l.M_3 (McGregor Mus. 435; cast Amer. Mus. 26968). It was first thought by Professor Osborn to be referable to *Archidiskodon subplanifrons*, but on further study of the original specimen kindly loaned by Curator Wilman of the McGregor Museum he was inclined to regard it as belonging to the genus *Palæoloxodon* (see Osborn, 1934.925). The description and figure, therefore, will be found below on page 1278 of Chapter XIX (the Loxodontinæ).

Archidiskodon hanekomi Dart, 1929

From the old river bed of the Vaal River at a depth of 20 feet at Delpoort's Hope, South Africa.

In 1929 Dart described a ?third right upper molar, r.M³, in the McGregor Museum (No. 2930), which he named *Archidiskodon hanekomi*. Professor Osborn, however, in his article "Primitive *Archidiskodon* and *Palaeoloxodon* of South Africa" (Osborn, 1934.925) referred this species to the genus *Palæoloxodon*. The description and figure will be found on page 1279, figure 1140 of Chapter XIX (the Loxodontinæ).

Genus: METARCHIDISKODON Osborn, 1934

Original reference: "Primitive *Archidiskodon* and *Palaeoloxodon* of South Africa," Amer. Mus. Novitates, No. 741, August 24, 1934 (Osborn, 1934.925, p. 12).

Genotypic species: *Loxodonta griqua* Haughton, 1922.

Generic Characters.—(Osborn, 1934.925, p. 12): "This group [*Metarchidiskodon griqua* group] includes the fragmentary type (Fig. 3 [= Fig. 882 of present Memoir]) of '*Loxodonta*' *griqua* Haughton, 1922. . . . This specimen appears to belong to a distinct form of grinding tooth to which the new generic name *Metarchidiskodon* may be applied, and distinguished from *Archidiskodon* as follows: (1) M 3 with a relatively long narrow crown; index cannot be estimated at present. (2) Deep U-shaped valleys filled with cement. (3) Enamel ridge plates extending to the bottom of the crown. (4) Very prominent post-sinus folds instead of median sinus expansion of the typical *Archidiskodon*. . . . Type species: *Loxodonta griqua* Haughton, 1922." See Table IX above (p. 985) under "*M. griqua* group."

Specific Characters of Metarchidiskodon griqua, by Osborn, 1934.—(Osborn, 1934.925, p. 12): "(1) Cement areas equal or exceed dentine areas; (2) pre-sinus folds absent or inconspicuous; very prominent post-sinus folds; (3) very deep U-shaped valleys extending to the bottom of the crown; this is a very important point. (4) These valleys are filled to the summit with cement. (5) Enamel ridge plates very deep, extending to the bottom of the crown, closely compressed with very narrow dentinal areas between."

"Type figure 3 [= Fig. 882 of present Memoir] to be compared with the relatively narrow grinding teeth of similar molars observed in the Val d'Arno specimens and in British Museum M12641, M12642."

Metarchidiskodon griqua Haughton, 1922

Figures 882, 883

Vaal River gravels, Griqualand West, South Africa. ?Lower Pleistocene.

From these gravels Fraas (1907) described *Equus* cf. *zebra*, *Hippopotamus amphibius* var. *robustus*, *Damaliscus* sp. and *Mastodon* sp.; Felix (see Beck, 1906.1, p. 49) described *Mastodon* (*Bunolophodon*) sp., and Haughton (1922) described a new giraffe (*Griquatherium cingulatum*).

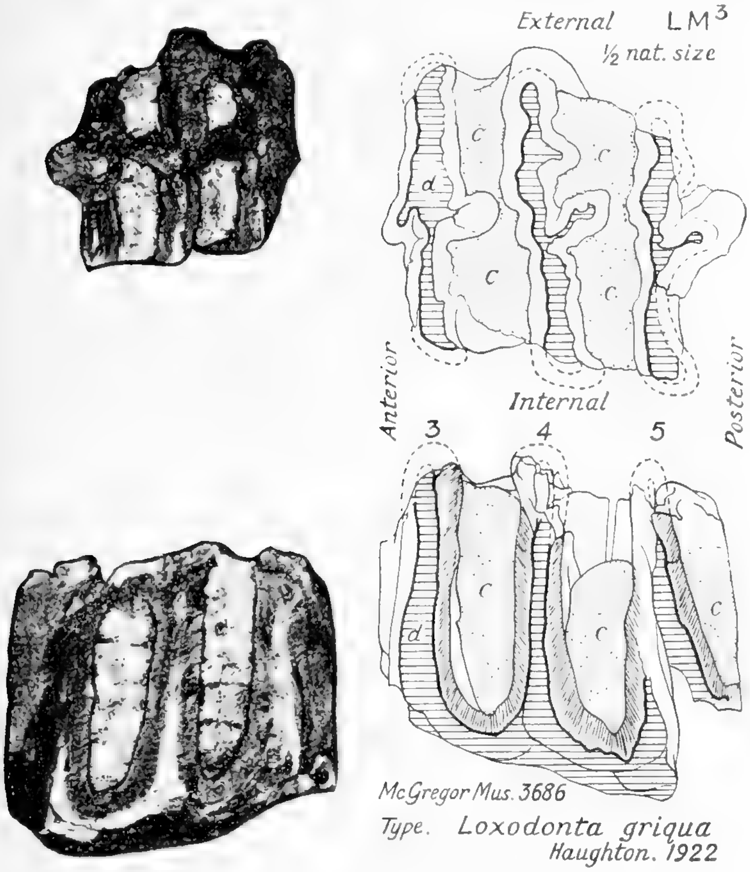
History.—Originally described by Haughton in 1922 as *Loxodonta griqua* this extremely fragmentary superior molar proves to belong to a new genus, *Metarchidiskodon*. The new type figure (Fig. 882, right) is reconstructed from the original specimen (McGregor Mus. 3686) kindly loaned by Miss Wilman, Director of the Museum. It apparently represents three central ridge-plates ["Supposed third, fourth and fifth" (*fide* Osborn 1934.925, p. 8, fig. 3)] of a third left upper true molar (?l.M^3), as compared with *Archidiskodon planifrons* (Fig. 829); the elevation of the ridge-plates and approximation of the valleys are less extreme than in the type of *A. planifrons* (Fig. 825); the more worn anterior plate is to the left, the less worn posterior plate is to the right; the concave side of each plate opens backward as in *A. planifrons*; the backward enamel loops are much more prominent than in *A. subplanifrons*; width of central ridge-plate 90e mm., height of same ridge-plate 90e mm.

Loxodonta Griqua Haughton, 1922. "A Note on Some Fossils from the Vaal River Gravels." Trans. Geol. Soc. S. Africa, 1922, Vol. XXIV, pp. 11–13. Type.—Fragmentary molar. Horizon and Locality. From the river gravels of the Vaal River, Griqualand West (*op. cit.*, p. 11, quoted from du Toit, 11th Ann. Rept. Geol. Comm., 1907, pp. 171, 172): "The gravels are situated at various levels as well as at varying distances from the river, and though they form a number of fairly distinct terraces, it is not always easy to determine their relative age. . . . On the west of the Vaal the terrace is finely developed at Klipdam, where it has an altitude of 200 feet above the river and a distance from it of 3½ to 6 miles." (Osborn, 1934.925, pp. 2, 3) ?Middle terrace (upper levels), 60–80 feet, ?Lower Pleistocene. Type Figure.—Haughton, *op. cit.*, 1922, Pl. I, figs. 1 and 2.

Type Description.—(Haughton, *op. cit.*, 1922, p. 12): ". . . a portion of an Elephant molar. . . . The fragment consists of three plates of which one side is imperfect and shows a vertical longitudinal section. . . . Although the molar is incomplete, it was obviously large and broad and fairly low. The enamel is thick, the borders show no strong crimping but a considerable amount of unevenness. The cement wedges are large, the plates are wide apart and were certainly few in number. In vertical section the tooth has an appearance intermediate between those of *E. africanus* and *E. planifrons* figured by Falconer and somewhat similar to that from the Red Crag of Suffolk assigned by Leith Adams to *E. antiquus* (Brit. Foss. Elephants, Pl. XXVI., fig. 3 [2]). The cement wedges between the plates are as thick as the plates; and their bases are more rounded than wedge-shaped. The sides of the plates are more parallel than in *planifrons*, thus approximating to those of *africanus*. The most characteristic feature of the tooth, however, is the shape of the wearing surface of the plates. . . . [p. 13] The present tooth seems to differ considerably from that of *E. zulu* and also from that of *E. antiquus*. These show a central angular notch on the enamel, but never to the same extent; while the strong crimping of the enamel in both these forms is a distinguishing feature, as well as the comparative lowness and width of the tooth in this fragmentary specimen."

SPECIFIC CHARACTERS OF ARCHIDISKODON [=METARCHIDISKODON] GRIQUA, BY OSBORN, 1928.—(1) Superior ridge-plates much more elevated, i.e., 3½e in. = 90e mm., than in the type of *A. subplanifrons*, i.e., 2½–2¾ in. = 64–70 mm. (2) Central enamel loops much more prominent than in *A. subplanifrons*. (3) Width of central ridge-plate 90e mm.; height of central ridge-plate 90e mm.

KAISO BONE-BEDS (Hopwood, 1926, pp. 33, 34).—From the Kaiso Bone-beds, near Albert Nyanza, Hopwood describes a fragmentary tooth (Brit. Mus. M12641), see figure 883, as follows: "The chief specimen consists of three lamellae and the loxodont sinus of a fourth. At the anterior end is part of the posterior wall of a fifth plate which has been deeply abraded. The one behind it has been worn in such a manner as to reveal the great depth of the digitations. This specimen has been cut across in order to show the enamel figures [Fig. 883, lower]. . . . These characters, taken together with the lamellar frequency of four, indicate a very primitive form, which might be compared with *E. planifrons* Falconer."



TYPE THIRD LEFT SUPERIOR MOLAR OF METARCHIDISKODON GRIQUA

Fig. 882. Original (upper, ¼ lower, ½ nat. size) and new (right pair, ½ nat. size) type figures of *Loxodonta griqua* Haughton, 1922, Pl. I, figs. 1 and 2; both drawings after fractured type specimen (?l.M³) in the McGregor Museum at Kimberley (McGregor Mus. 3686). From the river gravels of the Vaal, Griqualand West, South Africa. Original type figures (left): "Fig. 1.—Grinding surface of fragmentary molar. . . . Fig. 2.—Profile view of same."

(Right) New figure after Osborn, 1934.925, p. 8, fig. 3: Supposed third, fourth, and fifth ridge-plates of an l.M³. Observe very deep U-shaped valleys, thick simply folded enamel with very prominent looped post-sinus folds.

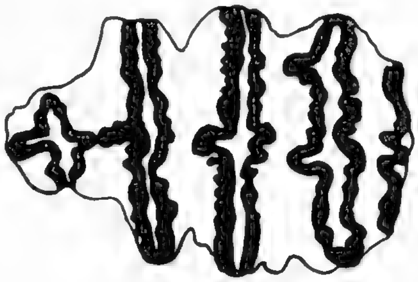


FIG. 13.—*Elephas* aff. *meridionalis* Nesti. Enamel pattern of larger fragment. Regd. M12641. 1/2 nat. size.

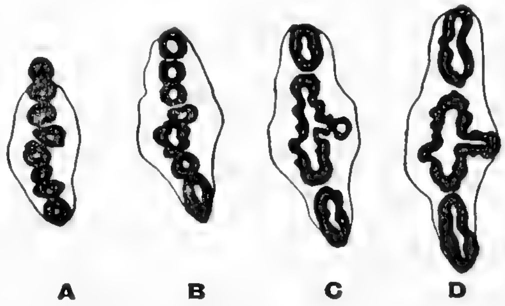


FIG. 14.—*Elephas* aff. *meridionalis* Nesti. Development of the enamel pattern in an isolated plate. *A* is 13.5 mm. from the top; *B* 6 mm. from *A*; *C*, 8 mm. from *B*; and D 12.5 mm from *C* Regd. M12642. 1/2 nat. size.

Fig. 883. REFERRED METARCHIDISKODON GRIQUA (NON MERIDIONALIS)

(Upper) A fragmentary molar from the Kaiso Bone-beds of Africa, doubtfully referred by Hopwood to *Elephas* [= *Archidiskodon*] *meridionalis* but which proves to be closer to *Metarchidiskodon griqua*. After photograph kindly furnished the present author by Dr. A. Tindell Hopwood (cf. Hopwood, 1926, Pl. III, fig. 2). Brit. Mus. M12641. Natural size.

(Middle) Mid-section of the worn coronal surface. After Hopwood, 1926, fig. 13, p. 34. One-half natural size. Brit. Mus. M12641. Observe the very prominent median 'loxodont sinus.'

(Lower) Summit of the worn coronal surface. After Hopwood, 1926, fig. 14, p. 34. One-half natural size. Brit. Mus. M12642.

This tooth, the enamel plate characters of which are best shown in figure 883 (lower), appears to resemble *Metarchidiskodon griqua* more closely than *Archidiskodon subplanifrons*, because the enamel ridge-plates are more elevated, the measurements given by Hopwood being (*op. cit.*, 1926, table, p. 35), length of four lamellae 100 mm., breadth 72 mm., height 105 mm., as compared with the following corresponding measurements in the type of *M. griqua*, breadth of center ridge-plate 90e mm., height 90e mm. This ridge-plate height exceeds that of the fifth ridge-plate of *A. subplanifrons*, namely, 53e mm., with a breadth of 92 mm.

3. ARCHIDISKODONTS OF THE UNITED STATES AND MEXICO

This noble genus appears to have been given origin in Africa, then to have migrated to Eurasia along the south temperate parallels, and finally to have reached its climax of evolution in the United States from Nebraska southward to the high plateau of Mexico[1].

Two quite distinct lines of descent, referable to *Parelephas* and *Archidiskodon* respectively, are found in the United States and Mexico, in which the low ridge formulæ are very similar, namely:

Elephas [=*Parelephas*] *columbi* Falconer, 1857–1868. Upper Pleistocene of southern United States and of Mexico. Smaller animal than *Archidiskodon*, with narrower grinders (Fig. 887), thin cement outer coating; maximum ridge-plate formula, M 3 $\frac{18\text{-}19}{15\text{-}16+}$.

Elephas [=*Archidiskodon*] *imperator*, Leidy, 1858. Lower[2] Pleistocene of southern United States and of Mexico. Larger animal in size, with broader grinders (Fig. 887), very broad enamel plates, and heavy cement outer coating; ridge-plate formula, M 3 $\frac{17\text{-}18}{18\text{-}20}$.

Geologic Age.—Falconer erred in considering these animals of the same species; they are really very distinct. They were not geologically contemporaneous; to our knowledge the true *Archidiskodon imperator* and true *Parelephas columbi* are not found in the same horizons. *A. imperator* is a late Pliocene and early Pleistocene species (Nebraskan and Aftonian glacial stages, cf. Hay, 1923, p. 15), while *P. columbi* is probably a late Pleistocene species (during Iowan to Wisconsin stages, abundant in the phosphate beds of South Carolina and Florida, cf. Hay, *op. cit.*, p. 431, map 12, also pp. 430 and 155). The true *P. columbi* of Georgia, South Carolina, and Florida are not to be confused with the *Parelephas jeffersonii* of the northern states (cf. Hay, *op. cit.*, map 12, p. 431, error). Gidley held that *A. imperator* and *P. columbi* were contemporaneous.

Gidley, 1928.—Gidley observes (letter, December 6): "There can be no question that remains of *Archidiskodon imperator* and *Parelephas columbi*, as these two species are now defined by Osborn [in the present Memoir], are found associated in the No. 2 beds of Sellards at Melbourne and Vero, and it is equally certain, I think, that these species were contemporaneous in Florida. From my work at Melbourne and Vero last winter I conclude that the 'No. 2' deposit is almost entirely of wind-blown sand origin, slowly accumulated, and that stream action had little or nothing to do with its formation. On this theory mixtures of material of different periods would not be possible. . . . I believe it . . . probable that descendants of *A. imperator* existed in Florida as well as in Mexico and the south, until Upper Pleistocene times." Recently described from Melbourne and Vero, Florida, by Gidley, are:

Parelephas floridanus: Nat. Mus. 11806, 11808, and 11810 (see *Parelephas*, Chap. XVII, footnote, p. 1078).

Archidiskodon imperator: Nat. Mus. 11805, 11814, and 11620 (see below, p. 1005).

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[1] [For Professor Osborn's final opinion on the migration of *Archidiskodon* from the Vaal River of South Africa to the Niobrara River of Nebraska, see Chap. XXIII, p. 1580.—Editor.]

[2] [Early and Middle Pleistocene (*fide* Lugn and Schultz, 1934.1, pp. 373–376).—Editor.]

ORDER OF DISCOVERY IN AMERICA OF ARCHIDISKODON AND PARELEPHAS

Since the opening sections of the present chapter were written several years ago, our knowledge of the two distinct lines of Mammontine descent found in the United States and Mexico has been greatly enriched by three more or less complete fossil skeletons of *Parelephas* discovered in Florida, also by intense and more extended observation on the differences between the *Parelephas* and the *Archidiskodon* crania as well as by careful comparison of the *Parelephas columbi* grinding teeth with those of *Archidiskodon imperator*.

Falconer's type of '*Elephas*' *columbi* is the middle portion of a third inferior grinder in which the ridge-plates are very far apart, thus resembling the widely separated ridge-plates of *Archidiskodon imperator*; he concluded, therefore, that Leidy's '*Elephas*' *imperator* was the same species as his own '*Elephas*' *columbi*. Osborn was long misled by these widely separated ridge-plates and erroneously concluded that the type of '*E.*' *columbi* belonged in the genus *Archidiskodon*; whereas the newly discovered materials above mentioned prove that '*E.*' *columbi* belongs within the phylum *Parelephas*. But, as will be shown in a subsequent chapter (Chap. XVII), the species *Parelephas columbi* Falc., 1857, is clearly distinct from the species *Parelephas jeffersonii* Osborn, 1922. Thus the two quite distinct lines of descent found chiefly in the southern United States[1] and in Mexico appear as follows in the order of discovery:

ARCHIDISKODON PHYLUM

1858 *Elephas imperator* Leidy, Nebraska = *Archidiskodon imperator*
1915 *Elephas hayi* Barbour, Nebraska = *Archidiskodon hayi*
1922 *Elephas Columbi* var. *silvestris* Freudenberg, Mexico = *Archidiskodon imperator silvestris*
1922 *Elephas Columbi* var. *Falconeri* Freudenberg, Mexico = *Archidiskodon imperator falconeri*
1925 *Elephas scotti* Barbour, Nebraska = *Archidiskodon imperator scotti* (or juvenile *A. imperator*)
1925 *Elephas* (*Archidiskodon*) *maibeni* Barbour, Nebraska = *Archidiskodon imperator maibeni*
1928 *Elephas haroldcooki* Hay, Oklahoma = *Archidiskodon haroldcooki*
1928 *Elephas exilis* Stock and Furlong, California = *Archidiskodon exilis*
1929 *Archidiskodon sonoriensis* Osborn, Mexico = *Archidiskodon sonoriensis*

Very broad grinding teeth; thick enamel ridge-plates; heavy cement outer coating; enamel ridge-plates widely separated from the wearing surface of the crown downwards to the face of the plates. Ridge-plate formula not known to exceed M 3 $\frac{18}{20}$.

PARELEPHAS PHYLUM

1838 *Elephas jacksoni* Mather, Ohio = *Parelephas jacksoni*(?)
1857 *Elephas columbi* Falconer, Georgia = *Parelephas columbi*
1859–1861 *Elephas texianus* Owen-Blake, Texas = *Parelephas columbi*
1922 *Elephas Columbi* var. *Felicis* Freudenberg, Mexico = *Parelephas columbi felicis*
1922 *Elephas jeffersonii* Osborn, Indiana = *Parelephas jeffersonii*
1927 *Elephas roosevelti* Hay, Illinois = *Parelephas jeffersonii*
1929 *Parelephas floridanus* Osborn, Florida = *Parelephas floridanus*
1929 *Parelephas columbi cayennensis* Osborn, French Guiana, South America = *Parelephas columbi cayennensis*

Narrower grinding teeth; thinner enamel ridge-plates; thin cement outer coating; enamel ridge-plates widely separated or arcuate at the base (as in type of '*E.*' *columbi*), more closely convergent at the summit; ridge-plates increasing from M 3 $\frac{19}{16+}$ (*P. columbi*) to M 3 $\frac{30}{26}$ (*P. progressus*).

It would be natural to suppose that from the progressive *A. meridionalis* stage these southern mammoths migrated across Asia and through the United States southward, but the present palæontologic and geologic evidence does not support this direct derivation of the imperial mammoth from the progressive *A. meridionalis* type,[2]

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[1] [In 1932 Professor F. H. Edmunds of the Department of Geology of the University of Saskatchewan forwarded to the American Museum for identification a proboscidean molar from the vicinity of Wiseton, Saskatchewan, which proved upon examination by Dr. Edwin H. Colbert of the Museum staff to be referable to *Archidiskodon imperator*. This is important as establishing the most northerly range of the genus in North America.—Editor.]

[2] [Subsequently Professor Osborn became convinced that the "*Elephas meridionalis*" of France was the direct ancestor of the "*Elephas imperator*" of North America, a conclusion arrived at through the discovery of a skeleton (named by Osborn *Archidiskodon meridionalis nebrascensis*), found one mile northwest of Angus, Nuckolls County, Nebraska (see Osborn, 1932.893, p. 1): "New and positive evidence of the correctness of this theory is now afforded by the discovery of the complete skeleton which forms the subject of the present paper. This skeleton with the lower jaw in a complete state of preservation proves to resemble very closely indeed in every detail the '*Elephas meridionalis*' of Durfort, France, as fully described by Albert Gaudry."—Editor.]

because since the year 1915 there have been discovered at least two specific stages very much more primitive than *A. imperator*. These are the *Archidiskodon hayi* Barbour, from near Crete, Saline County, Nebraska, also the *Archidiskodon sonoriensis* from Sonora, Mexico, with its prominent elongate protuberance of the rostrum (Fig. 923, cf. Fig. 903). Of these relatively primitive forms, *A. hayi* (Fig. 913, lower) has an elongate mandibular ramus, with a third inferior molar exhibiting from ten to eleven ridge-plates set very far apart. This not only appears to be the most primitive species of proboscidean thus far discovered in America, but it seems to resemble very closely the primitive lower jaws (Fig. 849) of *A. planifrons* of southern France and of India.

The *Archidiskodon sonoriensis* is a far more progressive species than *A. hayi*, but it exhibits an elongated mandibular rostrum of a much more primitive character (Fig. 923) than the brevirostral mandibular symphysis of *A. imperator* (Fig. 892 A, B, 898 A, A1).

These discoveries render it highly probable that the first migration from Eurasia to America occurred during the Upper Pliocene *Archidiskodon planifrons* phase; they also render it possible that the typical *A. planifrons* of the Pinjor horizon of India migrated to America at about the same period, and perhaps as a traveling companion of the ancestors of *Stegomastodon mirificus*.

SYSTEMATIC DESCRIPTION OF SPECIES

Archidiskodon imperator Leidy, 1858

Figures 805, 810, 812, 815, 817, 818, 865, 884–889, 891, 892, 894–902, 906–909, 912, 915, 916, 920, 937, 1030, 1226, 1231, Pl. xxi

Lower Pleistocene, (?)*1st Interglacial*, or (?)Aftonian age, Central and Southern United States, 40th parallel southward into Mexico. Osborn, 1921–1924: The unrecorded level is probably equivalent to the *Equus* beds of Cope, the *Equus excelsus-Elephas imperator* zone of Osborn (Osborn, 1918.473, p. 34).

Hay, 1924, p. 100: "Seneca, Thomas County (6 [see map, Fig. 890]).—Somewhere along Middle Loup Fork River, probably in Thomas County, was found, by F. V. Hayden's party, the tooth which forms the type of *Elephas imperator*. A more exact locality has not been determined. In the region about Seneca, as reported to the writer by Dr. W. D. Matthew, were found, in 1916, remains of *Equus, Camelops, Platygonus, Canis, etc.* Here, too, Hayden probably found the type of *Stegomastodon mirificus*."[1]

Synonyms or related forms (Mexico): *El. Columbi* var. *silvestris* Freudenb., 1922, Oaxaca, Mexico; *El. Columbi* var. *Falconeri* Freudenb., 1922, Tequixquiac, Mexico; *El. Columbi* var. *imperator* Freudenb., 1922.

Synonyms or related forms (United States): *Elephas scotti* Barbour, 1925; (?)*Elephas* (*Archidiskodon*) *maibeni* Barbour 1925, 1926, *Elephas haroldcooki* Hay, 1928. See type descriptions of these synonymous or related forms below.

This imperial species, well named *Elephas imperator* by Leidy because of its commanding size, appears to be a direct descendant[2] of *Archidiskodon meridionalis* and of *A. planifrons* of southern Eurasia. It progresses beyond the *A. meridionalis* stage, the number of plates in its grinding teeth rising to eighteen (max. twenty), but it retains the very thick enamel and the wide borders of cement. Inasmuch as *A. meridionalis* extended from Upper Pliocene into Lower Pleistocene time in western Europe, it may by migration have given rise to *A. imperator*[2] which seems to characterize Lower Pleistocene (?Aftonian) time, especially in the western and southwestern United States and in Mexico; then this imperial mammoth appears to have become extinct.[3]

Specific Characters, Osborn, 1928.—(1) Relatively short and broad superior and inferior grinding teeth completely surrounded by a heavy layer of cement. (2) Ridge-plate formula: M 3 $\frac{17\text{-}18}{18\text{-}19\text{-}20}$; no superior molars observed in which the ridge-plates exceed eighteen. (3) Brachycephalic and hypsicephalic portions of cranium correlated with the excessively short, broad, and elevated superior molar teeth (Figs. 889B, 888), also with the relatively broad and short inferior molar teeth (Figs. 889A, 892B, left, 898). (4) Lower jaw short, deep, excessively broadened or swollen to accommodate the broad inferior grinding teeth (Figs. 898, 892); inferior ridge-plates normally 16–18, may include imperfect ridge-plates 19–20 (Fig. 892A). Jaws much more abbreviate than in *Archidiskodon planifrons* (Fig. 865), much more massive and swollen than in *A. meridionalis* or any other species of proboscidean; rostrum deep and short; symphysis rounded; the superior border of the coronoid process greatly raised above the grinding surface (Fig. 898).

Elephas imperator Leidy, 1858. [On new species of Mastodon and Elephant from Nebraska, *Mastodon mirificus, Elephas imperator*.] Proc. Acad. Nat. Sci. Phila., March, 1858, Vol. X, p. 10 (Leidy, 1858.2); also "Notice of Remains of Extinct Vertebrata, from the Valley of the Niobrara River," . . . *op. cit.*, p. 29 (Leidy, 1858.4). Type.—(*Op. cit.*, 1858.2, p. 10): ". . . part of an upper molar tooth of an Elephant from the Niobrara; . . . The species he proposed to distinguish by the name *Elephas imperator*." (*Op. cit.*, 1858.4, p. 29): "The fragment of the tooth has been assumed to belong to an unnamed species from the fact that it was found in association with a fauna very distinct from any previously noticed." Nat. Mus. 185; cast Amer. Mus. 2568.

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[1] [Lugn and Schultz (1934.1, p. 373) give the type locality of *Elephas* [*Archidiskodon*] *imperator* as: "Pawnee Loup Branch of Platte River = Middle Loup, probably Hooker Co. [Nebraska], 1858."—Editor.]

[2] [See footnote 2 on previous page—Editor.]

[3] [See footnote 2 on page 996 above.—Editor.]

Horizon and Locality.—(Leidy, 1858.2): "Valley of the Niobrara river, Nebraska." (Leidy, 1869, p. 254): "The fragment of a molar tooth originally referred to a species with the name of *Elephas imperator* was obtained by Prof. Hayden on the Loup Fork of the Platte River." (Hay, 1914, pp. 421, 422) Type collected from Loup Fork of Platte River, now in the National Museum, designated Nat. Mus. 185. (As quoted above from Hay, 1924, p. 100) Probably Seneca, Thomas County, Nebraska. (Lugn and Schultz, 1934.1, p. 373) "Pawnee Loup Branch of Platte River = Middle Loup, probably Hooker Co. [Nebraska], 1858." Type Figure.—Leidy, 1869, Pl. xxv, fig. 3.

Type Third Right Superior Molar of Archidiskodon imperator, and Reconstruction

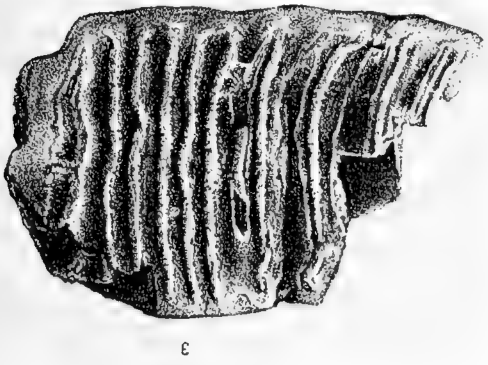


Fig. 884. Type figure of *Elephas imperator* Leidy, 1858. After Leidy, 1869, Pl. xxv, fig. 3. One-third natural size. Fragment of a third right superior molar, r.M^3, from Nebraska (Nat. Mus. 185; cast Amer. Mus. 2568). Inverted.

The anterior surface is to the left; ridge-crests 1–8 are preserved (cf. Fig. 886), ridge-plates concave posteriorly.

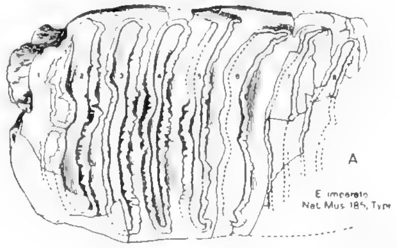


Fig. 885. Type molar, r.M^3, of *Elephas imperator*, crown view. After Osborn, 1922.555, p. 4, fig. 4.

This tooth is in the same position as in Leidy's type drawing (Fig. 884), namely, anterior surface to the left, posterior surface to the right.

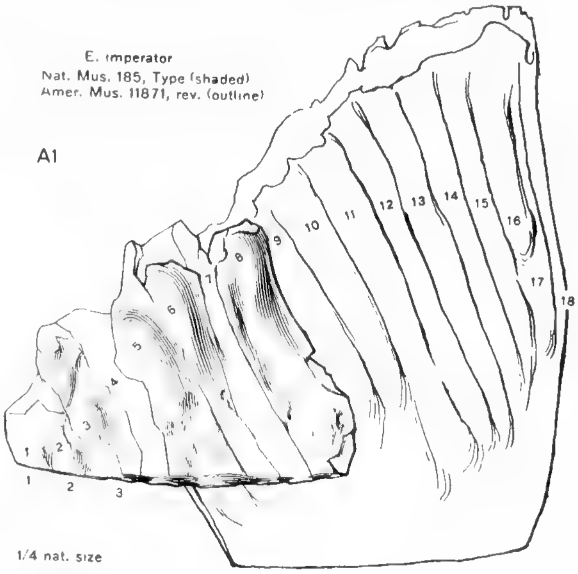


Fig. 886. Leidy's type molar (shaded) and Osborn's neotype (outline) combined, both belonging to M^3 of the right side. After Osborn, 1922.555, p. 4, fig. 4. Neotype (Amer. Mus. 11871) from Guadalajara, Jalisco, Mexico. See figure 888, showing eighteen ridge-plates.

Type Description, 1858.—(Leidy, 1858.4, p. 29): "The Niobrara collection also contains the anterior portion of an upper molar tooth [Figs. 884–886] of an Elephant of larger proportions than any which are known to us. The triturating surface is within a line or two of five inches in breadth, and within a space of seven inches only eight enamel folds or double plates exist. In the most thick plated variety of teeth of the *Elephas americanus* which we have seen, in the same space ten folds were counted. As in the latter, *E. primigenius*, and the recent Elephant of India, the enamel plates become worn on the triturating surface into transverse, strongly crenulated ellipses."

Second Description, 1869.—(Leidy, 1869, pp. 254, 255): "The fragment of a molar tooth originally referred to a species with the name of *Elephas imperator* was obtained by Prof. Hayden on the Loup Fork of the Platte River. I was led to refer it to a species different from the more ordinary American Elephant, from its greater size, the comparative coarseness of the constituent elements, together with the fact that it appeared to be a member of a peculiar fauna, an associate of the *Mastodon mirificus*, as the ordinary *E. americanus* was of the *M. americanus*. . . . The specimen assigned to *E. imperator* is represented in figure 3, plate xxv, one-third the diameter of nature. It exhibits the characters attributed by Dr. Falconer to *E. Columbi*, compared with the supposed American variety of *E. primigenius*. The specimen is the fore part of an upper molar, probably the fifth. The triturating surface, extending the breadth of the fragment, is nearly five inches at its widest part. The breadth on the less broken side is about seven and a half inches, and contains only as many ridges,—that is to say, one ridge to an inch of breadth. There is, however, a thick talon in front, and the ridges curve considerably backward on the less broken side of the tooth. The four more perfect ridges of the specimen at the middle of the triturating surface occupy a space of a little over three inches, including the three intermediate plates of cementum. The widest ridges measure four and a half inches. The enamel is thick and strongly crimped, and the dentinal tracts are slightly dilated at their middle. *Elephas imperator*, if not regarded as a peculiar species of a peculiar fauna, may be viewed, together with those teeth which have been referred to *E. Columbi*, as belonging to the *Elephas americanus*."

Osborn, 1924: (1) In his second description Leidy correctly designated the type horizon as "the Loup Fork of the Platte River," Nebraska. (2) Doubtless influenced by the high authority of Falconer (1863, pp. 58, 59 cited below), Leidy was inclined to abandon the name *Elephas imperator* and to refer this type to *Elephas columbi*, and finally (see Leidy, 1869, pp. 251, 252, 255; 1871, p. 359; 1877, p. 213) to *E. americanus* De Kay, a species representing the American variety of *Elephas primigenius*, namely, *Mammonteus primigenius americanus* of the present Memoir (see p. 1156). This was clearly a series of unfortunate errors on Leidy's part, due to lack of material.

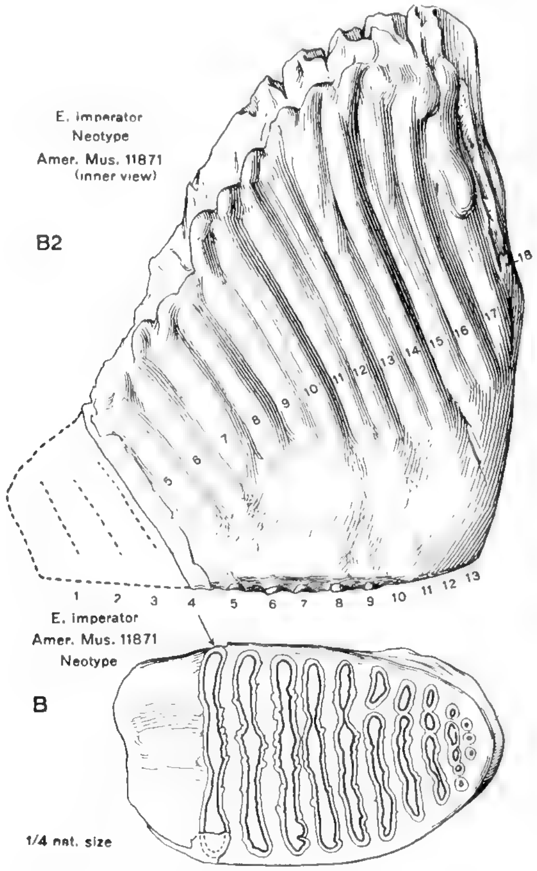
FALCONER ERRONEOUSLY UNITES (1863) ELEPHAS IMPERATOR WITH ELEPHAS COLUMBI

(Falconer, 1863, pp. 58, 59, 67): "The second case is more remarkable and important, being that of the fossil Elephant of the Pliocene Fauna of Niobrara, an affluent of the Missouri River, in Nebraska, the account of which, by Dr. Leidy, has excited much interest and surprise among Palæontologists. [Footnote: 'Proceed. Acad. Nat. Scien. Philadelp., 1858, p. 20, *et seq.*'] . . . 1 Mastodon of the sub-genus *Tetralophodon*, *M. mirificus*, Leidy, and a huge Elephant, *E.* (*Eueleph.*) *imperator*, Leidy. The published descriptive details of this Elephant are as yet but very meagre. One specimen only is mentioned, being the anterior portion of an upper molar, of larger dimensions than any known to the author. The crown is stated to be 'within a line or two of five inches in breadth, and within a space of seven inches, only eight enamel folds or double plates exist.' This would give an average of nearly nine-tenths of an inch to each ridge, corresponding closely with the proportions yielded by *E. Columbi*. The ridges are described as becoming worn into transverse strongly crenelated ellipses. Dr. Leidy adds, 'that the fragment of the tooth has been assumed to belong to an unnamed species, from the fact that it was found in association with a fauna very distinct from any previously noticed.' "

In a subsequent passage in the same paper (1863, p. 67), Falconer observes that in his opinion there are "but two well-determined species of fossil Elephant known in North America," namely: (1) *E. primigenius* (syn. *E. americanus*). (2) *E. columbi* (syn. *E. primigenius*, *pro parte*; *E. texianus*). He concludes (p. 67): "The same, with our present knowledge, must be said of the *E. imperator* of Leidy, from Niobrara. Until a perfect molar is figured and described, no satisfactory opinion can be formed as to what the species is. Dr. Leidy, as already stated, assumed it to be distinct, and gave it the name upon the assumption."

TYPES OF ARCHIDISKODON IMPERATOR (UPPER) AND PARELEPHAS COLUMBI (LOWER)

Fig. 887. *Elephas columbi* (lower figure), fragment of a third right inferior molar, r.M_3, two-sevenths natural size, and *Elephas imperator* (upper figure), fragment of a third right superior molar, r.M^3, two-fifths natural size, photographed directly from the type casts of *E. columbi* (Amer. Mus. 1747) and *E. imperator* (Amer. Mus. 2568). Compare figures 948 and 884.



NEOTYPE OF ARCHIDISKODON IMPERATOR

Fig. 888. From Guadalajara, Jalisco, Mexico. B 2, Neotype superior molar of *Archidiskodon imperator*, M^3 of the right side (Amer. Mus. 11871), inner view, eighteen ridge-plates. B, The same, crown view. One-fourth natural size. After Osborn, 1922.555, p. 5, fig. 5. See figure 886 A1, in outline.

That Falconer erred as to synonymy is clearly demonstrated in the accompanying figure (Fig. 887) in which we observe that while the enamel ridges are equidistant in *Archidiskodon imperator* and in *Parelephas columbi*, and that while the ridge formula is approximately similar in the two species, namely, M 3 $\frac{17\text{-}18}{18\text{-}20}$ (*A. imperator*), $\frac{18\text{-}19}{15\text{-}16+}$ (*P. columbi*), we also observe that the molar of *A. imperator* (upper) is much broader and is surrounded with a broad layer of cement, while the molar of *P. columbi* (lower) is much narrower and is lacking in cement.

OSBORN SEPARATES (1922) ELEPHAS IMPERATOR LEIDY FROM ELEPHAS COLUMBI FALCONER

In reëxamining and comparing the fragmentary molar types of *Elephas columbi* and *E. imperator*, Osborn (1922.555, pp. 1–7) determined with great care the exact position and character of both type fragments as shown in figures 949, 951A, 951B (for *E. columbi*), and in figure 886 (for *E. imperator*) of the present Memoir. The *E. imperator* type proves to be the anterior portion of a third right superior molar containing portions of the first to the eighth ridge-plates greatly worn, and broken away from ridge-plates nine to seventeen, as clearly shown in outline in the accompanying figure 886 A1. At the same time Osborn selected as a *neotype* the third superior molar tooth (Amer. Mus. 11871) from Guadalajara, Jalisco, Mexico, from which the outline in figure 886 A1 is drawn.

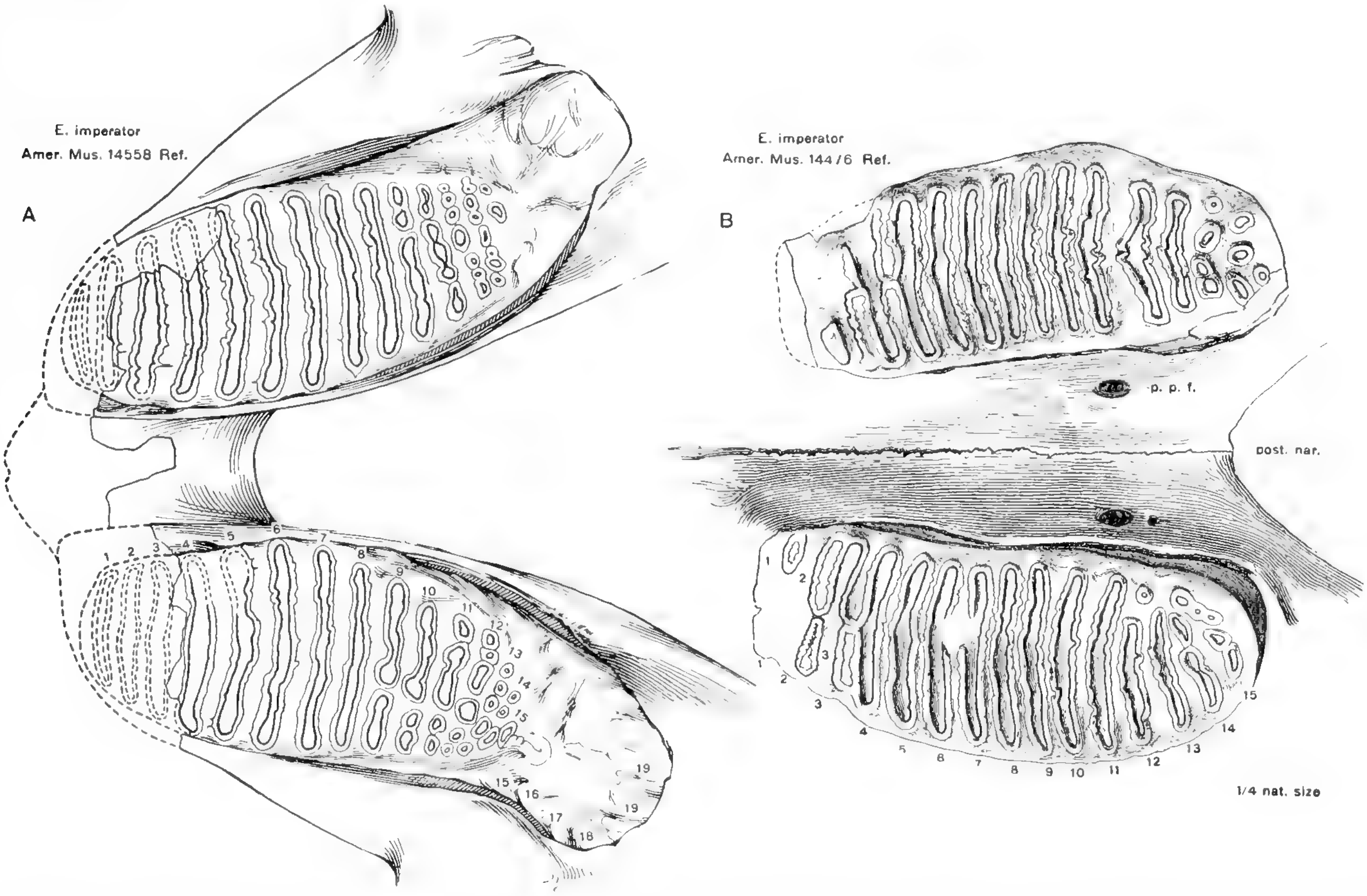


Fig. 889. Superior (B) and inferior (A) molars of *Archidiskodon imperator*, referred American Museum specimens, one-fourth natural size. These two individuals are believed to be of corresponding age. They exhibit (M^3, M_3) mechanical reversal of the convex and concave surfaces both in the crown contours, crown surfaces, and ridge-plates. After Osborn, 1922.555, p. 6, fig. 6.

A, Inferior molars (Amer. Mus. 14558), from Ness County, Kansas, with 14–15 ridge-plates in use, a total of 19 visible in left molar. See also figure 892A, where a total of 20 ridge-plates are visible owing to artificial exposure.

B, Superior molars (Amer. Mus. 14476), from Victoria, Victoria County, Texas, with 14–15 ridge-plates in use, a total of 15+. Inferior view of this skull shown in figure 897. See also figure 896.

Characters of the Archidiskodon imperator Type and Neotype.—(Cf. Osborn, 1922.555, pp. 3–5): "We are indebted to the National Museum for the loan of the *Elephas imperator* type specimen (Fig. 4 [=Fig. 886 of the present Memoir]), enabling us to determine exactly to what portion of the complete neotype tooth (Fig. 5 [=Fig. 888 of the present Memoir]) this ancient and much battered type belonged; the eight ridge-plates of the type [Nat. Mus. 185] which are preserved, in comparison with those of the neotype (Amer. Mus. 11871), constitute the anteroposterior portion of a much-worn molar, M^3 of the right side, in which thirteen ridge-plates were in use out of an estimated total of seventeen [eighteen]. Of these plates five occupy a line 100 mm. long; this is because the ridge-plates are arcuate and widest apart in the middle portion of the crown. The neotype tooth (Amer. Mus. 11871), from Guadalajara, Jalisco, Mexico, appears to attain the full size of the superior grinders of this species of mammoth; the ridge formula may be written M 3 $\frac{17\text{-}18}{18\text{-}19}$ [M 3 $\frac{17\text{-}18}{18\text{-}19\text{-}20}$]. This accords with the actual average count of the ridge-plates in *E. imperator* by Hay (1914) and by Osborn (1921–1922) in individuals which can without question be referred to *E. imperator*. . . . In the neotype (Fig. 5 [=Fig. 888 of the present Memoir]) thirteen plates were in use; in the referred skull (Amer. Mus. 14476) fifteen plates were in use (Fig. 6 B [=Fig. 889 B of the present Memoir]); in the referred lower jaw (Amer. Mus. 14558) fifteen plates were in use (Fig. 6A [=Fig. 889 of the present Memoir]). The total ridge-plates in M_3 attain nineteen [twenty], as clearly shown in Fig. 6A [=Figs. 889A and 892A of the present Memoir]." We have, therefore, the following ridge formulæ (cf. specific definition above).

Upper Pleistocene. *Elephas* [=*Parelephas*] *columbi* of the southern United States: M 3 $\frac{18\text{-}19}{15\text{-}16+}$.

Lower Pleistocene[1]. *Elephas* [=*Archidiskodon*] *imperator* of the southeastern and western United States: M 3 $\frac{17\text{-}18}{18\text{-}19\text{-}20}$.

Upper Pliocene to Lower Pleistocene. *Elephas* [=*Archidiskodon*] *meridionalis,* ancestral, of western Europe: M 3 $\frac{13\text{-}14}{11\text{-}14}$.

(Osborn, 1922.555, p. 5): "The cranial characters observed in three more or less complete skulls referred to *Elephas imperator* tend to support the direct descent of this animal from the *E. meridionalis* of the Val d'Arno, Upper Pliocene of Italy."

Osborn, 1924: Thus *E.* [=*Archidiskodon*] *imperator* appears to be firmly established in its dental characters and ridge-plate formula as a probable successor of *E.* [=*A.*] *meridionalis,* whereas *E.* [=*Parelephas*] *columbi* is clearly distinguished as a smaller form with narrow molar teeth which lack the very broadly encircling layer of cement but exhibit practically the same ridge formula. Freudenberg (1922) has suggested that the true *E.* [=*P.*] *columbi* is geologically a successor of the true *E.* [=*A.*] *imperator* stage.

Meanwhile Hay (1914) made a series of observations on the type and other grinding teeth truly referable to *E.* [=*A.*] *imperator* in various museums, from which the following citations may be made.

HAY'S (1914, 1923, 1924) OBSERVATIONS ON ELEPHAS IMPERATOR

Osborn summarizes below (pp. 1087, 1088) Hay's observations on *Elephas* [=*Parelephas*] *columbi* and geographic distribution records, as well as of *E.* [=*Archidiskodon*] *imperator* in the region west of the Mississippi River (Fig. 890); also Osborn points out (p. 699) the clear distinction between the true *E.* [=*P.*] *columbi* (as limited by Osborn) and the true *E.* [*A.*] *imperator* of Leidy.

DENTAL CHARACTERS (HAY, 1914, p. 421).—It now remains to summarize Hay's observations of 1914 on the grinding teeth discovered near the type locality of Nebraska and on those found in Oklahoma and Kansas (see Fig. 890): "Tooth formula not well known; the hindermost molars having apparently from sixteen to twenty ridge-plates; the teeth large, with thick ridge-plates and thick enamel; the ridge-plates often concave on their hinder face and more or less warped; those of the hinder half of the lower teeth leaning strongly forward. This is a species not yet well known, although various parts of its skeleton have been collected." The chief materials observed and enumerated by Hay are:

Nat. Mus. 185 Type	M^3 fragment (Loup Fork of Platte River, Neb.), eight anterior ridge-plates. (*Op. cit.*, p. 422): "The breadth of the grinding face is 125 mm., but of this about 5 mm. on each side belong to the cement. There are hardly five ridge-plates in a line 100 mm. long and crossing the plates at right angles. The enamel plates are each nearly as thick as the layer of dentine enclosed by them. The plates of cement intervening between the ridge-plates are somewhat, but not greatly thicker than the plates of dentine. The face of each enamel plate which is directed toward the plate of cement is moderately striated from the base to the summit, but this striation is not deep enough to be called crimping. At their inner and outer margins the ridge-plates are turned backward so as to make each one deeply concave on the hinder face, convex on the front face."
Nat. Mus. 2216	M^3 (Afton, Okla.). (*Op. cit.*, p. 422): "The surface of wear extends back to the ninth plate. There are counted sixteen plates. The anterior talon is missing on account of wear, and the posterior one is broken off. It seems not unlikely that at least two ridge-plates are missing, either in front or behind. The plates are very thick, there being hardly five of them in a 100 mm. line." (*Op. cit.*, p. 422): "In another tooth, which is broken, it is seen that the hinder faces of the plates are considerably dish-shaped. It will be observed likewise, that the plates converge toward their summits. The base of the tooth is very convex. The length of the tooth, from the base of the first ridge-plate to that of the hindermost, is 350 mm. The thickness is 126 mm., more than one-third the length of the tooth. The height of the ninth plate is 250 mm. As will be noted, the plane of wear, at the stage represented by this tooth, strikes the summits of the plates very obliquely."
Nat. Mus. 2217	M_3 (Afton, Okla.). (*Op. cit.*, p. 423): "The length from the base of the anterior plate present to that of the hinder one, is 297 mm. The greatest width, taken at one-half the height of the tenth plate, is 125 mm.; the height of the ninth plate is, in a straight line, 170 mm. At the middle of the inner and outer faces there are only three and a half ridge-plates crossed by a line 100 mm. long. At the rear there are five plates in such a line. There are to be counted sixteen ridge-plates and a posterior talon. These are about as thick as the cement plates. The enamel is thick and considerably crimped."
Phil. Acad.	M_3 (Wellington, Kan.?). (*Op. cit.*, p. 424): "It is pretty certain that one ridge-plate is missing in front, and one or more at the rear. Eighteen plates are present. From the front of this tooth to the base of the hindermost plate is 435 mm., a little more than seventeen inches. The height of the tenth plate, in a straight line, is 180 mm. . . . On the hinder end of the tooth, on the grinding surface, six plates outcrop in a distance of 100 mm.; but on the side of the tooth, at one-half of the height, there are only three and one-half plates in 100 mm."

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[1] [See footnote 2 on page 996 above regarding the Early and Middle Pleistocene age of *A. imperator.*—Editor.]

Nat. Mus. 6662 Dp_3 (Afton, Okla.), length 135 mm., width 69 mm.; ridge-plates 7+; 5½ or 6 ridge-plates in 100 mm.; enamel thick (see Hay, *op. cit.*, Pl. LXI, figs. 7, 8).

Nat. Mus. 6663 Dp^4 or M^1 (Afton, Okla.), doubtfully referred. 12 estimated ridge-plates (Hay, *op. cit.*, p. 414).

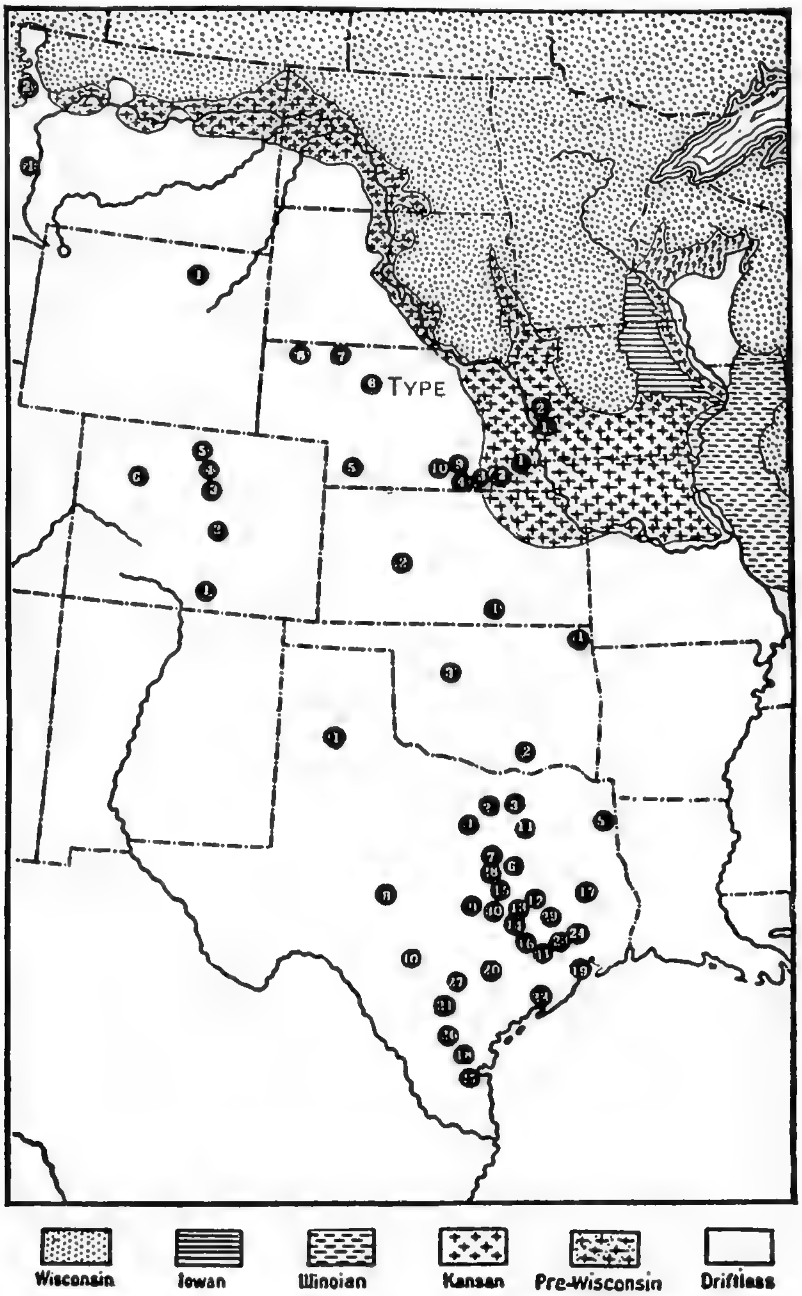


Fig. 890. Distribution of Archidiskodon imperator west of the Mississippi River. After Hay, 1924, Map 10, p. 337, and explanation of Map, p. 336 (Texas omitted).

Nebraska. (6) Near type locality "Loup Fork of Platte River" [probably Seneca (*fide* Hay)], also eight other localities, Holmesville, Fairbury, Reynolds, Wauneta, Cody, Grayson, Hebron, and Sutton. [Lugn and Schultz (1934.1, p. 373) give "Pawnee Loup Branch of Platte River = Middle Loup, probably Hooker Co.," as the type locality.—Editor.]

Oklahoma. (1) Afton, Ottawa County; type region of the Aftonian or *1st Interglacial* stage, in which age *A. imperator* was very abundant. Also three other localities, Kinlock, Okeene, and Kingfisher. Kingfisher not on map.

Kansas. Localities 1 to 3, Wellington, Ness City, Russell (Russell not on map).

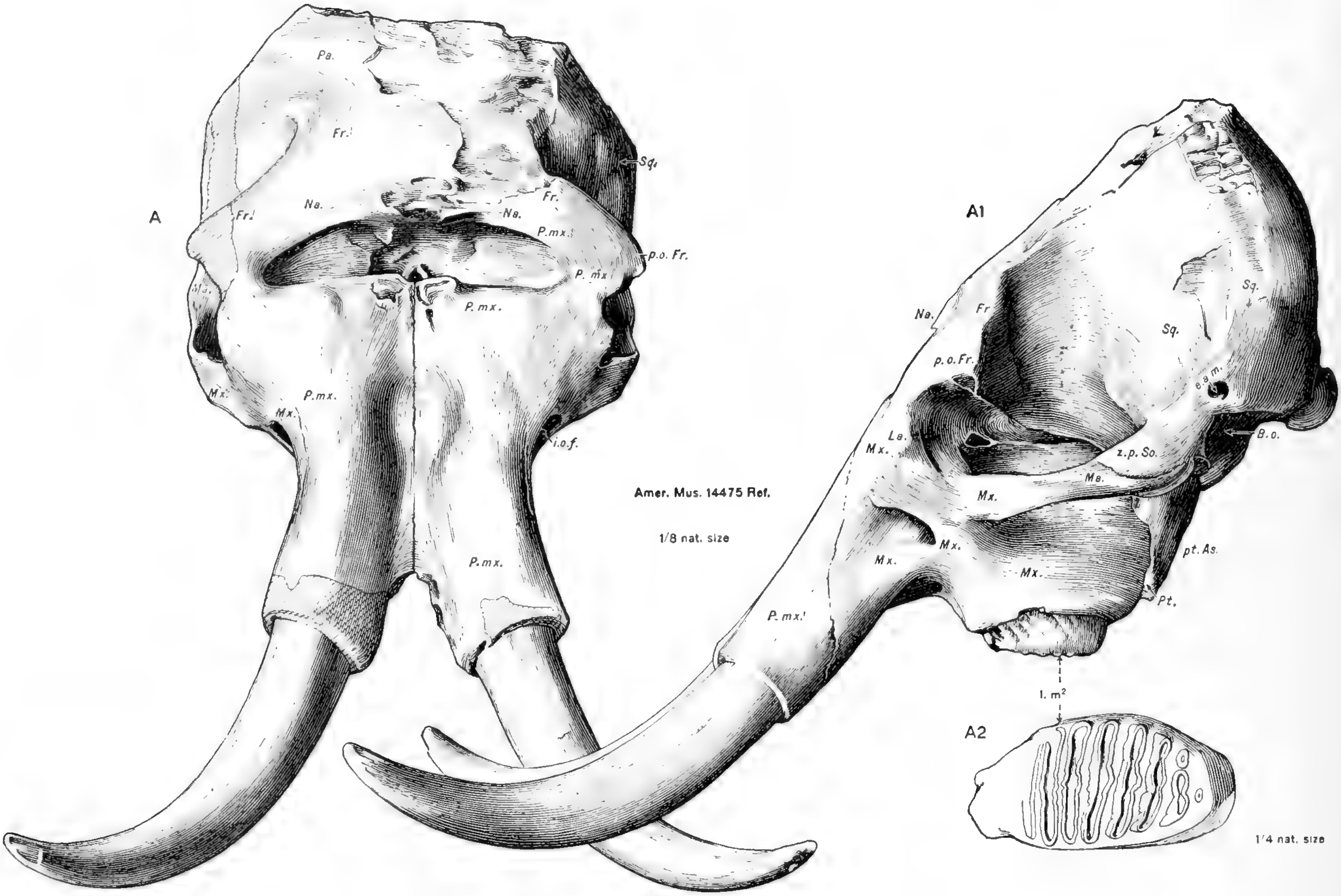
Colorado. Localities 1 to 6, Laveta, Colorado Springs, Denver, Boulder, Fort Collins, Glenwood Springs.

Iowa. Localities 1 and 2, Mt. Pisgah and Mapleton.

Wyoming. (1) Powder River.

Montana. Localities 1 and 2, Helena and Valier.

These grinding teeth are recorded as exhibiting the specific characters of *Archidiskodon imperator* or of *A. hayi*.



Cranium of a Young Male of Archidiskodon imperator of Texas in the American Museum

Fig. 891. Referred young male skull of *Archidiskodon imperator* Leidy (Amer. Mus. Cope Coll. 14475), discovered near Dallas, Texas. Compare figures 895, 896 (restored), also figure 805.

A, Frontal aspect. One-eighth natural size. A1, Left lateral aspect. One-eighth natural size. A2, Partly worn left M^2. One-fourth natural size.

This young male skull was described by Cope in 1889 (1889.2) as "*Elephas primigenius columbi* Falc." and figured by him in Pl. xiv, also on p. 208, fig. 9. It was erroneously referred by Osborn (1922.555, p. 15) to *Elephas* [=*Parelephas*] *jeffersonii*. Both the profile and front views as well as the wire mid-section (Fig. 805, Chapter XV) of this cranium indicate that it is more closely related to *Archidiskodon* than to *Parelephas*. The single molar tooth preserved, l.M^2, enables us to determine this individual as probably belonging to *Archidiskodon imperator*.

Second left superior molar, l.M^2, length	140e
Ridge-plates estimated (?12); exposed	8+
Width at broadest ridge-plate	80
Ridge-plates in 10 cm.	6
Tip of left tusk to occipital condyle	1,400e
Alveolus of left tusk to occipital condyle	960e
Breadth across cranium, posterior portion of occiput	632
Breadth across jugals	610e
Breadth between orbits	484
Breadth between temporal fenestræ	330

We observe that this Texas skull (Amer. Mus. Cope Coll. 14475) belongs to a young male mammoth in which the superior tusks are partly erupted; it was at first regarded as a female skull and was so labeled, but the diameter of the tusks forbids such a reference. In vertical section (Fig. 810) this cranium closely corresponds with the two other crania in the American Museum collection certainly referable to the species *Parelephas jeffersonii*. The young grinding tooth shown herewith (A2), a left second superior molar, l.M^2, does not so clearly display the characters of *P. jeffersonii* as to preclude the possibility of this cranium belonging to a juvenile *Archidiskodon imperator*; consequently the reference is somewhat doubtful. The skull was found in the Texas geographic region characteristic of *A. imperator* in early Pleistocene times, a region which was also traversed by the migrations of *P. jeffersonii* in late Pleistocene times.

Geographic Distribution and Nomenclature (Hay, 1914, 1923, 1924).—Hay (1923, 1924) has made interesting and important observations on the geographic distribution of the remains of *Elephas* [=*Archidiskodon*] *imperator* in the central region of the United States which are summarized on pages 434 and 435, map and legend, 1923, and pages 336 and 337, map and legend, 1924 [=Fig. 890 of the present Memoir].

Unfortunately (1) some of the specimens referred in Hay's work (1914, 1923, 1924) to *E. imperator* may belong to the true *Elephas* [=*Parelephas*] *columbi* and *vice versa*, owing to the confusion which has existed in the minds of practically all American writers up to July 8, 1922 (Osborn, 1922.555), when Osborn clearly distinguished the true *E. columbi* from the true *E. imperator*. (2) In Hay's volume of October, 1924, the northerly mammoths previously (1914–1923) named by him "*Elephas columbi*," as plotted on map 5, p. 327, and map 6, p. 329, are partly named by him "*Elephas boreus*," a name preoccupied by *Parelephas jeffersonii* Osborn; also, on maps 7 to 9, are partly named *Elephas columbi*. As above noted, Hay (1924, pp. 57–84, "Finds of Elephas columbi in the Middle Region of North America") fails to recognize the now well-determined typical ridge formula of *Parelephas columbi*, namely, $M\ 3\ \frac{18\text{-}19}{15\text{-}16+}$.

ARCHIDISKODON IMPERATOR IN THE U. S. NATIONAL MUSEUM FLORIDA COLLECTION

Specimens collected for the U. S. National Museum by James W. Gidley in the locality of Melbourne, Florida, and presumably all from the "No. 2" bed of Sellards, are as follows:

Nat. Mus. 11805. A third inferior molar, M_3, with 15–18 ridge-plates; laminar frequency 5 ridge-plates in 10 cm.

Nat. Mus. 11814. A much worn third inferior molar, M_3; laminar frequency 5 ridge-plates in 10 cm. Total ridge-plates 12+ (tooth worn to base).

Nat. Mus. 11620. The Venice mammoth from near Melbourne, Florida. Aged individual, with third superior and inferior molars much worn, also jaw, portions of skull, right tusk, and hind foot. Third superior molar, l.M^3, total ridge-plates estimated at 18½–19, 3 to 4 anterior worn off, length 200 mm., breadth 106 mm., 5½ ridge-plates in 10 cm.; maximum breadth 106 mm. as compared with 125 mm. in Leidy's Nebraska type (Fig. 884). Third inferior molar, r.M_3, estimated ridge-plates 16–17, 3 to 4 anterior worn off, length 228 mm., breadth 97 mm.

Gidley (letter, Oct. 27, 1928) adds that the specimen from Venice has an extremely deep jaw but otherwise is like *A. imperator*; that both *A.* [=*Parelephas*] *columbi* and *A. imperator* occur at Melbourne and at Vero. "I think, therefore, there can be no doubt that these two species were contemporaneous in Florida, and perhaps also in other localities of the southern and southwestern United States."

Osborn, 1922-1928: This is a very important case of the apparent association of *Archidiskodon imperator* ref. and of *Parelephas columbi* ref. in the same geologic locality, if not actually from the same level.

ARCHIDISKODON IMPERATOR IN THE AMERICAN MUSEUM COLLECTION

See figures 885, 886, 888, 889, 891, 892, 896–898, 900, 906–908, 912, 920 of the present Memoir.

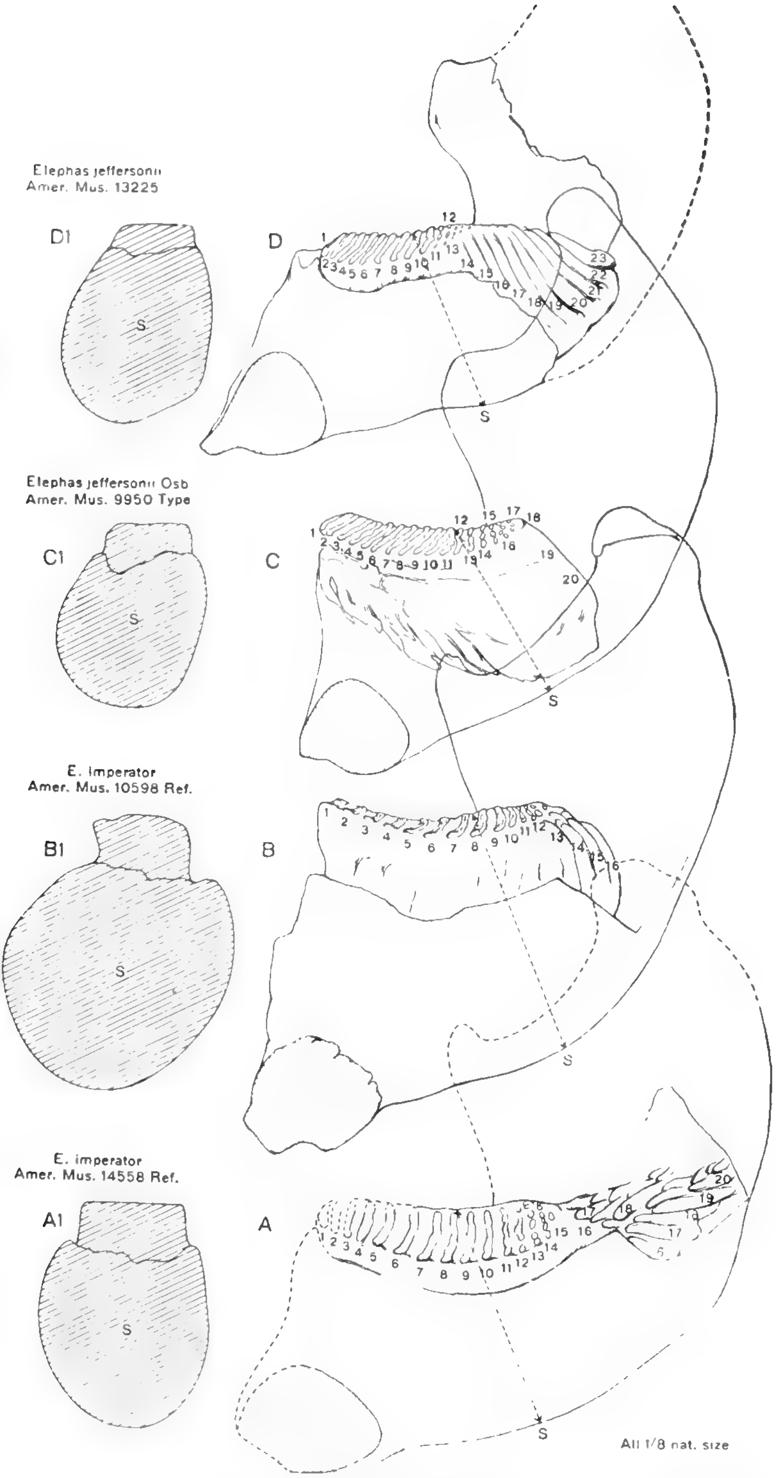
The type cast, the neotype, and the finest referred specimens referable to *Archidiskodon* in the American Museum collection are listed herewith (bottom of this page). These superb materials are illustrated in various figures of the present Memoir and add greatly to our knowledge of this imperial species of southern mammoth. They display clearly the specific characters enumerated above.

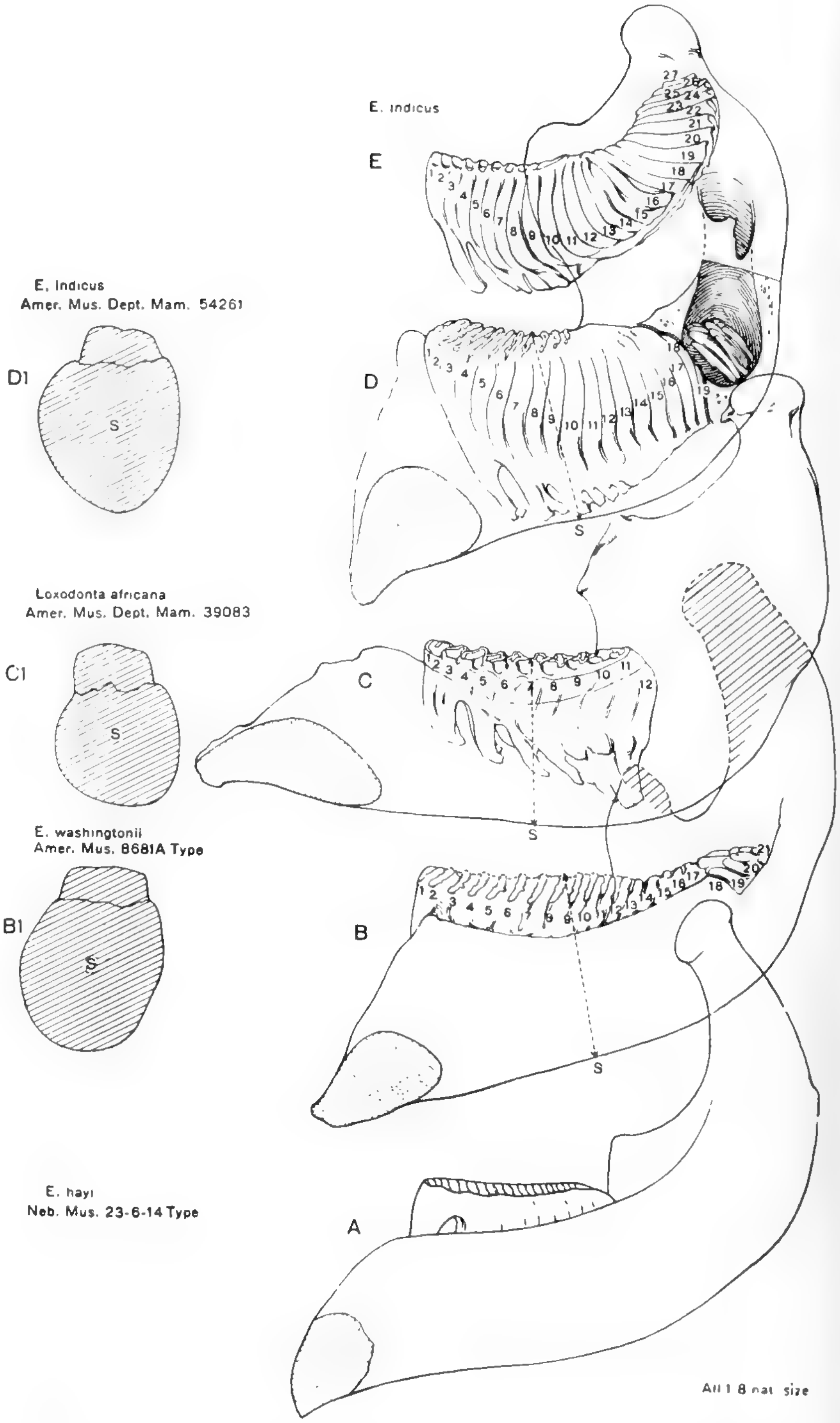
COMPARISON OF THE JAW AND DENTITION WITH OTHER PROBOSCIDEANS

A great deal of study has been given to comparison of the jaws of various types of the Proboscidea, especially in correlation with: (1) Abbreviation (brachycephaly) and elevation (hypsicephaly) of the cranium, also with (2) insertion of the third inferior molar tooth which naturally is the chief functional organ of the body. It is seen in the accompanying diagram (Figs. 892, 893) that the progressive jaws of *Archidiskodon imperator* (Fig. 892 A, B) are profoundly different from the relatively elongate jaws represented in figures 893, A, B, C (*Archidiskodon hayi*, *Parelephas washingtonii*, *Loxodonta africana*). The jaws of *Archidiskodon imperator* (Fig. 892 A, B) are also readily distinguished both from those of *Parelephas jeffersonii* (Fig. 892 C, D) and of *Elephas indicus* (Fig. 893, D, E).

It is observed that in the Texas jaw (Amer. Mus. 10598—see Fig. 892 B) M_3 exhibits sixteen ridge-plates, while in the Kansas jaw (Amer. Mus. 14558—see Fig. 892A) M_3 exhibits five accessory ridge-plates, namely, 16, 17, 18, 19, 20; this difference cannot be due

Amer. Mus. 2568 United States	*Type* r.M^3 of *Elephas imperator*, cast (Amer. Mus. 2568) after original in U. S. National Museum (Nat. Mus. 185). See figures 884, 886, 887.
Amer. Mus. 11871 Mexico	*Neotype* (Osborn) of *Elephas imperator*, right third superior molar, r.M^3, from Guadalajara, Jalisco, Mexico. See figures 886 A1, 888.
Amer. Mus. 14476 Texas	Lower portion of cranium with tusks, here represented in figures 889B, 896, 897, 906. From Victoria, Victoria County, Texas.
Amer. Mus. 14558 Kansas	Imperfect lower jaw, right and left third inferior molars. Crown view (Fig. 889A); side view (Figs. 892A, A1). Total of 19–20 ridge-plates, of which the 19th and 20th are extremely short and rudimentary (see Fig. 892). From Ness County, Kansas.
Amer. Mus. 10598 Texas	Lower jaw with partly worn M_3 (see Figs. 892, 898), also right forelimb (see Figs. 906, 907, 908, 912). From near Tule Cañon, Briscoe County, Texas.
Amer. Mus. Cope Coll. 14475 Texas	Referred young male skull of *Archidiskodon imperator*, with tusks and l.M^2, discovered near Dallas, Texas, and described by Cope in 1889 (1889.2) as "*Elephas primigenius columbi* Falc." (see Fig. 891).





JAWS OF ARCHIDISKODON IMPERATOR IN COMPARISON WITH PARELEPHAS JEFFERSONII, P. WASHINGTONII, LOXODONTA AFRICANA, AND ELEPHAS INDICUS

Fig. 892. Internal aspect of the lower jaws and M_3 of *Elephas* [=*Parelephas*] *jeffersonii* (paratype and type) and *Elephas* [=*Archidiskodon*] *imperator*, also sections D1, C1, B1, A1, cut at point indicated by the dotted line S. One-eighth natural size.

D, *Elephas* [=*Parelephas*] *jeffersonii* paratype (Amer. Mus. 13225); M_3 *in situ* with fifteen worn plates and eight unworn plates, a total of twenty-three plates. [See Fig. 960 for final count of twenty-four ridge-plates in this paratype specimen.]

C, Type of *Elephas* [=*Parelephas*] *jeffersonii* (Amer. Mus. 9950), a very aged individual, M_3 with seventeen worn plates and three additional unworn plates *in situ*, a total of twenty plates. This, as explained elsewhere, is a very aged individual and it is probable that one or two of the extreme anterior plates have been worn off.

B, Jaw of *Elephas* [=*Archidiskodon*] *imperator* ref. (Amer. Mus. 10598), M_3 with fourteen worn plates and a total of sixteen plates *in situ*; a very robust individual. From Tule Cañon, Texas.

A, *Elephas* [=*Archidiskodon*] *imperator* ref. (Amer. Mus. 14558), from Ness County, Kansas, M_3 with fourteen to fifteen (est.) worn plates and five additional, a total of twenty plates. See also figure 889A, crown view of same tooth.

Fig. 893. Internal views of jaws of *Elephas indicus*, *Loxodonta africana*, *Elephas* [=*Parelephas*] *washingtonii*, and *E.* [=*Archidiskodon*] *hayi*, for comparison with figure 892. One-eighth natural size.

E, *Elephas indicus*, a fully developed M_3 of the right side with twenty-seven plates. Drawn after de Blainville, 1839–1864, Pl. IX, fig. 6^c (reversed).

D, *Elephas indicus*, right jaw (Amer. Mus. Dept. Mam. 54261); M_3 with nineteen plates fully formed and five imperfect plates in the jaw, a total of twenty-four plates.

C, *Loxodonta africana* jaw (Amer. Mus. Dept. Mam. 39083, Akeley Coll.); ?M_2 with twelve plates developed.

B, Type jaw of *Elephas* [=*Parelephas*] *washingtonii* Osborn (Amer. Mus. 8681A), with twenty-one plates developed in M_3. Compare figure 969, type of *Parelephas progressus*.

A, Type jaw of *Elephas* [=*Archidiskodon*] *hayi* Barbour (Neb. Mus. 23 6–14).

to age or to sex; it is more probably due to the progressive addition of ridge-plates in the Kansas specimen. Majestic as are these imperial mammoths from Texas the largest pair of tusks known is from Mexico and is described below, with change of name, by Osborn (Fig. 894).[1]

Apposition of the Grinders.—In the American Museum collection there is no case of skull and jaws being found together, so that we cannot positively determine the apposition of the grinders; it is almost certain that an equal number of ridges are in use at the same time in animals of the same age. Consequently the superior and inferior molars represented in figure 889, in each of which *fifteen* ridge-plates are in use above and below, probably represent animals of the same age, although they may not be exactly in the same stage of dental progression. The teeth from Kansas (Amer. Mus. 14558—Fig. 889A, 892A) have 14–15 ridge-plates in use, also the maxillary teeth from Texas (Amer. Mus. 14476—see Fig. 889B) have fifteen ridge-plates in use. These grinders (Fig. 889) are examples of typical *A. imperator* molars exhibiting the following characters: (1) Inferior ridge-plates concave *anteriorly*, partly worn summits of ridge-plates exhibiting 7–8 conelets; (2) superior molars, l.M^3, ap. 290 mm. (restored), tr. 111 mm., index 38; r.M^3, ap. 295 mm. (restored), tr. 120 mm., index 41; (3) M^3, ridge-plates concave *posteriorly*, thus following the mechanical principle of reversal; (4) breadth-length index, $M^3 = 41$.

Fig. 894. A right superior tusk of record size (16+ ft.) of *Archidiskodon imperator* (Amer. Mus. 22481), from Post, Texas, one-twentieth natural size, in comparison with the superb left tusk (13 ft. 9¼ in.) formerly in the National Museum, Mexico, after photograph of original taken by Barnum Brown in 1910. A letter from Sr. Francesco Contreras of the Universidad Nacional de Mexico, May, 1935, states that the original tusk was unfortunately destroyed.

Incisive Tusks.—The characters of the tusks are superbly displayed in the cranium (Amer. Mus. 14476) as shown in figure 896; these tusks curve downwards, outwards, upwards, inwards, until finally they cross each other on the median line, forming a complete superior arch, as in the aged type specimen of *Elephas* [=*Parelephas*] *jeffersonii*. The tusks are parallel but not closely opposed to each other where they issue from the alveoli, as in the specimens referred to this species in the Nebraska State Museum (Fig. 899) found at Hay Springs, Sheridan County, Nebraska.

This comparative study of the superior and inferior teeth and jaws enables us to define the species *A. imperator* much more closely than before.

Record Proboscidean Tusk

A record proboscidean tusk (Amer. Mus. 22481) was presented to the American Museum in 1934 by Mr. George D. Doughty of Post, Texas. This tusk was found in the vicinity of Mr. Doughty's home, namely, Post, Garza County, Texas, in which region the Imperial Mammoth (*Archidiskodon imperator*) seems to have flourished in Pleistocene time. This gift was first noted in the January, 1935, number of Natural History, page 84, followed in the April number, page 357, by a brief description with comparative estimated measurements. Since that time the tusk has been restored conservatively to conform to the measurements given by Mr. Doughty, who was unable to save the anterior end; in life it

Fig. 895. Referred young male(?) skull of *Archidiskodon imperator* from the tar pools of Rancho La Brea, California. Los Angeles Museum 3800-1 (skull), 3801-1 (jaws).

Although partly restored at the summit of the occiput, this is one of the most highly characteristic skulls ever found, in the sharp concavity of the forehead and the peaked cranium, resembling closely the skull of *Mammonteus*.

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[1] [This statement was true at the time it was written about eight or ten years ago. In 1934, however, Mr. George D. Doughty of Post, Texas, presented the American Museum with a giant tusk of *Archidiskodon imperator* (Amer. Mus. 22481), the size and weight of which establishes the record for this species, or, as a matter of fact, for any proboscidean, namely, a length of 16+ feet. This gift was noted in 1935 in the January number of "Natural History," page 84, followed in the April number (p. 357) by a brief description with measurements (see Fig. 894).—Editor.]

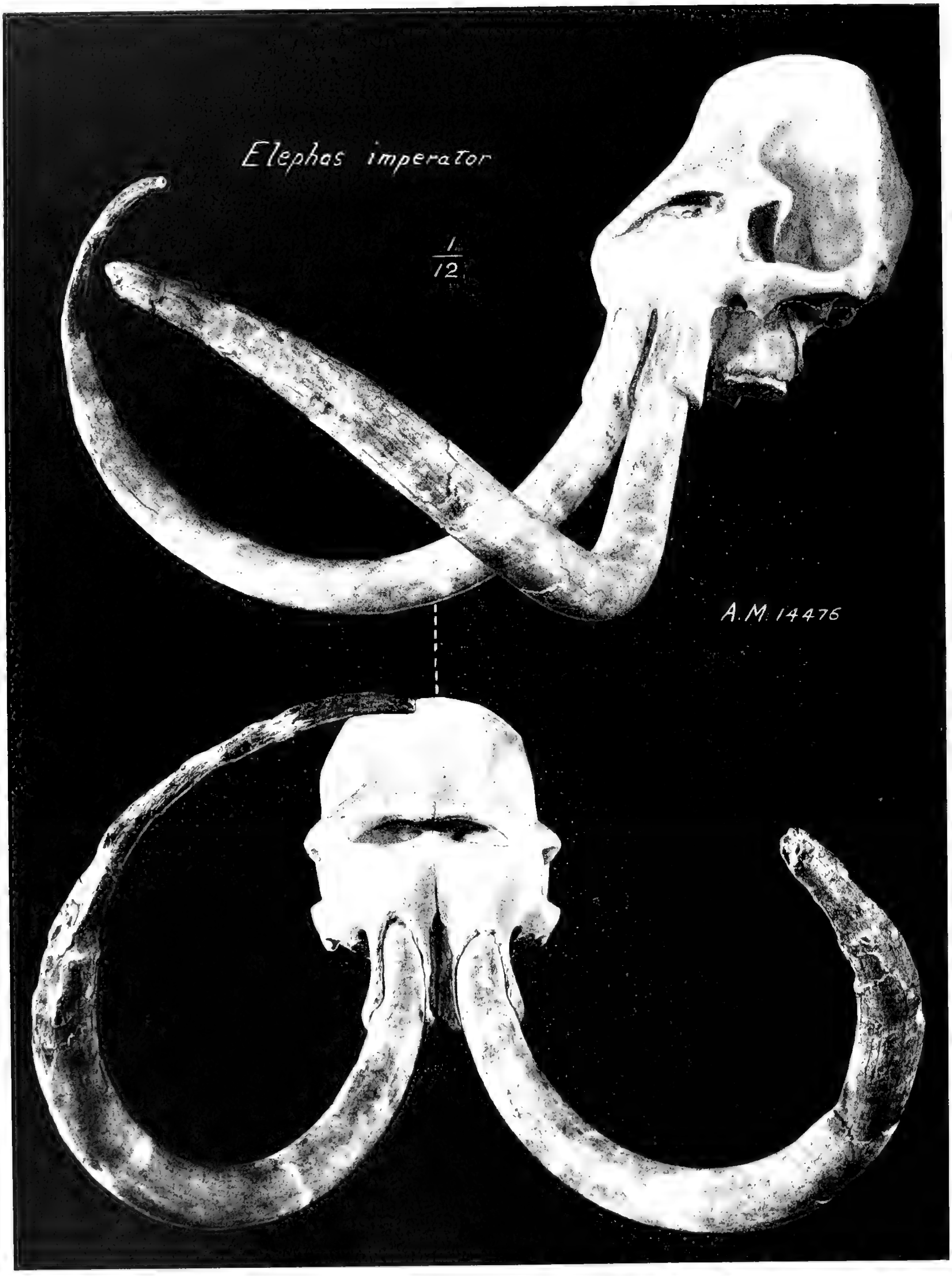

Fig. 896. Skull of *Archidiskodon imperator* (Amer. Mus. 14476), found at Victoria, Texas. The upper portion of this skull is entirely restored. The premaxillaries, the palate, and the superior grinding teeth are perfectly preserved. The palate and grinding teeth of this specimen are also represented in figures 897 and 889. The tusks are complete and natural, without restoration; they measure 4 m. 21.5 cm. or 13 ft. 10 in., as compared with 4 m. 20 cm., est., or 13 ft. 9¼ in., the measurement of the tusks of *A. imperator* in the Geological Institute of the City of Mexico (Fig. 894), as remeasured by Barnum Brown. [See footnote on preceding page which gives the length of the record tusk of this species (Amer. Mus. 22481) as 16 + ft. Editor.]

was evidently longer than now restored, namely, 16+ feet. Associated with this giant tusk were two superior molars (M^2), probably belonging to the same individual.

CRANIAL CHARACTERS OF ARCHIDISKODON

Compare Chapter XV, pp. 915–926, also figures 865, 891, 895, 896, 897, 902, and 906 of the present Memoir.

In the progress from youth to maturity, the occipital summit and profile of the *Archidiskodon* cranium changes profoundly with growth, with sex, and with the development of the enormous superior tusks; these progressive stages are displayed in a comparison of the following eight more or less complete crania in the Los Angeles, American, and Nebraska State museums, and the Geological Institute of Mexico:

Fig. 895. California. Primitive stage. Young male(?) skull from Elephant Pit No. 9, Rancho La Brea tar pool (Los Angeles Mus. Nos. 3800-1 (skull) and 3801-1 (jaws). [=*Archidiskodon imperator.*]

Fig. 891. Texas. Young male stage. Skull from near Dallas (Amer. Mus. 14475). [=*Archidiskodon imperator.*]

Fig. 902. Mexico. Adult male stage. Skull from Tepexpan (Geol. Inst. 212). [=*Archidiskodon imperator.*]

Fig. 897. Texas. Aged stage. Skull (summit restored) from Victoria, Victoria County (Amer. Mus. 14476). [=*Archidiskodon imperator.*]

Fig. 918. Nebraska. 'Lincoln County Mammoth.' Type skull, mandible, and tusks from near Curtis, Lincoln County (Neb. Mus. 5-9-22). [=*Archidiskodon imperator maibeni.*]

Nebraska. 'Adams County Mammoth.' Not figured in present Memoir. Skull, mandible, and teeth from sandpit 6 miles due south of Hastings (Neb. Mus. 11-3-13). [=*Archidiskodon imperator.*]

Nebraska. 'Howard County Mammoth.' Skull, mandible, teeth, and tusks, from near Dannebrog (Neb. Mus. 2-7-17B). [=*Archidiskodon imperator.*]

Nebraska. 'Custer County Mammoth.' Skull, tusk, and teeth from Callaway (Neb. Mus. 16-6-16). [=*Archidiskodon imperator.*]

Texas, Victoria, Skull (Amer. Mus. 14476—Figs. 896, 897, 906).—Only the lower portion of the cranium, including the palate, condyles, and paired grinding teeth, is preserved, the upper portion, as shown in figure 896, being entirely restored above the white dotted line; as the summit of the Victoria, Texas, skull (Amer. Mus. 14476) is restored, we have not ventured to give this hypsicephalic character full expression; it characterizes all the young speci-

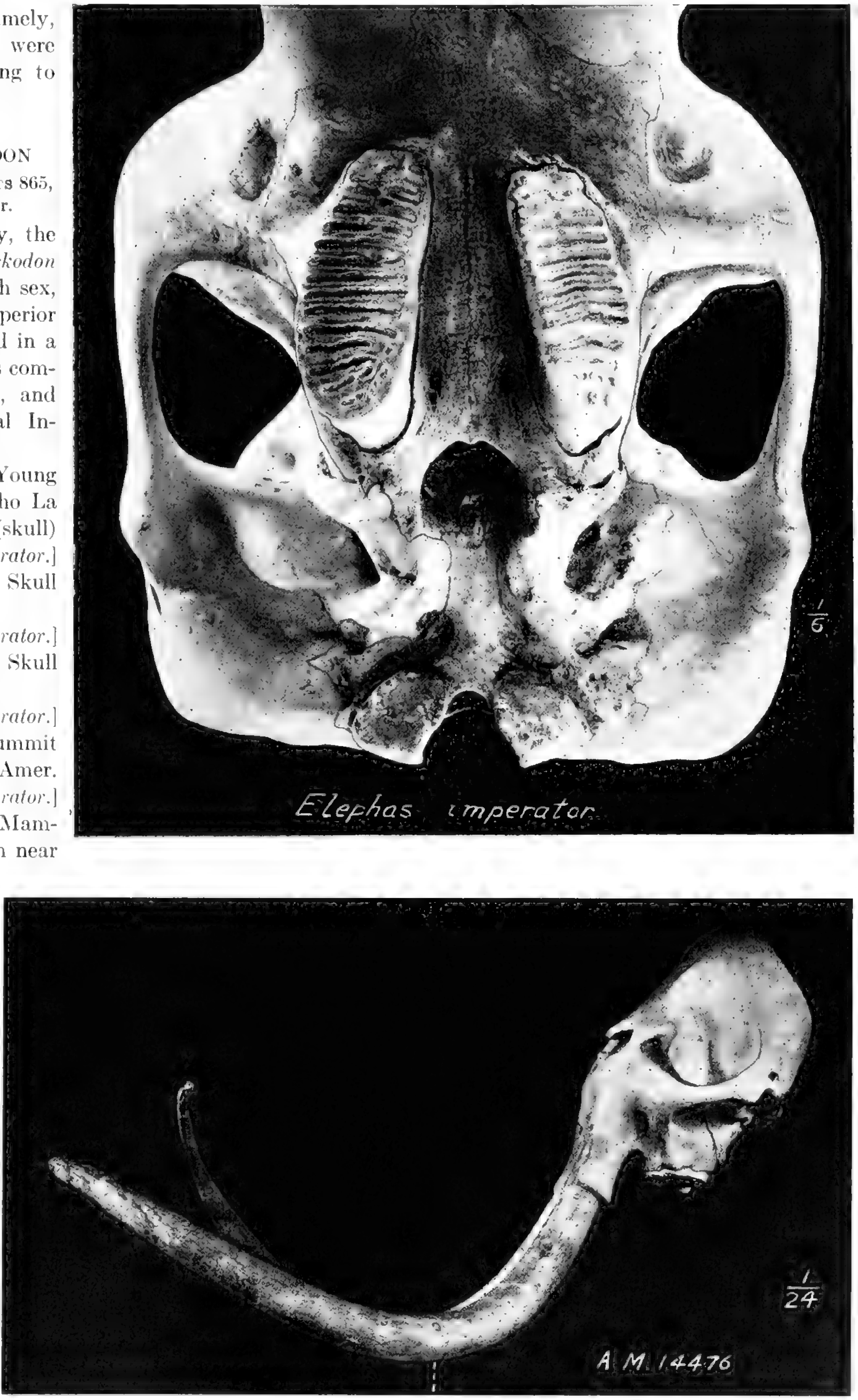

Fig. 897. Skull of *Archidiskodon imperator* from Texas, as largely restored and mounted in the American Museum.

Skull (Amer. Mus. 14476) found near Victoria, Victoria County, Texas; upper part of cranium entirely restored. Side view one twenty-fourth natural size; palatal view one-sixth natural size. See also figure 889 for view of palate; figure 896 for front view of same skull.

mens of the species *A. imperator*; but an aged Mexican skull (Fig. 902) has a broad, massive occiput.

The hypsicephaly or peaked contour of the superior crest is based upon a beautiful cranium of a young male (?) in the Los Angeles Museum, from Rancho La Brea (Figs. 865, No. 10, and 895); we observe a remarkable similarity between the profile of this Los Angeles cranium and that of the true *Mammonteus primigenius*, namely: (1) Forehead concave; (2) parieto-occipital union acute, hypsicephalic; (3) occipital condyles and orbits approximate, i.e., brachycranial; (4) depth extreme from peak of cranium to base of lower jaw. Reverting to figure 865, these distinctive cranial characters of *Archidiskodon imperator* are closely analogous if not genetically related to those of the true mammoth (*Mammonteus primigenius*), while they are widely distinct from those of the trogontherian elephant (*Parelephas trogontherii*) or from the typical elephant (*Elephas indicus*).

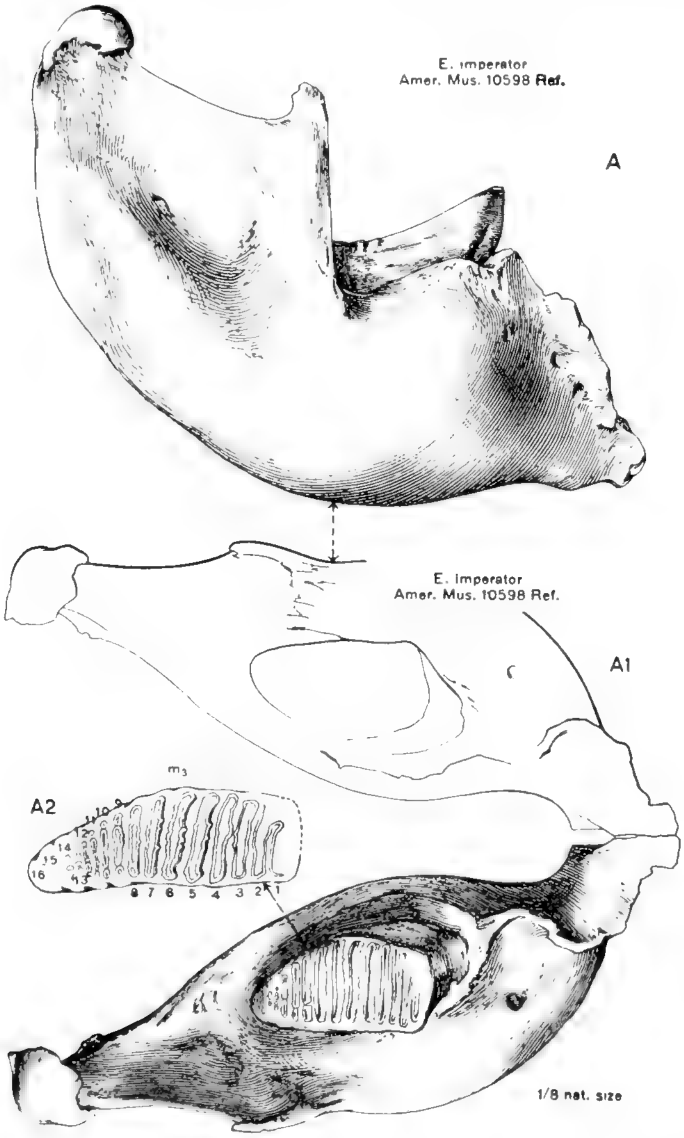

Fig. 898. Jaw of *Archidiskodon imperator* ref. (Amer. Mus. 10598), found at Tule Cañon, Texas, by the American Museum Expedition of 1899. One-eighth natural size. Section and inside view of the same jaw, completely exposing M_3, shown in figure 892B, B1.

A, Right ramus, outer aspect; jaw uptilted.

A1, Top view; tooth greatly shortened by perspective.

A2, Same tooth in perpendicular view of crown, showing sixteen ridge-plates, fourteen of which are worn, indicating that this was a fully adult animal.

See figure 907 for forelimb of same individual.

Comparing the profile and palate of this cranium with that of *Archidiskodon planifrons* and of *A. meridionalis*, we observe the close similarity in fore-and-aft compression (cyrtocephaly) and corresponding vertical elevation (hypsicephaly, acrocephaly).

FLATTENED CRANIA OF ARCHIDISKODON IMPERATOR FROM HAY SPRINGS, NEBRASKA, IN THE NEBRASKA AND AMERICAN MUSEUMS. AFTONIAN AGE.

As provisionally determined by Matthew (1902.1, pp. 317, 318, and 1918.1, pp. 226, 227) from the American Museum collections of 1893 and 1897 (modified by Hay and by Osborn), also by Frick (1929.1, p. 107, and 1930.1, p. 79), [and finally by Barbour and Schultz who have published a preliminary list of the Hay Springs fauna (1937.1, pp. 3–6)], the following includes the species so far recorded by the above-mentioned authors:

Edentata
    Mylodon garmani Allen
    Mylodon nebrascensis (Brown)
    Megalonyx leidyi Lindahl

Rodentia
    Cynomys niobrarius Hay
    Geomys sp.
    Thomomys sp.
    Castoroides ohioensis nebraskensis Barbour
    Castor sp.
    Ondatra nebrascensis (Hollister)
    Microtus?

Carnivora
    Canis latrans? Say
    Canis (Aenocyon) dirus nebrascensis Frick
    Arctodus simus nebrascensis Frick
    Mustela vison? Schreber
    Smilodon nebrascensis Matthew

Proboscidea
    Archidiskodon imperator (Leidy)

Perissodactyla
    Equus excelsus Leidy
    Equus excelsus niobrarensis Hay
    Equus calabatus nebrascensis Frick

Artiodactyla
    Platygonus vetus Leidy
    Camelops kansanus Leidy
    Camelops vitakerianus? (Cope)
    Tanupolama americanus (Wortman)
    Odocoileus sheridanus Frick
    Capromeryx furcifer Matthew
    Tetrameryx (Hayoceros) falkenbachi Frick
    Bovid

It is a striking fact that two extremely flattened crania have been discovered in the deposits of Hay Springs, Sheridan County, Nebraska, which are considered of Lower Pleistocene (Aftonian) age. The first is the flattened cranium (Fig. 899) in the Nebraska Museum; the second is the flat cranium (Fig. 900) in the American Museum of Natural History. The flattening of these crania is a proof of the heavy geologic pressure to which these beds were formerly subjected.

Nebraska Museum.—In figure 899 is represented the palate of a flat skull referred by Prof. E. H. Barbour to *Elephas imperator* (Neb. Mus. 1–11–8–17E); it was found in 1917 at Hay Springs, Sheridan County, Nebraska, in a bed of diatomaceous earth, flattened to four inches in thickness. The broad-plated grinding teeth enable us to confirm this reference, the molars presenting marked resemblance to those of the typical *Archidiskodon imperator*. The geologic age of this specimen is very important, since the Hay Springs fauna is now regarded as of Lower Pleistocene (Aftonian) age.[1] In describing this skull, Barbour observed ten exposed ridge-plates, also three on the deeply worn anterior portion of the tooth, thirteen worn ridge-plates in all; the total number of ridge-plates is unknown. The tusks are very massive in transverse section and closely approximated where they issue from the alveoli; when found the left tusk was 9 feet long, but it was partly destroyed by careless collecting.

American Museum Crushed Skull (Fig. 900).—This

Fig. 899. *Archidiskodon imperator* cranium of aged male (Neb. Mus. 1–11–8–17E) found in a bed of diatomaceous earth, flattened to four inches in thickness; discovered in 1917 at Hay Springs, Sheridan County, Nebraska.

Fig. 900. *Archidiskodon imperator* cranium of adult male (Amer. Mus. 17355), extremely flattened, exhibiting small posterior nares and cranial foramina. Discovered in 1916 at Hay Springs, Sheridan County, Nebraska.

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[1] [Middle Pleistocene (see Barbour and Schultz, 1937.1, p. 3).—Editor.]

crushed cranium (Amer. Mus. 17355) closely resembles in size and character that in the Nebraska Museum (Neb. Mus. 1–11–8–17E). It was discovered in 1916 by Albert Thomson in the famous Hay Springs quarry, Sheridan County, Nebraska. The cranium belongs to a fully adult male, somewhat less aged than the Nebraska Museum cranium (Fig. 899), because the third superior molars, r.M^3, l.M^3, are less worn, displaying anterior ridge-plates. Besides the anomalous crushing, this specimen finely displays the characters of the palate, especially the *'backward' posterior nares*, which contrasts with the very large 'forward' posterior nares of the superb *Parelephas jeffersonii* cranium (the Franklin County Mammoth) in the Nebraska Museum (Neb. Mus. 1–4–15—see Fig. 963), which for a time was erroneously referred to *E.* [=*Parelephas*] *columbi*. This palate of *Archidiskodon imperator* (Amer. Mus. 17355—Fig. 900) should be compared with that of *Parelephas jeffersonii*, which more nearly resembles that of *Elephas indicus bengalensis* (Fig. 800). The backwardly placed opening of the posterior nares appears to be a very distinctive character of *Archidiskodon*.

HAY SPRINGS, NEBRASKA, FRICK COLLECTION.—The following specimens, collected under the direction of Mr. Childs Frick, serve to confirm *Archidiskodon imperator* as the characteristic proboscidean of the Hay Springs horizon.

Amer. Mus. numbers: 25501A, fragment of superior molar, ridge-plate maximum height 244 mm.; 25501, posterior portion of inferior molar, ridge-plate maximum height 164 mm.; 25501B, anterior portion of extremely worn superior molar, maximum width 111 mm.; 25500A, middle portion of an aged inferior molar, width 97 mm., laminar frequency 6½ in 10 cm.; 25500, portion of half-worn superior molar, width 107 mm., laminar frequency 6 in 10 cm.; 25505 A–D, portions of inferior milk molars; 25506, portion of first milk molar.

CRANIAL MATERIAL IN THE NEBRASKA STATE MUSEUM

The finest *Archidiskodon* collection is in the Nebraska State Museum as recently listed by Director Barbour (1925.3, pp. 117, 118) in connection with his description of the "Columbian Mammoth Elephas Maibeni." This list is entitled "Columbi Material in the State Museum"; as revised by Barbour to July, 1925, it is as follows:

SKULLS

11–3–13 Skull, mandible, and teeth from sandpit 6 miles due south of Hastings, Adams Co., Nebraska. ADAMS COUNTY MAMMOTH. [=*Archidiskodon imperator.*]

1–4–15 Skull, mandible, and tusks complete, of extraordinary size. Campbell, Franklin Co., Nebraska. FRANKLIN COUNTY MAMMOTH (compare Figs. 963 and 964 of present Memoir). [=*Parelephas jeffersonii.*]

16–6–16 Skull, tusk, teeth, and femur. Callaway, Custer Co., Nebraska. CUSTER COUNTY MAMMOTH. [=*Archidiskodon imperator.*]

2–7–17B Skull, mandible, teeth, tusks, two tibiæ, scapula, and ribs. Found 7 miles south of Farwell, near Dannebrog, Howard Co., Nebraska. HOWARD COUNTY MAMMOTH. [=*Archidiskodon imperator.*]

5–9–22 Skull, mandible, tusk, forelimbs, six cervicals, several dorsals, four lumbars, sacrum, femur, part of pelvis, ribs, etc. Lincoln Co., Nebraska. Described as *Elephas* (*Archidiskodon*) *maibeni.* LINCOLN COUNTY MAMMOTH. [=*Archidiskodon imperator maibeni.*]

1–4–26 Skull, teeth, and tusks of a form apparently identical with *A. maibeni*; the same type of teeth and the same size and curvature of tusk (see Barbour, 1926.1, p. 122). From Lingle, Wyoming. [=*Archidiskodon imperator maibeni.*]

[1–11–8–17E Palate of a flat skull referred by Barbour to *Elephas imperator*, Hay Springs, Sheridan County, Nebraska. SHERIDAN COUNTY MAMMOTH. [=*Archidiskodon imperator.*]

MANDIBLES

19–9–17 Mandible, left half, with teeth. Powell, Jefferson Co., Nebraska. [=*Archidiskodon imperator.*]

29–25–11–18 Mandible and teeth. Inland, Clay Co., Nebraska. [=*Archidiskodon imperator.*]

2½–3–8–19 Mandible and teeth. Republican City, Harlan Co., Nebraska. [=*Archidiskodon imperator.*]

8–7–08 Mandible and teeth. Young. Benkleman, Dundy Co., Nebraska. [=*Archidiskodon imperator.*]

18–2–22 Mandible with teeth. In Aftonian gravels, Staplehurst, Seward Co., Nebraska. Type of *Elephas scotti* Barbour, 1925. [=*Archidiskodon imperator scotti*, or juvenile *A. imperator.*]

23–6–14 Mandible with teeth. From Crete, Saline Co., Nebraska. Type of *Elephas hayi* Barbour, 1915. [=*Archidiskodon hayi.*]

GRINDING TEETH

Largely as plotted by Hay (1924) under *Elephas* [=*Archidiskodon*] *imperator*, thirty-two or more upper and lower grinding teeth, usually associated, from the following counties in Nebraska, Kansas, Indiana, and Wyoming:

Dawes, Furnas, Jefferson, Platte, Richardson, Gage, Cass, Thayer, Howard, Adams, Fillmore, Buffalo, Cheyenne, Valley, Harrison, Clay, Butler—of Nebraska; also Herndon—of Kansas, Tipton—of Indiana, and Goshen—of Wyoming.

Neb. Mus. 1–4–26 *Archidiskodon imperator maibeni* ref. of Lingle, Goshen County, Wyoming. Walls of cranium very sloping; maximum transverse measurement of palate 30 in., breadth of nasal opening 20 in.; circumference of tusk 25 in.; ridge-plates as thick as those in *A. imperator.*

5–11–20 *Archidiskodon imperator* ref., from Bellwood, Butler County, Nebraska (cast Amer. Mus. 20069). Posterior half of a third right inferior molar, r.M_3, with eight broad ridge-plates; six arched ridge-plates in 20 cm. as compared with nine arched ridge-plates in 20 cm. in the corresponding tooth of *Parelephas columbi* (Amer. Mus. 13707, l.M_3); breadth 4½ in. = 112 mm. This is the most broadly ridge-plated molar on record.

4–12–13 Portions of inferior molars and femur. Arched laminæ of inferior molar, four in 10 cm., as compared with three arched laminæ in 10 cm. (Neb. Mus. 5–11–20). Femur 56 in. long or 1422 mm.; same measurement as that of Neb. Mus. 13–24–10–14 (see Fig. 908).

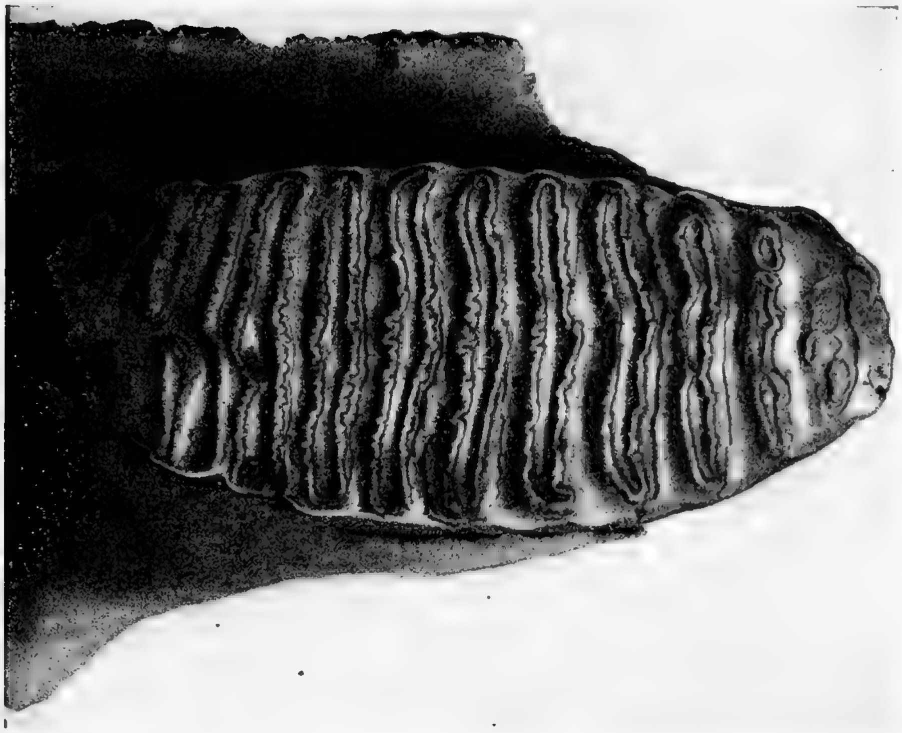

Fig. 901. Referred superior molar, r.M^3, of *Archidiskodon imperator* in the Geological Institute of the City of Mexico (No. 207). After photograph kindly furnished by Señorita Reyes. One-half natural size. Compare Reyes, 1923, fig. 3. This tooth was described by Señorita Reyes (1923, p. 229) as follows: "Fig. 3. Escala: ¼. Ejemplar núm. 207 del I. Geológico. Elephas imperator, Leidy. Molar derecho." Locality: Zumpango, Mexico.

Observe that there are 5½ ridge-plates in 10 cm. as compared with 9½ in *P. columbi felicis*. Length of worn surface 220 mm., breadth 82 mm.

ARCHIDISKODON IMPERATOR IN THE MUSEUMS OF THE CITY OF MEXICO

See *Parelephas columbi* below (Chap. XVII)

We owe to Osborn (1905.270), to Freudenberg (1922), and finally and most fully to Señorita Reyes (1923) descriptions of the superb materials referable to *Archidiskodon imperator* and to *Parelephas columbi* in the museums of the City of Mexico.

Progressive Stages (Mexico).—As described by Osborn (1905.270, p. 931): "The elephant remains in the National Museum have usually been ascribed to *Elephas columbi*; but they include molar teeth not only of this species, but of the much larger form, *Elephas imperator*. In the collection of the Geological Survey of Mexico in the new survey building are the skull and tusks of an *E. imperator* of magnificent proportions, the tusks measuring 5 m. 10 cm., or 16 feet 10 inches [4 m. 20 cm. est., or 13 ft. 9¼ in., as remeasured by Barnum Brown] in length; this specimen was secured during the excavations for the great drainage canal of the Mexican Valley."

In the collection of the Geological Institute of Mexico, under the direction of Dr. José G. Aguilera, there are also several single teeth of *Archidiskodon imperator*, molars of the *Parelephas columbi* type from the village of Zacapú in Michoacan and of *A. imperator* from the valley of Puebla (cf. Osborn, *op. cit.*, p. 931).

Reyes, 1923.—The specimens described and figured (1923) by Señorita Reyes, are as follows:

Elephas imperator

Escuela de Ingenieros No. 1. Jaw containing M 3, with 6 ridge-plates exposed. From Tequixquiac. Figs. 1 and 2, p. 228.

Geol. Inst. 207. Palate with r.M^3, 13 ridge-plates exposed; length 220 mm., breadth 82 mm. From Zumpango. Fig. 3, p. 229 (see Fig. 901 of the present Memoir).

Geol. Inst. 210. R.M^3, length 300 mm., breadth 115 mm., 12½ ridge-plates in 25 cm. From Tepexpan. Fig. 4, p. 230.

Geol. Inst. 212. Cranium of young [adult] individual, a beautiful specimen well conserved. It is without tusks. Enormous prominence of occipital crest. Associated lower jaw. Dimensions of second superior molar, M^2: length of worn area 168 mm., breadth 108 mm. From Tepexpan. Fig. 7, p. 233, Fig. 8, p. 234, and Fig. 9, p. 235 (see Fig. 902 of the present Memoir).

Posterior view (Fig. 7).

Anterior view (Fig. 8), forehead concave. Summit of occipital crest broadly rugose.

Crown view of lower jaw (Fig. 9).

Geol. Inst. 211. Left ramus of jaw[1] with l.M_3, 12½ ridge-plates in 25 cm., length 220 mm., breadth 98 mm.; length of femur 1360 mm. From Tepexpan. Fig. 5, p. 231, Fig. 6, p. 232 (see Fig. 903 of the present Memoir).

Archidiskodon (?)hayi Ref. in Mexico.—A mandible[1] (Fig. 903) from Mexico (Geol. Inst. v-211), referred by Señorita Reyes to *Elephas hayi*, supports the evidence afforded by Barbour's type of *E. hayi* that an Upper Pliocene stage of *Archidiskodon*, apparently similar in progression to the *A. planifrons* of Asia and of southern France, entered North America.

Osborn, 1924: This mandible from Mexico is intermediate between the *E. hayi* type of Barbour and the *E. imperator* type of Leidy; it shows a prolonged rostrum (see Fig. 903); it appears to us like a progressively modified rostrum derived from an ancestor with a jaw like that of *A. planifrons*. While this mandible has been referred to *Elephas hayi* by Señorita Reyes, it seems to Osborn to

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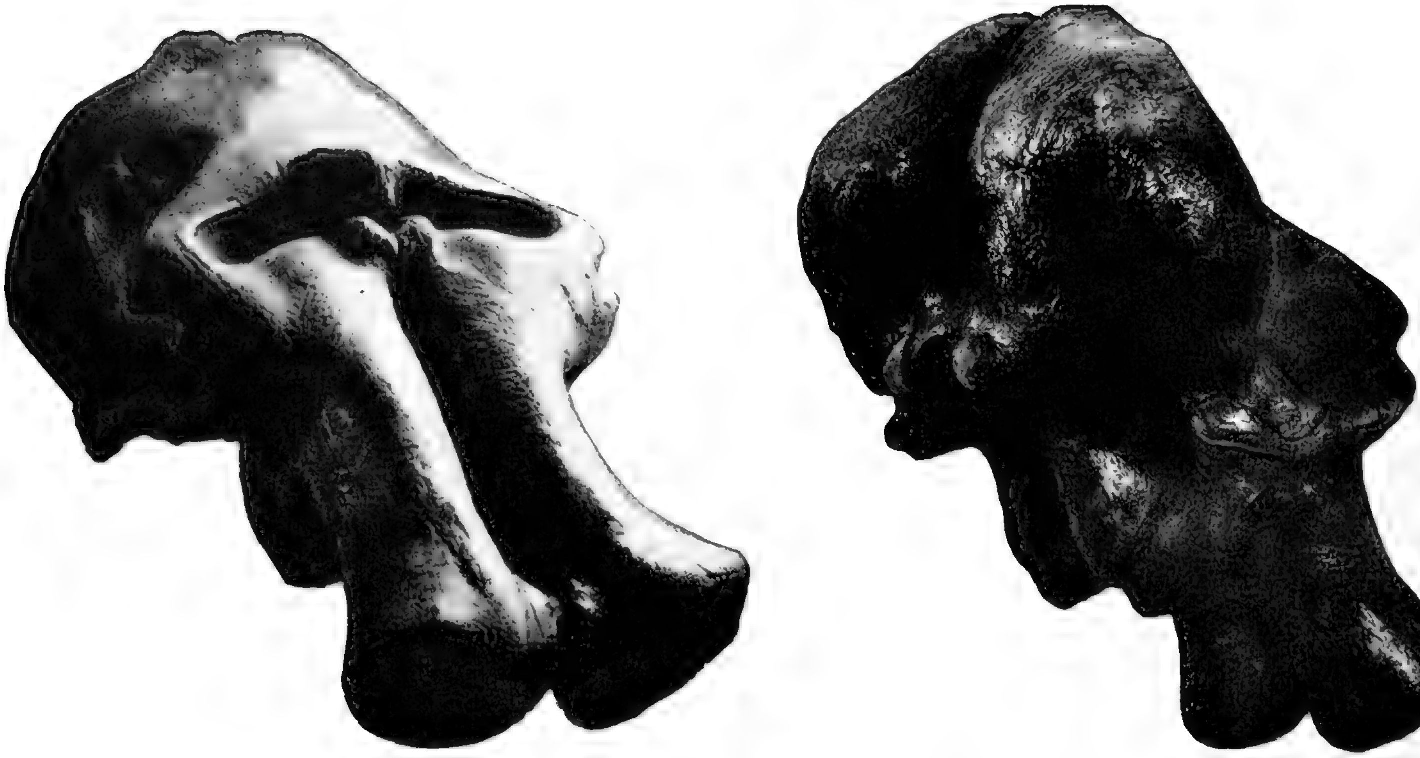
[1] Osborn, 1929: A similar mandible is described below (p. 1033) as *Archidiskodon sonoriensis*, to which species this specimen may also be referable.



CRANIUM OF AN ADULT MALE OF ARCHIDISKODON IMPERATOR IN THE GEOLOGICAL MUSEUM OF MEXICO

Fig. 902. Referred mature cranium of *Archidiskodon imperator* in the Geological Institute of the City of Mexico (Geol. Inst. 212), reduced to one-twelfth natural size. After photograph kindly furnished the present author by Señorita Reyes. Locality: Tepexpan, Mexico. Compare Reyes, 1923, figs. 7, 8, and 9.

This robust male cranium lacks the sharply peaked, acrocephalic, occipital crest structure seen in the young male(?) cranium from Rancho La Brea (Fig. 895). Judging by the elongated and massive alveoli and rugose exoccipital muscular attachments this cranium supported an enormous pair of tusks. The adult male tusks are estimated at 13+—16+ feet in length (see Fig. 894).

represent rather an intermediate and distinct species in which there is a much larger number of ridge-plates than in the type of *E. hayi*. It is another proof of how much we have still to learn regarding the characters and migrations of *Archidiskodon* in North America.

Doubtless future excavation will reveal additional material of great value. We turn to Freudenberg (1922) for his views regarding the relationship of the true *Elephas columbi* Falconer to the true *E. imperator* of Leidy (see p. 1017 below); also for his remarks on the relationship of *A. imperator* to the *A. meridionalis* of Europe and to the *A. planifrons* of Asia and southern France.

ANCESTRY OF ELEPHAS IMPERATOR (FREUDENBERG, 1922, SOERGEL, 1915[1]).—(Freudenberg, 1922, p. 171): "Die Mastodonten wanderten früher nach Amerika über, die Elefanten später. Die innerasiatischen Hochländer, die den meisten Säugetierstämmen den Ursprung gaben, sind auch hier in diesem Fall als Heimat der mexikanischen Arten anzusehen. [Footnote: 'Vgl. W. D. Matthew, Climate and Evolution. Annals of the New York Acad. of Science. Vol. 24. pag. 171–318.']. Für die Elefanten gilt das mit ziemlicher Sicherheit. Eine Ableitung des *El. imperator* von *El. meridionalis* Europas, wie Soergel [Footnote: 'W. Soergel, Die Stammesgeschichte der Elefanten. IV. Die amerikanischen Elefanten. Centralbl. f. Mineralog., Geolog. u. Paläontolog. 1915. No. 9. pag. 278–283.'] das will, ist gesucht. *El. planifrons* ist weit eher der Stammvater aller späterer Elefantiden als der *El. meridionalis*,

Fig. 903. Mandible of *Elephas* [=*Archidiskodon*] *hayi*(?) ref. in the collection of the Geological Institute of the City of Mexico (v-211). Photograph through the courtesy of Señorita Reyes (compare Reyes, 1923, figs. 5 and 6). About one-seventh natural size. The prolongation of the symphyseal rostrum suggests a remote resemblance to the type of *Archidiskodon hayi* Barbour (Fig. 913 of the present Memoir); this feature, however, is more characteristic of *A. sonoriensis*. [See footnote on p. 1013.—Editor.]

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[1] See citation below, page 1015.

der auch sicher mit Unrecht als der Ahne des *El. antiquus* von genanntem Autor angesprochen wird."

Ancestry of Elephas imperator, Soergel, 1915, p. 281.—"Wir müssen annehmen, dass die nach Amerika überwandernden Formen der *Meridionalis-Trogontherii*-Reihe schon beim Überwandern resp. kurz vorher besondere Charaktere gegenüber dem europäischen *El. trogontherii meridionalis* ausgebildet hatten, Charaktere, die in der weiteren Entwicklung sich zum '*Imperator*-Typus' steigerten. Es war also im ältesten Diluvium im Kreis der kontinentalen Elephantenformen eine Variationsbreite mit 2 Polen, *El. trogontherii meridionalis* im Westen und dem direkten Vorfahren des *El. imperator* im Osten vorhanden. Es ist klar, dass als direkter Vorfahr beider Pole die nächstältere Mutation in der kontinentalen Reihe zu gelten hat, das ist *El. meridionalis* des ältesten Diluviums, vielleicht auch des Oberpliocän. Als Vorfahr des *El. imperator* Leidy hat also jedenfalls *El. meridionalis* Nesti zu gelten."

In our judgment Freudenberg was less fortunate in his treatment of *Elephas imperator* as a subspecies of *E. columbi*. For reasons originally stated by Osborn (1922.555) the type of *Elephas columbi* Falc. is readily distinguishable from the type of *Elephas imperator* Leidy; consequently the treatment of *E. imperator* as a subspecies of *E. columbi* is invalid; it should stand *E.* [= *Archidiskodon*] *imperator*.

Synonyms of Archidiskodon imperator.—The four subspecies of *Elephas columbi* proposed by Freudenberg (1922) in this manner are redetermined by Osborn as follows:

El. Columbi var. *Felicis* Freudenberg, 1922, p. 147, Taf. xvi (viii), fig. 4, Tecamachalco, Puebla, Mexico
= *Parelephas columbi felicis.*
El. Columbi var. *silvestris* Freudenberg, 1922, p. 152, fig. 19, Ejutla, Oaxaca, Mexico = *Archidiskodon imperator silvestris.*
El. Columbi var. *Falconeri* Freudenberg, 1922, p. 153, fig. 21, Tequixquiac, Mexico = *Archidiskodon imperator falconeri.*
El. Columbi var. *imperator* Freudenberg, 1922, pp. 160–171
= *Archidiskodon imperator.*

The subspecific value of *Archidiskodon imperator silvestris* and of *A. imperator falconeri* remains to be determined. We may here quote in full Freudenberg's description of these subspecies and reproduce his type figures.

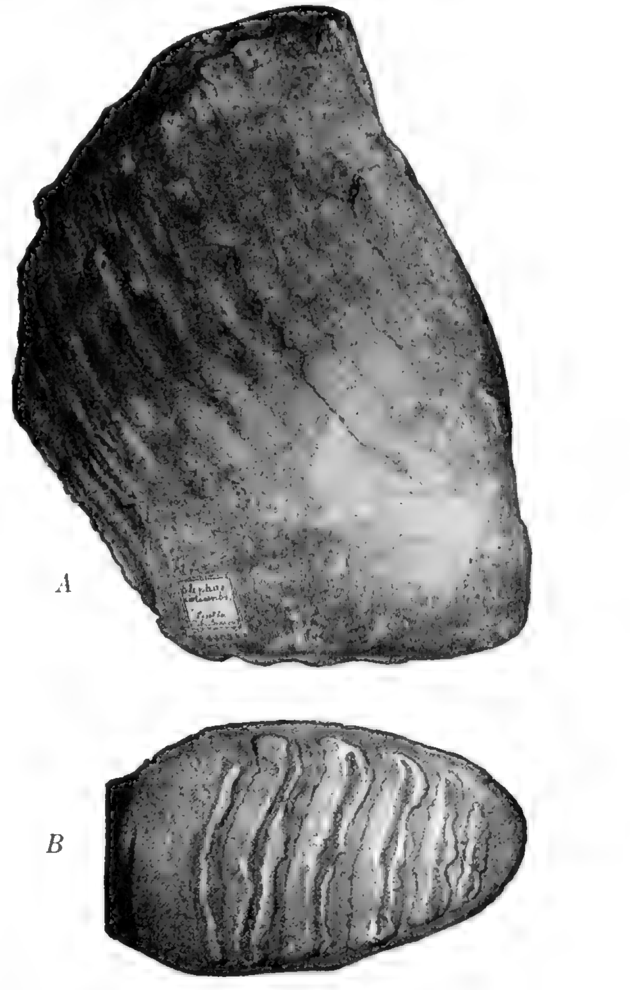
Archidiskodon imperator silvestris Freudenberg, 1922

Figure 904

Ejutla, State of Oaxaca, Mexico. Probably Lower(?) Pleistocene.

The type of this subspecies, related by Freudenberg to the species *Elephas* [= *Parelephas*] *columbi*, is obviously referable as a synonym or subspecies of *Archidiskodon imperator*. The type (Fig. 904), with at least 16 ridge-plates, is too elevated to be regarded as an M^2; it appears rather to be a left M^3; the six ridge-plates exposed (Fig. 904 B) resemble those of *A. imperator* rather than of *P. columbi*; this Ejutla type has the very broad outer coating of cement characteristic of *A. imperator* and lacking in *P. columbi*.

El. Columbi var. *silvestris* Freudenberg, 1922. "Die Säugetierfauna des Pliocäns und Postpliocäns von Mexiko." Geol. und Palæont. Abhand., N. F., Band XIV, Heft 3, pp. 152, 153. Type.—Second [third] superior molar of the left side, M^2 [l.M^3]. Pal. Coll. Univ. Leipzig 4402. Horizon and Locality.—Ejutla, Estado de Oaxaca, Mexico. Type Figure.—(*Op. cit.*, p. 146, fig. 19): "Fig. 19. a. *El. Columbi* var. *silvestris*. Kronenansicht des zweiten oberen Molaren, in ⅔ nat. Gr. b. Seitenansicht in etwa ⅓ nat. Grösse. Original in Leipzig, von Ejutla, Estado de Oaxaca in Mexiko. Coll. Felix, wohl aus jüngerem Diluvium. Subtropische Waldform."



Freudenberg's Type of Archidiskodon imperator silvestris

Fig. 904. Type, left M^3, of *Elephas Columbi* var. *silvestris* Freudenberg, 1922, p. 146, fig. 19, reduced to one-third natural size. From Ejutla, Estado de Oaxaca, Mexico. After photographs sent by Doctor Freudenberg. Original in Leipzig (Pal. Coll. Univ. Leipzig, 4402), Coll. Felix. B, Crown view; A, side view.

Type Description.—(*Op. cit.*, p. 152): "3. Der Zahn von Ejutla (*El. Columbi* var. *silvestris* Freudenberg). Wenden wir uns genauer dem oberen Molaren von Ejutla (Estado de Oaxaca) zu, welchen Felix als '*El. Columbi*' etikettiert und nur mit Vorbehalt wegen der relativ enggestellten Lamellen unter *El. primigenius* Blumenbach var. angeführt hat. Dieser Zahn trägt jetzt die No. 4402 der paläontologischen Sammlung der Universität Leipzig. Es ist ein zweiter oberer Molar der linken Seite. Ich bilde ihn ab von der Seite als Textfig. 19b und a und von der Kaufläche aus. Das Hinterende weist eine merkliche Einwärtsdrehung der Lamellen auf und zugleich eine Vertiefung in 5 cm Entfernung unter der letzten angekauten Lamelle. Diese Grube halte ich trotz ihrer Rauhigkeit für eine Pressionsmarke, hervorgebracht vom nachdrängenden M^3. Die vordersten 4 Lamellen sind abgebrochen; einige davon dürften abgekaut sein. Dadurch ist die Lamellenzahl im Minimum = 16." The author rightly contrasts this species as identical in the ridge formula of M^3 with that of the subspecies *Parelephas columbi felicis*. He remarks (*op. cit.*, p. 153):

"In der Art der Abkauung gleicht dieser Zahn sehr dem von Pohlig—Nova Acta Acad. C. L. C. G. Nat. Cur. Vol. 57 abgebildeten M^2 des *El. Americae* Pohlig aus Chihuahua, Mexiko. Es wird auch ein M^3 von dort an gleicher Stelle abgebildet mit derselben schiefen Stellung der Lamellen zur Längsachse des Zahns wie an den Molaren von Ejutla und ganz verschieden von den Hochplateauformen der Mesa central von Mexiko oder Puebla. Es empfiehlt sich aus oben genannten Gründen nicht, Pohligs Namen *El. Americae* [= *Elephas americanus* De Kay, 1842] für die Waldform des *El. Columbi* anzuwenden, dessen Verbreitungsgebiet die südwestlichen Randgebirge des mexikanischen Hochplateaus waren. Ihnen gegenüber stehen die als *El. Columbi* var. *Felicis* aus der Mesa central bezeichneten Steppenformen.

Archidiskodon imperator falconeri Freudenberg, 1922

Figure 905

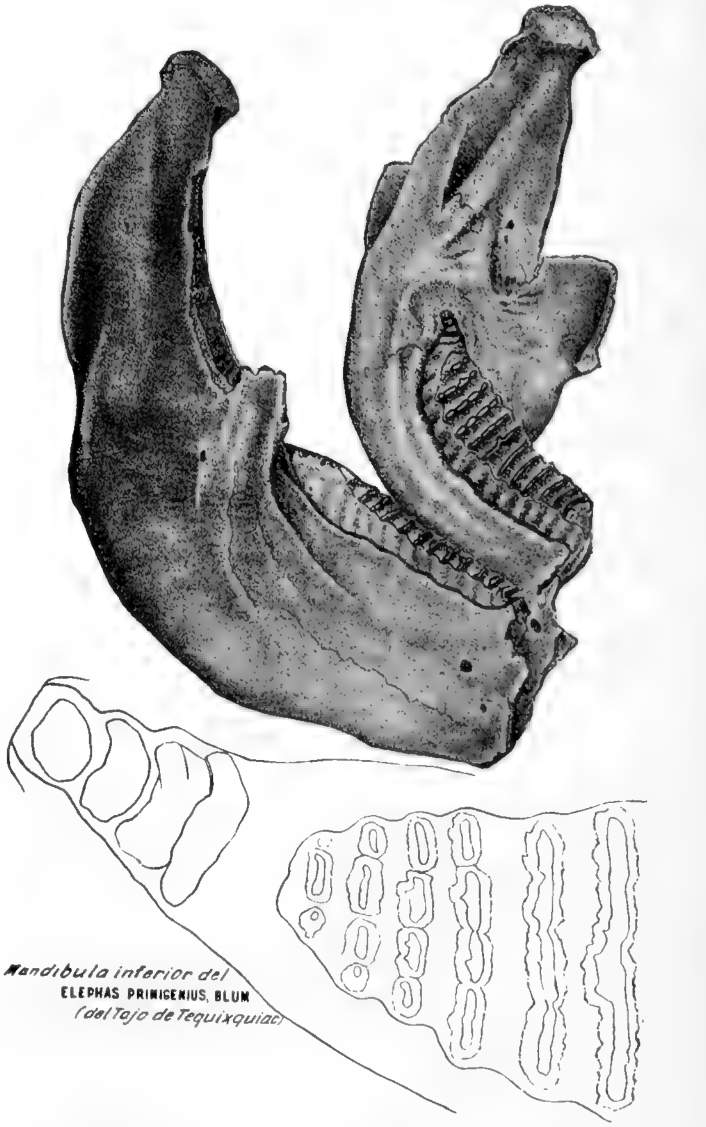
Tequixquiac, Valley of Mexico; probably Lower(?) Pleistocene.

This Tequixquiac jaw (Fig. 905) represents the cotype and is undoubtedly related to *Archidiskodon imperator* rather than to *Parelephas columbi*. From the figure it is difficult to give the characters of this jaw, but it appears to be somewhat longer and more primitive than the type of *A. imperator*. The lower grinding teeth apparently present the following formula: $M\ 3_{\overline{16\text{-}17}}$. In this jaw the 16+ ridge-plates exposed in the $l.M_3$ are too widely separated to be related to *P. columbi*; the $l.M_3$ measures ap. 175+ mm., tr. 95 mm., the dimensions apparently equal those of *P. columbi*, namely, neotype $l.M_3$ ap. 298 mm., tr. 91 mm. The locality of Tequixquiac yields both *A. imperator* and *P. columbi*, according to Reyes.

El. Columbi var. *Falconeri* Freudenberg, 1922. "Die Säugetierfauna des Pliocäns und Postpliocäns von Mexiko." Geol. und Palæont. Abhand., N. F., Band XIV, Heft 3, pp. 153–160. LECTOTYPE.—First left lower molar, $l.M_1$, Mus. Royal Coll. Surg. 741a.[1] COTYPE.—Lower jaw with both third molars M_3 *in situ*. HORIZON AND LOCALITY.—Tequixquiac, Mexico. LECTOTYPE FIGURE.—After Falconer, 1863.1, Pl. II, fig. 1. COTYPE FIGURE.—Freudenberg, 1922, p. 154, fig. 21.

DESCRIPTION.—(*Op. cit.*, p. 153): "Als Typus der Form gilt mir der von Falconer abgebildete M_1 von Mexiko (London) und ein M_3, den ich auf S. 54 [154], Fig. 21 abbilde. Dieser M^3 [M_3] gehört wohl der linken Seite an. Er stammt vermutlich aus dem Valle de Mexico. Die Hinterseite des Zahnes ist abgebrochen. Die Zahl der fehlenden Disken lässt sich nicht mehr bestimmen. Ebensowenig weiss man, wie viele Lamellen vorn durch Abkauung verschwunden sind. Die Kaufläche ist intakt und wurde in natürlicher Grösse abgebildet. Die Länge der Kaufläche misst 175 mm, die Breite in der Mitte, einschliesslich des Zements, misst 95 mm. Die Kaufläche ist also etwa doppelt so lang wie breit. Der Verschmelzungstypus der eben erst angekauten Disken (im Sinne der Soergelschen Nomenklatur) ist median lamellar, lateral anular. Besonders an den drei ersten Jochen ist dieser Bau der Schmelzpfeiler zu beobachten. Ein mir vorliegender M^3 von *El. trogontherii* Pohlig [Footnote: '1) Abgebildet in meiner Arbeit: Die Säugetiere des älteren Quartärs von Mitteleuropa etc. Geolog. u. pälaont. Abh. N. F. Bd. 12. Heft 4/5. Jena 1914. t. 3. f. 5. Siehe auch unsere Taf. IX [XVII].'] von Jockgrim in der Pfalz hat eine Kaufläche von 195 mm bei einer maximalen Breite von 82 mm. Das Verhältnis von Länge zu Breite ist also über 2: 1 (Breite = 1). Während bei *El. Columbi* die Verhältniszahl für die Länge (Breite = 1) unter 2 ist."

CHARACTERS.—(*Op. cit.*, p. 154): "Als altquartär haben sich jene Formen herausgestellt, welche wir nach Falconer als *Elephas Columbi* var. *Falconeri* bezeichnen müssen. Ihre Lamellen sind kürzer und stehen isolierter (wie z. B. an dem Taf. VIII [XVI], Fig. 1 abgebildeten Molaren) verglichen mit der var. *silvestris* und erst recht mit der var. *Felicis*. Bei der typischen (altquartären)



COTYPE OF ARCHIDISKODON IMPERATOR FALCONERI FREUDENBERG

Fig. 905. Cotype jaw (one-sixth natural size) of *Elephas Columbi* var. *Falconeri* Freudenberg, 1922, p. 154, fig. 21; crown view one-half natural size. From Tequixquiac, Mexico. Originally figured by Villada, 1903, Lám. VIII.

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[1] [By inference this is Professor Osborn's lectotype. It is not figured, however, in the present Memoir.—Editor.]

Columbi-Form, der gerade auch das Original Pohligs aus Mexiko zugehört, kommen am oberen M³ vier Lamellen auf 53 mm, während deren 6 sich auf die gleiche Strecke verteilen bei dem jungdiluvialen Zahn von Mexiko Taf. VIII [XVI], Fig. 4. Es mag nun dieser weniger Waldform als Steppenform gewesen sein."

El. Columbi var. **imperator** Leidy
[=**Archidiskodon imperator**] Freudenberg, 1922

Spokam Bar near Helena, Montana.

Under the true specific name *Archidiskodon imperator* should apparently be included the *El. Columbi* var. *imperator* of Freudenberg, 1922, in the Geological Museum of Bonn.

El. Columbi var. *imperator* Leidy Freudenberg, 1922. "Die Säugetierfauna des Pliocäns und Postpliocäns von Mexiko." Geol. und Palæont. Abhand., N. F., Band XIV, Heft 3, pp. 160–171.

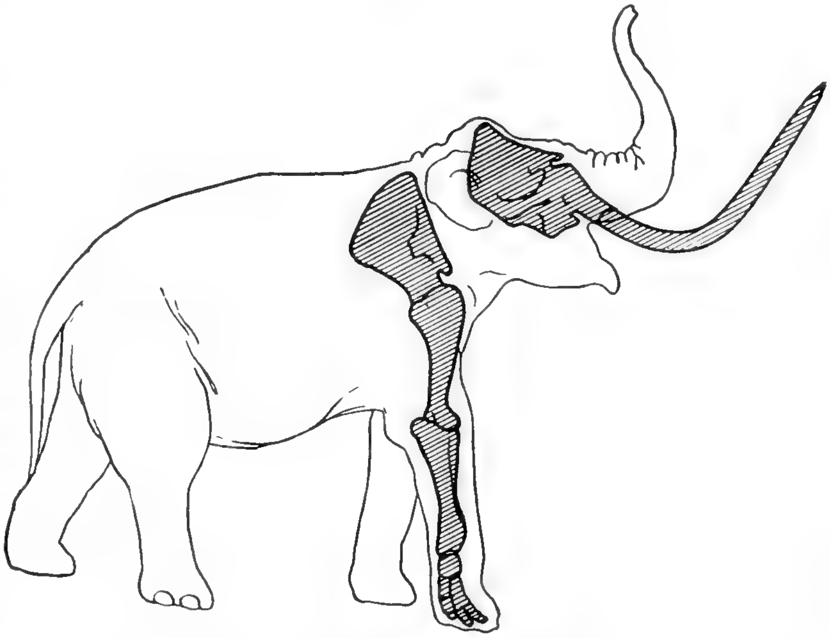
Freudenberg frequently introduces the subspecific name *Elephas columbi* var. *imperator* Leidy (*op. cit.*, pp. 155, 156) and finally definitely employs it on page 160. TYPE DESCRIPTION.—(*Op. cit.*, p. 160): "5. *El. Columbi* var. *imperator* Leidy. Wegen der vielfachen Verwechslungen und wegen der mutmasslichen Abstammung des *El. Columbi* von *El. imperator* ist es nötig, näher auf diese Form einzugehen. Es ist das um so notwendiger, als H. F. Osborn [Footnote: 'Recent Vertebrate Palaeontology. Fossil mammals of Mexico. Science. Vol. 21. 1908 [1905]'.] diese Art aus Mexiko anführt. Osborn gründete seine Bestimmung wohl in erster Linie auf den gewaltig langen Stosszahn, der 16 Fuss misst und somit der längste Stosszahn ist, von dem eine Kunde vorliegt. Aber warum sollte nicht ein *El. Columbi* gelegentlich riesige Dimensionen erreichen, zumal da diese gute Art in eine ganze Anzahl von Unterarten einmal zerlegt werden muss, sowie Matschie 4 Arten des afrikanischen Elefanten heute unterscheidet."

CHARACTERS.—After quoting Leidy, Osborn, Lull, Lucas, Holmes, Pohlig, Soergel, and Cope (*op. cit.*, pp. 160–169), Freudenberg concludes (p. 170): "'*El. imperator*' gewinnt mit seinem Aufsteigen ins jüngere Diluvium immer mehr Aehnlichkeit mit den englamelligen, schmalkronigen, eigentlichen '*Columbi*-Rassen.' Vielleicht lösen sich die letzten Herde des waldlebenden Kaiserelefanten auf im *Columbi*-Hauptstamm als sogenannte var. *silvestris*. Das hängt doch wohl mit dem immer weiter zürückweichenden Seen- und Waldklima zusammen, das offenbar der Existenz der *Imperator*-Rasse in der Sonorischen Faunenprovinz günstig war. Die zunehmende Austrocknung der diluvialen Seengebiete förderte die Entstehung von mammutähnlichen *Columbi*-Rassen, die wohl vorwiegend auf die spärliche Koniferenkost und auf harte Steppenpflanzen angewiesen waren. Die im tropischen Laubwald äsenden *Imperator*-Rassen, die, wie *El. indicus* auf Ceylon gute Bergsteiger gewesen sein mochten, haben bei Afton wie im Becken von Puebla, Chihuahua und Mexiko als deutlichen Hinweis auf einstige Holzäsung tief ausgehöhlte Zementintervalle zwischen den äusserst kräftig gebauten Dentinpfeilern und ihrer oft stark gefalteten Schmelzhülle."

SKELETAL CHARACTERS OF ARCHIDISKODON

Much remains to be done in establishing the skeletal characters of *Archidiskodon imperator*. In the fluviatile sand and gravel deposits of early Pleistocene time, in which these imperial mammoths occur, skulls, jaws, and skeletal parts are widely scattered. The principal partly or fully associated materials hitherto described are the following:

Figs. 907 and 906.	Forelimb from Tule Cañon, Briscoe County, Texas (Amer. Mus. 10598).
Fig. 908.	Femur from near Reynolds, Jefferson County, Nebraska (Neb. Mus. 13–24–10–14).
Fig. 912.	Forelimbs associated with numerous vertebræ, skull, jaw, one tusk, and parts of hindlimbs—the finest material thus far discovered [=*Archidiskodon imperator maibeni*] from near Curtis, Lincoln County, Nebraska (Neb. Mus. 5–9–22).



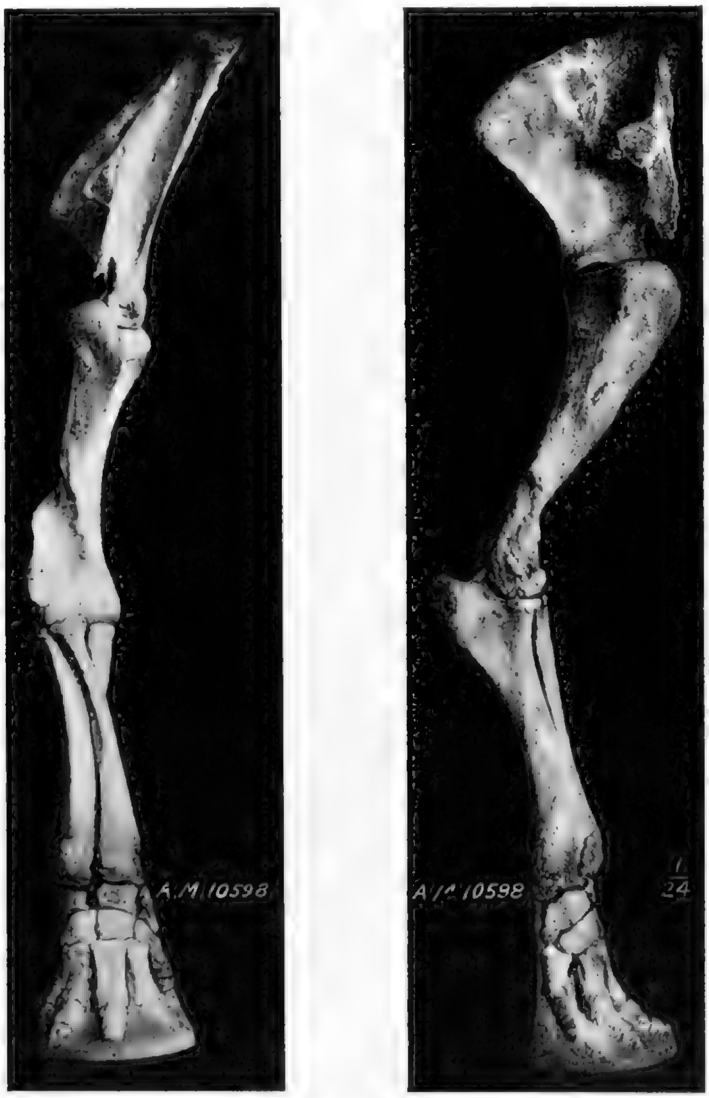
ARCHIDISKODON IMPERATOR. AGED MALE

Fig. 906. Outline reconstruction from right forelimb in the American Museum (Amer. Mus. 10598—Fig. 907) and from skull (Amer. Mus. 14476—Fig. 896), one-sixtieth natural size.

The *forelimb* (Amer. Mus. 10598) measures 348 2mm. or 11 ft. 5 in., as shown in figure 912. This gives a shoulder height in the flesh of 3702 mm., which may be taken as a conservative estimate of the shoulder height in the flesh of a nine-tenths grown *Archidiskodon imperator*. Compare figure 912, also figure 907, lateral and front views of the same forelimb, one twenty-fourth natural size. The diagram of the forelimb, found in 1899 near Tule Cañon, Texas, is taken from the mounted forelimb in the American Museum (Amer. Mus. 10598). The diagram of the skull is taken from *Archidiskodon imperator* (Amer. Mus. 14476), found at Victoria, Texas.

FORE- AND HINDLIMBS OF A. IMPERATOR (FIG. 907).—Fortunately the complete right forelimb (Amer. Mus. 10598), discovered in 1899 near Tule Cañon, Briscoe County, Texas, along with other parts of the skeleton belonging to a single individual, gives us the means of estimating the height of *Archidiskodon imperator*, namely, 12 ft. 1¾ in. = 3702 mm. at the withers, 13 ft. = 3960 mm. at the top of the head when elevated. This elevation is shown diagrammatically in figure 906 which combines the skull (Amer. Mus. 14476) from Victoria, Victoria County, Texas, with the forelimb (Amer. Mus. 10598) from Tule Cañon, Briscoe County, Texas.

In the rich collections made by Professor Barbour for the State Museum, University of Nebraska, are a femur (Fig. 908) and a humerus which may be compared with corresponding limb elements in the skeleton of "Jumbo" (*Loxodonta africana oxyotis*) in the American Museum. The specific reference is somewhat uncertain. The femur probaby does not represent a full-grown *Archidiskodon imperator*, which would greatly exceed the specimen here represented in the photograph (Fig. 908) kindly furnished by Professor Barbour.



FORELIMB OF ARCHIDISKODON IMPERATOR. AMERICAN MUSEUM
Compare Figure 912

Fig. 907. Right forelimb referred to *Archidiskodon imperator*, as mounted in the American Museum (Amer. Mus. 10598). one twenty-fourth natural size, found by Alban Stewart in 1899 near Tule Cañon, Briscoe County, Texas, along with other parts of the skeleton belonging to a single individual.

The same forelimb is represented, vertically extended, in figure 912. The vertical measurements of the separate segments are: Scapula 1017 mm., humerus 1095 mm., radius 890 mm., manus 480 mm., sum of total vertical height 3482 mm. or 11 ft. 5 in. As the limb is always somewhat flexed, the cartilages, foot pads, and the flesh and skin above the shoulder give this animal a total height of 3702 mm., or 12 ft. 1¾ in., a conservative estimate of the height of this animal.

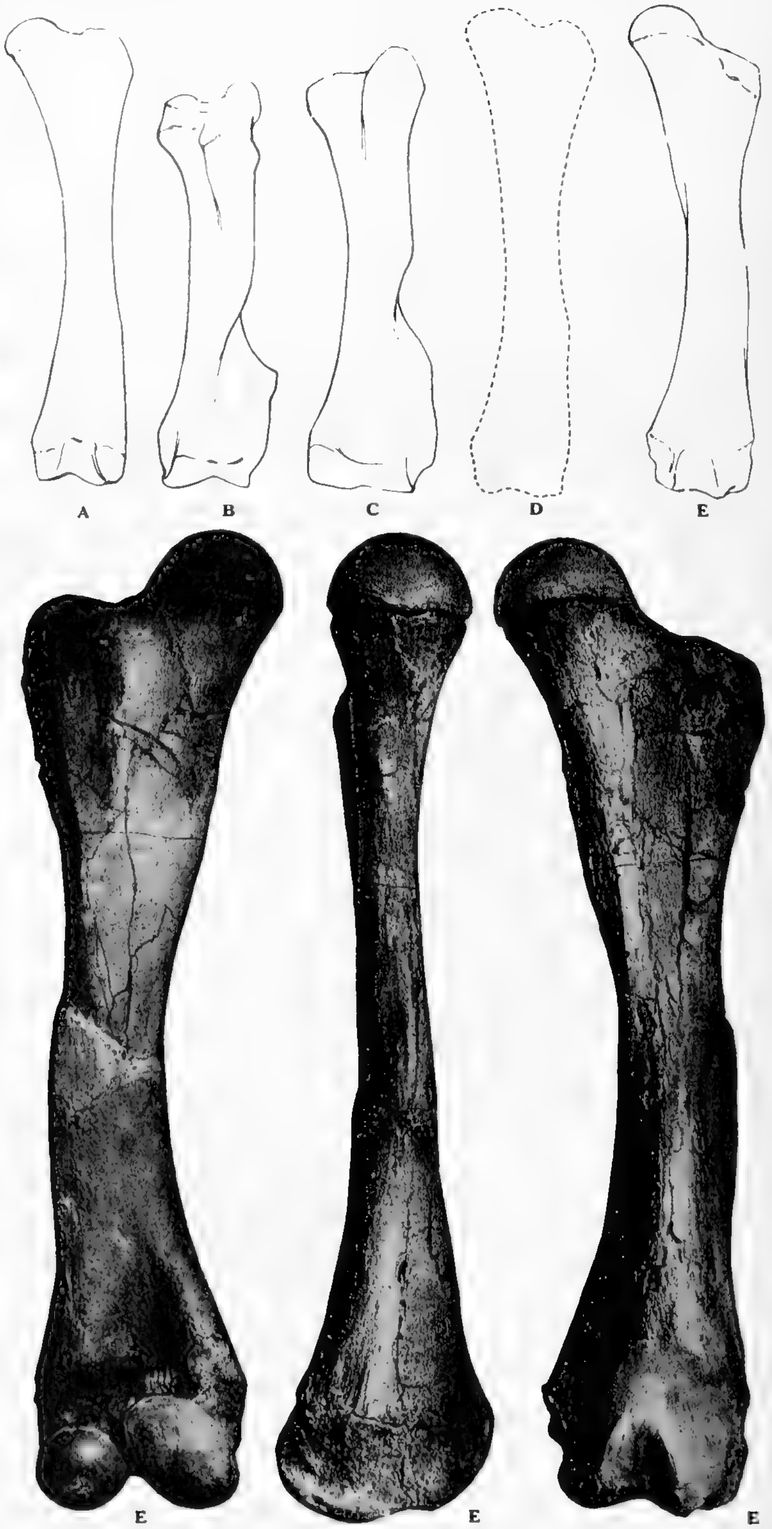


Fig. 908. LIMB BONES OF ARCHIDISKODON IMPERATOR (YOUNG ADULT) AND LOXODONTA AFRICANA OXYOTIS COMPARED

(Lower) Three views (E) of femur of referred *Archidiskodon imperator* (Neb. Mus. 13-24-10-14) from Reynolds, Jefferson County, Nebraska, one-tenth natural size. Height of femur 1422 mm. = 56 in. (Barbour, 1925.3, p. 116), same measurement as the femur (Neb. Mus. 4-12-13), namely, 4.8 feet.

(Upper) The same femur (Neb. Mus. 13-24-10-14), one-twentieth natural size, compared with (A, B) femur and humerus of *Loxodonta africana oxyotis* (skeleton of "Jumbo") in the American Museum; also with (C, D) humerus and femur (latter computed) referred to *Archidiskodon imperator* (Amer. Mus. 10598). Compare figure 907 opposite.

BARBOUR'S DESCRIPTION (1925) OF THE SKELETON OF ARCHIDISKODON MAIBENI

(See type description of skull, jaws, and dentition below.)

As above noted, this is the most nearly complete skeleton of *Archidiskodon* thus far discovered. The following is a free rather than a literal citation from Professor Barbour's valuable paper of August, 1925 (Barbour, 1925.3), entitled, "Skeletal Parts of the Columbian Mammoth, Elephas maibeni, sp. nov." For reasons shown in the systematic treatment of *E.* (*Archidiskodon*) *maibeni* below, there appears to be no doubt that this skeleton is properly referable to *Archidiskodon* rather than to *Elephas*; also that it is closely related to *Archidiskodon imperator* rather than to *Parelephas columbi*. The narrative of discovery is as follows:

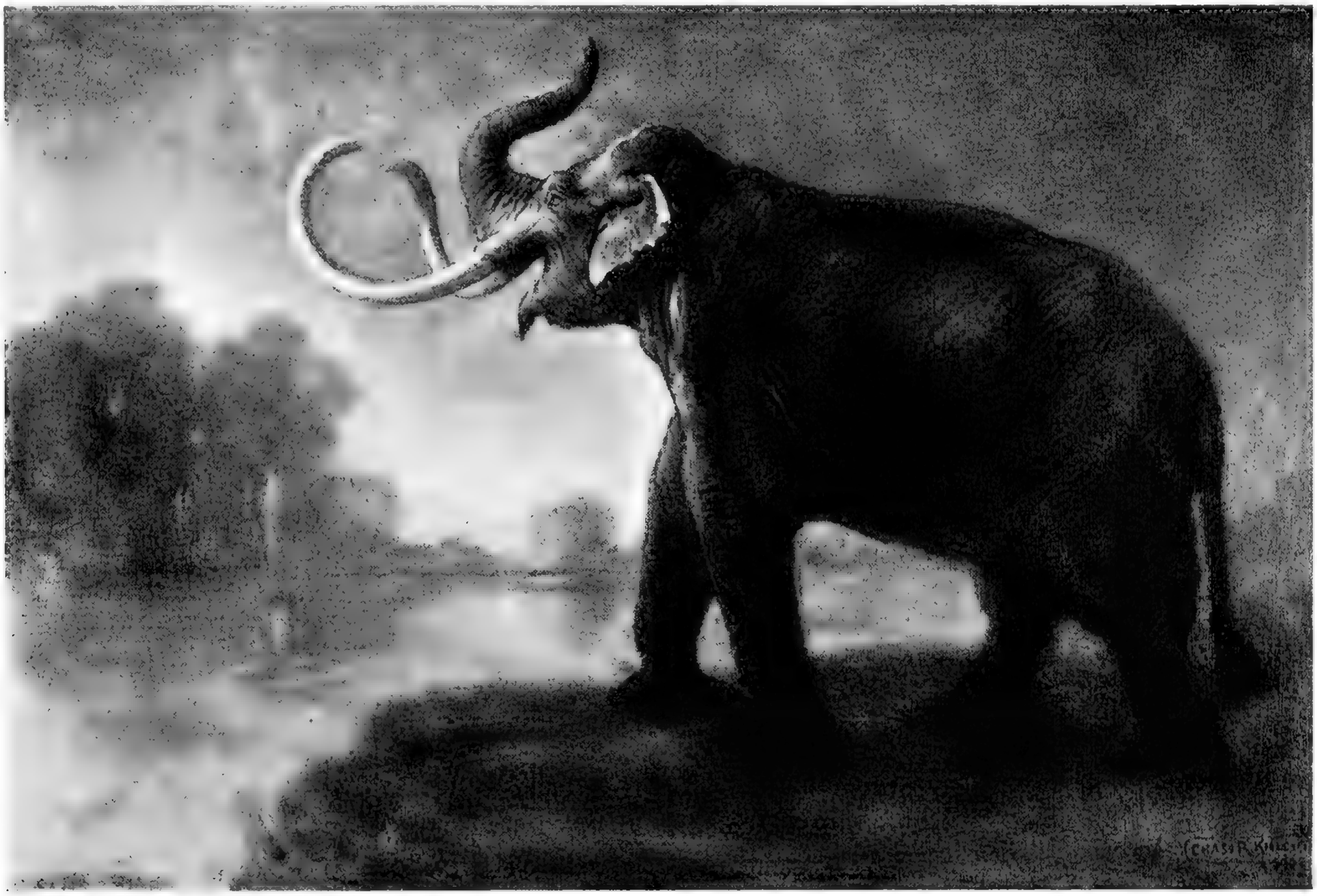


Fig. 909. Imperial Mammoth (*Archidiskodon imperator*) of Nebraska and Texas. After restoration by Osborn and Knight, 1908. About one-fiftieth natural size.

"The last and most remarkable specimen of the columbi [imperator] type was found in Lincoln County, about 16 miles north of Curtis, on the Karriger farm. It was discovered by Mr. and Mrs. H. S. Karriger, and was dug out and preserved by them. Later it was procured of them for the palaeontological collections of Mr. Hector Maiben, who, next to Mr. Charles H. Morrill has been the most generous contributor of funds for the purchase and preservation of choice Nebraska specimens. . . . It should be recorded in connection with this specimen that an unknown number of bones and parts of bones were pounded up to furnish lime for the large flocks of poultry on the Karriger farm, before it was realized that they were out of the ordinary, after which the remaining parts were dug out and cared for with unusual appreciation and discernment. . . . The bones of Elephas maibeni were found projecting from a loessial wall at the bottom of a small canyon. The general thickness of the loess at this point is about 100 feet. In an attempt to find additional material the writer, aided by Mr. William Hall and Mr. H.S. Karriger, blasted out many cubic yards of the loessial wall."

"The skeletal parts preserved are the skull, mandible, one tusk, the atlas, axis, and four other cervicals, several thoracics, lumbars, and the sacrum, ribs, and *double ribs*, both fore limbs and parts of the hind limbs. Both fore limbs are practically complete and are essentially perfect save that but one foot bone was found, hence the feet must be supplied. The hind quarters are represented by parts of the pelvis, the shaft of a femur, and the major portion of a fibula. The dentition is perfect. The molars have 14 ridges bonded together by an uncommon thickness of cement, which is a character of columbian elephants. Even the great columbian elephant from Franklin County [referred to *Parelephas jeffersonii* in the present Memoir] seems surpassed in size. Heretofore, the tusks of the Franklin County elephant [Neb. Mus. 1-4-15] have been considered the largest reported, namely about 13½ feet long with a maximum circumference, near the incisive sheath, of 29 inches. The skull and mandible of Elephas maibeni is noticeably larger. The incisive sheath shows that the tusk had a diameter of 10½ inches and the incredible circumference of 33 inches."

"The outstanding characters of *Elephas* [=*Archidiskodon*] *maibeni* are size, extreme curvature and divergence of tusks and incisive sheaths, unusual shortness of centra coupled with great width. The tusk must have lain in a plane or nearly so and must have described a circle, the radius being 28 inches (711 mm.). The diameter of the tusk is 6½ inches (165 mm.) at the tip, 7½ inches (190 mm.) four feet back of the tip, and 10½ inches (297 mm. [267]) at the incisive sheath. Originally it was a magnificent piece of ivory."

"The fore quarters have bones unexpectedly large and massive, especially the humerus. The humerus is huge beyond the visualization of those who have not seen it, hence must judge of it from figures and measurements. In the hind quarters the bones are, if anything, less massive than might be expected. They seem in contrast to those of the fore limbs. Judging from the very short vertebræ the body must have been unduly foreshortened."

"The centra of the vertebrae are very short, compared with their width, consequently certain ribs, presumably the fifth and sixth pairs, came in contact and became completely fused into one shaft with a double head and double tubercle, making huge and peculiar mammal ribs. A slight longitudinal depression is a vestige of the original boundary between the two shafts. It is interesting to note that the cancellous portion is uniform and continuous and is without partitions or vestiges of the dual origin. From this it may be inferred that they had been in coalescence for ages and that the character may have become fixed. At any rate it is not a case of pathology. The great fore limbs, several vertebrae, and their corresponding ribs, have been mounted as an arch, a palaeozoologic arch [Fig. 910 of the present Memoir], through which all students and visitors must pass on entering the main floor. It is but a temporary mount which must be dismantled and moved into the new museum sometime in 1926, where the complete skeleton will be carefully articulated and properly installed. So many skeletal parts are at hand that this huge elephant when ready for exhibition will seem complete. Its proper installation demands a ceiling 18 feet high." [See Fig. 911 for present mount.—Editor.]

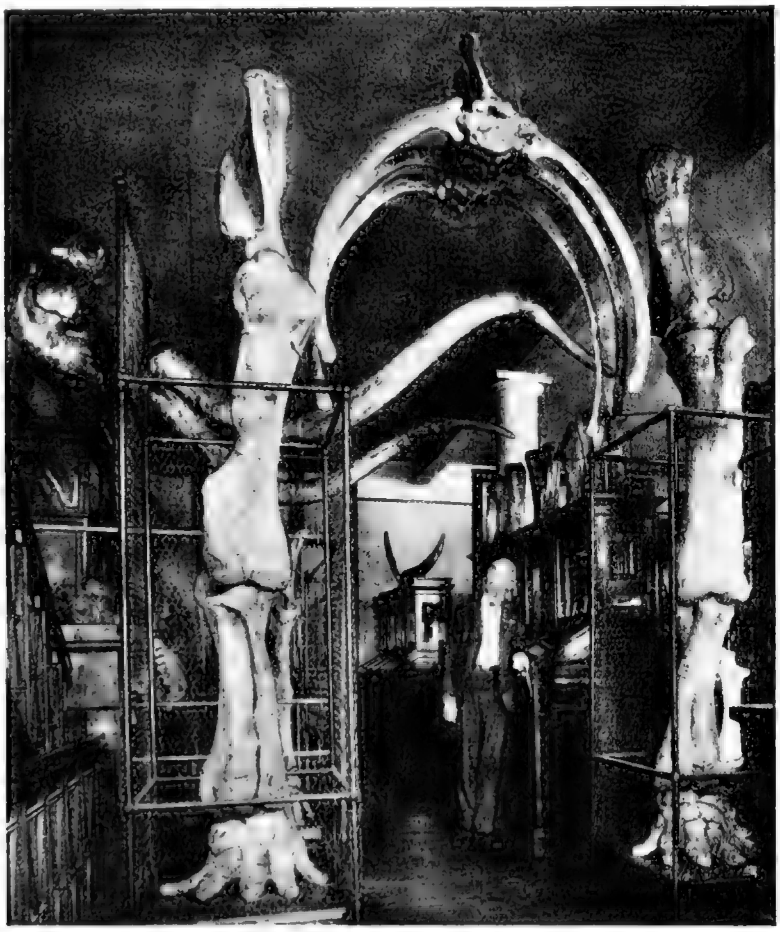


Fig. 910. Forelimbs of type skeleton of *Archidiskodon imperator maibeni* as mounted in the Nebraska State Museum (Neb. Mus. 5-9-22) in the year 1925. Professor Barbour is standing in the background. The dimensions of this superb skeleton are shown (Fig. 912) in direct comparison with the forelimbs of *A. imperator* from Texas, of *Loxodonta africana*, and of *Elephas indicus*.

The cranium and tusks in the background to the left, from Franklin County, Nebraska, belong to *Parelephas jeffersonii*. Barbour notes (1925.3, legend to Fig. 58): "The great skull and tusks in the background are those of Elephas columbi from Jefferson [Franklin] County."

[For present mount, see figure 911 on following page.—Editor.]

"Mammoth scapulae are large, heavy, and very thin in portions, so it seems the more remarkable that the two huge shoulder blades should have been preserved practically without blemish. The right humerus is likewise perfectly preserved; in the left the head is wanting but has been modeled on from the right humerus. The right ulna is perfect save that the distal epiphysis is missing. This has been modeled after the left ulna in which the epiphysis is present but the shaft missing. . . . The fore limbs, four vertebrae, two pairs of single ribs, and one pair of double ribs of this exceptional mammoth are mounted in approximate position and make an impressive arch, the height of which is 13 feet from the tip of the toe to the top of the spine, see fig. 58 [Fig. 910 of the present

Memoir; see also Fig. 912]".

"In the flesh the height of Elephas [=*Archidiskodon*] maibeni at the shoulder must have been about 13 feet, and the top of the head of this magnificent beast must have been about 14 feet above the ground."

"From the tip of the toes to the top of the scapula is 11 feet, 6 inches."

"This specimen is believed to hold the record for size amongst the Columbian group of mammoths."

"In point of size, Elephas [=*Archidiskodon*] maibeni was a rival of the Imperial elephant itself, which stood 13½ feet high. The tallest living African elephant stands 11 feet high and the average elephant of the menagerie and circus 8 to 9 feet."

Referring to figure 912 of the present Memoir, we observe that A 1 (right) is foreshortened, while A, B, C, D represent orthogonal full length projections of each limb segment, with the actual measurement of each segment in millimeters. This affords an absolutely reliable comparison of the ascending height of these four animals.

The following entirely consistent comparative measurements appear to demonstrate that *Archidiskodon imperator* and the more primitive giant species *A. maibeni* towered in height far above the largest existing elephants:

	Manus		*Forearm*	*Humerus*	*Scapula*
Fig. 912, A, *Archidiskodon imperator maibeni*	297	(as mounted)	1085	1251	1066+
	424e	(fully extended)			
B, *Archidiskodon imperator*	480	(fully extended)	890	1095	1017
C, *Loxodonta africana oxyotis* ("Jumbo")	361	(fully extended)	830	1078	925
D, *Elephas indicus*	391	(fully extended)	744	1008	864
Fig. 1083, *Hesperoloxodon antiquus* (Upnor)				1290	1170

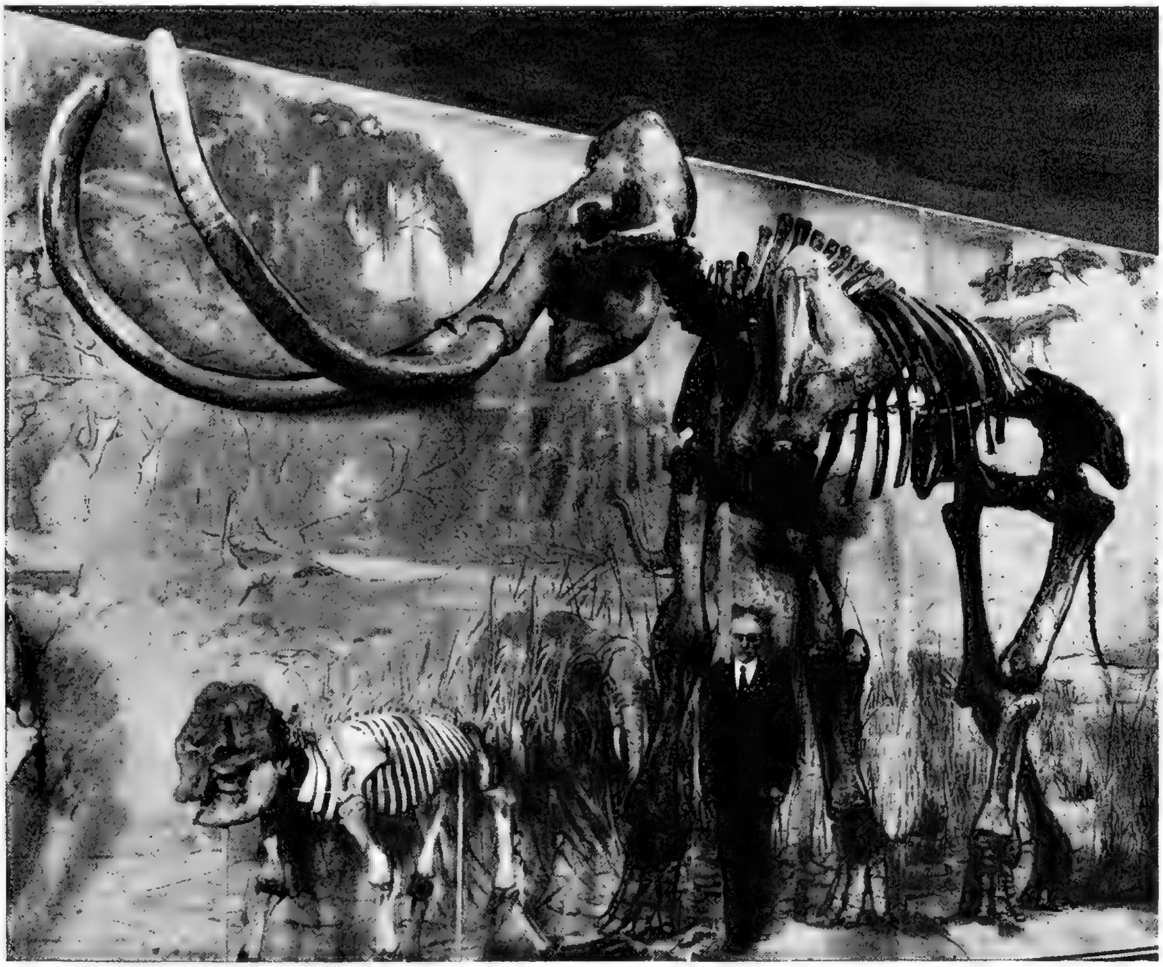


Fig. 911. Present mount of the type skeleton of *Archidiskodon imperator maibeni* in Morrill Hall of the University of Nebraska (Neb. Mus. 5-9-22): for dimensions of the forelimbs of this superb specimen, see figure 912, which was based on figure 910 showing the forelimbs as first mounted in 1925. In the left foreground is a skeleton of a juvenile *Elephas indicus*. After original photograph kindly furnished the present author by Professor Erwin H. Barbour.

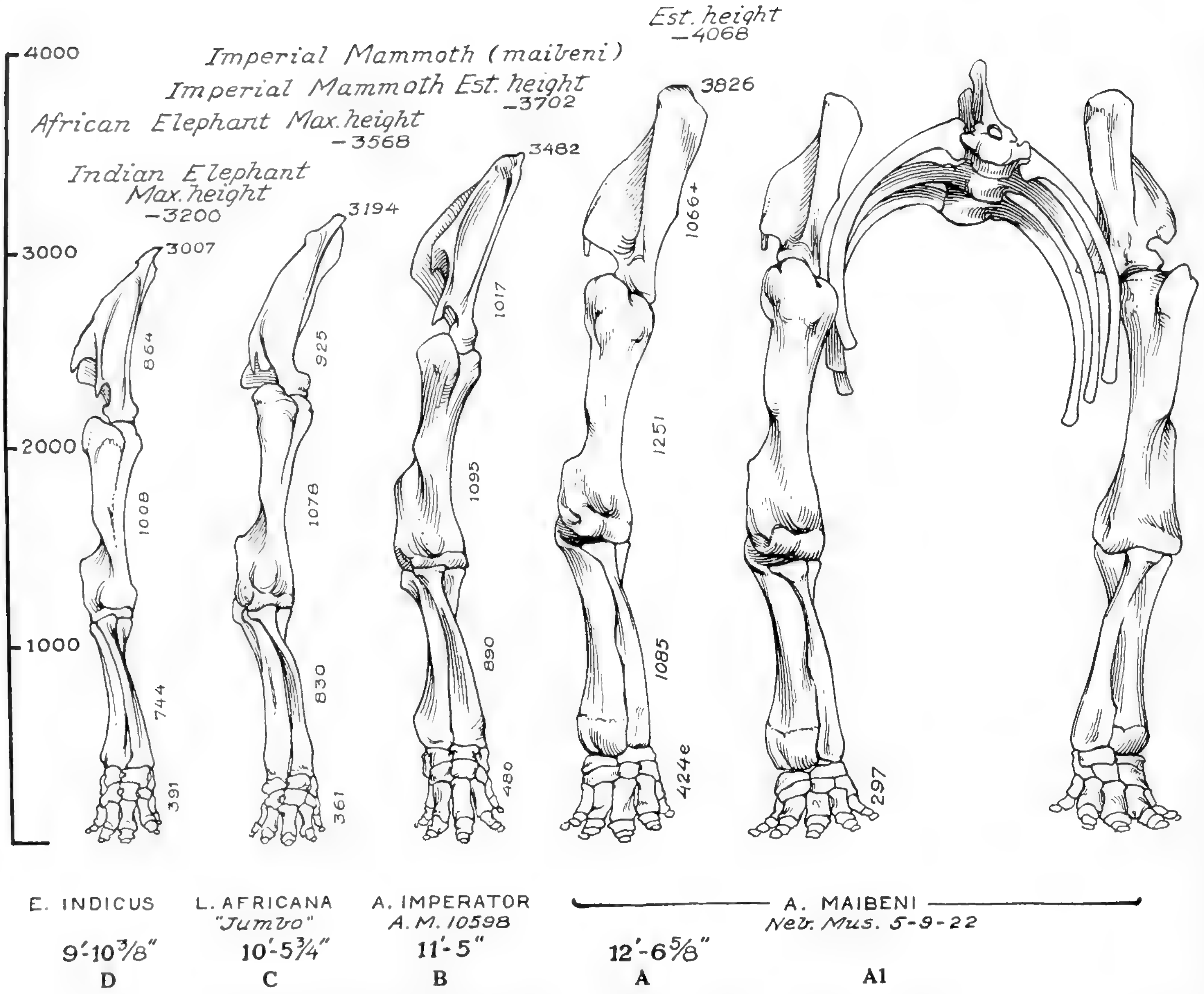


Fig. 912. Shoulder Heights of Living and Extinct Elephants. Compare Figure 1194

[Professor Osborn's method, used in the present Memoir, of estimating the height in the flesh is to add six and a third per cent. to the skeletal height.—Editor.]

	Skeleton	Flesh
Elephas indicus:		
Standard skeletal height of full-grown male	3007 mm., 9 ft. 10⅜ in.	3200 mm., 10 ft. 6 in. est.[1]
Loxodonta africana oxyotis ("Jumbo"):		
Adult male, extended skeletal height at shoulder	3194 mm., 10 ft. 5¾ in.	3396 mm., 11 ft. 1¾ in. est.
Archidiskodon imperator (Amer. Mus. 10598); sex unknown:		
Extended skeletal height	3482 mm., 11 ft. 5 in.	
Estimated height in flesh		3702 mm., 12 ft. 1¾ in.
Archidiskodon imperator maibeni (Neb. Mus. 5-9-22):		
(Right) Perspective drawing after mount in the Nebraska Museum.		
(Left) Right forelimb, also bony projection of each segment.		
Skeletal height:		
Fully extended forelimb	3826 mm., 12 ft. 6⅝ in.	
Estimated, at shoulder, in flesh		4068 mm., 13 ft. 4¼ in.

[1] [Rowland Ward's "Records of Big Game," 1922, p. 468. A subsequent record (Ward, edition of 1928, p. 451) gives a height of 10 ft. 8 in.—Editor.]

[2] [The record skeletal height of the African elephant (*Loxodonta africana*) is 3290 mm. = 10 ft. 9½ in. ("set up forelimb in Quex Museum," Birchington, England—letter of January 6, 1931, from Major P. H. G. Powell-Cotton to Mr. J. W. Walker of Michigan) or 3520 mm. = 11 ft. 6½ in., in the flesh, as measured on the same specimen in the field by Major Powell-Cotton (*op. cit.*, Ward, 1928, p. 456).—Editor.]

The principal measurements of the type skull and skeleton of *Archidiskodon imperator maibeni* (see Barbour, 1925.1, pp. 114–117) are as follows:

	Mm.	Inches
SKULL		
Occipital condyle, greatest diameter	125	5
Molar (r.M^3), length of grinding surface	245	9⅝
Molar (r.M^3), breadth	110	4¼
Breadth-length index	45	
Molar (r.M^3), greatest thickness of cement	13	½
MANDIBLE		
Molar (M_3), length of grinding surface	240	9½
Molar (M_3), greatest breadth	95	3¾
Breadth-length index	40	
Transverse ridges 14		
SCAPULA		
Total height	1,257[1]	49½
Extreme width suprascapular border	889	35
Length of glenoid border	556	22
HUMERUS		
Total length	1,226[1]	48¼
Transverse diameter of head	330	13
ULNA		
Total length	1,080[1]	42½
FORE LIMB		
Total height	3,505[1]	11 ft. 6 in.[1]
In the flesh this huge creature must have stood not less than 13 feet high at the shoulders [13 ft. 4¼ in. est.]		
TUSK		
Diameter 8 inches from tip	165	6½
Diameter at incisive sheath	267	10½
ATLAS		
Total width	440	17½
Length	140	5½
AXIS		
Height	336	13¼
CERVICAL 5		
Posterior centrum, vertical diameter	186	7¼
Posterior centrum, transverse diameter	192	7½
CERVICAL 6		
Centrum, height	175	6⅞
Centrum, length measured at center	39	1½
CERVICAL 7		
Posterior centrum, vertical diameter	185	7¼
Posterior centrum, transverse diameter	192	7½
DORSAL 9		
Centrum, vertical diameter, anterior	167	6½
Centrum, transverse diameter, anterior	144	5⅝
DORSAL 10		
Posterior centrum, vertical diameter	175	6⅞
Posterior centrum, transverse diameter	156	6⅛
LUMBAR		
Centrum, length	80	3⅛
Centrum, height	131	5⅛
Average length of 4 lumbars	83	3¼
SACRUM		
Length	325	12½
Greatest breadth	296	11⅝
Centrum, anterior, transverse diameter	205	8
FEMUR		
Circumference at slimmest point, about middle	432	17
Transverse diameter at narrowest point of shaft	157	6¼
Anteroposterior diameter at narrowest point of shaft	115	4½

Archidiskodon hayi Barbour, 1915

Figures 893A, 903, 913, 915

Crete, Saline County, Nebraska. Lower Pleistocene.

This appears to be the most primitive species of proboscidean thus far discovered in America, distinguished by its shallow jaw and elongated rostrum. It obviously belongs to the broad-plated *Archidiskodon* phylum, but with 10–11 ridge-plates like *A. planifrons.* The relatively long, shallow jaw, the prominent rostrum, the low coronoid process are totally different from the adult *Archidiskodon imperator*, also from the adult *A. meridionalis*, and there is certainly a very strong resemblance to the jaws of *A. planifrons* as figured by Mayet and Roman (Figs. 894 above and 914). A juvenile jaw of *A. imperator* would have this shallow character but Professor Barbour, who discovered this important specimen, remarks: (Letter of January 17, 1923): ". . . we both examined it [the type] as well as we know how, and count it an old not a young individual. I feel quite sure of this. [*E.*] *hayi* is very distinctive."

Elephas hayi Barbour, 1915. "A New Nebraska Mammoth, *Elephas hayi.*" Amer. Journ. Sci., (4), XL, No. 236, pp. 129–134 (1915.2). TYPE.—Mandible and teeth. Associated with this jaw were fragments of a large tusk. (Barbour, *op. cit.*, 1915, p. 132): "The distinguishing character on which this new mammoth must depend is derived, first of all, from the teeth. Especial care was exercised to determine whether the teeth in the jaw of *E. hayi* are penultimate or ultimate molars. If penultimate, a successor should be in evidence in each ramus, but not a fragment of a tooth or plate could be found in the cavities, which were filled with compact sand and gravel; nor could any such fragments be found in the surrounding gravels when screened. Undoubtedly the two teeth are the sixth molars, a point of consequence in this connection." Collections of Hon. Charles H. Morrill, the Nebraska State Museum (Neb. Mus. 23–6–14). TYPE LOCALITY AND HORIZON.—(*Op. cit.*, p. 129): "Hurlbert sand pit at Crete, Nebraska, eight blocks east and three blocks north of the center of the town. . . . Aftonian. . . . 11 feet below the surface." TYPE FIGURE.—Barbour, *op. cit.*, 1915, p. 130, fig. 1, p. 133, fig. 3, p. 134, fig. 5*d*.

TYPE DESCRIPTION.—(Barbour, *op. cit.*, p. 129): "The chief distinguishing characters of *Elephas hayi* are: unusual length of mandible; the last molar small, narrow, and anterior to the coronoid; transverse ridges 10 to 11; angle distinct and sharp posteriorly; coronoids uncommonly prominent, deeply pitted, and set very obliquely. . . . The mandible . . . measures 29½ inches (750$^{\text{mm}}$) from the tip of the symphysis to the angle, ... The depth of the jaw at the coronoids is 9½ inches (241 $^{\text{mm}}$), ... The coronoid

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[1] Letter of E. H. Barbour, May 8, 1929, gives corrected measurements of Barbour, Colbert, and Shanafelt, namely, scapula 1066+ mm. =42 + in.; humerus 1251 mm. =49⅜ in.; ulna 1085 mm. =42¾ in.; forelimb 3826 mm. =12 ft. 6⅝ in.; length of grinding surface of left lower molar 238 mm.

process is conspicuously robust, being 2¾ inches (70^{mm}) through near its base, and an inch (25^{mm}) near the summit. It stands 4 inches (102^{mm}) above the superior mandibular border, and 2 inches (51^{mm}) above the crown of the teeth. It is set more obliquely than in other mammoths. Its inner surface is deeply pitted, and extends from the outer to the inner alveolar border. . . . The teeth are those of a mature individual, with the crowns well worn. Though well cemented and strong, the teeth of *E. hayi* are noticeably small. The postero-anterior diameter is but 9 inches (229^{mm}), and the greatest transverse diameter 3 inches (76^{mm}). . . . The dimensions of these teeth agree more closely with those of our earlier Nebraska mastodons than with those of our mammoths. The number of transverse plates is noticeably reduced, for there are but 10 in one tooth, and 11 in the other, with no plates missing. . . . In *E. hayi*, there are 4 and a fraction transverse enamel ridges to the decimeter. The valleys are deep and bordered by highly crenulated enamel ridges. The great anterior prong branches widely and carries 3 plates. The teeth lack the symmetrical development common to mammoths. They are noticeably constricted back of the anterior prong, and taper posteriorly to 1½ inches (38^{mm}) . . . there are but 11 transverse ridges at most [to each molar tooth], the last being small, perhaps a heel. This form seems to be an earlier and more primitive type of mammoth than any other known to the State [Nebraska]. The inferior dental foramen is small, and has a circular border, while in *E. imperator* it is very large and deeply notched, as shown in the accompanying

BARBOUR'S TYPE JAW OF ARCHIDISKODON HAYI

Fig. 913. Type of *Elephas hayi* Barbour, 1915, p. 130, fig. 1 (Neb. Mus. 23–6–14), one-eighth natural size. Ramus perfect to summit, condyle only restored.

Compare jaw of *Archidiskodon planifrons* of Chagny, France (Fig. 914).

Professor Barbour (letter of January 17, 1923) remarks: ". . . we both examined it [the type] as well as we know how, and count it an old not a young individual. I feel quite sure of this. [*E.*] *hayi* is very distinctive."

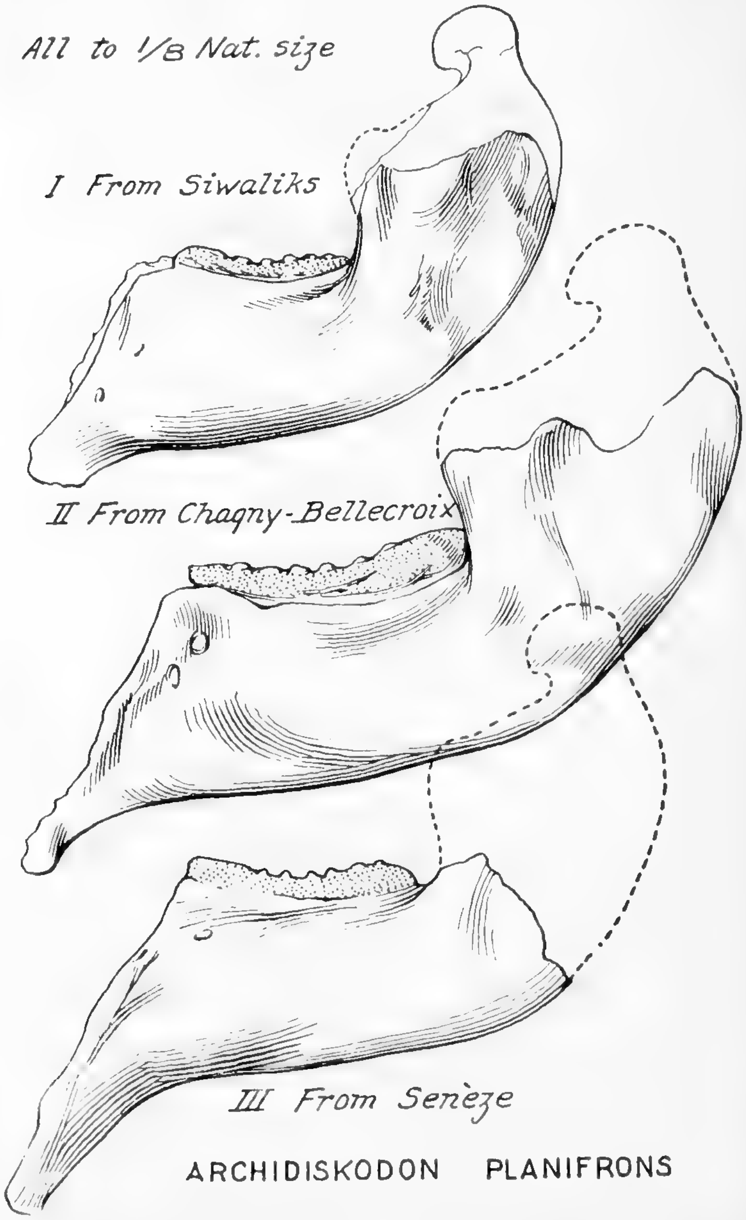

Fig. 914. Primitive mandibles of *Elephas* [*Archidiskodon*] *planifrons* of the Siwaliks, India, Chagny-Bellecroix and Senèze of France, after Mayet and Roman, 1923, p. 81, fig. 13, inserted for comparison with type figure of *E.* [*Archidiskodon*] *hayi* (Fig. 913 opposite). See caption to figure 849, p. 962 above. One-eighth natural size. Observe similarity to the Chagny mandible.

figures. Although inferior dental foramina differ in individuals, and even between opposite sides of the jaw, the differences shown by the cuts are significant. The ascending rami of our proboscideans also vary between wide limits."

Specific Characters.—(1) Mandibular ramus elongate, depressed, coronoid process low. (2) Third inferior molars broad in center, with ten to eleven ridge-plates set very far apart; laminar frequency 4⅓ in 10 cm.; molars narrowing posteriorly. (3) Ramus of jaw shallow, moderately expanded; rostrum relatively prominent. (4) Agreeing with *Archidiskodon planifrons* in ridge formula, differing in greater width of M_3. (5) Dimensions of M_3, length 229 mm., maximum breadth 76 mm., index 33.

Comparison with Archidiskodon planifrons (Osborn, 1924).—It is remarkable that the type of *Archidiskodon hayi* resembles closely in the profile of the jaw the *Archidiskodon planifrons* of India and of southern France, apparently justifying Barbour's statement that *A. hayi* seems to be an earlier and more primitive type of mammoth than any other known to the state [Nebraska], and suggesting the possibility that we have to do with the arrival in North America in the late Pliocene or early Pleistocene of a primitive proboscidean, displaying some of the chief *A. planifrons* characters, namely: (1) Jaw long and shallow; (2) rostrum prominent; (3) coronoid relatively depressed; (4) grinding teeth broad with 10–11 transverse ridge-plates. Supplementary figures and sketches of the jaw and teeth of *A. hayi* (jaw, Fig. 893 A) serve to emphasize the wide contrast between this type jaw and the adult jaw of *A. imperator* (Fig. 892 B, A).

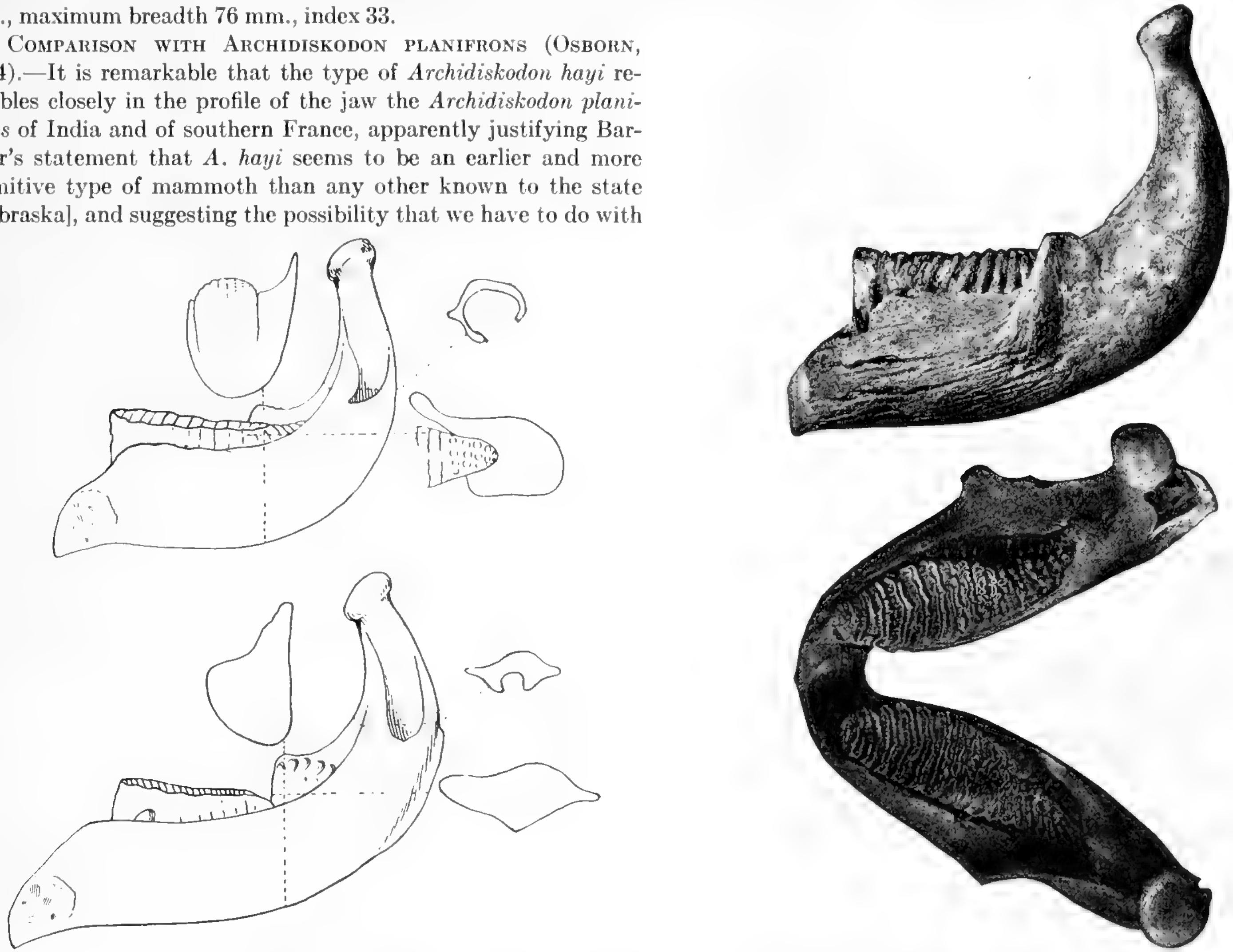

Fig. 915. Barbour's Type of Archidiskodon hayi compared with A. imperator Ref.

(Left lower) Type right mandible of *Archidiskodon hayi*, sectioned at three points, grinding teeth with 10–11 ridge-plates.
(Left upper) *Archidiskodon imperator* ref. Same aspect of right mandibular ramus, grinding teeth with 18 ridge-plates.
(Right upper and lower) *Archidiskodon imperator* with 18 ridge-plates, lateral and superior aspects of mandible.
Both specimens in the Nebraska State Museum, Morrill Collection. After Barbour, 1915.2, figs. 2, 3, and 4.

Archidiskodon imperator scotti Barbour, 1925
[=**A. imperator** ?juvenile]

Figures 916, 917, Pl. xxi

Five miles south of Staplehurst, Seward County, Nebraska. Lower Pleistocene, Aftonian gravels.

Awaiting further evidence, Osborn is inclined to regard the type of '*Elephas scotti*' as representing a young individual of *Archidiskodon imperator*.

This Archidiskodont, discovered in 1922 in the Aftonian gravels, 5 miles south of Staplehurst, Seward County, Nebraska, and 20 miles south of Crete, Saline County, where the type of *Elephas* [=*Archidiskodon*] *hayi* was found (1914), is regarded by Barbour (1925.1, p. 22) as a mature individual, as primitive as *A. hayi*, if not more so. This statement rests upon the identification of the small 8 ridge-plated molars as representing third inferior molars, M_3, which appears to Osborn very doubtful, especially as the jaws of the type of '*Elephas scotti*' (Fig. 916) are very robust in section with greatly abbreviated symphysis, altogether different from the relatively slender, elongated mandibular rami of *A. hayi*. Consequently it seems probable that they are second inferior molars, M_2.

Elephas scotti Barbour, 1925. "Elephas scotti, A New Primitive Mammoth from Nebraska." The Nebraska State Museum, Bull. 2, Vol. I, April, 1925, pp. 21–24 (Barbour, 1925.1). TYPE.— Mandible with last [second?] lower molar of each side (Neb. Mus. 18–2–22, the Maiben Palæontological Collections. Cast of type right M_3 [r.M_2], Amer. Mus. 14610). HORIZON AND LOCALITY.—Discovered on farm of Mr. E. J. Hartman, five miles south of Staplehurst, Seward County, Nebraska. TYPE FIGURE.—*Op. cit.*, text figures 7–10.

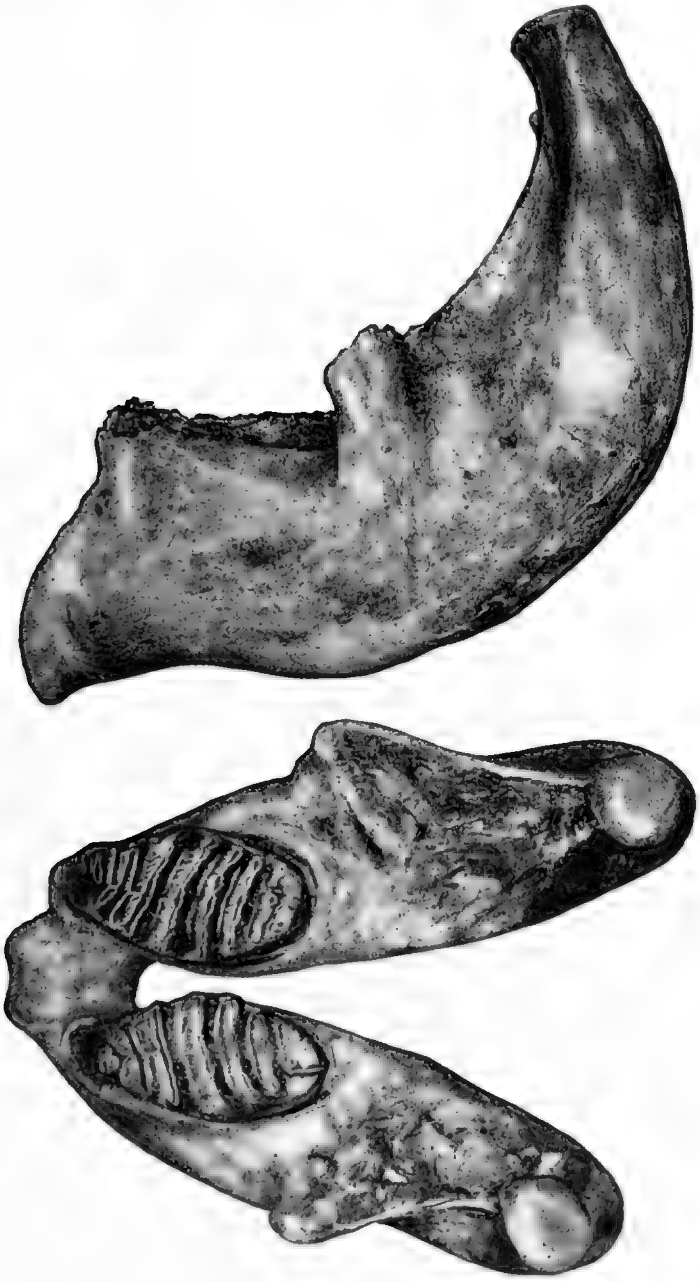

Fig. 916. Juvenile jaw of *Archidiskodon imperator* ref. (Neb. Mus. 18-2-22), from Seward County, Nebraska. After photograph by Prof. E. H. Barbour who in 1925 made this the type of *Elephas scotti*. Compare figure 917. Scale about one-sixth natural size.

These 8 ridge-plated grinding teeth, described as third inferior molars, M_3, are regarded by Osborn as second inferior molars, M_2 (cast of r.M_2, Amer. Mus. 14610).

TYPE DESCRIPTION.—(Barbour, 1925.1, pp. 21–24): "On February 18, 1922, the mandible of an unusually primitive mammoth was secured for the palaeontological collections of Mr. Hector Maiben by Mr. E. T. Engle. . . . The peculiarities of this mammoth seem to entitle it to a position as a distinct species, for which we are proposing the name, Elephas scotti, named for Professor William D. [B.] Scott. It cannot be compared with the later and more advanced mammoths, such as imperator, jeffersoni (columbi), or primigenius. It is comparable instead, with the earlier and more conservative mammoth, Elephas hayi. . . . The new mammoth is as primitive as Elephas hayi, if not more so. Like hayi, it is undoubtedly a mature individual. Its teeth are taken to be last [second] molars. The enamel plates, which are highly crenulated, incline noticeably backward, and are worn with extreme obliquity. At the same time the valleys, or dental spaces, are so deeply indented, as to still further heighten and exaggerate the effect. There are but five pronounced ridges, and in all, but eight and a cone. Two of the anterior ridges are so confluent that the count is rendered somewhat uncertain, as shown in figure 10 [our figure 917A, A1, A2]. The transverse ridges in E. hayi are eleven. The molars of scotti measure 219 mm. (8⅝ in.) in length, by 117 mm. (4⅝ in.) in extreme width. They are short and abruptly expanded in the middle. In the mammoths the number of enamel ridges to the decimeter serves, in a general way, in the recognition of species. In E. scotti there are three and a fraction, transverse, grinding ridges to the decimeter; in E. hayi four and a fraction; in E. imperator five to six; in E. jeffersoni (columbi) six to eight; and in E. primigenius nine to ten. It is a noteworthy feature that the robust jaws of Elephas scotti come within three-fourths of an inch of meeting on the middle line, as is plainly shown in the figures [see Figs. 916 and 917A of the present Memoir]. This is not due to crushing, as far as can be learned, for the specimen in hand is essentially perfect. The coronoids of the earlier and the later mammoths differ widely and are worthy of notice. Those of scotti and hayi are much more robust, thick, and heavy, and flare outwardly, and are posterior to the molars. The inner wall is broader and more heavily roughened and pitted for ligamentous attachment. Each ramus, measured back of the molar, has a width of 185 mm., ($7\frac{5}{16}$ in.) and a depth of 180 mm., (7⅛ in.). On the middle line the jaws are but 19 mm., (¾ in.) apart."

Osborn, 1928: The Seward County jaw (Neb. Mus. 18–2–22 —see Fig. 916, and as seen from above, Fig. 917A) in Osborn's opinion resembles a juvenile jaw of *A. imperator* rather than the type jaw of *E. hayi* Barbour. In superior view (Fig. 916) the jaw appears fairly robust, less swollen than that of *A. imperator*, with highly characteristic outwardly flaring coronoid processes. In lateral view (Fig. 916) it is relatively short and deep, the rostrum is short and depressed, in wide contrast to the long, shallow jaw of the type of *A. hayi*. The single grinding tooth, in which 8–9 ridge-plates appear, may represent M_2 of a young *A. imperator*; the tooth is obliquely worn and consequently the dental space between the broad enamel ridges appears to be much greater than it actually is; the disparity in the actual distance between the ridge-plates (Fig. 917 A2) and the apparent distance due to obliquity of wear (Fig. 917 A1) are clearly shown in this diagrammatic representation.

Archidiskodon imperator maibeni Barbour, 1925

(See full description above, page 1019, of the skeleton of *A. maibeni*)

Figures 815, 824, 910–912, 917, 918, 1239, Pl. xxi

Lincoln County, about sixteen miles north of Curtis, Nebraska.

Aftonian,[1] loess 100 feet in general thickness. Upper Pleistocene (see Fig. 1239, also Pl. viii, Vol. I).

The type of this species is an unusually complete skeleton, entitled the 'Lincoln County Mammoth,' in the Nebraska State Museum, described by Barbour in 1925 (1925.3) as the "Columbian Mammoth Elephas maibeni, sp. nov." and subsequently (June, 1926) transferred by him to *Archidiskodon maibeni*, now mounted in the new Museum, Morrill Hall, University of Nebraska. To the above full description of the skeleton (p. 1019) by Barbour (1925.3) may now be added the type description and characters of the skull and dentition (Barbour, 1926.1), as follows:

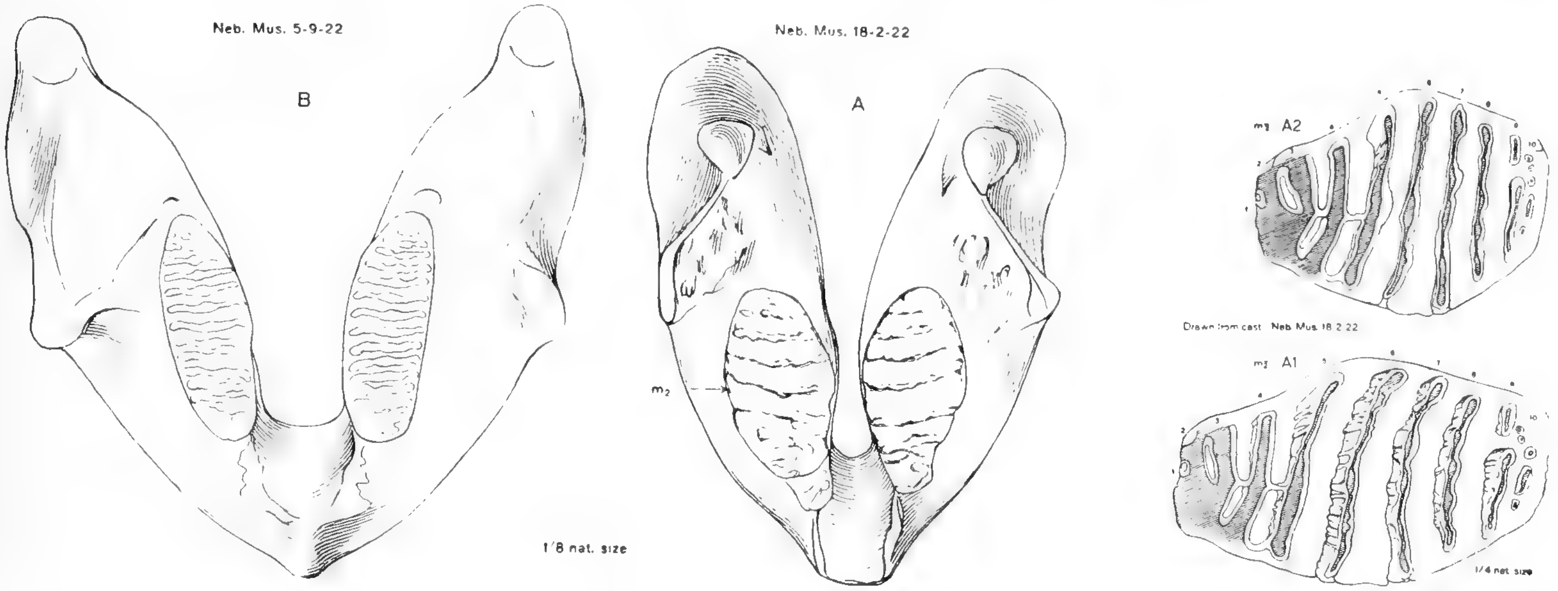

Fig. 917. Comparison of: (B) Mandible of the type of *Elephas* (*Archidiskodon*) *maibeni* [=*Archidiskodon imperator maibeni*] (Neb. Mus. 5–9–22), with third inferior molars, M_3, in place, exhibiting 15+ ridge-plates, 14 exposed; and (A) type jaw of *Elephas scotti* [=*Archidiskodon imperator scotti* or ?juvenile *A. imperator*] (Neb. Mus. 18-2-22), containing second inferior molars, M_2, exhibiting 8 ridge-plates, and measuring ap. 219 mm., tr. 117 mm., i.e., short and abruptly expanded in the middle; A1, A2, enlarged views of right second inferior molar of the type of '*E. scotti*' (cast Amer. Mus. 14610).

Archidiskodon maibeni Barbour, 1926. Professor Barbour in his supplementary description ("Archidiskodon maibeni," Nebraska State Museum, Bull. 11, Vol. I, June, 1926, pp. 119–122) states: "Archidiskodon maibeni was first described in Bulletin 10 of the Nebraska State Museum under the title 'Skeletal Parts of the Columbian Mammoth, Elephas Maibeni, sp. nov.'" Under this designation Barbour gives additional measurements and comments on the skeleton. He also mentions the discovery of another skull (Neb. Mus. 1–4–26) referable to *A. maibeni*.

Elephas maibeni Barbour, 1925. "Skeletal Parts of the Columbian Mammoth, Elephas Maibeni, sp. nov.," Nebraska State Museum, Bull. 10, Vol. I, August, pp. 95–118. Type.—(*Op. cit.*, p. 98): "The skeletal parts preserved are the skull, mandible, one tusk, the atlas, axis, and four other cervicals, several thoracics, lumbars, and the sacrum, ribs, and *double ribs*, both fore limbs and parts of the hind limbs. . . . The hind quarters are represented by parts of the pelvis, the shaft of a femur, and the major portion of a fibula. The dentition is perfect." Neb. Mus. 5–9–22. Horizon and Locality.—Discovered by Mr. and Mrs. H. S. Karriger about sixteen miles north of Curtis, Lincoln County, Nebraska, on the Karriger farm. Type Figure.—*Op. cit.*, Figs. 58–60, 63–70, 72, 74, 76–87.

Type Description.—(Barbour, 1925.3, pp. 97–111): "Confusion has long surrounded the columbian and jeffersonian mammoths. But the one under consideration is undoubtedly of the true columbian type. The bones of Elephas maibeni were found projecting from a loessial wall at the bottom of a small canyon. The general thickness of the loess at this point is about 100 feet. . . . The outstanding characters of Elephas maibeni are size, extreme curvature and divergence of tusks and incisive sheaths, unusual shortness of centra coupled with great width. The tusk must have lain in a plane or nearly so and must have described a circle, the radius being 28 inches (711 mm.) The diameter of the tusk is 6½ inches (165 mm.) at the tip, 7½ inches (190 mm.) four feet back of the tip, and 10½ inches (297 [267] mm.) at the incisive sheath. Originally it was a magnificent piece of ivory. . . . The humerus is huge beyond the visualization of those who have not seen it, hence must judge of it from figures and measurements. In the hind quarters the bones are, if anything, less massive than might be expected. . . . Judging from the very short vertebrae the body must have been unduly foreshortened. . . . The skull is broken into several large, and numerous small pieces, which have not been set permanently in place. . . . The

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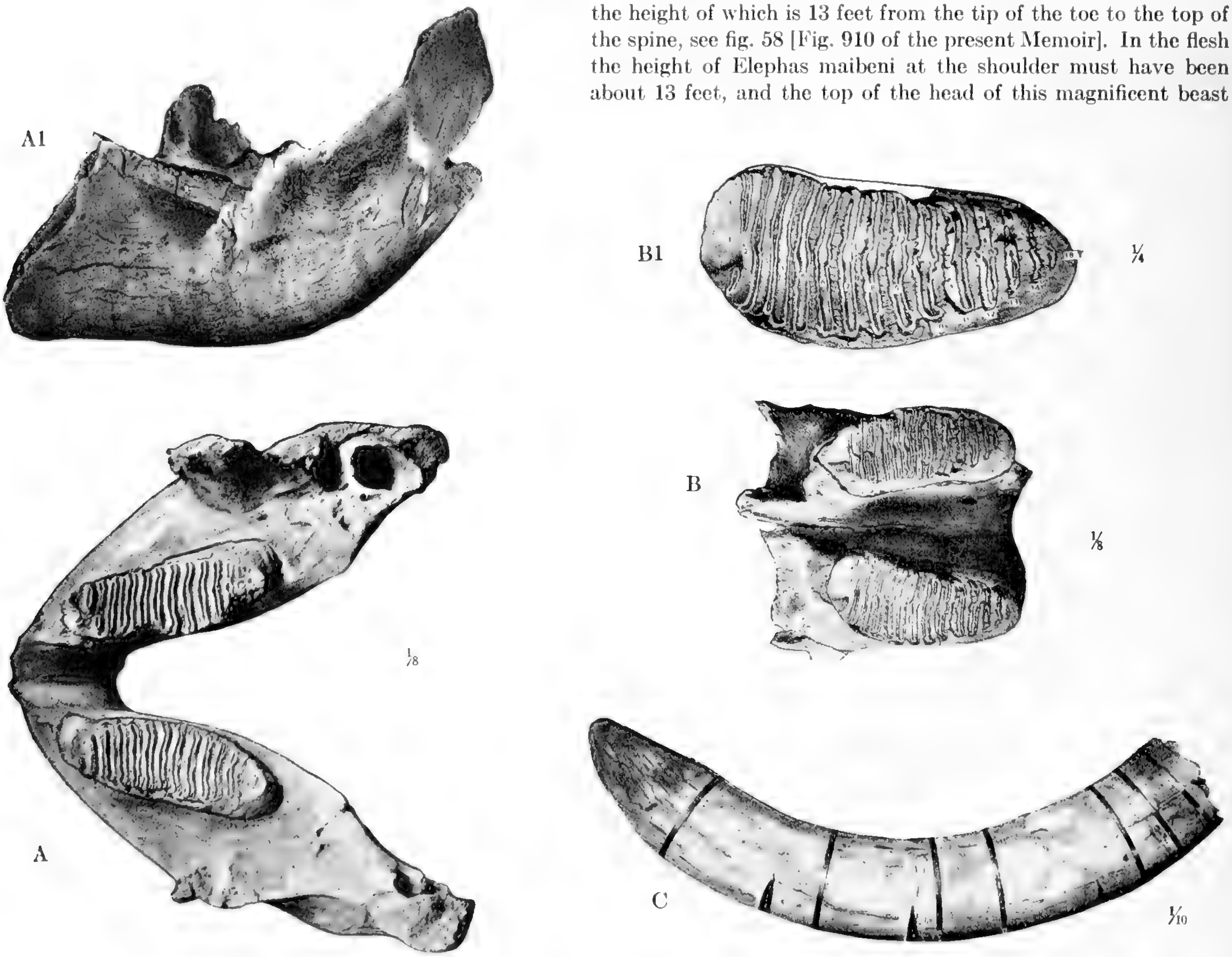
[1] [Lugn and Schultz (1934.1, p. 376, also Table A) regard it as of Iowan, late Pleistocene age.—Editor.]

accompanying free hand sketches were made with the pieces set approximately in position, and give our impressions of the skull. . . . The head must have presented a bull-dog effect or aspect. It might be called the bull-dog mammoth. . . . The mandible is well preserved, and in point of size passes the largest in our collections. The rami are widely divergent and the condyles far apart. . . . The anterior borders of the coronoids are excessively roughened; they are even nodular, and we find no parallel. . . . The lachrymal process, which is uncommonly large, prominent, and acorn-shaped, is dissimilar to all others available for study and comparison. . . . The fore limbs, four vertebrae, two pairs of single ribs, and one pair of double ribs of this exceptional mammoth are mounted in approximate position and make an impressive arch, the height of which is 13 feet from the tip of the toe to the top of the spine, see fig. 58 [Fig. 910 of the present Memoir]. In the flesh the height of Elephas maibeni at the shoulder must have been about 13 feet, and the top of the head of this magnificent beast



Barbour's Type of Archidiskodon imperator maibeni

Fig. 918. *Archidiskodon imperator maibeni*, the 'Lincoln County Mammoth,' superior and inferior dentition of the type skeleton (Neb. Mus. 5-9-22). After photographs kindly furnished the present author by Prof. E. H. Barbour (compare Barbour, 1925.3, figs. 64, 65, 67, 68).

A, Mandible of *A. imperator maibeni* from above, about one-eighth natural size.

Right and left inferior molars, r.M_3, l.M_3, with 15+ ridge-plates, 14 exposed, more or less worn, broad cement, somewhat sinuous, but slightly concave posteriorly, crown externally plane, internally convex.

A1, The same in lateral view. One-eighth natural size.

B, Palate containing right and left third superior molars, r.M^3, l.M^3. One-eighth natural size.

B1, Right third superior molar, r.M^3. One-fourth natural size.

C, Extremity of tusk 4 feet in length measured on outer curve. About one-tenth natural size.

Observe in B, B1, 16+ ridge-plates, of which 1–13 show signs of wear, quite strongly concave posteriorly with heavy border of cement; crown externally convex, internally slightly concave. Very similar in contour and ridge formula to *A. imperator* (Amer. Mus. 14476—Fig. 889B), from Victoria, Texas. Observe in A, A1, 15+ ridge-plates, 14 exposed.

must have been about 14 feet above the ground. From the tip of the toes to the top of the scapula is 11 feet, 6 inches. This specimen is believed to hold the record for size amongst the Columbian group of mammoths. In point of size, Elephas maibeni was a rival of the Imperial elephant itself, which stood 13½ feet high. The tallest living African elephant stands 11 feet high and the average elephant of the menagerie and circus 8 to 9 feet."

TYPE OF ARCHIDISKODON HAROLDCOOKI

Fig. 919. Type mandible and third inferior molar of the right side *in situ* of *Elephas haroldcooki* Hay, 1928. After Hay and Cook, 1930, Pl. III, fig. 1. One-fifth natural size.

Archidiskodon haroldcooki Hay, 1928

Figure 919

Found in Holloman's gravel quarry, Frederick, Oklahoma. Aftonian? gravels.

Elephas haroldcooki Hay, 1928. "Preliminary Descriptions of Fossil Mammals Recently Discovered in Oklahoma, Texas and New Mexico." Proc. Colo. Mus. Nat. Hist., Vol. VIII, No. 2, Pt. 1, February 2, 1928, p. 33. TYPE.—Nearly complete lower jaw containing last right and left molars *in situ* (Colo. Mus. 1057). HORIZON AND LOCALITY.—Holloman's gravel quarry, at Frederick, Oklahoma. TYPE FIGURE.—Hay and Cook, 1930.1, Pls. III, fig. 1, V, fig. 1, XIII and XIV.

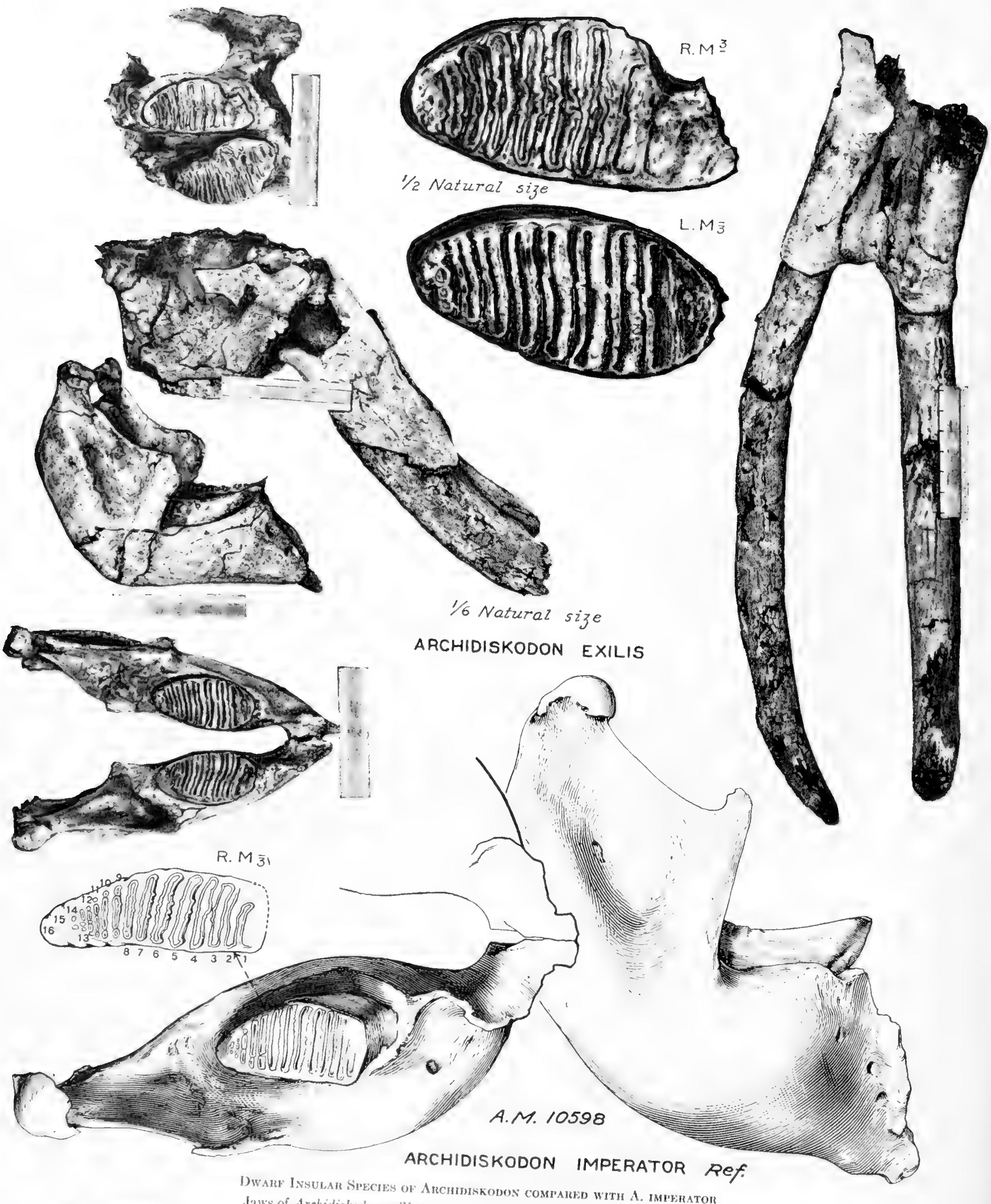
TYPE DESCRIPTION.—(*Op. cit.*, 1928, p. 33): "*Elephas haroldcooki* Hay. Based on a nearly complete lower jaw containing the right and left last molars. Anterior fang and 2 ridge-plates absent through wear. 12 ridge-plates and the rear talon present. 4.4 ridge-plates in 100 mm. Enamel thick, moderately folded. A loxodont expansion present in some of the ridge-plates. The crown very high. Found in Holloman's gravel quarry at Frederick, Oklahoma. No. 1057, Colorado Museum of Natural History, Denver."

SUPPLEMENTARY DESCRIPTION (HAY AND COOK, 1930.1, PP. 32, 33).—"This jaw was embedded in the cemented gravel very close to the Permian red clay . . . It will be seen that nearly all of the jaw behind the teeth is lacking. These teeth are in fine condition and show that the animal was somewhat beyond middle age. The height of the jaw where the ascending ramus arises is a little more than 200 mm. Its thickness, where greatest, at the middle of the tooth is 155 mm.; the width of the bone, taken at the rise of the ascending rami, is about 390 mm."

"As will be observed from the views of the jaw, it is wholly without a beak in front; and does not turn downward, also the symphysis is short, about 60 mm. in length. The teeth present are parts of the hindmost molars. This is shown by the arrangement of the rear ridge-plates, only partly shown in the figures. In front of each tooth (plate III, figure 1 [=Fig. 919 of present Memoir]), especially of the one of the right side, is seen a cavity in which was lodged the anterior fang. The tooth had been worn down to the bar of bone separating this fang from the part behind it and the fang had fallen out. With it went three worn-out ridge-plates. Behind the bar of bone may be counted on the grinding face 11 ridge-plates, the tenth being represented by a small circle of enamel, the eleventh by a dot of enamel. The length of the abraded surface of the molar (plate V) is 182 mm.; its width, with the cement, is 85 mm.; without it, 80 mm."

"Behind this eleventh ridge-plate is a mass which may be regarded as a talon, a ridge-plate as yet undeveloped. Adding now to these eleven ridge-plates the two supported by the anterior fang and the one by the bar of bone behind it, we have 14 ridge-plates for the hindmost molar of the species. From plate XIV it is seen that the ridge-plates are very thick. Measured at one-half their height three are spanned by a line just a little less than 75 mm. Measured at one-half their height 4.44 plates are crossed by a 100 mm. line. The hind end of the crown is almost 6 inches high, nearly as high as the grinding surface was long."

"The view (plate XIV) of the inner face of the tooth shows that the ridge-plates are at first directed strongly forward, then are turned abruptly upward and (in relation to the grinding face) somewhat backward. It is due to this obliquity that the front enamel plate of the hinder ridge-plates is more exposed to view than they are farther forward. It will be seen that the outer ends of the loops of enamel are rather strongly turned forward. The enamel, as usual in primitive elephants, is thick, here about 3 mm. It is moderately crimped. A feature of interest is the presence of a lozenge-shaped expansion at the middle of each ridge-plate. This is a characteristic of the earlier elephants, as *E. planifrons*, *E. meridionalis*, and *E. imperator*."



Dwarf Insular Species of Archidiskodon compared with A. imperator

Jaws of *Archidiskodon exilis* to same one-sixth scale as jaws of *A. imperator*

Fig. 920. Comparison of *Elephas* [*Archidiskodon*] *exilis* (Calif. Inst. Tech. Coll. Vert. Pal. 11) with *Archidiskodon imperator* (Amer. Mus. 10598) from near Tule Cañon, Texas, to the same one-sixth scale, with the exception of r.M^3 and l.M$_3$, crown views, which are one-half natural size, reveals the marked diminution in size of the species from Santa Rosa Island, California, described in 1928 by Stock and Furlong. After photographs kindly forwarded to the present author by Dr. Chester Stock of the California Institute of Technology.

Archidiskodon exilis Stock and Furlong, 1928

Figures 815, 920, 921, Pl. xxi

Santa Rosa Island, California. Pleistocene.

This dwarfed insular form of imperial mammoth, estimated at 6–8 feet in height measured at the shoulder, as compared with 12 ft. 1¾ in., distinctive height of *Archidiskodon imperator*, is of the greatest interest. There is little doubt from the drawings received (Fig. 920) that this is a diminutive insular form related either to *A. imperator* or to *Parelephas columbi*.

Elephas exilis Stock and Furlong, 1928. "The Pleistocene Elephants of Santa Rosa Island, California," Science, Vol. LXVIII, No. 1754, p. 140. TYPE.—"A skull and mandible including four cheek-teeth and two tusks" (Calif. Inst. Tech. Coll. Vert. Pal. 14). HORIZON AND LOCALITY.—Santa Rosa Island, California, the second largest of four islands separated from the mainland by the Santa Barbara Channel. Pleistocene. TYPE FIGURE.—Stock, 1935.1, p. 210, fig. 6. SUPPLEMENTARY DESCRIPTION.—Stock, "Exiled Elephants of the Channel Islands, California," Scientific Monthly, 1935, XLI, September, pp. 205–214, text figs. 1–10.

RESTORATION OF ARCHIDISKODON EXILIS OF SANTA ROSA ISLAND

Fig. 921. Facial portion of the skull, with tusks and lower jaw, of *Elephas exilis* Stock and Furlong, 1928. From Quaternary deposits, Santa Rosa Island, California. After unpublished photograph kindly furnished by Dr. Chester Stock.

TYPE DESCRIPTION.—(Stock and Furlong, 1928.1, pp. 140, 141): "W. G. Blunt's discovery of fossil teeth of an elephant on Santa Rosa Island, one of the Channel Islands off the coast of southern California, was recorded by Stearns [Footnote: 'Stearns, R. E. C., Proc. Calif. Acad. Sci., Vol. 5, p. 152, 1873.'] in 1873. Since that time this interesting and significant occurrence has been referred to by several authors. Hay [Footnote: 'Hay, O. P., Carnegie Inst. Wash. Pub. 322B, pp. 42, 43 and 51, 1927.'] has recently summarized the available information and recognizes the presence of *Elephas imperator* and of an undetermined species. During the past year Dr. Spencer Atkinson and Mr. J. A. Barbieri, of Pasadena, secured a fragmentary elephant skull on Santa Rosa Island and presented the specimen to the California Institute of Technology. Through the courtesy of the Vail Company of Los Angeles, owners of the island, the California Institute, with the cooperation of the Carnegie Institution of Washington, have been given the opportunity to investigate the occurrence, and facilities were kindly made available to collect further remains. . . . The collections secured by the California Institute include a number of teeth, parts of skulls and skeletal material. Occasionally several skeletal elements and teeth are found associated in the deposits. Usually the remains are scattered. One curious feature of the occurrence is the apparent total absence of associated mammalian types. The proboscidean remains are referable to the genus *Elephas*. The individuals exhibit considerable variation in size, and this is undoubtedly to be ascribed in part to differences in age. A survey of the collection as a whole yields the impression rather strongly that the elephant types were of relatively small size. Some of the forms may have a height of six to eight feet as measured at the shoulder. The larger individuals are perhaps comparable in size to the American mastodon and are certainly smaller, possibly considerably smaller, than the Pleistocene mammoths of the southwestern United States. While the Santa Rosa Island elephant has been determined as representing the species *Elephas primigenius* Blumenbach and *E.* (*Archidiskodon*) *imperator* Leidy, the difference in size, coupled with differences noted in the skull and dentition, seem quite clearly to distinguish the island form as a distinct species for which the name *Elephas exilis* is here proposed."

Supplementary Description (Stock, 1935.1, pp. 206, 207, 212–214).—"Remains of extinct elephants are now known to occur on three of the Channel Islands, namely, on San Miguel, Santa Rosa and Santa Cruz (see Fig. 1 [=Fig. 922 of present Memoir]). The first material was found on Santa Rosa more than sixty years ago, and this island has furnished by far the largest collection of fossil specimens representing these types. Similar material has been brought to light on San Miguel. In contrast to the rather numerous finds of elephant remains in Quaternary deposits of Santa Rosa, the presence of elephants on Santa Cruz is known thus far by only two fragmentary enamel plates of a cheek-tooth."

"*San Miguel*: Although this island is wind-swept and shifting sand dunes mantle much of the area underlain by sediments of Tertiary and Quaternary age, the incision of the present land surface by ravines and gullies and the constant though gradual recession of the sea-cliffs develop exposures on which occasionally the weathered-out materials of fossil mammals have been discovered. Several tusks and cheek-teeth of elephants were found in a thin series of Quaternary alluvial deposits lying beneath a table-like surface and exposed in the sides of gullies near the northwest end of San Miguel. Scattered proboscidean teeth have been found from time to time elsewhere on this island. Among the fossil materials are specimens which clearly point to the fact that the San Miguel elephants are among the largest types to be obtained in the insular region."

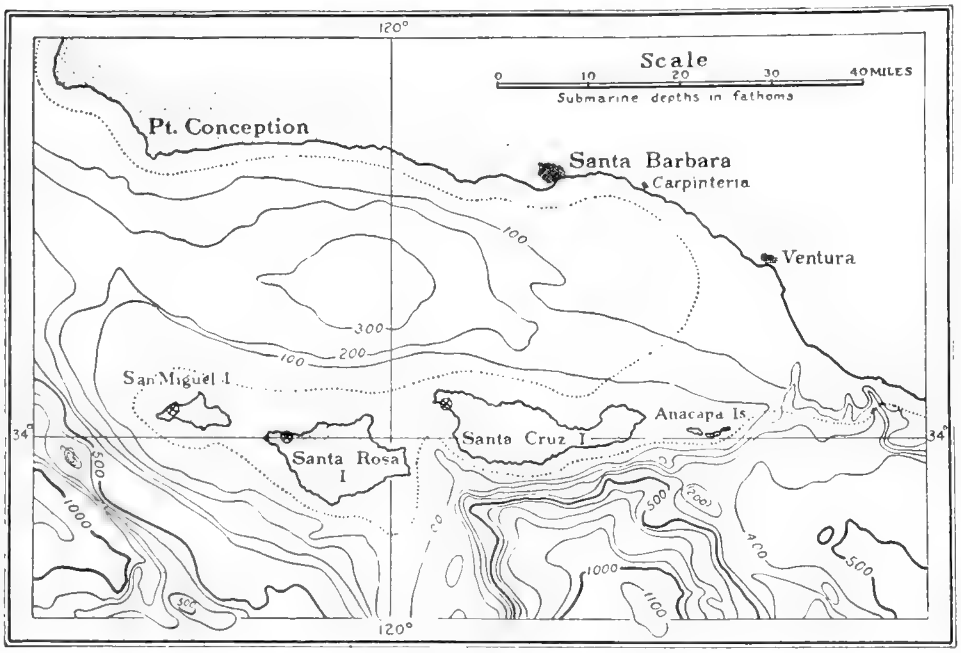


Fig. 922. "Map of coastal province of southern California in vicinity of Santa Barbara. Location of some occurrences of fossil elephants on Channel Islands shown by x. Dotted line indicates hypothetical border of land during Pleistocene time, after Chaney and Mason." Reproduced from Stock, 1935.1, p. 206, fig. 1.

Conclusions (pp. 212–214).—"Whether or not more than one species of elephant is present among the island forms remains to be definitely determined. In this connection, it should be recognized that an interesting and perhaps significant difference may exist between those forms on Santa Rosa and the types of San Miguel."

"Numerous cheek-teeth and tusks, fragmentary jaws and skeletal elements comprise the bulk of the collections obtained on Santa Rosa. Individuals of all ages are preserved, from an unborn type to fully grown adults. The youngest specimen, evidently belonging to a foetus, is represented by a lower jaw (Fig. 6 [not figured in present Memoir]) in which the enamel plates had not firmly consolidated to form the lower cheek-teeth and had not erupted through the gums. One fairly complete skull represents an adult individual and furnishes valuable information as to the specific characters of the island elephants. When found in Quaternary strata, exposed in the sea-cliff near the mouth of the Cañada Corral, only the weathered cranial portion was visible. . . . Excavation revealed the rest of the skull and upper tusks . . . with the lower jaw in position below the palate. [This is the type.] Illustrations of this specimen and of a young adult skull of the imperial mammoth (*Archidiskodon imperator*), drawn to the same scale, are shown in Figure 9 [not figured in present Memoir]."

"Comparison of fossil remains of elephants found on Santa Rosa with comparable materials occurring on the mainland establishes clearly the fact that the island forms were smaller in stature than their relatives of the mainland. Considerable variation in size exists among the island types, but the difference in stature between island and mainland forms remains a notable feature. . . . While the elephants of the mainland ranged in height from approximately 10½ feet to 13½ feet as measured at the shoulders, those of the islands presumably never exceeded 8 or 9 feet in height and the smaller individuals were probably no taller than 6 feet. Thus, the smaller size of these elephants presents a character wherein they resemble the fossil or subfossil, dwarfed elephants described from the Maltese Islands of the Mediterranean. The diminution in size, however, has not been carried so far in the Channel Island elephants as in the Maltese species."

"As mentioned before, the elephants of San Miguel are among the largest types to be recorded from the island region. Tusks of these forms have been found which measure 5 feet in length and 6 inches in diameter at the base. While some of the fossil materials on Santa Rosa likewise indicate the former presence of relatively large individuals, it is possible that the average size of the San Miguel elephants was larger than that of the Santa Rosa types. Were this ultimately established to be the case, on the basis of a comparison with more extensive collections than are now available from San Miguel, it is interesting to speculate whether the difference may not have been the result of an earlier extinction of elephants on the smaller of the two islands."

Archidiskodon sonoriensis Osborn, 1929

Figure 923

One mile east of Arizpe, northern Sonora, Mexico. Lower Pleistocene.

Archidiskodon sonoriensis Osborn, 1929. "New Eurasiatic and American Proboscideans," Amer. Mus. Novitates, No. 393, Dec. 24, 1929, p. 18. Type.—"Nearly complete skeleton,[1] of which the palate with third superior molar, M^3, of both sides, right lower jaw (lacking ascending ramus), with third inferior molar, r.M_3, *in situ*, also symphysis, are in the American Museum." Amer. Mus. 22637 (Osborn, 1929.797). Horizon and Locality.—"One mile east of Arizpe, northern Sonora, Mexico, on the Sonora River, 60 miles southeast of Cananea and approximately 100 miles north of La Prietas and San José de Pimas. . . . The Arizpe horizon is regarded by Barnum Brown as Lower Pleistocene (lake deposit)." Type Figure.—*Op. cit.*, p. 18, fig. 18.

Fig. 923. *Archidiskodon sonoriensis*, anterior portion of type mandible and maxilla showing r.M_3, r.M^3 (Amer. Mus. 22637), one-sixth natural size. Compare Osborn, 1929.797, p. 18, fig. 18.

Specific Characters.—"Mandibular rostrum prolonged obliquely downwards, with downturned beak, as seen both in front and side views; length from symphysial groove to tip of rostrum 230 mm., exposed length of M^3 246 mm., of M_3 346 mm.; depth from third unbroken plate to bottom of jaw 244 mm. A total of 11+2(?) exposed ridge-plates in M^3, of 2(?)+11+3 in M_3."

Archidiskodon meridionalis nebrascensis Osborn, 1932

Figures 815, 924, 927, 928, 1239, Pl. xxi

One mile northwest of Angus, Nuckolls County, Nebraska. Lower to Middle Pleistocene.

Archidiskodon meridionalis nebrascensis Osborn, 1932. "The 'Elephas meridionalis' Stage Arrives in America," Proc. Colo. Mus. Nat. Hist., XI, No. 1, Sept. 7, 1932, pp. 1–3 (Osborn, 1932.893). Type.—Skeleton, lacking cranium also tusks, excepting mid-portion of left tusk, with lower jaw in complete state of preservation. Colo. Mus. 1359. Horizon and Locality.—Found "one mile northwest of Angus, Nuckolls County, Nebraska, some fourteen or fifteen years ago." Lugn and Schultz (1934.1, Table A) regard this species as of Yarmouth (Upland) age, equivalent to Lower to Middle Pleistocene. Type Figure.—Osborn, 1932.893, figs. 1 and 2.

Characters.—"The inferior grinding teeth similar in character and in ridge formula to the '*Elephas meridionalis*' of Durfort, but somewhat broader with much thicker surrounding layer of cement. . . . *Mandible*: (1) A very prominent rostrum. (2) A relatively elongate and shallow ramus. (3) Measurements as follows:

Length mandibular condyle to symphysis	943 mm.
Depth below M3 of mandibular ramus.	220 mm.

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[1] [Remainder of skeleton unintentionally destroyed by discoverer.—Editor.]

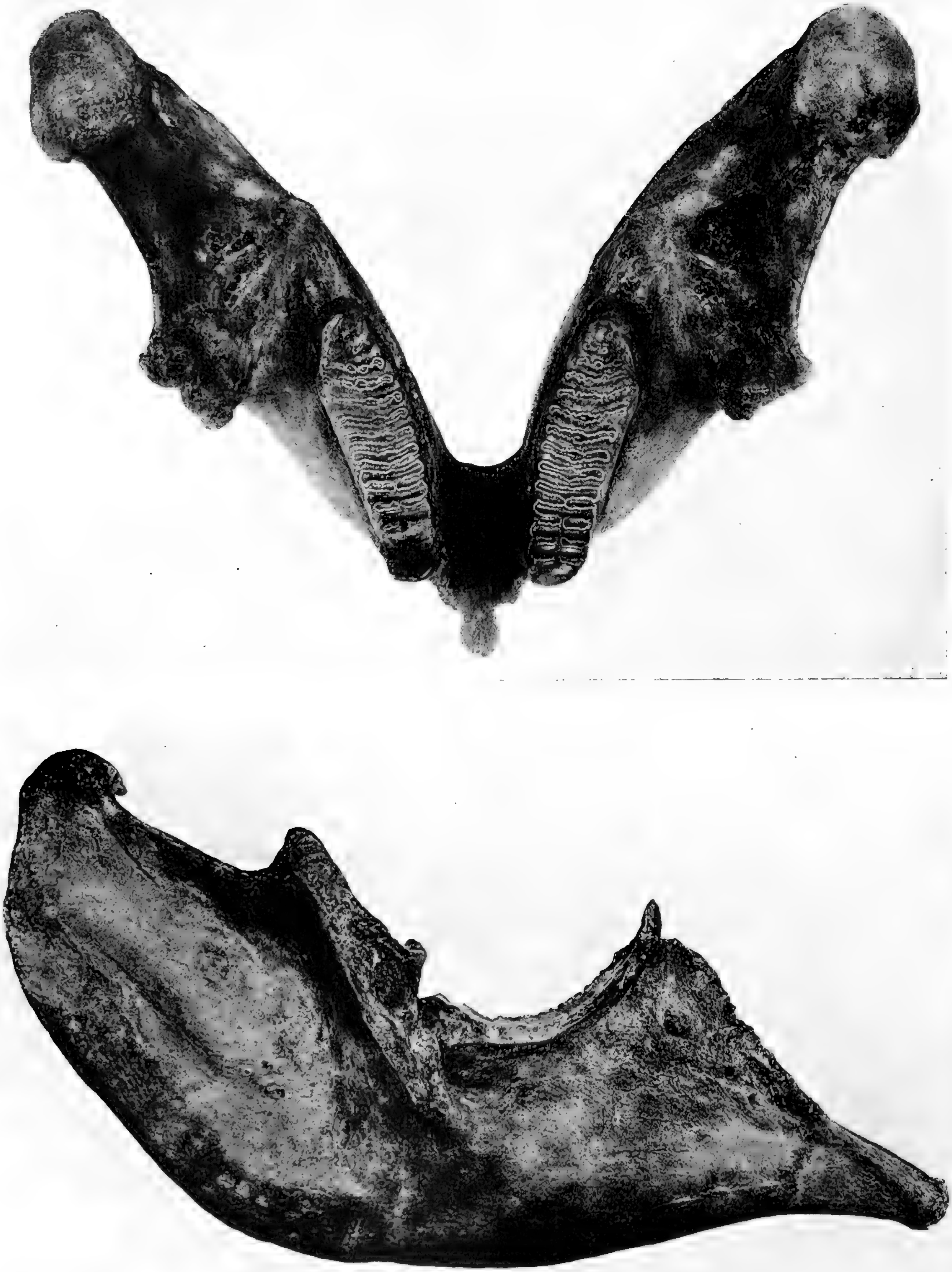


Fig. 924. Type Mandible of Archidiskodon meridionalis nebrascensis (Colo. Mus. 1359). Both figures one-fifth natural size

(Upper) Crown view of mandible with right and left third molars *in situ*. After Osborn, 1932.893, fig. 1.

(Lower) Lateral view of mandible and rostrum. After Osborn, 1932.893, fig. 2.

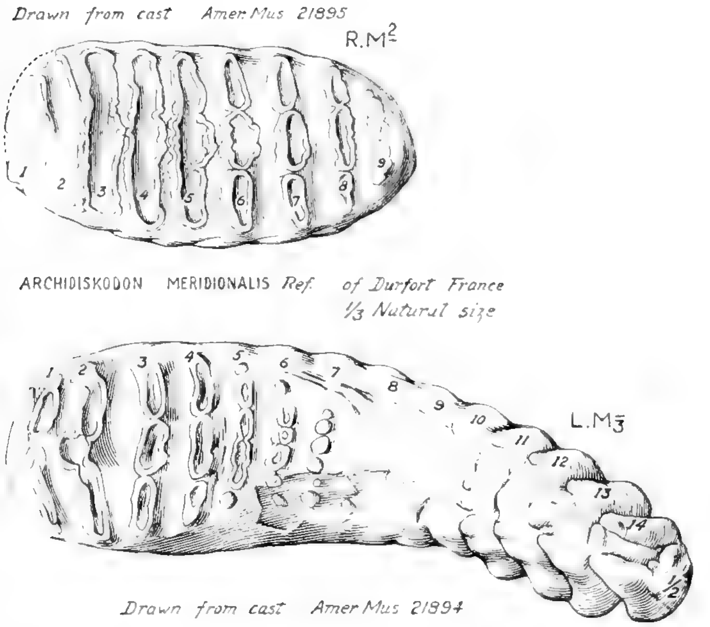


Fig. 925. Referred superior and inferior molars found associated with Durfort skeleton (*Archidiskodon meridionalis*) in the Muséum d'Histoire Naturelle, Paris, after casts kindly furnished the present author by Dr. Marcellin Boule in January, 1930. Both figures one-third natural size.

(Upper) Right second superior molar, r.M^2 (cast Amer. Mus. 21895), with +8 worn ridge-plates; $5\frac{1}{2}$ ridge-plates in 10 cm.; coronal surface length 162 mm., maximum breadth 81 mm.

(Lower) Summit of crown of left third inferior molar, l.M_3 (cast Amer. Mus. 21894), with $14\frac{1}{3}$ ridge-plates, 6 partly worn; 5 anterior ridge-plates in 10 cm.; maximum length 276 mm., maximum breadth 83 mm.

Length of r.M3, Third Inferior Molar........	289 mm.
Width of r.M3, Third Inferior Molar........	84 mm.
R.M3 total ridge-crests....	+ 13 +
L.M3 total ridge-crests....................	$\frac{1}{3}$ 13 $\frac{1}{3}$
Ridge-crests in 10 cm.....................	$5\frac{1}{2}$
Widest ridge-crest........................	73 mm.

The above ridge-crest formula, together with the dimensions of the third grinders, agree closely with those which prevail among most of the specimens referred to '*Elephas meridionalis*' in the British Museum as described and figured by Falconer."

"Unfortunately, the cranium was the first part of this animal to be exposed and was completely weathered out. Only the extremity of one of the superior incisive tusks remained; this was lost; a mid-portion of the left incisive tusk remains. Fortunately, every other part of the skeleton was preserved in absolutely complete condition on one side of the animal or on both sides so that the skeleton is now superbly mounted and becomes a classic in all its dimensions as follows:

Vertebral column:

7 cervical vertebrae measuring..........	543 mm.
19 dorsal vertebrae measuring..........	1640 mm.
4 lumbar vertebrae measuring..........	400 mm.
Sacrals not preserved.	
7 caudals only preserved.	
Height dorsal spine to ground (as mounted)........................	3695 mm.

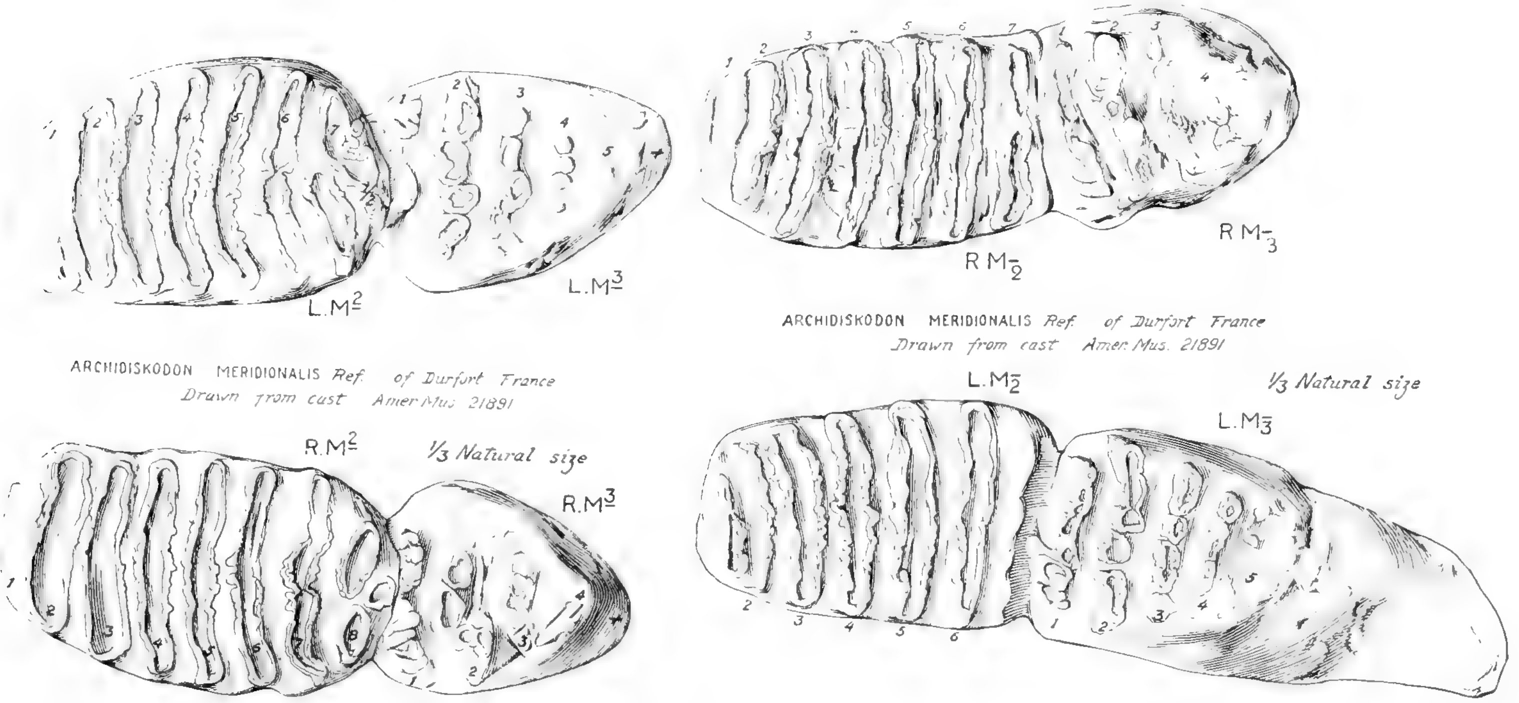


Fig. 926. Superior and inferior molars of Durfort skeleton (*Archidiskodon meridionalis*) in the Muséum d'Histoire Naturelle, Paris, after casts kindly furnished the present author by Dr. Marcellin Boule in April, 1930. All figures one-third natural size. Compare with figure 924, showing type mandible of *A. meridionalis nebrascensis* of Nebraska, with third inferior molars *in situ*.

(Left) Left and right second and third superior molars ($M^{2\text{-}3}$), after cast (Amer. Mus. 21891).

(Right) Right second and third inferior molars (r.$M_{2\text{-}3}$), same as opposite figure, and left second and third inferior molars (l.$M_{2\text{-}3}$), after cast (Amer. Mus. 21891).

Fore and Hind Limbs:

Height fore-limb scapula to ground	3454 mm.
Scapula, length of	1020 mm.
Humerus, length of	1220 mm.
Ulna, length of	910 mm.
Radius, length of	980 mm.
Median metacarpus III	200 mm.
Pelvis, length of os innominatum	1350 mm.
Pelvis, width of os innominatum	1754 mm.
Femur, length of	1390 mm.
Tibia, articular length of	840 mm.
Pes: astragalus to tip of Mts. III	475 mm.
Pes: depth of Mts. III	150 E.”

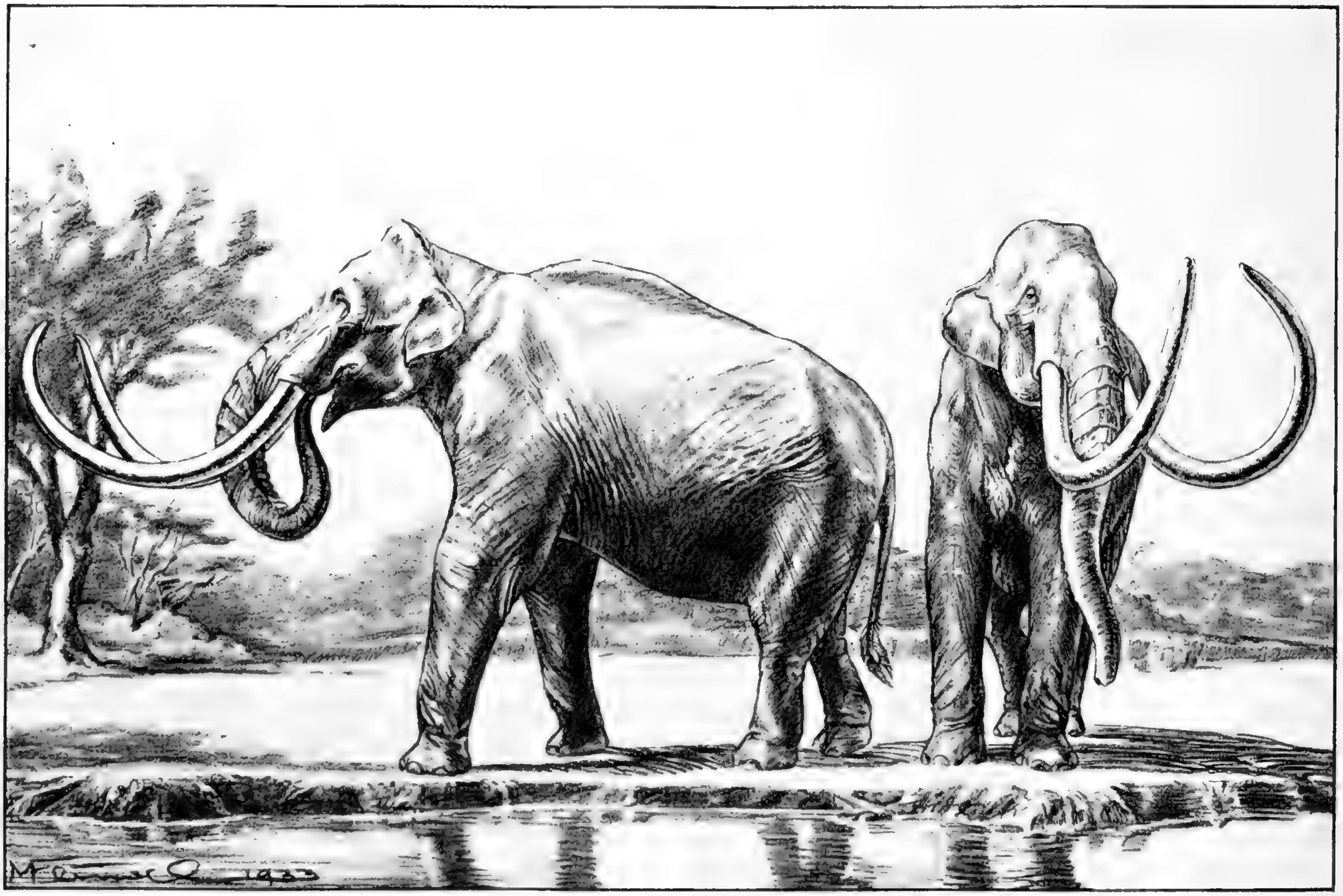


Fig. 927. Restoration of *Archidiskodon meridionalis nebrascensis* Osborn, 1932, from the complete skeleton and mandible with lower portion of the tusks, lacking only the cranium. One-fiftieth natural size.

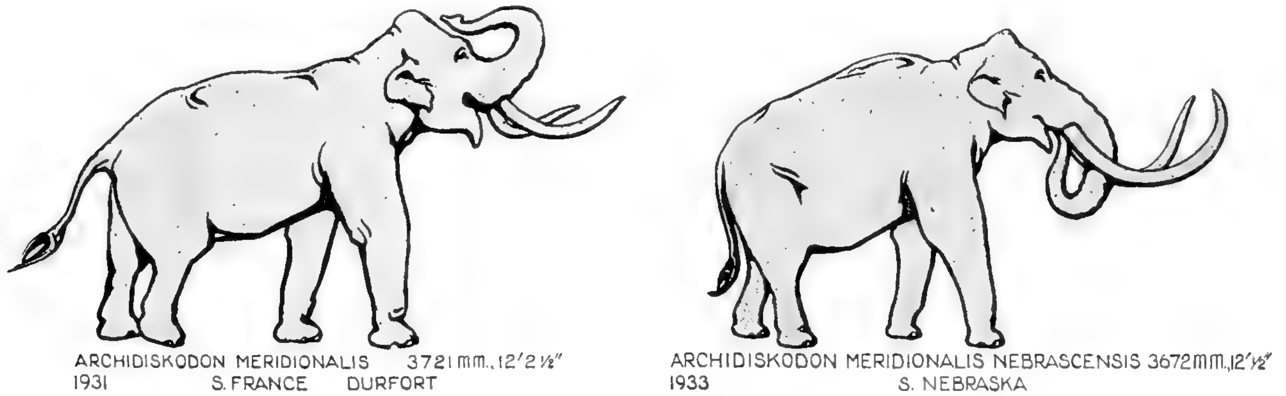
The grinding teeth of this priceless specimen are in the same stage of evolution as those of the famous '*Elephas*' *meridionalis* of Durfort, France, as established by casts of the Durfort grinding teeth kindly sent to the American Museum by Director Marcellin Boule (see Figs. 925, 926).

TABLE XI. Measurements of Molars of Archidiskodon meridionalis of Durfort (cf. Figs. 925,926, also Fig. 924, Mandible and Third Molars of A. meridionalis nebrascensis)

		Length	Breadth	Ridge-plates	
Cast Amer. Mus. 21891	L. M^2	152	94	½–7	5½ ridge-plates in 100 mm.
	R. M^2	157	93	½–7	5½ ridge-plates in 100 mm.
	L. M^3		85+	4 partly exposed, heavy cement	
	R. M^3		82+	3 exposed	
	R. M_2	140	86	⅓–6	5 ridge-plates in 100 mm.
	L. M_2	143	92	⅓–6	5 ridge-plates in 100 mm.
	R. M_3		90	4 exposed	
	L. M_3		85	4 only exposed	
Associated molars					
Cast Amer. Mus. 21894	L. M_3	278	83	14½	5½ ridge-plates in 100 mm.
Cast Amer. Mus. 21895	R. M^2	157	81	⅓–7–½	5½ ridge-plates in 100 mm.

[This species was described by Professor Osborn in 1932, while visiting the Colorado Museum of Natural History at Denver. In his article in the Proceedings of the Colorado Museum (Osborn, 1932.893) he states: "In the years of study which the present writer has devoted to the evolution of the fossil elephants, he became convinced that the '*Elephas meridionalis*' of France is the direct ancestor of the '*Elephas imperator*.' New and positive evidence of the correctness of this theory is now afforded by the discovery of the complete skeleton which forms the subject of the present paper. This skeleton with the lower jaw in a complete state of preservation proves to resemble very closely indeed in every detail the '*Elephas meridionalis*' of Durfort, France, as fully described by Albert Gaudry. . . . In August, 1931, it [the skeleton] was brought to the attention of Director Figgins of this Museum [Colorado Museum], who immediately took steps not only to rescue the fragments from careless visitors but to institute the complete excavation by the most skillful modern methods. The result will be most gratifying to palaeontologists all over the world, mainly for two reasons; first, because it is by far the most complete and perfectly preserved skeleton of *Archidiskodon* ever found, lacking only the cranium; second, because it enables us to record the early migration of '*Elephas meridionalis*' to North America, and thereby establish a direct ancestral relationship of the Durfort form to the present Nebraska mammoth."

"Fortunately, the writer had recently secured from Director Boule of the Paris Museum a series of casts of the upper and lower grinding teeth of the Durfort specimen [Figs. 925 and 926 above]. Placed side by side with corresponding teeth of the Nebraska specimen, there can be no doubt that the two forms are closely related."—Editor.]


ARCHIDISKODON MERIDIONALIS 3721 mm., 12′2½″
1931 S. FRANCE DURFORT

ARCHIDISKODON MERIDIONALIS NEBRASCENSIS 3672 mm., 12′½″
1933 S. NEBRASKA

Fig. 928. Restoration by Margret Flinsch Buba of *Archidiskodon meridionalis* of Durfort and *A. meridionalis nebrascensis* of Nebraska, under the direction of Henry Fairfield Osborn. One-fiftieth natural size.

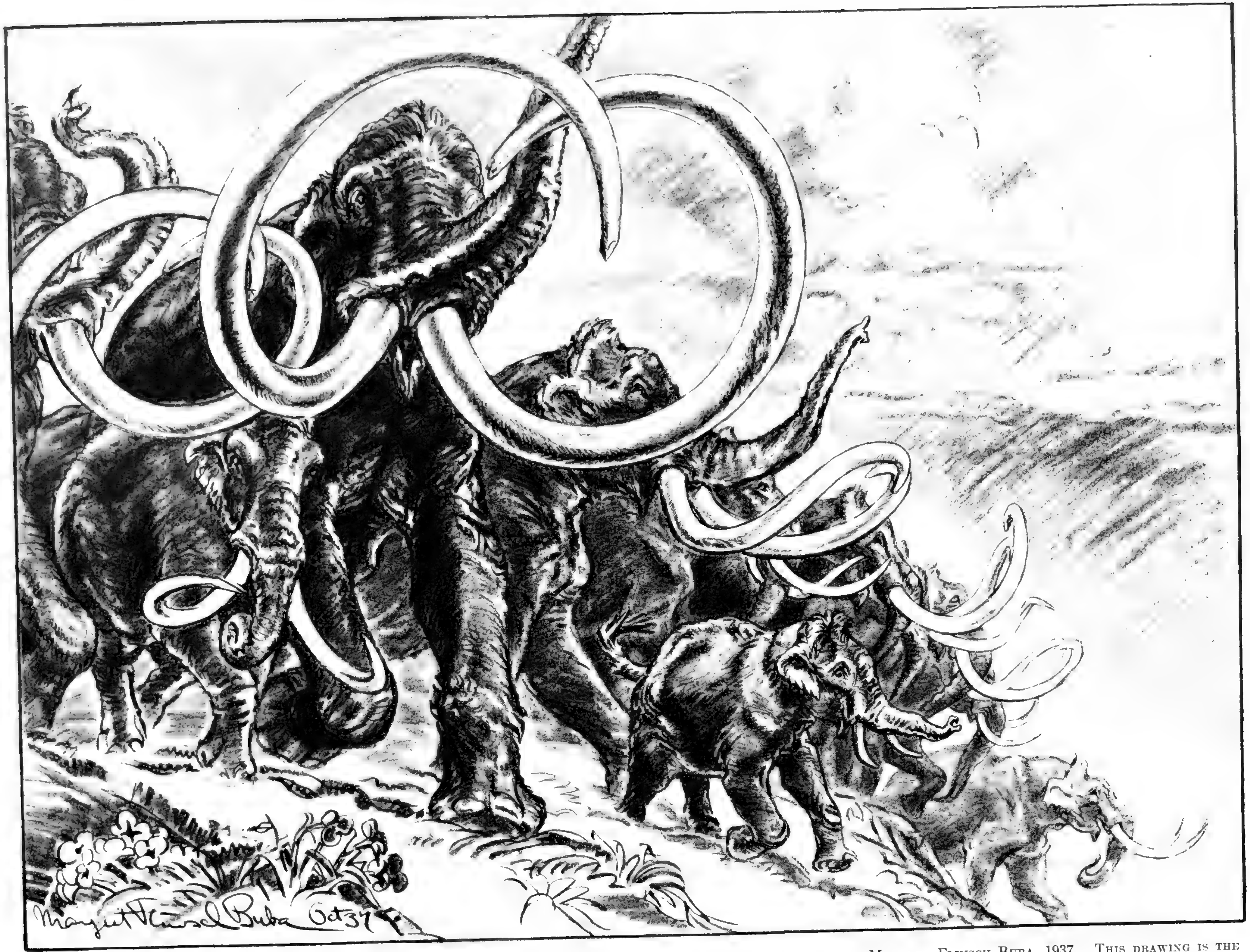


Fig. 929. Parelephas trogontherii of Mosbach, the Largest Species of the Parelephas Phylum. Restored by Margret Flinsch Buba, 1937. This drawing is the generous Contribution of the Artist to Professor Osborn's Memoir.

CHAPTER XVII

THE GENUS PARELEPHAS (SUPERFAMILY ELEPHANTOIDEA), OF THE SUBFAMILY MAMMONTINÆ, INTERMEDIATE BETWEEN ARCHIDISKODON AND MAMMONTEUS, DISTRIBUTED IN THE NORTH TEMPERATE ZONE OF EURASIA AND NORTH AMERICA

PROFOUND CRANIAL AND INCISIVE TUSK RESEMBLANCES TO ARCHIDISKODON AND MAMMONTEUS. CLEAR DISTINCTIONS FROM THESE GENERA IN GRINDING TOOTH STRUCTURE. FIRST APPEARANCE IN THE UPPER PLIOCENE[1] AND LOWER PLEISTOCENE OF EUROPE. MIGRATION THROUGH ASIA MINOR AND ASIA TO THE UNITED STATES—WASHINGTON, NEBRASKA, TEXAS, ILLINOIS, INDIANA, OHIO, SOUTH CAROLINA, GEORGIA, FLORIDA—AND FRENCH GUIANA, SOUTH AMERICA. EXTINCTION IN UPPER PLEISTOCENE OR POSTGLACIAL(?) TIMES.

1. European north temperate origin. History of separation from other extinct proboscideans.
    - Complete separation by Osborn of the phylum *Parelephas*.
    - Order of discovery and description of species of *Parelephas*.
    - Phylogenetic order of succession of *Parelephas*.
    - Distinctive cranial characters of *Parelephas*.
2. Systematic description of European and Asiatic species in ascending progressive order.
    - *Parelephas trogontherioides*, Italy.
    - *Parelephas trogontherii*, Germany.
    - *Parelephas*(?) *trogontherii nestii*, England.
    - *Parelephas armeniacus*, Asia Minor.
    - *Parelephas* unrecorded in China and Japan.
    - *Parelephas intermedius*, France.
    - *Parelephas wüsti*, South Russia.
3. North and South American species of *Parelephas*.
    - *Parelephas jacksoni*, Ohio, exact locality unrecorded.
    - *Parelephas*(?) *mississippiensis*(?), Indiana.
    - *Parelephas columbi*, Georgia.
    - *Parelephas columbi felicis*, Mexico.
    - *Parelephas columbi cayennensis*, French Guiana, South America.
    - *Parelephas jeffersonii*, Indiana.
        - *Elephas roosevelti* (synonym of *P. jeffersonii*), Illinois.
    - *Parelephas progressus*, Ohio.
    - *Parelephas washingtonii*, Washington.
    - *Parelephas eellsi*, Washington.
    - *Parelephas floridanus*, Florida.

1. EUROPEAN NORTH TEMPERATE ORIGIN. HISTORY OF SEPARATION FROM OTHER EXTINCT PROBOSCIDEANS

The generic phylum separated as *Parelephas* by Osborn in the year 1924 is briefly mentioned in Chapter II of the present Memoir and distinguished especially in its cranial characters in Chapter XV, in which it appears that *Parelephas* is linked with *Archidiskodon* and *Mammonteus* in its cranial resemblances and great incurved incisive tusks, while in its grinding teeth and ridge-plate formulæ it is so nearly intermediate between these two genera as to have been mistaken for an actual connecting link. In the present chapter it is shown to be an entirely distinct generic phylum which during the more temperate interglacial periods (Fig. 795) occupied the same geographic range as that of the true woolly mammoth (*Mammonteus*) during the glacial periods.

HISTORY.—The sixteen species which are grouped in the genus *Parelephas* constitute a very ancient and distinct generic phylum for which Osborn's name (*Parelephas*) seems appropriate, in reference to the convergence or parallelism of the grinding teeth in this phylum with those of the true *Elephas*. For more than half a century, owing to the similarity in appearance of the grinding teeth to those of the true mammoth (*Mammonteus*), all English and American authors, including Falconer, Leith Adams, and Lydekker, confused the grinding teeth of specimens which Osborn now refers to *Parelephas* with those of the northern mammoth *Elephas* [*Mammonteus*] *primigenius*, and this accounts for the great discrepancies in the collective ridge formulæ attributed to the species *E. primigenius*, i.e., M 3 $\frac{18-27}{18-27}$ as given by Leith Adams (1877-1881, p. 127) and by Lydekker (1886.2, p. 175), and copied by Hay (1914, p. 395). This unfortunate confusion in the ridge formula arose despite the fact that Falconer

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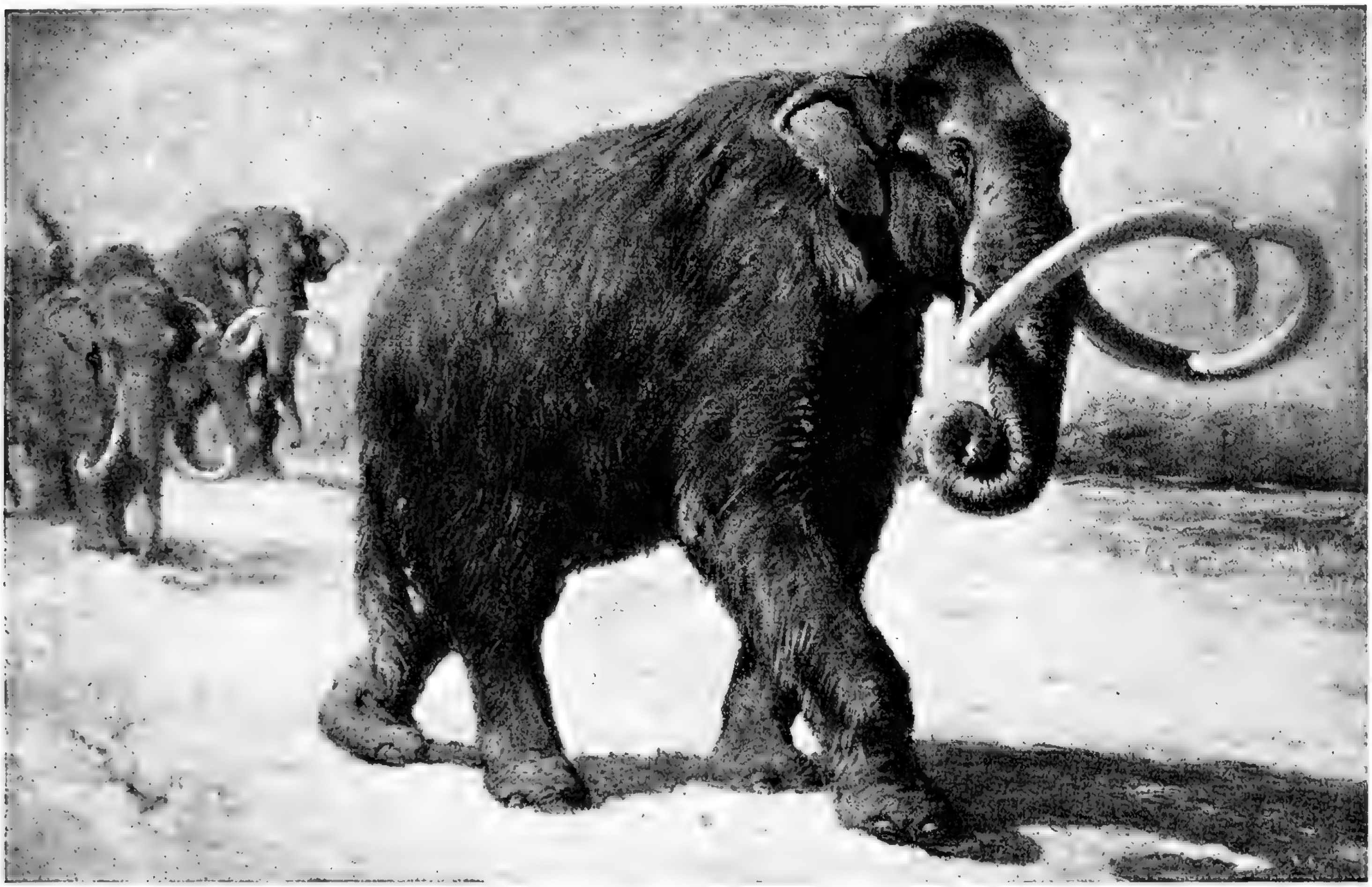
[1] [See footnote 1 on page 1049 below.—Editor.]

as early as 1863 (p. 65) had correctly defined the ridge-plate formula of *E. primigenius* as M 3 $\frac{24}{24}$, a formula which is fully confirmed by Osborn's researches for this Memoir (see Chapter XVIII). The lower ridge-plate count (M 3 $\frac{18}{18}$) attributed by Adams and Lydekker to *Elephas primigenius* really belongs to grinding teeth of primitive Middle Pleistocene species of *Parelephas*, such as *P. trogontherii*, which exhibits M 3 ${}^{15+}_{16+}$ ridge-plates. As described in detail below, Jourdan (1861) was the first to separate from *E. primigenius* one of these species of *Parelephas* under the name *Elephas intermedius*, a stage which exhibits M 3 ${}^{22}_{21}$ ridge-plates; he was followed by Pohlig (1885) who clearly defined the more primitive *Elephas trogontherii*.

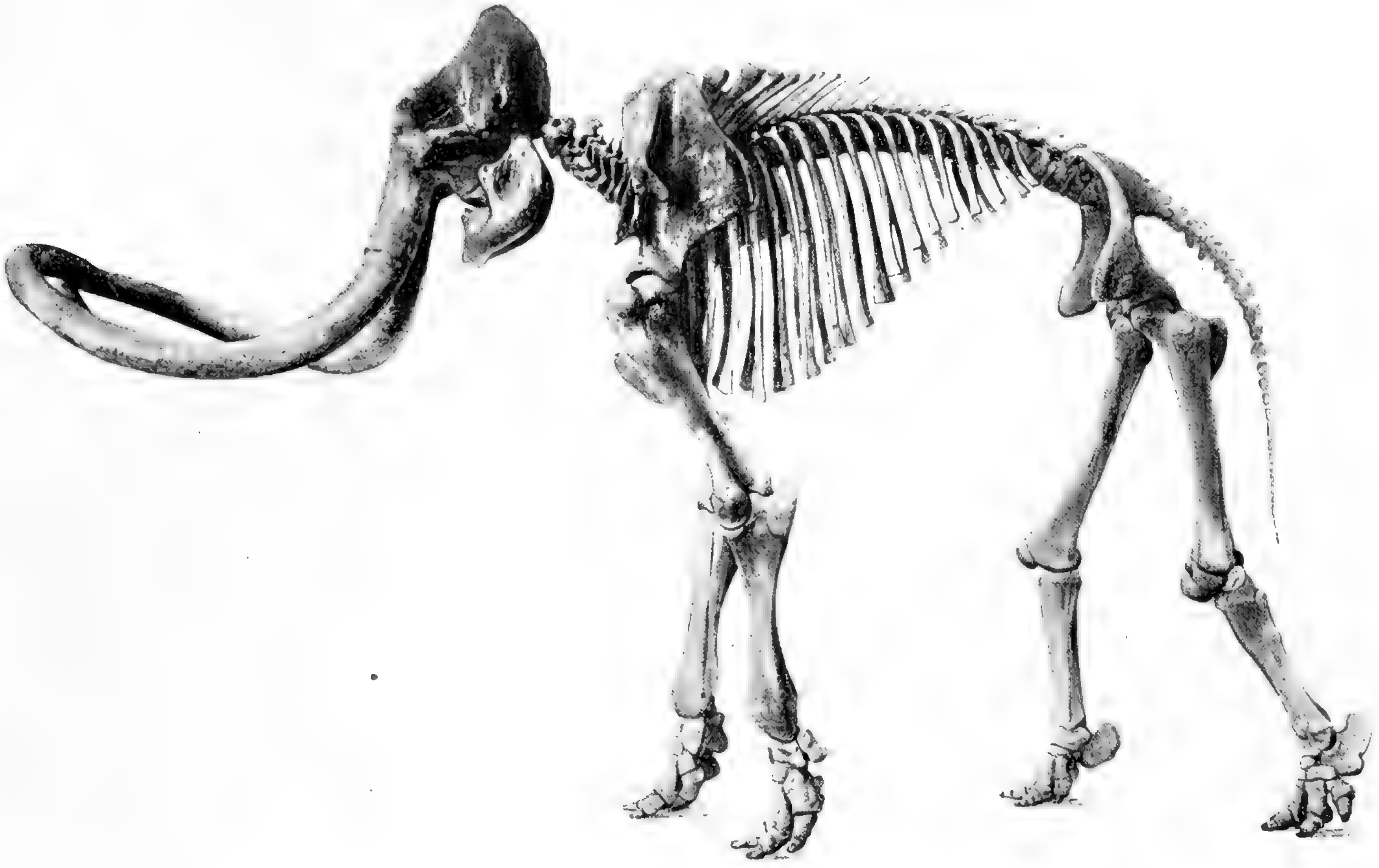


RESTORATION OF THE TYPE OF PARELEPHAS JEFFERSONII
One-thirtieth natural size

Fig. 930. This painting by Charles R. Knight, in the year 1909, was taken directly from the type skeleton of *Parelephas jeffersonii* in the American Museum of Natural History. The characters of the typical *Parelephas* cranium and tusks are particularly well shown, with short concave forehead and prominent convex occipitofrontal crest. The shape of the ears is entirely conjectural. The hairy covering, unlike the hairy and woolly covering of *Mammonteus primigenius*, is a wholly conjectural character, because no remains of the hair have been discovered, but the presence of this Jeffersonian mammoth in north temperate regions, appearing in post(?)-Wisconsin times, furnishes indirect evidence of a hairy if not of a woolly coat.

In the present chapter, chiefly from the researches of Depéret, Mayet, and Osborn, it is shown that the *phylum Parelephas constitutes a long line of progressive ascent wholly distinct from that of Mammonteus primigenius.* Its first appearance is in Upper Pliocene time in Italy. Its final appearance in IV GLACIAL and Postglacial times, principally on or near the 40th parallel of the United States, in the species *Parelephas jeffersonii* (M 3 ${}^{25}_{24}$), is followed by the closing stage *Parelephas progressus* (M 3 $\frac{30}{26}$).

It has also been a long and difficult matter both in Europe and America to clearly separate the members of the generic phylum *Parelephas* from the newer phylum of the broad-toothed, narrow-plated true mammoth (*E.* [=*Mammonteus*] *primigenius*) on the one hand, and from the older phylum of the broad-toothed, broad-plated southern (*Elephas meridionalis*) and imperial (*E. imperator*) mammoths of the genus *Archidiskodon* on the other. The chief grounds of separation are as follows: (1) The cranium in *Elephas intermedius*, *E. trogontherii*, and *E. jeffersonii* is now known to be readily distinguishable from the crania of either *E.* [=*Mammonteus*] *primigenius* or *E.* [=*Archidiskodon*] *imperator*; (2) the grinding teeth are *intermediate* in form and in the number of plates, as observed by Jourdan in 1861 in applying the name *Elephas intermedius*; (3) it is noteworthy that both in France and Germany the grinding teeth of *Parelephas* have been independently described as intermediate in structure between those of *E.* [=*Archidiskodon*] *meridionalis* and *E.* [=*Mammonteus*] *primigenius*, as shown in the full historic notes below. *Elephas columbi* proves to be *Parelephas columbi*.



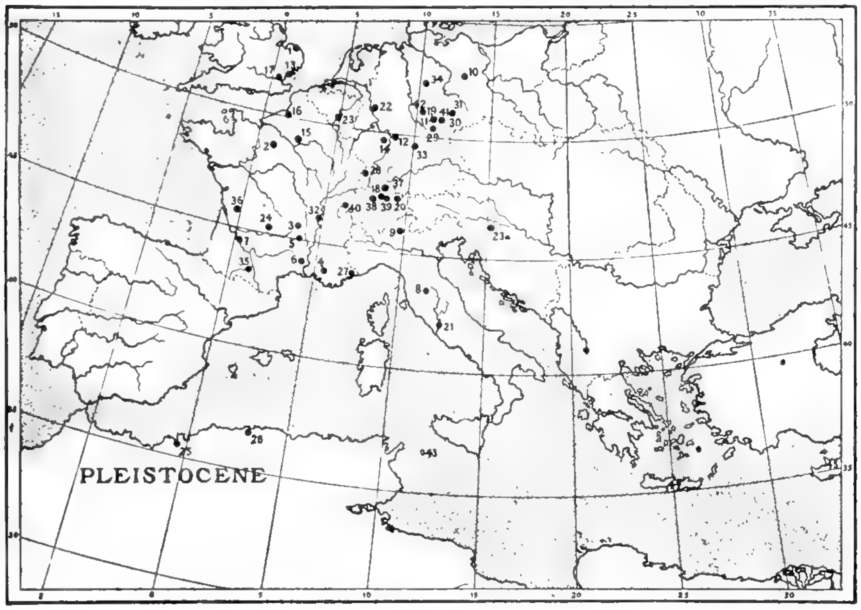
SECOND FIGURE OF THE TYPE SKELETON OF PARELEPHAS JEFFERSONII
One-thirtieth natural size

Fig. 931. Second figure of the aged *type* skeleton of *Parelephas jeffersonii* Osborn, 1922, p. 11, fig. 10, as mounted in the American Museum (Amer. Mus. 9950). For further information about this type skeleton, see legend of figure 966, also the description below.

FRANCE: JOURDAN, 1861.—Despite the early separation by Jourdan of *Elephas intermedius* from *E. primigenius* and description of the grinding teeth as intermediate between *E. primigenius* and *E. meridionalis* (1861), Gaudry, who was very conservative in the matter of applying new names to species, continued to describe (1876, p. 40, also Pl. IX) these animals as "*Elephas primigenius* à lames écartées." The steps in the gradual separation of this phylum by palæontologists of France are clearly described by Depéret and Mayet (1923, pp. 176–190).

Fig. 932. Chief Lower to Upper Pleistocene localities in which occur species of *Archidiskodon*, *Parelephas*, *Mammonteus*, *Loxodonta*, and *Palæoloxodon* (syn. *Pilgrimia*), after Osborn, 1910.346, p. 391, fig. 176.

Fossils attributed to the phylum *Parelephas*, and of large size, are especially abundant in the Middle Pleistocene of Süssenborn (Fig. 932,11), of Mosbach (12), and of Taubach (19). At Mosbach (in *1st? Interglacial* times) they occur in the same layers, but with much greater frequency, than those of *E.* [*Hesperoloxodon*] *antiquus*, namely, three to one (Soergel, 1912, p. 32); more recently it is estimated (Schmidtgen, 1926) that in the Mosbach sands *E.* [*Parelephas*] *trogontherii* is about ten times as abundant as *E.* [*Hesperoloxodon*] *antiquus*; in Mosbach also this elephant attains its greatest size.



PLEISTOCENE EUROPE.—**1** *Forest Bed of Cromer* (Norfolk). Sables de **2** *St. Prest* near Chartres (Eure-et-Loire). **3** *Malbattu* (Puy-de-Dôme). **4** *Peyrolles* (Bouches-du-Rhône). **5** *Solhilac* near Puy. Clay deposits of **6** *Durfort* (Gard). **7** *Cajarc* (Lot-et-Garonne). **8** *Val d'Arno* (Tuscany). **9** *Leffe* near Bergamo (Lombardy). **10** *Rixdorf* near Potsdam (Brandenburg). Gravels of **11** *Süssenborn* near Weimar. Sands of **12** *Mosbach* in northern Baden. Freshwater deposits of **13** *Clacton* (Essex). Sands of Mauer near **14** *Heidelberg* (western Germany). **15** *Chelles* on the Marne, near Paris. **16** *St. Acheul* (Somme). **17** *Ilford* and *Grays Thurrock* (Essex). Lignites of **18** *Dürnten* and of *Utznach*, near Zürich. **19** *Taubach* near Weimar. **20** *Wildkirchli cave* on *Mont Säntis* (eastern Switzerland). Tuffs of **21** the *Tiber Valley*, near Rome. Caves of **22** *Neandertal*, near Düsseldorf (western Germany), **23** *Spy*, near Amur (Belgium), **23a** *Krapina* (Croatia), **24** *Chapelle-aux-Saints* (Corrèze). Caves and alluvial deposits of **25** *Ternifine* (or *Palikao*) near Oran (Algeria), **26** *Pointe Pescade*, near Algiers (Algeria). **27** *Prince's Cave* (Monaco). Sandy clays of **28** *Vöklinshofen* (Alsace). **29** *Saalfeld* (Saxe-Meiningen). Travertines, etc., of **30** *Gera*, *Jena* (Saxe-Weimar). **31** *Leipzig* (Saxony). **32** *Solutré*, north of Lyons. Loess of **33** *Würzburg* (Bavaria). **34** *Thiede* near Braunschweig (Prussia). Cave of **35** *Montmaurin* (Haute-Garonne). **36** *Châteauneuf-sur-Charente* (Charente). Caves of **37** *Schweizersbild* near Schaffhausen, and *Kesslerloch* near Thayngen (northern Switzerland). Remains of lake dwellings at **38** *Wauwyl* (Lucerne), **39** *Robenhausen*, south of Lake Pfäffikon, **40** *Concise* on Lake Neuchâtel (Switzerland). Peatbogs of **41** *Hassleben*, near Weimar. Travertines of **42** *Langensalza* (Erfurt) in central Germany. Caves of the **43** *Island of Malta*, **44** *Island of Crete*, **45** *Island of Cyprus*.

[Not on map: **46** San Paolo de Villafranca (Piedmont), Italy. **47** Erzerum, Armenia. **48** Plateau loess, Lyon, France. **49** Tiraspol, S. Russia]

ITALY: FALCONER, 1868.—As early as 1868 (see below under *Parelephas armeniacus*), Falconer entertained a strong suspicion that a form closely related to *E. armeniacus* occurred at St. Paolo, Italy, which he identified (1868, II, pp. 249, 250) as resembling *E. armeniacus*, but which we now know belonged to *Parelephas trogontherioides* (see p. 1055). This is a fine example of Falconer's unerring sense of form.

GERMANY: POHLIG, 1885.—In 1885 Pohlig, on discovering two grinding teeth of one of these mammoths in the *Interglacial* sands of Süssenborn near Weimar, proposed the specific name *Elephas trogontherii*; he maintained that both geologically and zoologically this species was a link, or intermediate, between *Elephas primigenius* [i.e., *Mammonteus*] and *Elephas meridionalis* [i.e., *Archidiskodon*]. To quote Pohlig's own language (*op. cit.*, 1885, p. 1027): "Unter der Bezeichnung '*Elephas trogontherii* Pohl.' führe ich in meiner Monographie eine europäische Molarenform auf, welche zwischen denjenigen des *E. primigenius* und *E. meridionalis* zoologisch, wie ihrer geologischen Lagerstätte nach, in der Mitte steht."

Pohlig also observed the relationship of *E. trogontherii* to the species which Falconer named *Elephas armeniacus* in 1857. At the same time Pohlig erred in suggesting the relationship of *E. trogontherii* to *Elephas* [*Palæoloxodon*] *namadicus* Falc.; he also erred in suggesting that both in craniology and dentition there was a direct phylogenetic or ancestral succession between *E. meridionalis*, *E. trogontherii*, and *E. primigenius* (i.e., "directer Verwandtschaft").

In 1886, p. 181, Pohlig remarks: "Under the name of *Elephas trogontherii*, Pohlig, I have described European molars which hold a middle place, both zoologically and geologically, between those of *E. primigenius* and *E. meridionalis*, most closely approaching those of *E. antiquus* in the ridge-formula, but differing more from them than from the other two in the form of the crown. The position of *E. trogontherii* with regard to *E. armeniacus*, Falc., and *E. namadicus*, Falc., still remains to be investigated."

France: Depéret, 1923.—In 1923, Depéret and Mayet in their invaluable review of "Les Éléphants Pliocènes," Deuxième Partie, out of respect for Pohlig's clear distinction and definition of the species *E. trogontherii*, decided not to adopt the term *Elephas intermedius* of Jourdan, but to name this phylum "Rameau de l'*Elephas trogontherii*." They recognized its remote kinship to *Elephas primigenius* (see "III Groupe des *Elephas trogontherii* et *E. primigenius* (Mammouths)") but established it (p. 176) as a distinct branch of the "groupe des Mammouths." Osborn believes this to be its true phyletic position, resting on two chief characters, namely: (a) The *intermediate* character of the grinding teeth, observed by Jourdan, by Gaudry, by Pohlig, and by Depéret and Mayet; (b) the dome-shaped cranium, figured and observed by Pohlig and by Depéret and Mayet.

In their analytical treatment of the geologic succession of species, Depéret and Mayet clearly pointed out that the type locality (*3d Interglacial* plateau loess near Lyons) of *Elephas intermedius* Jourd. is of more recent geologic age than the type locality (*2d Interglacial* sands) of *Elephas trogontherii* Pohl.; moreover in seeking a Pliocene ancestor of this phylum, they believe they have discovered it in the Upper Pliocene subspecies of Italy, named by Zuffardi in 1913 *Elephas antiquus* var. *trogontherioides*. They thereby confirmed Falconer's observation of 1868 that an elephant closely similar to *E. armeniacus* occurred in northern Italy (see *Parelephas armeniacus* description, p. 1060 below).

Consequently the actual geologic succession of the three types of *Parelephas* thus far discovered in France and Italy is as follows:

Pleistocene (*3d Interglacial* plateau loess), Lyons, France	*Elephas intermedius* Jourdan, type
Pleistocene (*2d Interglacial* sands), Süssenborn near Weimar, Germany	*Elephas trogontherii* Pohlig, type
Upper Pliocene (Villafranchian), Italy [see footnote, p. 1049 below.—Ed.]	*Elephas antiquus* var. *trogontherioides* Zuffardi, type

America: Osborn, 1922.—Among the abundant remains of members of this phylum in America, a precisely similar confusion between specimens belonging to *Archidiskodon*, *Parelephas*, and *Mammonteus* arose in the minds of American palæontologists (Cope, Osborn, and Hay). Cope (1889.2, pp. 208, 209) referred the remains of a very fine skull of *Archidiskodon* (Fig. 891) from Texas to "*Elephas primigenius columbi* Falc." Osborn also saw only resemblances to "*Elephas columbi*" in the fine skeleton found in Indiana (type of *Parelephas jeffersonii* Osborn, Figs. 961, 931); whereas Hay (1914) referred the same skeleton to *Elephas primigenius*. No stronger proof could be given of the truly *intermediate* character of members of this phylum in America than this alternate reference of the same skeleton by Osborn to *Elephas columbi* and by Hay to *Elephas primigenius*. In Hay's exhaustive summary (1914) of grinding teeth and other remains from various parts of the United States (Alaska to Florida) which he referred to "*Elephas columbi*," he includes teeth which certainly belong to *Parelephas columbi* as well as to the truly intermediate form (*P. jeffersonii*).

Osborn (1922.555) was the first to separate these intermediate animals, previously described by Cope, Hay, and himself as "*E. columbi*" and "*E. primigenius*," under the new specific name of *Elephas jeffersonii*, a species which he subsequently (1924.633, p.4) made the genotype of *Parelephas*. This separation was based principally upon cranial characters (Osborn, 1922.555, p. 15): "Still more obvious are the differences between the relatively long, broad, and shallow crania of *E. jeffersonii* and the relatively short, narrow, and deep crania of *E. primigenius*, proportions which are correlated respectively with the corresponding proportions just described and figured in the teeth."

Phylogenetic Relationships (Pohlig, Soergel).—Inasmuch as the same species of animal had previously been erroneously described by Cope and Osborn under the name of "*Elephas columbi*," we must credit Soergel (1921, p. 60) with the prior observation that this supposed "*Elephas columbi*" of America (=*Elephas* [*Parelephas*] *jeffersonii* Osborn) shows phyletic relationships to the *Elephas* [=*Parelephas*] *trogontherii* of Pohlig.

Schmidtgen and Freudenberg (1926, pp. 62, 68) describe and discuss *Elephas* [*Parelephas*] *trogontherii* of Mosbach, especially the supposed phylum ("Stammreihe") *Elephas meridionalis—E. trogontherii—E. primigenius,* which in unbroken succession lived in the region of Wiesbaden.

Osborn, 1924–1928: It has remained, however, for Osborn in the present Memoir to institute a close comparison between all the known characters of the *Elephas trogontherii* phylum of Europe and the *Elephas jeffersonii* of America and to establish the fact that there is a close phyletic relationship which justifies the linking of the European and American species in the new and distinct genus *Parelephas.* This affinity is most clearly indicated in the cranium, as shown in the resemblance of several crania, erroneously figured as "*Elephas primigenius*" by Falconer, to those of *E. trogontherii* as figured by Pohlig, and to the cranium of *E. jeffersonii* as figured in the present Memoir; there can be no doubt that this relatively broad, elongate, and rounded cranium is entirely distinct from the extremely short, compressed, and peaked cranium of the true mammoth *Elephas primigenius.*

Habitat of Parelephas trogontherii (Soergel, 1912).—In his masterly monograph of 1912, entitled "Elephas trogontherii Pohl. und Elephas antiquus Falc.," Soergel observes (pp. 105, 106) that the Steppe [plains] and Wald [forest] faunas lived contemporaneously in central Europe; as observed in the *1st Interglacial* period, they are found in the lower sands of Mosbach, the "kiese" [gravels] of Mauer, the sands of Petersdorf bei Gleiwitz in Schlesien, the "Tone" [clays] and "grauen Rheinsande" [gray sands of the Rhine] near Jockgrim in Pfalz, and the gravels of Süssenborn (which persist into II Glacial time).[1] He divides the plains or "Steppe" and forest or "Wald" faunas of the *1st Interglacial* period as follows:

Chiefly Inland Steppes or Plains	Chiefly Ocean Borders and Forests
E. [*Parelephas*] *trogontherii* Pohl.	*E.* [*Hesperoloxodon*] *antiquus* Falc.
Very abundant in Mosbach; absent in Mauer.	Very abundant in Mauer.
Dicerorhinus etruscus Falc.	*Dicerorhinus etruscus* Falc.
Equus stenonis Cocchi, *E. süssenbornensis* Wüst, *E. mosbachensis* v. Reich.	*Equus stenonis* Cocchi, *E. mosbachensis* v. Reich.
Leptobos etruscus Falc.	
Bison priscus Boj.	*Bison priscus* Boj.
Cervus elaphus Linn., *C. elaphus trogontherii* Pohl., *C. capreolus* Linn., *Alces latifrons* Johns.	*Cervus elaphus antiqui* Pohl., *C. capreolus* Linn., *Alces latifrons* Johns.
Ursus arvernensis Croiz. and Job., *U. Deningeri* v. Reich.	*Ursus arvernensis* Croiz. and Job., *U. Deningeri* v. Reich.
Felis leo fossilis Goldf.	*Felis leo fossilis* Goldf.
Hyæna arvernensis Croiz. and Job.	
Canis neschersensis Croiz. and Job.	*Canis neschersensis* Croiz. and Job.
	[*Homo heidelbergensis* Schoet. (lower sands of Mauer)].

Certainly *Hesperoloxodon antiquus,* a forest loving form with coarser teeth, occurred nearer the ocean borders, whereas *Parelephas trogontherii,* with finer teeth, frequented both the steppes (plains) and forests. Since animals of both habitats are buried together in river sands, gravels, and clays, there is an intermingling of plains and forest faunas, as shown in Mosbach and Mauer (Osborn).

Of the habitat and geographic distribution, Soergel (*op. cit.,* p. 110) observes that whereas *Hesperoloxodon antiquus* preferred a warmer ocean bordering climate, not under the direct influence of the northern inland ice masses, *Parelephas trogontherii* sought the cooler northern-northeastern continental localities. Accordingly in Italy, Spain, and Greece it is almost entirely wanting; in France *P. trogontherii* is less abundant than *H. antiquus,* at least, it appears in less characteristic forms. The homeland of the *P. trogontherii* type appears to be confined to England and Germany, perhaps also to Russia. During the arid *1st Interglacial* peroid we find *P. trogontherii* distributed from southern England over middle Germany and eastward to southern Russia, as shown in the Forest Bed of Cromer, the sands of Mosbach, the gravels of Süssenborn, the sands of Petersdorf in Schlesien, and the clays of Jockgrim in Pfalz. Already in this *1st Interglacial* period migration towards the east may have begun.

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[1] [See p. 1056 below, where *Parelephas trogontherii* type is placed by Professor Osborn in the *2d Interglacial.*—Editor.]

In the *2nd Interglacial* period we observe practically the same geographic distribution of *Parelephas trogontherii*; its southernmost appearance in Germany at this time is at Steinheim on the river Murr; its northernmost appearance is at Rixdorf near Berlin. In Thuringia it is found in the Ilm gravels below the older travertines of Taubach, also in the stream gravels at Vieselbach near Erfurt, etc.

For the better understanding of the geologic as well as the geographic distribution of the *Parelephas trogontherii* phylum in Germany may be cited the following geologic correlation by Soergel (*op. cit.*, p. 106):

Dem I. 'Interglazial' gehören an:	Dem II. 'Interglazial' gehören an:	Dem III. Interglazial gehören an:
die Sande von Mosbach [n. Baden], die Kiese von Mauer [b. Heidelberg], die Sande von Petersdorf b. Gleiwitz in Schlesien, die Tone und grauen Rheinsande b. Jockgrim i. d. Pfalz, die Kiese von Süssenborn [bei Weimar], die allerdings bis in die II. Eiszeit hineingehen.	die Bachkiese bei Vieselbach, die Saalekiese von Uichteritz b. Weissenfels, die Ilmkiese unter dem älteren Travertin von Taubach-Ehringsdorf [b. Weimar], die Schotter von Steinheim (II. Glazial-Interglazial). . . . die Sande von Rixdorf b. Berlin für eine Ablagerung des II. 'Interglazial.'	der Travertin von Taubach-Ehringsdorf-Weimar, der Travertin von Burg-Graefentonna, der Travertin von Bilzingsleben und verschiedene andere Travertinvorkommen Thüringens.
[Plains ("Steppe") and forest ("Wald") faunas, as listed above.] The Süssenborn deposits extend into II GLACIAL time (*fide* Soergel, 1912.)	[Plains and forest faunas not clearly separated; *Parelephas trogontherii* and *Hesperoloxodon antiquus* occur in the same horizon.]	[Plains and forest faunas again appear partly separated, as in Mauer and Mosbach. *Hesperoloxodon antiquus* survives *Parelephas trogontherii*, which disappears. In the tundra fauna appears *Mammonteus primigenius.*]

COMPLETE SEPARATION BY OSBORN OF THE GENERIC PHYLUM PARELEPHAS

Osborn finally (1924.633, p. 2) concluded to cut the Gordian knot and terminate this confusion by distinguishing the generic phylum *Parelephas* throughout from both *Mammonteus* and *Archidiskodon*, as shown in the following citation:

> [p. 2] Much more difficult has been the separation of the third generic series of the Mammontinæ, which hitherto has been referred to the genus *Elephas* but which we now remove to the new generic phylum *Parelephas.*
>
> [p. 4] The eight or ten species included within this genus constitute a very ancient and wholly distinct generic phylum, for which the name *Parelephas* seems appropriate, because in certain characters these animals parallel the true *Elephas*, although in profound cranial and dental structure they are closely related to and convergent with the mammoths *Archidiskodon* and *Mammonteus.*
>
> GENERIC CHARACTERS.—A phylum of the Mammontinæ. *Elephas jeffersonii*, genotypic species, *E. armeniacus*, *E. intermedius*, *E. trogontherii*, *E. trogontherioides.* Cranium intermediate in form between that of *Archidiskodon* and that of *Mammonteus*, namely, brachycephalic, acrocephalic. Frontals concave, occipital crest elevated; occiput more or less convex. Molars in the Upper Pliocene and Lower Pleistocene stages with relatively few ridge-plates, i.e., M 3 $\frac{15+}{16+}$; progressive Upper Pleistocene stages with multiple ridge-plates, i.e., M 3 $\frac{30}{26}$. Ridge-plates compressed to 7–8–9 in 100 mm. Molar crowns broad, M^3 short, with enamel of intermediate thickness, more or less crimped or sinuous.
>
> The progressive ridge formulæ in *Parelephas* are distinct throughout from those of *Mammonteus*, and the final ridge formulæ in the two generic phyla are different, namely:
>
> *Mammonteus primigenius compressus*, M 3 $\frac{27}{27}$ = final stage.
> *Parelephas jeffersonii progressus*, M 3 $\frac{30}{26}$ = final stage.
>
> The crania of *Parelephas* throughout are readily distinguishable both in frontal and lateral aspects, and especially in vertical section, from those of *Mammonteus*, as can be seen in all of Falconer's beautiful plates of *E. primigenius* and in Pohlig's excellent figures of *P. trogontherii.*
>
> The jaws of *Parelephas* and of *Mammonteus* are less readily distinguishable, but by more profound study they can also be separated from those of *Mammonteus*. The contrasts in the crania of the two genera may be summed up as follows:
>
> *Mammonteus.*—Cranium and jaws extremely compressed fore-and-aft (cyrtocephalic); extremely elevated and pointed above (hypsicephalic); extremely depressed and foreshortened below (bathycephalic).
>
> *Parelephas.*—Cranium moderately compressed fore-and-aft (cyrtocephalic); moderately elevated occipitofrontal borders (acrocephalic); moderately depressed molar-grinding area (bathycephalic).
>
> Thus, while the intermediate forms of crania and teeth of *Parelephas* and of *Mammonteus* may prove difficult to separate, the two finally progressive forms are readily separable, namely, *Parelephas jeffersonii progressus* and *Mammonteus primigenius compressus.*

To this phylum certainly belongs the *Elephas armeniacus* of northern Asia Minor, as first observed by Falconer, as well as many specimens to the eastward described under other names. The connection of this phylum with the *Parelephas jeffersonii* of late Glacial times in the United States seems highly probable; the resemblance both of the teeth and cranium has been repeatedly observed between *E. trogontherii* and the northerly type formerly known as "*Elephas columbi*," now known as *Parelephas jeffersonii.*

The southerly type (Georgia, South Carolina, Florida) of *Elephas* [=*Parelephas*] *columbi*, with rather primitive ridge formula (M 3 $\frac{19}{16+}$), has recently been reinforced by the large and more progressive *Parelephas floridanus* (M 3 $\frac{22+}{21+}$), apparently a late Pleistocene stage distinguished by its larger size, more robust tusks, and coarser ridge-plates from the northerly (Indiana) *Parelephas jeffersonii* type.

A branch of the *Parelephas columbi* stage appears to have migrated to South America, as mentioned by Lull 1908, p. 204) and Freudenberg (1922, p. 159) on the authority of Lartet (1859, pp. 500, 505).

> Lartet, 1859, pp. 500[1] and 505.—L'existence des Éléphants n'est encore indiquée dans l'Amérique méridionale que par un fragment de molaire à lames épaisses, rapporté de Cayenne par le capitaine Perret et donné par lui au Musée de Marseille. . . . Dans l'Amérique du Sud, deux formes spécifiques du genre Mastodonte se montrent dans des dépôts *post-pliocènes*; mais peut-être se sont-elles aussi retrouvées dans des formations plus anciennes et rapportables à l'âge précédent ou pliocène. Quant au type Éléphant, il n'y est encore indiqué que par le seul fragment déjà cité d'une molaire à lames épaisses, rapporté de Cayenne par le capitaine Perret.
>
> Freudenberg, 1922, pp. 159, 160.—Wir haben Lartets Autorität für den Fund eines Zahnes von *Elephas* im unteren Pleistocän von Cayenne (Französisch-Guayana). Nach der Beschreibung der dickrückigen Schmelzplatten ist das Exemplar offenbar von *El. imperator*. Wahrscheinlich vollzog sich eine Wanderung nach dem Süden, bevor die Bedingungen geschaffen waren, welche später die Wanderung der Proboscidier nach Südamerika ermöglichten. . . . Es ist das einzige mir bekannt gewordene Beispiel eines wahren Elefanten im Süden des Hochlands von Mexiko.

Osborn, 1929: Through the extreme courtesy of Mm. Laurent and Repelin of the Faculté des Sciences de Marseille, this priceless molar fragment from French Guiana has been located in the Muséum d' Histoire Naturelle de Marseille, photographs taken, and casts made, especially for the purpose of specific and generic identification for the present Memoir. As shown in figure 957, on a one-half scale, this specimen consists of three ridge-plates of coarse enamel, as described by Lartet, remotely resembling in crown and side views the posterior ridge-plates of a superior grinding tooth of *Parelephas columbi* (Fig. 952). In 1929 the present writer (Osborn, 1929.797, p. 20) made this the type of a new subspecies, namely, *Parelephas columbi cayennensis.*

The recently discovered *Parelephas floridanus* includes parts of three full skeletons collected by the Holmes Florida Expedition of the year 1929. In this stage, intermediate in ridge-plate formula (M 3 $\frac{22+}{21+}$) between *Elephas* [*Parelephas*] *columbi* (M 3 $\frac{19}{16+}$) and *P. jeffersonii* (M 3 $\frac{25}{24}$), the ridge-plates are broad at the base and compressed at the summit; the incisive tusks extremely massive and relatively short. The males attain very large size. The femora measure, according to age, 1230 mm. to 1393 mm., as compared with 1250 mm. in the adult Indiana type of *P. jeffersonii.*

Summary of Migration

The restudy of long-known specimens like *Elephas jacksoni* (1838), *Elephas columbi* (1857), *Elephas armeniacus* (1857), and *Elephas intermedius* (1861), together with the recent recognition of *Parelephas columbi cayennensis* in French Guiana, builds up a *Parelephas* phylogeny and migration second only to that of *Archidiskodon* (Chapter XVI). We await the discovery (probably in northern Africa) of an ancestral stage more primitive than *Parelephas trogontherioides* of the Upper Pliocene[2] of Italy.

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[1] Dr. Richard S. Lull (letter, Sept. 24, 1928) writes: "From this description, mentioning the fragment of a molar with 'thick plates,' I drew my own conclusion as to the genus and species of that elephant. It seemed to me that that it would be *Elephas* [=*Archidiskodon*] *imperator*."

[2] [See footnote 1 on page 1049 below.—Editor.]

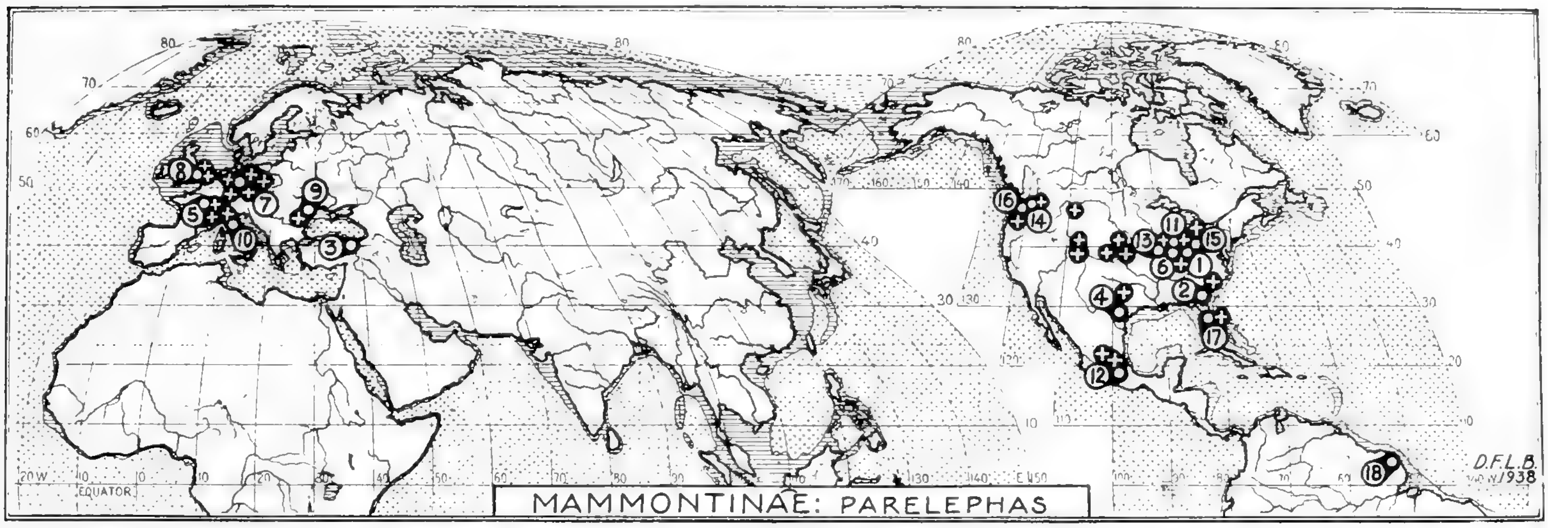

Fig. 933. Geographic distribution (according to the numbers in the accompanying list) of species of *Parelephas.* The white dots within the black areas represent the approximate localities where the types of these species were discovered. The white crosses represent referred specimens. It will be noted that Professor Osborn regarded *Elephas texianus* Owen, Blake (1859–1861) as a synonym of *Parelephas columbi,* and *Elephas roosevelti* Hay (1922) as a synonym of *Parelephas jeffersonii.*

ORDER OF DISCOVERY AND DESCRIPTION OF SPECIES OF PARELEPHAS

See Figure 933

		Original Name	Specific Reference in Present Memoir
1838	1. Jackson County, Ohio	*Elephas jacksoni* Mather	= *Parelephas jacksoni*
1857–1868	2. Brunswick Canal, Georgia	*E.* (*Euelephas*) *Columbi* Falconer	= *Parelephas columbi*
1857	3. Armenia, Asia Minor	*Elephas armeniacus* Falconer	= *Parelephas armeniacus*
1859–1861	4. San Felipe de Austen on Brazos River, Texas	*Elephas texianus* Owen, 1859, Blake, 1861	= *Parelephas columbi*
1861	5. France, *3d Interglacial* loess	*Elephas intermedius* Jourdan	= *Parelephas intermedius*
1872	6. Indiana	*Elephas Indianapolis* Foster. Later in same year changed to *Elephas mississippiensis*—see below	= *Nomen nudum*
1872	6. Indiana	*Elephas mississippiensis* Foster	= Indeterminate, possibly *Parelephas*(?) *mississippiensis*(?)
1885	7. Süssenborn near Weimar, Germany, *2d Interglacial* sands	*Elephas trogontherii* Pohlig	= *Parelephas trogontherii*
1891	8. Cromer Forest Bed, East Anglia, England	*Elephas* (*antiquus*) *Nestii* Pohlig	= *Parelephas*(?) *trogontherii nestii*
1910	9. Tiraspol, southern Russia	*Elephas Wüsti* Pavlow	= *Parelephas wüsti*
1913	10. Piedmont (Villafranchian), Italy	*Elephas antiquus* var. *trogontherioides* Zuffardi	= *Parelephas trogontherioides*
1922	11. Jonesboro, Grant Co., Indiana	*Elephas jeffersonii* Osborn	= *Parelephas jeffersonii*
1922	12. Mexico, Tecamachalco, Puebla	*El. Columbi* var. *Felicis* Freudenberg	= *Parelephas columbi felicis*
1922	13. Ashland, Cass Co., Illinois	*Elephas roosevelti* Hay	= *Parelephas jeffersonii*
1923	14. Pine Creek, Whitman Co., Washington	*Elephas washingtonii* Osborn	= *Parelephas washingtonii*
1924	15. Zanesville, Ohio	*Parelephas jeffersonii progressus* Osborn	= *Parelephas progressus*
[1924	Province of Kazusa, Japan	*Euelephas* (*Parelephas*) *protomammonteus* Matsumoto	= *Palæoloxodon protomammonteus*—see Chap. XIX]
[1926	Province of Kazusa, Japan	*Parelephas protomammonteus proximus* Matsumoto	= *Palæoloxodon protomammonteus proximus*—see Chap. XIX]
1926	16. Port Williams, Clallam Co., Washington	*Elephas eellsi* Hay	= *Parelephas*(?) *eellsi*
1929	17. Florida, near Bradenton, Manatee County	*Parelephas floridanus* Osborn	= *Parelephas floridanus*
1929	18. Cayenne, French Guiana, South America	*Parelephas columbi cayennensis* Osborn	= *Parelephas columbi cayennensis*

SUPERFAMILY: ELEPHANTOIDEA Osborn, 1921

FAMILY: ELEPHANTIDÆ Gray, 1821

SUBFAMILY: MAMMONTINÆ Osborn, 1921

GENUS: **PARELEPHAS** Osborn, 1924

Original reference: Osborn, Amer. Mus. Novitates, No. 152, pp. 4 and 5 (Osborn, 1924.633).

GENERIC CHARACTERS (CF. OSBORN, 1924.633, p. 4).—Genotypic species, *Elephas jeffersonii* Osborn, of Indiana; species referred to this genus, *Elephas armeniacus, E. intermedius, E. trogontherii*, and *E. trogontherioides*. Cranium intermediate in form between that of *Archidiskodon* and that of *Mammonteus*, namely, bathycephalic, acrocephalic. Frontals concave, occipital crest elevated; occiput more or less convex. Molars in the Upper Pliocene to Middle Pleistocene stages with relatively few ridge-plates, i.e., M 3 $\frac{14+}{14+}$; progressive Upper Pleistocene stages (*P. progressus*) with multiple ridge-plates, i.e., M 3 $\frac{30}{26}$. Ridge-plates compressed to 6-6.5-7-8-9 in 100 mm. Molar crowns broad, M^3 short, with enamel of intermediate thickness, more or less crimped or sinuous. Adapted to continental plains or steppe environment, grazing and browsing.

APPROXIMATE PHYLOGENETIC ORDER OF SUCCESSION OF PARELEPHAS

			RIDGE FORMULA	LENGTH	BREADTH	HEIGHT
Upper Pleistocene	Ohio	*Parelephas progressus* Osborn	Type: M 3 $\frac{30}{26}$	205 221	109 97	203 161
Pleistocene	Ohio	*Parelephas jacksoni* Mather (Imperfectly known)	Type: M 3 M 2 $\frac{}{16}$			
Upper Pleistocene	Indiana	*Parelephas jeffersonii* Osborn	Type: M 3 $\frac{+17}{+20}$	203+ 208	108 86	. . . 168
Pleistocene	Illinois	*Elephas roosevelti* Hay = syn. *Parelephas jeffersonii*	Type: M 3 $\frac{25}{24}$	282 304e	98 92	202 154
Upper(?) Pleistocene	French Guiana So. America	*Parelephas columbi cayennensis* Osborn	Type: M 3 superior—fragmentary			
Upper(?) Pleistocene	Florida	*Parelephas floridanus* Osborn	Type: M 3 $\frac{22+}{21+}$	320 290	88 79	235 180
Upper(?) Pleistocene	Georgia	*Parelephas columbi* Falconer	Ref.: M 3 Type: M 3 $\frac{18\text{-}19}{15\text{-}16+}$	249 241e	96 82e	207 152e
Pleistocene	Washington	*Parelephas washingtonii* Osborn	Ref.: M 3 Type: M 3 $\frac{23}{21}$	348	88	. . .
THEORETIC PERIOD OF MIGRATION TO NORTH AMERICA						
Pleistocene *3d Interglacial*	France	*Parelephas intermedius* Jourdan	Ref.?: M 3 $\frac{20\text{-}22}{20\text{-}21}$	270	92	150
Upper Pleistocene	S. Russia	*Parelephas wüsti* Pavlow	Cotypes: M 3 $\frac{22}{20}$	340e	100e	198
Pleistocene	Asia Minor	*Parelephas armeniacus* Falconer	Type: M 3 $\frac{+17\frac{1}{2}}{}$	299	105	181
Middle Pleistocene *2d Interglacial* [Abundant, attaining greatest size (Mosbach)]	Germany (Süssenborn)	*Parelephas trogontherii* Pohlig	Type: M 3 $\frac{15+}{16+}$	225 270+	101 75	138 100
Lower Pleistocene *1st Interglacial*	Germany (Basal Mosbach)	*Parelephas trogontherii* ("kleinere Var.") Freudenberg	Ref.: M 3 Not available			
Lower Pleistocene *1st Interglacial*	England Forest Bed (Cromer)	*Parelephas*(?) *trogontherii nestii*	Cotypes: M 3 $\frac{18}{14+}$	302 243+	80 83	167 103
Upper Pliocene Villafranchian[1] (type) English Crag (ref.)	Italy	*Parelephas trogontherioides* Zuffardi	Lectotype: Cotype: M 3 $\frac{\frac{1}{2}\text{-}14\text{-}\frac{1}{2}}{\frac{1}{2}\text{-}14\text{-}\frac{1}{2}}$	210+ 340	110 148	150 188

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[1] [See footnote 1 on opposite page.—Editor.]

Only an approximate phylogenetic order of succession may be given at the present time. In this phylogenetic list we include with some doubt the imperfectly known *Elephas jacksoni* Mather, also the recently described *Elephas washingtonii* Osborn. In phylogenetic order it would seem that this *Parelephas* phylum first appears in *Elephas trogontherioides* of the Upper Pliocene (Villafranchian)[1] of Italy. Doubtless there were many intermediate forms or ascending mutations between this Pliocene stage and the Mid-Pleistocene *Elephas trogontherii* of Pohlig at the close of the *2d Interglacial* period when this animal was quite abundant. The type of *E. trogontherii* of Germany is in fact in about the same stage of evolution of the third upper molar as the type molar of the *E. armeniacus* of Asia Minor.

The phylum is next represented in the *3rd Interglacial* in the plateau loess of southern France in the form of *Elephas intermedius* of Jourdan. Depéret and Mayet consider the type of *Elephas intermedius* as more progressive than the type of *E. trogontherii*. Pohlig also states that a form related to *E. trogontherii* survived into *3rd Interglacial* times in Germany and was then replaced by *Elephas primigenius*; whereas Depéret and Mayet consider that the *Elephas trogontherii-intermedius* phylum of Europe became extinct before *3d Interglacial* time. This *3d Interglacial* period may possibly mark (Fig. 795) its time of migration across Asia into North America.[2]

PRIORITY OF DEPÉRET IN SEPARATING THE E. TROGONTHERII PHYLUM.—To Charles Depéret and his colleague Lucien Mayet belongs the credit of clearly distinguishing the origin and geographic distribution of the "Rameau de l'*Elephas trogontherii*," to which phylum Osborn has assigned the generic name *Parelephas*. Depéret and Mayet (1923, pp. 176–183) first distinguished the "A. Rameau de l'*Elephas trogontherii* Pohlig" from "B. Rameau de l'*E. primigenius* Blumenbach," both of which they included within the "Groupe des *Elephas trogontherii* et *E. primigenius* (Mammouths)." They credit Jourdan with the recognition of *E. intermedius* as distinguishable from *E. primigenius*, followed by Gaudry (1876) and by Leith Adams (1877) who traced this form back to the Forest Bed of England, then by Pohlig (1889 [1888]) who described *E. trogontherii* of Süssenborn near Weimar, but which Depéret and Mayet remark is absolutely identical with the *E. intermedius* of Jourdan. Finally they trace the "Rameau de l'*Elephas trogontherii*" down into the Pliocène supérieur (Villafranchian of Italy), confirming a note by Pohlig (1889 [1888], p. 208) as to the tooth subsequently made by Zuffardi (1913, p. 174, Tav. XII [VI], figs. *3a*, *3b*) the type of *Elephas primigenius* var. *trogontherii*. Depéret and Mayet observe (p. 177) that the molars of this *E. trogontherii* var. are readily distinguished from those of the contemporary *E.* [*Archidiskodon*] *meridionalis* Nesti and *E.* [*Hesperoloxodon*] *ausonius* Major-Depéret. Zuffardi also described and figured another molar under the name of *Elephas antiquus* var. *trogontherioides* (Zuffardi, Tav. IX [III], fig. 6), and two other molars of the *E. trogontherii* form (Pl. IX [III], figs. 4 and *5a*, *5b*). They state (p. 179) that these four molars of *E. trogontherii* described from the "Villafranchien de l'Astésan" are the only ones thus far observed in Italian Museums, although there are probably others, and that they are clearly distinguishable from '*E. meridionalis*' and '*E. antiquus*,' concluding (p. 180) as follows:

> On peut donc dire seulement que la forme pliocène de l'*E. trogontherii* possède des molaires de dimensions plutôt un peu réduites, sans qu'il puisse être question d'une véritable *mutation de petite taille* de l'espèce. On doit s'attendre à découvrir un jour dans le Pliocène ancien de quelque région éloignée les types ancestraux nains du rameau de l'*E. trogontherii*.

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[1] [There is a tendency among many geologists (see Chap. XXII of this Memoir by Dr. Edwin H. Colbert, where the views of Haug, Hopwood, Pinkley, et al are cited) to regard the Villafranchian as of Lowest Pleistocene (or Quaternary) rather than of Upper Pliocene age. Apparently one of the most reliable factors in the determination of the boundaries between the Pliocene and the Pleistocene, aside from the geological evidence, is a change in fauna, for example, the presence of *Bos* (including *Bison*), *Elephas*, or *Equus*, would indicate the Pleistocene age of the deposit in which they were found. Compare also Haug, 1911.1, pp. 1761 and 1767, Hopwood, 1935.2, pp. 46 and 47.—Editor.]

[2] [See page 1071 below where Professor Osborn expresses the opinion that migration to America may have taken place during *2d Interglacial*, and possibly as early as *1st Interglacial* time.—Editor.]

They also recognize (p. 180) the "Rameau de l'*Elephas trogontherii*" in the Lower Pleistocene Forest Bed of Cromer, but find no trace of it in the Pliocène supérieur Crags of England.

From the Forest Bed they trace (p. 181) the phylum *E. trogontherii*, with gradual increase in size, through the terraces of 30 meters (Chellean or Tyrrhenian stage) in the valley of the Thames, also at Gray's and at Ilford where Lydekker (1886.2, pp. 127, 134) mistook *E. trogontherii* for *E. antiquus*.

In Germany observations fail to indicate the Pliocene age of *E. trogontherii*, but this species appears in a *1st Interglacial* stage corresponding to the Forest Bed (Sicilien, Lower Pleistocene), also according to Wüst (1901, p. 61) in the ancient gravels of the Ilm at Süssenborn near Weimar, where it was very abundant. This level they regard as contemporaneous with the *1st Interglacial* sands of Mosbach near Wiesbaden and of Mauer near Heidelberg (Chellean). They also state (p. 182) that Pohlig records *E. trogontherii* from Süssenborn, Heinthurm and Denstedt, near Weimar; Brucksdorf near Halle; Sulza, Angelhausen, near Armstadt; Apolda, Mosbach, near Wiesbaden; the lower gravels of Taubach, and of Rixdorf near Berlin; the gravels of the terrace of 30 meters at Mauer near Heidelberg, and the travertines of Taubach and of Weimar. It became extinct, without extending higher, in the Quaternary.

Osborn, 1929: Observe the constantly ascending ridge formula in M 3 $\frac{14+}{14+}$ (in the Upper Pliocene) to M 3 $\frac{30}{26}$ (in the Upper Pleistocene), a period of perhaps 1,250,000 years. Observe also that during *3d Interglacial* times *Parelephas* disappears in western Europe and in early Pleistocene times it appears in North America.

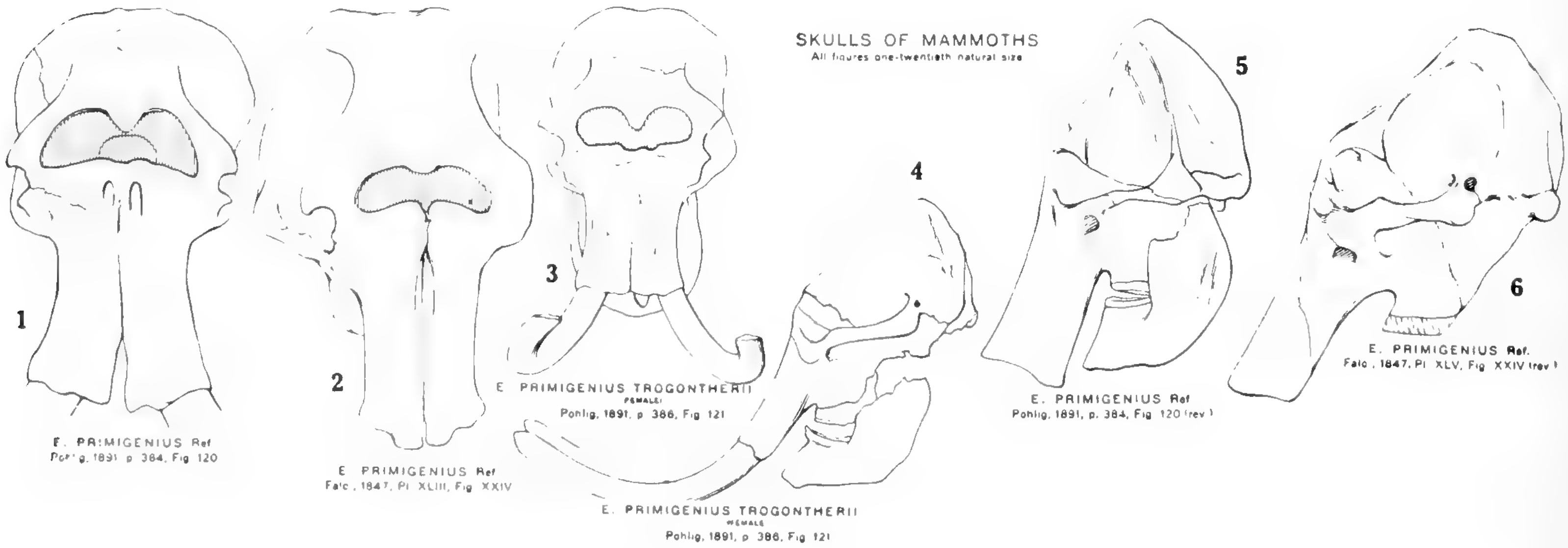


Fig. 934. Cranial Profiles of Mammonteus primigenius (1,2,5) and Parelephas trogontherii (3,4,6) of Europe

One-twentieth natural size. The plate lettering is incorrect (compare Fig. 865, upper row, and key, p. 977)

3. *Parelephas trogontherii* (female); front view of cranium. After Pohlig, 1891.
4. *Parelephas trogontherii* (female); side view of same cranium. After Pohlig, 1891.
6. *Parelephas trogontherii*; adult male cranium in side view. After Falconer, 1847.
5. *Mammonteus primigenius;* adult cranium. After Pohlig, 1891.
1. *Mammonteus primigenius*; front view of cranium (after Pohlig, 1891), which resembles *Parelephas* in certain characters.
2. *Mammonteus primigenius*, front view of cranium (after Falconer, 1847), which appears to be typical of '*E. primigenius*.'

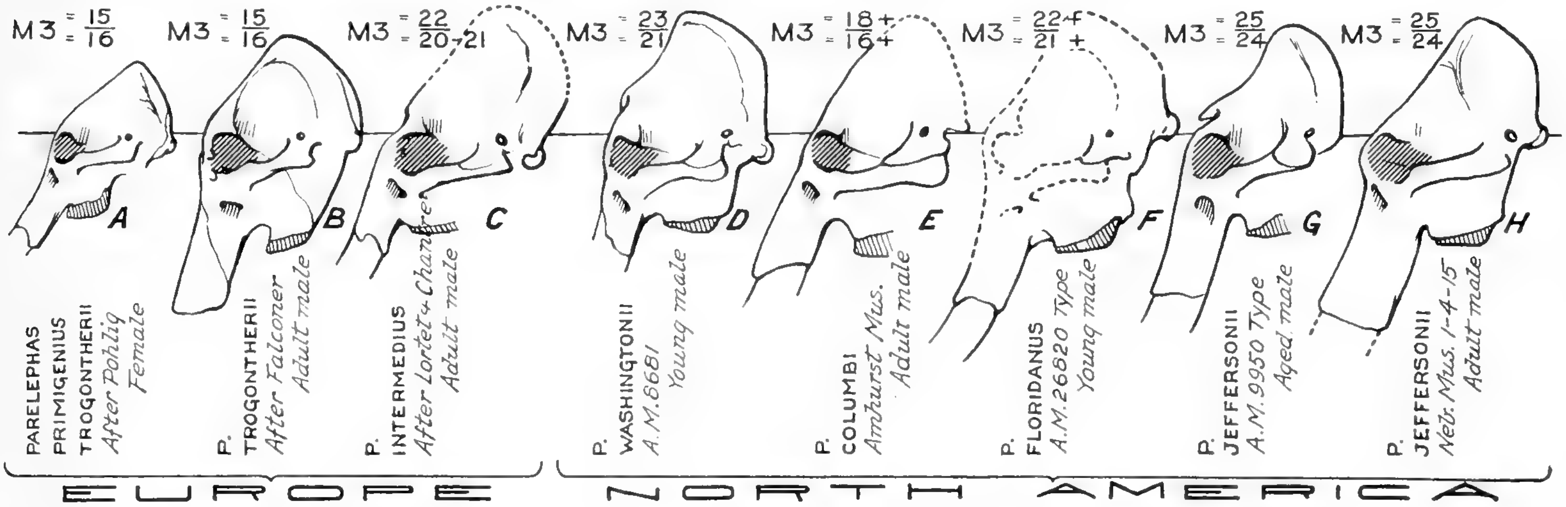
Observe that the *Parelephas trogontherii* cranium, both in the male (6) and in the female (3, 4), is relatively lower, broader, and less compressed fore and aft than the *Mammonteus primigenius* male (5); in other words, it is less hypsicephalic and less bathycephalic, with broader space between condyle and orbit. Compare especially (5) *M. primigenius* and (6) *P. trogontherii*, both males.

Distinctive Cranial Characters of Parelephas

Up to the time that Pohlig separated the grinding teeth of *Parelephas trogontherii* from the grinding teeth of *Mammonteus primigenius* the crania in these two distinct lines of generic descent were confused, as well as the grinding teeth, yet, as shown in figures 865, 934, 935, and 937, the crania of *Parelephas* are readily distinguishable from those of *Mammonteus*.

The principal characters by which we distinguish the *Parelephas* crania are the following: (1) In frontal aspect the crania of *Parelephas* are relatively broader, more spreading, and more brachycephalic than those of *Mammonteus*, which are deeper and more bathycephalic; (2) in lateral aspect (a) the orbit is more widely separated from the occipital condyle, (b) the occiput is much more convex, thus throwing the occipitoparietal apex farther forward, (c) the height from the occipital apex to the superior molar crowns is less deep, i.e., less bathycephalic, (d) the apex formed at the summit of the cranium is less acute, (e) the facial front is shorter and more deeply concave, (f) the maxillo-premaxillary sockets are less vertical and the tusks emerge in a less vertical plane; (3) in frontal aspect (a) the premaxillary sockets are more expanded at the extremities, whereas in *Mammonteus* they are more elongate and more closely compressed, (b) the transverse diameter of the frontals is relatively broader than in *Mammonteus*, (c) the anterior nares are proportionately broader transversely and less deepened vertically; (4) in brief, the proportions of the cranium of *Parelephas* throughout are harmonious with those of the grinding teeth, i.e., less compressed anteroposteriorly, less bathycephalic and less hypsicephalic than those of *Mammonteus*.

Profiles (Fig. 935) of juvenile, adult, and middle-aged crania of *Parelephas* reveal a contour which is readily distinguishable from that of the larger *Archidiskodon* cranium, on the one hand, and that of the smaller and much more compressed *Mammonteus* cranium, on the other; but it is not at all surprising that Falconer confused the *Parelephas* and *Mammonteus* crania, because they present so many points of subfamily (i.e., Mammontinæ)



Left Lateral Profiles of Seven Species of Parelephas with Progressive Ridge Formulæ

One-thirtieth natural size

Fig. 935. This series is remarkably uniform in its progressive characters:

1) M 3 $\frac{15}{16}$ to M 3 $\frac{25}{24}$; superior ridge-plates exceeding the inferior ridge-plates in number.

2) The orbits lie just below the level of the occipital condyles, with relatively wide separation.

3) The occipitofrontal profile is restored in *P. intermedius* (C), *P. columbi* (E), and *P. floridanus* (F), but is perfectly preserved in *P. trogontherii* (A, B), female and male of Mid-Pleistocene time, also in *P. washingtonii* (D), *P. jeffersonii* (G), aged type, and *P. jeffersonii* (H), giant male in the Nebraska Museum.

4) All the profiles present a concave forehead, a moderately elevated summit, and a rather angulate occipital contour.

5) As shown by comparison with figure 934, the hypsicephaly, acrocephaly, and bathycephaly of the cranium are much less acute than in *Mammonteus*.

resemblance. The relation (Figs. 806, 816) of the *basis cranii* to the fronto-occipital contours reveals a very profound difference between the fully adult *Parelephas jeffersonii* (Nat. Mus. 10261) and the adult *Elephas indicus* profile, on the one hand, and the *Loxodonta africana* profile, on the other. In all stages *Parelephas* agrees both with *Archidiskodon* and *Mammonteus* in the *concave* frontal plane or forehead.

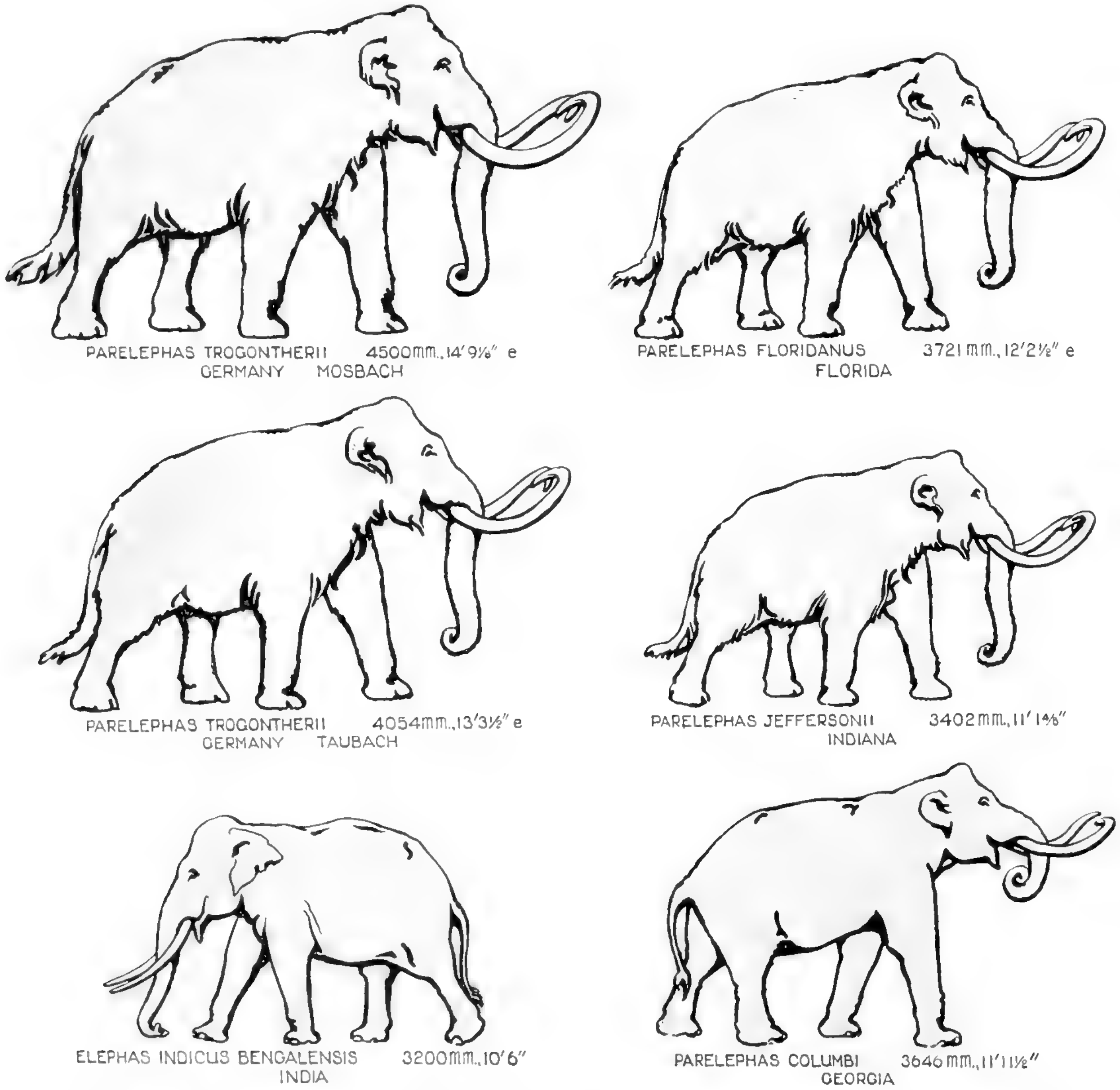


Fig. 936. Parelephas of Europe and America in comparison with Elephas indicus bengalensis
Restorations to a one-fiftieth scale by Margret Flinsch Buba, under the direction of Henry Fairfield Osborn.

The crania conform in size with the three skeletons more or less fully known, namely, of *Parelephas intermedius* of France (Fig. 944), said to attain a skeletal height of 3750 mm., or 12 ft. 3½ in., of *P. jeffersonii* in the American Museum (Fig. 966), with an estimated height of 3200 mm., or 10 ft. 6 in., of the giant *P. jeffersonii* of the Nebraska Museum (Neb. Mus. 1-4-15), the skeleton of which is unknown, and of *P. columbi* of the Amherst Museum (Fig. 955), with an estimated height of 3430 mm., or 11 ft. 3 in., finally of the giant *P. floridanus*, known from an associated humerus and femur in the American Museum to attain an estimated height of 3584 mm., or 11 ft. 9 in., probably influenced by the favorable climatic conditions of Florida in contrast to the more severe northern conditions which produced *P. jeffersonii.* For estimated height in the flesh, compare figure 936 on opposite page.

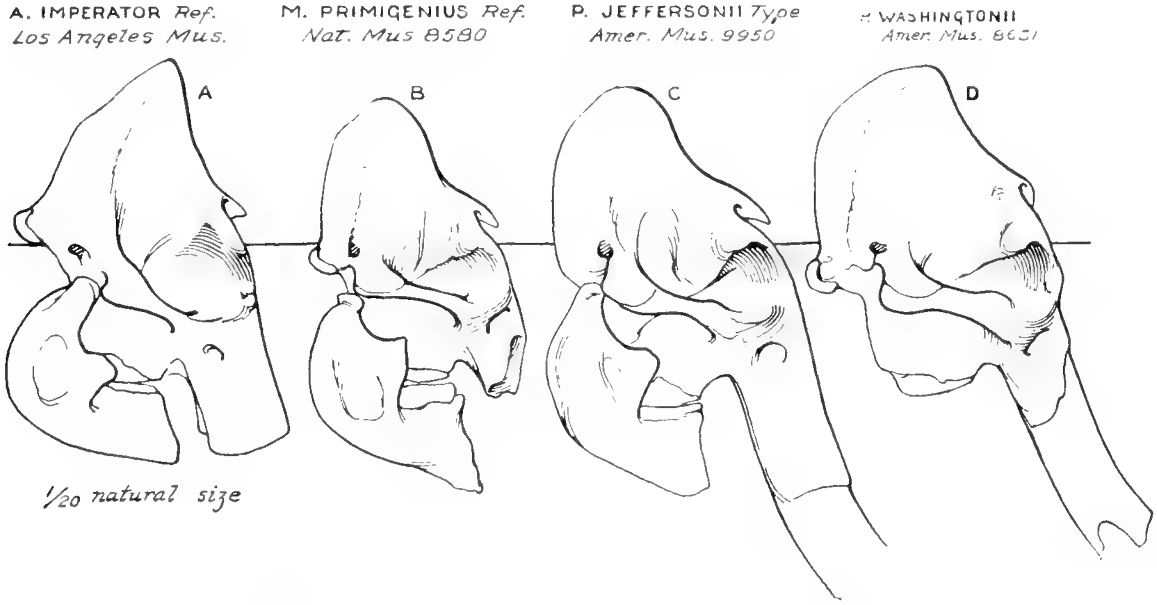


Fig. 937. Cranial Profiles of the Mammontinæ of America

One-twentieth natural size

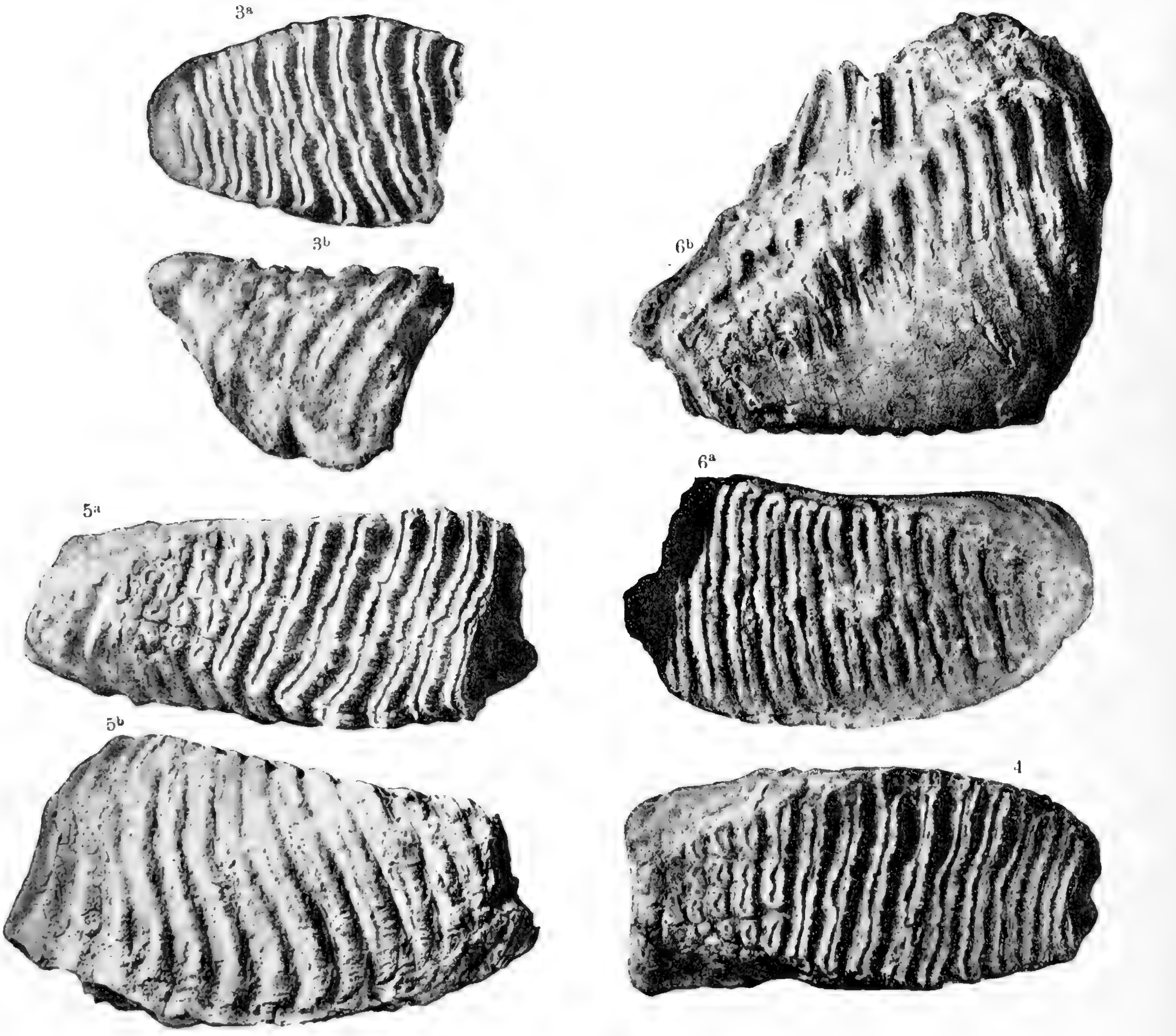
(A) *Archidiskodon imperator*, young male in the Los Angeles Museum.

(B) *Mammonteus primigenius*, adult male, dwarfed, in the U. S. National Museum.

(C) *Parelephas jeffersonii*, type aged male in the American Museum of Natural History.

(D) *Parelephas washingtonii*, referred young adult male in the American Museum of Natural History, the least progressive of the series.

Observe extreme progressive hypsicephaly, cyrtocephaly, and bathycephaly as we pass from right (D) to left (B, A); thereby the occipital crest is elevated, the grinders are depressed, the orbits are approximated to the condyles (B), the face is flattened or concave.



LECTOTYPE AND COTYPES OF PARELEPHAS TROGONTHERIOIDES

About two-fifths natural size

Fig. 938. Lectotype and cotypes of *Elephas antiquus* Falc. var. *trogontherioides* Zuffardi, 1913, Tav. IX (III), figs. 3*a*-6*b*, namely: Lectotype from Nizza della Paglia (Astésan), third left superior molar, l.M^3 (*6a, 6b*), with 14+ ridge-plates; cotypes from near San Paolo de Villafranca, third right inferior molar, r.M_3 (4), with +14+ ridge-plates, third left inferior molar, l.M_3 (*5a, 5b*), with ½14½ ridge-plates and talon, and second left inferior molar, l.M_2 (*3a, 3b*), with at least 10 ridge-plates. Compare Zuffardi, *op. cit.*, pp. 130, 155–158, also Depéret and Mayet, 1923, pp. 177–179. These figures are designated by the author as follows:

"[Fig.] 3*a*.—Molare probabilmente quinto inferiore sinistro (*G*),—pag. 155 [35].
" 3*b*.—Lo stesso visto dal fianco esterno.
" 4 .—Molare ultimo inferiore destro ('8'),—pag. 156 [36]. [Mus. Palais Carignan, Turin.]
" 5*a*.—Molare ultimo inferiore sinistro ('9'),—pag. 156 [36].
" 5*b*.—Lo stesso visto dal fianco interno.
6*a*.—Molare ultimo superiore sinistro ('5'),—pag. 158 [38]. [Geol. Mus. Turin.]
6*b*.—Lo stesso visto dal fianco esterno. [Geol. Mus. Turin.]"

2. SYSTEMATIC DESCRIPTION OF EUROPEAN AND ASIATIC SPECIES IN ASCENDING PROGRESSIVE ORDER

Parelephas trogontherioides Zuffardi, 1913

Figure 938

Type: Upper Pliocene (Villafranchian stage),[1] Piedmont, northern Italy, Nizza della Paglia and San Paolo de Villafranca (Astésan). Referred: Red and Norwich Crags of East Anglia.

Third superior and inferior molars, M^3, M_3, described as a mutation of small size of *Elephas trogontherii*; grinding teeth of reduced dimensions; ridge-plates of similar character to *E. trogontherii*; laminar frequence 6 to 6.5 in 10 cm.; total estimated ridge-plates in $M\ 3\ \frac{\frac{1}{2}\text{-}14\text{-}\frac{1}{2}}{}$ as preserved in the lectotype (Fig. 938, 6*a*, 6*b*), in the cotype $M\ 3\ \frac{}{\frac{2}{3}\text{-}14\text{-}\frac{1}{3}}$ (Fig. 938, 4), in the cotype $M\ 3\ \frac{}{\frac{1}{2}\text{-}14\text{-}\frac{1}{2}}$ (Fig. 938, 5*a*, 5*b*); estimated ridge-plate formula $M\ 3\ \frac{\frac{1}{2}\text{-}14\text{-}\frac{1}{2}}{\frac{1}{2}\text{-}14\text{-}\frac{1}{2}}$ somewhat inferior to that of *E. trogontherii*, as we should anticipate. We may depend upon the observations of Falconer, Pohlig, Zuffardi, and Depéret as to the resemblance of these cotypes to *E.* [=*Parelephas*] *trogontherii*, which, if corroborated by future discovery, make this the most primitive species.

As to size, Osborn observes that whereas the typical molars of *Parelephas trogontherioides* exhibit fewer ridge-plates ($M\ 3\ \frac{+14+}{+14+}$), they are about equal in size (length, M^3, 210+mm., breadth 110 mm., height 150 mm.) to Pohlig's type (Fig. 939) of *P. trogontherii* (M^3, length 225 mm., breadth 101 mm., height 138 mm.), also superior in size to the smallest M^3 of *P. trogontherii* from Süssenborn near Weimar (length 213 mm., breadth 74 mm., height 118 mm.); consequently *P. trogontherioides* cannot be described as a "mutation de petite taille"; it is, however, inferior in size to one of the largest superior molars of Süssenborn, namely, length 317 mm., breadth 76 mm., height 183 mm. (see Soergel, 1912, Pl. VIII).

E. [*Elephas*] *antiquus* var. *trogontherioides* Zuffardi, 1913. "Elefanti Fossili del Piemonte." Palaeont.-Italica, XIX, pp. 130, 155–158. LECTOTYPE AND COTYPES.—Lectotype, third left superior molar, l.M^3 (Fig. 938, 6*a*, 6*b*); cotypes, third right inferior molar, r.M_3 (4), third left inferior molar, l.M_3 (5*a*, 5*b*), and second left inferior molar, l.M_2 (3*a*, 3*b*). HORIZON AND LOCALITY.—Upper Pliocene (Villafranchian stage),[1] Nizza della Paglia and San Paolo de Villafranca (Astésan), Piedmont, northern Italy. LECTOTYPE AND COTYPE FIGURES.—Zuffardi, *op. cit.*, 1913, Tav. IX (III), figs. 3*a*-6*b*.

DESCRIPTION.—(Zuffardi, 1913, p. 130): "Però pensando che il Jourdan considerava la sua specie *E. intermedius* come specie di passaggio dall' *E. antiquus* all' *E. primigenius*, per evitare dannose confusioni, proporrei ora il nome di *E. antiquus* var. *trogontherioides* alla varietà in questione, in ricordo del nome specifico dapprima dato al materiale attualmente ad essa attribuito. . . . [p. 155] Ricordo prima un dente [cotype l.M_2] (Tav. IX [III], fig. 3*a*, 3*b*) che si trovava in raccolta senza indicazione alcuna e che distinguo colla lettera *G*. La corona larga con fianchi non molto convessi, termina anteriormente con una faccia ristretta e arrotondata, e posteriormente è tronca. La superficie di abrasione è concava e di forma ovale. . . . Lunghezza della corona m. 0,156. Larghezza massima della corona, m. 0,105. Altezza massima della corona m. 0,094. Indice dentale 0,015. Frequenza laminare 6½. Simbolo [ridge-plate formula] *x* 10—." Zuffardi states on page 156 that the two third inferior molars [cotypes] (Tav. IX, figs. 4, 5*a*, 5*b*) were [erroneously] referred to *Elephas antiquus* Falconer and Cautley, from the Pliocene lacustrine of Astigiana S. Paolo, according to the label attached to the specimens in the Turin Museum, numbered 8 and 9 respectively. No. 5 [lectotype] of the collection (Tav. IX, figs. 6*a*, 6*b*), also [erroneously] referred to *Elephas antiquus*, is from Nizza della Paglia (cf. p. 158); length of crown 210 mm., maximum breadth of crown 110 mm., maximum height of crown 150 mm., laminar frequence 6½ to 7, ridge-plate formula—15 *x*. Depéret and Mayet (1923, p. 178) estimate the total ridge-plates of this type specimen at about 20. Zuffardi's full type description is as follows:

(Zuffardi, 1913, p. 158) "La stessa discussione può farsi in riguardo di un altro grosso molare superiore (Tav. IX [III], fig. 6*a*, 6*b*). Esso porta l'indicazione '5' *Euelephas antiquus* Cautl. et Falc. Nizza della Paglia—Dono del sig. cav. Pio Corso Bosenasco' ed è accompagnato da un biglietto cosi concepito 'n.° 20—Rinvenuto nel 1819 in un podere della famiglia Corso Bosenasco dal sig. Pio Corso Bosenasco Sindaco di Nizza Lapaglia, a Nizza Lapaglia.' È un dente alto e massiccio, troncato davanti, arrotondato e assottigliato in dietro. I fianchi della corona, ancora rivestiti dal cemento, sono verticalmente quasi diritti, e longitudinalmente convesso l'interno, concavo l'esterno. La superficie di abrasione, quasi rettangolare-arrotondata, è composta di dodici lamine, tortuose, larghe come gli interspazi di cemento e tendono ad allargarsi bruscamente nel mezzo in modo da originare una espansione ovolare. Le corna piegano più o meno sentitamente all' indietro, le lamelle sono leggermente pachiganali e fittamente increspate. Della 1.ª lamina è presente solo la metà interna della lamella di smalto posteriore, e della 2.ª manca la metà esterna della lamella anteriore. Sino all'8.ª compresa, le lamine hanno figura completa; la 9ª, 10ª, 11.ª hanno tre elementi laminaroidi di cui il mediano più sviluppato, e assai meno l'estremo interno ridotto quasi a un semplice anulo. La 12.ª è composta di quattro cercini appena usati. Segue l'altra parte della superficie di abrasione non usata che forma con la precedente un angolo di poco superiore al retto. Essa quantunque ricoperta ancora da cemento, dalle costolature laterali può ritenersi constituita da cinque lamine delle quali l'ultima, strettissima e arrotondata, può considerarsi come tallone prossimale."

"Le radici, per la massima parte perdute, si iniziano in un brusco restringimento laterale della corona e vi si vedono i tronconi basali di un paio di robusti rami anteriori probabilmente liberi, e i resti dell'ammasso delle altre radici. Dall'andamento di queste e dalla forma della corona sembra manchino al massimo altre due amine."

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[1] [See footnote 1 on p. 1049 above regarding the possible Lowest Pleistocene age of the Villafranchian.—Editor.]

"Valori metrici:

Lunghezza della corona	m.	0,210
Larghezza massima della corona	"	0,110
Altezza massima della corona	"	0,150
Indice dentale	"	0,015
Frequenza laminare		6½–7
Simbolo		–15*x*"

"È d'uopo notare però che il Falconer ([40], vol. II, pag. 249–250) si riferiva forse anche a questo dente quando parlando del suo *E. armeniacus,* che credeva ravvisare in un grosso molare segnato col n.° 7 nella nostra raccolta, e che ci occuperà più avanti (pag. 174 [54]), affermava che altri ve n'erano tra i molari di S. Paolo."

Pliocene of Italy (Depéret and Mayet, 1923, pp. 176–183).—According to Falconer (1868), Pohlig (1889 [1888]), and Zuffardi (1913), this *Parelephas trogontherioides* branch [i.e., phylum] although rare first appears in the Upper Pliocene (Villafranchian) of Italy. As discovered near San Paolo de Villafranca this [lectotype] M^3 exhibits so closely all the characters of the corresponding tooth of *Elephas trogontherii* that it can only be separated as a variety. Falconer (1868) mentioned San Paolo as one of the localities in Italy containing teeth resembling the type of *E. armeniacus* of Asia Minor, which he accordingly referred to the Armenian species (see p. 1060 below).

For this and other Upper Pliocene teeth found at or near San Paolo and described and figured both by Zuffardi and by Depéret and Mayet, the subspecific name *Elephas antiquus* var. *trogontherioides* was given, the characters being summed up as follows (Depéret and Mayet, 1923, p. 179): "Ces molaires présentent tous les caractères essentiels de l'*E. trogontherii* quaternaire, savoir: une couronne très large et très haute, avec des lames épaisses et assez écartées (fréquence laminaire de 6 à 6, 5); un émail tortueux et fortement plissé, orné sur sa longueur de quelques sinus aigus irréguliers, mais ne ressemblant en rien au sinus loxodonte médian des *E. meridionalis* et *antiquus.* . . . [p. 180] On peut donc dire seulement que la forme pliocène de l'*E. trogontherii* possède des molaires de dimensions plutôt un peu réduites, sans qu'il puisse être question d'une véritable *mutation de petite taille* de l'espèce. On doit s'attendre à découvrir un jour dans le Pliocène ancien de quelque région éloignée les types ancestraux nains du rameau de l'*E. trogontherii.*"

First Interglacial of Germany (Freudenberg, 1926).—In the basal layers of the Mosbach sands, near Wiesbaden (Fig. 932, 12), Freudenberg records small mutations ("kleinere Variante") which he refers to *Elephas trogontherii,* associated with artificially broken off ("künstlich abgetrennte") portions of the horns of *Cervus verticornis,* charred wood ("Holzkohlen"), and earth colored by fire ("rotgebrannte Erde"), also bones belonging to an ancient camping place of primitive man which might well have belonged to *Homo heidelbergensis*; of the same geologic age as the Cromer Forest Bed which is quite as old as the deposits of Jockgrim (Freudenberg, 1909). The very ancient characteristics of this small *E. trogontherii* mutation at once confirm the great antiquity of this basal Mosbach sands horizon, which also contains the Etruscan rhinoceros (*Dicerorhinus etruscus*), *Trogontherium cuvieri,* and *Hippopotamus.* In this lower Mosbach stage of this small *E. trogontherii* mutation, the third inferior molar, M_3, exhibits 8 ridge-plates in 10 cm., exactly as in the primitive *trogontherii* molars of Jockgrim, whereas the true *Elephas primigenius* M_3 exhibits 7 ridge-plates in 10 cm. These basal sands of Mosbach cannot be more recent than the *1st Interglacial* (Günz-Mindel) stage of the Alps, or the Elephant Bed of Cromer (Forest Bed series). Still more ancient are the underlying layers at Mosbach containing *Elephas* [=*Archidiskodon*] *meridionalis* and an Upper Pliocene fauna with *Mastodon* [=*Anancus*] *arvernensis* and the Red Crag species.

Osborn, 1928: The above note by Dr. Wilhelm Freudenberg is deeply interesting as tending to confirm the great antiquity of the *Parelephas* phylum in western Europe and the possible coexistence of a primitive species of *Parelephas* (?sp. *trogontherioides*) with Heidelberg man (*Homo heidelbergensis*).

Parelephas trogontherii Pohlig, 1885, 1888-1891

Figures 794, 865, 871, 929, 934–936, 939, 940, Pl. xxii

Type: *2d Interglacial* deposits at Süssenborn near Weimar (Fig. 932, 11), northern Germany. Referred: *1st–2d Interglacial.* Pohlig (1887.2, p. 274). "vom mir zuerst in den alten Flusskiesen Thüringens zu Süssenborn etc. bei Weimar in grösserer Menge aufgefundene altdiluviale Elephantenzahnform beschrieben."

This very important species, widely distributed in *2d Interglacial* times in western Europe, is, with the more progressive *Elephas intermedius* of Jourdan, a member of the distinct phyletic series *Parelephas. Parelephas trogontherii* belongs to a phylum by itself which appears sparsely in Europe at the close of Pliocene time and reappears in the *1st* and *2d Interglacial* periods. We do not agree with Pohlig's opinion that the species *E. trogontherii* is a connecting ancestral link between *Elephas meridionalis* and *E. primigenius.* With Depéret we regard it rather as a distinct phylum. The estimated ridge-plate count of the type, M^3 (Fig. 939, upper) is $\frac{15+}{16+}$, somewhat exceeding the ridge-plate count of *E.* [*P.*] *trogontherioides* Zuffardi.

Soergel (1912.2, Tab. vii, viii) records three inferior and five superior molars from the type locality of Süssenborn (*1st to 2d Interglacial* deposits), in the Rebling and Weimar Museum collections, which vary widely in length, breadth, and height, as follows:

Süssenborn: Rebling and Weimar Mus.	Ridge formula	Length	Breadth	Height
R.M_3 No. 46 (Weimar)	x18x (x17x)	270	62	160
17 (Weimar)	16x	255	83	105
10 (Weimar)	x21x	316	73	137
R.M^3 No. 80 (Rebling)	x18x	302	91	192
69 (Rebling)	20x	291	88	160
32 (Weimar)	x20x	296	66	137
89 (Rebling)	x18x	264	71	162
87 (Rebling)	x20x	274	85	171

Elephas trogontherii Pohlig, 1885. "Ueber eine Hipparionen-Fauna von Maragha in Nordpersien, über fossile Elephantenreste Kaukasiens und Persiens und über die Resultate einer Monographie der fossilen Elephanten Deutschlands und Italiens." Zeitschr. deutsch. geol. Ges., 1885, XXXVII, Heft IV, p. 1027. Type.—Apparently a last superior molar, M^3, of the right side, also a last inferior molar, M_3, of the same side. Horizon and Locality.—*2d Interglacial* deposits, Süssenborn near Weimar, northern Germany. Type Figure.—Pohlig, 1888, p. 193, fig. 79, and p. 195, fig. 82 (Fig. 939 of the present Memoir). Schwabe Coll., Weimar. Referred Specimens.—The Süssenborn stage of the upper and lower grinding teeth of *Elephas trogontherii*, illustrated by Wüst, 1901, Taf. ii, figs. 4–12 (Fig. 940), appears in comparison with the stage erroneously referred to '*Elephas*' [*Hesperoloxodon*] *antiquus* in figures 3 and 18.

RELATIONSHIPS OF ELEPHAS TROGONTHERII POHLIG (1885, 1887, 1888–1891, 1907, 1912) AND SOERGEL (1921)

Relationships.—(Pohlig, 1885, p. 1027): "6. Unter der Bezeichnung '*Elephas trogontherii* Pohl.' führe ich in meiner Monographie eine europäische Molarenform auf, welche zwischen denjenigen des *E. primigenius* und *E. meridionalis* zoologisch, wie ihrer geologischen Lagerstätte nach, in der Mitte steht, dem *E. antiquus* in der Lamellenformel am nächsten kommt, aber durch die Kronenform und geologische Lagerstätte von dieser Art weit schärfer gesondert ist als von den anderen beiden Species. Das Verhältniss von *E. trogontherii* zu *E. armeniacus* Falc. und auch *E. namadicus* Falc.-Cautl. bleibt noch genauer zu untersuchen.—*E. meridionalis* und *E. primigenius* stehen nach Kranologie und Dentition über *E. trogontherii* hin in directer Verwandtschaft."

Description (Pohlig, 1887.2, p. 274): "Unter diesem Namen *Elephas trogontherii* habe ich in meiner Monographie eine, wie es scheint, in Europa allgemein verbreitete, von mir zuerst in den alten Flusskiesen Thüringens zu Süssenborn etc. bei Weimar in grösserer Menge aufgefundene altdiluviale Elephantenzahnform beschrieben, welche geologisch sowohl als zoologisch die beiden Arten *E. meridionalis* Nesti aus dem Pliocaen und *E. primigenius* Blum. aus dem Plistocaen völlig mit einander verkettet: in der Form der Krone und Kaufläche und in dem Charakter der einzelnen Schmelzfiguren auf letzterer stimmt jene altdiluviale Rasse mit den zuletzt genannten beiden Arten überein, steht jedoch, was die Anzahl der Schmelzlamellen und die Dicke der Schmelzwände anbetrifft, zwischen diesen beiden Species in der Mitte,—in den unterplistocaenen Schichten mehr dem *E. meridionalis*, in den mittelplistocaenen Lagerstätten mehr dem Mammuth in dieser Beziehung angenähert."

Pohlig (1885–1887) from the first expressed the opinion that *Elephas trogontherii* forms a connecting ancestral link between *Elephas meridionalis* and *Elephas primigenius*, its earlier representatives resembling the former, its more recent representatives resembling the latter, accordingly he wrote the specific name at the time *E. primigenius trogontherii*. He held that this species entered Europe during the second glaciation (Saxonian-Mindel) and survived during the *2d Interglacial* period (Helvetian, Mindel-Riss); thus *E. trogontherii* was contemporary with the appearance of the Chellean industry in France (Penck). Pohlig (1888–1891, p. 458) pointed out that while *Elephas trogontherii* resembles *E. antiquus* in ridge formula, in the structure of the crowns of the molar teeth it is sharply separated, because the grinders of *E. trogontherii* are different in proportion from those of *E. antiquus*; the enamel

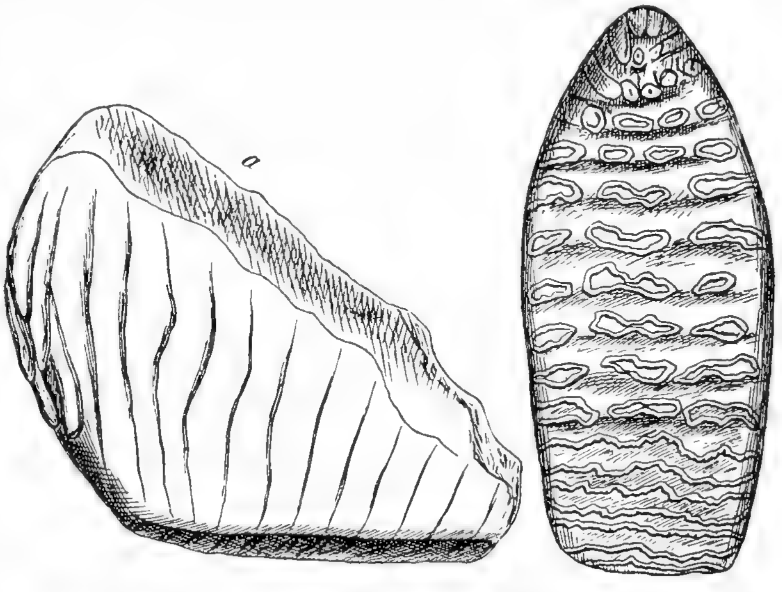

Fig. 79. Letzter Maxillenmolar von *Elephas trogontherii*. Original zu Weimar (Dr. Schwabe), $^1/_3$

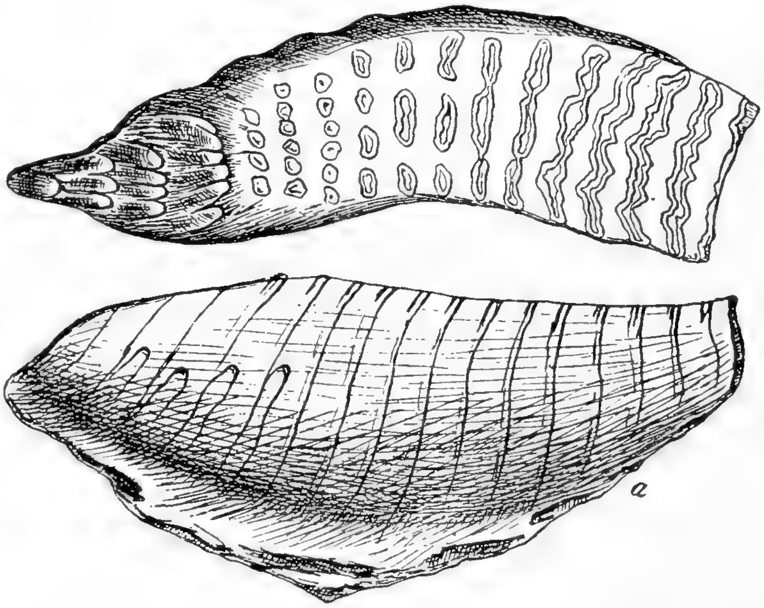

Fig. 82. Letzter Mandibelmolar von *Elephas trogontherii*. Original zu Weimar (Dr. Schwabe), $^1/_3$.

Types of Parelephas trogontherii. Compare Soergel, 1912.2, Tab. vii
One-third natural size

Fig. 939. Type third superior and inferior molars of *Elephas trogontherii* Pohlig, 1885. After Pohlig, 1888–1891, p. 193, fig. 79, and p. 195, fig. 82. These are the specimens first mentioned by Pohlig (1885, p. 1027) and figured by him in his Memoir of 1888–1891: "Fig. 79. Letzter Maxillenmolar von *Elephas trogontherii*. Original zu Weimar (Dr. Schwabe), $\frac{1}{3}$." This is apparently a last superior molar of the right side, r.M^3; it is complete and displays 15 ridges. "Fig. 82. Letzter Mandibelmolar von *Elephas trogontherii*. Original zu Weimar (Dr. Schwabe), $\frac{1}{3}$." This is a last inferior molar of the right side, r.M_3; it is broken in front and displays 16+ ridges. The incomplete ridge formula of these types of *Elephas trogontherii* is: $M\,3\frac{15+}{16+}$. See text below.

bands rise above the cement not vertically but obliquely, after the manner of the Asiatic elephant. *E. trogontherii* bespeaks a relatively moist climate but is also occasionally mingled with remains of the reindeer (*Rangifer*) where the forest bordered on the open country, as attested by the appearance of both animals in Süssenborn and Steinheim. Pohlig (1888–1891, p. 386, fig. 121) figures the female skull as *Elephas* (*primigenius*) *trogontherii* (reproduced in Fig. 865, Nos, 3, 4 above), in which the superoccipital region is imperfect and restored. Pohlig's opinion as to the *transitional* character of this animal between *E. meridionalis* and *E. primigenius* is indicated in the names he has successively assigned to it, namely:

Elephas trogontherii Pohlig, 1885, p. 1027.

Elephas (*primigenius* bezw. *meridionalis*) *trogontherii,* 1887, p. 274.

Elephas (*primigenius*) *trogontherii* Pohlig, 1887 [1888[1]], p. 799.

Soergel (1921.2, p. 68) in his comprehensive review entitled '*Elephas columbi* Falconer'' likewise adopts Pohlig's opinion and places *Elephas meridionalis-trogontherii-primigenius* as successive phyletic stages in the same west European phylum. He assigns (*op. cit.*, p. 55) the following collective ridge formula to the *Elephas trogontherii* specimens of Süssenborn and Mosbach:

$$\text{Dp}\,2\tfrac{3}{4}\quad \text{Dp}\,3\,\tfrac{5\text{-}7}{7}\quad \text{Dp}\,4\,\tfrac{9}{10}\quad \text{M}\,1\,\tfrac{10\text{-}12}{11\text{-}13}\quad \text{M}\,2\,\tfrac{11\text{-}15}{11\text{-}15}\quad \text{M}\,3\,\tfrac{16\text{-}21}{16\text{-}21}.$$

Soergel is of the opinion that *Elephas trogontherii* (western Europe) and the typical *Elephas columbi* (southern U.S.A.) are in similar stages of evolution. He points out that the typical *Elephas meridionalis* may be regarded as the *direct ancestor* of the *Elephas columbi-imperator* phylum: (*Op. cit.*, 1921, p. 68) "Diese Tatsache berechtigt zu der Annahme, 'dass die nach Amerika überwandernden Formen der *Meridionalis-trogontherii*-Reihe schon beim Ueberwandern resp. kurz vorher besondere Charaktere gegenüber dem europäischen *El. trogontherii meridionalis* ausgebildet hatten, Charaktere, die in der weiteren Entwicklung sich zum '*Imperator*-Typus' steigerten. Es war also im ältesten Diluvium im Kreis der kontinentalen Elefantenformen eine Variationsbreite mit zwei Polen, *El. trogontherii meridionalis* im Westen und dem direkten Vorfahren des *El. imperator* im Osten vorhanden." Soergel (*op. cit.*, pp. 69–97) concurs with Pohlig in the opinion that *Elephas trogontherii* is ancestral to *Elephas primigenius.*

HABITAT.—In a letter of June 30, 1922, Soergel states: According to my interpretation *E. trogontherii* lived during a period of limited rainfall, in a half-arid climate, not migrating during glacial times into the colder ice-clad regions of middle Europe (compare also Soergel: 'Die Ursachen der diluvialen Aufschotterung und Erosion,' Verlag Bornträger, 1921). *E. trogontherii* therefore occupied the region later traversed by the mammoth. We still regard *E. trogontherii* as the direct ancestor of *E. primigenius.* We possess in the museums of Europe all the transition forms in large numbers and are unable to make any sharp distinction between the two species. If one seeks a complete understanding of the chief literature of value on this subject, it may be found in the following works: M. Pavlow, 'Les éléphants fossiles de la Russe,' Nouv. Mém. d. l. Soc. Imp. des Nat. de Moscou, T. XVII, 1910; W. Soergel, '*Elephas trogontherii* und *Elephas antiquus* etc.' Palæontographica, 1912; E. Wüst, 'Das Pliozän und das älteste Pleistozän Thuringens. Abhand. d. naturf. Gesellsch. zu Halle, Bd. XXIII, 1900. I rejoice that in the principal points we agree as to the diluvial elephants and their phylogeny.

PHYLOGENETIC CONCLUSION (OSBORN, 1924).—Osborn does not agree with either Pohlig or Soergel that the typical *Elephas trogontherii* is a descendant of *E.* [*Archidiskodon*] *meridionalis;* nor does he agree that it should be regarded as transitional or ancestral to the typical *E.* [*Mammonteus*] *primigenius.* The profound difference between the broad-plated molars of the *Archidiskodon planifrons-meridionalis-imperator* phylum widely distinguishes this phylum from *Elephas trogontherii*; Osborn accepts rather the view of Depéret and Mayet that *E. trogontherii* represents a distinct branch of the mammoths. Moreover, the extreme hypsicephalic, acrocephalic, bathycephalic cranium of *Elephas primigenius,* with corresponding hypsodont, finely compressed, and laminated molars, cannot be derived from the cranium and molars of the *Elephas trogontherii* type. Osborn agrees entirely with Depéret and Mayet that we have to do with three distinct phyla, certainly separate from the close of Pliocene time. Again Osborn does not accept the opinion of Soergel that *E. trogontherii*

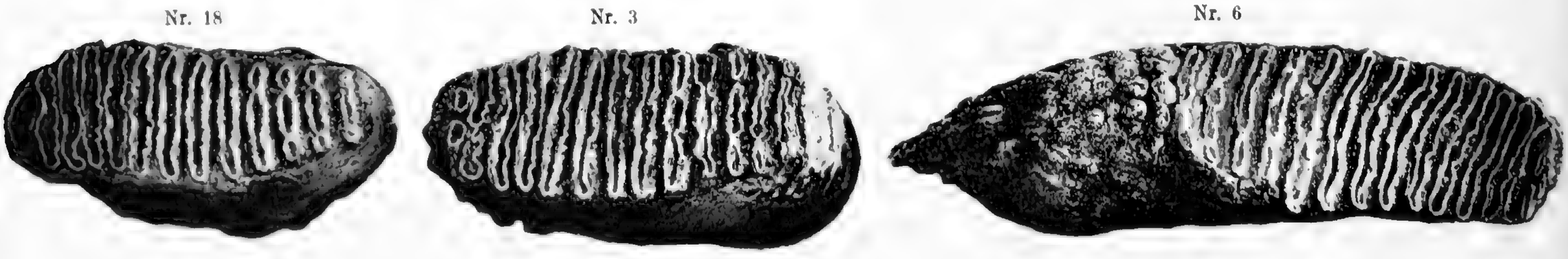

Fig. 940. Referred molars (r.M_3 with 18+ ridge-plates) of '*Elephas trogontherii*' Pohlig from the *2d Interglacial* of Süssenborn and Weimar, Germany. After Wüst, 1901, Taf. II. Wüst erroneously refers r.M^3 (Nr. 3) and r.M^2 (Nr. 18) to *Elephas antiquus*; they are *Parelephas trogontherii* molars from the type locality (Süssenborn near Weimar).

"Nr. 3. *Elephas antiquus Falc.* M.III max. dextr. Süssenborn. . . .
" 6. Desgl. M.III max. dextr. Süssenborn. . . .
" 18. *Elephas antiquus Falc.* M.II max. dextr. Weimar."

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[1] In the Bibliography of the present Memoir (p. 795), it is possible that 1887.1 should read 1888.

is related to the true *E.* [=*Parelephas*] *columbi* of the southern United States, although it may well prove to be related to the animal described by Cope, Hay, Osborn, and others as "*Elephas columbi*" but which now proves to represent a distinct species, namely, the *Parelephas jeffersonii* of Osborn. Consequently, Osborn, as cited above, has placed *E. trogontherii* in the distinct phylum *Parelephas,* the generic characters of which are defined by cranial and dental characters in the chapter on the "Classification of the Elephantoidea" (Chap. XV).

Parelephas (?) **trogontherii nestii** Pohlig, 1891

Figure 941

Type locality: "Jungpliocaenen," Forest Bed (Norfolk), Walton (Essex), and Southwold (Suffolk), England. Lower Pleistocene.

Regarded by Depéret and Mayet (1923, p. 163) as a synonym of *Elephas* [*Hesperoloxodon*] *ausonius* F. Major. Cotypes regarded by C. W. Andrews as belonging to *E.* [=*Parelephas*] *trogontherii.*

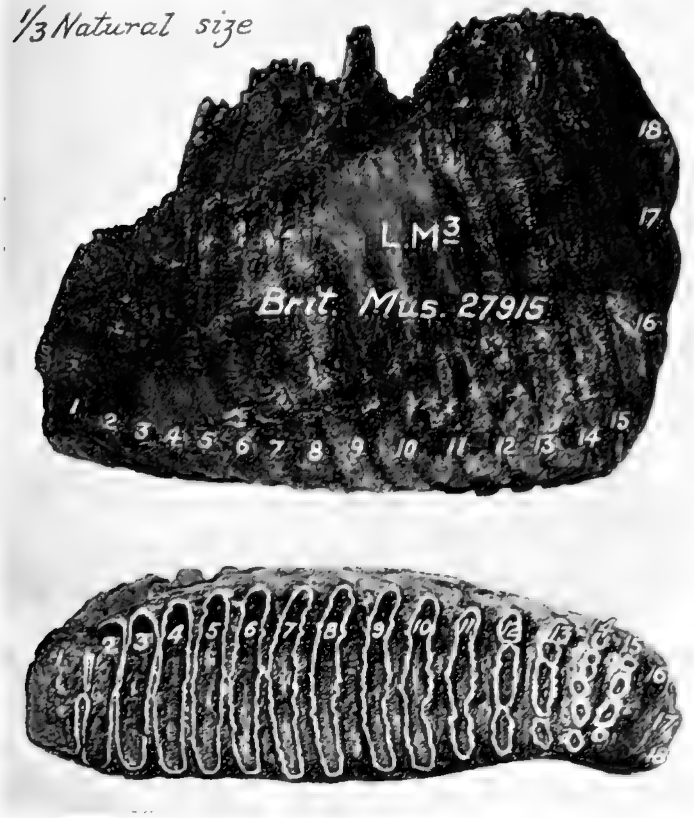
Pohlig (*op. cit.*, p. 303) in reviewing Leith Adams' Monograph on *Elephas antiquus* observed that certain teeth of the Thames Valley (Adams, 1877–1881, p. 33), of Norfolk (p. 40) and of Southwold (p. 38), do not agree with the continental molars [of Germany] referred to *E. antiquus.* Pohlig continues, that part of the "jungpliocaenen . . . Forestbed stammenden" molars do belong to the typical *E. antiquus,* but that the majority belong to an inferior race; he then separates this race as *E. Nestii.* Pohlig's *types* or *cotypes* of *E. Nestii* are therefore molars of Forest Bed age.

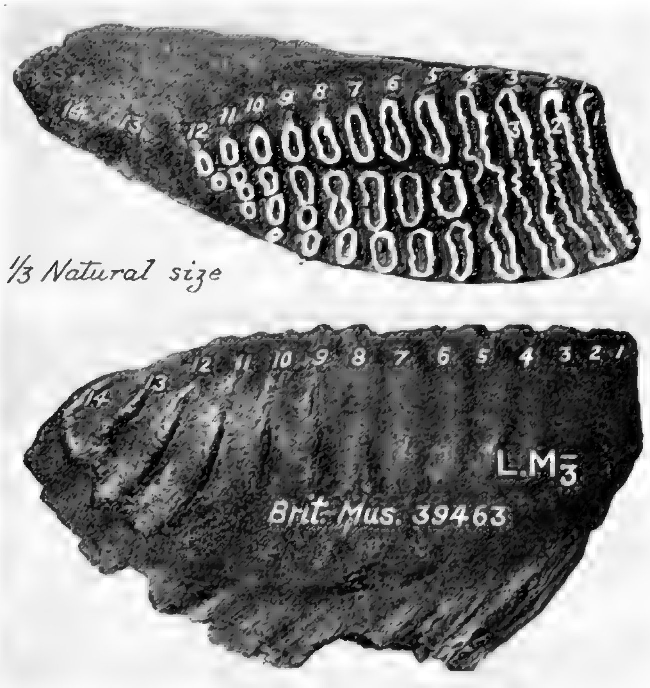
COTYPES.—As shown above, the subspecies *Elephas antiquus Nestii* was erroneously based on cotype specimens selected from Leith Adams' Monograph of 1877–1881, pp. 37 and 38, namely, Brit. Mus. 33327, a dredged lower molar from Happisborough with +16+ridge-plates in 11.5 inches [catalogued by Lydekker, 1886.2, p. 128, as a "right third upper true molar"]; Brit. Mus. 27915 [given as No. 27515 by Leith Adams], a 14+ ridge-plated third left upper true molar from Walton (Essex), with 13+ ridge-plates in 8.5 inches, and Brit. Mus. 39463, a half-worn third left lower true molar from Southwold (Suffolk), compare Lydekker's "Catalogue of the Fossil Mammalia in the British Museum," 1886.2, pp. 128, 129, and 135. All these cotypes are of Lower Pleistocene Cromerian or Forest Bed age; their generic and specific reference to '*E. antiquus*' is doubtful; C. W. Andrews refers Brit. Mus. 27915 and 39463 to '*E. trogontherii*;' Hopwood (letter, August 6, 1929) kindly furnished photographs and detailed measurements which tend to confirm Andrews' reference to '*E. trogontherii.*'

Happisborough (Forest Bed), England. Brit. Mus. 33327, r.M^3, length 268 mm., breadth 92 mm., height 196 mm.; ridge-plates +16+, 6.3 in 10 cm.

Walton (Essex), England. Brit Mus. 27915, l.M^3, length 302 mm., breadth 80 mm., height 167 mm.; ridge-plates 18, 6½ in 10 cm. (referred to '*E. trogontherii*' by C. W. Andrews).

Southwold (Suffolk), England. Brit. Mus. 39463, l.M_3, length 243+ mm., breadth 83 mm., height 103 mm., ridge-plates





COTYPES OF ELEPHAS ANTIQUUS NESTII POHLIG NOW TRANSFERRED TO PARELEPHAS(?) TROGONTHERII NESTII

Fig. 941. Cotypes or syntypes of *Elephas antiquus Nestii* Pohlig, 1891, after photographs kindly furnished by Dr. A. Tindell Hopwood of the British Museum, August 6, 1929. From the Lower Pleistocene of eastern England. One-third natural size.

(Left) Brit. Mus. 27915. Left third superior molar, l.M^3, from Walton (Essex), England, exhibiting 1–18 ridge-plates; also crown view of same.

(Right) Brit. Mus. 39463. Incomplete left third inferior molar, l.M_3, from Southwold (Suffolk), England, exhibiting 1–14 posterior ridge-plates; anterior ridge-plates broken off. Lateral and crown views of same.

14+, 7½ to 8 in 10 cm. (referred to '*E. trogontherii*' by C. W. Andrews).

Unfortunately these specimens were not figured by Leith Adams or Pohlig, but they were described by Leith Adams as belonging to his '*Elephas antiquus*.' It is to be regretted that the name *Elephas antiquus Nestii* has been adopted and widely quoted in the literature, for we cannot agree with Depéret and Mayet (1923) that '*Elephas antiquus Nestii*' Pohlig, erroneously based on Lower Pleistocene cotypes, is synonymous with '*Elephas ausonius*' Major-Depéret-Mayet, correctly based on an Upper Pliocene type of the Villafranchian stage.[1]

History.—In 1891 Pohlig imperfectly established this subspecies (named after Filippo Nesti) as of Upper Pliocene age, whereas the cotypes selected by him, as mentioned by Leith Adams in his Monograph of 1877–1881, are said to be from Walton, Southwold, and Norfolk, the latter from the Cromer Forest Bed level which is of Lower Pleistocene age. This subspecies, founded on a misconception as to its Pliocene age, is invalid; it is certainly not in the same geologic stage as the Upper Pliocene '*Elephas*' *ausonius* Major-Depéret-Mayet, from the Villafranchian of Italy.[1] Although not figured, the ridge formula was said by Pohlig (1891, p. 305) to agree with that of *E. antiquus*: "In der Lamellenformel würde *E. Nestii* sowohl mit *E. antiquus typus*, als auch mit *E. trogontherii* übereinstimmen."

E. Nestii Pohlig, 1891. "Dentition und Kranologie des Elephas antiquus Falc. mit Beiträgen über Elephas primigenius Blum. und Elephas meridionalis Nesti. . . . Nachträge," pp. 303, 304, 465. On page 465 the name appears as *Elephas antiquus Nestii* n.f. Type.—(Letter, Pohlig, Sept. 10, 1924): "As type specimens of *E. Nestii* from the forest bed are named in my monograph (p. 304) those of L. Adams' [monograph], p. 38, from Walton and Southwold, and the Nr. 33327 of the British Museum, from Norfolk." Locality and Horizon.—Forest Bed (Norfolk), Walton, and Southwold, England; Lower Pleistocene. Type Figure.—Not figured. See figure 941 of the present Memoir after photographs. Referred skull of northern Italy figured by Pohlig, *op. cit.*, 1891, p. 350 = Cranium B of Nesti (*Elephas meridionalis*); referred to *Elephas antiquus* by Weithofer 1890, and erroneously referred by Pohlig to his subspecies *E. antiquus Nestii*.

Type Description.—(Pohlig, 1891, pp. 303–305): "b. Ein Theil der letzteren—die aus dem jungpliocaenen [Footnote: 'Vgl. u. (sub *E. meridionalis*).'] Forestbed stammenden—lassen die Zugehörigkeit wenigstens zu der Species *E. antiquus* zu, manche mögen selbst als typische Molaren derselben gelten; die meisten haben jedoch Abweichungen von der typischen Gleichmässigkeit der Kronenbreite nicht nur, sondern auch von dem charakteristischen Lamellenbau der diluvialen Ausgangsform, besonders von dem ausgeprägten Loxodontismus, der complicirteren Festonirung und der grösseren Dicke des Schmelzes bei jener. Da nun diese Eigenthümlichkeiten zum Theil mit den im ersten Abschnitt erörterten, ebenfalls jungpliocaenen Erfunden von der Species aus dem Arnothal übereinstimmen, so scheint es mir nunmehr doch geboten, diesen pliocaenen *E. antiquus* von dem diluvialen durch eine Rassenbezeichnung, etwa *E. Nestii*, vorläufig zu trennen. . . . Es müsste danach die in dem ersten Abschnitt ausgesprochene Vermuthung, dass Loxodon von unbekannten Mastodontenformen sich ableite, fallen gelassen werden; denn ganz wie *E. Nestii* zum typischen *E. antiquus* verhält sich nach Mitgetheiltem das Wenige, was man vom *E. priscus* weiss . . . , zum modernen *E. africanus*,—es zeigt den Charakter des letzteren minder markirt, mit Eigenthümlichkeiten archidiskodonten Gepräges, wenn auch in geringem Grade, vermengt. . . . In der lamellenformel würde *E. Nestii* sowohl mit *E. antiquus typus*, als auch mit *E. trogontherii* übereinstimmen; und da an mehreren Punkten der englischen Ostküste, wie bei Mundesley-Cromer, Clacton etc. interglaciale Schichten mit *E. antiquus* und *E. primigenius*—an ersterem sogar mit ganz ähnlichem Erhaltungszustand—die jungpliocaenen mit *E. meridionalis*, *E. Nestii* und *E. trogontherii* überlagern, also Molaren aller dieser Formen in die Brandung und von da in die Museen gelangen: so war die Schwierigkeit, alles das nunmehr Vermengte in der rechten Art wieder voneinander zu sondern, anfangs begreiflicher Weise selbst für den Geübten zu gross. Und doch sind eben grade diese Verhältnisse von grösstem Interesse."

Osborn, 1930: We are therefore obliged to regard *Elephas antiquus Nestii* as comparable to the species '*Elephas*' [=*Parelephas*(?)] *trogontherii* Pohlig (cf. *Parelephas trogontherioides* Zuffardi).

Parelephas armeniacus Falconer, 1857

Figure 942

Pleistocene, near Khanoos, Province of Erzerum, Armenia.

We note that Falconer in 1868 (Vol. II, pp. 187, 192, 193, 248, 249, 250) observed a strong resemblance between his type of *E.* (*Euelephas*) *armeniacus* and Upper Pliocene molars from the locality of San Paolo, or near it, Nizza della Paglia, Italy, recently chosen by Zuffardi as the types of *Elephas antiquus* var. *trogontherioides*. It is probable, therefore, that the species *Elephas armeniacus* of Falconer belongs in the generic phylum *Parelephas*, but we cannot be certain of this reference until the cranial characters of the species become known. The specific distinctions are: Ridge-plates of M 3 $\frac{+17\frac{1}{2}}{}$ (Fig. 942), worn anteriorly. This appears to be a more progressive stage than *Parelephas trogontherii* and much more progressive than *P. trogontherioides*.

E. (Eueleph.) Armeniacus Falconer, 1857. "On the Species of Mastodon and Elephant occurring in the fossil state in Great Britain. Part I. Mastodon." Quart. Journ. Geol. Soc. London, Vol. XIII, Synoptical Table opp. p. 319. Type.—(Falconer, 1863, p. 74): ". . . two last upper molars in fine preservation, and a portion of a lower, all apparently of the same individual." Brit. Mus. 32250, 32251, and 32252; also fragment of tusk, head of femur, and portion of tibia (Brit. Mus. 32256, 32254, 32253), which Lydekker (1886.2, p. 174) regards as belonging to the same individual as the teeth. Horizon and Locality.—Pleistocene. Near Khanoos, Province of Erzerum, Armenia. Type Figure.—Falconer, 1863, Pl. ii, fig. 2.

History.—Falconer first named this species in his "Synoptical Table" of 1857, facing page 319: "Spec. 14. E. (Eueleph.) Armeniacus . . . Armenia: Erzeroom . . . In the Brit. Mus. Coll. Discovered between Erzeroom and Moosh in 1856. The molar

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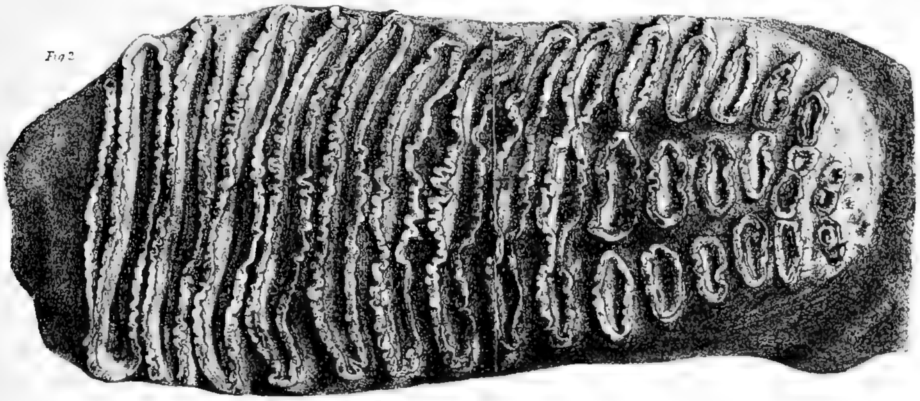
[1] [See footnote 1 on page 1049 above regarding the possible Lowest Pleistocene age of the Villafranchian.—Editor.]

plates closely approximated, and the enamel-edges very undulated." In 1863, pp. 74–76, he renewed his description as follows: "These Khanoos molars are intermediate in character, between the Mammoth and the Indian Elephant, but more nearly allied to the latter. . . . In the synoptical table appended to my Memoir on the 'Species of Mastodon and Elephant, &c.,' the Khanoos fossil form is ranged between *E. indicus* and *E. primigenius,* under the provisional name of *E. Armeniacus.* [Footnote: 'Quart. Journ. Geol. Society, 1857, vol. xiii, p. 319.'] . . . [p. 76] while *E. Armeniacus,* as stated above, approaches nearer to the existing Indian species." Falconer also speaks of the remains of fossil elephants on the banks of the Bosphorus and the northern shores of the Black Sea and of the Sea of Azof (*op. cit.*, p. 75). On page 74 he gives what may be called the type description.

TYPE DESCRIPTION (FALCONER, 1863, P. 74).—"The specimens presented by Colonel Giels to the national collection, consist of two last upper molars in fine preservation, and a portion of a lower, all apparently of the same individual. These molars strike a practised eye, at the first glance, as presenting something intermediate between the Mammoth and the existing Indian Elephant. The case is of so much interest, that I shall venture on some of the details. The left upper molar (m.3, being No. 32,250 Museum Regist. Palæont. Gallery) is entire from behind the large front fang, the portion borne upon which had been ground down by protracted wear. [Footnote: 'Pl. II, fig. 2, shows the crown-view of the tooth.'] The anterior part of the crown to the extent of 2.7 inches is also worn out, presenting merely a smooth surface of ivory, behind which there are seventeen ridges and a posterior talon. Of these, fifteen are more or less worn. The anterior nine form transverse narrow discs; the next six are divided nearly equally by two rather wide longitudinal channels into three divisions, consisting each of a flattened elliptical disc. The transverse discs, in their general character, bear a close resemblance to those of the Indian Elephant, the enamel-plates being rather thick, with very pronounced close-set crimping in the middle, but diminishing towards the cornua. These discs are narrower than is commonly seen in the existing species, less open and less parallel across. The crown is broad, and the enamel plates are high. To render these descriptive details more appreciable and available for comparison, I append the principal dimensions [l.M^3]:—

	[In.]	[Mm.
Extreme length of crown	11.75	299
Length of crown surface in use (partly worn out)	9.5	242
Space occupied by the anterior ten discs measured at top of crown	5.7	146
Ditto ditto, at base of crown	6.1	156
Width of crown at 3rd ridge (greatest) . .	4.1	105
Ditto at 11th ditto	3.7	95
Height of crown at 12th ridge	7.1	181]"



ONE OF THE TYPE MOLARS OF PARELEPHAS ARMENIACUS
One-half natural size

Fig. 942. Third superior molar, l.M^3, of *Elephas Armeniacus* Falconer, 1857. After Falconer, 1863, Pl. II, fig. 2, p. 114: "Represents the crown-aspect of the last true molar, (m.3) upper jaw, left side, of *E. Armeniacus,* from a specimen in the British Museum, No. 32,250, procured by Col. Giels, in the province of Erzeroum, in Armenia."

(?) E. ARMENIACUS IN ITALY (FALCONER, 1868).—The same description is found in the "Palæontological Memoirs," 1868, Vol. II, p. 247, in which Falconer again treats *Elephas armeniacus* as intermediate between *Elephas primigenius* and *E. indicus* but more nearly allied to the latter. He adds (p. 249): "I now entertain a strong suspicion that remains of *E. Armeniacus,* or of a form closely allied to it, occur in Italy. This impression is founded upon specimens which I observed in the Natural History Museum of Turin, in the University Museum of Pisa, in the private collection of the Marchese Carlo Strozzi at Leghorn, and in those of Professor Ponzi and Signor Ceselli at Rome, the satisfactory specific identification of which puzzled me greatly. . . [p. 250] The space occupied by the twelve discs of wear, measured along the summit of the crown, is 7 inches, yielding an average of about .6 inch to each, which comes very near that indicated above in the *E. Armeniacus* of Khanoos, *i.e.* .57. The principal dimensions are:—Length of crown (not quite entire), 13.75 in. Extreme width of crown, 4.5 in. Height of crown at 12th ridge, 8. in. Space occupied by the 12 discs of wear, 7. in. I have detailed notes of numerous other molars, exhumed on the same occasion, from the same locality, St. Paolo, or near it, 'Nizza della Paglia,' which yield similar characters. . . . I have been led to identify the 'Khanoos' and St. Paolo molars as being of the same species, *E. Armeniacus,* and to consider that they are not referable either to *E. primigenius* or *E. antiquus* [Footnote: 'See *antea,* pages 187 and 192, *note.*—[ED.]']."

Osborn, 1928: (1) It is now known that these Upper Pliocene[1] Italian specimens thus *referred* by Falconer to *E. armeniacus* actually belong to *Elephas antiquus* var. *trogontherioides* Zuffardi, as confirmed by Depéret and Mayet (see above). (2) Leith Adams (1877–1881, p. 241) mentions *E. armeniacus* but does not add to our knowledge. (3) Lydekker (1880.1, p. 285) erroneously gives the ridge formula of *E. armeniacus* as M 3 $\frac{24}{\quad}$, whereas Falconer's type figure shows: M 3 $\frac{+17\frac{1}{2}}{\quad}$. (4) Lydekker (1886.2, p. 174) remarks: "Elephas armeniacus, Falconer [Footnote: 'Quart. Journ. Geol. Soc. vol. xiii, table facing p. 319 (1857).']. Syn.

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[1] [See footnote 1 on page 1049 above.—Editor.]

Euelephas armeniacus, auct. This species is definitely known only by the following [six] specimens, which belong to an animal of very large size. The structure of the molars indicates a species intermediate between *E. primigenius* and *E. indicus*, which is probably an ancestral form closely connected with both [Footnote: '*Ibid.* vol. xlii, p. 174 (1886).']. The crowns of the molars are extremely wide, the ridges approximated, with their extremities curving backwards, the enamel is moderately thick and much plicated, and the wear of the crown irregular. In their great width these teeth agree with those of *E. primigenius*, but in the other characters with those of *E. indicus* [Footnote: 'See Leith-Adams, British Fossil Elephants (Mon. Pal. Soc.), p. 241.']."

(5) Lydekker (1886.3, p. 174) remarks: "From strata of unknown age at Erzerum, in Armenia, Dr. Falconer many years ago described some elephant molars under the name of *Elephas armeniacus*; and as Erzerum is comparatively near to Tabriz, it may be suggested that some of the Maragha elephants' teeth may not improbably belong to this species; but be this as it may, the Erzerum and Maragha faunas may be geographically grouped together."

PHYLOGENETIC CONCLUSION (OSBORN): The extremely able and acute observations of Falconer (1857–1868) on this species from Armenia and on allied forms from Italy, confirmed by Zuffardi's observations on the resemblance of this animal to *Elephas trogontherii* of Pohlig, as signified by the specific name *trogontherioides*, also the recent observations by Depéret and Mayet (1923), all emphasize the *intermediate* character of this species and its phyletic relationship to the *Elephas intermedius* of Jourdan and to the *E. trogontherii* of Pohlig.

The ridge formula, M 3 $\frac{+17\frac{1}{2}}{}$, indicates that *E. armeniacus* Falconer is in about the same stage of evolution as the type of *E. trogontherii* Pohlig, in which the ridge formula is said to be M 3 $\frac{15+}{16+}$. While Falconer repeatedly described the type of *E. armeniacus* as intermediate in character between *E. primigenius* and *E. indicus*, but approaching the latter species more closely, Osborn regards it rather as belonging to the same phylum as *E. intermedius* and *E. trogontherii* and refers it to the independent genus *Parelephas*.

PARELEPHAS ERRONEOUSLY RECORDED IN CHINA AND JAPAN

Erroneous are the records of *Parelephas* in China and Japan. The supposed *Elephas armeniacus* (Brit. Mus. 29007) is related (Lydekker, 1886.2, p. 169, Hopwood, letter, 1928) to *Elephas* [*Palæoloxodon*] *namadicus*. Matsumoto's types of *Parelephas protomammonteus* and *P. protomammonteus proximus* of Japan also belong to *Palæoloxodon*. The following literature may be quoted:

LYDEKKER (1886.3, P. 174).—"There is in the British Museum an elephant's molar from China (No. 29007), which has been suggested to belong to this species [*Elephas armeniacus*]; and if this were correct it would seem that the range of *E. armeniacus* was somewhat the same as that of *Rhinoceros Blanfordi*, *i.e.* that it extended from western Asia through the regions lying to the north of India and China; I am, however, disposed to refer the specimen to *E. namadicus*."

PARELEPHAS ARMENIACUS REF.—(Leith Adams and G. Busk, 1868, pp. 496–499): "In the British Museum there is a large part of a fossil molar tooth from China, which, on comparison with the teeth presented by Colonel Gills [Giels] from Armenia, so exactly resembles them in every respect, that no doubt can be entertained as to its belonging to the same species, namely, *E. Armeniacus* of Dr. Falconer; and as such, I believe, it was regarded by that eminent palæontologist. The occurrence, therefore, of the same form in Japan would not have been very surprising; but, so far as I am able to judge, it is impossible to identify Dr. Duggan's specimen with *E. Armeniacus*."

JAPAN.—The Japanese tooth found by Dr. Duggan, in company with Mr. Hodgson, in 1859, is referred to *Palæoloxodon* (see figure by Leith Adams, 1868.1, p. 497).[1]

Parelephas intermedius Jourdan, 1861

Figures 935, 943, 944

Pleistocene plateau loess, near Lyons, Rhone Valley, France. Type locality believed to be more recent (i.e., *?3d Interglacial*) than the *2d Interglacial* deposits of Süssenborn, containing the type of *Elephas* [=*Parelephas*] *trogontherii*.

Jourdan applied this name to the species of mammoth which he regarded as *intermediate* or transitional between *Elephas primigenius* and *E. indicus*. The name is appropriate today for the specific stage more progressive and geologically younger than *Parelephas trogontherii*. The history of this stage is very interesting, as detailed below. In referred grinding teeth from the same locality (Fig. 943), the ridge-plate formula is: M 1 $\frac{?}{12\text{-}13}$ M 3 $\frac{22}{}$. Depéret (letter, Sept. 10, 1924) assigns the following ridge formula: M 3 $\frac{20}{20\text{-}21}$.

In his original description of this species, Jourdan remarked that of all fossil elephants this approached most nearly to *Elephas indicus*. He applied the name *intermedius* to certain *broad* molars resembling in breadth the molars of *E. primigenius* but with thicker and more widely separated lamellæ, in distinction from the *narrow* molars of *E. antiquus*. Unfortunately the type molars of *E. intermedius* have been misplaced and no type figure was published; consequently the specific name *Elephas intermedius* Jourdan, 1861, although repeatedly cited, has not gained acceptance; none the less it is certainly valid. The species is related to but not identical with the widely known *Elephas* [=*Parelephas*] *trogontherii* of Pohlig, which in turn resembles the *Parelephas jeffersonii* of Osborn. Depéret and Mayet (1923) describe this animal throughout as *Elephas trogontherii*.

Elephas intermedius Jourdan, 1861. "Des terrains sidérolitiques," Compt. Rend. Acad. Sci., Tome LIII, 1861, p. 1013. TYPE DESCRIPTION.—(*Op. cit.*, p. 1013): "La faune du sidérolitique du néocène ou étages les plus supérieures des terrains tertiaires se caractérise donc dans ses couches inférieures par l'*Elephas meridionalis*, dans les couches moyennes par l'*Elephas antiquus*, et dans les supérieures par l'*Elephas intermedius*, qui, de tous les Éléphants fossiles, est celui qui présente le plus de rapport avec l'Éléphant actuel des Indes."

HISTORY.—Lortet and Chantre (1872, p. 79) observe: "*Elephas intermedius* (Jourdan, mss.).—Cette espèce, créée par M. Jourdan sur une forme de l'*Elephas antiquus* de Falconer, est celle qui est la plus commune dans le bassin du Rhône lyonnais; elle paraît même y avoir été cantonnée. Les caractères transitoires

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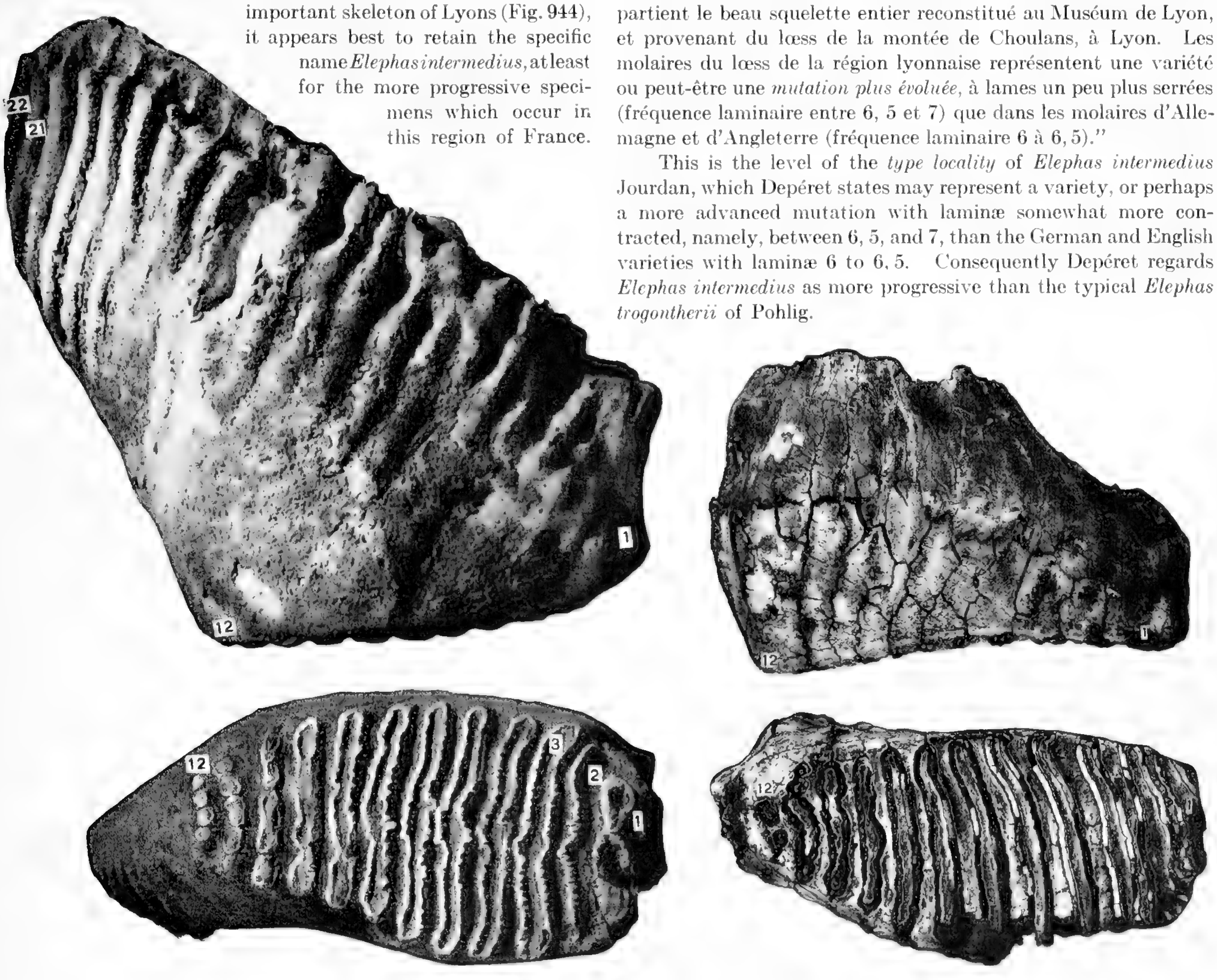
[1] [See page 1334 below.—Editor.]

entre l'*Elephas primigenius* et l'*Elephas antiquus*, faciles à constater sur de nombreuses pièces, ont engagé M. Jourdan à élever au rang d'espèce cette forme, et de lui assigner le nom spécifique d'*intermedius*. Ces caractères sont très-apparents sur certaines dents; cependant, parmi celles qui ont été considérées comme appartenant à l'*Elephas intermedius*, un grand nombre de pièces peuvent être rangées dans la catégorie de l'*Elephas antiquus*."

VALIDITY OF THE SPECIES ELEPHAS INTERMEDIUS (OSBORN, 1924).—Inasmuch as Jourdan's type description (1861, p. 1013) characterizes the species as being closely related to *Elephas indicus*, and inasmuch as Lortet and Chantre (1872, p. 79) cited the name, amplified the specific characters, and referred to this species the important skeleton of Lyons (Fig. 944), it appears best to retain the specific name *Elephas intermedius*, at least for the more progressive specimens which occur in this region of France. It appears best also to conserve the name *Elephas trogontherii* Pohlig for less progressive specimens from Pohlig's type locality, especially since according to Depéret, Mayet, and Pohlig this phylum (i.e., "rameau de l'*Elephas trogontherii* Pohlig") is of long duration.

TYPE LOCALITY OF E. INTERMEDIUS.—In the environs of Lyons remains of this species are found abundantly in the loess covering the plateaus (Depéret and Mayet, 1923, p. 182): "Aux environs de Lyon, il abonde dans le lœss des plateaux (Saint-Cyr, Saint-Romain-au-Mont-d'Or, la Duchère, Fourvière, Caluire, Margniole, Croix-Rousse, Saint-Clair, le Vernay, etc.), où Jourdan l'a décrit sous le nom d'*E. intermedius*. C'est à cette espèce qu'appartient le beau squelette entier reconstitué au Muséum de Lyon, et provenant du lœss de la montée de Choulans, à Lyon. Les molaires du lœss de la région lyonnaise représentent une variété ou peut-être une *mutation plus évoluée*, à lames un peu plus serrées (fréquence laminaire entre 6, 5 et 7) que dans les molaires d'Allemagne et d'Angleterre (fréquence laminaire 6 à 6, 5)."

This is the level of the *type locality* of *Elephas intermedius* Jourdan, which Depéret states may represent a variety, or perhaps a more advanced mutation with laminæ somewhat more contracted, namely, between 6, 5, and 7, than the German and English varieties with laminæ 6 to 6, 5. Consequently Depéret regards *Elephas intermedius* as more progressive than the typical *Elephas trogontherii* of Pohlig.



REFERRED MOLARS OF PARELEPHAS INTERMEDIUS, LYONS MUSEUM

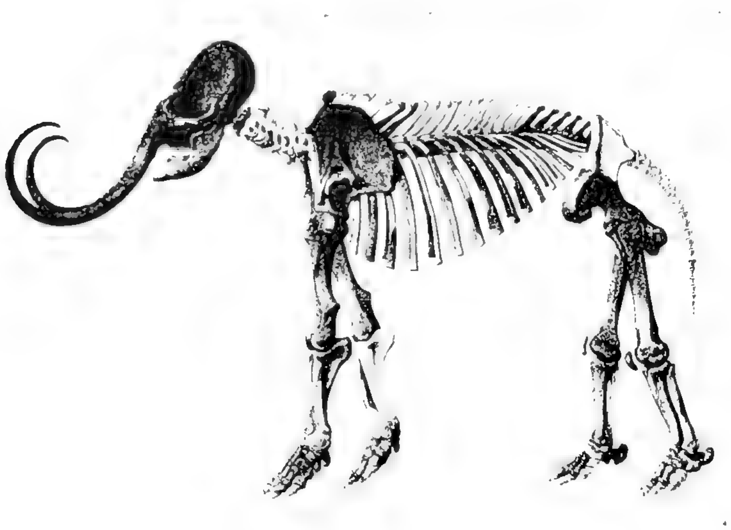
One-half natural size

Fig. 943. Superior molar teeth referred to *Elephas intermedius* Jourdan from the collection of the Muséum de la Ville à Lyon. After photographs, prepared under the direction of Doctors Depéret and Mayet (see letter of September 10, 1924).

(Left) This beautifully preserved r.M^3 exhibits 22 ridge-plates, of which the 12 anterior are worn.

(Right) This first inferior molar, l.M_1, exhibits 12 worn ridge-plates, but the formula appears to be (with an additional unworn ridge-plate): l.M 1_{13}.

Depéret (Translation of a Letter dated Lyons, August 26, 1921).—The *Elephas intermedius* was created by Jourdan, a former palæontologist of Lyons, who applied the name, unfortunately without a figure, to certain broad molars, which he ob-



Restored Skeleton of Parelephas intermedius, Lyons Museum
One-sixtieth natural size

Fig. 944. Restored skeleton referred by Jourdan to his species *Elephas intermedius.* The plate was prepared under Jourdan's direction but was first printed by Lortet and Chantre in the frontispiece of their Memoir of 1872[1876], from which it is here reproduced one-sixtieth natural size. The height is said to be 3 m. 75 cm. = 12 ft. 3½ in.

(Lortet and Chantre, *op. cit.*, p. 79): "*Elephas intermedius* (Jourdan, mss.).—Cette espèce, créée par M. Jourdan sur une forme de l'*Elephas antiquus* de Falconer, est celle qui est la plus commune dans le bassin du Rhône lyonnais; elle paraît même y avoir été cantonnée. Les caractères transitoires entre l'*Elephas primigenius* et l'*Elephas antiquus,* faciles à constater sur de nombreuses pièces, ont engagé M. Jourdan à élever au rang d'espèce cette forme, et de lui assigner le nom spécifique d'*intermedius.* Ces caractères sont très-apparents sur certaines dents; cependant, parmi celles qui ont été considérées comme appartenant à *l'Elephas intermedius,* un grand nombre de pièces peuvent être rangées dans la catégorie de l'*Elephas antiquus.* Dans la vallée de la Saône on a trouvé des ossements d'*Elephas intermedius,* dans le lehm ou à la limite des alluvions, à Lyon et aux environs. (Saint-Rambert-l'Ile-Barbe, le Vernay, Caluire, la Duchère, Vaise, la Demi-Lune, Saint-Just, Fourvière et la Quarantaine.) C'est à la Quarantaine que M. Jourdan a trouvé, en 1862, le squelette de l'individu qui a pu être remonté dans les galeries du Muséum de Lyon par les soins de M. Charles Révil, l'un de nos préparateurs. Ce squelette, un des plus grands et des plus complets que l'on puisse voir en Europe, mesure 3 mètres 75 centimètres de hauteur au garrot. Il est surtout remarquable par la courbure très-prononcée des ses énormes défenses et par les formes trapues et massives de ses membres."

This animal, discovered in the Pleistocene loess of the hill of St. Foy, Lyons, France, is regarded by Depéret and Mayet as similar to *Elephas trogontherii* Pohlig. Plateau loess ("provenant du lœss de la montée de Choulans, à Lyon." Depéret et Mayet). Depéret and Mayet remark (1923, p. 176): "Lortet et Chantre (1876) n'ont figuré de cette espèce que le squelette reconstitué du lœss de Choulans qui se trouve au Muséum de Lyon et forme le frontispice de leur ouvrage; mais ils n'ont donné malheureusement aucune figure des molaires de l'*E. intermedius,* devenu ainsi une espèce purement *nominale,* qui ne saurait être retenue." The skull is said to be *erroneously restored* at the summit of the occiput. The rounded summit of the cranium in the above figure agrees fairly well with the rounded summit characteristic of *Parelephas trogontherii;* the tusks appear to be recurved rather than incurved as in *Parelephas jeffersonii.*

served to be very distinct from the narrow molars of the *Elephas antiquus* type, molars resembling in breadth those of *Elephas primigenius,* but with thicker and more widely separated lamellæ. Lortet and Chantre in their memoir on the Mastodons and the Elephants (Archiv. Mus. Lyon, T. I., 1872, et T. II, 1879) cited this species and figured other pieces which could be related to it. I believe that *E. intermedius* is probably the same animal as that named by M. Gaudry *Elephas primigenius* var. à *lames écartées* and by Pohlig *Elephas trogontherii.* We have at Lyons in the University Museum also in the Municipal Museum numerous molars of this species and even a *complete skeleton* discovered in the loess of the hill of St. Foy at Lyons. It is this complete skeleton [Fig. 944] which has been figured by Lortet and Chantre, but in the *absence of figures of the type* itself I fear that it may be necessary for us to adopt the name of *trogontherii* which appears to have priority.

Depéret and Mayet, 1923, p. 176.—Depéret and Mayet, while regarding *E. intermedius* as conspecific with *E. trogontherii,* treat this animal as follows: "III Groupe des Elephas trogontherii et E. primigenius (Mammouths). Le groupe des Mammouths comprend des Eléphants de taille moyenne, au crâne allongé, au vertex trés élevé et étroit en haut (crânes en dôme), aux défenses fortement spiralées, aux molaires généralement larges et hautes (type *hypsélodonte*), avec lames nombreuses plus ou moins serrées dont les bandes d'émail sont parallèles et ne présentent pas de sinus loxodontes médians. Nous y distinguerons deux rameaux ayant vécu parallèlement depuis le Pliocène supérieur jusque dans le Quaternaire: A. Le rameau de l'*E. trogontherii* Pohlig. B. Le rameau de l'*E. primigenius* Blumenbach."

Depéret and Mayet continue: "A. Rameau de l'Elephas trogontherii.—Jourdan avait reconnu le premier, voici plus d'un demi-siècle, parmi les molaires de Mammouth de la région lyonnaise, une forme aux lames plus épaisses, plus écartées et moins nombreuses que dans le Mammouth normal et lui avait donné le nom d'*E. intermedius.* Lortet et Chantre (1876) n'ont figuré de cette espèce que le squelette reconstitué du lœss de Choulans qui se trouve au Muséum de Lyon et forme le frontispice de leur ouvrage; mais ils n'ont donné malheureusement aucune figure des molaires de l'*E. intermedius,* devenu ainsi une espèce purement *nominale,* qui ne saurait être retenue."

Gaudry (1876, p. 40 also Pl. ix) and Leith Adams (1877, p. 31) observe similar intermediate forms of teeth in Louverné (Mayenne), France, and in England in the Forest-bed, to the middle of the Pleistocene.

Finally (Depéret and Mayet, 1923, p. 177): "C'est à Pohlig que nous devons d'avoir distingué, parmi les Eléphants quaternaires d'Allemagne, sous le nom d'*E. trogontherii* (1889, p. 189), une forme particulière du groupe des Mammouths, dont les molaires ont une couronne large, comme chez les *E. meridionalis* et *primigenius,* mais avec un nombre total de lames (14 à 22 aux Miii) supérieur à la moyenne de l'*E. meridionalis* (12 à 14), mais inférieur à celle de l'*E. primigenius* (18 à 27). Cet *E. trogontherii* est d'ailleurs absolument identique à l'*E. intermedius* de Jourdan, comme nous avons pu nous en assurer sur les nombreux sujets du lœss de la région lyonnaise."

Thus Depéret and Mayet first concluded that the *Elephas trogontherii* of Pohlig is absolutely identical with the *Elephas intermedius* of Jourdan, but subsequently stated (p. 183) that it belongs to a more progressive stage, thus agreeing with Osborn's opinion in the present Memoir.

Geographic Distribution of E. intermedius-trogontherii Phylum.—Depéret and Mayet (*op. cit.*, p. 180) declare that with the exception of the rare molars of the Upper Pliocene of Astésan, *Elephas trongontherii* represents a very distinctive Quaternary branch or phylum:

(1) "La *distribution géographique* s'étend de l'Est à l'Ouest depuis la Russie jusqu'à l'Europe occidentale et du Sud au Nord depuis l'Italie jusqu'aux Iles Britanniques. Laissant de côté les détails de cette dispersion géographique, nous essayerons seulement de préciser l'étendue de sa répartition stratigraphique dans le terrain quaternaire."

(2) In England the species [i.e., phylum] appears very abundantly at the beginning of the Quaternary period in the Forest-bed of Cromer, or Sicilian stage, where it has been described and figured under different names by Leith Adams (1877); it persisted in England to higher Quaternary levels, namely, to the gravels of the terrace of 30 meters (Tyrrhenian stage of Depéret, Chellean industry).

(3) In Germany the species *E. trogontherii* was first[1] observed in the ancient gravels at Süssenborn near Weimar, contemporaneous with the deposits of Mosbach, and of Mauer near Heidelberg; this is *2d Interglacial* time of the Osborn-Reeds Table (Pl. xxiv) of the present Memoir; at this time the species appears to be very abundant in Europe.

(4) In Europe the species [i.e., phylum] *E. trogontherii* becomes extinct in *3d Interglacial* time and is replaced by the true mammoth *Elephas primigenius* during the period of the Fourth Glaciation.

(5) In southern France *E. trogontherii* does not occur in the Sicilian stage (Durfort, Solilhac, Malbattu, Rozières) in which *Elephas meridionalis* is abundant.

Ridge Formula (Letter, Depéret, September 10, 1924).—"Ces jours derniers, nous avons pu enfin faire avec M. Mayet quelques recherches au Muséum de la ville où se trouvent environ une trentaine de molaires de cette espèce. Malheureusement il y en a fort peu qui soient des M^3 intactes et susceptibles de fournir des mensurations.

De l'ensemble de mes mesures vous pouvez en toute sécurité inscrire le chiffre $\frac{20\text{-}(22)}{20\text{-}21}$ pour la formule des M^3 de l'*Elephas intermedius*: c'est donc une mutation de passage entre le *trogontherii* et votre *E. roosevelti* [*P. jeffersonii*]. J'ai déjà eu cette impression dans mon Mémoire sur les Eléphants pliocènes et j'ai été très sensible à l'éloge que vous voulez bien faire de ce travail."

Parelephas wüsti Pavlow, 1909

Figure 945

Upper Pleistocene gravels of Tiraspol (gouv. Kherson), southern Russia.

This most welcome discovery by Pavlow (1909.1[2] – supplemented by letters of May 31 and August 22, 1924) probably represents an Upper Pleistocene stage about as progressive (M 3 $\frac{22}{20}$) as the *Elephas intermedius* of Jourdan, namely, M3 $\frac{22}{21}$. It is the most easterly record of this phylum, with the possible exception of the tooth erroneously recorded from China, as noted above, page 1062.

This specific stage of *Parelephas* is certainly more progressive than the *P. trogontherii* of the *1st Interglacial* gravels of Süssenborn, a level containing *Dicerorhinus etruscus* and *Equus süssenbornensis* (see Table, p. 1044 above) and now regarded as of Lower Pleistocene age, and the ridge-plate formula agrees closely with that of *P. intermedius* of the plateau loess near Lyons. The upper level of Süssenborn, containing *Elephas trogontherii* type, is attributed to the *2d Interglacial* stage, that is, more recent than II Glacial.

Pavlow (1910, pp. 6–18), in describing the dentition of *Elephas wüsti* of Tiraspol, bases her description on a series of superior and inferior molars (Dp 3–M 3) from the Tiraspol collection of Moscow, excellently figured (as reproduced in our Fig. 945) from photographs in Pl. i, figs. 1–12 inclusive. In the same plate (fig. 23) appears a third inferior molar from Tiraspol in the Geological Collection of the University of Moscow which she refers to *Elephas hysudricus*.

Pavlow at first states (p. 7) that the second molars [= Dp 3] approach those of *Elephas meridionalis* of the Val d'Arno (Weithofer, 1890, Pl. xii) and of *Elephas antiquus* of Weimar (Pohlig, 1891, Taf. 2 bis, fig. 8), but on the final page (p. 18) she concludes: "Prenant en considération que les dents de Süssenborn, décrites par Wüst sous le nom de l'*El. trogontherii* Pohl., se distinguent des formes pour lesquelles Pohlig a créé ce nom, nous proposons un nouveau nom spécifique de l'*El. Wüsti* pour nos formes, celles de Süssenborn, décrites par Wüst, et les formes de Tiraspol, décrites par Mr. Sinzow." It is therein suggested that *Elephas wüsti*, a species dedicated to Doctor Wüst, is not remote from the *Elephas trogontherii* Pohl. of Süssenborn. So far as we can judge from Pavlow's figures (Pl. i) and description (pp. 6–18) the cotype molars of either side have the following ridge formula:

Parelephas wüsti: Dp 3 $\frac{5\text{-}6}{?}$ Dp 4 $\frac{10}{10}$ M 1 $\frac{14\text{-}15}{13\text{-}14}$ M 2 $\frac{16\text{-}18}{15\text{-}16}$ M 3 $\frac{20\text{-}22}{19\text{-}20}$.

Parelephas trogontherii: Dp 3 $\frac{5\text{-}7}{7}$ Dp 4 $\frac{9}{10}$ M 1 $\frac{10\text{-}12}{11\text{-}13}$ M 2 $\frac{11\text{-}15}{11\text{-}15}$ M 3 $\frac{16\text{-}21}{16\text{-}21}$.

Geologic Level.—(Pavlow, *op. cit.*, 1910, pp. 1 and 4): "Une grande collection de dents et d'ossements d'*Eléphants fossiles*, provenant du gravier de Tiraspol (gouv. Kherson) et se trouvant dans le Cabinet géologique de l'Université de Moscou, a dû servir de matériaux pour l'ouvrage présent. . . . Le fait est que les dents sont bien représentées, elles forment presque une série complète et peuvent donner une bonne idée des caractères généraux du système dentaire; tandis que jusqu'à présent il n'y a que quelques dents isolées de ces dépôts qui ont été décrites par Mr. Sinzow sous le nom d'*Elephas trogontherii* Pohl. . . . Je commencerai mon travail par la description des *Eléphants de Tiraspol*, autant qu'ils m'ont servi de base dans mon étude; après quoi j'en ferai la comparaison avec les autres formes d'éléphants pour déterminer leur position dans la ligne du développement. J'ai déjà signalé que les dents d'éléphants provenant de cette localité ont été citées par plusieurs savants, Mrs Sokolow, Sinzow, Laskarew, sous les noms

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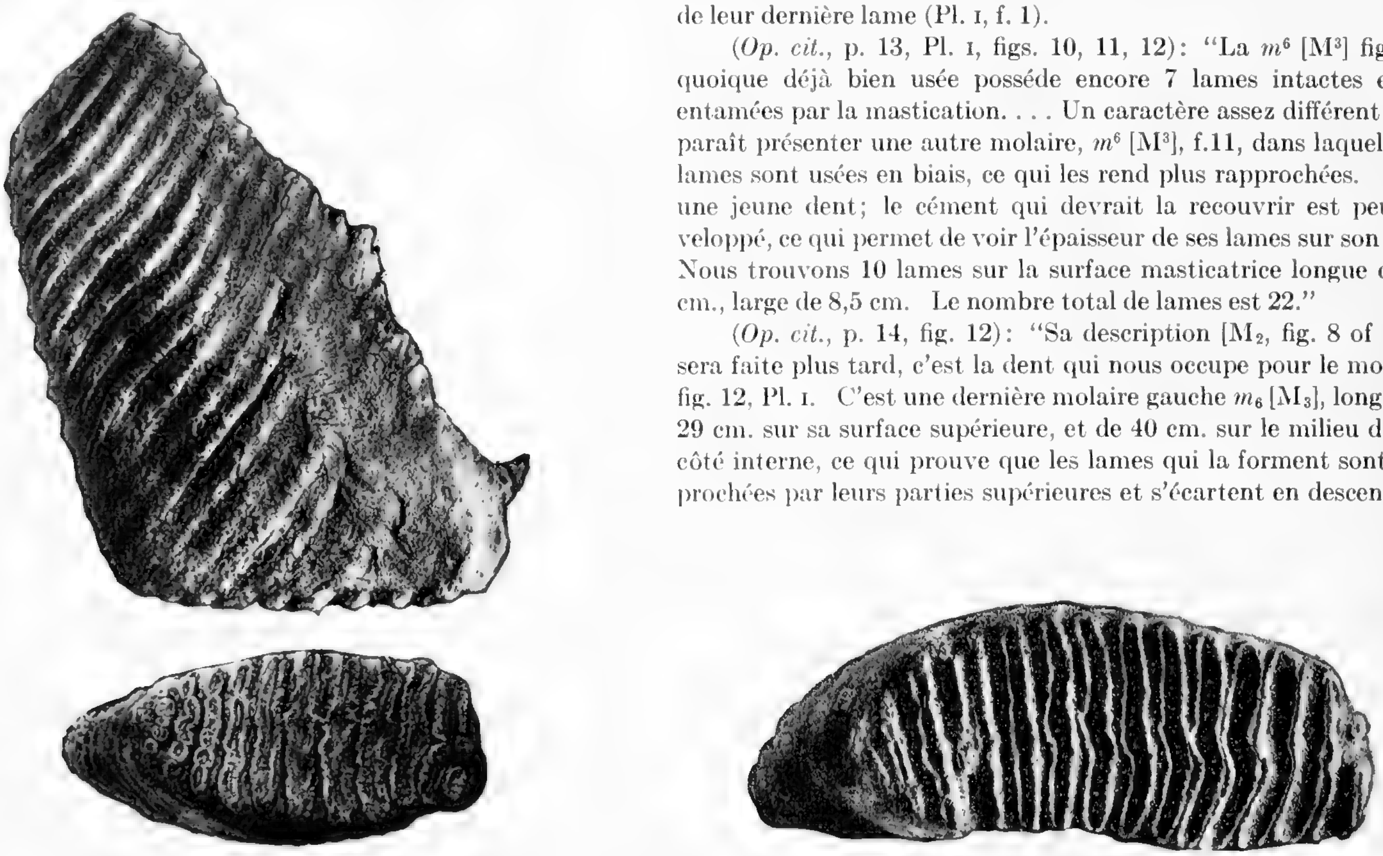
[1] [See page 1044 above where Soergel lists *Parelephas trogontherii* as abundant in Mosbach in *1st Interglacial* times.—Editor.]

[2] Original description in Russian (French translation) "Les éléphants posttertiaires de diverses localités en Russie (Annuaire géol. et minéral. Russie, 1909, Vol. XI, Livr. 6–7, pp. 171–174, Pl. v, figs. 1,2); supplementary description "Les Éléphants Fossiles de la Russie" (Nouv. Mém. Soc. Imp. Naturalistes, Moscou, 1910, Tome XVII, Livr. 2, pp. 6–18, Pl. i, figs. 1–12).

divers: tantôt c'était *El. meridionalis,* tantôt *El. antiquus,* mais dans ces derniers temps on est arrivé à les rapporter à l'*El. trogontherii* Pohl. et c'est sous ce nom que Mr. J. F. Sinzow les a décrites et figurées dans son ouvrage [Footnote: 'J. Sinzow. Geol.-Palaeonth. Beobacht. in. Südrussland. 1900. Odessa. Pl. IV, V.']."



Cotypes of Parelephas wüsti
One-fourth natural size

Fig. 945. Cotypes (M^3) of *Elephas wüsti* Pavlow, 1910, Pl. I, fig. 10 (lower right), same as Pavlow, 1909.1, Pl. V, fig. 1; figs. 11 (lower left), and 11*a* (upper left). From Tiraspol, southern Russia. Originals in the Tiraspol Collection, University of Moscow.

Elephas Wüsti Pavlow, 1910. "Les Éléphants Fossiles de la Russie," Nouveaux Mémoires de la Société Impériale des Naturalistes de Moscou, Tome XVII, Livr. 2, pp. 6–18. Cotypes.—Series of superior and inferior molars (Dp3–M 3), indicated by Pavlow as M 2-M 6, in the Cabinet géologique de l'Université de Moscou. Horizon and Locality.—Gravels of Tiraspol (gouv. Kherson), South Russia. Upper Pleistocene. Cotype Figures.—Pavlow, 1909.1, Pl. V, figs. 1 and 2; 1910.1, Pl. I, figs. 1–12 inclusive. Two of the cotypes are shown in figure 945 of the present Memoir.

Supplementary Description.—(Pavlow, *op. cit.,* 1910.1, p. 6, fig. 1): "Je commence par les dents qui doivent être rapportées à la même espèce. Nous avons déjà indiqué que les premières molaires supérieures et inférieures (les m^1, m_1 [$=$ Dp^2, Dp$_2$]) manquent dans la collection de Tiraspol. Pour les *deuxièmes molaires* [= Dp 3] nous avons deux exemplaires presque identiques, privés de leur dernière lame (Pl. I, f. 1).

(*Op. cit.,* p. 13, Pl. I, figs. 10, 11, 12): "La m^6 [M^3] fig. 10, quoique déjà bien usée possède encore 7 lames intactes et 13 entamées par la mastication. . . . Un caractère assez différent nous paraît présenter une autre molaire, m^6 [M^3], f.11, dans laquelle les lames sont usées en biais, ce qui les rend plus rapprochées. C'est une jeune dent; le cément qui devrait la recouvrir est peu developpé, ce qui permet de voir l'épaisseur de ses lames sur son côté. Nous trouvons 10 lames sur la surface masticatrice longue de 16 cm., large de 8,5 cm. Le nombre total de lames est 22."

(*Op. cit.,* p. 14, fig. 12): "Sa description [M$_2$, fig. 8 of Pl. I] sera faite plus tard, c'est la dent qui nous occupe pour le moment fig. 12, Pl. I. C'est une dernière molaire gauche m_6 [M$_3$], longue de 29 cm. sur sa surface supérieure, et de 40 cm. sur le milieu de son côté interne, ce qui prouve que les lames qui la forment sont rapprochées par leurs parties supérieures et s'écartent en descendant. Les 6 lames antérieures sont les seules usées, quoique faiblement; les deux suivantes sont à peine entamées; les 12 qui suivent sont intactes."

Conclusion, Osborn, 1928: It would appear that the molars of *Parelephas wüsti* are closely related in their ridge-plate formula to the collective formula of *P. trogontherii* and *P. intermedius.* From a comparison, however, of the above formulæ, it would also appear that *P. wüsti* is a somewhat more progressive species, with a slightly higher dental ridge-plate formula, than that of *P. trogontherii.* Consequently it appears to be closest to the *P. intermedius* stage of Jourdan.

3. NORTH AND SOUTH AMERICAN SPECIES OF PARELEPHAS

Migration from Eurasia.—As shown above, the *Parelephas* phylum becomes known in the Upper Pliocene[1] of Italy in *Parelephas trogontherioides* (M 3 $\frac{\frac{1}{2}\text{-}14\text{-}\frac{1}{2}}{\frac{1}{2}\text{-}14\text{-}\frac{1}{2}}$); it reappears in the *1st Interglacial* stage of the Cromer Forest Bed, East Anglia, in *P. trogontherii* ref.? (M 3 $\frac{15+}{21+}$—see Fig. 871); it is very abundant in the *2d Interglacial* of Süssenborn near Weimar (M 3 $\frac{15+}{16+}$, type—see p. 1056); it continues in *P. intermedius* of southern France (M 3 $\frac{20\text{-}22}{20\text{-}21}$—see p. 1062); again it is found in *P. wüsti* of southern Russia (M 3 $\frac{22}{20}$—see p. 1065 above). During the *3d Interglacial* period it apparently migrated from western Eurasia, but future discoveries may reveal its presence in eastern Eurasia in northerly latitudes. The next record is in the state of Washington in *Parelephas washingtonii* (M 3 $\frac{-}{21}$), with the least progressive ridge formula thus far observed in America; it then becomes very abundant, under favorable conditions of the Middle United States, in *Parelephas jeffersonii* (M 3 $\frac{25}{24}$), appearing to culminate in the highly progressive *P. progressus* (M 3 $\frac{30}{26}$). Meanwhile the giant *Parelephas floridanus* (M 3 $\frac{22+}{21+}$) appeared in Florida.

In the opening section of this chapter we have briefly described the steps taken by Osborn toward the separation of species of the genus *Parelephas* from *Mammonteus primigenius*, on the one hand, and from the true *Elephas columbi* of the southern United States, on the other. To our present knowledge the order of description of the American species has been as follows (see p. 1047 and fig. 933):

1838	Jackson County, Ohio	*Elephas jacksoni* Mather	=*Parelephas jacksoni*
1857–1868	Brunswick Canal, Georgia	*E.* (*Euelephas*) *columbi* Falconer	=*Parelephas columbi*
1859–1861	Texas	*Elephas texianus* Owen, 1859, Blake, 1861	=*Parelephas columbi*
1872	Indiana	*Elephas mississippiensis*	=*Parelephas*(?) *mississippiensis*(?)
1922	Jonesboro, Indiana	*Elephas jeffersonii* Osborn	=*Parelephas jeffersonii*
1922	Mexico	*El.* [*Elephas*] *columbi* var. *Felicis* Freudenberg	=*Parelephas columbi felicis*
1922	Ashland, Cass County, Illinois	*Elephas roosevelti* Hay	=*Parelephas jeffersonii*
1923	Pine Creek, Whitman County, Washington	*Elephas washingtonii* Osborn	=*Parelephas washingtonii*
1924	Zanesville, Ohio	*Parelephas jeffersonii progressus* Osborn	=*Parelephas progressus*
1926	Port Williams, Clallam County, Washington	*Elephas eellsi* Hay	=*Parelephas*(?) *eellsi*
1929	Florida, near Bradenton	*Parelephas floridanus* Osborn	=*Parelephas floridanus*
1929	French Guiana, So. America	*Parelephas columbi cayennensis* Osborn	=*Parelephas columbi cayennensis*

As to the generic reference of the above species, the type jaw of '*Elephas jacksoni*' Mather, 1838, has been lost,[2] fortunately, however, the figure (Fig. 946), intentionally published by the author side by side with that of *Elephas primigenius*, enables us, by comparison with the jaws of the type and paratype of *Parelephas jeffersonii* (Figs. 960, 967, 892) to determine positively the generic reference to *Parelephas* of this classic American species. It is important to credit W. W. Mather, Geologist of the Geological Survey of Ohio, with being the first to point out the clear distinctions which separate the jaw and inferior dentition of *Parelephas* from the jaw and inferior dentition of *Mammonteus primigenius*.

The second species, *Elephas columbi*, originally described by Falconer in 1857 and more fully defined in 1868, has been referred by the writer to the genus *Parelephas*, as set forth below in the present chapter under the heading "The Columbian Mammoth (Parelephas columbi)."

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[1] [See footnote 1, page 1049 above.—Editor.]

[2] With the aid of Prof. Raymond C. Osburn and Prof. J. Ernest Carman of the Ohio State University, the museums of the state have been thus far searched in vain. A "supposed type" (a lower jaw from Jackson County), found by Prof. Ralph W. Whipple in the collection of Marietta College, does not agree with Mather's type figure, which was of a younger individual.

The third species, *Elephas texianus*, first named (1859) by Owen and later (1861, 1862) described by Blake, is treated in the present Memoir as a synonym of *Parelephas columbi*.

The fourth species named, but neither described nor figured, is the *'Elephas' Indianapolis* or *mississippiensis* of Foster, 1872, an indeterminate species probably referable to *Parelephas*.

Fortunately the fifth species described, namely, *Elephas* (*Parelephas*) *jeffersonii* Osborn, 1922, is based upon a superb type specimen (Fig. 966) which had previously been erroneously described by Osborn (1907) as *Elephas columbi*, and redescribed by Hay (1914) as *Elephas primigenius*. This genotypic species is now the most completely known of all the extinct proboscideans, for the aged grinding teeth (Fig. 959) of the senescent type specimen are supplemented by superb paratype[1] specimens (Figs. 960, 967, 892), also by very large numbers of teeth and jaws collected from the great geographic belt of the 40th parallel northward occupied by species of this genus.

The type ridge formula of *Parelephas jeffersonii*, in comparison with that of other American species, is given on page 1070 below.

Osborn would gladly surrender priority in specific nomenclature to Mather, if Mather's type should be located and compared. It appears from the above ridge-plate formulæ, actual and estimated, that if we are able to locate the type of *Parelephas jacksoni* (indirectly named after President Andrew Jackson), we may be able to determine that it is conspecific with *Parelephas jeffersonii* (named after President Jefferson). In the same presidential line of nomenclature is also *Elephas* [=*Parelephas*] *roosevelti* Hay, 1922 (named after President Roosevelt), herein shown to be a synonym of *Parelephas jeffersonii*. Finally, *Parelephas washingtonii* was named after the first President of the United States. It will be observed that *P. washingtonii* is apparently the least progressive in its ridge formula, namely, $M\,3\,\frac{}{21}$, which is similar to that of *P. intermedius* of southern France, namely, $M\,3\,\frac{20\text{-}22}{20\text{-}21}$, also to that of *P. wüsti* of southern Russia, $M\,3\,\frac{22}{20}$, as shown in the comparative table above (p. 1048).

Parelephas jacksoni Mather, 1838

Figure 946

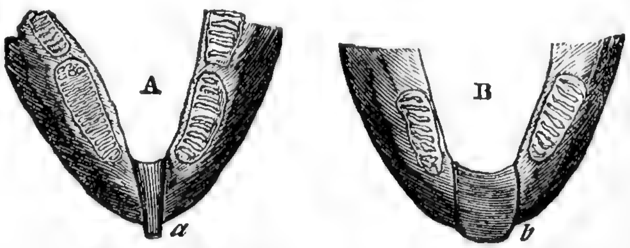
Pleistocene, Jackson County, Ohio.

Compare *Elephas indianapolis* or *mississippiensis* Foster, 1872; also *Elephas (Parelephas) jeffersonii* Osborn, 1922–1924.

Compare Leidy, 1869, p. 399, who suggested that if *E. jacksoni* were adopted, to be correct, it should read *E. jacksonensis*.

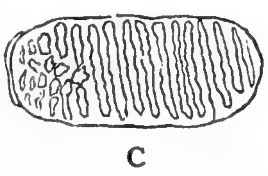
Elephas jacksoni Mather, 1838, is interesting as the earliest name given to any species of American mammoth, even antedating *Elephas americanus* De Kay (1842) and *E. columbi* Falconer (1857). The figure and description indicate that this is a valid species, which will be recognized if the type can be located; Hay states (letter dated March 14, 1922) that in his examination of the Pleistocene mammal collections of the United States he has not been able to locate this type jaw. Mather's description of *E. jacksoni* was reviewed by Falconer (1863, p. 57) and the species regarded as indeterminate. Hay (1923, p. 147) also regarded the species as "wholly indeterminable."

E. [*Elephas*] *jacksoni* Mather, 1838. "First Annual Report on the Geological Survey of the State of Ohio," embodying Report of C. Briggs, Jr., Fourth Assistant Geologist, pp. 96, 97, with geologic section (1838.1 Fig. 947 of present Memoir); review of First Annual Report on the Geological Survey of Ohio, quoting portions of Report by C. Briggs, Jr., Amer. Journ. Sci. and Arts, Vol.



A. Lower jaw of the Elephant found at Jackson.

B. Lower jaw of the fossil Elephant.



TYPE OF PARELEPHAS JACKSONI

Fig. 946. Juvenile type jaw (A) of *Elephas jacksoni* Mather, 1838, from Jackson County, Ohio, as distinguished from a lower jaw (B) referred by Mather to *Elephas primigenius*. Type specimen not located at present. Also (C) supplementary drawing of r.M_2 exhibiting sixteen *worn ridge-plates*. Reproduced after Mather's type figure (1838.3, p. 363).

A young jaw exhibiting the right and left second inferior molars and a few ridge-plates of the third inferior molars, unevenly worn on the opposite sides, consequently exhibiting an unequal number of worn ridge-plates.

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[1] Technically ideotype (see Schuchert, 1905.2, p. 15), because strictly speaking a paratype must be one of the specimens mentioned in the original description.

XXXIV, p. 358 (1838.2); "Remarks in addition to and explanation of the Review of the Report of the Geological Survey of Ohio—in a letter to the Editor," Amer. Journ. Sci. and Arts, Vol. XXXIV, pp. 362–364 (description, name, and figure—1838.3). TYPE.—Lower jaw from Jackson County, Ohio. TYPE FIGURE.—*Op. cit.*, 1838.3, p. 363, fig. A, also supplementary figure on the same page of the crown of r.M_2, exhibiting 16 worn ridge-plates.

This type jaw, according to the following citation from Mather (*op. cit.*, 1838.2, p. 358) appears to be part of the skeleton found on "one of the branches of Salt creek, in the northwest part of Jackson county," Ohio:

"Among the most interesting details of this report [Report of C. Briggs, Jr., to the Geological Survey of Ohio, on the work of J. W. Foster and himself], are those respecting the fossil elephant discovered during the past season. As there is some doubt as to the geological position of the deposits in which these bones are found, we will extract the description."

'About two years ago, some bones, so large as to attract the attention of the inhabitants, became exposed in the bank of one of the branches of Salt creek, in the northwest part of Jackson county. They were dug out by individuals in the vicinity, from whom we obtained a tooth, a part of the lower jaw, and some ribs. In the examinations at this place, during the past season, it was concluded to make further explorations, not only with the hope of finding other bones, but with a view of ascertaining the situation, and the nature of the materials, in which they were found. The explorations were successful. There were found some mutilated and decayed fragments of the skull, two grinders, two patellæ, seven or eight ribs, as many vertebræ, and a tusk. Most of these are nearly perfect, except the bones of the head. The tusk, though it retained its natural shape as it lay in the ground, yet, being very frail, it was necessary to saw it into four pieces in order to remove it.'

'The following are the dimensions of the tusk, taken before it was removed from the place in which it was found:—

Length on the outer curve,	10 feet	9 inches.
" " inner curve,	8 "	9 "
Circumference at base,	1 foot	9 "
" 2 feet from base,	1 "	10 "
" 5 " " "	1 "	11 "
" 7½ " " "	1 "	7½ "

'This tusk weighed, when taken from the earth, 180 lbs. The weight of the largest tooth is 8¼ lbs.'

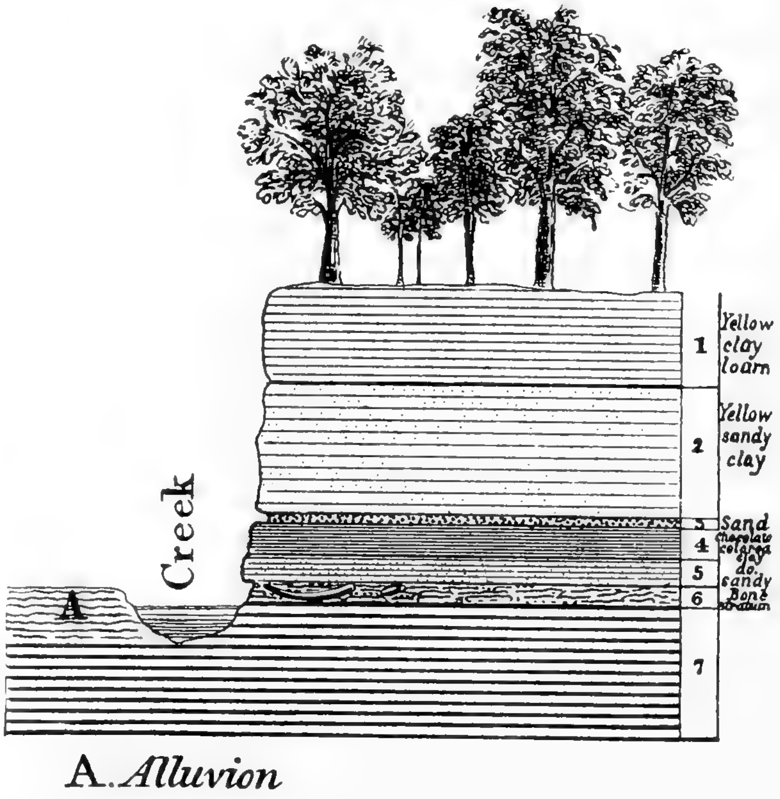
'These bones were dug from the bank of a creek, near the water, where they were found under a superincumbent mass of stratified materials, fifteen to eighteen feet in thickness.'

"The place where these bones occur is evidently a lacustrine deposit, consisting of horizontal layers of sand, loam and marly clay. The layer in which the bones occurred is dark blue, colored by phosphate of iron."

TYPE DESCRIPTION.—(*Op. cit.*, 1838.3, pp. 362, 363). Distinguished from "*E. primogeneus*" and "*E. recens.*" "You will perceive . . . that the jaw A converges more than B. In this respect, it approaches the existing species. There is also a remarkable difference in the construction of the canals, *a* and *b*. The tusk of the Jackson elephant is cornuform, more so than those of the existing elephant, but less so than in the fossil elephant. . . . From these differences, we think that it cannot belong to the *E. primogeneus* of Cuvier, and yet we are not prepared to say that it is identical with the *E. recens.*"

REFERRED SPECIMEN.—(Hay, 1923, p. 147): "2. *Hamilton, Wentworth County* [Ontario, Canada].—In 1863 (Canad. Nat. and Geol., vol. VII, p. 135) a lower jaw of an elephant was described under the name *Euelephas jacksoni* Briggs and Foster. This had been found near Hamilton, at the extreme western end of Lake Ontario. It was mentioned and figured as *Euelephas jacksoni* in the same year by W. E. Logan (Rep. Geol. Surv. Canada, p. 914, figs. 495, 497). The specific name, however, is not to be credited to Briggs and Foster, for it was proposed by W. W. Mather in 1838

Fig. 3



TYPE LOCALITY OF PARELEPHAS JACKSONI

Fig. 947. Diagrammatic cross-section of the bank of Salt Creek, Jackson County, Ohio, including the stratum containing the type of *Elephas jacksoni* Mather. After Mather, 1838.1, fig. 3.

(*Op. cit.*, 1838.1, p. 97): "No. 6 is the stratum containing the bones. It consists, judging from external characters, of sand and clay, containing a large proportion of animal and vegetable matter—1 to 1½ foot. [Footnote: 'All these layers, with the exception of the ferruginous sand, contain so much carbonate of lime as to effervesce briskly with acids'.] These bones, from their position, had evidently been subjected to some violence before they were covered with the stratified deposits which have been described. The jaw and grinders, with the other bones which we have thus slightly noticed, evidently belong to an extinct species of the elephant, now found in a fossil state. As the teeth differ from any which are figured and described in the books to which I have access at the present time, it is possible they may belong to an undescribed species."

(Amer. Jour. Sci., vol. XXXIV, p. 362, figures) for a lower jaw of an elephant found in Jackson County, Ohio. This jaw is, however, from the description and the figure, wholly indeterminable."

Referred to Parelephas (Osborn, 1924): Osborn observes that the type figure (Fig. 946 A, C) is sufficiently characteristic, accompanied by Mather's quaint description, to distinguish this jaw from that of *Mammonteus primigenius* and to relate it rather to *Parelephas*. Allowing for the primitive wood engraving, the rostrum (*a*) of *Elephas jacksoni* resembles quite closely the rostrum of *Parelephas jeffersonii* paratype (Amer. Mus. 13225) shown in figure 960 B of the present Memoir; this rostrum would be more prominent in an immature jaw like the type of *Elephas jacksoni* than in a mature jaw.

The second feature of note is the fact that M_2 is still in use and that M_3 is coming into use; this individual is therefore younger than either of the paratypes of *P. jeffersonii* (cf. Fig. 960). The number of ridge-plates shown in this wood engraving is M 2 $\frac{}{\text{r.16, l.10+}}$ M 3 $\frac{}{\text{r.7, l.6+}}$ (incomplete) which agrees fairly well with the ridge-plate formula of M 2 $\frac{18\text{-}19e}{19e}$ assigned to *Parelephas jeffersonii.* Consequently it appears probable that *Elephas jacksoni* is related to the genus *Parelephas* rather than to the genus *Mammonteus.* It would be of the utmost interest to discover this young type jaw and to determine more closely its actual relationships. The tusk measurements cited above from Mather (outer curve 10 ft. 9 in.) accord in size with those of the type of *Parelephas jeffersonii* (outer curve 11 ft. 4⅝ in.), since the type of *P. jacksoni* belongs to a much younger animal than the type of *P. jeffersonii*, an aged bull.

Parelephas (?) **mississippiensis** (?) Foster, 1872

From Indiana, exact locality not recorded.

Elephas indianapolis Foster, 1872. "Elephas Indianapolis. A New Species of Fossil Elephant." Proc. Amer. Assn. Adv. Sci., August, 1872, p. 259.

Calvin, 1911, p. 213 (footnote) states: "*Elephas indianapolis*, a new species of fossil elephant, by J. W. Foster. Proceedings of the American Association for the Advancement of Science, twenty-first meeting, held at Dubuque, August, 1872, p. 259. The title only is printed in the Proceedings. After the reading of the paper, and at the suggestion of some of the naturalists present, Foster proposed to change the name to *Elephas mississippiensis,* and under this designation there is a short reference to the paper and the proposed species in "Nature," Vol. VI, p. 443.

"Nature," 1872, September 26, p. 443: "Prof. J. W. Foster of Chicago, read a paper on what he considers a new species of fossil elephant, called by him *Elephas Mississippiensis.* He presented to the association a fossil tooth found in Indiana, and which he regards as differing specifically from that of any other fossil elephant found in America or on the Continent. The differences are so great that he holds them sufficient to constitute the new species."

Calvin, 1911, p. 213: "At the meeting of the American Association for the Advancement of Science, in Dubuque, in 1872, the writer had the privilege of seeing the tooth, which Foster regarded as the type of a new species of fossil elephant, *Elephas indianapolis,* and of hearing his description of it, and one at least of the distinguishing characters of the supposed new species was the looping of the enamel from the middle of the grinding surface to the sides, instead of the usual arrangement of this tissue in elongated ellipses surrounding plates of dentine. In the bibliography and catalogue of the fossil vertebrata of North America, by Hay, Bulletin of the United States Geological Survey, No. 179, page 714, the tooth described by Foster is assumed to be one of the forms of molars of *Elephas primigenius.*"

Osborn, 1929: Genus and species indeterminate.

THE COLUMBIAN MAMMOTH (PARELEPHAS COLUMBI)

The second member of the *Parelephas* phylum to be described, figured, and named was the '*Elephas columbi*' of Falconer, 1857, representing a specific stage which has become widely known among all palæontologists as the Columbian Mammoth. As narrated in the early part of Chapter XVI, Falconer believed this animal to be identical with Leidy's '*Elephas* [=*Archidiskodon*] *imperator*.' Osborn for several years treated it under the genus *Archidiskodon* but as a species quite distinct from *A. imperator*; finally Osborn, with the accession of the new and rich materials now to be described, perceived its true phyletic relationship to the phylum *Parelephas*. It is, however, clearly separable from *Parelephas jeffersonii*, being much more primitive in its ridge formula, as shown in the following comparison of the five known outstanding American species of the genus *Parelephas*.

Parelephas progressus		M 3 $\frac{30}{26}$	*Parelephas floridanus*	M 3 $\frac{22+}{21+}$
Parelephas jeffersonii	M 2 $\frac{18\text{-}19e}{19e}$	M 3 $\frac{25}{24}$	*Parelephas columbi*	M 3 $\frac{19}{16+}$
Parelephas washingtonii		M 3 $\frac{}{21}$		

The low ridge formula of the true *Parelephas columbi* of Georgia and South Carolina (M 3 $\frac{19}{16+}$) is very surprising and significant; this low ridge formula of *P. columbi* appears to prove that its ancestors migrated into America early in Pleistocene time. This theory of the early geologic entrance into America of relatively primitive species of

Parelephas is supported by the primitive character of the lower jaw of *P. washingtonii* (Fig. 972), in which the type and referred ridge formula is M 3 $\frac{23}{21}$; as pointed out below, the ridge formula of *P. washingtonii* agrees quite closely with that of *P. intermedius* (M 3 $\frac{20\text{-}22}{20\text{-}21}$) of southern France. Taken altogether this evidence appears to indicate that the ancestors of *P. columbi* and of *P. washingtonii* may have passed across Europe and Asia and migrated far southward in North America during the *2d* and even possibly during the *1st Interglacial* period, following the migration wave into America of *Archidiskodon.*

Parelephas columbi Falconer, 1857, 1863, 1868

Figures 887, 935, 936, 948–952, 954, 955, Pl. XXII

Type: Upper(?) Pleistocene, Brunswick Canal, near Darien, Georgia.

Referred: Upper(?) Pleistocene, South Carolina, Florida, and Mexico.

Syn.: *Elephas texianus* Owen, 1859 (name); Blake, 1861 (name), 1862 (definition and figure).

Specific Characters (Osborn, 1924).—(1) Type and neotype ridge-plates: M 3 $\frac{18\text{-}19}{15\text{-}16+}$. (2) Ridge-plates typically 6½ in 100 mm. (3) Third superior and inferior molars relatively short anteroposteriorly and deep vertically, corresponding with a hypsicephalic or acrocephalic cranium. (4) Ridge-plate height of third superior molar, M^3, 145 mm. (min.), 207 mm. (max.); of third inferior molar, M_3, 147 mm. (min.), 166 mm. (max.).

(5) The ridge-plate formula of the third molars, compared with that of primitive species and of more progressive species of *Archidiskodon*, may be written as follows:

Upper Pleistocene	*Parelephas columbi*	M 3 $\frac{18\text{-}19}{15\text{-}16+}$, thin cement outer coating.
Lower Pleistocene	*Archidiskodon imperator*	M 3 $\frac{17\text{-}18}{18\text{-}19\text{-}20}$, heavy cement outer coating.
Upper Pliocene to Lower Pleistocene	*Archidiskodon meridionalis*	M 3 $\frac{13\text{-}14}{11\text{-}14}$, moderate cement outer coating.
Upper Pliocene	*Archidiskodon planifrons*	M 3 $\frac{10+}{11+}$, no cement outer coating.

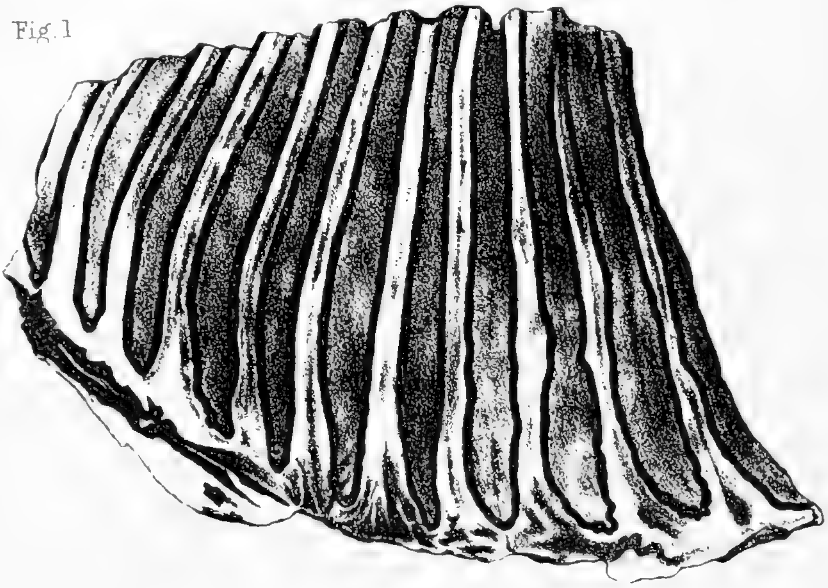
This species, clearly established by Falconer in 1857 and subsequently described in great detail (1863) from a type molar found in 1838–1839 while digging the Brunswick Canal, near Darien, Georgia, has had a most checkered history and synonymy. There is no question as to the validity of Falconer's type, type locality or region, and type description; '*Elephas columbi*' is a clearly distinguished species of the southern United States. With this species other specimens have been sadly confused by Cope, Osborn, Hay, and others; in fact, '*E. columbi*' is one of the most sadly misused names in the American proboscidean literature. Let us first turn to Falconer's type description and to his application of the type characters in a number of referred specimens from Texas and Mexico.

HISTORY: LYELL, FALCONER, OWEN, BLAKE, OSBORN (1846-1924)

E. (*Eueleph.*) *Columbi* Falconer, 1857. "On the Species of Mastodon and Elephant occurring in the fossil state in Great Britain. Part I. Mastodon." Quart. Journ. Geol. Soc. London, Vol. XIII, 1857, synoptic table opposite p. 319, including dental characters. "Subgen. 3. Euelephas . . . Spec. 12. E. (Eueleph.) Columbi . . . Post-Pliocene? . . . Mexico; Georgia; Alabama. . . . A Syn. *E. Jacksoni?* (Sillim. Journ. 1838, vol. xxxiv. p. 363)."

Of this description Falconer observes (Nat. Hist. Rev., 1863, p. 45): "Thus, the leading points of the dental characters, and the precise place in the natural series occupied by the species, were distinctly indicated, together with its range of habitat along a stretch of nearly 20° of longitude in the regions bordering the Gulf of Mexico." Type and Locality.—(Falconer, *op. cit.*, 1863, p. 43): "My first knowledge of this form dates from the year 1846, when Sir Charles (then Mr.) Lyell submitted to me, for examination, some fossil mammalian remains, which he had brought with him on his return from his second visit to America [Footnote: 'Second Visit to N. America, 3rd edit. 1855. Vol. i. p. 347.']. They formed part of a collection which had been exhumed in 1838–39, in digging the Brunswick Canal, near Darien in Georgia. A selected series of these remains was presented by Mr. Hamilton Couper, the discoverer, to the Academy of Natural Sciences of Philadelphia, where they were identified by Dr. Harlan, some of

Fig. 1

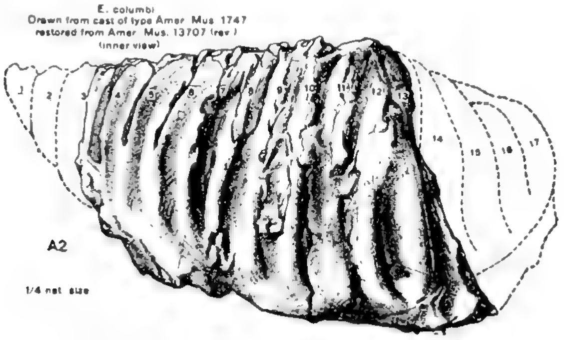


Type Figure of Parelephas columbi

Fig. 948. Type of *Elephas columbi* Falconer, 1857. After Falconer, 1868, Vol. II, Pl. x, fig. 1. Middle portion of the third right lower molar, r.M_3, longitudinally and vertically bisected. From the Brunswick Canal, near Darien, Georgia. Charles Lyell Collection, 1846. Brit. Mus. 40769. Cast Amer. Mus. 1747. (Lydekker, 1886, p. 173): "The greater part of the second [third] right lower true molar which has been longitudinally and vertically bisected; from the Pleistocene of the Brunswick canal, Darien, Georgia. Described and figured in the 'Nat. Hist. Rev.,' 1863, p. 52, Pl. i. and in the 'Palæontological Memoirs,' vol. ii. pp. 221, 222, Pl. x. fig. 1. *Presented by C. Falconer, Esq.*, 1867."

whose determinations were corrected by Professor Owen, and those of the latter more recently by Dr. Leidy."

(Lydekker, 1886.2, Pt. IV, p. 173): "The greater part of the second [third] right lower true molar which has been longitudinally and vertically bisected; from the Pleistocene of the Brunswick canal, Darien, Georgia." Brit. Mus. 40769. Cast Amer. Mus. 1747. TYPE FIGURE.—Falconer, *op. cit.*, 1863, pp. 52, 114, Pl. I; reproduced in the "Palæontological Memoirs," Vol. II, 1868, Pl. x, fig. 1. (Explanation Pl. I, 1863) "Section of the middle portion of an adult lower molar, of *Elephas Columbi*, from the post-pliocene deposit of the Brunswick Canal, near Darien, in Georgia (p. 52); showing the disposition and relative proportions of the ivory, enamel, and cement, as compared with corresponding sections of *E. Indicus*, and *E. primigenius*, contained in the Fauna Antiqua Sivalensis, Pl. I. (Nat. size)."



RESTORED TYPE OF PARELEPHAS COLUMBI

Fig. 949. Type r.M_3 of *Elephas columbi*, internal aspect, redrawn for the present Memoir from British Museum cast of type (Amer. Mus. 1747). Anterior and posterior plates restored from *neotype* (Amer. Mus. 13707). Compare Osborn, 1922.555, p. 1, fig. 1.

This fractured type agrees exactly in size with a complete third inferior molar found in the phosphate beds near Charleston, South Carolina, which contains seventeen ridge-plates, three of which belong in front and four behind the ridges 4 to 13 contained in the type specimen, showing that the full number of ridges in M_3 is probably seventeen.

TYPE DESCRIPTION (Falconer, 1863, pp. 43–52).—"[1] The specimens brought by the latter [Sir Charles Lyell] included some fragments of the molars of a fossil Elephant, which, after careful examination, I satisfied myself belonged to a species wholly distinct from the prevailing fossil form of North America, namely, *E. primigenius*; . . . .[2] I applied to it, in my notes of a systematic classification of the Proboscidia [referring to his description of 1857], the designation of *E. Columbi*, after the great discoverer; . . . [3] proving the co-existence of a distinct species of Elephant with the extinct Edentate Fauna of the Southern States of the Union." [4] Confirmed by other specimens from Mexico, Texas, and other of the Southern States of North America. [5] "I resorted to the crucial test of sawing up the principal molar of the Brunswick Canal series longitudinally and vertically, in the manner figured in the plates devoted to the Elephants, in the 'Fauna Antiqua Sivalensis,' a procedure which commonly quashes at a glance all doubts as to the specific distinctness, or otherwise, of Elephant molars, in critical cases. The section yielded *colliculi*, showing rather thick plates of enamel folded upon cuneiform cores of ivory, of very considerable width at their base, and separated by correspondingly open interspaces filled with thick masses of cement. These characters were strongly in contrast with the attenuated, parallel, and pectiniform disposition of the materials seen in molar sections of *E. primigenius*; combined with the dilated outline of the 'discs of wear,' and the decided crimping in the plates of enamel, they led me to regard the form as occupying a place in the series between *E. antiquus* and *E. Indicus*, and as differing more from the Mammoth than does the latter from the existing Indian Elephant." [6] These facts were epitomized in the table of April 8, 1857, in which *E. columbi* is included in the same group as *E. indicus*. [7] "Sir Charles Lyell's Georgian specimen, from the Brunswick Canal, upon which my first knowledge of *E. Columbi* was founded, consists of the middle portion of the penultimate or last true molar, probably the latter (m.3) lower jaw right side, broken off, both at the anterior and posterior ends. The fragment comprises ten complete ridges, with part of two others, of which the anterior seven are more or less worn. All the fangs are broken off, together with the basal mass of ivory. The summit of the crown is concave from back to front, and the tooth is also concave with a little torsion on the outside, and convex inwards, showing that it was considerably arcuated laterally, like the specimen last described. The discs of wear are of moderate width, as in the Indian Elephant, with a tendency in some of them to expansion in the middle. This is most pronounced in the second, where the expansion nearly attains half an inch. The plates of enamel are thicker than in the Mammoth, and about equal to those of the Indian Elephant; they present a considerable amount of parallel shallow plaiting, which is prominently shown where they rise above the level of the cement. The wear of the crown takes place in a succession of steps, from the front backwards, which it is of importance to notice with reference to the inferred food of the species. These steps rise like a flight of stairs, each being composed of the whole mass of cement of one of the valleys, and the combined enamel plates and ivory of the ridge immediately behind it. There are five of these steps in the Georgian specimen, the posterior ridges being intact. The [type] dimensions are as follows:

	[Falconer]	[Osborn
Length of crown measured at the base	9.5 inch.	241e mm.
Ditto ditto at summit of crown	6.9 "	176 "
Width of crown in front	3.2 "	81 "
Ditto at 4th remaining ridge	3.5 "	89 "
Ditto behind at widest part	3.3 "	82e "
Height of ditto at 8th plate where unworn	6.2 "	158 "
Ditto of anterior worn plate	2.5 "	64 "]"

"Pl. I [Fig. 948 of present Memoir] represents a longitudinal section of the specimen, by which the specific distinction from the Mammoth is best shown. The plates converge from the convex base to the summit irregularly, but somewhat like the *voussoirs* [arch-stones] of an arch; so that the same number of plates, diminishes from 9.5 inches at the base to about 7 at the crown. The ridges are not so high as in the Mammoth, and their constituent elements, *i.e.* the enamel, ivory, and cement are thicker. In the interval between the 10th and 11th ridges, the cement attains, near the base, the excessive thickness of six-tenths of an inch, being about twice as much as what is ordinarily seen in the section of the Mammoth. For the contrasted difference, I refer to the sections, pl. I, fig. 1, of the 'Fauna Antiqua Sivalensis.' "

FALCONER, 1863.—In the introductory remarks to his invaluable paper of 1863 cited above, Falconer treats most fully the dentition, habits, and range of *Elephas columbi* and associated fossil mammals. He then considers the origin and range in time of the mammoth (*Elephas primigenius*) and the persistence of its distinctive characters, followed by a discussion of the unity or plurality of the species of the existing Indian elephant (*Elephas indicus*). Finally he gives the fullest exposition of the food of living and extinct species, *E. indicus, E. africanus, E. primigenius.* In this paper Falconer classifies the species of elephants by ridge formulæ, grouping those with a high ridge formula in *Euelephas*, those with a low ridge formula in *Loxodon.*

ESTIMATED RIDGE FORMULA.—In this species Falconer finally (1863, p. 56) estimates the ridge formula, based on referred specimens some of which certainly belonged to *Elephas imperator*, as follows:

E. COLUMBI: $\mathrm{Dp}\,2\frac{4}{4}$ $\mathrm{Dp}\,3\frac{8}{8}$ $\mathrm{Dp}\,4\frac{12}{12}$ $\mathrm{M}\,1\frac{12}{12}$ $\mathrm{M}\,2\frac{16}{16}$ $\mathrm{M}\,3\frac{20\text{-}?}{20\text{-}?}$.

Falconer's formula (1863) was shown by Osborn (1922.555, p. 2) to be probably too high. Osborn's formula of M_3 (1929) is given above in the definition of the species and is discussed below in the analysis of the Cohen Collection.

SYNONYMY.—Falconer (*op. cit.*, 1863, p. 67) finally concludes: (1) That his *Elephas columbi* of 1857 includes in part specimens described by American palæontologists as *Elephas primigenius*; (2) that the *Elephas texianus* Owen is a synonym of it; (3) that *Elephas imperator* Leidy is also a synonym, and that until a perfect molar is figured and described, no satisfactory opinion can be formed as to what *E. imperator* is.

ELEPHAS TEXIANUS OWEN, 1859, BLAKE, 1861, 1862.—*Elephas texianus* Owen-Blake, given as a name only by Owen in 1859, was defined by Blake in 1862 (1862, p. 58), as follows: "The figure by Mr. Mackie [Fig. 950 of the present Memoir] gives a better idea of its appearance than any mere verbal description. I however define it as *Elephas texianus, dentium molarium* (m.6), *colliculi undulati, magis remoti quam in E. Indico.*" It is antedated, however, by *Elephas columbi* Falconer, and was the subject of an animated controversy between Falconer, Owen, and Blake.

Elephas texianus Owen. "Address of the President." Brit. Assn., 1859, p. lxxxvi. "Geology tells us that at least two kinds of Elephant (*Mastodon Andium* and *Mast. Humboldtii*) formerly did derive their subsistence, along with the great Megatherioid beasts, from that abundant source [tropical America]. Nay more; at least two other kinds of Elephant (*Mastodon ohioticus* and *Elephas texianus*) existed in the warm and temperate latitudes of North America." Name only. (Owen, 'Palæontology,' 2d Edit., 1861, p. 395, quoted by Falconer, Nat. Hist. Rev., 1863, p. 46): ". . . where it [the Mammoth] existed not only with the gigantic *Mastodon Ohioticus*, but also with a second species of true Elephant (*Elephas texianus*, Blake) the teeth of which were adapted to a succulent vegetable diet." (Blake, The Geologist, Vol. IV, 1861, p. 470): "South of the 30th degree of N. latitude it [(the Mammoth) *E. primigenius*], however, gives place to a totally different species of true Elephant (*Elephas Texianus*, Owen, *E. Columbi?* Falconer), the molars of which, by their less degree of complexity, were more adapted to triturate the soft succulent herbage of Texas and Mexico."

BLAKE, 1862.—"Molar tooth of Elephas texianus (N.S.)," after figure by Charles Carter Blake, in The Geologist, 1862, Pl. IV, p. 57, in his article "On a Fossil Elephant from Texas (*E. Texianus*)." This tooth appears to be the one referred to by Owen in September, 1858, and designated by Blake as follows (Blake, 1862, p. 58): "This opinion [that it was a distinct species of elephant, closely allied to the Indian type] was confirmed by Professor Owen, and after the name of *Elephas Texianus* had been given to the species, the specimen was deposited in the British Museum, and now forms one of the most conspicuous objects in the gallery devoted to Proboscidea. Professor Owen, in September, 1858, thought fit to adopt the name of *E. Texianus* for the species, in his eloquent address to the British Association (and also in the second edition of 'Palæontology,' p. 395). . . . This is the only specimen which I have seen of this type, as Dr. Falconer has not stated where the specimens are on which he described his species. He appends as a doubtful synonym, '*E. jacksoni?*, Silliman's Journal, 1838, vol. xxxiv. page 363'; but after examination of the very bad drawings contained in that page, I cannot make any distinction between them and *E. primigenius.* The tooth of *E. Texianus* (m.6, lower jaw) has enamel-folds much wider and much more waved and undulated than that of the *E. Jacksoni.* The canals of cement are consequently of much greater width, and the whole aspect of the tooth is much more like *E. Indicus.*"

OWEN-BLAKE ELEPHAS TEXIANUS TYPE [=PARELEPHAS COLUMBI REF.]

Fig. 950. Type right third inferior molar, r.M_3, of *Elephas texianus* Owen, 1859, Blake, 1861, after Blake, 1862, Pl. IV. Scale not given by Blake, but estimated at approximately one-third natural size from dimensions given by Falconer, 1868, Vol. II, p. 223, namely, exteme length of crown 12.5 in. or 318 mm., width at eighth disc 3.8 in. or 99 mm. These dimensions somewhat exceed those of Osborn's neotype (Amer. Mus. 13707), length 298 mm., breadth 91 mm.

(Lydekker, 1886, p. 172): Brit. Mus. 33218, "The well-worn third right lower true molar; from [San Felipe de Austin, on the Brazos River, Texas]. Described and figured by Blake in the 'Geologist,' vol. v. p. 57, pl. IV. (as *E. texianus*), and also described by Falconer in the 'Nat. Hist. Rev.' 1863, p. 52, and in the 'Palæontological Memoirs,' Vol. ii. p. 222. *Purchased.* About 1858." Known as the "Bollaert molar." Estimated ridge-plates 17+.

Osborn, 1924: This figure and description appear to confirm Falconer's opinion that *Elephas texianus* Owen, 1859, Blake, 1861, 1862, is a synonym of *E. columbi* Falc.

OSBORN (1922) SEPARATES PARELEPHAS COLUMBI FROM PARELEPHAS JEFFERSONII[1]

Consistent with the researches on which the present Memoir throughout has been based, Osborn reëxamined Falconer's type specimen and description and realized that in common with Cope, Hay, and other American palæontologists, he had previously erred in confusing this with an entirely different species of fossil elephant, which, as a consequence, he (Osborn, 1922.555, pp. 1–3) separated as *Elephas jeffersonii* and subsequently (Osborn, 1924.633, p. 4) as *Parelephas*.

(Osborn, (1922.555, pp. 1–3): "The present article relates explicitly to the type characters of *Elephas columbi*, of *E. imperator*, and of the American specimens referred to *E. primigenius*, three species which have become more or less confused in all the previous literature because the characters of the type specimens have not been precisely determined and compared. The object of the present communication is to clear up this confusion and to propose *Elephas jeffersonii* as a new species of American Pleistocene mammoth. . . . We thus find by the characters of the type and neotype specimens [see Fig. 951 of the present Memoir] that the real *Elephas columbi* is not the animal we have been describing under this name; it is a dwarf form, perhaps a dwarf female, of the animal which we have been describing under the name *Elephas imperator*."

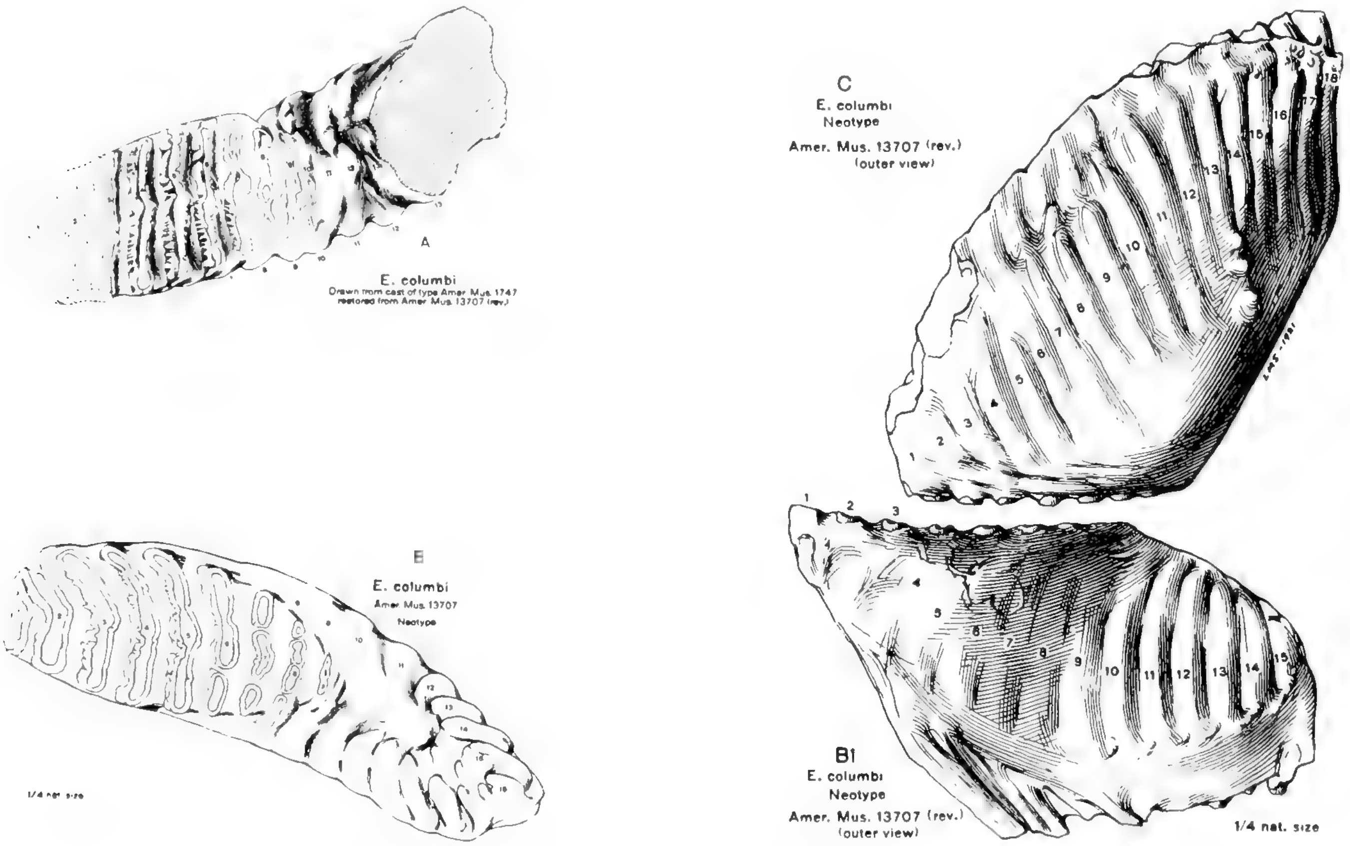


FIG. 951. FALCONER'S TYPE (A) AND OSBORN'S NEOTYPE (B, C) OF ELEPHAS [PARELEPHAS] COLUMBI
One-fourth natural size

(Left) Crown view of the type, r.M_3 (upper figure) and neotype, l.M_3 (lower figure) of *Elephas columbi* (cast Amer. Mus. 1747). (A) Shaded portions represent ridge-plates 4–13 which are preserved in the type, ridge-plates 1–3 being restored from the neotype. (B) Crown view of neotype, a complete third lower molar of the left side, l.M_3, showing ridge-plates 1–15 and rudiment of ridge-plate 16 [observe that in the restored type specimen (Fig. 949) the estimated ridge-plate count is 16+ (17).] After Osborn, 1922.555, p. 2, fig. 2.

(Right) Neotype molars of *Elephas columbi*, one-fourth natural size, from the phosphate beds of South Carolina (Amer. Mus. 13707). Two individuals. (C) External view of r.M^3, eighteen ridge-plates plus a probable posterior one and a half ridge-plate. B1, External view of l.M_3; same tooth as figure (B) opposite, with fifteen complete ridge-plates and an incipient sixteenth plate. After Osborn, 1922.555, p. 3, fig. 3.

The affinity between *Parelephas columbi* and *Archidiskodon imperator* he found by no means so close as Falconer believed; the distinctions have been pointed out in the full description of *A. imperator* above. Prior to, and independently of, Osborn's observations, Freudenberg had revived Falconer's opinion as to the close relationship of the true *Elephas columbi* of Mexico and the true *E. imperator*.

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[1] At this time (1922) Osborn placed '*Elephas columbi*' within the phylum *Archidiskodon;* in the present Memoir it is placed within the phylum *Parelephas*.

TYPE CHARACTERS

Consequently the reëstablishment of the type and neotype characters of *E.* [=*Parelephas*] *columbi* is based upon the following materials:

Falconer's type of *Elephas* [=*Parelephas*] *columbi*, r.M_3 (Brit. Mus. 40769, cast Amer. Mus. 1747). Georgia.

Owen-Blake type of *Elephas texianus*, r.M_3 (Brit. Mus. 33218). Texas.

Osborn's neotypes of *Elephas* [=*Parelephas*] *columbi*, r.M^3, l.M_3 (Amer. Mus. 13707). Phosphate beds of Charleston, S. C.

	Number of Specimens
SUPERIOR MOLARS	
R.M^3–L.M^3—one-third worn, one-half worn, two-thirds worn, greatly worn, very aged, complete or fragmentary, preserving from 8–18½ ridge-plates	14
R.M^2–L.M^2—one-third worn, one-half worn, complete or fragmentary, preserving 10–13½ ridge-plates	6
R.M^1–L.M^1—one-third to one-half worn, preserving 10½–11½ ridge-plates	3
INFERIOR MOLARS	
R.M_3–L.M_3—one-third to one-half worn, adult, aged, young, preserving from 6–16 ridge-plates	7
R.M_2–L.M_2—one-third worn, two-thirds worn, aged, fractured, preserving from 9–12½ ridge-plates	5
R.M_1–L.M_1—one-fourth worn, one-half worn, preserving from 10½–12½ ridge-plates	2
R.Dp_4 —one-fourth worn, preserving 10½ ridge-plates	1
Total number of grinding teeth	38

Thirty-six inferior and superior grinding teeth of *Elephas* [=*Parelephas*] *columbi* (Amer. Mus. 13708 a–z and 13709).

The type and neotype molar characters of *Parelephas columbi* may be summarized as follows:

Type:

R.M_3 17e ridge-plates, 11 worn, 6 unworn, 6 in 10 cm., breadth 82e mm., length 241e mm., index 34e.

Neotypes:

R.M^3 19½e ridge-plates, 8 worn, 10+ unworn, 5½–6½ in 10 cm., breadth 96 mm., length 249 mm., index 39.

L.M_3 15–16 ridge-plates, 9 worn, 6 unworn, 4½–5½ in 10 cm., breadth 91 mm., length 298 mm., index 31.

The variations in the ridge-plate count in 10 cm. and the compression depend upon the level of the crown from which the ridge-plate count is made and approximate *Parelephas columbi* to *Archidiskodon imperator* with which it was long confused. *P. columbi* is much more distinct from *P. jeffersonii*, which has a higher ridge-plate formula and a higher ridge-plate compression, namely, ridge-plate formula $M3\frac{25}{24}$, ridge-plate compression 7 (min.), 9 [11½] (max.), according to the level of the crown from which the compression is counted.

They show, as illustrated in figure 949, that in Falconer's type molar three ridge-plates are missing in front and four to five ridge-plates are missing behind. Thus the type and neotype ridge formula of *Parelephas columbi* is as follows: $M\,3\frac{18\text{-}19}{15\text{-}16+}$.

OSBORN ESTABLISHES THE CHARACTERS OF PARELEPHAS COLUMBI BY THIRTY-EIGHT NEOTYPE AND REFERRED MOLARS FROM THE PHOSPHATE BEDS OF SOUTH CAROLINA

See Figure 952 of the present Memoir

The very extensive Cohen Collection from the phosphate beds near Charleston, South Carolina, presented to the American Museum in 1908 by Mrs. Morris K. Jesup, includes a complete series of thirty-eight upper and lower grinding teeth to which the

COHEN COLLECTION: NUMBER OF RIDGE-PLATES

Amer. Mus. No.		Total	Worn	Unworn	in 10 cm.	Breadth	Length	Index	Height		Remarks
13707 (Neotype)	R.M^3	19½e	8	10+	5½–6½	96	249	39	207	9th pl.	One-fourth worn, preserving 18½ ridge-plates. Finely preserved.
13708-e	L.M^2	+12½	11		6–7	92	197½	47	106	8th pl.	One-half worn, preserving 11¾ ridge-plates. Finely preserved.
13708-m	R.M^1	+11½	+10	½	7–8	77	169	45			One-half worn, preserving 10½ ridge-plates.
1747 (Type cast)	R.M_3	17e	11	6	6	82e	241e	34e	152e	10th pl.	One-third worn, preserving 10½ ridge-plates.
13708-i	L.M_2	+12¾e	11	1½	5½–6½	74	210	35			Two-thirds worn, preserving 12½ ridge-plates. Very aged.
13708-k	R.M_1	13	12	1	7½–8	67	167	40			One-half worn, preserving 12½ ridge-plates. Finely preserved.
13708-n	R.Dp_4	½–11–½	9	4	8–10	49	133	37	94	6th pl.	One-fourth worn, preserving ½–11–½ ridge-plates. Finely preserved.

following numbers have been assigned: Amer. Mus. 13708 a–z (35 specimens in all); and Amer. Mus. 13709; also Amer. Mus. 13707, a third inferior molar and a third superior molar chosen by the present author (1922.555, pp. 2, 3) as the neotypes.

These thirty-eight specimens agree entirely in their generic and specific characters, thus positively establishing the grinding tooth characters of *Parelephas columbi*; the largest specimens are the *males*, the smaller specimens are the *females* or *dwarfed males*.

The summary of the Cohen Collection is as above (p. 1075).

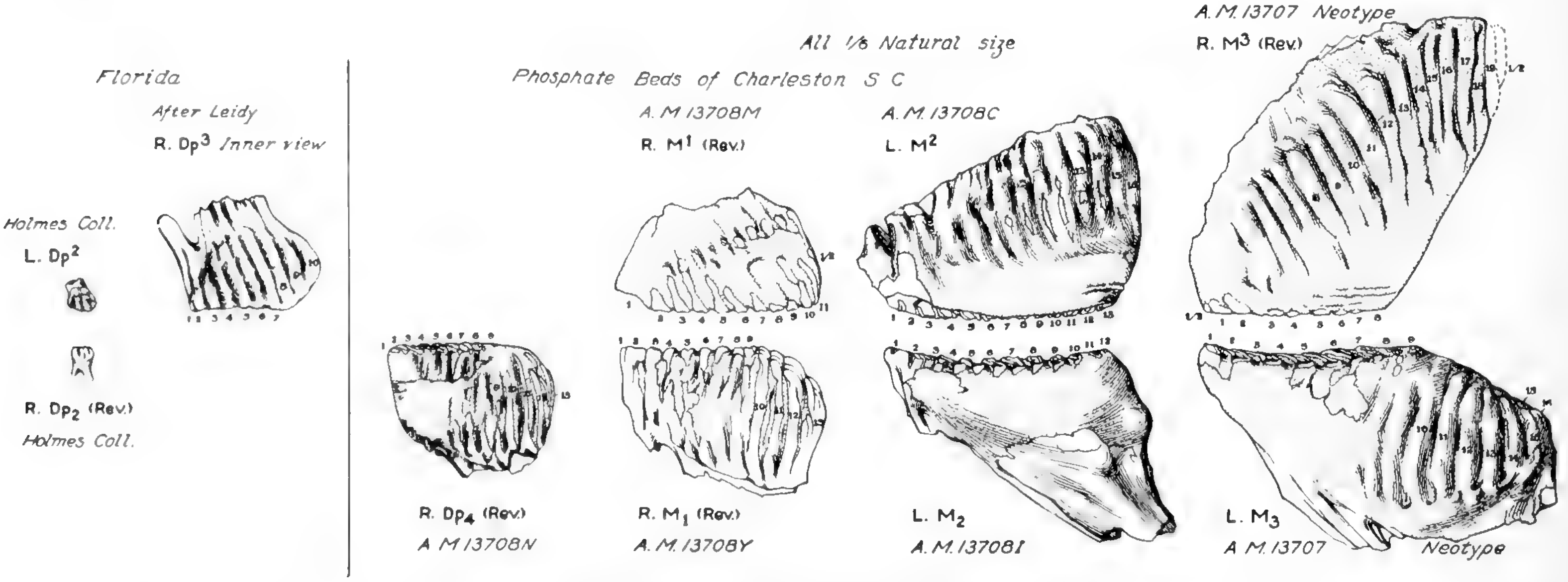
Constant Ridge Formula.—From an examination of these fourteen third superior molars, the prevailing ridge-plate formula (M 3 $\frac{18\text{-}19}{15\text{-}16+}$) agrees very closely with that of the molars in the Amherst specimens (Fig. 954), namely, M 3 $\frac{18+}{16\frac{1}{2}}$, and appears to firmly establish four facts: (1) The low ridge-plate formula of the third superior molars is typical and constant; (2) there are more ridge-plates in the third superior than in the third inferior molars —a characteristic of all known species of *Parelephas*, as shown in the phylogenetic table above (p. 1048); (3) on the contrary, in the *Archidiskodon* phylum the inferior ridge-plates exceed the superior ridge-plates in number, e.g., *A. imperator* (M 3 $\frac{18}{20}$), *A. planifrons* (M 3 $\frac{10+}{11+}$), *A. meridionalis* (M 3 $\frac{13\text{-}14}{11\text{-}14}$); (4) as shown in the section of Falconer's type (Figs. 948, 949, 951), the arcuate ridge-plates are widely separated in mid-section, thus, in extremely worn grinding teeth of *Parelephas columbi* the ridge-plates appear to be as far apart as in *A. imperator*.

From these exceptionally fine materials subjected to the most careful study and comparison by the author and Dr. C. C. Mook, the ridge formula of *Parelephas columbi* may now be written as follows:

$$\text{Dp } 4\ \frac{}{\frac{1}{2}\text{-}11\text{-}\frac{1}{2}}\ \text{M } 1\ \frac{12}{12\frac{1}{2}}\ \text{M } 2\ \frac{13\text{-}16}{+12\frac{1}{2}}\ \text{M } 3\ \frac{18\text{-}19}{15\text{-}16+}.$$

The maximum and minimum measurements of the larger (male) and the smaller (female) grinding teeth are probably due to sexual differences; certain of the Cohen specimens agree exactly in size with Falconer's type. The details are as follows:

	Breadth		Length		Index		Height	
	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.
M^3	86	106	249	288	36	39	130	207
M^2	66	92	186c	229	39	49c	106	145
M^1	77	83	159	174	45	51		
M_3	69	95	241c	298	31	34c	87c	166
M_2	70	78	210		35			
M_1	57	67	167	183	31	40	111	
Dp_4	49		133		37		94	



Key to Parelephas columbi Upper and Lower Grinding Teeth

Fig. 952. Characteristic superior and inferior molars selected from the Cohen Collection, phosphate beds, Charleston, S. C. (Amer. Mus. 13707, 13708 a–z, 13708 aa–kk, 13709), in all thirty-eight specimens, also milk teeth in part, r.Dp³, after Leidy, l.Dp², l.Dp₂, from the Holmes Collection, Florida. The key to the grinders in this figure is as follows:

Neotype (Amer. Mus. 13707) r.M³ (rev.), length 249 mm., breadth 96 mm., 19½c ridge-plates.
Neotype (Amer. Mus. 13707) l.M₃, length 298 mm., breadth 91 mm., 16c ridge-plates.
Referred (Amer. Mus. 13708–c) l.M², length 229 mm., breadth 90 mm., ridge-plates 13+ worn, 3 unworn, total 16c.
Referred (Amer. Mus. 13708–i) l.M₂, length 210 mm., breadth 74 mm., very aged, preserving 12½ ridge-plates.
Referred (Amer. Mus. 13708–m) r.M¹, length 169 mm., breadth 77 mm., half worn, preserving 11½ ridge-plates.
Referred (Amer. Mus. 13708–y) r.M₁, length 183 mm., breadth 57 mm., one-fourth worn, preserving 13 ridge-plates, 9 worn, 4 unworn.
Referred (Amer. Mus. 13708–n), r.Dp₄, length 133 mm., breadth 49 mm., preserving 13 ridge-plates, 9 worn, 4 unworn.
Referred r.Dp³, after Leidy, in the Wagner Free Inst. Sci., Philadelphia, 10 ridge-plates.
Referred l.Dp², Holmes Collection, Florida, 3 ridge-plates.
Referred r.Dp₂, Holmes Collection, Florida, 3 ridge-plates.

The ridge-plate formula of *Parelephas columbi* of the phosphate beds and Florida, as illustrated in the above key figure, is as follows:

$$\text{Dp } 2\ \frac{3}{3}\quad \text{Dp } 3\ \frac{10}{}\quad \text{Dp } 4\ \frac{}{13}\quad \text{M } 1\ \frac{+11\frac{1}{2}}{13}\quad \text{M } 2\ \frac{13\text{-}16}{12\frac{1}{2}}\quad \text{M } 3\ \frac{18\frac{1}{2}\,(19)}{16+}$$

We observe that the three intermediate molars, Dp 4, M 1, M 2, while increasing rapidly in size, exhibit a substantially similar number of ridge-plates below, namely, 13.

Laminar Frequency.—The ridge-plates are typically divergent at the unworn summit of the crown (5½–6½ laminæ in 10 cm.), more contiguous as we descend toward the base of the crown (6–7½ laminæ in 10 cm.); in mid-crown the ridge-plates are set widely apart as in *Archidiskodon imperator*, more widely apart than in *Parelephas jeffersonii.* In all degrees of age and wear the minimum laminar frequency is 5½ in 10 cm.; the typical laminar frequency is 6½ in 10 cm., the maximum laminar frequency is 8½ in 10 cm. The above variations accord with the point at which the measurement is taken. This explains why certain of these fractured, broad-plated grinders have been mistakenly referred to *Archidiskodon imperator* by Hay and others, while certain of the narrow-plated molars have been referred to *Parelephas jeffersonii.* The grinders (Fig. 954) of the Amherst skeleton belong to the narrow-plated variety. See also Florida specimens of *P. floridanus*, (Nat. Mus. 11808, 11806, 11810), page 1079 below.

PARELEPHAS COLUMBI ABUNDANT IN THE SOUTHEASTERN UNITED STATES

This is Hay's interesting account of the geology and fauna of the important and distinct type of *Elephas columbi* Falconer. (Hay, 1923.1, p. 157): "1. *Brunswick, Glynn County* [Georgia].—This is the type locality of *Elephas columbi.* This species was based by Falconer (Quart. Jour. Geol. Soc. Lond., XIII, 1857, table opposite p. 219 [319]) on a part of a tooth received from the geologist Charles Lyell and which had been found in the Brunswick Canal. The specimen consisted of 10 median plates of a lower second or third molar. Falconer figured it in 1868 (Palæont. Mem., vol. II, pp. 214, 221, plate x). Lyell (Second Visit, etc. vol. I, p. 348) noted that an elephant had been found in excavating the canal. Richard Harlan, in 1842 (Proc. Acad. Nat. Sci. Phila., vol. I, p. 189), stated that a large collection of bones of various animals had been presented to the Academy by J. Hamilton Couper, of Darien, Georgia. Among these were teeth of *E. primigenius.* Couper, in 1848 ([1846.1] Hodgson's Memoir, etc., p. 45), stated that two lower jawbones with teeth, several loose teeth, two tusks, and several vertebræ of *Elephas primigenius* had been collected in the canal during 1838 and 1839. These remains quite certainly belonged to *Elephas columbi* unless possibly some belonged to *E. imperator.* Leidy (Jour. Acad. Nat. Sci. Phila., vol. VII, 1869, p. 254) records the presence in the collection of the Academy of a lower molar of *E. columbi.* The present writer has seen in this collection parts of four teeth of this species which had been sent from the Brunswick Canal, doubtless parts of the Couper collection. The species are listed on page 369. . . [p. 369] The most striking was the great ground-sloth, of the genus *Megatherium,* and which Leidy afterwards called *Megatherium mirabile* . . . .[p. 370] Elephas columbi (p. 157). Mammut americanum (p. 120). Bison [*latifrons?*] sp. indet. (p. 261). . . . E. [*Equus fraternus*] leidyi (p. 193). . . . Megatherium mirabile (p. 36)."

(*Op. cit.*, p. 370): "J. Hamilton Couper (Hodgson's Memoir, pp. 37–40) has given an account of the topography and geology of the region through which the Brunswick Canal was being constructed (map 40). On one of the plates of the work is a section from the ocean westward 21 miles. About 10 miles west of St. Simon's Island the canal passed through Six-mile Swamp. This is connected at its northern end with Altamaha River, at the southern with Turtle River. The swamp has thus the appearance of a lake which has become filled with alluvial deposits. These consist of a compact clay, usually yellow and impregnated with iron. There are thin strata of soft, chalky marl and many fragments of petrified wood. At the bottom of this deposit were found the bones of *Megatherium, Elephas, Mammut, Equus,* and *Bison.* Beneath the clay stratum was sand with marine shells."

From Hay's faunistic tables of 1914.1, 1923.1, and 1924.1, the following species may be selected as characteristic of the Upper Pleistocene life zone, to which *Parelephas columbi* probably belongs:

FAUNA OF THE TYPE LOCALITY OF ELEPHAS [= PARELEPHAS] COLUMBI NEAR DARIEN, BRUNSWICK CANAL, GEORGIA	FAUNA OF THE PHOSPHATE BEDS NEAR CHARLESTON, S. C., WHERE ELEPHAS [= PARELEPHAS] COLUMBI OCCURS IN ABUNDANCE
Parelephas columbi type	*Parelephas columbi* ref.
Megatherium mirabile type	*Ocalientinus* (*Serridentinus*) *obliquidens* type
Mastodon americanus ref.	*Mastodon americanus* ref.
Equus [*fraternus*] *leidyi* type	*Bison latifrons* ref.
Bison latifrons (?) ref.	*Tapirus haysii* ref.

Upper Pleistocene Age.—Besides the above and numerous other species, Hay (1923, p. 363) includes many specimens referred to several other species found in South Carolina but not definitely recorded from the "Charleston phosphate beds," for example, *Archidiskodon imperator* ref., which may have been washed in or dredged from an older horizon.

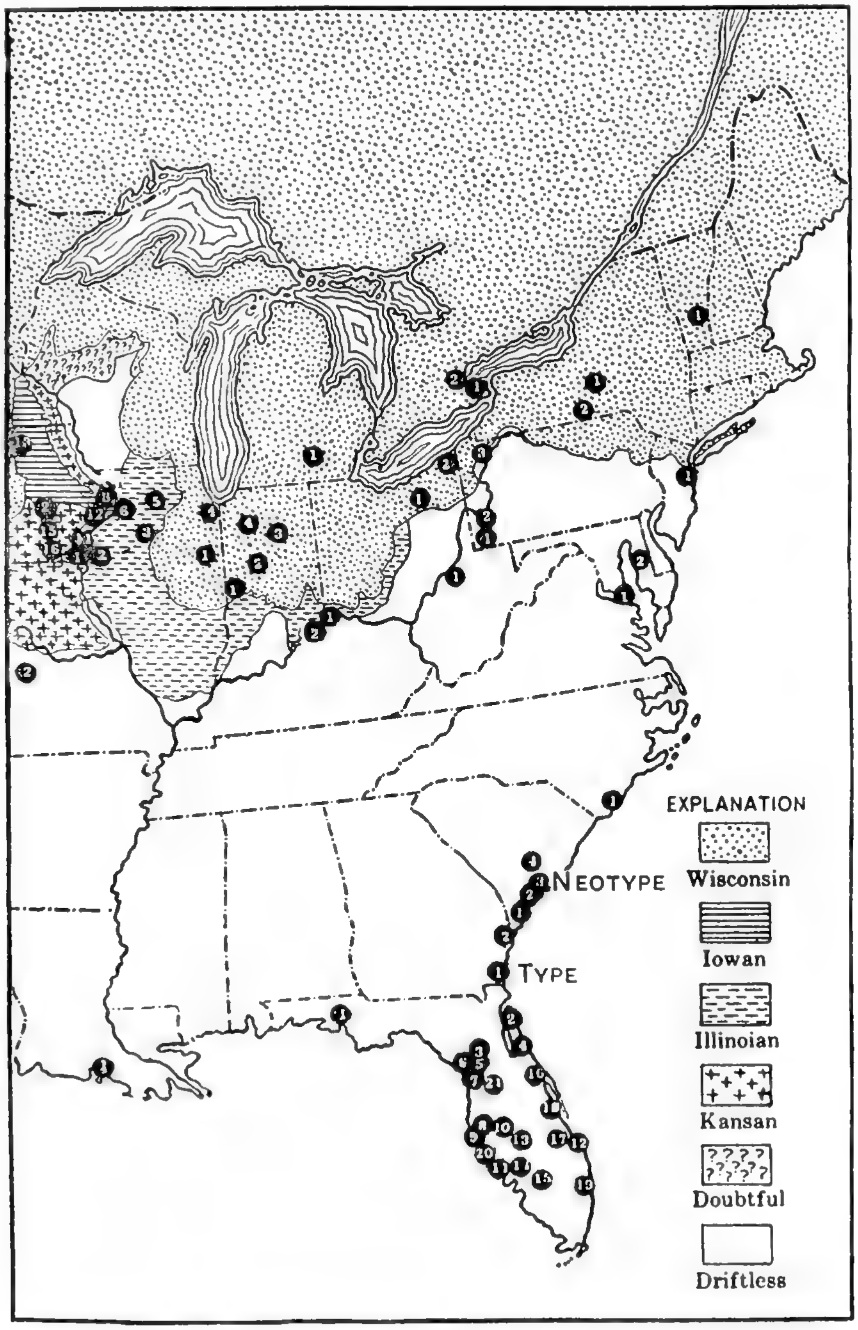
Hay, 1914, 1923.—In his Memoir of 1914 and again in 1923 Hay grouped together as one species, namely, "*Elephas columbi*" (Hay, 1914, pp. 410–421, also 1923, pp. 430, 431, map 12), the mammoths now separated by Osborn into *Parelephas columbi* [southeasterly range in Fig. 953] and *Parelephas jeffersonii* [northerly range in same figure]. Those in the northerly range probably include some specimens referable to *Mammonteus.*

Osborn, 1928: Osborn determines as *Parelephas columbi* two of the grinding teeth from the Charleston phosphate beds of South Carolina and from Ocala, Florida, described and figured by Hay, 1914, p. 413, Pl. LXI, as follows:

	Dp^2 (Ocala, Florida), see Leidy, Trans. Wagner Inst. Sci., Vol. II, p. 17, Pl. III, figs. 6 and 7, also Hay, 1914, p. 413, Pl. LXI, figs. 2 and 3.
	Dp^3 (Ocala, Florida, *fide* Leidy), length 110 mm.; ridge-plates 8–9 (see Hay, *op. cit.*, Pl. LXI, figs. 5, 6).
Nat. Mus. 1614	Dp^3 (phosphate beds, South Carolina), length 101 mm., height fourth ridge-plate 94 mm.; ridge-plates 8+ (see Hay, *op. cit.*, Pl. LXI, fig. 4).

PARELEPHAS COLUMBI[1] OF FLORIDA

FLORIDA.—*Parelephas columbi* is fairly abundant in Florida; relatively few specimens of *Archidiskodon imperator* are recorded from Florida, the most perfect being the Venice mammoth (Nat. Mus. 11620), an aged individual recently described by Gidley (see page 1005 above). The true *P. columbi*, relatively abundant, agrees very closely in size and ridge-plate formula with Falconer's type from Georgia (Fig. 948) and with Osborn's neotype from the South



NORTHERLY CIRCLES = DISTRIBUTION OF PARELEPHAS JEFFERSONII AND MAMMONTEUS PRIMIGENIUS. SOUTHEASTERLY CIRCLES = DISTRIBUTION OF PARELEPHAS COLUMBI AND ARCHIDISKODON IMPERATOR

Fig. 953. Range of *Parelephas jeffersonii* and *P. columbi*, including the type locality (1) of *P. columbi* in Georgia, also the neotype locality (3) from the phosphate beds of South Carolina. Modified from Hay (1923, map 12, p. 431), who erroneously treated *Parelephas jeffersonii* and *P. columbi* as belonging to the same species.

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[1] Since this Florida section was written (1928) the more progressive *Parelephas floridanus* stage, M3 $\frac{2\,2+}{2\,1+}$, has been described (Osborn, 1930.837). The grinding teeth (Nat. Mus. 11806, 11808, 11810) belong to *P. floridanus* (*op. cit.*, p. 17).

Carolina phosphates (Fig. 951). Recently described by Gidley, from Melbourne and Vero, Florida, presumably from the "No. 2" bed of Sellards, are three *P. columbi*[1] molars:

Nat. Mus. 11808. Third superior molar, r.M^3, adult; laminar frequency 6–6½ ridge-plates in 10 cm. Total ridge-plates 19–20, 13 preserved (tooth not complete).

Nat. Mus. 11806. A second superior molar, l.M^2; laminar frequency 8 ridge-plates in 10 cm., +12+ ridge-plates preserved.

Nat. Mus. 11810. A third superior molar, r.M^3, aged individual; laminar frequency 7–8 ridge-plates in 10 cm. Total ridge-plates 18 to 20, 15 preserved, 3 to 5 missing.

Gidley (June 14, 1928) observes that while in *Parelephas columbi* ref. (Nat. Mus. 11808) the laminar frequency is only 6 measured on the outer side and 6½ measured on the inner side of the crown, in 10 cm., at the same level, Nat. Mus. 11806 (*P. columbi* ref.) exhibits a laminar frequency at the base of nearly 8 ridge-plates in 10 cm., the compression being much greater. Can such a difference be accounted for on the ground of individual variation?

Gidley (letter, December 6, 1928) observes in Nat. Mus. 11806 (*P. columbi*) 12 ridge-plates plus 7 to 10 missing, a total of 19 to 22, hence an M^3; in Nat. Mus. 11810 (*P. columbi*) he observes 15 worn ridge-plates plus 3 to 5 missing, a total of 18 to 20.

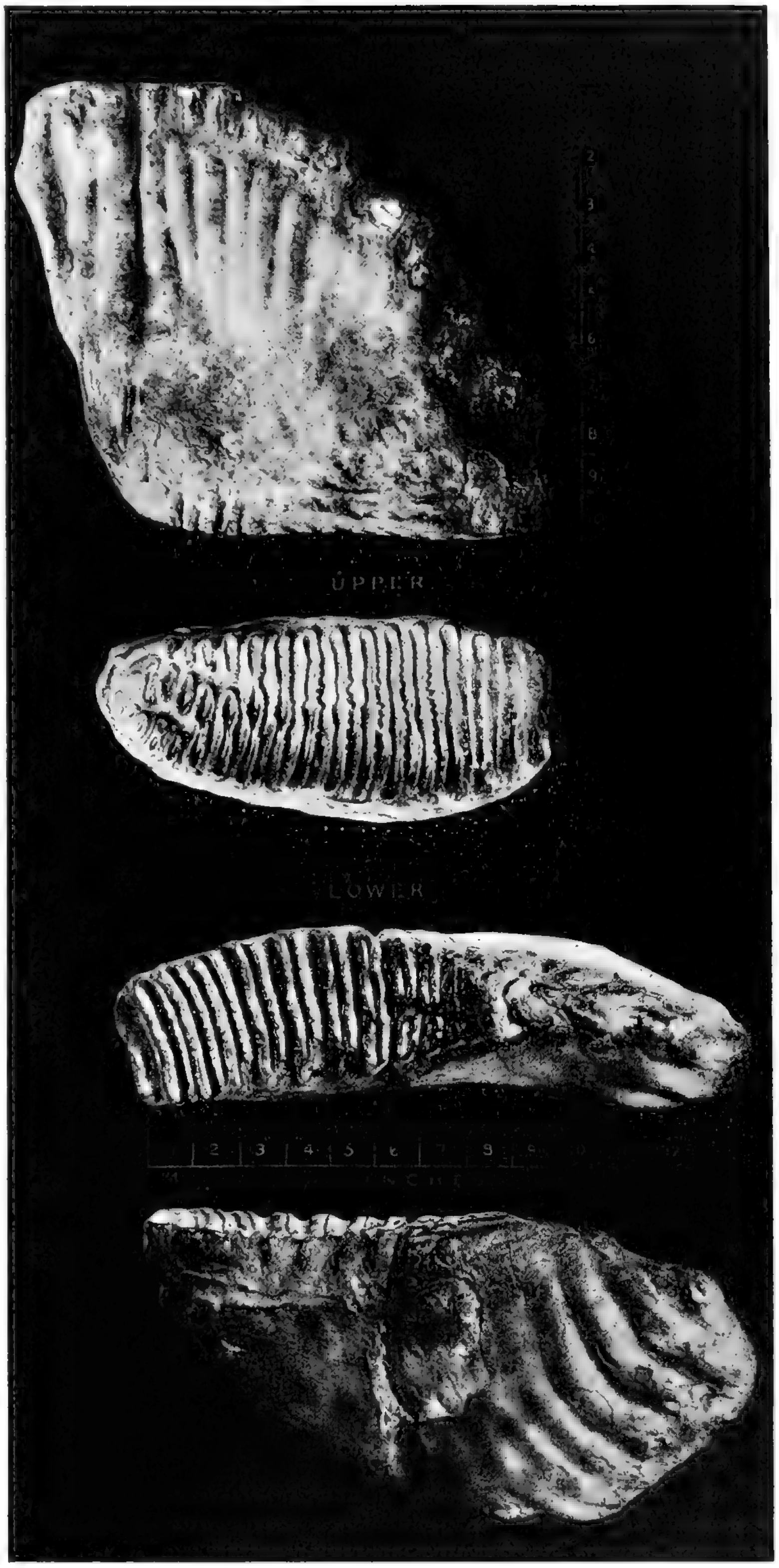
Loomis (1923–1928) collected in the No. 2 horizon, latest Pleistocene, near Melbourne, Brevard County, Florida, for the Amherst Museum, the invaluable specimens now assembled in the mounted skeleton (Amherst Mus. 25–1) of the typical *Parelephas columbi* represented in our figures 954 and 955 and fully described below.

AMHERST SKELETON OF PARELEPHAS COLUMBI

One of the most fortunate discoveries in the recent history of mammalian palæontology is that of the Amherst skeleton referred to *Parelephas columbi*, found in 1923 and exhumed in December of that year. It is recorded from the Sellards "No. 2" horizon, latest Pleistocene, Brevard County, Florida, near Melbourne. Through Prof. Frederic B. Loomis of Amherst College it came into the possession of the Amherst Museum; it bears the number Amherst Mus. 25–1. The materials were assembled under the direction of Professor Loomis, and mounted, as shown in figure 955, about one fifty-sixth natural size.

Typical of P. columbi.—The beautifully preserved third superior and inferior grinding teeth in the Amherst specimen (Fig. 954) agree very closely in their ridge-plate formula (M 3 $\frac{18+}{16½}$) with the typical *Parelephas columbi* of Georgia and the phosphate beds of South Carolina, in which the prevailing ridge-plate formula is M 3 $\frac{18\text{-}19}{15\text{-}16+}$.

Skeletal Characters.—Professor Loomis writes (cf. letter, July 28, 1928): In regard to our skeleton of *Archidiskodon* [*Parelephas*] *columbi* the four posterior grinding teeth [Fig. 954] and about 4 feet of each tusk are original, but most of the skull is



Molars of the Amherst Skeleton (cf. Fig. 955)

Fig. 954. Superior and inferior molars found in incomplete skull of *Parelephas columbi* (Amherst Mus. 25–1). About one-third natural size.

(Upper figures) Third left superior molar, l.M^3, crown and internal views, displaying 18+ ridge-plates, of which 15+ are worn. Height 206 mm.

(Lower figures) Third left inferior molar, l.M_3, crown and external views, displaying 16+ ridge-plates, of which 12+ are worn. Length 318 mm. = 12½ in.

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[1] [See footnote on opposite page.—Editor.]

restored. All the vertebral column, excepting four dorsals, and all of the ribs, excepting a few gaps, were found together. Of the forelimb, the right scapula is complete and half of the left scapula; both humeri were present, the right humerus lacking the head. The left radius and ulna were complete and fortunately the carpals, metacarpals, and phalanges of the forefeet, excepting three digits. Of the pelvic region, the ischium and pubes, and the lower portion of the ilium, including some 12 inches above the acetabulum, are present, but the upper part of the ilium is restored. The hindlimbs, including the femora, tibiæ, and left fibula, are complete, also the lower end of the right fibula.

It is very interesting to give the principal measurements in comparison with those of *Archidiskodon imperator* (Amer. Mus. 10598) and of *A. imperator maibeni* (Neb. Mus. 5-9-22):

NEW FORELIMB ESTIMATES OF PARELEPHAS AND ARCHIDISKODON

	P. columbi Amherst Mus. 25-1			*A. imperator* Amer. Mus. 10598			*A. imperator maibeni* Neb. Mus. 5-9-22		
	Ft.	In.	Mm.	Ft.	In.	Mm.	Ft.	In.	Mm.
Complete height at shoulder from summit of scapula to base of manus, as mounted	11	3	3430	11	5	3482	12	1⅝	3699
With fully extended manus							12	6⅝	3826
FORELIMB—Vertical diameter									
Right scapula	3	4¾	1037	3	4⅛	1017	3	6	1066+
Right humerus	3	4½	1030	3	7⅛	1095	4	1¼	1251
Left radius	3	1½	952	2	11	890	3		
Left ulna	3	5¾	1060				3	6¾	1085
Manus and carpus fully extended	1	10	559						
Manus and carpus, as mounted	1	4¼	412	1	6⅞	480	1	4⅝	424e
HINDLIMB—Vertical diameter									
Right femur	4	4¾	1340				[4	8	1422*]
Right tibia	2	8½	825						
Fibula	2	8½	825						
Complete length of hindlimb, acetabulum to base of pes, as mounted	8	1½	2477						

The above comparative measurements (see also Fig. 912) indicate the following shoulder heights, that is, summit of scapula and neural spines of anterior dorsals to the tip of the fully extended digits of the manus.

	Ft.	In.	Mm.	Ft.	In.	Mm.	Ft.	In.	Mm.
Skeletal shoulder height	11	3	3430	11	5	3482	12	6⅝	3826
Height in the flesh	11	11½	3644	12	1¾	3702	13	4¼	4068e

PARELEPHAS COLUMBI RELATIVELY RARE IN MEXICO

The true *Archidiskodon imperator* (see p. 1013 above) is evidently very abundant in Mexico, whereas *Parelephas columbi* appears to be relatively rare. Recent descriptions are those of Freudenberg (1922) and of Señorita Reyes (1923).

FREUDENBERG, 1922—We owe to this author a full history of this much misrepresented species (see his Memoir, p. 138. "I. *Elephas Columbi Falconer* und seine Rassen. Geschichtliches."). On pages 138-140 he clearly distinguishes this species but wrongly, as we believe, compares (Fig. 18, p. 140) Falconer's types of *Elephas columbi* and *E. armeniacus* with a second inferior molar from Mexico. After thus comparing the broad-plated grinding tooth of *E.* [=*Parelephas*] *columbi* with the narrow-plated grinder of *E.* [=*Parelephas*] *armeniacus*, he proceeds to describe a number of new subspecies, namely, *El. Columbi* var. *Felicis*, *El. Columbi* var. *silvestris*, *El. Columbi* var. *Falconeri*, and *El. Columbi* var. *imperator*, based on type grinding teeth. Osborn consequently describes these four subspecies under *Parelephas columbi* (*El. Columbi* var. *Felicis*) and *Archidiskodon imperator*, giving facsimile reproductions of the broad-plated type figures directly after Freudenberg. We also reproduce herewith (Fig. 901) the figure of a 13-plated grinding tooth after a photograph loaned by Señorita Reyes, referable to *A. imperator*.

Osborn, 1928: Probably members of this phylum migrated into Mexico in Upper Pleistocene time, long after *A. imperator* had become extinct.

REYES, 1923.—The Proboscidea collections from the Valley of Mexico were described by Señorita Alicia E. Reyes in her paper entitled "Los Elefantes de la Cuenca de Mexico," 1923, p. 227:

"Entre los numerosos mamíferos fósiles de la Cuenca de México, quizá ninguno tan ampliamente repartido como el elefante. Sus restos se encuentran en mayoría en nuestros museos, y son incontables las instituciones extranjeras que conservan en sus colecciones molares de Elephas procedentes de la cuenca.

Estos restos, sólo por excepción han sido debidamente clasificados, entre otras causas, porque las dos especies a que pertenecen, E. imperator y E.Columbi, presentan muchas formas de transición. Este hecho me ha inducido a revisar los ejemplares existentes en los museos de la Ciudad, con el objeto de intentar una clasificación, basándome en los datos así obtenidos."

In her valuable paper she fully describes and figures five specimens of *Elephas imperator* and five specimens of *E. columbi* chiefly from the localities of Tequixquiac, from the region of Zumpango, at Tepexpan, in the deposits above the basalt emitted by the volcano

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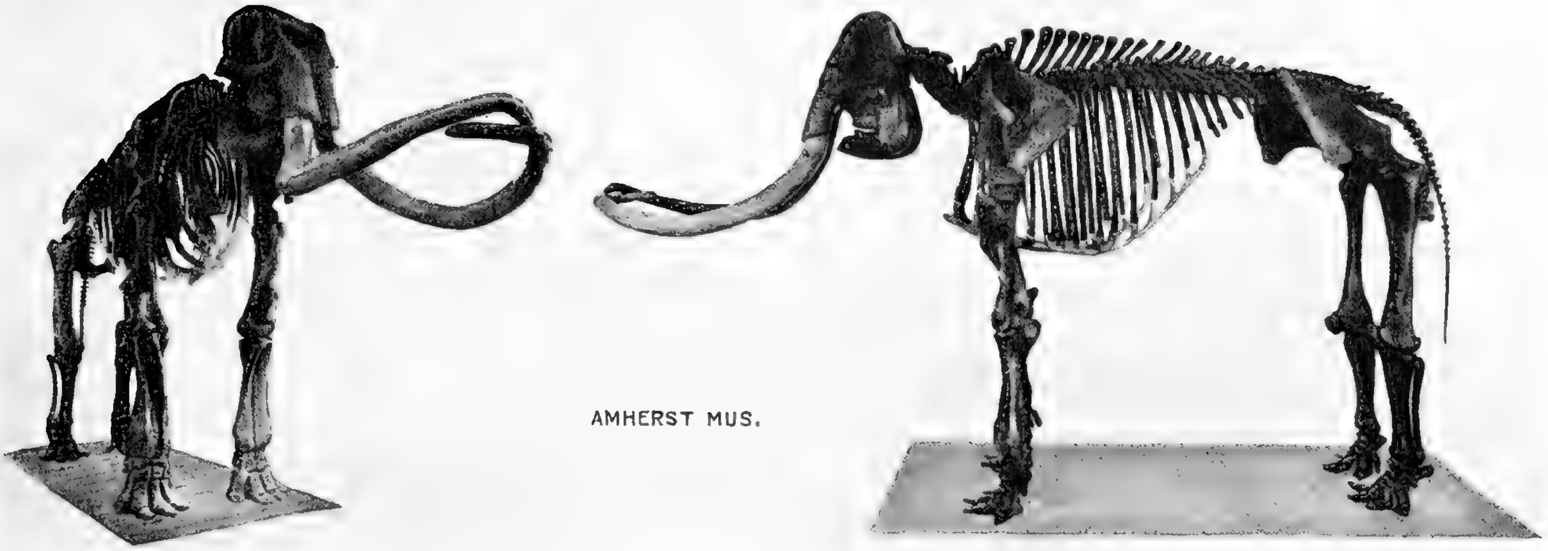
*Femur, Neb. Mus. 13-24-10-14 and 4-12-13.



Amherst Skeleton of Parelephas columbi from near Melbourne, Florida
About one fifty-sixth natural size

Fig. 955. Materials for the mounted skeleton of *Parelephas columbi*, bearing the number Amherst Mus. 25–1, were collected by Prof. Frederic B. Loomis of Amherst College in the No. 2 horizon, latest Pleistocene, Brevard County, Florida, near Melbourne. While the specimen was found in 1923 and taken up that December, it did not come into the possession of the Amherst Museum until 1925.

Skull mostly restored, also portions of both tusks, four dorsals, parts of the limb bones, ilium, manus, and pes; otherwise largely original (see below).

Superior and inferior molars shown in figure 954.

of Chiconautla, and in Villa de Guadalupe. Her observations relating to localities and to *E. columbi* are as follows, those relating to *E. imperator* are presented in abstract above.

Elephas [=*Parelephas*] *columbi.*

Escuela de Ingenieros No. 2. R.M^3 with 18 ridge-plates, 14 in 25 cm.; length 280 mm., breadth 110 mm., height 200 mm. From Tequixquiac. Fig. 10, p. 236.

Instituto Geologico (without number). R.M_3 with 15½ ridge-plates in 25 cm.; length 290 mm., breadth 102 mm., height 180 mm. From Zumpango.

Instituto Geologico 213. Fragment of skull and erroneously restored left tusk; also both third molars, length of r.M^3 350 mm., breadth 115 mm., height 190 mm. Total ridge-plates 19½; 16 in 25 cm. From Tequixquiac. Fig. 11, p. 237.

Instituto Geologico 214. Inferior mandible with l.M_3; 16 to 17 ridge-plates in 25 cm.; length 268 mm., breadth 90 mm., height 190 mm. From Villa de Guadalupe. Fig. 12, p. 238.

Escuela Ingenieros No. 3. L.M^3, with 21 ridge-plates, 20 in 25 cm.; length 275 mm., breadth 88 mm., height 190 mm. From Tequixquiac. Fig. 13, p. 239.

GEOLOGIC AGE OF THE PROBOSCIDEA FAUNA OF MEXICO

See Cope, 1884.2, "The Extinct Mammalia of the Valley of Mexico," also Furlong, 1925, "Notes on the Occurrence of Mammalian Remains in the Pleistocene of Mexico," etc., and Villada, 1903, "Apuntes Acerca de la Fauna Fósil del Valle de México."

Reyes, 1923.—This author concludes (1923, p. 239) with a comparison of *Parelephas columbi* and *Archidiskodon imperator* and a discussion of the observations of Leidy, Osborn, and Falconer. She dismisses the observations of Bárcena and Castillo (1882–1884) as to the human remains being contemporaneous with the mammoth at Tequixquiac, from which locality both *P. columbi* and *A. imperator* are recorded. It is not stated whether *P. columbi* is geologically more recent than *A. imperator*, as is probably the case. Reyes writes (June 12, 1924): "The little data which we have concerning the stratigraphy of the Valley [of Mexico] seem to confirm your hypothesis that *E. columbi* is more recent than *E. imperator*; but they are insufficient. It is not possible to correlate Quaternary strata of the Valley with "las Nordicas," because glacial periods or extremely cold periods do not exist. Diaz Lozano informs me that the flora is constantly tropical. All the examples which I have examined seem to me to belong to the two species *columbi* and *imperator*. More intensive study would perhaps permit a subdivision into varieties."

Faunal Succession.—A brief summary of our present knowledge of the Proboscidea and other mammals of this region in Upper Pliocene and in Pleistocene times is as follows:

Pleistocene	*Parelephas columbi*: Tequixquiac, Zumpango, Villa de Guadalupe. *Archidiskodon imperator*: Tepexpan, Tequixquiac, Zumpango, Villa de Guadalupe.
Pliocene or Pleistocene	*Cordillerion tropicus* (cf. *Mastodon humboldtii*). *Cordillerion oligobunis* Cope, Tequixquiac. *Cordillerion oligobunis progressus* Freudenberg, Canyon of Aculcingo.

PLIOCENE	*Cordillerion oligobunis antiquissimus* Freudenberg, Hidalgo, Valley of Amajaque.
PLIOCENE	*Cordillerion*(?) *oligobunis felicis* Freudenberg, Puebla.
PLIOCENE OR PLEISTOCENE	*Cordillerion*(?) *oligobunis intermedius* Freudenberg, Mexico.
	Hipparion castilli [*Protohippus*] Cope.
PLIOCENE	*Rhynchotherium tlascalæ* Osborn, type from Valley of Mexico, neotype from Sonora.

Other Pleistocene and Upper Pliocene faunas are the following (Cope, 1884, Villada, 1903, Furlong, 1925):

Tequixquiac:	*Equus* [*curvidens* Owen], *E. tau* Owen, *E. crenidens* Cope, *E. barcenæi* Cope, *E. occidentalis* Leidy, ref.
	Bison latifrons Harlan, ref.
	Camelops hesternus Leidy, ref.
	Platygonus (?)*compressus* Le Conte, ref.
	Capromeryx mexicana Furlong.
	Ænocyon dirus.
	Teleoceras (?)*fossiger* Cope, ref. [Pliocene].
Near Monterey:	*Glyptodon* [*mexicanus*].
	Nothrotherium.
	Neotoma, near *occidentalis*, ref.

Furlong concludes (1925.1, p. 152): "[1] The mammalian remains obtained at the four localities, Tequixquiac, Zumpango, Saltillo, and Monterey, in central and north-central Mexico, are indicative of the large and varied mammalian faunas that will be found in the Pleistocene deposits of Mexico when intensive work is carried on. [2] The two types of deposits recognized in the quarry at El Tajo, near Tequixquiac, and the mammalian forms found in each of these accumulations, indicate apparently two distinct stages in the Pleistocene history of this region. [3] The presence of *Ænocyon dirus*, a coyote-like form, and of *Capromeryx mexicana* in the brecciated fissure deposits suggests a faunal horizon comparable perhaps to that found at Rancho La Brea, California. The assemblage of mammals thus far found in the beds overlying the fissure deposits indicates a somewhat later horizon in the Pleistocene. [4] The paucity of mammalian remains found in the cave-fissure deposits in Cerro de la Silla offers little opportunity to add to our knowledge of the upland mammalian fauna of the Pleistocene or to make comparisons with the faunas from the California caves. The presence of *Nothrotherium* sp., *Equus* sp., and *Neotoma*, near *occidentalis*, a form related to the recent wood rat, are close to the types found in Samwel Cave, Shasta County, California."

Parelephas columbi felicis Freudenberg, 1922

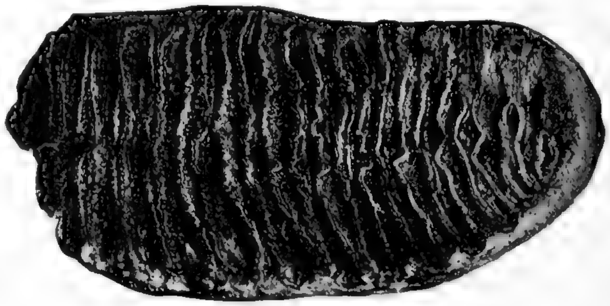
Figure 956

Pleistocene, Tecamachalco, Puebla, Mexico

Freudenberg's excellent figure and description of the type, an r.M^3, which he named *El. Columbi* var. *Felicis*, enables us to relate this type to the genus *Parelephas*, a species probably more progressive than the typical *P. columbi*.

El. Columbi var. *Felicis* Freudenberg, 1922. "Die Säugetierfauna des Pliocäns und Postpliocäns von Mexiko," Geol. und Palaeont. Abhand., N. F., 1922, Band XIV, Heft 3, pp. 147–152. TYPE.—Third right superior molar, r.M^3. Original in Leipzig (Pal. Coll. Univ. Leipzig 4403), Coll. Felix. Steppenform. HORIZON AND LOCALITY.—Tecamachalco, Puebla, Mexico. Pleistocene. TYPE FIGURE.—*Op. cit.*, Taf. VIII (XVI), fig. 4: "*Elephas Columbi* var. *Felicis* nov. forma."

TYPE DESCRIPTION.—(1925.1, p. 148): "Ein von Tecamachalco . . . im Staate Puebla stammender Molar, No. 4403 der paläontologischen Sammlung der Universität Leipzig, gleicht ebenfalls sehr einem solchen von *El. primigenius*, unterscheidet sich jedoch durch eine etwas bedeutendere Dicke der Schmelzlagen und ist vielleicht schon der folgenden Art zuzurechnen; doch stehen die Schmelzbüchsen ausserordentlich gedrängt. Das gleiche gilt für einen ebenfalls in unserer Sammlung befindlichen Zahn von Ejutla im Staat Oaxaca [Footnote: 'Unsere Textfigur 19a und 19b. *El. Columbi* var. *silvestris*.']. Herr Prof. Dr. Felix hatte die Liebenswürdigkeit, mir aus dem paläontologischen Museum der Universität Leipzig diesen Zahn neben einigen anderen aus Mexiko zur Untersuchung zu senden. Es handelt sich bei dem Elefantenzahn von Tecamachalco um einen M^3 des rechten Oberkiefers. Er trägt die Katalognummer 4403 des dortigen Museums. Der Zahn hat aussen weisse Farbe, welche auch das Innere aufweist, und oberflächlich einzelne Hämatitflecken. Diese Art der Erhaltung begegnete mir nur bei einigen mitteldiluvialen Fossilien, z. B. von San Luis."



TYPE OF PARELEPHAS COLUMBI FELICIS

Fig. 956. Type, r.M^3, of *Elephas Columbi* var. *Felicis* Freudenberg, 1922, Taf. VIII (XVI), fig. 4, one-half natural size. From Tecamachalco, Puebla, Mexico. Original in Leipzig (Pal. Coll. Univ. Leipzig 4403), Coll. Felix.

Observe that of the 14+ ridge-plates exposed by wear there are 9½ in 10 cm., slightly exceeding the maximum number attributable to this species as noted in the specimens of the Cohen Collection from the Charleston phosphate beds.

CHARACTERS.—Freudenberg (*op. cit.*, pp. 147–152) points out the confusion by Cope and Felix of the races of *Elephas columbi* Falc. with those of *E. primigenius*; he also points out the characters of Falconer's type of *E. columbi*; following Falconer's estimate of 1863, p. 56, he gives (p. 141) the ridge formula of *E. columbi* as: M 1 $\frac{12}{12}$, M 2 $\frac{16}{16}$, M 3 $\frac{20-?}{20-?}$. He concludes (p. 145) that *E. columbi* Falc. is related to *E. imperator* Leidy; he then proceeds to describe a number of races or varieties of these species of "*Elephas columbi*," of which *E. columbi* var. *Felicis* is the first mentioned; he distinguishes this subspecies by its closely compressed lamellæ as most nearly resembling *E. primigenius*, in contrast to a second subspecies *El. Cloumbi* var. *Falconeri* (cf. *A. imperator*) in which the lamellæ are less compressed.

Osborn, 1930: The relatively compressed ridge-plates (see legend of Fig. 956) together with the estimated ridge formula of M 3 $\frac{20\text{-}?}{20\text{-}?}$ may range this subspecies *Parelephas columbi felicis* beyond the limit of the typical *P. columbi* (M 3 $\frac{19}{16+}$) into the ridge-plate estimates of the more progressive species *P. floridanus* (M 3 $\frac{22+}{21+}$) or *P. jeffersonii* (M 3 $\frac{25}{24}$).

Parelephas columbi cayennensis Osborn, 1929

Figures 957, 979

Cayenne, French Guiana, South America. Probably Upper Pleistocene.

As set forth on page 1046 of the present chapter, the sole elephant so far known to have reached South America is a subspecies of *Parelephas columbi* reported by Captain Perret and successively mentioned by Lartet (1859), Lull (1908), and Freudenberg (1922), located in the Marseille Museum by Doctors Laurent and Repelin in 1929, and finally described by Osborn (1929.797, p. 20) as *Parelephas columbi cayennensis.* Lartet (1859, p. 500) characterized this specimen as "un fragment de molaire à lames épaisses," which led Freudenberg (1922, pp. 159, 160) to refer it to *El.* [*Archidiskodon*] *imperator*, from which it proves to be positively distinguished by the very narrow molar crown as described below.

Parelephas columbi cayennensis Osborn, 1929. "New Eurasiatic and American Proboscideans." Amer. Mus. Novitates No. 393, December 24, 1929, pp. 20, 21. TYPE.—"Three and a half ridge-plates of a third right superior molar, r.M^3, collected by Captain Perret in Cayenne (French Guiana), South America, and now preserved in the Muséum d'Histoire Naturelle, Marseille, France, as No. 8449 (cast Amer. Mus. 21933)." HORIZON AND LOCALITY.—Probably Upper Pleistocene. Cayenne, French Guiana, South America. TYPE FIGURE.—*Op. cit.*, p. 21, fig. 20.

SPECIFIC CHARACTERS.—The superior type fragments, photographs and casts of which have been kindly furnished the present writer through the courtesy of Director W. Laurent of the Muséum d'Histoire Naturelle of Marseille, and Prof. W. Repelin, Conservateur, is characterized by Professor Repelin (translation of letter of March 30, 1929) as follows: "They were in rather bad condition and so badly cemented together that I had to take away the larger part of the cement. One of these fragments, A–1, is represented in side view on one of these photographs. The lamellæ are very worn and they show the plate of blackish or brownish enamel rather in relief and the ivory forms a small median depression. The cement which separates the lamellæ is not very thick in this specimen. In the other photograph, A–2, the specimen is shown as seen from above. Finally another fragment, B, is also represented as seen from above. It has been worn in the direction of the lamellæ, but this worn part shows only a very irregular section of ivory and enamel."

The fragment consisting of three and a half lamellæ or ridge-plates is made the type of the new subspecies *Parelephas columbi cayennensis.* These ridge-plates appear to belong to the posterior portion of the crown of a third superior molar of the right side, r.M^3; they are strongly concave posteriorly and are composed of coarse enamel, deeply grooved or crenulated on the sides; the external cement, formerly present, has been dissolved or worn away; the apices of the three ridge-plates present a convex profile, hence supporting the superior molar reference indicated by the posterior concavity. They correspond broadly with ridge-plates 16, 17, and 18 of an r.M^3 of *Parelephas columbi*; in size they correspond with ridge-plates 19, 20, and 21 of *floridanus*; they seem relatively narrow, thus agreeing with the narrow ridge-plated *P. columbi* rather than with the broad-plated *Archidiskodon imperator*.

Geographically the nearest representative of *Parelephas columbi cayennensis* to the north is the *Parelephas columbi felicis* Freudenberg, 1922, from Puebla, described on the opposite page 1082 and illustrated in figure 956 of the present Memoir, in which the posterior ridge-plates are broader, with less coarse enamel, than in the present type specimen.

TYPE OF PARELEPHAS COLUMBI CAYENNENSIS OSBORN

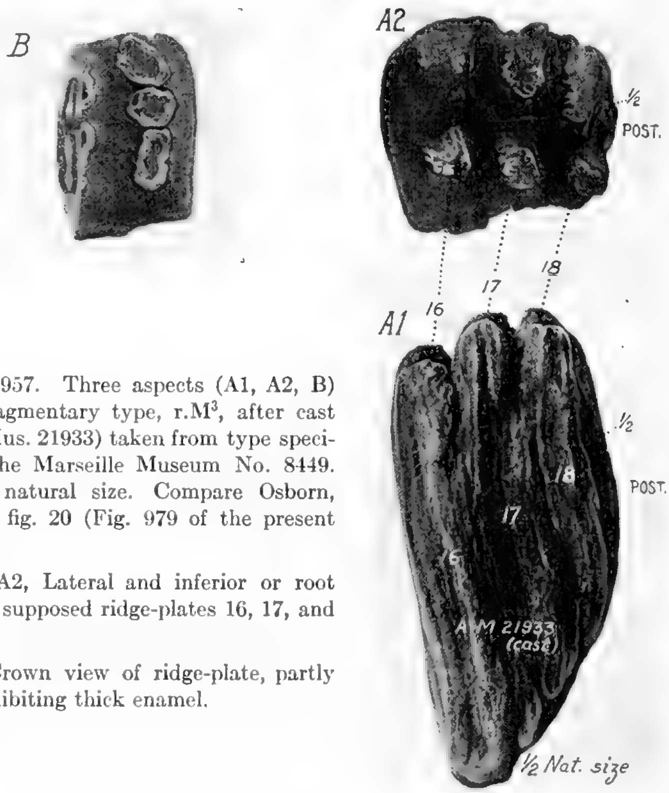


Fig. 957. Three aspects (A1, A2, B) of the fragmentary type, r.M^3, after cast (Amer. Mus. 21933) taken from type specimen in the Marseille Museum No. 8449. One-half natural size. Compare Osborn, 1929.797, fig. 20 (Fig. 979 of the present Memoir).

A1, A2, Lateral and inferior or root aspect of supposed ridge-plates 16, 17, and 18-½.

B, Crown view of ridge-plate, partly worn, exhibiting thick enamel.

Parelephas jeffersonii Osborn, 1922

Figures 806, 810–814, 818, 892, 930, 931, 935–937, 958–968, 975, 988, 1009, 1029, 1084, Pl. XXII

Upper Pleistocene, post(?)-Wisconsin, IV GLACIAL till (*fide* Leverett and Hay, 1923); Jonesboro, Indiana.

Syn.: *Elephas roosevelti* Hay, 1922. Compare also *Elephas* [*Parelephas*] *jacksoni* Mather, 1838, which may prove to antedate *Parelephas jeffersonii.*

This well-known and very important specific stage, genotypic of *Parelephas,* is widespread throughout the Middle United States and gives us a complete knowledge of the skeletal and dental characters. The ridge-plate formula is:

$$\text{Dp } 3\,\frac{8+}{} \text{ Dp } 4\,\frac{12}{13} \text{ M } 1\,\frac{11+}{} \text{ M } 2\,\frac{18\text{-}19e}{19e} \text{ M } 3\,\frac{25}{24}$$

History of the Name.—This species is very abundant in the latter part of the Pleistocene period in the northern United States and southward into Mexico; the type may even be of Postglacial age; it is the animal erroneously described by Cope and Osborn as "*Elephas columbi*," and by Hay as "*E. primigenius*," and finally separated by Osborn as *Elephas jeffersonii*. It now becomes the most fully known species of American mammoth. This species was described by Osborn July 8, 1922. Hay subsequently (Sept. 30, 1922) proposed the name *Elephas roosevelti*. Mather in 1838 gave the name *Elephas jacksoni* to a similar animal, the type of which has been lost rendering the species indeterminate at present. In 1924 Osborn made *Elephas jeffersonii* the genotypic species of the new genus *Parelephas*.

Elephas jeffersonii Osborn, 1922. "Species of American Pleistocene Mammoths. *Elephas jeffersonii*, New Species." Amer. Mus. Novitates No. 41, July 8, 1922, pp. 11–16. Type.—Skull, jaws, and greater part of skeleton (Amer. Mus. 9950). Horizon and Locality.—Upper Pleistocene, post(?)-Wisconsin, IV Glacial till; Jonesboro, Indiana, on the farm of Dora S. [E.] Gift. Type Figure.—Osborn, *op. cit.*, 1922.555, p. 11, fig. 10. Confusion as to Paratypes.—(1) A pair of upper and lower grinding teeth of both sides (Amer. Mus. Warren Coll. 10457) from Zanesville, Ohio, erroneously selected by Osborn (1922.555, pp. 11, 12, also figs. 11 and 12) as paratypes; (2) subsequently (1923.601, p. 4) referred by Osborn to *Elephas washingtonii*; (3) finally (1924.633, pp. 4 and 7) made by Osborn the type of a new subspecies, *Parelephas jeffersonii progressus* (=*Parelephas progressus*); (4) new paratype [ideotype, see footnote on p. 1068] jaws (Amer. Mus. 13225, 21892) selected by Osborn in the present Memoir.

History of Specific and Generic Separation by Osborn.—The following type description is reprinted in part from Osborn's paper cited above (Osborn, 1922.555). Osborn introduced the subject as follows (p. 1): "The present article relates explicitly to the type characters of *Elephas columbi*, of *E. imperator*, and of the American specimens referred to *E. primigenius*, three species which have become more or less confused in all the previous literature because the characters of the type specimens have not been precisely determined and compared. The object of the present communication is to clear up this confusion and to propose *Elephas jeffersonii* as a new species of American Pleistocene mammoth. . . . [*Op. cit.*, p. 15] The American elephant heretofore widely known as '*Elephas columbi*,' the Columbian Mammoth, will hereafter be known as *Elephas jeffersonii*, the Jeffersonian Mammoth."

OSBORN'S SPECIFIC (1922) TYPE DESCRIPTION AND TYPE FIGURES OF PARELEPHAS JEFFERSONII

(Osborn, 1922.555, p. 11): "The above diagnoses of the real specific characters of the grinding teeth of [the true] *Elephas columbi*. . . . and of the true *E. primigenius* leaves without a name the animal which previously has been described in all the literature (excepting Soergel's recent Memoir) as *Elephas 'columbi.'* This animal is better known than either of the others; it is represented in all the collections of the principal museums of the United States, as described by Hay (1914), and particularly in the American Museum by four especially fine specimens. Of these we select as the type Amer. Mus. 9950, including the skull, jaws, and greater part of the skeleton (Fig. 10), found near Jonesboro, Indiana, on the farm of Dora S. [E.] Gift; purchased for the Museum with the Jesup Fund in 1904, restored and mounted in 1906; described by Osborn in 1907 as *Elephas columbi*, determined [and described] by Hay (1914) as *Elephas primigenius*."

(*Op. cit.*, p. 15): "Cranial Characters.—Still more obvious are the differences between the relatively long, broad, and shallow crania of *E. jeffersonii* and the relatively short, narrow, and deep crania of *E. primigenius*, proportions which are correlated respectively with the corresponding proportions just described and figured in the teeth."

"The four complete skulls of this species known to the writer are those of (1) in the type mounted skeleton (Amer. Mus. 9950); (2) the fine male skull associated with the jaws and a large part of the skeleton (Amer. Mus. Cope Coll. 8681) from Whitman County, Washington, and labeled '*Elephas columbi*' [since referred to *Parelephas washingtonii*]; (3) the young male skull (Amer. Mus. Cope Coll. 14475) from Dallas, Texas, also labeled '*Elephas columbi*' [now referred to *Archidiskodon imperator*]. (4) To these should be added the very large male skull (Nat. Mus. 10261) collected near Cincinnati, Ohio; in this specimen the ridge formula is $\mathrm{M}\ 3\ \frac{26}{\ }$; seventeen plates were in use; the compression of the grinding teeth is greater, namely:

9 ridge-plates in 100 mm. on the outer [convex] side, at the worn edge,

9 ridge-plates in 100 mm. on the worn mid-coronal surface.

The cranial characters of this specimen are entirely similar to those of the three skulls in the American Museum collections, except that it is larger and more robust."

(*Op. cit.*, p. 12): "This typical American species is named in honor of the third president of the United States, Thomas Jefferson, in commemoration of his long-continued devotion to mammalian palæontology."

Type Locality and post(?)-Wisconsin Age (IV Glacial) of Parelephas jeffersonii Type.—The geologic age of the type of *Parelephas jeffersonii* is a very important matter; according to Leverett and Hay, the Glacial or Postglacial deposit where it was found is of post(?)-Wisconsin age, i.e., IV Glacial.

(Hay, 1923, p. 139): "6. Fairmount, Grant County [Indiana]. Here was found, in 1904, the nearly complete skeleton of the mammoth mounted in the American Museum of Natural History in New York City. It has been described and figured [as *Elephas primigenius*] by the writer (36th Ann. Rep. Geol. Surv. Indiana, p. 718, figs. 63, 64 [1912.2]; Iowa Geol. Surv., vol. XXIII, p. 396, fig. 133) [1914.1]. It was found on the farm of Mrs. Dora C. [E.] Gift, about 4 miles east of Fairmount. The location is in the southeast quarter of section 23, township 23 north, range 8 east. This information has been furnished by Mr. George Swisher, surveyor of Grant County."

"This whole region is mapped by Leverett as being occupied by ground moraine of till plains, and the animal must have lived after the Wisconsin ice cleared away. A tract more or less morainic, an extension of the Union City moraine, is indicated by Leverett on his latest map as passing further south than Fairmount. At the earliest it must have been after the withdrawal of the ice from the Union City moraine that the animal lived. Considering the character of the surrounding country, the nature of the deposit inclosing the skeleton, and the depth at which it was buried, it might be supposed that it was not long after the formation of the Union City moraine that this elephant existed."

Genotypic Species of Parelephas (Osborn, 1924.633).—After the establishment (Osborn, 1922.555) of *Elephas jeffersonii* as a species distinct from *Elephas columbi* and from *Elephas primigenius,* Osborn finally (1924.633) reached the conclusion that *Elephas jeffersonii* could be placed neither in the phylum of *Archidiskodon* nor in the phylum of *Mammonteus* (e.g., *Mammonteus primigenius*) and for the reasons above recited he selected it as the genotypic species of the new genus *Parelephas.*

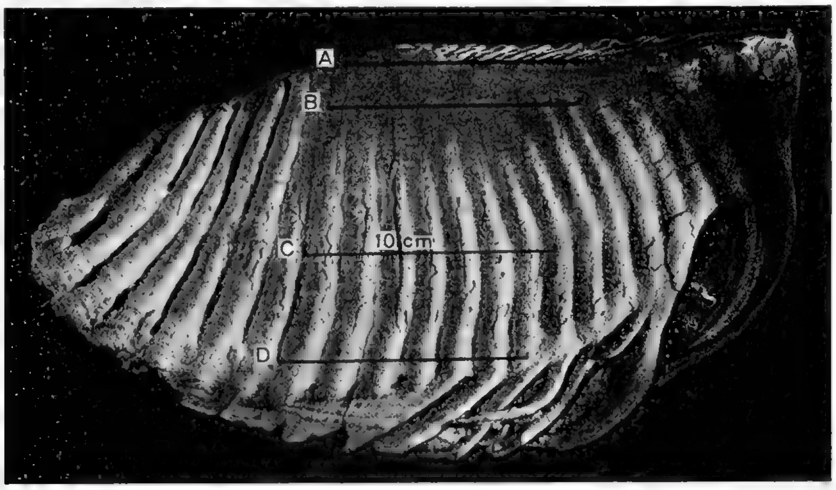
SPECIFIC CHARACTERS OF PARELEPHAS JEFFERSONII

Osborn's Error (1922.555) as to Ridge Formula based on Zanesville Paratype (since made the Type of Parelephas jeffersonii progressus Osborn, 1924).—In the above original description of *Elephas* (*Parelephas*) *jeffersonii,* Osborn *erroneously* selected as a *paratype* two upper and lower grinders from Zanesville, Ohio, contained in the Warren Collection (Osborn, 1922.555, p. 11): "As the paratype of this species we select a pair of upper and lower grinding teeth of both sides (Amer. Mus. 10457) acquired with the Warren Collection in 1906 and described by Warren in 1855 (p. 163, Pl. xxviii, fig. C) as *Elephas 'Primigenius.'*" In 1923, Osborn corrected this error (1923.601, p. 4), but remained in doubt as to the true relationship of the Zanesville teeth: "Related to this species [*Elephas washingtonii*] may be a pair of upper and lower grinding teeth of both sides from Zanesville, Ohio (Amer. Mus. Warren Coll. 10457) acquired with the Warren Collection in 1906 and described by Warren in 1855 (p. 163, Pl. xxviii, fig. C) as *Elephas 'Primigenius.'*"

It appears (Osborn, 1924.633, pp. 4, 7) that these Zanesville 'paratype' molars are typical of a progressive mutation of *Parelephas* with a higher ridge formula, namely, M $3\frac{30}{26}$. To this subspecies the name *Parelephas jeffersonii progressus* was assigned. It becomes *Parelephas progressus* in the present Memoir.

DENTAL CHARACTERS OF PARELEPHAS JEFFERSONII

Ridge Formulæ.—It has been a very difficult matter to determine the ridge formula of the species *P. jeffersonii;* as noted above, the high ridge formula (M $3\frac{30}{26}$) originally given by Osborn, as based on the original paratypes from Zanesville, Ohio, was erroneous; the finally corrected ridge formula of the type, new paratypes, and referred specimens of *Parelephas jeffersonii* is: M $3\frac{25}{24}$.



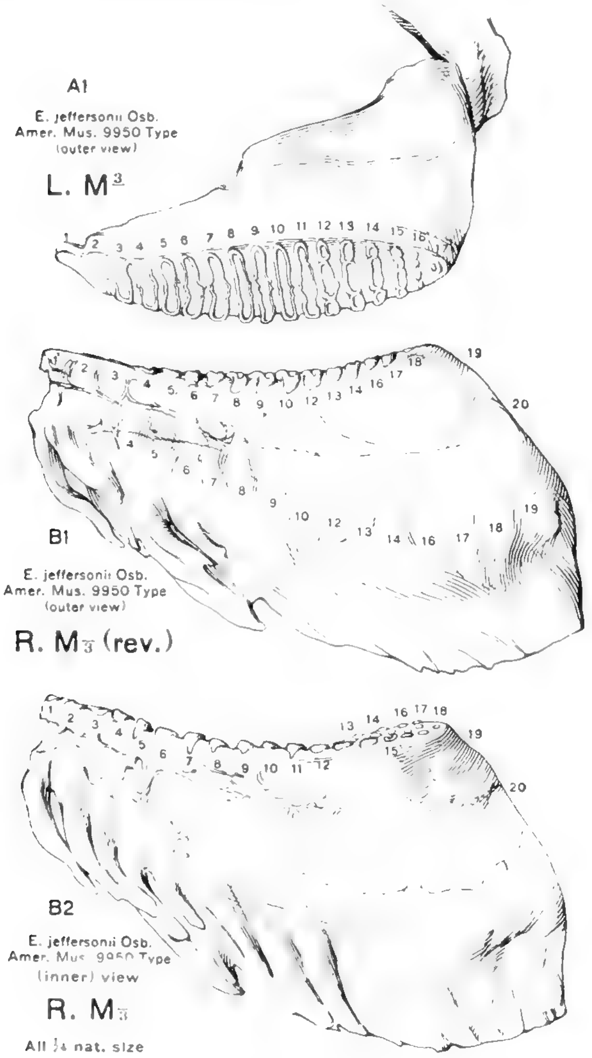
Parelephas jeffersonii Ridge-plate compression at three levels of R.M_3
One-third natural size

Fig. 958. Right third lower molar, r.M_3, of *Parelephas jeffersonii* new paratype [ideotype] (Amer. Mus. 13225). Observe: (1) The arcuate arrangement of the typical *twenty-three* ridge-plates of this partly worn molar. By counting the ridge-plates at different levels, as indicated by the horizontal lines **A, B, C, D,** we observe that the upper plates are much more closely compressed than the lower plates, as follows:

A, Summit of crown, 11½ plates in 10 cm.
B, One-sixth below summit, 10 plates in 10 cm.
C, Four-sixths below summit, 7½ plates in 10 cm.
D, Near base of crown, 6½ plates in 10 cm.

The *type dentition* (Amer. Mus. 9950) is that of a very aged male (Fig. 959), as indicated *first* by the remarkable length (= 11 ft. 4½ in. or 3.47 m.), incurvature, and crossing of the tusks (Fig. 966); *second* by the fact that in the third superior and inferior molars the anterior ridge-plates are worn off. Consequently Osborn was unable to give the type ridge formula correctly in his type description (1922.555) and made the error of depending upon the erroneously associated Zanesville paratype; in his second description, Osborn (1923.601, p. 4) wrote: "Since the original description of *Elephas jeffersonii* was written the molars [Fig. 959] in the aged type specimen (Amer. Mus. 9950) have been cut out of the jaw of the skull and carefully sectioned; it has thus been found that they are relatively short and deep and present a different ridge formula, namely: $M\ 3\frac{\quad}{20+}\left[\frac{+17}{+20}\right]$. There can be no question that the type of *E. jeffersonii* has a shorter jaw and shorter and deeper molar teeth than those of the erroneously associated paratype which may now be referred to *E. washingtonii.*"

The result of sectioning the molar teeth in the aged type specimen proved that the *anterior* ridge-plates were entirely worn off; the *aged* type ridge formula may therefore be written: $M\ 3\ \frac{+17}{+20}$. The *adult* ridge formula, however, is $M\ 3\,\frac{25}{24}$.



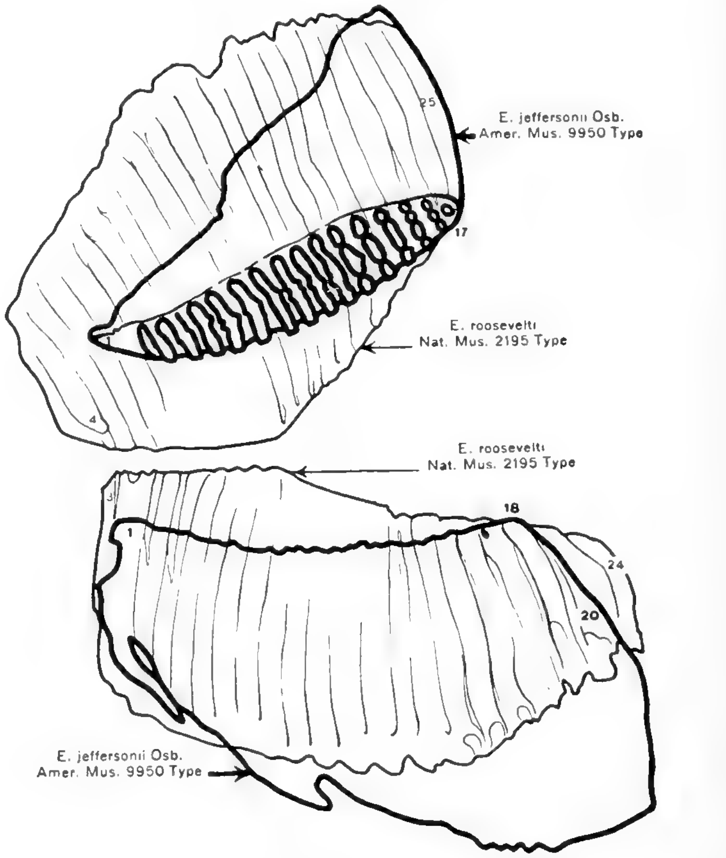


Fig. 959. (Left) Aged Type Third Superior and Inferior Molars of Parelephas jeffersonii
(Right) The same superposed on Elephas roosevelti [=Syn. Parelephas jeffersonii]

(Left) Aged *type* superior and inferior molars of *Parelephas jeffersonii* (Amer. Mus. 9950), viewed upon the *outer* surface with the anterior portion of the crown to the *left.*

Superior molar, M^3, partly encased in the maxilla, consequently the fangs are not displayed. Inferior molar, M_3, completely removed from the jaw and sectioned to show the incomplete posterior ridge-plates.

A1, Outer view of left superior molar, $1.M^3$, 1–4 anterior ridge-plates worn off; remaining ridge plates (5–17) exposed; 17 ridge-plates in use. Total estimated ridge-plates 25.

B1, Right inferior molar, $r.M_3$ (rev.), 4 anterior ridge-plates worn off; 18 ridge-plates in use (1–18); incomplete ridge-plates 19–20 demonstrated by vertical and horizontal sections of this tooth. Total estimated ridge-plates 24.

B2, Inner aspect of right M_3, showing 18 ridge-plates in use (1–18); incomplete ridge-plates 19 and 20, at posterior border. Total estimated ridge-plates 24.

(Right) Diagram showing in *heavy* lines type superior and inferior molars of *Parelephas jeffersonii* projected upon the type superior and inferior molars of *Elephas roosevelti* (light lines). This diagram was constructed by superposing type figure 959, left, upon type figure 968.

This diagram shows: (1) That the young adult molar teeth of *E. roosevelti* (light lines) exhibit a ridge formula of $M\ 3\ \frac{25}{24}$, whereas the aged molar teeth of *P. jeffersonii* (heavy lines) exhibit a ridge formula of $M\ 3\,\frac{+17}{+20}$; (2) the anterior ridge-plates in this species are worn off before the posterior ridge-plates attain their full length; (3) in the type of *E. roosevelti* 10–13 ridge-plates are in use, in the type of *P. jeffersonii* 17–18 ridge-plates are in use; (4) the long diameter of M^3 is oblique, while the long diameter of M_3 is horizontal; (5) following the rule in the Elephantidæ, approximately the same number of ridge-plates is in use at the same time in the superior and inferior molars, namely, in the young *E. roosevelti* $\frac{13}{10}$; in the aged *P. jeffersonii* $\frac{17}{17\text{–}18}$. (6) The worn ridge-plate surface of M^3 is convex; that of M_3 is concave.

It is proven by comparison of the aged type teeth (Fig. 959) of *Parelephas jeffersonii* with the adult type teeth (Fig. 968) of its synonym *Elephas roosevelti*, that in the aged type of *P. jeffersonii* *five* to *six* ridge-plates have been worn off in front of the upper molars and *four* ridge-plates in front of the lower molars, by extreme use. This is shown diagrammatically in figure 959, in which the aged teeth of the type of *P. jeffersonii* are superposed upon the adult teeth of the type of *E. roosevelti*. This diagram also illustrates that the *anterior* ridge-plates begin to be worn off while the *posterior* ridge-plates have not attained their full depth and are still growing.

Corrected Ridge Formulæ.—Fortunately it is now possible to verify this interpretation of the ridge formulæ of these two types and positively to establish the adult ridge formula of *Parelephas jeffersonii* (*E. roosevelti* syn.) by comparison of *five* different specimens as follows:

Indiana	Type skull and jaws of *P. jeffersonii* (Amer. Mus. 9950), aged ridge formula: M $3\,\frac{+17}{+20}$. In M_3, 17 ridge-plates in use, 3 rudimentary.
Kansas	New paratype[1] jaw of *P. jeffersonii* (Amer. Mus. 21892), a young jaw. Ridge formula: M $3_{\overline{24}}$. In M_3, 12 ridge-plates in use.
Kentucky	New paratype[1] jaw of *P. jeffersonii* (Amer. Mus. 13225), a middle-aged jaw. Ridge formula: M $3\,\frac{}{24+}$. In M_3, 14–15 ridge-plates in use.
Ohio	Referred skull of *P. jeffersonii* (Nat. Mus. 10261), adult male. Ridge formula: M $3^{\underline{26}}$. In M^3, 17 ridge-plates in use.
Illinois	Type grinding teeth of *Elephas roosevelti* Hay (Nat. Mus. 2195). Ridge formula: M $3\frac{25}{24}$.

Thus from the recurrent evidence of five different specimens, young, middle-aged, adult, and extremely aged (i.e., type), we conclude as follows:

Typical adult ridge formula of *Parelephas jeffersonii* type and four referred specimens: M $3\,\frac{25}{24}$.

Typical Ridge-plate Compression.—Osborn (1922.555, p. 12) carefully described the ridge-plate compression in the *type inferior* molars of *Parelephas jeffersonii* (Amer. Mus. 9950) as follows:

7 ridge-plates in 100 mm. on the convex internal surface.

7–7½ ridge-plates in 100 mm., obliquely worn on mid-coronal surface; 17 ridge-plates in use.

8 ridge-plates in 100 mm. on the concave external surface.

Thus the number of the ridge-plates in the type of *Parelephas jeffersonii* is: 7, or 8, or 9 in 100 mm., depending upon where the count is taken.

Ridge-plate Count at Different Crown Levels (Fig. 958.—(1) As observed in the diagram and figure (Figs. 958, 959) the ridge-plates are arcuate and the ridge-plate arches *converge* toward the summit, the greatest number of ridge-plates may be counted at the *summit* of the unworn crown, e.g., 11½ ridge-plates in 100 mm., a ridge-plate compression approaching that of *Mammonteus primigenius*. (2) As we descend down the side of the crown (B), we may find 10 ridge-plates in 100 mm. (3) As we reach the point of maximum expansion of the ridge-plate arches (C), we may count 7½ ridge-plates in 100 mm. In general the compression is greater in the *short superior* molars than it is in the *long inferior* molars; consequently we get the highest count in the superior teeth. (4) This difference in the compression of the arcuate ridges explains the discrepancy in the records of the "laminaire fréquence" of Depéret and the ridge-plate counts of Hay. Similar discrepancies are observed in the ridge-plate compression of *Archidiskodon* and of *Mammonteus*. According to the observations of Hay (1914), as accepted or modified by Osborn, the ridge-plate compression characteristic of different specimens of *Parelephas jeffersonii* may be summarized as follows:

In the *inferior* molars: 7 ridge-plates (at base) to 11½ (at summit of crown) in 100 mm.

In the *superior* molars: 7 ridge-plates (at base) to 10 (at summit of crown) in 100 mm.

REFERRED RIDGE FORMULÆ OBSERVED BY HAY AND OSBORN

The majority of the teeth from the middle and northern United States described as "*Elephas columbi*" by Hay (1914, pp. 410–421) actually belong to *Parelephas jeffersonii* and are readily distinguishable from the teeth of the true type of *Elephas columbi* Falc. of the Southern States as well as from the true teeth of *Mammonteus primigenius* and of *Archidiskodon imperator*. Eliminating six of Hay's specimens from Afton, Oklahoma, which may belong to *A. imperator* Leidy, also three specimens from the phos-

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[1] [See footnote on page 1068 above.—Editor.]

phate beds of South Carolina, which may belong to the true *Elephas columbi* Falc., Hay's detailed observations on teeth probably or possibly (Alaska?) referable to *Parelephas jeffersonii* or to *P. washingtonii* (Washington, Oregon, Alaska) may be summarized as follows:

Kentucky	Phil. Acad.	Dp^4 (Big Bone Lick, Ky.), length 145 mm., width 75 mm., height of first plate 143 mm.; ridge-plates 12, front and rear talons. "A line 100 mm. long passes across eight of these plates, a number greater than one might expect in this species;"
Alaska	Nat. Mus. 6669	Dp_4 (Alaska, Yukon), length 180 mm., width 67 mm., height 135 mm.; 13 ridge-plates. "There are seven ridge-plates in a 100 mm. line."
Montana	Nat. Mus. 6052	Dp_4 (Glendive, Mont.), length 155 mm., width 75 mm.; ridge-plates 8+.
?	Nat. Mus. 287	M^2 (Loc. unrec.), length 300 mm., width 78 mm., height of thirteenth plate 195 mm.; ridge-plates 18 or 19; eight plates in a 100 mm. line; amount of cement between the plates small.
Iowa	Univ. Iowa 167	M^2 (Logan, Iowa), length 192 mm., width 70 mm., height of eighth plate 160 mm.; eight plates in a 100 mm. line.
Alaska	Nat. Mus. 6668	M_2 (Alaska), length 277 mm., width 90 mm., height of sixth plate 140 mm.; ridge-plates 19; seven ridge-plates in a 100 mm. line.
Oregon		M^3 (Mt. Angel, Clack. Co., Ore.), length 355 mm., height of thirteenth plate 193 mm.; ridge-plates 21+; 5½ ridge-plates in a line 100 mm. long.
Indiana	Neb. Mus.	M_3 (Tipton Co., Ind.), length 280 mm., height of fourth plate 152 mm.; ridge-plates 22+.

To the above *eight* specimens observed by Hay from Kentucky, Iowa, Indiana, Montana, Oregon, and Alaska, we may add the following six specimens observed and included by Osborn in the species *Parelephas jeffersonii* or *P. washingtonii*:

Indiana	Amer. Mus.	9950 (type skull) M^3, M_3 (Jonesboro, Ind.), type aged male, anterior ridge-plates worn off. $\text{M}\,3\frac{+17}{+20}$.
Washington	Amer. Mus.	8681 (referred *Parelephas washingtonii* skull) $\text{M}^{2\text{-}3}$ (Whitman Co., southwest Washington), male: M^2, 10+ ridge-plates; M^3, 23 ridge-plates. (See Fig. 976.)
Kentucky	Amer. Mus.	13225 (paratype jaw) M_3 (Twin Cr. near Sanders, Ky., Big Bone Lick region), middle aged, paratype of *P. jeffersonii*: M_3, 24 ridge-plates.
Kansas	Amer. Mus.	21892 (paratype jaw) M_3 (near Pendennis, Lane Co., Kan.), young adult, paratype of *P. jeffersonii*: M_3, 24 ridge-plates.
Ohio	Nat. Mus.	10261 (referred skull) M^3 (Cincinnati, O.): M^3, 26 ridge-plates.
Illinois	Nat. Mus.	2195 (type teeth) M^3, M_3 (Ashland, Cass Co., Ill.). Type of *Elephas roosevelti*: M^3, 25 ridge-plates; M_3, 24 ridge-plates. (See Fig. 968.)

The type and referred ridge formula of *Parelephas jeffersonii* is: $\text{Dp}\,2^{?}\,\text{Dp}\,3\frac{8+}{}\,\text{Dp}\,4\frac{12}{13}\,\text{M}\,1\frac{11+}{}\,\text{M}\,2\frac{18\text{-}19e}{19e}\,\text{M}\,3\,\frac{26}{24}$.

According to these fourteen specimens, as described by Hay and Osborn, the *average* specific ridge-plate frequency of *Parelephas jeffersonii* in 10 cm., as compared with that in *Mammonteus primigenius, Archidiskodon imperator*, and *Parelephas columbi*, is as follows:

Mammonteus primigenius and *M. primigenius compressus*: 8–10–11–12–13
Parelephas jeffersonii: 7–8–9
Archidiskodon imperator: 5–6–7
Parelephas columbi: 5–6

Other Specific Characters of the Teeth (Hay, 1914, p. 395, Osborn, 1922–1924).—(1) Ridge-plates more widespread than those of *E. primigenius*. (2) Enamel plates thicker and more channeled and crimped. (3) Superior ridge-plates transverse or concave posteriorly; inferior ridge-plates transverse or concave anteriorly, i.e., disc shaped or bent. (4) Rear or last superior molars, M^3, usually strongly arched. (5) Superior ridge-plates, M^3, not known to exceed 25 to 26; inferior ridge-plates of M_3 not known to exceed 23 to 24. (6) Bony sheaths of superior tusks shorter and more divergent than those of *Elephas primigenius*. (7) Superior tusks in young males diverging rapidly, in middle age beginning to rotate, in adult males converging, so that in aged males the tips cross.

Detailed Structure of the Teeth.—The detailed structure of the superior and inferior teeth of *Parelephas jeffersonii* is beautifully shown in the following figures of this Memoir which have been prepared with the utmost care and precision:

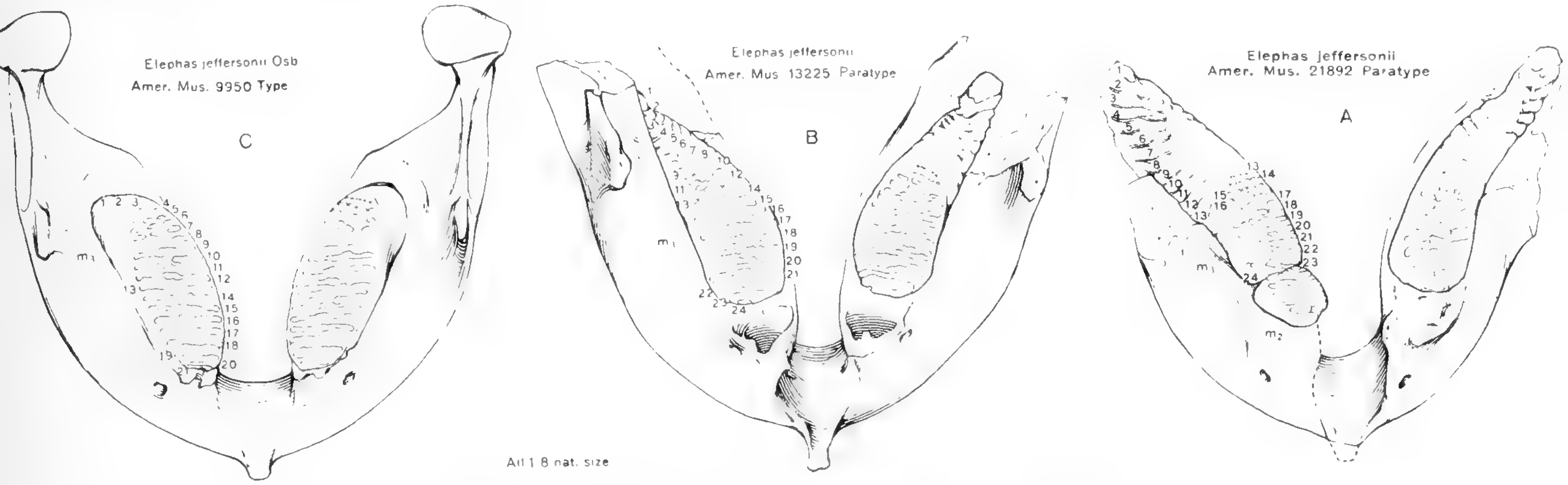
Fig. 959. Vertical view of the aged superior and inferior molars of the type of *Parelephas jeffersonii* (Amer. Mus. 9950).

Fig. 960. Superior view of the type and paratype [ideotype] inferior grinding teeth and jaws of *Parelephas jeffersonii*.

Fig. 968. Exterior and crown views of superior and inferior grinding teeth of the type of *Elephas roosevelti* (Nat. Mus. 2195).

Fig. 959. Diagram showing superior and inferior grinding teeth of type of *Parelephas jeffersonii* and *of Elephas roosevelti.*

Fig. 967. Middle-aged paratype [ideotype] jaw of *Parelephas jeffersonii* (Amer. Mus. 13225).



JAWS OF PARELEPHAS JEFFERSONII FROM INDIANA, KENTUCKY, AND KANSAS

One-eighth natural size

Fig. 960. Superior view of type and paratype [ideotype] grinding teeth and jaws of *Elephas jeffersonii.* Compare (B) with Mather's type of *Elephas* [=*Parelephas*] *jacksoni* (Fig. 946).

A, Ideotype *young adult* jaw (Amer. Mus. 21892) with M_2 *in situ*, eight plates in use; M_3 with twelve plates in use; total number of ridge-plates in M_3 twenty-four. From near Pendennis, Lane Co., Kansas. Compare Amer. Mus. 14558 (*Archidiskodon imperator* ref.—Fig. 889).

B, Ideotype *middle-aged* jaw (Amer. Mus. 13225), M_2 shed, M_3 with fourteen to fifteen plates in use; total number of plates in M_3 twenty-four; jaws somewhat more massive. From Twin Creek, near Sanders, Kentucky, Big Bone Lick region.

C, Type of aged *Parelephas jeffersonii* Osborn (Amer. Mus. 9950); jaw with M_3 worn to the edge of the anterior fang; one or possibly two plates have been worn off, seventeen plates in use, three posterior plates shown in section (Fig. 959, right). Jaws still more massive. From Jonesboro, Indiana.

Fig. 892. Comparative figure of jaws of *Parelephas jeffersonii* and other species.

Fig. 958. Right third lower molar paratype [ideotype] of *Parelephas jeffersonii* (Amer. Mus. 13225).

JAWS OF PARELEPHAS JEFFERSONII

The first to distinguish the jaw of *Elephas* [=*Parelephas*] *jacksoni* from the jaw of *Elephas* [=*Mammonteus*] *primigenius* was Mather in his description and figure (Fig. 946) of 1838. When all the jaws figured in the present chapter, both in superior and lateral view, are compared with the jaws figured in the *Mammonteus* chapter (Chap. XVIII), the latter, it will be observed, are shorter, deeper, and more compressed anteroposteriorly, while relatively broader, with a broader groove above the rostrum.

Specific Characters of the Jaws.—Certainly belonging to this species are the three specimens shown from above in figure 960, namely, the aged type (Amer. Mus. 9950), the paratype [ideotype] middle-aged jaw (Amer. Mus. 13225) from the Big Bone Lick region, Kentucky, and the paratype [ideotype] young adult jaw (Amer. Mus. 21892) from Lane County, Kansas. The lateral and superior views of the middle-aged paratype [ideotype] are shown in detail in figure 967. In figure 892 is shown the internal aspect of the type jaw (Amer. Mus. 9950) also the internal aspect of the middle-aged paratype [ideotype] jaw (Amer. Mus. 13225).

Comparisons.—These comparative figures, which have been prepared with the greatest care to a uniform one-eighth and one-fourth scale, will enable the student to distinguish these jaws of *Parelephas jeffersonii* very readily from those of *Archidiskodon imperator* and somewhat less readily from those of *Mammonteus primigenius.* (1) The jaws in all these species of Mammontinæ are correlated with the *brachycephaly* and *acrocephaly* of the cranium, that is, the jaws are excessively short and deep. (2) The ramus in *P. jeffersonii* (see Fig. 892 D, D1, C, C1) is far less robust than the ramus in *A. imperator* (Fig. 892 B, B1, A, A1). (3) The ramus of *P. jeffersonii* with rounded inferior border differs from that of *Elephas indicus* (Fig. 893 D, D1) in which the inferior border is more pointed. (4) The deeply depressed ramus of *P. jeffersonii* is readily distinguished from the horizontal ramus of *Loxodonta africana* (Fig. 893 C, C1) or from the relatively shallow ramus of the *Elephas* [=*Parelephas*] *washingtonii* type (Fig. 893 B, B1).

Rostrum.—The most characteristic feature is the prominent rostrum perfectly preserved in the paratype [ideotype] of *P. jeffersonii* (Fig. 960 B) which projects conspicuously beyond the line of the chin. This prominent rostrum apparently distinguishes the *Parelephas jeffersonii* jaw from the *Mammonteus primigenius* jaw. This rostrum is the feature especially shown in Mather's type figure (Fig. 946) of *Elephas jacksoni*; it is also pointed out in Mather's type description which leads us to believe that *E. jacksoni* is more closely related to *Parelephas jeffersonii* than to the true *Mammonteus primigenius,* although in certain specimens referred to *E. primigenius* the *rostrum* is quite prominent, so that we cannot place too great reliance on this character.

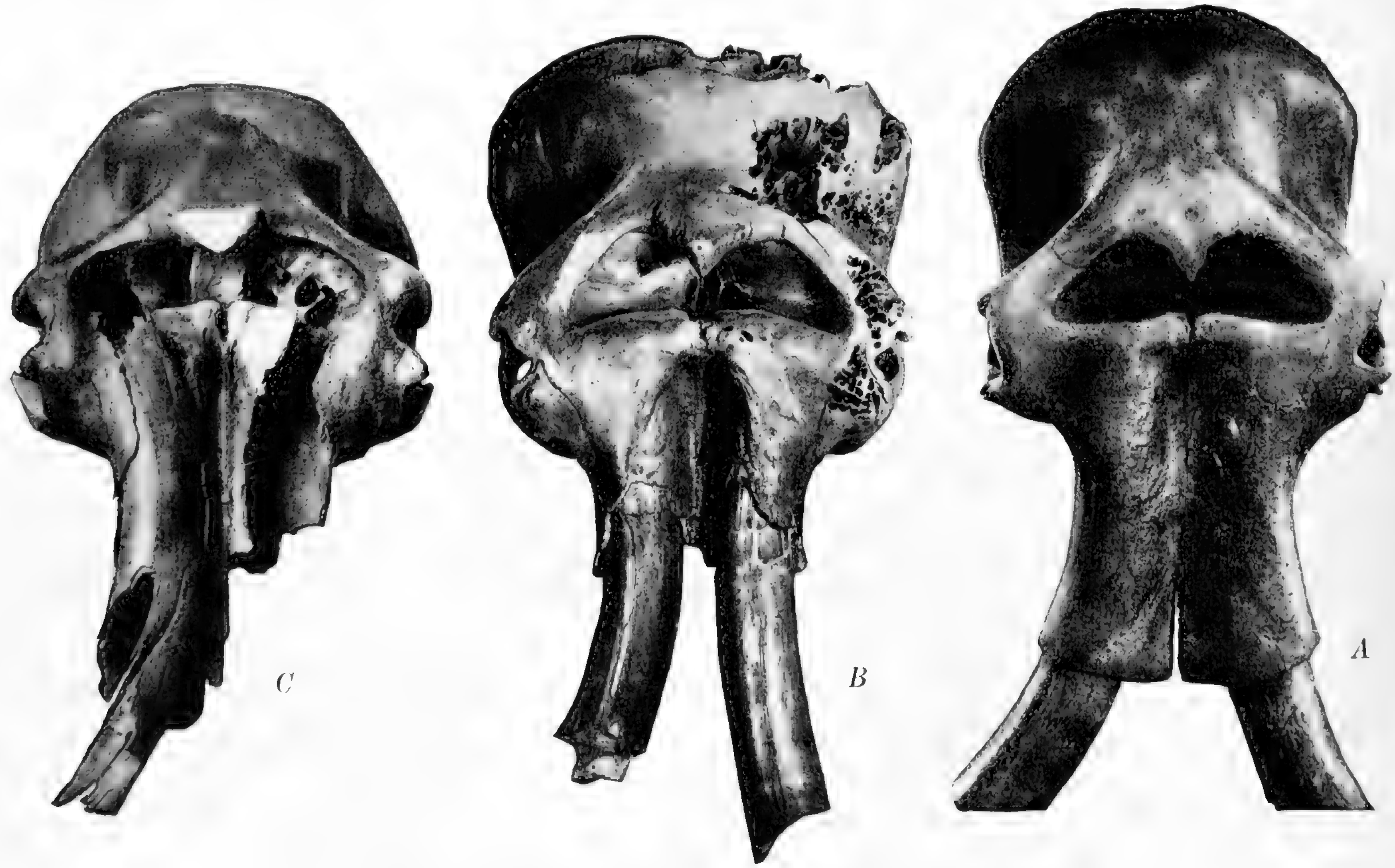
TYPE AND REFERRED SKULLS OF PARELEPHAS JEFFERSONII

We may fortunately compare five finely preserved crania of different ages referable to this species in American collections with a number of European crania referred to *Elephas intermedius* (Fig. 935) and to *E. trogontherii* (Fig. 934). Thus we may establish the fundamental similarity of cranial structure which distinguishes all the species referable to the genus *Parelephas*.

Cranial Characters (Figs. 934, 935, 961-963).—As pointed out in the introduction to the Mammontinæ, superficially the profile aspect of the cranium of *Parelephas jeffersonii* (Fig. 962A) resembles that of *Elephas indicus*, but the midcranial section shows that it is fundamentally distinct. The cranial form of *P. jeffersonii* is actually *intermediate* between the cranial form of *Archidiskodon imperator* and that of *Mammonteus primigenius*. Close comparison with *M. primigenius* is afforded in figure 962, in which two crania, one of *P. jeffersonii* (A) and the other of *P. washingtonii* (B) are shown on the right side of the profile in comparison with a single cranium of *M. primigenius* (C,C¹). In this comparison it is apparent that *M. primigenius* is even more brachycephalic and acrocephalic than *P. jeffersonii* or *P. washingtonii*.

COMPARISON OF PARELEPHAS AND MAMMONTEUS CRANIA

We observe (Fig. 961) that in the frontal aspect these three crania of *Parelephas* are remarkably similar and readily distinguishable from crania of *Mammonteus* (Fig. 962 C). In frontal aspect: (1) The occipital crest, which is perfectly preserved in the aged type skull from Indiana (A) is broad and swelling at the summit; it is also well preserved on the right side in the adult skull of the specimen from the state of Washington (B); it is erroneously restored in the specimen from Ohio (C). (2) The anterior narial openings are very broad and widely open, whereas in *Mammonteus* they are smaller and more contracted. (3) The orbital sockets are



Frontal Views of Three Parelephas Crania: (A, C) P. jeffersonii, (B) P. washingtonii

All figures one-twelfth natural size

Fig. 961. Front view of the (A) type skull of *Parelephas jeffersonii* Osborn (Amer. Mus. 9950), from Jonesboro, Indiana, compared with one skull (B) in the American Museum and one (C) in the U. S. National Museum, as referred to in the original type description.

A, Front view of the aged type skull of *Parelephas jeffersonii* (Amer. Mus. 9950); actual measurement 28.8 inches across the outside of the orbits.

B, Referred skull of *Parelephas washingtonii* (Amer. Mus. Cope Coll. 8681) from Whitman County, Washington, heretofore designated as "*Elephas columbi*," and subsequently referred by Osborn (1922.555, p. 15) to *Parelephas jeffersonii*. This skull was never figured or described by Cope, it was found in an unopened box in his collection. For full description of this specimen, see pages 1101, 1103, and figures 937, 973, 974, 971, and 976 of the present Memoir.

C, A very large male skull in the National Museum (Nat. Mus. 10261), collected near Cincinnati, Ohio, referred to *P. jeffersonii* in Osborn's type description (1922.555, p. 15): "The cranial characters of this specimen are entirely similar to those of the three skulls in the American Museum collections, except that it is larger and more robust." Occiput incorrectly restored.

much more prominent than in *M. primigenius*, as perfectly shown in all three skulls (A,B,C). (4) The maxillo-premaxillary sockets of the superior tusks are relatively less elongate and less parallel than in *Mammonteus*; they diverge widely where the tusks issue from the skull. (5) In profile view (Fig. 962 B) the orbits are more widely separated from the occipital condyles than in *M. primigenius* (Fig. 962 C). (6) In profile view the occiput is more prominent and bulging (Fig. 962 B) than the relatively vertical occiput of *M. primigenius* (Fig. 962 C). (7) In its proportions the *M. primigenius* cranium is broader, shorter, higher, deeper, i.e., more brachycephalic and hypsicephalic, than the *P. jeffersonii* cranium. (8) In all these characteristics the cranium of *P. jeffersonii* appears to agree more closely with the crania of the European species *Parelephas intermedius* (Fig. 944), and *P. trogontherii* as shown in profile in figure 934, than it does with either profile or front views of the cranium of *Mammonteus primigenius.*

SKULL OF PARELEPHAS JEFFERSONII (KNOWN AS THE FRANKLIN COUNTY MAMMOTH) IN THE NEBRASKA STATE MUSEUM

Discovered in the loess of Wisconsin or late Pleistocene time.

Nebraska Skull.—Since the crania above described come from the states of Indiana, Ohio, and Washington, it is interesting to add the description and figures of the superb skull and tusks from Nebraska preserved in the Museum of the University of Nebraska (Neb. Mus. 1–4–15), photographs of which (Figs. 963 and 964) we are able to reproduce through the courtesy of Prof. E. H. Barbour. Like the two crania from Indiana and Ohio previously described, this Nebraska skull was originally referred by Professor Barbour to *"Elephas columbi,"* but it agrees in all particulars with the two crania above described as *Parelephas jeffersonii* and is the largest and in many respects one of the finest representatives of this type of cranium, the tusks exceeding in length and in circumference those of the type skull of *P. jeffersonii* from Indiana.

The left profile view of this Nebraska cranium (Neb. Mus. 1–4–15) is shown in figure 963; the profile is closely similar to that of the type of *Parelephas jeffersonii*, except that the concave plane of the forehead is relatively more elongate; we observe that the orbital region is very prominent, the summit of the occiput is rounded, the postoccipital profile is very convex, the occipital condyle is elevated; the entire profile is similar to that of the male skull of *Parelephas* figured by Falconer (Fig. 934). The palatal view (Fig. 963) displays the third superior grinding teeth *in situ* and exhibits (Fig. 965) nineteen ridge-plates, of which the anterior

Mammonteus primigenius (C, C^1), Parelephas jeffersonii (A), P. washingtonii (B)

All figures one-twelfth natural size

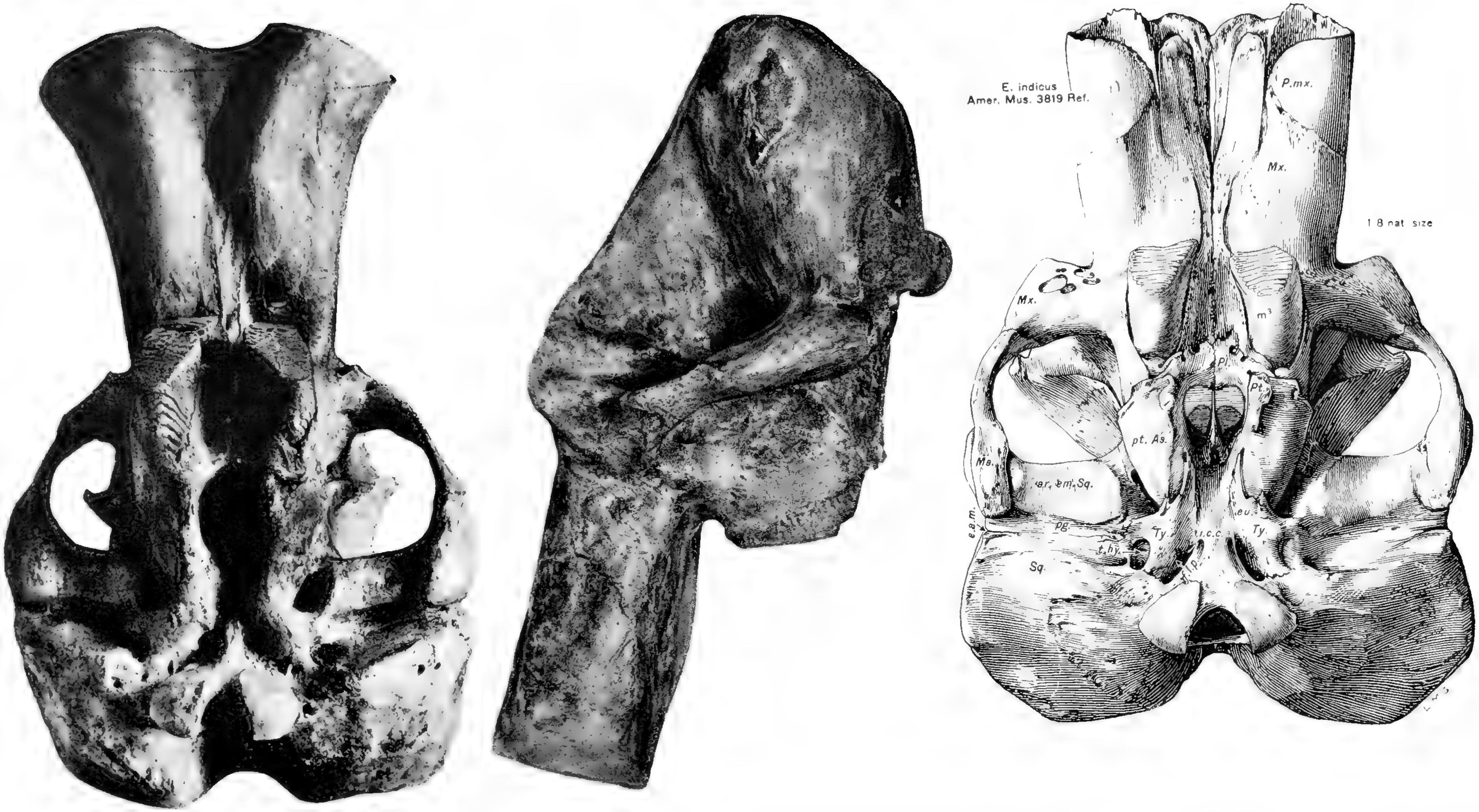
Fig. 962. Profile views of type and referred skulls of *Parelephas jeffersonii* (A), *P. washingtonii* (B), and *Mammonteus primigenius* (C) in the American Museum and United States National Museum, also front view of *M. primigenius* (C^1).

A, Type of *Parelephas jeffersonii* (Amer. Mus. 9950), reversed. An aged individual. Main portion of the tusks not included. From Jonesboro, Indiana.

B, Referred skull of *Parelephas washingtonii* (Amer. Mus. Cope Coll. 8681). From Whitman County, Washington.

C, Referred skull of *Mammonteus primigenius* (Nat. Mus. 8580) from Siberia, with jaws belonging to another individual (Nat. Mus. 8579), from Alaska.

C^1, Front view of same skull and jaws.



Crania of the Franklin County Mammoth of Nebraska (Parelephas jeffersonii) and of Elephas indicus bengalensis

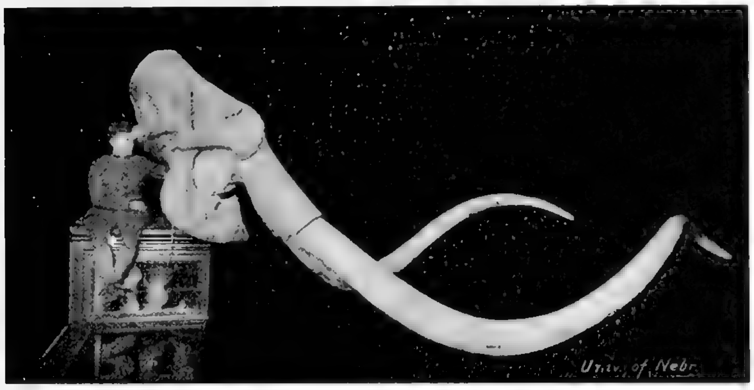
Fig. 963. *Parelephas jeffersonii*, palatal (left) and left lateral (middle) aspects (Neb. Mus. 1–4–15), known as the Franklin County mammoth. Skull, mandible, and tusks complete. Discovered in the loess near Campbell, Franklin County, Nebraska, April 1, 1915. After photograph by Prof. E. H. Barbour. Observe the greatly expanded premaxillary and maxillary sockets of the superior tusks. One-tenth natural size. A description of this cranium and the teeth will be found on pages 1091 and 1093. Compare figures 964 and 965 of the same specimen.

Measurement from crest of occiput to base of premaxilla............................1355 mm.
Measurement across zygomatic arches 800

(Right). Palatal view of cranium of *Elephas indicus* (Amer. Mus. Dept. Mam. 3819), exhibiting all the component elements and the cranial foramina, including the posterior nares and the external auditory meatus (e.a.m.). Observe the resemblances and contrasts to *Parelephas jeffersonii*. One-eighth natural size.

thirteen are in use. Behind these thirteen more or less worn ridge-plates (Fig. 963) are observed seven to eight unworn ridge-plates making an estimated total of twenty to twenty-three ridge-plates. The widely divergent maxillo-premaxillary region presents the usual contrast with the parallel and convergent bony sockets of the *Mammonteus primigenius* type of cranium. Comparison is afforded in figures 899 and 900 with the palatal view of two crushed skulls of *Archidiskodon imperator* from Hay Springs, Sheridan County, Nebraska (see Chap. XVI).

Locality and Geologic Level.—This skull was discovered from 11 to 12 feet underground while digging for the foundation of the new high school of Campbell, Franklin County, Nebraska; the date of discovery was April 1, 1915. The geologic deposit was a bed of loess which we may infer belongs to late Pleistocene times. As restored under Professor Barbour's direction and mounted in the University of Nebraska Museum, the skull and tusks are shown in side view in figure 964. The tusks are 12½ feet in length and 29 inches in circumference at the thickest point; the cranium and jaws are essentially without restoration; the enormous depth of the skull from the occipital condyle to the inferior border of the jaw is shown by the seated figure of a student whose forehead rests just opposite the occipital condyle.



The Franklin County Mammoth of Nebraska

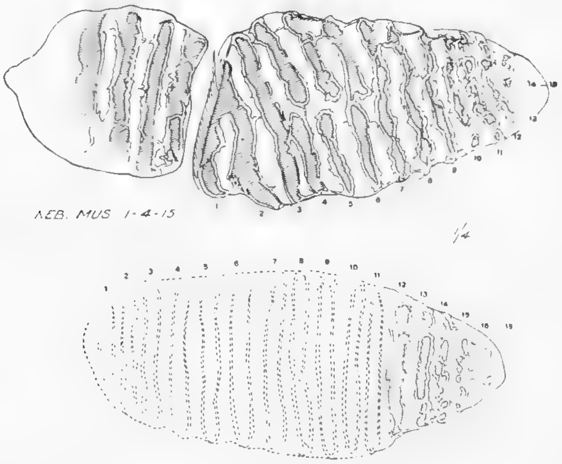
Fig. 964. Nebraska Skull.—Complete skull, jaws, and tusks of *Parelephas jeffersonii* (Neb. Mus. 1–4–15) discovered in the loess near Campbell, Franklin County, Nebraska. After photograph by E. H. Barbour. Skull essentially without restoration. Part of the coronoid region of the jaw restored in plaster; symphysis of the jaw perfect; both mandibular rami broken. Tips of the tusks weathered off and restored with characteristic curvature. One-tenth natural size.

TYPE SKELETON OF PARELEPHAS JEFFERSONII

See figures 931 and 966 of mounted skeleton

The type skeleton of *Elephas jeffersonii* was found near Jonesboro, Indiana, in 1903. It was purchased for the Museum with the Jesup Fund in August, 1904, from Dora E. Gift and others. As found the skeleton was imbedded in a muck deposit of late Pleistocene age, fifteen feet below the surface; this deposit is considered of IV Glacial, post(?)-Wisconsin age, by Leverett and Hay. The whole upper portion of the skeleton was complete and intact, including the remarkably incurved tusks, which were preserved for their entire length although requiring surface restoration and thorough soaking, and reinforcing with an internal steel rod in plaster to prevent them from crumbling away. Vigorous efforts were made to find the missing lower bones of the limb and the feet but without success.

Mounting of Parelephas jeffersonii Type.—The missing parts are the radius and ulna of both sides, the right tibia and fibula, the fore- and hindfeet. These parts are restored from the more massive limbs of two specimens of *Archidiskodon* and it is doubtful whether they are of the proper proportions for *Parelephas*. Thanks to the kind coöperation of Dr. Marcellin Boule of the Museum of Palæontology, Paris, casts were secured of the lower portions of the limbs and of the feet of the great skeleton of *Elephas meridionalis* (Fig. 866) in the Paris Museum; on arrival in the American Museum these casts were remodeled, recourse being had for comparison to remains of the feet and limbs of *Archidiskodon imperator*; all this work of restoring and remodeling was done by Otto Falkenbach under the direction of head preparator Adam Hermann. Mr. Hermann himself restored the missing surfaces of the upper parts of the skeleton which were, however, in exceptionally complete condition.



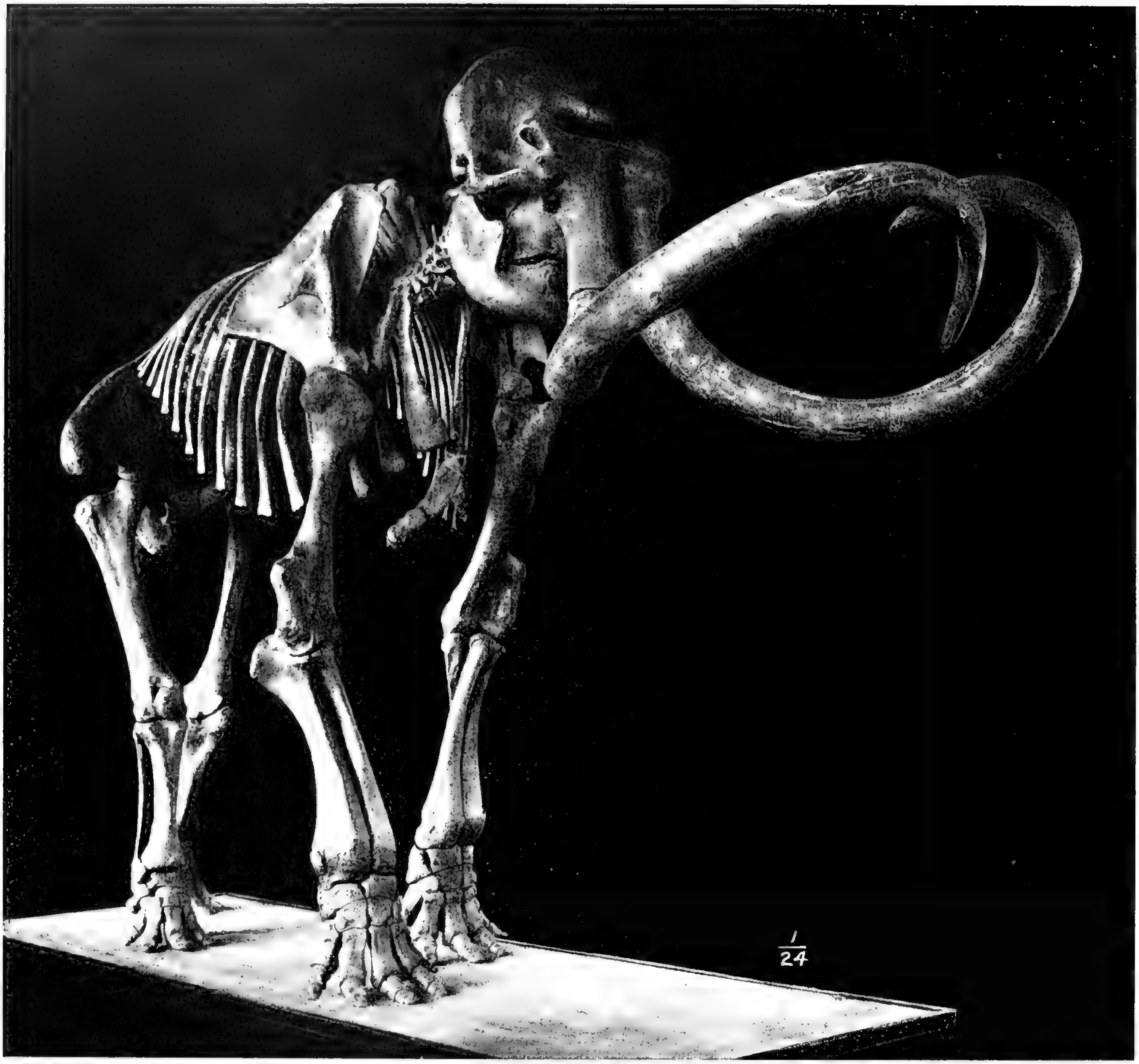
Molar Ridge-plates of Franklin County Mammoth of Nebraska.
Aged Parelephas jeffersonii

Fig. 965. Franklin County Mammoth. Diagram drawn from casts showing the (13) superior and (16) inferior worn ridge-plates of *Parelephas jeffersonii* ref. (Morrill Coll., Neb. Mus. 1–4–15). Outlines furnished by Professor E. H. Barbour, August 29, 1924.

(Upper) Crown view of M^2, M^3. (Lower) Portion of the crown of M_3 of the same specimen. See figure 963 for cranium of this specimen before restoration, figure 964 after restoration.

Pose.—The animal is represented with uplifted head and as if just starting to walk. For the pose of the skeleton the coöperation of Director Hornaday of the Zoological Park was secured; the tracks of the Indian elephant "Gunda" slowly walking over a sandy surface fifty feet long were carefully plotted by park engineer Beerbower (Fig. 1243 of this Memoir); through this means it is believed that the fore- and hindfeet are correctly placed. The author also made a special study of the position of the bones of all parts in the living elephant. The result of all this work is a pose and gait which are believed to be true to life.

The most striking features of this skeleton of an aged in-



Type Skeleton of Parelephas jeffersonii in the American Museum
One twenty-fourth natural size

Fig. 966. First published type figure of the aged skeleton of *Elephas jeffersonii* Osborn, 1922 (Amer. Mus. 9950), as mounted in the American Museum. This specimen, including the skull, jaws, and greater part of the skeleton, was found near Jonesboro, Indiana, on the farm of Dora E. Gift; purchased for the American Museum with the Jesup Fund in 1904; parts of limbs restored and mounted in 1906; described and figured by Osborn in 1907 (1907.295) as *Elephas columbi*; redescribed by Hay (1914) as "*Elephas primigenius*," and again in February, 1923, p. 139, as *E. primigenius* of post(?)-Wisconsin age. This skeleton was finally selected and figured by Osborn in 1922 (1922.555, p. 11, fig. 10) as the type of *Elephas jeffersonii* new species.

(Cf. Osborn, 1907.295, p. 256): As found the skeleton was imbedded in a muck deposit of late Pleistocene age, fifteen feet below the surface. The whole upper portion of the skeleton was complete and intact, including the remarkably incurved tusks, which were preserved for their entire length although requiring surface restoration and thorough soaking, and reinforcing with an internal steel rod in plaster to prevent them from crumbling away. Vigorous efforts were made to find the missing [restored] lower bones of the limb and the feet but without success.

The missing parts [restored] are the radius and ulna of both sides, the right tibia and fibula, the [both] fore-and hindfeet. Thanks to the kind coöperation of Dr. Marcellin Boule of the Museum of Palæontology, Paris, casts were secured of the lower portions of the limbs and of the feet of the *Elephas meridionalis* (Fig. 866) in the Paris Museum; on arrival in the American Museum these were remodeled, recourse being had for comparison to remains of the feet and limbs of *Elephas imperator*; all this work of restoring and remodeling was done by Otto Falkenbach under the direction of head preparator Adam Hermann. The animal is represented with uplifted head and as if just starting to walk. For the pose of the skeleton the cooperation of Director Hornaday of the Zoölogical Park was secured; the tracks of the Indian elephant "Gunda" (Chap. XXIII, p.1598) slowly walking over a sandy surface fifty feet long (Fig. 1243 of the present Memoir) were carefully plotted by park engineer Beerbower; through this means it is believed that the fore- and hindfeet are correctly placed. The author also made a special study of the position of the bones of all parts in the living elephant.

dividual of *Parelephas jeffersonii* are the following: (1) The complete incurvature and crossing of the tusks, indicating that this animal is an old bull which had retired from the herd. (2) The relatively small size of the skull. (3) The abbreviation of the back and body in contrast to the vertical elongation of the limbs.

Dietrich (1916, p. 76, 1924, p. 13 — p. 1276 below), in describing *Elephas antiquus recki*, discusses the size of the humerus of recent and fossil proboscideans and gives a number of measurements which we may compare with those of the type of *Parelephas jeffersonii* as follows:

	Length of Humerus	Estimated Shoulder Height
Parelephas trogontherii of Mosbach	1480 mm.[1]	4500 mm. [Schmidtgen, 1926, p. 64]
[*Parelephas jeffersonii* type	1085+	3200]
Hesperoloxodon antiquus of Taubach	1300	
Mammonteus primigenius	1270	
Palæoloxodon recki	1235	4000 ca.[2]

Parelephas of Intermediate Size

Vertebral Column.—The vertebral formula of this generic and specific type is here shown in comparison with that of specimens of *Loxodonta*, of *Elephas*, and of *Mammonteus*:

	Loxodonta africana		*Elephas indicus*	*Mammonteus primigenius*		*Parelephas jeffersonii*
	Flower, 1885	"Jumbo" Amer. Mus. Dept. Mam. 3283	Flower, 1885	Falconer and Amer. Mus. 14559 (*M. p. compressus*)	Felix, 1912	Type Amer. Mus. 9950
Cervicals	7	7	7	7	7	7
Dorsals	19	20	19–20	18–19	19	19
Pairs of ribs	..	..	..	18–19	19	19
Lumbars	4	3	5–3	4–3	5	4
Sacrals	5	4	4	4–3	4	5
Caudals	24+	21	24–30+	21	21(Zalensky)	12+

The size of the animal is indicated by the following comparisons with the great *Archidiskodon meridionalis* of the Paris Museum:

	P. jeffersonii Amer. Mus. 9950	*A. meridionalis* Paris Mus. (Measurements given by Gaudry)
Length, incurved tip of tusks to vertical line of tail	17 ft. 9¾ in. (5430 mm.)	22 ft. 3¾ in. (6800 mm.)
Length, base of tusks to vertical line of tail	13 ft. 3½ in. (4050 mm.)	17 ft. 10½ in. (5450 mm.)
Height at withers (to top of scapula)	10 ft. 6 in. (3200 mm.)	12 ft. 6¾ in. (3830 mm.)
Length of femur	4 ft. 1¼ in. (1250 mm.)	4 ft. 5½ in. (1360 mm.)
Length of right tusk (outside curve)	11 ft. 4⅝ in. (3470 mm.)	

Compare also the fully adult skeleton of *Parelephas jeffersonii* with the recently described titanic skeleton of *Archidiskodon maibeni* (Figs. 910, 912). We reach the interesting conclusion that the adult *Parelephas* of the north temperate regions of Eurasia and North America is midway in size between the giant *Archidiskodon imperator* of the more southerly latitudes and the relatively dwarfed *Mammonteus primigenius* of the northerly latitudes. Broadly speaking the proportions of these members of the subfamily Mammontinæ may be estimated from the extreme height at the withers as follows:

Archidiskodon imperator maibeni	12 ft. 6⅝ in. = 3826 mm.
Parelephas jeffersonii	10 ft. 6 in. = 3200 mm.
Mammonteus primigenius	9 ft. 3 in. = 2820 mm.

ELEPHAS ROOSEVELTI HAY, 1922

This Pleistocene species from Ashland, Illinois, based on superior and inferior molar teeth, r.M^3, r.M_3 (Nat. Mus. 2195), was described by Hay September 30, 1922. Hay observes (*op. cit.*, p. 100): "The peculiarity of all these teeth is the low elongated form and the approximate parallelism of the upper and the lower borders." This species appears to represent a stage of evolution very close to that shown in the type and paratype teeth of *Elephas jeffersonii* described by Osborn about two months previous, namely, July 8, 1922. Consequently we may regard *Elephas roosevelti* as a synonym of *Parelephas jeffersonii*.

Elephas roosevelti Hay, 1922. "Further Observations on Some Extinct Elephants," Proc. Biol. Soc. Washington, Vol. XXXV, Sept. 30, 1922, p. 101.

The author's designation of the type specimen, locality, formation, and characters of *Elephas roosevelti*, new species, is as follows (Hay, *op. cit.*, p. 101):

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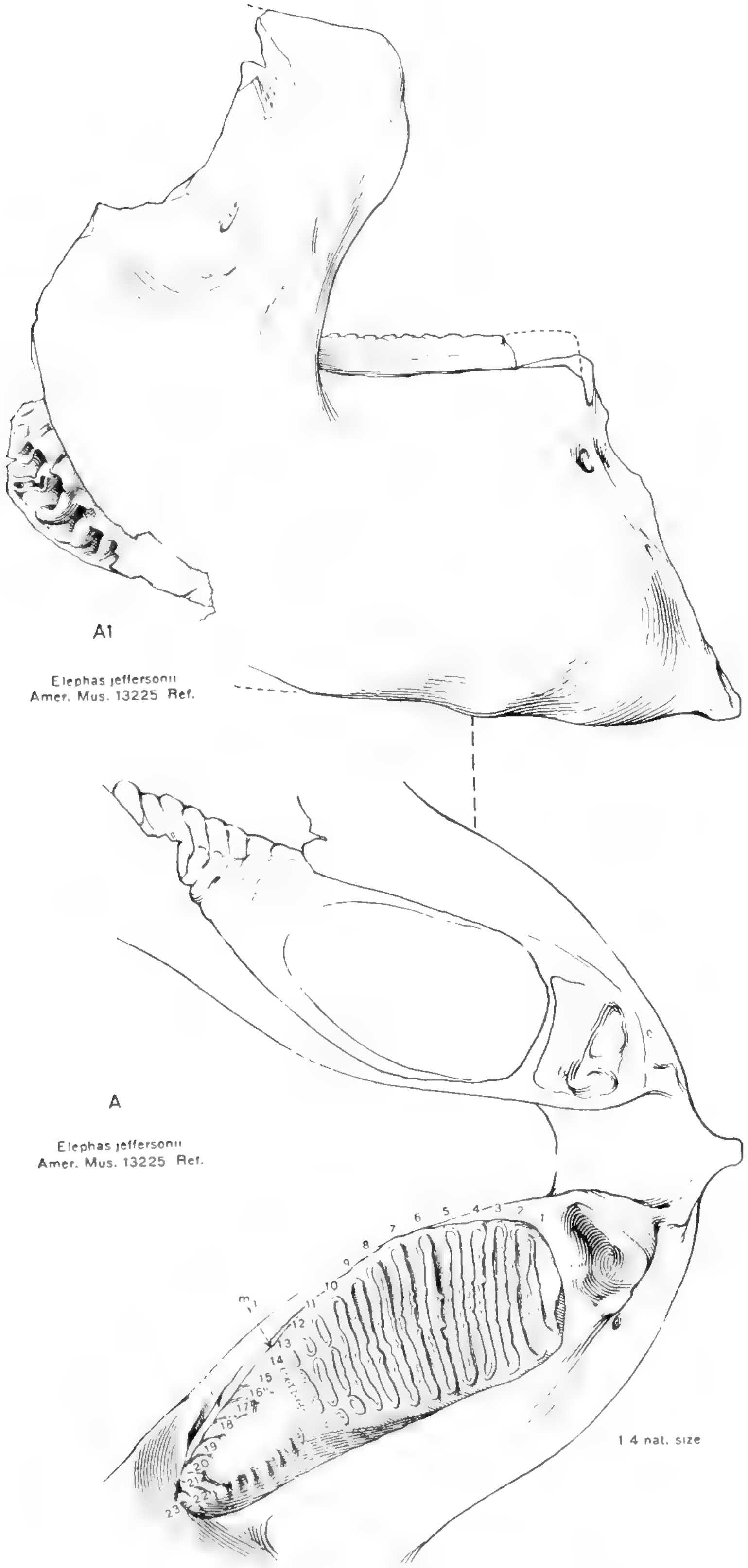
[1] 1440 mm., *fide* Schmidtgen, 1926, p. 63.

[2] 4030 mm., *fide* Schmidtgen, 1926, p. 64; see Osborn's estimate of 3600 mm. (p. 1277 below).

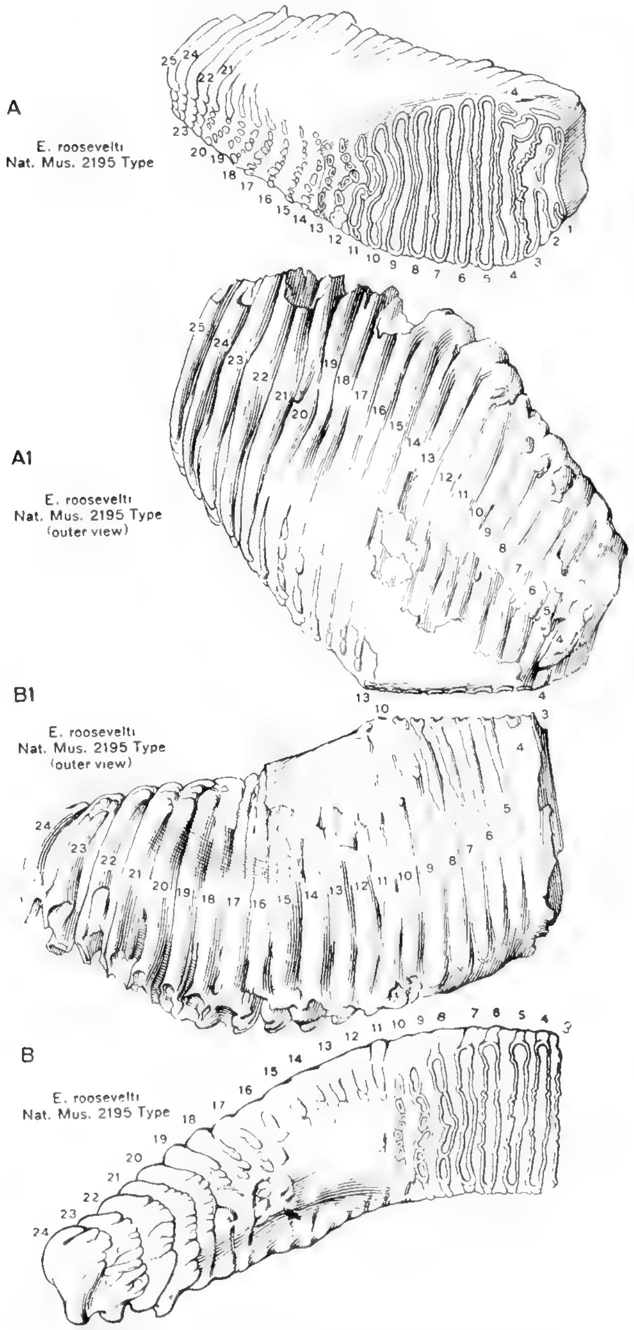
"*Type specimen.* Upper and lower hindermost molars, No. 2195, U. S. National Museum. *Type locality.* Ashland, Cass County, Illinois. *Type formation.* Pleistocene. *Diagnosis.* Hindermost molars long and low, the base and the summit approximately parallel, consisting apparently of 25 plates; of these 8 in



PARATYPE OF PARELEPHAS JEFFERSONII

Fig. 967. Jaw of middle-aged paratype [ideotype] of *Parelephas jeffersonii* (Amer. Mus. 13225) from Twin Creek, near Sanders, Kentucky, Big Bone Lick region.

The rudiment of M_2 has been recently shed; M_3 exhibits twenty-three ridge-plates (see Fig. 960B, showing 24 ridge-plates) of which the anterior *fourteen* are in use.



PARELEPHAS JEFFERSONII (SYNONYM ELEPHAS ROOSEVELTI)
THIRD SUPERIOR AND INFERIOR MOLARS

Fig. 968. Figured for the present Memoir. Type superior and inferior molars of *Elephas roosevelti* Hay (Nat. Mus. 2195), from Ashland, Cass County, Illinois. One-fourth natural size.

A, A1, Crown and external views of the right superior molar, r.M^3, showing twenty-five ridge-plates (1–25 in the figure).

B, B1, Crown and side views of the right inferior molar, r.M_3, showing ridge-plates 3–24, the anterior ridge-plates being broken away.

a 100 mm. line; enamel thin, delicate, and little folded. [*Type figure.* None. See figure 968 of the present Memoir]."

TYPE DESCRIPTION OF ELEPHAS ROOSEVELTI.—The type description was introduced by the following notes: (Hay, Sept. 30, 1922, p. 100): "Professor Osborn in his paper of July 8 [Osborn 1922.555] has published an interesting figure of upper teeth of an elephant (his fig. 8) ["Fig. 8. Fourth and third superior molars of . . . *Elephas primigenius*"] found in Indiana. On plate LIX of the twenty-third volume of the Iowa Geological Survey, I published a figure of very similar teeth found at Milwaukee, Wisconsin, and preserved in the Public Museum of that city. The hindermost molar had just begun to suffer wear. In the U. S. National Museum are right and left hindermost molars (No. 2195) of similar form, found at Ashland, Cass County, Illinois; also an upper left hindermost molar (No. 4761) hardly different, discovered in Wayne Township, Darke County, Ohio. The peculiarity of all these teeth is the low elongated form and the approximate parallelism of the upper and the lower borders. Inasmuch as the molar descends at a nearly right angle with the grinding face of the tooth in front it seems probable that the skull was short. Professor Osborn has referred his specimen to *Elephas primigenius;* but I find no teeth from Alaska or the Old World which present similar characters. I believe that a hitherto unrecognized species is indicated. This I propose to call *Elephas roosevelti* in honor of another statesman and naturalist, one whose multifarious interest led him to pursue living elephants in their African wilds."

"The Ashland teeth are chosen because with them came the nearly complete lower right hindermost molar. The length of the molars is close to 300 mm., the height 170 mm., the width of the upper teeth 90 mm., of the lower 85 mm."

Osborn, 1924: Hay's type description, in which he compares this animal with *E. primigenius,* was not accompanied by a figure and for the purposes of this Memoir the type teeth of *Elephas roosevelti* (Nat. Mus. 2195) were kindly loaned to the American Museum by Curator Merrill for examination and execution of the type figure which is reproduced herewith (Fig. 968).

This type figure, including its very careful enumeration of the ridge-plates as preserved, namely, 24–25 ridge-plates preserved above, 21 ridge-plates preserved below, agrees with the type description of Hay. The mid-coronal ridge-plate count is 8 in a 100 mm. line. The diameters of the molars are as follows:

	Left	Right
Third superior molars, length across 25 ridge-plates.	227 mm.	282 mm.
Third superior molars, height of tallest ridge-plate.	202	192
Third superior molars, max. width	95	98
Third superior molars, breadth-length index.	tooth incomplete	
Third inferior molars, length, estimated, of 22 ridge-plates.		304e
Third inferior molars, height of tallest ridge-plate.		154
Third inferior molars, max. width		92
Third inferior molars, breadth-length index.	tooth incomplete	

The diameters, ridge-plate measurements, and indices of these young molars closely resemble those of the aged molars of the type of *Elephas jeffersonii* (Fig. 959, left) as clearly shown in the diagram (Fig. 959, right), in which the superior and inferior molars of the aged *E. jeffersonii* type are projected to the same scale upon the type superior and inferior molars of the young adult *E. roosevelti.* Consequently we have been able to amplify the specific characters of *E. jeffersonii* by a study of these grinding teeth of *E. roosevelti,* which compare so closely in all respects except in age and wear. The ridge-plate compression is as follows:

	Left	Right
M^3 ridge-plates in 100 mm. on convex external surface.	9½	9
ridge-plates in 100 mm. on mid-coronal surface.	10	9½
ridge-plates in 100 mm. on mid-coronal concave internal surface.	8	9
M_3 ridge-plates in 100 mm. on mid-coronal concave external surface.	7	7–8½
ridge-plates on worn mid-coronal surface, that is, in 100 mm	incomplete	
ridge-plates in 100 mm. on convex internal surface.		6–7½

Parelephas progressus Osborn, 1924

Figures 969, 970

Upper Pleistocene, post(?)-Wisconsin (IV GLACIAL) age, Zanesville, Muskingum County, Ohio.

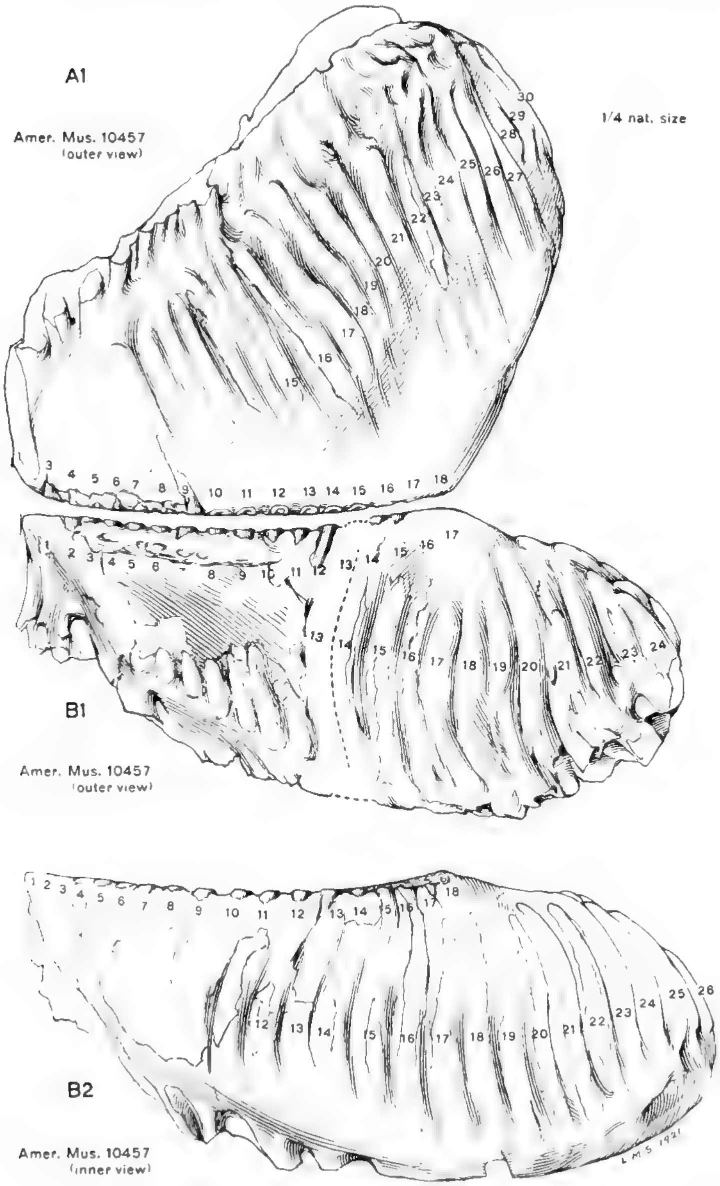
This very progressive species is based on a pair of superior and inferior grinding teeth described by Warren in 1855 as *Elephas 'Primigenius';* erroneously selected by Osborn (1922.555, pp. 11, 12) as a paratype of *Elephas jeffersonii.* The type teeth belong to a much larger animal than the type and referred specimens of *Elephas jeffersonii* and present a more progressive ridge-plate formula, namely: M 3 $\frac{30}{26}$. Its descent from the *P. jeffersonii* stage is indicated by the similarity in the ridge-plate compression, indicating that the cranium of this species will prove to have the same distinctive proportions as the cranium of *P. jeffersonii.*

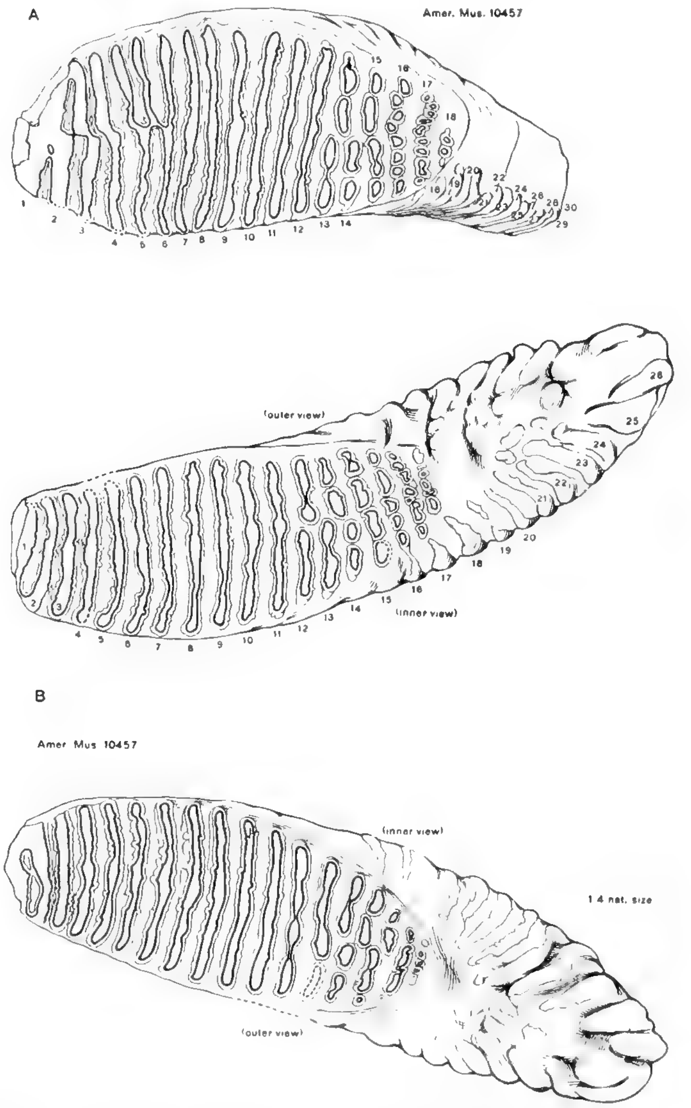
Parelephas jeffersonii progressus Osborn, 1924. "Parelephas in Relation to Phyla and Genera of the Family Elephantidæ." Amer. Mus. Novitates, No. 152, December 20, 1924, pp. 1, 4, and 7 (Osborn, 1924.633). TYPE.—Amer. Mus. Warren Coll. 10457. A pair of superior and inferior grinding teeth of both sides. HORIZON AND LOCALITY.—Zanesville, Muskingum County, Ohio; Upper Pleistocene, Wisconsin or post(?)-Wisconsin (IV GLACIAL) age. TYPE FIGURE.—Osborn, 1922.555, p. 13, fig. 11, and p. 14, fig. 12.

TYPE DESCRIPTION.—(Osborn, 1924.633, pp. 4, 7): "These progressive grinders, described by Warren in 1855 as *Elephas primigenius,* by Osborn in 1922 as a paratype of *Elephas jeffersonii,* belong to a much more progressive stage than the type of *Elephas jeffersonii,* and referred specimens, presenting a progressive ridge-plate formula of M 3 $\frac{30}{26}$, as compared with the typical ridge-plate formula of *Parelephas jeffersonii,* namely M 3 $\frac{25}{24}$. It is interesting to observe that these type molars (Osborn, 1922.555, p. 14, fig. 12) show eighteen ridge-plates in use in both M^3 and M_3; the superior molars show from four to six ridge-plates in excess of the inferior molars; thus they are readily distinguishable from those of *Mammonteus primigenius compressus*, as described above. In all other characters these type grinding teeth (Osborn, 1922.555, fig. 12) are related to those of *Parelephas jeffersonii*. Consequently, we assign the subspecific name *progressus* to denote this extreme stage in the long *Parelephas* series."

TYPE, ZANESVILLE, OHIO.—A pair of upper and lower grinding teeth of both sides (Amer. Mus. 10457) acquired by the American Museum with the Warren collection in 1906. It was described by Warren in 1855 (p. 163, Pl. XXVIII, fig. C) as *Elephas* '*Primigenius*' and described and figured by Osborn in 1922 (1922.555, p. 13, fig. 11) as *Elephas jeffersonii*. This type affords a complete comparison with the species *Parelephas jeffersonii* (as defined above with a ridge-plate formula of $M\,3\,\frac{25}{24}$), the ridge-plate formula in *P. progressus* being $M\,3\,\frac{30}{24\frac{1}{2}\text{-}26}$, the right M_3 presenting the last lower ridge-plates more fully developed than in the left lower M_3.

CHARACTERS OF TYPE.—It is interesting to observe that these





TYPE MOLARS OF PARELEPHAS PROGRESSUS (SIDE AND CROWN VIEWS) ORIGINALLY FIGURED BY OSBORN AS PARATYPES OF ELEPHAS JEFFERSONII

One-fourth natural size

Fig. 969. Side views of type molars of *Parelephas jeffersonii progressus* (Amer. Mus. Warren Coll. 10457), Zanesville, Ohio, one-fourth natural size. After Osborn, 1922.555, p. 13, fig. 11.

A1, External aspect of left superior molar, l.M^3, showing 30 ridge-plates, of which 18 are in use.

B1, External aspect of left inferior molar, l.M_3, showing 24 ridge-plates, of which 17 are in use.

B2, Internal aspect of right inferior molar, r.M_3, showing 26 ridge-plates, of which 18 are in use.

Fig. 970. Crown views of type molars of *Parelephas jeffersonii progressus* (Amer. Mus. Warren Coll. 10457), the same individual as in figure 969, one-fourth natural size. After Osborn, 1922.555, p. 14, fig. 12.

A, Crown view of left superior molar, l.M^3, showing 30 ridge-plates, of which 18 are in use.

B, Crown view of right and left third inferior molars containing respectively 26 and 24½ ridge-plates, of which 17 are in use.

type molars show 18 ridge-plates in use in both M^3 and M_3, but that the superior molars show from *four* to *six* ridge-plates in excess of the inferior molars, the ridge formula being $M\ 3\ \frac{30}{24\frac{1}{2}\text{-}26}$. The ridge-plate compression, however, corresponds with that of *Parelephas jeffersonii* and is directly intermediate between that of *Parelephas columbi-Archidiskodon imperator* and that of *Mammonteus primigenius*, the internal, external, and coronal ridge-plate measurements being as follows:

M^3 7–8 ridge-plates in 100 mm. on the external convex surface
  8–8½ ridge-plates in 100 mm. on the oblique mid-coronal grinding surface
  9–10 ridge-plates in 100 mm. on the internal concave surface
M_3, 6½–7 ridge-plates in 100 mm. on the external concave surface
  7–7½ ridge-plates in 100 mm. on the oblique mid-coronal grinding surface
  6–6½ ridge-plates in 100 mm. on the internal convex surface

This compression with averages of 6–7–8–8½–9–10 ridge-plates in 100 mm., according to the point of measurement of the ridge-plates, concurs with the measurements given by Osborn in the six type and referred specimens of *Parelephas jeffersonii*.

Comparing the ridge-plate formula of *Parelephas progressus* ($M\ 3\ \frac{30}{24\frac{1}{2}\text{-}26}$) with that of the most progressive form of *Mammonteus primigenius* from Alaska and Indiana, namely, *M. primigenius compressus* ($M\ 3\ \frac{27}{(?)27}$), we observe that *P. progressus* has a higher ridge-plate formula, but *M. primigenius compressus* (Alaska) has a much closer ridge compression.

As shown in the type figures of *Parelephas progressus*, herewith reproduced (Fig. 969), the ridge-plates in external and internal aspects have the sinuous and arcuate forms, such as are observed in *Parelephas jeffersonii*, more pronounced than the simple, arcuate ridge-plates of *Mammonteus primigenius* of Alaska (Fig. 1008).

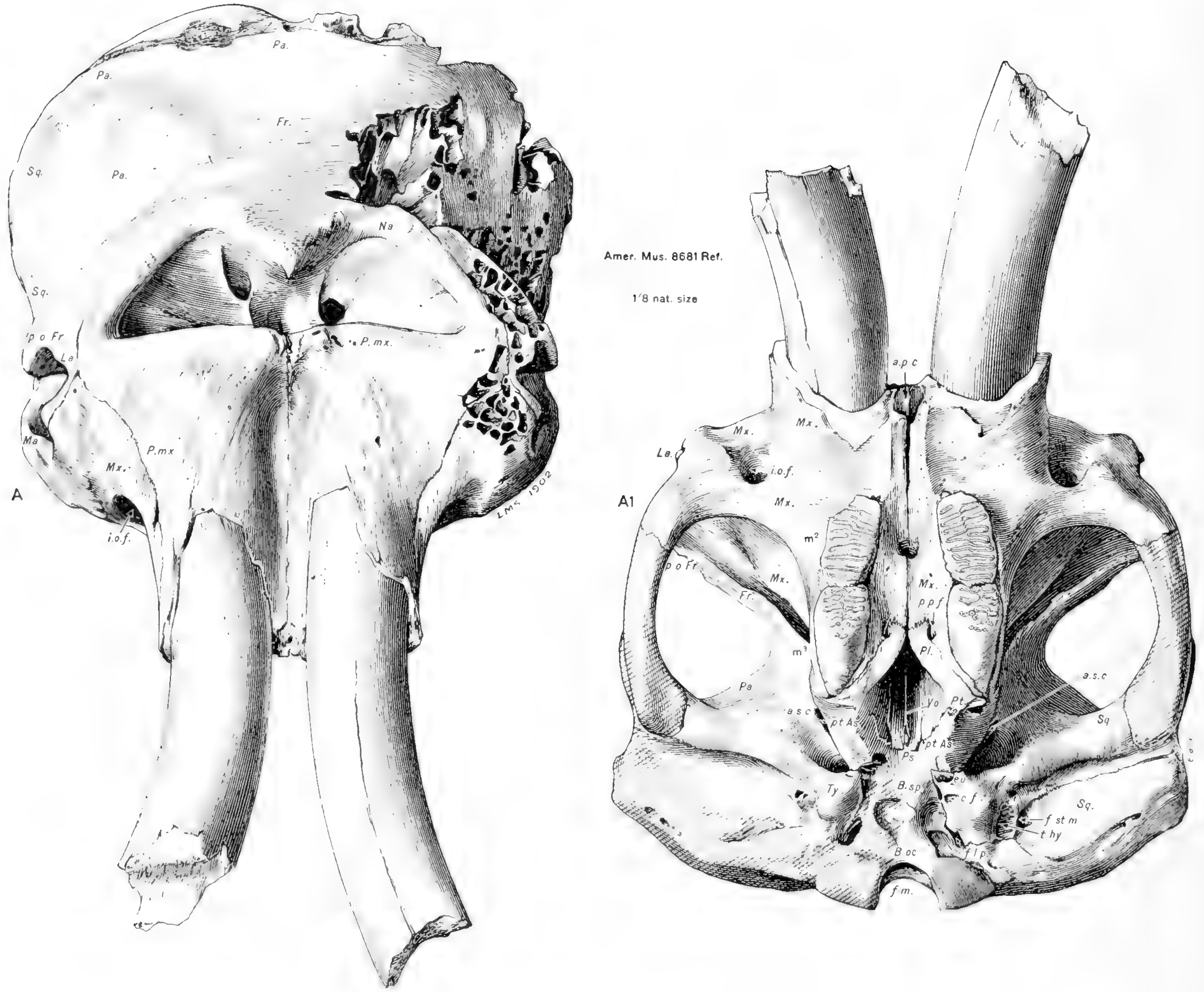
GEOLOGIC LOCATION AFTER HAY.—(Hay, 1923, p. 134): "2. *Zanesville, Muskingum County*, [Ohio].— . . . Zanesville is situated in the unglaciated part of the State [of Ohio]; but outwash from both the Illinoian and the Wisconsin glaciers has been deposited along the river. For a knowledge of the Pleistocene epoch in that region, Leverett's work may be consulted (Monogr. U. S. Geol. Surv., vol. XLI, p. 158, plate II). . . . In 1853 (Amer. Jour. Sci., ser. 2, vol. XV, pp. 146–147) is found a brief account of the discovery of elephant remains at Zanesville. One tusk and four molars were found. Two of the latter weighed (probably while wet) 20 pounds each and two others 14 pounds each. They had been found on the line of what was then called the Ohio Central Railroad and in the eastern part of the city. At about the same time (Proc. Boston Soc. Nat. Hist., vol. IV, p. 377) Warren exhibited a tooth of an elephant, one of three received by him from Zanesville (misprinted Lanesville). In the second edition of his monograph on "Mastodon giganteus" Warren figured one of these teeth (his plate XXVIII). It was stated that he had four of the teeth, all belonging to *Elephas primigenius*. These are now in the American Museum of Natural History, New York [Amer. Mus. 10457]. The right upper hindermost molar is a fine large tooth. The large front root is missing, as are quite certainly about 3 plates. There are now 28 present. The length along the nearly straight base is 335 mm. The rear is high and arched. There are 9 plates in a 100-mm. line and the enamel is little festooned. Foster, in 1857 (Proc. Amer. Assoc. Adv. Sci., 10th meeting, p. 156), described the discovery and exhumation of these remains, publishing a geological section illustrated by a figure. The elephant bed is 37 feet above the river and over 20 feet from the surface."

MEASUREMENTS OF INDICES.—It is interesting to make a close comparison of the measurements and indices of this historic pair of grinding teeth with the type grinding teeth of *Elephas jeffersonii* and of *Elephas roosevelti*.

From the following comparative measurements of the grinding teeth it appears that *Parelephas progressus* was undoubtedly an animal of larger size than the type of *P. jeffersonii*; in the grinding teeth the ridge-plates, while more numerous, are much more compressed, so that the total length of M^3 (205 mm.) is longer than the total length of M^3 in *P. jeffersonii* (203+ mm.); the grinding teeth are relatively broader (109 mm.) as compared with 108 mm.; the average thickness of the superior enamelled ridge-plates in the two species is the same, namely, 12.5 mm. In the lower grinding teeth the ridge-plates of *P. progressus* occupy 221 mm. as compared with 208 mm. in *P. jeffersonii* (cf. table below).

PROGRESSIVE SPECIFIC CHARACTERS.—From these comparisons we observe that this Zanesville mammoth may be regarded as a distinct species, namely, *Parelephas progressus*, possibly the last member of its race, lingering probably into post-Wisconsin or early Postglacial times.

	Parelephas jeffersonii type	*Elephas roosevelti* type	*Parelephas progressus* type
M^3 Total mid-length of crown including all the ridge-plates	203+	282	205
Maximum height of crown, height of tallest ridge-plate	. . .	202	203
Maximum width of crown at the broadest portion	108	98	109
Breadth-length index	53e	. . .	53
Height-length index	. . .	. . .	99
Average thickness of superior ridge-plates	12.5	11	12.5
M_3 Total mid-length of crown including all the ridge-plates	208	304e	221
Maximum height of crown, height of tallest ridge-plate	168	154	161
Maximum width of crown at the broadest portion	86	92	97
Breadth-length index	41	. . .	44
Height-length index	81	. . .	73
Average thickness of inferior ridge-plates	12.5	12	14



Referred Cranium of Parelephas washingtonii from the State of Washington

One-eighth natural size

Fig. 971. Referred skull of *Parelephas washingtonii* (Amer. Mus. Cope Coll. 8681). Pleistocene beds near Pine Creek, Whitman County, state of Washington. From the same locality is recorded the type jaw of *Elephas* [=*Parelephas*] *washingtonii* Osborn (Amer. Mus. 8681A). This superb skull was discovered by Charles H. Sternberg in 1876 and purchased by Prof. E. D. Cope, but the box containing it was never opened. Observe that M^2 exhibits 10+ worn ridge-plates, the anterior plates having disappeared; M^3 exhibits 6 worn ridge-plates, the posterior plates not having come into use.

A front view of the same skull is shown in figure 961 B; a perfect right lateral aspect is shown in figure 962 B; the l.M^3 is also shown in section in figure 976. This beautiful drawing and figure 973 were executed by Mrs. L. M. Sterling in 1902. The determination and lettering of the bones and foramina were under the direction of William K. Gregory.

Parelephas washingtonii Osborn, 1923

Figures 818, 893, 935, 937, 961, 962, 971–977, 1009

Pleistocene, pre(?)–Wisconsin age, Pine Creek, Whitman County, Washington.

The type of the species *Parelephas washingtonii* (Amer. Mus. 8681A) is one of the most primitive jaws thus far found in America; it comes from Pine Creek, Whitman County, state of Washington. The jaw has a very prominent rostrum, a long and shallow ramus, and a depressed sinus between the coronoid and the condyle, differing in every respect from the mandibular ramus referable to any of the known species of *Parelephas* and resembling only in the form of the mandibular ramus the primitive species *Elephas* [*Archidiskodon*] *hayi* of Barbour. Consequently the reference to the genus *Parelephas* (?) is largely provisional and we are uncertain as to its phylogenetic position; the relatively high ridge-plate formula ($\mathrm{M}\ 3\ \frac{}{21}$) clearly separates the lower grinders of this species from the type of *Archidiskodon hayi* ($\mathrm{M}\ 3\ \frac{}{10\text{-}11}$), as shown in the comparative figures 915, 893. It is noteworthy that the ridge formula of *P. washingtonii* ($\mathrm{M}\ 3\ \frac{23}{21}$) agrees with that of *P. intermedius* ($\mathrm{M}\ 3\ \frac{20\text{-}22}{20\text{-}21}$) of southern France.

Elephas washingtonii Osborn, 1923. "New Subfamily, Generic, and Specific Stages in the Evolution of the Proboscidea." Amer. Mus. Novitates, No. 99, Dec. 27, 1923, p. 4. Type.—Lower jaw containing two third inferior molars, with the ascending rami missing. Horizon and Locality.—Pine Creek, Whitman County, state of Washington. Pleistocene, pre(?)-Wisconsin age. Type Figure.—Figures 972, 975, 893, B, B1, of the present Memoir.

Type Description.—(Osborn, 1923.601, p. 4): "*Elephas washingtonii*, new species. As the *type* of the species *Elephas washingtonii* we select a lower jaw (Amer. Mus. 8681A) containing two third inferior molars, with the ascending rami missing, from Pine Creek, Whitman County, Washington. The ridge formula in these two teeth is: $\mathrm{M}\ 3\ \frac{}{21}$. The jaw has a depressed coronoid region as well as a long and shallow ramus, quite different in proportions from that of the true *E. jeffersonii* type. This species is named in honor of President Washington, in contrast to the species previously named in honor of President Jefferson."

This type jaw is specifically distinct from that of any known member of the *Parelephas phylum.* Comparison with the *Loxodonta* jaw (893, C, C1) demonstrates that this species (*P. washingtonii*) had a relatively long jaw but not quite so elongate as that of *Loxodonta.*

The measurements of the lower left grinding tooth, M_3, are as follows:

M_3 maximum length of crown, including 21 ridge-plates	348 mm.
maximum width of crown across the broadest ridge-plate	88
ridge-plates in 100 mm.	5
breadth-length index	25

Specific Characters.—Ramus long and shallow with very prominent rostrum, depressed coronoid and depressed sinus between coronoid and angle. Ridge formula: $\mathrm{M}\ 3\ \frac{}{21}$. Breadth-length index lower than in other species of *Parelephas.* Probably a primitive member of the *Parelephas* phylum.

State of Washington Skull.—The superb referred skull (Fig. 971) of *Parelephas washingtonii* (Amer. Mus. Cope Coll. 8681) is stated by Mr. Charles Sternberg to have been collected by himself in Pleistocene beds near Pine Creek, Whitman County, state of Washington. It had never been described or figured by Professor Cope, but was found in an unopened box in the Cope Collection when acquired by the American Museum. In previous literature by the present author, this skull has been referred to as "*Elephas columbi.*" The *brachycephalic* proportions of the Washington skull which relate it to *Parelephas* are shown both in the anterior aspect (Fig. 971A) and in the palatal aspect (A1). All three aspects

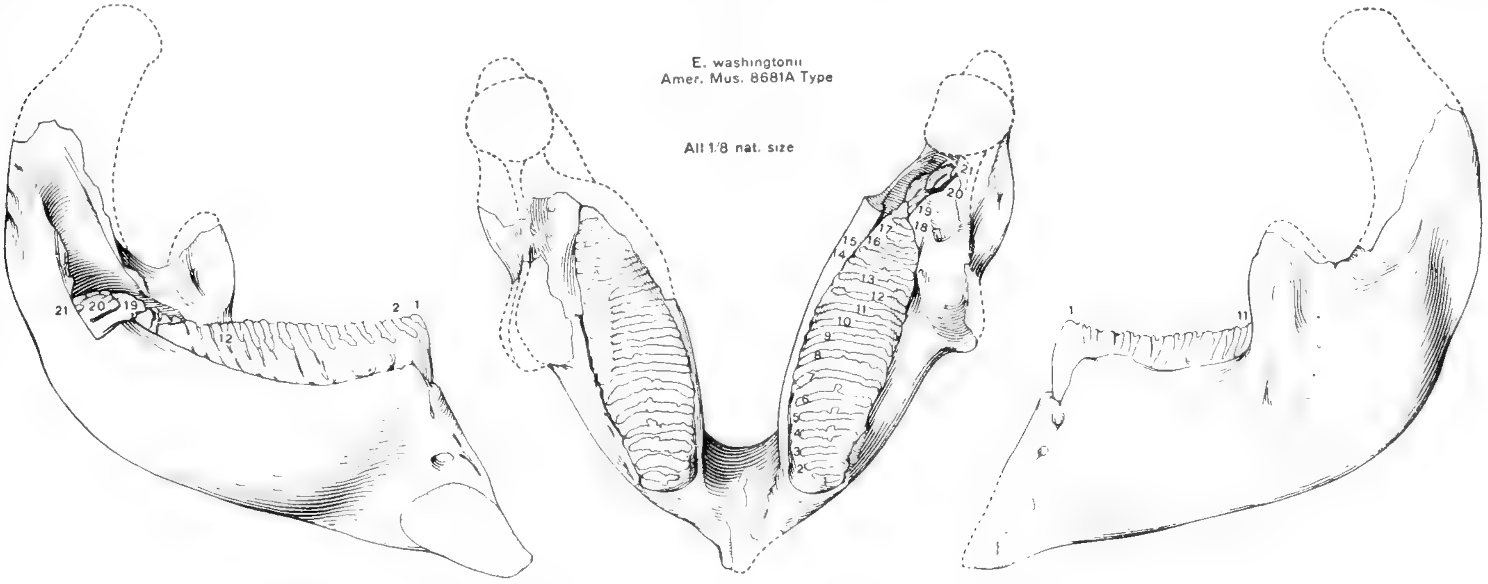


Fig. 972. New figure of the type adult jaw of *Parelephas washingtonii* Osborn (Amer. Mus. 8681A), one-eighth natural size, exhibiting twenty-one ridge-plates in M_3. Median (left), coronal (center), and internal (right) aspects. Compare with figures 974, 975 B, 893, B, B1.

As fully characterized in the type description and by the comparative figures, this jaw is readily distinguished by the greatly depressed coronoid region which gives it a wholly different aspect from the type jaw of *Parelephas jeffersonii.*

(Figs. 961 B, 962 B, 971 A) also palatal aspect (971 A1) should be compared with the corresponding aspects of the cranium of *Elephas indicus* (Fig. 963) to convince the student that the crania of *Parelephas jeffersonii* and *P. washingtonii are far more brachycephalic and bathycephalic* than the cranium of *E. indicus.*

GEOLOGY AND FAUNA (COMPARE STERNBERG, 1903, PP. 511, 512).—We owe to Charles H. Sternberg an interesting description of the beds and the conditions under which he discovered this very important skull. The following is a brief résumé of his description:

From a deposit of extinct animals, discovered in 1876 in 'mudsprings,' in the swamps of Pine Creek valley, Whitman County, Washington, about 100 miles north of Walla Walla. Skull dislodged and brought to the surface by means of a long iron rod with grappling hooks, on Mr. Copeland's farm.[1] First exhibited by a showman, then through Charles H. Sternberg purchased by E. D. Cope. The bed explored by Sternberg early in 1878 yielded recent buffalo crania, bones of the skeleton, and arrow-points. Copeland reported nine other mammoth specimens from this swamp which he had deposited in a college at Forest Grove, Oregon: "He discovered a flint spear-point in the gravel above the mammoth bones, associated with charred and partly petrified wood that bore the marks of tools upon it, also deer, buffalo and bird bones. . . . I never doubted, from what I saw and heard at the other excavations in the immediate neighborhood, and where the collectors went through the same kind of peat, clay and gravel as we had gone through, that man, the buffalo, elephant and many existing species once lived together in eastern Washington."

CHARACTERS OF THE SKULL (FIGS. 971, 973, 974, 976).—This superb skull is certainly referable to *Parelephas washingtonii*, and the specific reference is correct, because the exposure of the

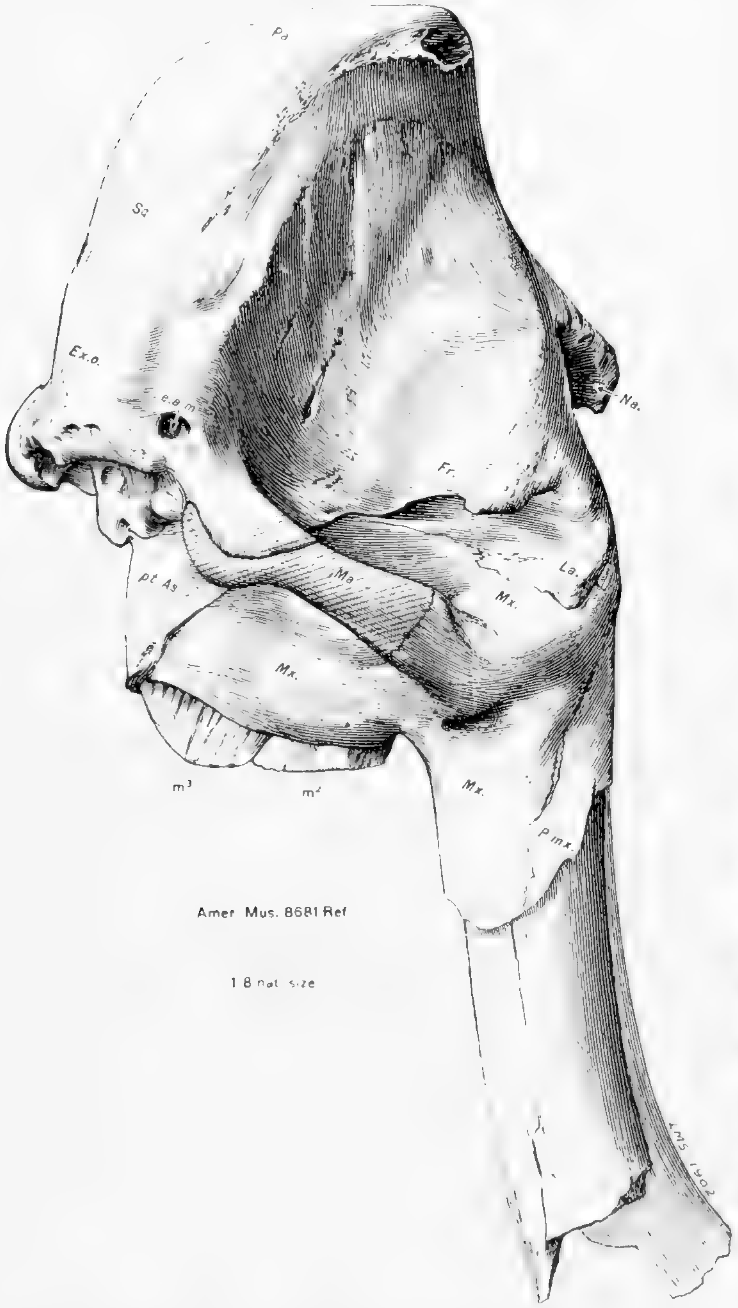


Fig. 973. Young adult male skull referred to *Parelephas washingtonii* Osborn (Amer. Mus. Cope. Coll. 8681), from the Lower Pleistocene of the state of Washington. Right lateral aspect. One-eighth natural size. Same skull as that shown in figures 961, 962, and 971; also figure 974 opposite from photograph of left lateral aspect.

Fig. 974. Young adult male skull (Amer. Mus. Cope Coll. 8681) referred to *Parelephas washingtonii* Osborn. Left lateral aspect of the same skull as that shown in figure 973 opposite. Also type jaw (Amer. Mus. 8681A).

The type jaw of *P. washingtonii* (Amer. Mus. 8681A), found in the same locality, namely, in the swamps of Pine Creek, Whitman County, Washington, about 100 miles from Walla Walla, belongs to a much older individual than the skull (Amer. Mus. Cope Coll. 8681). One-twelfth natural size.

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[1] A large part of the skeleton, beautifully preserved, was also recovered from the bed of gravel below (Science, N. S., 1903, Vol. XVII, p. 512).

third superior molar (Fig. 976) reveals the complete ridge formula. Although found in the same deposits as the type, it belongs to a much younger animal, because the third superior grinding teeth, M^3, are just coming into use, exhibiting only five or six worn ridge-plates (Fig. 971 A1), whereas in the type jaw (Fig. 972) the second molars are completely erupted and the third molars exhibit seventeen to eighteen ridge-plates of the total of twenty-one.

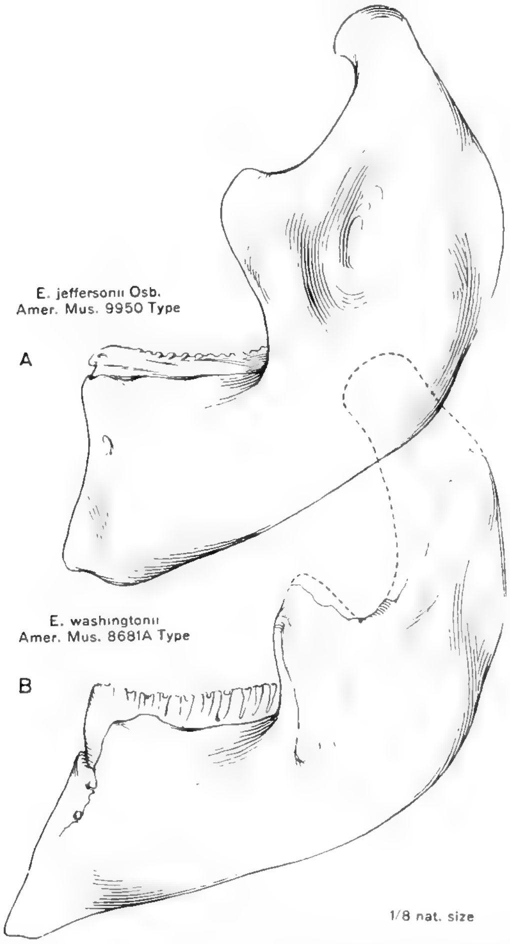


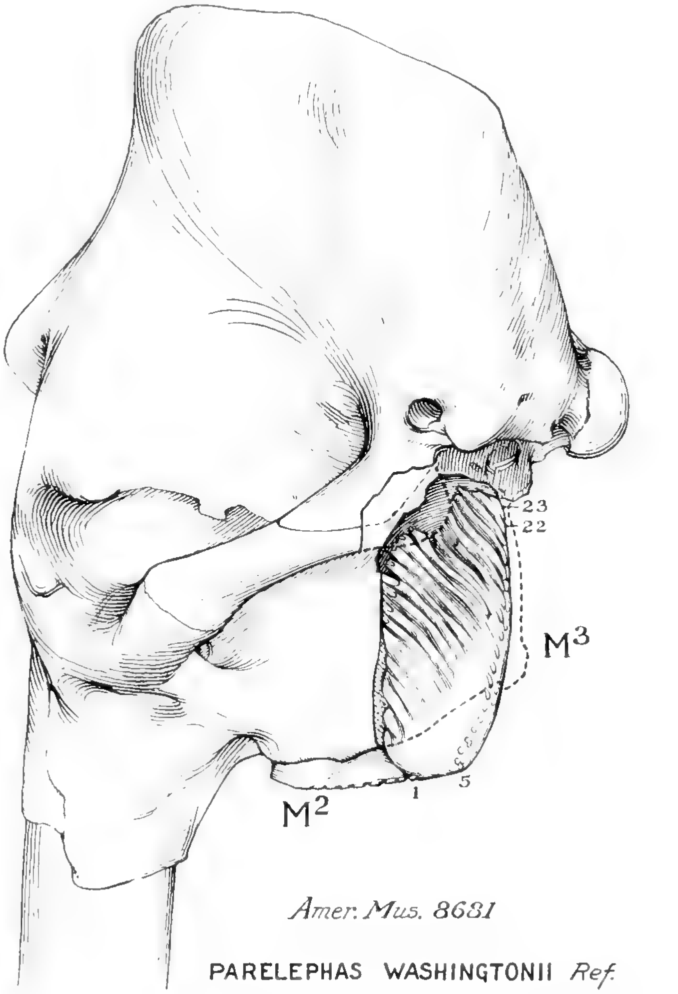
Fig. 975. Type jaw (B) of *Elephas* [*Parelephas*] *washingtonii* (Amer. Mus. 8681A), compared with type jaw (A) of *Elephas* [*Parelephas*] *jeffersonii* (Amer. Mus. 9950).

This comparative figure clearly shows the profoundly different form of the rostrum and of the coronoid region. The measurements of the jaw may readily be taken by multiplying the drawings in this figure and in figure 893 eight diameters; both figures are drawn to a one-eighth scale.

REFERRED PARELEPHAS WASHINGTONII, PETERSON, 1928

Peterson published the following description of a second left inferior molar, l.M$_2$, from Colorado, which he refers to *Parelephas washingtonii*.

Peterson, 1928, pp. 118–120.—"In the Pleistocene formation on Lay Creek, Moffat County, Colorado, about one half mile from Lay Post Office, Mr. M. A. Langley found a left lower molar of a Proboscidean, which was later presented to the Denver Museum of Natural History by Mr. A. G. Wallihan of Lay, Colorado. Upon comparison this lower molar (No. 472, Denver Museum Catalogue) compares very closely with *Parelephas washingtonii* Osborn. The posterior portion of the tooth is broken, but there are sixteen cross-crests present and there were probably from three to five additional crests in the complete tooth. The size of the tooth, the number of the cross-crests as well as their thickness and degree of crenulation is quite closely identical with the type in the American Museum of Natural History, of which an illustration is herewith published through the courtesy of Professor Henry Fairfield Osborn, President of the American Museum of Natural History, New York."



Referred Second and Third Superior Grinders of Parelephas washingtonii, in situ

Contrast with l.M^3 of *Parelephas floridanus* type (Fig. 982)

Fig. 976. Referred cranium of *Parelephas washingtonii* (Amer. Mus. Cope Coll. 8681), from Pleistocene beds near Pine Creek, Whitman County, state of Washington. Same cranium as that shown in palatal and frontal views in figure 971.

Observe that the premaxillaries of the left side have been removed to completely expose the left third superior molar, l.M^3, which exhibits 23 ridge-plates, of which only the 5 anterior are worn or in use (as shown in palatal view, Fig. 971). The second superior molar, l.M^2, is shown in profile, exhibiting 10+ ridge-plates, the anterior plates having disappeared. This figure shows admirably the enormous alveolus for the reception of this grinding tooth.

Parelephas? eellsi Hay, 1926

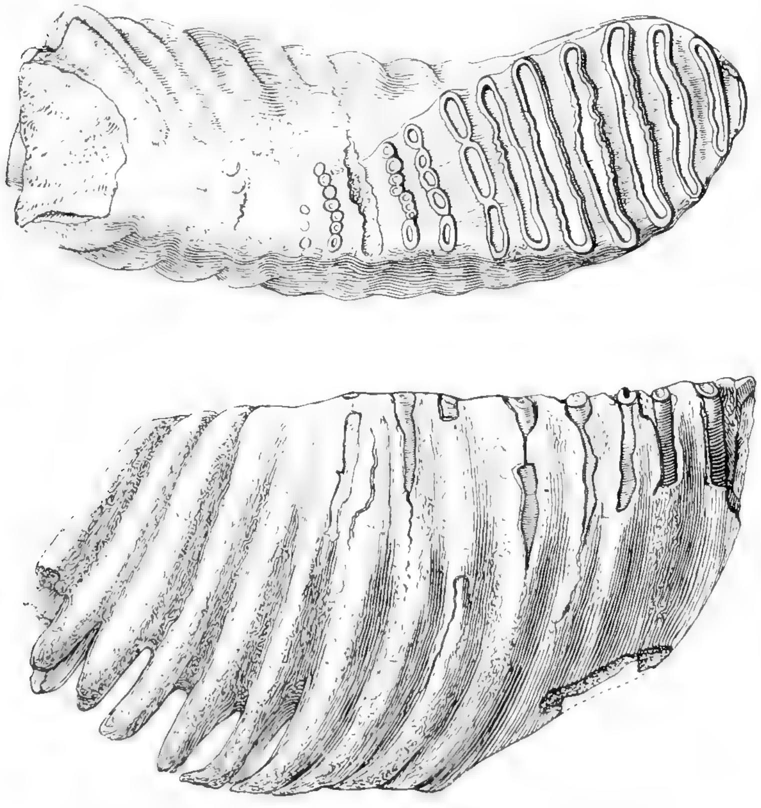
Figure 978

Port Williams, Clallam County, Washington.

Elephas eellsi Hay, 1926. "Description of remains of an elephant found at Port Williams, Washington." Journ. Washington Acad. Sci., Vol. XVI, No. 6, March 19, 1926, pp. 154-159. TYPE.—Fragment of a skull. HORIZON AND LOCALITY.—"Port Williams, Clallam County, Washington. This place is on the southern shore of the eastern end of the Strait of San Juan de Fuca." TYPE FIGURE.—*Op. cit.*, p. 156, figs. 1 and 2.

TYPE DESCRIPTION.—(Hay, *op. cit.*, 1926, p. 154): "The collection made by Mr. Eells consists of two third molars, an upper and a lower, which are referred to *Elephas columbi*, a fragment of a skull, which is here described, and tusks, one small and some others of large size. These tusks the writer has not seen. They may belong to *E. columbi* or to the elephant forming the subject of this paper. I regard the skull as belonging to a hitherto undescribed species, and, with the intention of honoring the finder [Rev. Myron Eells, a missionary among the Twana and Clallam Indians for over 30 years], I name it *Elephas eellsi*. At first view the specimen is an unpromising one. It consists of a part of the left maxilla and a smaller part of the right."

Osborn, 1929: Genus and species indeterminate (cf. *Parelephas washingtonii* referred cranium, Figs. 973, 974).



SECOND LEFT INFERIOR MOLAR OF PARELEPHAS WASHINGTONII REF.

Fig. 977. Left inferior molar, l.M_2, from Lay Creek, Moffat County, Colorado (Denver Mus. 472), referred by Peterson, 1928, fig. 23, to *Parelephas washingtonii*. Observe fifteen broad ridge-plates with a maximum of seventeen, as compared with twenty-one in the type, l.M_3 (Fig. 972), of *P. washingtonii*.

Fig. 978. Type figure of *Elephas eellsi* Hay, 1926, figs. 1 and 2, one-fourth natural size, found at Port Williams, Clallam County, Washington. Fragment of a skull. An indeterminate species (compare *Parelephas washingtonii*, Figs. 973, 974).

PARELEPHAS FLORIDANUS OF FLORIDA

A recent discovery of great interest is a deposit near Bradenton, Florida, apparently of Upper Pleistocene age, yielding the more or less complete remains of at least seven individual elephants, which represent a hitherto unrecognized specific stage described by Osborn (1930.837) as *Parelephas floridanus.* The importance of this discovery rests in the fact that it enables us to distinguish clearly this very large and progressive animal of Florida from the typical *Parelephas columbi*, a specific name which, as shown on pages 1043, 1046, 1067, 1070–1083, has embraced many quite distinct ascending mutations and specific stages. Near to this more primitive, true *Parelephas columbi* the French Guiana species (*Parelephas columbi cayennensis*) appears to be ranked.

Parelephas floridanus compared with P. columbi and P. jeffersonii

The fossil mammoths hitherto discovered in Florida have been determined by Hay, Gidley, and Osborn as belonging either to the relatively rare *Archidiskodon imperator* or to a stage very near to the typical *Parelephas columbi* from the Darien canal, Georgia, or contiguous phosphate beds of South Carolina. A third stage was distinguished by Osborn in 1930 (1930.837) as *Parelephas floridanus.*

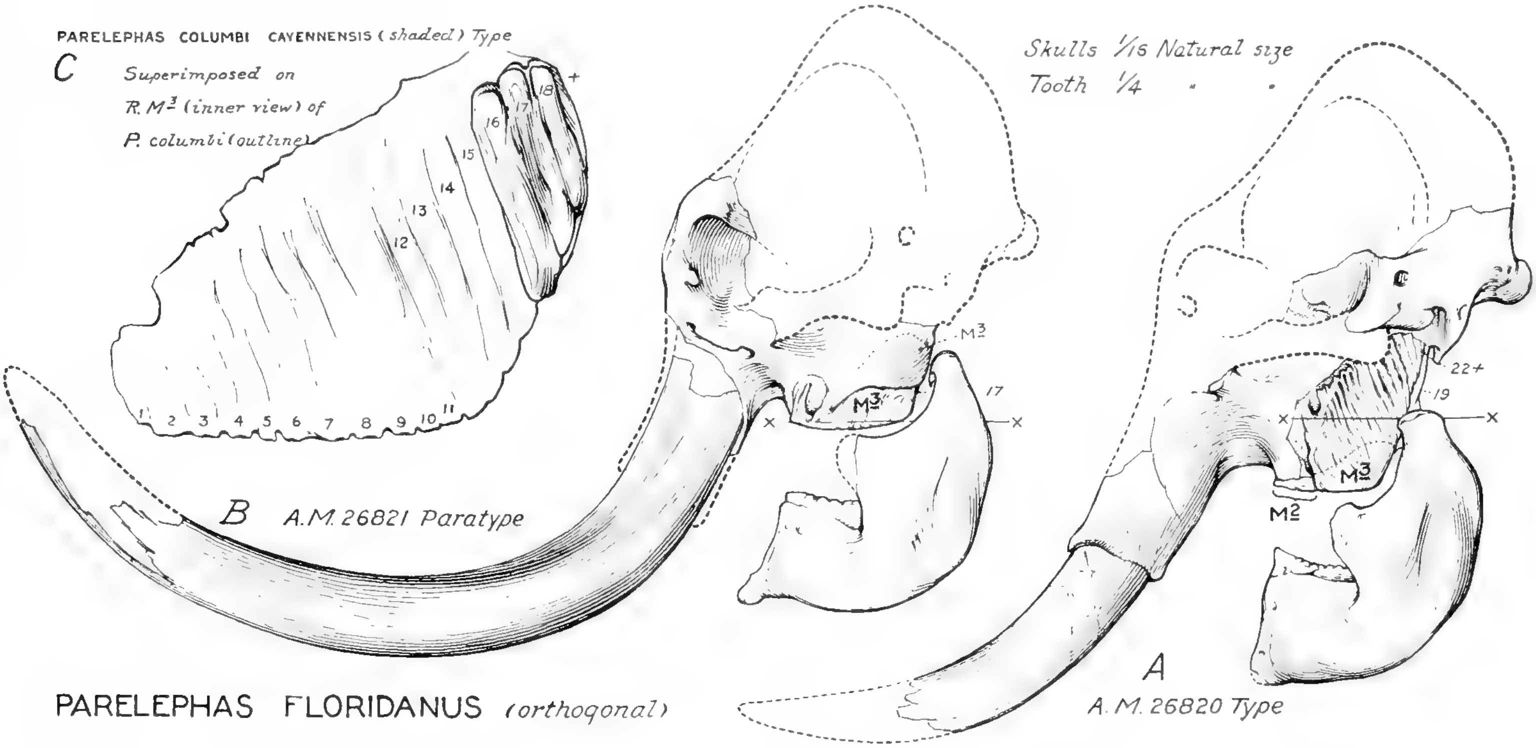


Fig. 979. Type (A) and Paratype (B) Crania and Jaws of Parelephas floridanus compared with Type (C) of P. columbi cayennensis
Crania one-sixteenth natural size; molar one-fourth natural size

A, Type (Amer. Mus. 26820), a middle-aged male with relatively short, obtuse tusks, exhibiting the second superior molar, M², still in use, the third superior molar, M³, just coming into function. Compare attritional surfaces displayed in figure 981. The horizontal line x———x indicates the attritional level attained in the more aged paratype bull (B), Amer. Mus. 26821.

B, Aged bull with maximum full-grown tusks; second superior molar, M², disappearing, third superior molar, M³, worn down to the very aged attritional level (x———x), as indicated in comparison with the younger bull (A).

Observe other age and growth differences in the depth of the jaw in A (cf. Figs. 983, 984). As detailed in the legend to figure 986, the outlines of the summit of the occiput were restored from the more complete crania of *Parelephas jeffersonii* and *P. washingtonii* in the American and Nebraska Museum collections.

C, Ridge-plates 16–18 of type of *Parelephas columbi cayennensis* superposed on outline of complete r. M³ of *Parelephas columbi* ref. (Amer. Mus. 13708a), from the phosphate beds near Charleston, S. C. Compare figure 957.

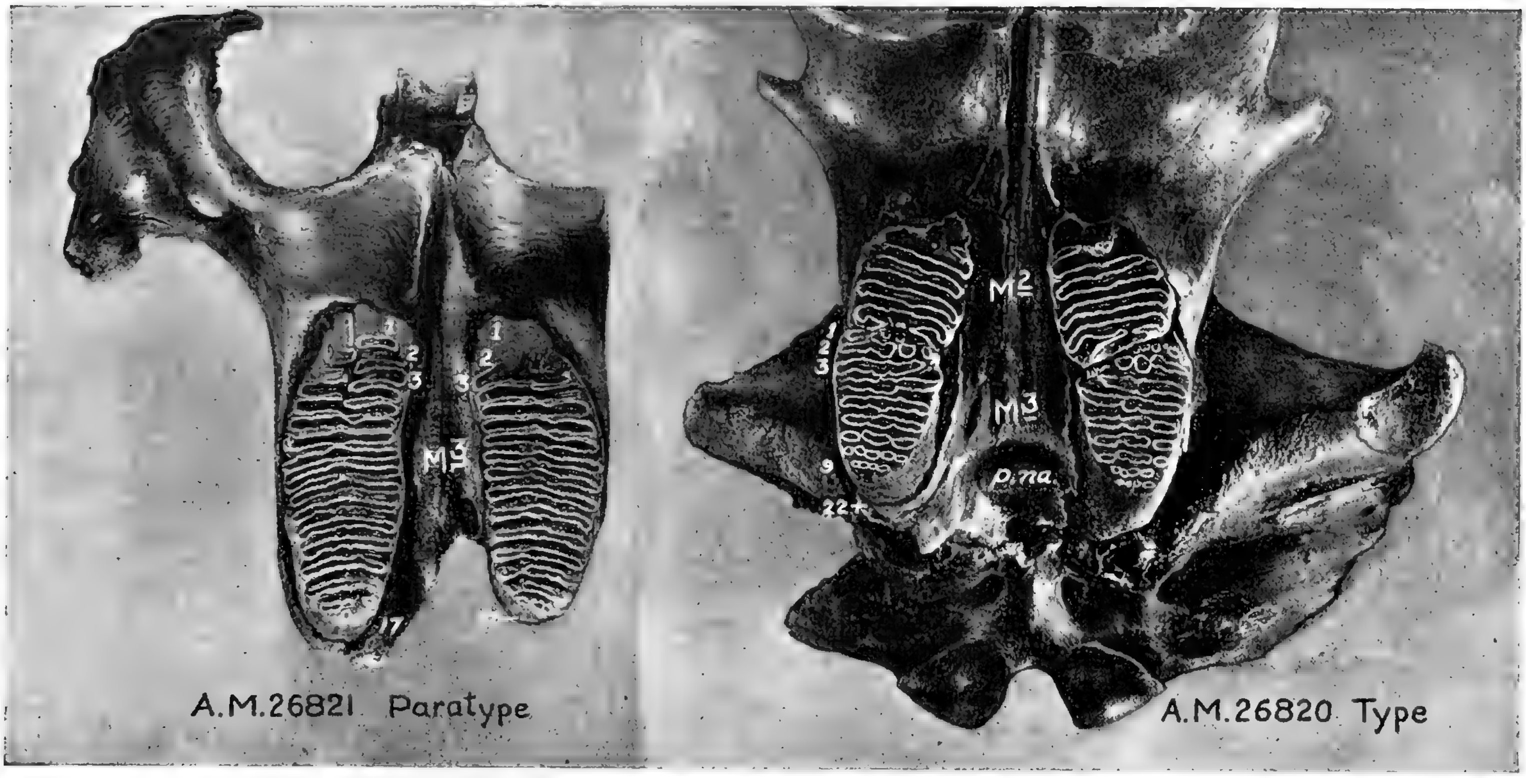


FIG. 980. PARELEPHAS FLORIDANUS TYPE AND PARATYPE, PALATAL ASPECT
ONE-SIXTH NATURAL SIZE
Gift of Mr. Walter W. Holmes, 1929

(Right) Type molar crowns of the middle-aged adult (Amer. Mus. 26820) with a total of 14–15 ridge-plates in use in the closely conjoined M^2 and M^3, which appear to function like a single grinder.

(Left) Aged paratype (Amer. Mus. 26821) in which the 16–17 ridge-plates of the single third superior grinders, M^3, are simultaneously in function.

Compare figure 979 showing the attrition level of the grinders in the middle-aged adult and aged specimens. Observe also that in the type younger bull 14–15 ridge-plates are in trituration, while in the aged bull paratype 16–17 ridge-plates are in use in correlation with the larger food requirements of the more aged specimen.

PARELEPHAS COLUMBI.—As shown on pages 1075–1077 of the present Memoir, in the typical *Parelephas columbi* the ridge formula is M 3 $\frac{19}{16+}$; to this typical stage, in which the grinding teeth are relatively small, belong all the thirty-eight specimens from the phosphate beds of South Carolina fully described on the above-mentioned pages, also the Amherst skeleton of *P. columbi* described by Loomis (1923–1928) on pages 1079–1081. In the Amherst specimen the ridge-plate formula (M 3 $\frac{18+}{16\frac{1}{2}}$) agrees closely with that of the South Carolina phosphate collection, in which the prevailing ridge-plate formula is M 3 $\frac{18\text{-}19}{15\text{-}16+}$.

PARELEPHAS FLORIDANUS.—The type and referred individuals of *Parelephas floridanus*, varying in sex, size, and age, are all distinguished by the ridge-plate formula M 3 $\frac{22+}{21+}$, indicating a much more advanced stage of evolution; moreover, the type and paratype skulls of *P. floridanus* indicate an animal of very large size, with crania and massive tusks differing in proportion from those of any *Parelephas* hitherto discovered, excepting perhaps the "Franklin County Mammoth" (Neb. Mus. 1–4–15), referred to *Parelephas jeffersonii*.

This fine type collection of *P. floridanus* was the gift in the year 1929 of Mr. Walter W. Holmes of St. Petersburg, Florida, who with enthusiasm and generosity has been promoting the American Museum explorations in Florida since the year 1923.

MATERIALS.—The deposit near Bradenton, Florida, yielding the type, paratype, and other specimens, was found in February of 1929 by Mr. J. E. Moore of Sarasota, who discovered the palate of the paratype specimen

(Amer. Mus. 26821) protruding from the side of the bank of a drainage canal. The whole deposit is 27 feet broad and 10 feet deep, the fine white river sand and black soil filling the interstices of the more or less broken crania; this deposit was thoroughly worked by Carl Sorensen during the period March 2 to April 2, 1929, where he recovered the remains of at least seven individual elephants. All the crania and jaws had been fractured to a greater or less degree, transported a considerable distance, and collected in what may have been a deep marginal pool of a low gradient river. These seven individuals, including type and paratype, are represented by parts of crania, jaws, and the included grinding teeth.

The chief materials in this Holmes-Moore collection are as follows:

Amer. Mus. 26820. Type. Middle-aged male. Skull and jaws (Figs. 979, 980, 981, with associated ribs, l. scapula, l. fibula, r. ulna, l. radius, two humeri, r. femur, two tibiæ, parts of pelvis, and certain foot bones of the skeleton. Smaller right femur, length 1250 mm. (4 ft. 1¼ in.). Smaller right humerus, length 1100 mm. (3 ft. 7¼ in.).

Amer. Mus. 26821. Paratype. Palate and jaws of an old male individual, third superior and inferior molars only. Right side of cranium (Figs. 981, 979, 980), palate, lower jaw, very large tusk, also associated large vertebræ (26833*b* in measurements below). Also larger left femur (1393 mm.). Larger left humerus complete, length 1200 mm. (3 ft. 11¼ in.).

Amer. Mus. 26822. Paratype. Palate with r.M^3 and l.M^3, of smaller size, supposed female.
Amer. Mus. 26823. Portion of right palate, with r.M^3, of larger size, supposed male.
Amer. Mus. 26824. Half of right palate, with r.M^3, of small size, supposed female.
Amer. Mus. 26825. Third left upper, l.M^3, and left lower grinder, l.M_3, complete, broad plated, of largest size, supposed male.
Amer. Mus. 26826. Right lower grinder, r.M_3, incomplete, (?)large size, supposed male.
Amer. Mus. 26833 *a, b, c, d, e, f*. Five vertebral series, scattered. See description and Table XIV on page 1114.

Geologic Age.—Important as bearing on the relatively recent geologic age of this Bradenton deposit are the horn and part of the cranium of a very large bison (perhaps *Bison regius* Hay), also part of the cranium of *Castoroides*. Dr. G. G. Simpson (1930), who surveyed the mammalian deposits of Florida with the aid of Chief Geologist Herman Gunter, considers this deposit as probably of late Pleistocene age.

Ridge-plate Distinctions.—The specific constancy both of the ridge-plates and of the molar measurements as a whole establish beyond question the clear separation of *Parelephas floridanus* from the more primitive typical *P. columbi*, on the one hand, and from the more progressive *P. jeffersonii* and *P. progressus*, on the other, as shown in the following comparison of the ridge-plate formulæ and of the maximum or male diameters of the molar crowns of M 3:

	Ridge-plates	Length	Breadth	Height
Parelephas progressus	$\frac{30}{26}$	205 mm.	109 mm.	203 mm.
Elephas roosevelti [=*Parelephas jeffersonii* ref.] . . .	$\frac{25}{24}$	282	98	202
Parelephas floridanus	$\frac{22+}{21+}$	320	88	235
Parelephas columbi	$\frac{19}{16+}$	288	106	207

In the "Franklin County Mammoth" of Nebraska, referred to *Parelephas jeffersonii* (pp. 1091–1093, Fig. 964 of the present Memoir), the tusks are 12½ ft. in length and strongly incurved; the third superior molar (M^3) exhibits 19 ridge-plates; with the possible exception of this Nebraska specimen, *P. floridanus* is the largest known member of the *Parelephas* phylum in America.

Parelephas floridanus Osborn, 1929

Figures 935, 936, 979–987, 989, Pl. XXII

Manatee County, Florida, two miles south of Bradenton. Upper(?) Pleistocene.

Parelephas floridanus Osborn, 1929. "New Eurasiatic and American Proboscideans." Amer. Mus. Novitates, No. 393, December 24, 1929, p. 20. TYPE.—"Anterior portion of cranium, maxilla with M^2, M^3 of both sides, and tusks, together with lower jaw, M_2 of both sides *in situ*, of a middle-aged individual, [M_3 partly erupted]; also associated (?) right femur and other skeletal parts." Amer. Mus. 26820. PARATYPES.—"Amer. Mus. 26821, adult jaw with M_2, M_3 in place, and Amer. Mus. 26822, fragment of palate with M^3 of both sides; also associated (?) left femur and other members of vertebral skeleton of an individual of larger size (Amer. Mus. 26821)." HORIZON AND LOCALITY.—Manatee County, Florida, two miles south of Bradenton. Fluviatile fine sand, (?)Upper Pleistocene. TYPE FIGURE.—*Op. cit.*, Osborn, 1929.797, p. 19, fig. 19.

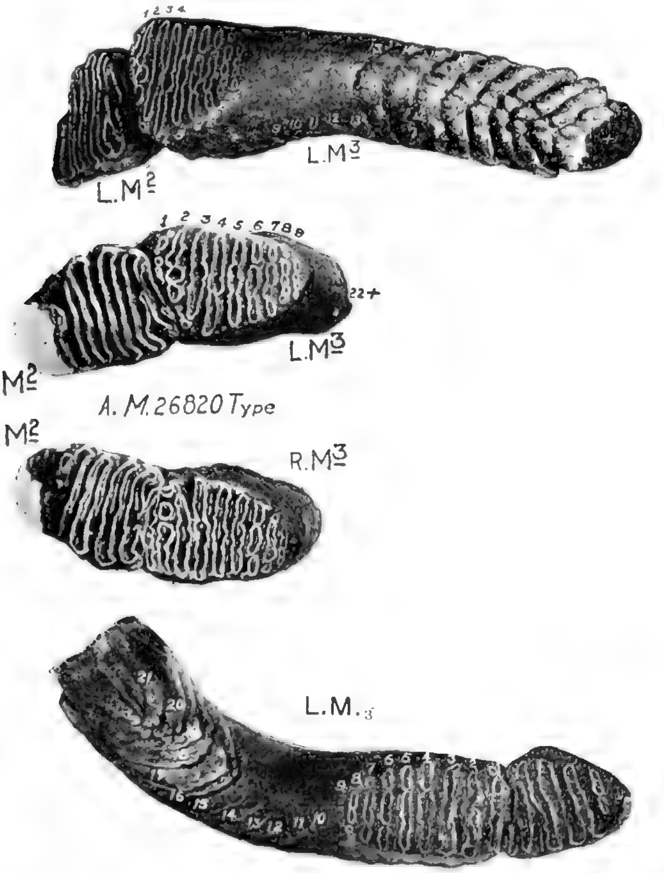


Fig. 981. Type right and left superior and inferior molars of *Parelephas floridanus* (Amer. Mus. 26820), one-sixth natural size. After Osborn, 1929.797, fig. 19.

Observe especially the equal attritional areas above and below; fifteen combined superior ridge-plates in $l.M^{2-3}$, opposed to 13–14 ridge-plates in $l.M_{2-3}$, a perfect mechanical balance. Compare $l.M^{2-3}$ (Figs. 980, 982, and legend), also $l.M_{2-3}$ (Fig. 985, and legend).

SPECIFIC CHARACTERS.—(*Op. cit.*, 1929.797, p. 20): "Superior and inferior ridge-plate formula: M 3 $\frac{22+}{21+}$, max. $\frac{23}{23}$, intermediate between *Parelephas columbi* ($\frac{19}{16+}$) and *P. jeffersonii* ($\frac{25}{24}$); ridge-plates broad and widely separated at base, more compressed at summit. Incisive tusks extremely massive and relatively short. Males attain very large size. Femora measure 1250 to 1410 [1393] mm."

Supplementary Description (Osborn, 1930.837): "*Parelephas floridanus* from the Upper Pleistocene of Florida compared with *P. jeffersonii*," Amer. Mus. Novitates, No. 443, December 18, 1930, pp. 1 17.

GENERAL CHARACTERS (CF. OSBORN, 1930.837).—Comparison is naturally made with the full-grown type skeleton of *Parelephas jeffersonii* (Fig. 988) and with the type dentition of *Elephas roosevelti* [=*P. jeffersonii* ref.] (Fig. 968). The incisive tusks are shorter and more robust; the grinding teeth, while exhibiting fewer ridge-plates, are of larger size and the ridge-plates are more widely separated (see Figs. 980 and 985), with thick enamel, yet clearly distinguishable from the broader crowns and still thicker enamel of *Archidiskodon imperator* of Florida. The type skeleton and limbs of this middle-aged bull of *Parelephas floridanus* type (Amer. Mus. 26820) slightly exceed in size those of the very aged bull (Fig. 988) of *Parelephas jeffersonii* type (Amer. Mus. 9950). In brief, the middle-aged *Parelephas floridanus* type agrees with the aged *P. jeffersonii* in size, whereas the aged male paratype of *P. floridanus* (Amer. Mus. 26821) greatly exceeds in size the aged male type of *P. jeffersonii*, and is not far inferior to the giant *Archidiskodon imperator maibeni* in the Nebraska Museum (Figs. 910, 911).

These general characters are very important in considering *Parelephas floridanus* as a most welcome new stage or ascending mutation in the long history of the *Parelephas* phylum first known in the Upper Pliocene[1] *Parelephas trogontherioides* of western Europe.

SEPARATION OF PARELEPHAS FLORIDANUS FROM P. COLUMBI

By the older method of ridge-plate count and molar crown proportions we may estimate the *ascending mutation* stage of three specimens listed as *P. columbi* in the National Museum and described on page 1079, namely:

Nat. Mus. 11810, r.M^3, with 18 to 20 ridge-plates, length 258 mm., breadth 90 mm., height 167+mm.

Nat. Mus. 11808, r.M^3, with +13 ridge-plates preserved, length 200 mm., breadth 89 mm., height 195 mm.; 7 to 8 anterior ridge-plates missing.

Nat. Mus. 11806, l.M^2, with +12+ridge-plates.

RIDGE-PLATE HEIGHTS.—By the newer height measurement *Parelephas floridanus* (M 3 $\frac{22+}{21+}$) not only exceeds *P. columbi* (M 3 $\frac{19}{16+}$) in the number of ridge-plates but in the height of the ridge-plates of the grinding teeth; M^3 is much taller or more hypsodont in *P. floridanus* than in *P. columbi*; in the type of *P. floridanus* the eight superior ridge-plates (12–19) measure 1309 mm. in collective height, whereas in the neotype of *P. columbi* the corresponding ridge-plates (12–19) measure 1117 mm. in their collective height. In Nat. Mus. 11808 the collective height of the eight

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[1] [See footnote 1 on page 1049 above.—Editor.]

ridge-plates (13–20) is 1196 mm.; it is therefore intermediate in collective height measurement between *P. floridanus* (1309 mm.) and *P. columbi* (1117 mm.) Consequently the National Museum specimens above are nearer to *Parelephas floridanus* in measurement than to the typical *P. columbi*, to which they were first referred by Osborn (see p. 1078).

The *ganometric* length (Osborn-Colbert, 1931.858) of the superior and inferior ridge-plates of an elephant grinder can only be measured in longitudinal section; measurements on unsectioned teeth are liable to be erroneous up to as much as twenty-five percent.

COMPARATIVE DENTAL MEASUREMENTS OF PARELEPHAS JEFFERSONII AND P. FLORIDANUS

Parelephas floridanus Type and Referred Molars (see Table XII).—The total number of ridge-plates in M^3 of *Parelephas floridanus* is 22+, in M_3 it is 21+, as compared with M $3\frac{25}{24}$ in *Elephas roosevelti* [=*Parelephas jeffersonii* ref.] (Fig. 968).

Ridge-plate Count.—According to the ridge-plate count of the type and paratype molars of *Parelephas floridanus* taken along the central line of the crown, in smaller males and females there are 6½ ridge-plates in 100 mm.; in the male type 7½ in 100 mm., as compared with 8 ridge-plates in a 100 mm. line in *P. jeffersonii.*

TABLE XII

Seven Individuals of Parelephas floridanus compared with P. jeffersonii Type

Measured as in Diagrams, Figs. 982, 985

	Parelephas jeffersonii A. M. 9950 Type Skeleton	*Parelephas floridanus* A. M. 26820 Type Male—middle-aged. Skull.	*P. floridanus* A. M. 26821 Paratype Male—aged. Skull.	*P. floridanus* A. M. 26822 Paratype ?Female. R. & L. M^3	*P. floridanus* A. M. 26823 ?Large male. R.M^3	*P. floridanus* A. M. 26824 ?Female. R.M^3	*P. floridanus* A. M. 26825 ?Large male. L.M_3	*P. floridanus* A. M. 26826 Large male. L.M^3, R.M_3
Third superior molar—length	203+	320	320±	278±				288
max. breadth. 9th	108+	88	99	106				91
max. height. 15th	Worn	235	215±	184+				195
Third inferior molar—length	208+	290	290±		312	273	355	333
max. breadth. 7th to 9th	86+	79	92		92	99	90	83
max. height. 12th to 15th	168	180±	180±		200	192	165	170
Total number of ridge plates. M^3		22+	17e	22e	19+	18+		20+
Total number of ridge plates. M_3		21+	12e				22	21
Crown—number ridge-plates in 10 cm. M^3		7½	7½	6½	6½	7		6½
number ridge-plates in 10 cm. M_3		6½	5½				6	6½
Tusk—exposed length, outside curve (free portion)	3020	1165	1960					
total length	3500		2320±					
max. diameter, transverse	$168^{R.}$	180	183					
max. circumference	505	545	$520^{L.}+$					

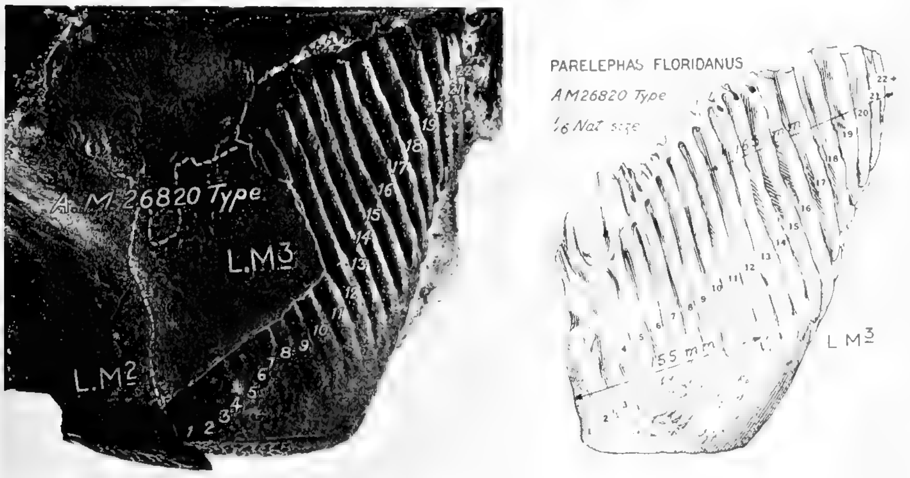


Fig. 982. (Left) Detailed photograph and (right) drawing of the third superior grinder, l.M^3, of the type of *Parelephas floridanus* (Amer. Mus. 26820) exhibiting a total of 22+ ridge-plates. One-sixth natural size. After Osborn, 1930.837, fig. 6.

(Right) Third left superior molar of type indicating the true method of measuring the *length* of a superior molar crown, namely, eleven ridge-plates on the lower level = 155 mm.; eleven ridge-plates on the upper level = 165 mm.; the total length of this third superior molar, accordingly, is 320 mm. Compare figure 979A.

The inferior ridge-plates are of coarse enamel set widely apart; in the unworn type (Amer. Mus. 26820) there are 6½ ridge-plates in 100 mm., in the much worn paratype (Amer. Mus. 26821) there are 5½ ridge-plates in 100 mm. For detailed measurements see Table XII.

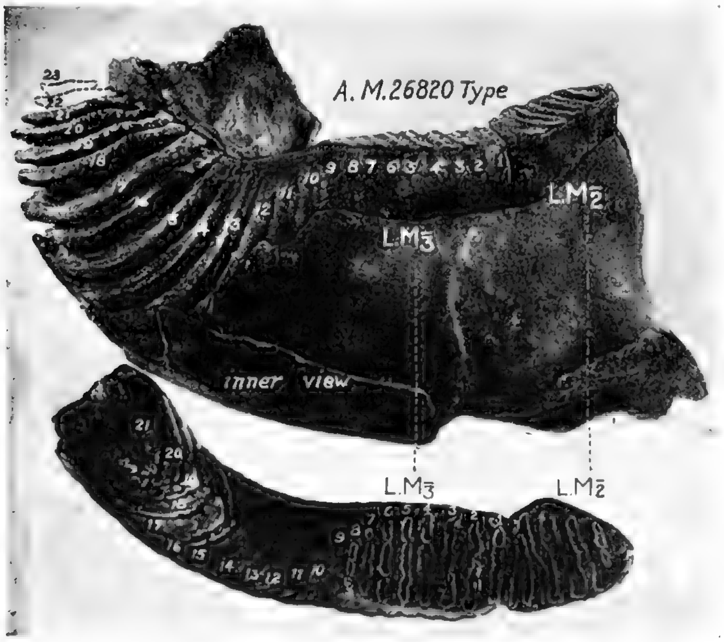
Ganometric Length.—In figure 982 (right) is shown the true method of measuring the collective length of the ridge-plates, namely, on two levels, a lower (=155 mm.) and a higher (=165 mm.), total =320 mm.; this agrees exactly with the above ridge-plate count of M^3, namely, from 6½ to 7½ ridge-plates in 100 mm. The *ganometric length*, i.e., of the unfolded enamel of the twenty-two rising and falling ridge-plates of M^3 in the type of *Parelephas floridanus* (Amer. Mus. 26820) is 8180 mm. as compared with 10231 mm. in the type of *P. progressus.*

Incisive Tusks.—The tusks are distinguished for their massiveness (Figs. 979 and 986), the maximum transverse diameter of the type being 180 mm., of the paratype 183 mm.; and the circumference, 545 mm., as compared with *P. jeffersonii* of which the maximum diameter is 168 mm., and the circumference 505 mm.

Type Mandible of Parelephas floridanus

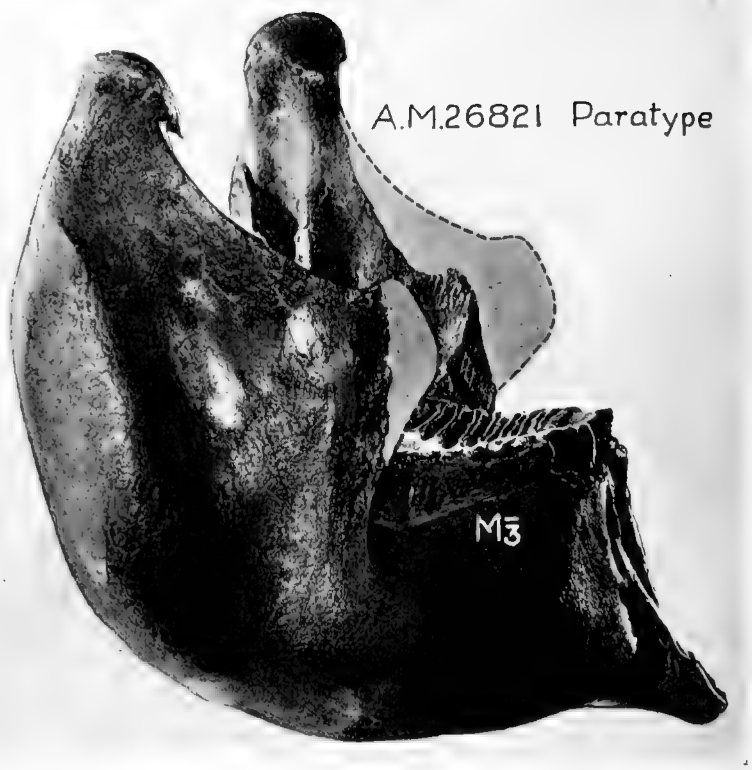
Fig. 983. Type mandible of *Parelephas floridanus* (Amer. Mus. 26820). One-sixth natural size. After Osborn, 1930.837, fig. 4.

Observe the very robust proportions, strongly abbreviated or truncated rostrum, wholly worn r.M_2, and partly worn r.M_3. Compare figure 981.



Type Inferior Molars of the Left Side of Parelephas floridanus

Fig. 985. Type (Amer. Mus. 26820) internal and crown views of second and third inferior grinding teeth, l.M_2, l.M_3; l.M_3 exhibits 21+ ridge-plates. One-sixth natural size. Compare figure 981, coronal aspect of type superior molars of both sides, and inferior of left side After Osborn, 1930.837, fig. 7.



Paratype Mandible of Parelephas floridanus

Fig. 984. Deeply depressed aged mandible of the paratype of *Parelephas floridanus* (Amer. Mus. 26821), exhibiting only M_3 *in situ*, M_2 having been shed. One-sixth natural size. After Osborn, 1930.837, fig. 5.

Observe the very prominent, peaked rostrum, also the relatively greater *bathycephaly* or depression of the lower border of the mandible below the level of the condyle, as compared with the more youthful type mandible opposite.

As newly restored (Fig. 986), the type tusk (Amer. Mus. 26820) is much longer than shown in figure 979. The paratype tusk (Amer. Mus. 26821) is correctly represented in figure 979; it is apparently full grown, judging from the extreme wear of M^3; it measures 2320 mm. as compared with 3500 mm., length of the type aged male tusk of *P. jeffersonii* (Amer. Mus. 9950). In brief, in the aged males of *P. floridanus* the tusks are more massive, less incurved, and relatively shorter (=2320 mm.) than the aged male tusks (=3500 mm.) of *P. jeffersonii.*

COMPARATIVE CRANIAL AND SKELETAL MEASUREMENTS OF PARELEPHAS FLORIDANUS AND P. JEFFERSONII

As shown in Table XIII and figures 979 and 984, the crania and jaws of *P. floridanus* greatly exceed in size and in massiveness the aged type cranium of *P. jeffersonii.* The ratio of increase in size in the jaw across the premaxillaries is about 10 per cent. The estimated bathycephalic measurement from the summit of the occiput to the occlusal surface of the grinding teeth is 1000e mm. as compared with 880 mm. in *P. jeffersonii.* The longitudinal measurement from the occipital condyle to the anterior rim of the orbit is 770e mm. as compared with 720 mm. in *P. jeffersonii.* It thus appears that *P. floridanus* is much more bathycephalic (1000e

Reconstructed Type Cranium of Parelephas floridanus beneath Restoration of Parelephas jeffersonii

Fig. 986. Type male cranium of *Parelephas floridanus* (Amer. Mus. 26820) as now exhibited in the American Museum, Hall of the Age of Man. Compare figure 979. After Osborn, 1930.837, fig. 8.

In this reconstruction, made under the direction of the author and Mr. Charles Lang, the height of the orbit is determined from the more complete paratype (Amer. Mus. 26821); the frontal profile and occipital region are determined partly from the cranium (Amer. Mus. Cope Coll. 8681) of the more primitive *P. washingtonii*, partly from the type (Amer. Mus. 9950) of *P. jeffersonii*, and partly from the giant *P. jeffersonii* in the Nebraska Museum known as the "Franklin County Mammoth" (Neb. Mus. 1-4-15).

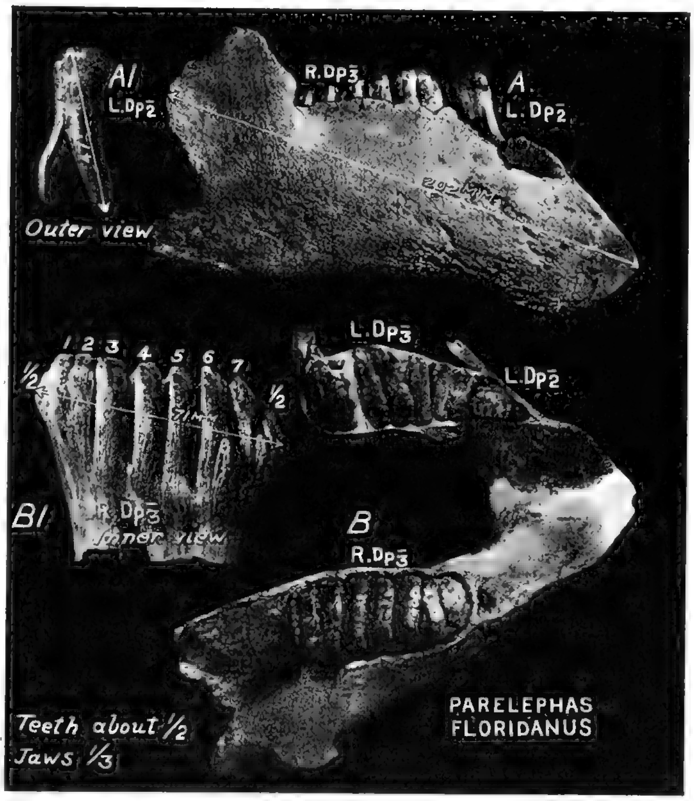
mm.) than the relatively primitive referred cranium of *P. washingtonii* (Amer. Mus. 8681) in which the bathycephaly is: height 880 mm., length 700 mm.

Increasing *bathycephaly* is also indicated in the mandible by comparison of the type jaw of the adult bull of middle age (Amer. Mus. 26820—Fig. 983), exhibiting the wholly worn M_2 and partly worn M_3, with strongly abbreviated rostrum. Much deeper or more bathycephalic is the aged paratype jaw (Amer. Mus. 26821—Fig. 984) retaining only the much worn third inferior molar, M_3.

Comparison of Shoulder Height.—As shown in Table XIII, the skeleton and limbs of the type middle-aged bull of *P. floridanus* (Amer. Mus. 26820) exactly equal or slightly exceed in size the very aged bull type of *P. jeffersonii* (Amer. Mus. 9950) measured as shown in figure 988. This statement is proved by the comparisons below.

The aged bull paratype (Amer. Mus. 26821) of *P. floridanus* (left humerus, 1185 mm.; left femur, 1393 mm.) exceeds in size the aged male type (Amer. Mus. 9950) of *P. jeffersonii*. In fact, the measurement of the humerus somewhat exceeds that of the Amherst skeleton of *Parelephas columbi* (Amherst Mus. 25–1) and is not far inferior to the measurements of both the humerus and femur of the giant *A. imperator maibeni* of the Nebraska Museum (Neb. Mus. 5–9–22).

	Parelephas jeffersonii, type. Aged bull. Amer. Mus. 9950	*P. floridanus*, type. Adult bull. Amer. Mus. 26820	*P. floridanus*, paratype. Aged bull. Amer. Mus. 26821
Articular Length			
Humerus, right	1120	1140	
Humerus, left	1085+	1143	1185
Femur, right	1250±	1230	
Femur, left	1255		1393
Tibia, right	690	698	
Tibia, left	685	685	



Inferior Mandible and Milk Dentition of Parelephas floridanus Ref.

Fig. 987. Teeth about one-half natural size; jaws one-third natural size. Relatively long (202 mm.) and shallow mandible, with prominent rostrum, containing small, bifanged second inferior milk molar, $l.Dp_2$ (as shown in A, A1, B); also right and left third inferior milk molars, r. and $l.Dp_3$, exhibiting ridge-plates ½-7-½ (as shown in B1). After specimen kindly loaned to the American Museum by Mr. J. F. Moore of Sarasota, Florida.

A few comparative measurements with *Parelephas columbi* and *Archidiskodon imperator* are also significant, as follows:

Right humerus of *A. imperator maibeni* of the Nebraska Museum	1251 mm.
Left humerus of aged male *P. floridanus* paratype	1185
Right humerus of type younger male *P. floridanus*	1140
Right humerus of *P. jeffersonii*, aged bull type	1120
Right humerus of *P. columbi*, Amherst skeleton	1030

Observe especially from the relative proportions of the humerus that the *aged* bull of *Parelephas floridanus* greatly exceeds in shoulder height, size, and all other dimensions the aged bull of *P. jeffersonii*. The comparative measurements of the *humerus* are very important, because the humerus always forms the most reliable method of estimating the shoulder height of any member of the elephant family.

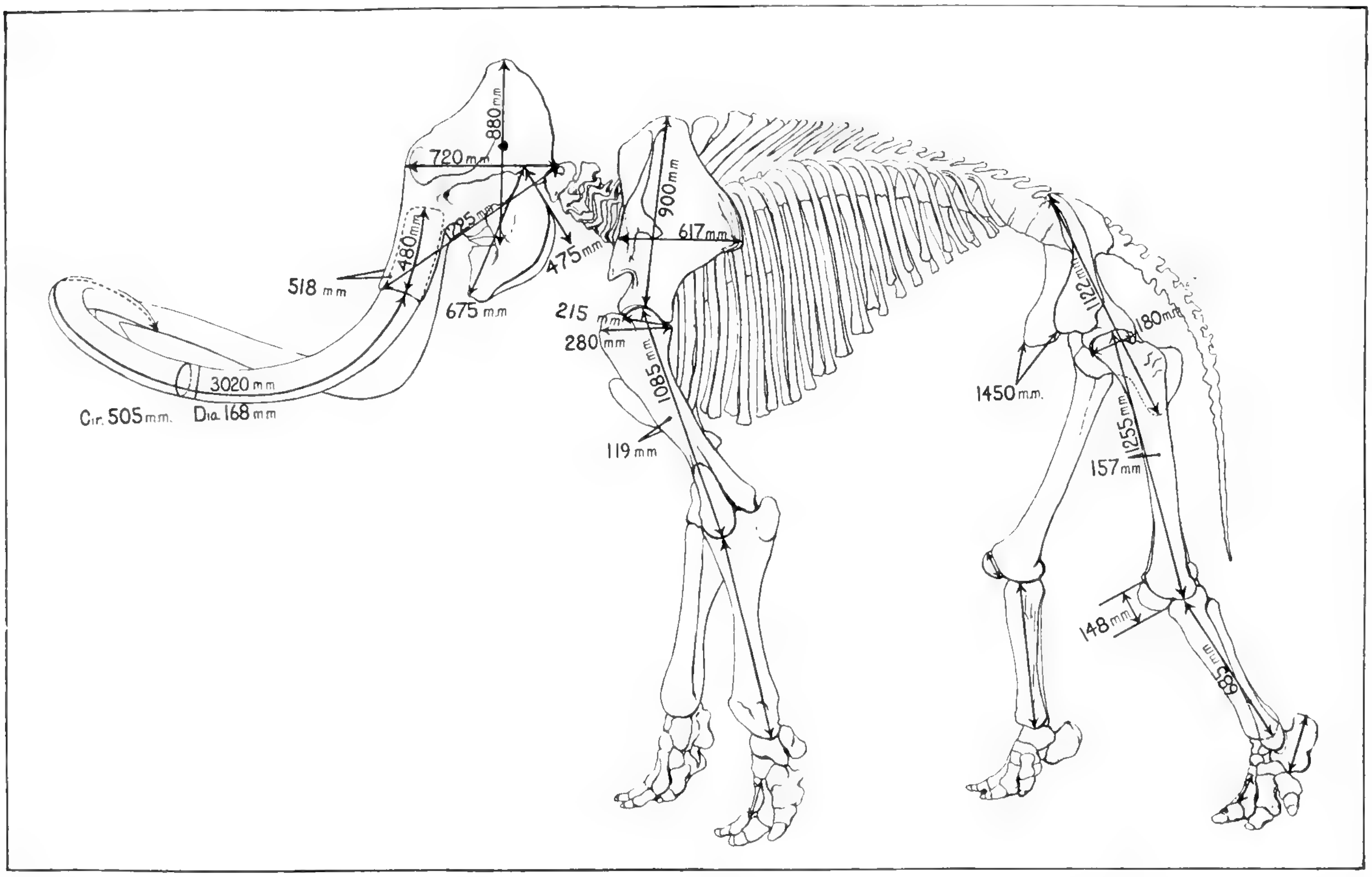


Fig. 988. New standard method (1930) of skeletal measurement in *Parelephas* and other extinct and living proboscideans, illustrated on the type skeleton (Amer. Mus. 9950) of *Parelephas jeffersonii* in the American Museum collection, Hall of the Age of Man. After Osborn, 1930.837, fig. 9.

Bathycephaly of cranium	
vertical	880 mm.
horizontal	720
Jaw	
length, condyle to tip of rostrum	675
Incisive tusks	
in socket 480 mm., exposed 3020 mm., total	3500
Scapula	
vertical	900
horizontal	617
Humerus, articular length	1085
Femur, articular length	1255

This method is uniform with that adopted throughout the present Memoir for the measurement of the cranium, tusks, and fore- and hindlimbs (cf. caption to Fig. 868). Observe the marked falling away of the posterior part of the vertebral column and the relative abbreviation of the hindlimbs, also characteristic of *Mammonteus primigenius* and in a less degree of *Archidiskodon meridionalis*.

TABLE XIII
Comparative Skeletal Measurements of Two Individuals of Parelephas floridanus compared with P. jeffersonii

	Parelephas jeffersonii Type A. M. 9950. Skeleton	*Parelephas floridanus* Type A. M. 26820. Skull and ref. limb bones. Male—middle aged	*P. floridanus* Paratype. A. M. 26821. Skull and ref. limb bones. Male—aged
Cranium—occip. condyle to mid-symphysis	980	1102	
occip. condyle to ant. orbit	720	770e	
trans. premaxillary	518	575	
bathycephaly	880	1000e	
Jaw—condyle to mid-symphysis	675	725	750
height or depth, condyle to lower border	475	535	560
Scapula—height, supra-scap. border to glenoid. R.	905		
ant.-post. glenoid borders. R.	220		
height, supra-scap. border to glenoid. L.	900		
ant.-post. glenoid borders. L.	215+	230	
ant.-post. diameter through metacromion. R.	622		
ant.-post. diameter through metacromion. L.	617		
Humerus—articular length. R.	1120	1140	
mid-diameter, ant.-post. R.	109+	130	
ant.-post. diameter of head. R.	279	255	
articular length. L.	1085+	1143	1185
mid-diameter, ant.-post. L.	119	120	128
ant.-post. diameter of head. L.	280	260	267
Radius—articular length	Rest.		
Ulna—articular length. R.	Rest.	750±	
articular length. L.	Rest.		
Manus—metacarpal III—articular length. R.	Rest.		
metacarpal III—articular length. L.	Rest.	208	
Pelvis—length of os innominatum	1122		
transverse diameter of ilia	1450		
max. diameter of acetabulum	180	183	
Femur—articular length. R.	1250±	1230	
mid-diameter, transverse. R.	155	144	
articular length. L.	1255		1393
mid-diameter, transverse. L.	157		154
Patella—diameter. R.	148		
diameter. L.	Rest.	151	160
Tibia—articular length. R.	690	698	
articular length. L.	685	685	
Calcaneum—length. R.	Rest.	231	
breadth. R.	Rest.	177	
length. L.	Rest.	232	
breadth. L.	Rest.	178	
Metatarsal III—articular length. R.	Rest.	155	
articular length. L.	Rest.		

FIVE VERTEBRAL SERIES PROBABLY ASSOCIATED WITH FIVE OF THE CRANIA OR JAWS. COMPARE TABLE XIV.

Several scattered series of vertebræ have been reassembled according to size which represent five, or at the most six, individuals, numbered as follows: Amer. Mus. 26833*a*, 26833*b*, 26833*c*, 26833*d*, 26833*e*, 26833*f*. Of these, one vertebral series (Amer. Mus. 26833*a*) may with some probability be associated with the type (Amer. Mus. 26820) cranium and jaws; while another series (Amer. Mus. 26833*b*) may be associated with the paratype cranium and jaws (Amer. Mus. 26821).

In the assembling, partly by order of size, these vertebral series present the following vertical and transverse measurements of the centra:

TYPE?

Amer. Mus. 26833*a*, probably associated with type (Amer. Mus. 26820).
- Cervicals, including C1, C5 (*tr.* 171×*ver.* 154), C6 (*tr.* 163×*ver.* 156).
- Dorsals, including D1, D11 (*tr.* 117×*ver.* 126), D13 (*tr.* 129×*ver.* 116), D15 (*tr.* 135×*ver.* 118), D18 (*tr.* 119×*ver.* 122), D19 (*tr.* 121×*ver.* 122).
- Lumbars, including L1 (*tr.* 127×*ver.* 118), L2 (*tr.* 143×*ver.* 116).

PARATYPE?

Amer. Mus. 26833*b*, probably associated with large aged paratype (Amer. Mus. 26821).
- Cervicals, including C1, C2, C3, C4, C5 (*tr.* 199×*ver.* 181), C6 (*tr.* 197×*ver.* 182).
- Dorsals, D4, D5 (*tr.* 130×*ver.* 156), D6, D7, D8, D9, D11, D12 (*tr.* 127×*ver.* 119), D14, D15, D16, D17 (*tr.* 136×*ver.* 131).
- Lumbars, L2, L3 (*tr.* 175×*ver.* 128).
- Sacrals 1–4, length 320+mm.

REFERRED?

Amer. Mus. 26833*e*, including a few dorsals of larger measurement, namely, D17 (*tr.* 127×*ver.* 128), D18 (*tr.* 126× *ver.* 127), D19.

Amer. Mus. 26833*d*, including four vertebrae of the largest measurement, namely
- Dorsals, D6 (*tr.* 150×*ver.* 165), D18 (*tr.* 137×*ver.* 135), D19 (*tr.* 136×*ver.* 139).
- Lumbars, L1 (*tr.* 144×*ver.* 136).

Amer. Mus. 26833*c*, of the smallest measurement,
- Cervicals, including C1 (*tr.* 225×*ver.* 122), C2, C3, C7 (*tr.* 148×*ver.* 150).
- Dorsals, including D6, D10 (*tr.* 117×*ver.* 123), D12 (*tr.* 114×*ver.* 117), D14 (*tr.* 127×*ver.* 113), D16 (*tr.* 120×*ver.* 110), D18 (*tr.* 115×*ver.* 114).
- Lumbars, including L1 (*tr.* 154×*ver.* 115), L3, L4.
- Sacrals, including sacrals 1–4, length 320e mm.

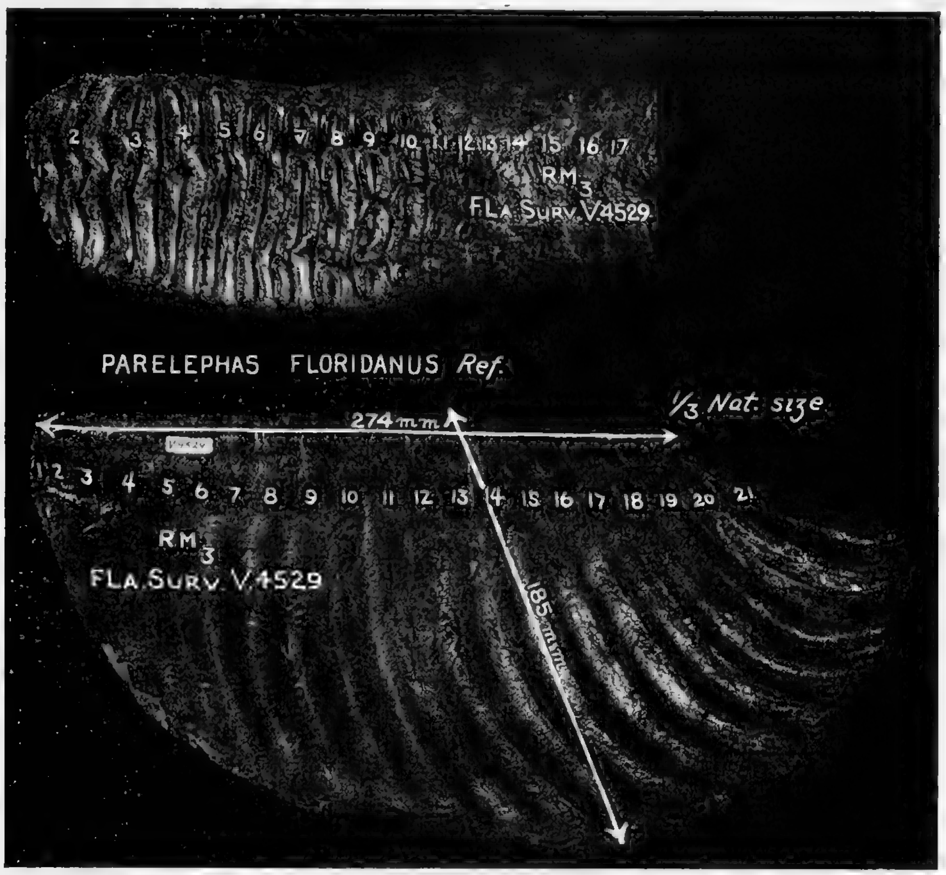
COMPARISON WITH PARELEPHAS JEFFERSONII (SEE TABLE XIV).—The transverse measurements of the type (Amer. Mus. 9950) of *Parelephas jeffersonii* in general agree most closely with the smallest *P. floridanus* (Amer. Mus. 26833*c*), omitting C7, D1 and D2 which could not be obtained. In the linear measurement of the sacrals 1–4, *P. jeffersonii* (377 mm.) exceeds the smaller *P. floridanus* (320e mm.). Very significant are the steadily increasing transverse diameters in the posterior dorso-lumbar vertebræ of *P. jeffersonii* D3 (*tr.* 121) Lumbar 4 (*tr.* 161). The anterior dorsals are wide transversely; in the middle region of the back the vertebræ become quite narrow, and near the lumbar series they become wider; this rule was also found to hold with *Elephas indicus*.

TABLE XIV

TRANSVERSE DIAMETERS OF VERTEBRAL CENTRA

		Parelephas jeffersonii Amer. Mus. 9950	*Parelephas floridanus* Amer. Mus. 26833c	*Parelephas floridanus* Amer. Mus. 26833a	*Parelephas floridanus* Amer. Mus. 26833e	*Parelephas floridanus* Amer. Mus. 26833b	*Parelephas floridanus* Amer. Mus. 26833d
Cervical	1	220	225				
	2	152					
	3	155					
	4	153					
	5	147		171		199	
	6	145		163		197	
	7		148				
Dorsal	1						
	2						
	3	121					
	4	132					
	5	135				130	
	6	133					150
	7	124					
	8	123					
	9	118					
	10	116	117				
	11	114		117			
	12	122	114			127	
	13	125		129			
	14	122	127				
	15	123		135			
	16	126	120				
	17	126			127	136	
	18	125	115	119	126		137
	19	127		121			136
Lumbar	1	142	154	127			144
	2	150		143			
	3	153				175	
	4	161					
Sacrals 1–4, length		377	320e			320e	

Whereas, as appears in Table XIV, the transverse measurements of *Parelephas jeffersonii* are fairly constant, similar transverse measurements of *P. floridanus* display great irregularity, owing to irregular disposition or distortion and to possible errors in our assemblage.



REFERRED RIGHT THIRD INFERIOR MOLAR OF PARELEPHAS FLORIDANUS
METHOD OF RIDGE-PLATE MEASUREMENT

Fig. 989. Total length 274 mm., maximum height of fourteenth ridge-plate, 185 mm. A finely preserved right third inferior molar, r.M_3 (Fla. Surv. V-4529) from Fig Island, Itchatucknee River, Florida, referred to *Parelephas floridanus*. Courtesy of the Florida Geological Survey.

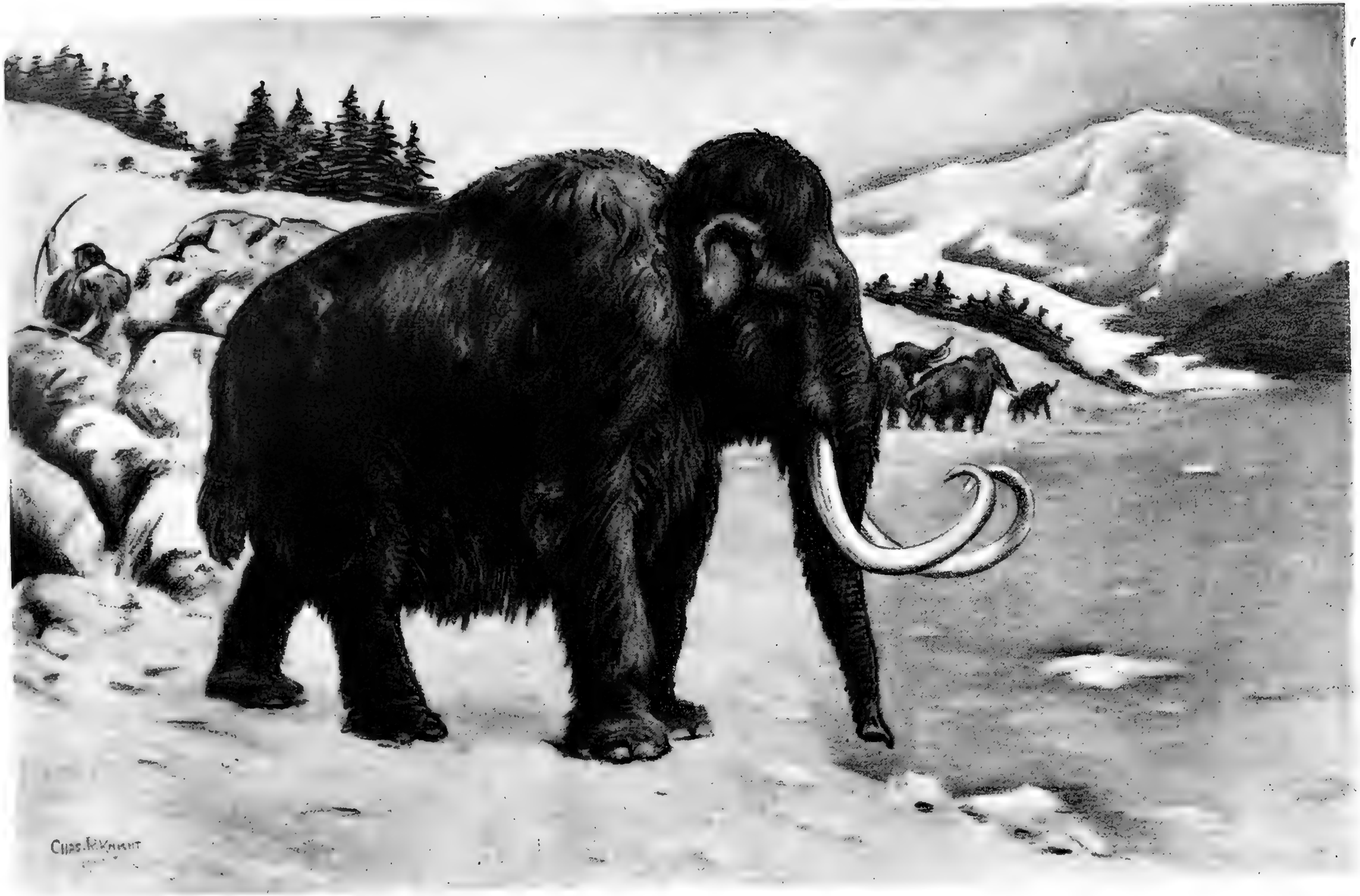


FIG. 990. THE WOOLLY OR NORTHERN MAMMOTH (MAMMONTEUS PRIMIGENIUS). AFTER PAINTING BY CHARLES R. KNIGHT IN THE AMERICAN MUSEUM OF NATURAL HISTORY, HALL OF THE AGE OF MAN.

CHAPTER XVIII

THE GENUS MAMMONTEUS[1] (SUPERFAMILY ELEPHANTOIDEA), OF THE SUBFAMILY MAMMONTINÆ, THE TRUE NORTHERN WOOLLY MAMMOTH

EARLY DESCRIPTIONS OF THE MAMMOTH DURING THE SEVENTEENTH AND EIGHTEENTH CENTURIES (1696–1788) IN EURASIA. HISTORY OF EURASIATIC AND NORTH AMERICAN DISCOVERY. CHARACTERS OF MAMMONTEUS PRIMIGENIUS AND OF SUPPOSED ANCESTRAL STAGES LEADING BACK TO UPPER PLIOCENE TIME. EXTREME STAGES OF EVOLUTION IN AMERICA. FEEDING HABITS AND GEOGRAPHIC DISTRIBUTION.

I. Historical Introduction (1696–1788).
   Names successively applied to the mammoth.
   Native Siberian origin of the word Mammut.

II. Characters of the Subfamily Mammontinæ, including the Genus Mammonteus.
   1. External characters and feeding habits.
   2. Skeletal characters of *Mammonteus primigenius*.
   3. Historical order of naming of species of *Mammonteus*.
   4. Geologic and provisionally ascending phyletic order of species and subspecies of *Mammonteus*. Eurasia and North America.

III. Systematic Description of Species of Mammonteus.
   1. Typical progressive Eurasiatic stages of *Mammonteus*.
      Mammonteus primigenius.
         Typical ridge formula.
         Skulls and jaws of the true *Mammonteus primigenius*.
         'Adams skeleton.'
   2. Primitive European stages of *Mammonteus primigenius*.
      Mammonteus primigenius leith-adamsi.
      Mammonteus primigenius hydruntinus.
      Mammonteus primigenius fraasi.
      Mammonteus primigenius astensis.
   3. American stages of *Mammonteus*.
      Mammonteus primigenius americanus.
      Mammonteus primigenius compressus.
      Mammonteus primigenius alaskensis.
   4. The frozen Mammoth of Siberia.

I. HISTORICAL INTRODUCTION (1696-1788)

The subfamily name Mammontinæ Osborn, 1921, replaces the name Euelephantinæ Osborn, 1918, because the subgenus *Euelephas* Falconer is invalid (see Chapter XIX, p. 1177); the term Mammontinæ, signifying '*les mammonts*,' the 'mammoths,' was substituted in 1921. As set forth in the two preceding chapters, the Mammontinæ embrace three genera, namely, *Archidiskodon* of the southern and south temperate zones, *Parelephas* of the intermediate and north temperate zones, and *Mammonteus*[1] of the northerly and circumpolar zones.

It is probable that these northerly or woolly mammoths were the first mammalian fossils of northern Eurasia to be discovered and recognized as extinct. The earliest descriptions are naturally lost in obscurity. Of this early period Falconer (1846, pp. 11 and 12) writes:

> Next, in regard to the establishment of the species.—The fossil remains of the Mammoth had, during ages, attracted more or less attention in every country in Europe, having been found in England and in all parts of the Continent, from Italy to Siberia. But it was only towards the close of the last century that definite notions as to the species, were arrived at. Pallas, who had better opportunities for determining the point than any of his contemporaries, upon the perfect remains so commonly met with in Russia, erroneously considered the fossil teeth to be identical with those of the Indian species. A great advance was made in the inquiry through the discovery, by Peter Camper, of the specific difference between the teeth of the Asiatic and African Elephants [Footnote: 'P. [A]. Camper, Déscript. Anatom. d'un Eléphant male, p. 16.'], when Blumenbach and Cuvier almost

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[1] [The generic name *Mammonteus* (Mammonteum Camper, 1788, pp. 251, 259; Osborn, 1924.633, p. 2) for the northern Mammoth is of doubtful validity as Camper's description has reference to an animal in America and not to the Mammoth, moreover he used the word "mammonteum" in an adjectival sense. Dr. A. Tindell Hopwood in his recent (1935) memoir on the "Fossil Proboscidea from China," p. 97, adopted the generic term *Mammuthus* Burnett, 1830, genotype *Mammuthus borealis*. For a historical account of the names applied to the Mammoth and the Mastodon, see Chapter XXI below on Nomenclature.—Editor.]

simultaneously entered upon the investigation, and arrived at the same result, viz., that the Mammoth was an extinct form, differing from both of the existing species. Struck with the length of the cranium, and of the incisive sheaths in the Mammoth, as represented in the figures of Messerschmidt's specimen attached to Breyne's excellent remarks in the Philosophical Transactions [Footnote: 'Phil. Trans. vol. xl. 1738 [1741], p. 124.'], and connecting these peculiarities with the great width of the crown, and the narrowness and number of the plates in the fossil grinders, Cuvier was conducted to his first happy conclusion. The probability of a similar difference characterizing the species in other fossil genera, flashed across his mind, and opened to him new views respecting the theory of the earth. Great and important were the results; and after they had been achieved, the illustrious Anatomist reverted, in terms of the liveliest acknowledgment, to the long neglected figures of Messerschmidt, which had helped him to the first idea [Footnote: 'Cuvier, Oss. Fossil. tom. i. p. 178.'].

Sceleto Elephantino Tonnæ, 1695, confused with the Mammoth, Blumenbach, 1799

In 1695 Ludolf described the mammoth of Siberia. The earliest account of the fossil elephant in Germany is that of Wilhelmus Ernestus Tentzelius[1] (Phil. Trans. Roy. Soc., London, 1698, Vol. XIX, pp. 757–776):

> Tentzelius (Tentzel), 1698, pp. 757, 758.—III. *Wilhelmi Ernesti Tentzelii Historiographi Ducalis Saxonici Epistola de Sceleto Elephantino Tonnæ.* . . . Tonna inter Thuringiæ Dinastias haud postrema, . . . quorum alter appellatur Burg-Tonna, . . . quam effodientes mense Decembri superioris anni ossa quædam maxima reperiunt, . . . Prior sententia mihi cumprimis placet, quam ita defendere aggredior, ut primo ostendam, sceleto nostro omnia convenire, quæ ad vera elephanti ossa requiruntur; deinde evincam, non esse minerale fossile, sed animale petrefactum; denique inquiram, quomodo in has terras ipsumque locum pervenerit Elephantus.

This classic or original description of the 'elephant' discovered in a sand-pit at Burgtonna near Gotha, Thuringia, is of the skeleton referred to by Blumenbach in his type description of *Elephas primigenius* cited below, but this is not to be regarded as the type specimen.[2] It is addressed "*ad Virum toto orbe celeberrimum Antonium Magliabechium, Serenissimi Magni Hetruriæ Ducis Bibliothecarium & Consiliarium.*" Following the dedication Tentzelius gives a description of the discovery in the month of December, 1695; he fully describes parts of the teeth, skull, and skeleton found, and discusses local opinion as to whether they were the remains of a petrified elephant or of a fossil unicorn (p. 758); he cites the descriptions of John Ray, of Pliny, and of Aristotle to prove that the specimen from Tonna was an elephant; he assures the most learned and celebrated Magliabechi that the bones and teeth correspond point by point with those of the elephant; he proceeds with a comparison with the Ceylon elephant (p. 771) and with Pigafetta's descriptions of the African elephant; he cites Steno as to the habits and distribution of the Indian and African elephants, and concludes that the Burgtonna remains (p. 774) constitute proofs of the Flood, of the rise of the waters even to the height of the Thuringian mountains.

The Editor of this classic contribution to the Philosophical Transactions, (Gothae, 1696, p. 776), concludes:

> *The Author of this Letter has favour'd the Royal Society with some pieces of the Bones of the Sceleton of this Elephant,* viz. *part of the Skull, wherein appear its Cells, some of the Teeth both of those that grind, and such as are called Elephants Teeth or Ivory, with some other pieces of Bones, all which they found agreable to his Description, and ordered they should be carefully preserv'd in their Repository.*

Thirty-one years later Sir Hans Sloane (Phil. Trans., 1729, pp. 457–494, 497–514) refers to this discovery as follows (p. 508):

> The Skeleton of an Elephant which was dug up in a Sand-pit near *Tonna* in *Thuringen*, in 1695, is one of the most curious, and also the most compleat in its Kind, forasmuch as they found the whole Head, with four Grinders, and the two *dentes exerti*, or Tusks, the Bones of the fore and Hind-legs, one of the Shoulder-bones, the Back-bones, with the Ribs, and several of the

---

[1] Karl von Zittel ("History of Geology and Palæontology," 1901, p. 134) refers to this discovery as follows: "The skeleton found at Burgtonna in 1696 was one of the most famous discoveries, as it gave rise to a dispute between Ernst Tentzel and the medical faculty in Gotha. The other professors saw in the large bones only sports of nature, but Tentzel proved to their discomfiture that the bones were real, and had belonged to elephants."

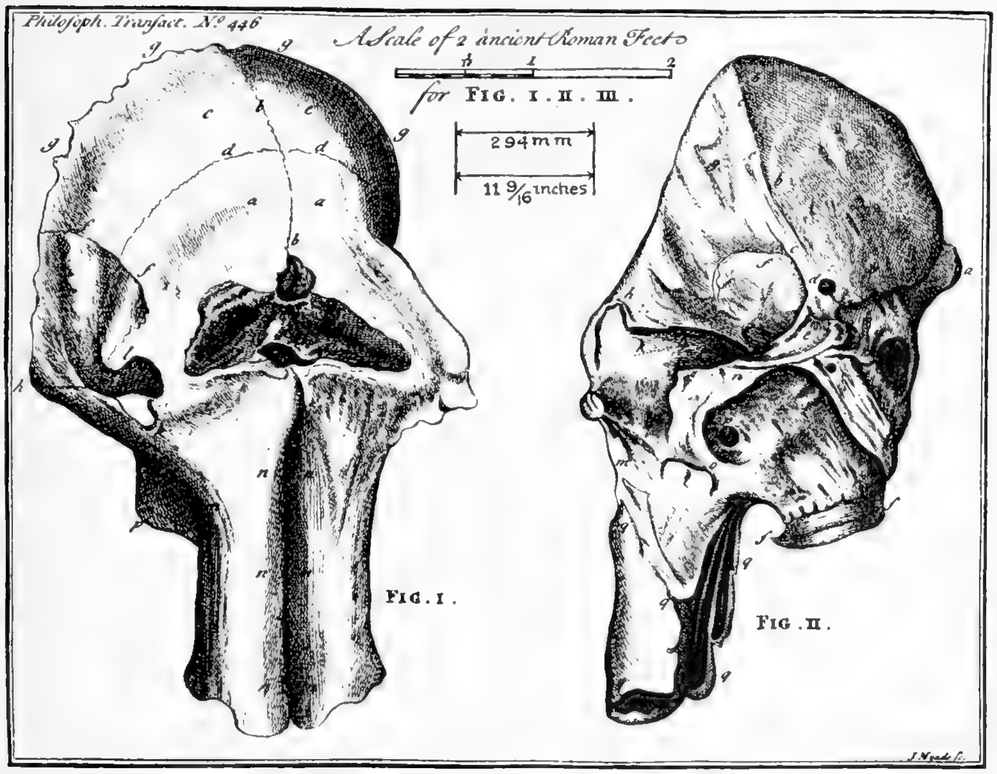
[2] The Burgtonna skeleton belongs (Dietrich, 1930) to *Elephas antiquus*; while first mentioned, it is not the type. In defining and describing *Elephas primigenius* (1799), Blumenbach had in mind the true mammoth of Siberia and Germany.

Vertebræ of the Neck. But the whole hath been so accurately described by *Wilhelmus Ernestus Tentzelius*, Historiographer to the Dukes of *Saxony*, in a Letter to the learned *Magliabechi*, printed in the *Philosophical Transactions* [Footnote: 'No. 234, *pag.* 737.'], that it is needless to add any thing, the rather, as that Gentleman was pleased to oblige the *Royal Society* with some Pieces of the Bones of this Elephant, with Part of the Skull, wherein appeared its Cells, some of the Grinders, and Part of the *dentes exerti*; all which being produced at a Meeting of the *Royal Society*, were found exactly agreeable to his Description, and ordered to be carefully preserved in their Repository. [See footnote 1 below.]

BREYNE'S DESCRIPTION (1735) OF THE ELEPHAS PRIMIGENIUS OF SIBERIA

A second scientific description of the mammoth, from the river Indigirka, Siberia, with figure of the skull (Fig. 991), was a communication to Sir Hans Sloane, President of the Royal Society, by John Phil. Breyne, in a letter dated "Dantzick, Sept. 28, 1735," from which the following excerpts are made (Phil. Trans. Roy. Soc., London, 1741, Vol. XL, pp. 124–138).

> *A Letter from* John Phil. Breyne, *M.D.F.R.S.* to *Sir* Hans Sloane, *Bart. Pres. R.S.* with *Observations, and a Description of some* Mammoth's *Bones dug up in* Siberia, *proving them to have belonged* to Elephants.
>
> *Sir,*
>
> Your very learned and instructive Accounts of *Elephants* Teeth and Bones found under Ground, I saw with great Pleasure in the *Philosophical Transactions*, N° 403. and 404. In the same Year, to wit 1728, I was busied about the very same Matter, especially to prove, that the extraordinary large Teeth and Bones found under Ground, and digged up in several Places of *Siberia*, by the Name of *Mammoth's*, or *Mammut's*, Teeth and Bones, were,
>
> I. True Bones and Teeth of some large Animals once living; and,
>
> II. That those Animals were *Elephants*, by the Analogy of the Teeth and Bones, with the known ones of *Elephants*.
>
> III. That they were brought and left there by the universal Deluge. I made likewise several useful Inferences about This Matter.
>
> At the same time there flourished in our City a Society of some learned and ingenious Gentlemen, who met once a Week in a certain Place: In one of those Meetings in the Month of *March*, I had the Honour to read and communicate my Thoughts and Observations about this Subject; which, as I believe, they will not be disagreeable to you, I have translated into the *English* Tongue, and joined to this present Letter.
>
> After that, *viz.* in the Year 1730, Dr. *Messerschmidt* returned to *Dantzick*, from his Travels thro' *Siberia*, and was pleased to communicate to me some curious Draughts of a Part of a Skeleton, to wit, of a very large Skull, *Dens exsertus & molaris*, with the *Os femoris*, belonging to the Animal commonly called *Mammoth*, found in *Siberia*; by which our Assertion, that the Teeth and Bones, called in *Rusland Mammoths* Bones, are the true Teeth and Bones of *Elephants*, is not only, as you wished in your first Account, put in a greater Light, but, if I am not mistaken, demonstrated beyond all Doubt.



THE MESSERSCHMIDT CRANIUM OF SIBERIA. COPIED BY CUVIER

Fig. 991. Cranium of the mammoth, as described and figured by Dr. John Phil. Breyne in the Philosophical Transactions of the Royal Society of London, 1737 (printed in 1741, Vol. XL, No. 446, pp. 124–138, Pl. I, figs. I, II). One-sixteenth natural size. This classical Breyne figure of the mammoth cranium was reproduced by Cuvier in his "Ossemens Fossiles" of 1806 and used as the basis of comparison of the *E. primigenius* cranium with the crania of *E. africanus* and *E. indicus* (Cuvier, 1806.1, Pl. XXXIX, fig. 1, and Pl. XLI, figs. 9.I, 10.A, 11.F.—our Fig. 992). Made by Brandt (1833.1,[2] p. XII) the type of *Elephas giganteus*.

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[1] Hopwood (letter, May 20, 1930) finds that the Royal Society records (November 3, 1697) reveal that the Tentzel specimens were assigned the number 120B in various lists up to the year 1712: "It would seem, then, as though the specimens were lost between 1733 and 1763." Fragments of the Burgtonna skeleton of *Elephas antiquus*, incisive tusks and other remains, are still preserved in the Gotha Museum (*fide* Dietrich, letter, April 14, 1930—see Chap. XIX, the Loxodontinæ, p. 1181).

[2] [See footnote on page 1136 regarding the date of description as 1832.—Editor.]

Observations on the Mammoth's Bones and Teeth found in Siberia: *Read in a Meeting of some learned Gentlemen at* Dantzick *in the Year* 1728. *by* J. P. B.

> That learned and curious Gentleman *Dr. Daniel Gottlieb Messerschmidt,* who was sent some Years ago, by his late *Czarish* Majesty, *Peter the Great,* into *Siberia,* to search after the Products of Nature in this uninhabited and cold Country, was pleased to send me in the Year 1722, amongst some other Samples of Natural Things out of *Siberia,* two very large Teeth, called there, *Mammoth* or *Mammut's* Teeth, with the following Inscription: *Dens molaris, ut videtur, diluvianus, Belluæ cujusdam hactenus incognitæ, nisi pro Elephantino habendus sit, cujus jam penes Te esto arbitrium, Russis* Mammoth, *repertus in Montium altissimis jugis ad Thomam fluvium. Alterum est frustum aliud Eboris Denti exerto Elephantis non absimile, ab aliis repertum in Thomæ Montibus.*

[p. 137] The bones of this Skeleton, with the Ribs, *Vertebræ,* and others thereto belonging, were found in the sandy Side of a steep Hill, on the Eastern Bank of the River *Indigirska* [Indigirka], which falls into the Northern Ocean, not far from the Mouth of the Rivulet *Wolockowoi ruçzei.*

NAMES SUCCESSIVELY APPLIED TO THE MAMMOTH

Among the first descriptions of species, to which Latin names were appended, are the following:

1696 MAMMONTOVA KOST [*Mammotovoi kost* in Ludolf, 1696.1,p. 92] (probably derived from the Tatar word *mama* signifying earth and *kost* signifying ivory =tusks) Ludloff [Ludolf]. Cited by Fischer de Waldheim, "Oryctographie," III, Fossiles du Gouvern. de Moscou, 1830–1837, p. 111.

"I. Elephant. 1. Le Mammont . . . *Elephas mammonteus.* m. [Fischer, 1830–1837] . . . Je conserve la dénomination la plus ancienne, et je n'écris point *Mammouth* parceque ce nom n'a pris origine que par corruption ou une fausse lecture du mot Mammont [Footnote: Маммонтъ en russe; le *Yer* (ъ) terminal a été changé par les anglais en h et le *n* a été pris pour un u. D'ailleurs Ludloff est le premier qui en parle (1696) et appelle ces ossemens Mammontova Kost et justifie ainsi ma dénomination systématique.']."

Cited by Cuvier (Ann. Mus. VIII, 1806, p. 45): "C'est sous le nom de *cornes de mammont, mammontova-kost,* qu'ils désignent les défenses."

1788 MAMMONTEUM Camper (Nova Acta Acad. Sci. Imp. Petropol. Communicanda, II, 1787, p. 251).

". . . os humanum petrifactum, aut fossile, etiamsi Mammonteorum, Elephantorum, . . . Adserere ex eodem principio audeo Mammonteum animal extinctum non modo esse, sed nullam omnino habuisse cum Elephanto similitudinem!"

1796 Mammoth, Cuvier [MS.] "Mémoire sur les espèces d'Eléphans tant vivantes que fossiles," etc.

(See Falconer, 1868, Vol. II, pp. 158, 159): "Whatever may have been the approximation previously made by Merk or Blumenbach towards a distinction of the Mammoth from the two living species, Cuvier was undoubtedly the first to characterize the extinct species with exactness, in his joint memoir with Geoffroy, under the name of *Elephas Mammoth,* in the year 1796 [Footnote: 'Mém. de l'Institut, 1re Classe, tom. ii.']. In the same year, he read a memoir at the first public meeting of the 'Institute,' but which was not published until 1806 [1799], in which the diagnostic marks are very pointedly expressed under the designation of *Elephas Mammonteus*: 'Maxillâ obtusiore, lamellis molarium tenuibus, rectis,' as distinguished from *Elephas Indicus*: Fronte plano-concava, lamellis molarium arcuatis, undatis.' Cuvier connected these dental and mandibular distinctions with others yielded by Messer Schmidt's [Daniel Gottlieb Messerschmidt—see Breyne, 1737 (1741), Pls. I, II, III] figure of the skull of the Mammoth, and combined the whole in the extended specific definition of the extinct form, which appeared in his memoir of 1806—'L'Éléphant à crâne allongé, à front concave, à très longues alvéoles des défenses, à machoire inférieure obtuse, à mâchelières plus larges, parallèles, marquées des rubans plus serrés.'[1] He abandoned the name *E. Mammonteus* of his memoir of 1796 [1799], and adopted the designation of *Elephas primigenius,* proposed by Blumenbach [Footnote:

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[1] Cuvier's definition (1806.1, p. 264) "*L'éléphant à crâne allongé,* . . . que nous nommons *éléphant fossile* (*elephas primigenius,* Blumenb.), est le *mammont* des Russes," in contrast to (*op. cit.*, p. 262) "*L'éléphant a crâne arrondi,* . . . (*elephas africanus*)," also to (*op. cit.*, p. 263) "*L'éléphant a crâne allongé* . . . (*elephas indicus*)," is clearly illustrated in his Plates XXXIX and XLI, in which he places Breyne's figure of *Elephas primigenius* with his own figures of *Elephas indicus* and *Elephas africanus.* This definition was literally repeated in the three successive editions of the "Ossemens Fossiles" (1812, 1825, 1834) and exerted a profound influence on other palæontologists, for it was not until 1825 that the mammoth of the south (*Elephas meridionalis*) was named by Nesti, in contrast to this elephant of the north (*Elephas primigenius*) with curved tusks, also to *Elephas antiquus* Falconer (1847), with straight tusks.

'Voigt's Mag. 1803, Band v. p. 16.'], in 1803, which is that now generally accepted among palæontologists [see Blumenbach, 1799, p. 697, for first use of name *Elephas primigenius*]. To this normal form, as already stated, Cuvier referred all the fossil remains of Elephants found over the whole of Europe, in Northern Asia, and in North America, however much at variance with the terms of his definition; and to the last he clung to the specific unity of the 'Éléphant fossile' with the jealous partiality of a discoverer for the earliest results of his most cherished labours.

The distinctive characters in the molars of the Mammoth, as compared with those of the existing Indian Elephant, upon which Cuiver relied, may be expressed in the following terms:—1. Great narrowness or compression and approximation of the crown-ridges, involving both a larger number in the same length of crown and in triturating use at the same time. 2. Tenuity of, and absence of crimping in, the enamel-plates. 3. Greater width of the molar-crowns, both absolutely and relatively to their length."

1796 *Elephas mammonteus* Cuvier (1796 [MS.], published August-September, 1799).

(Cuvier, 1799, p. 21): "les caractères distinctifs des quatre espèces que ja'i décrites dans le cours de ce mémoire. Les voici:

Espèces qu'on sait exister.

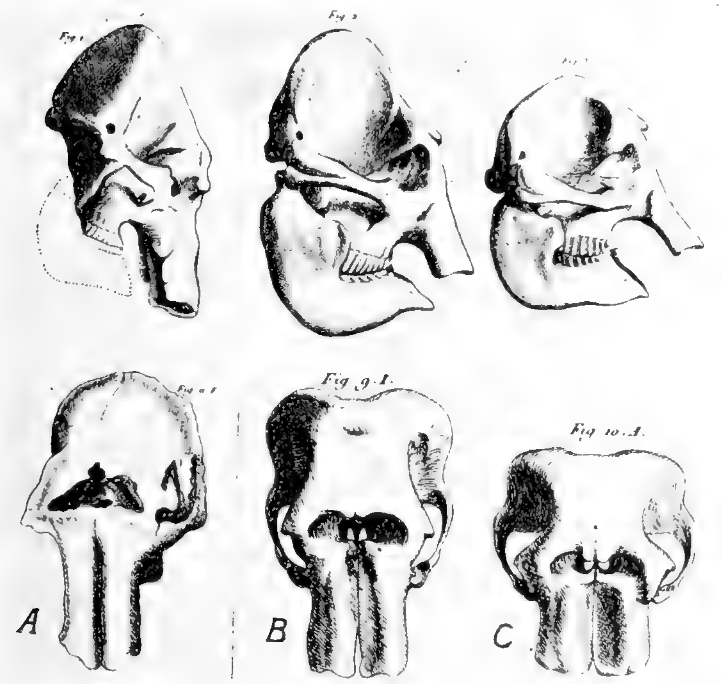
Elephas capensis [Cuv. = *Loxodonta africana* Blum.], *fronte convexâ, lamellis molarium rhomboïdalibus.*

Elephas indicus [Linn. = *Elephas indicus* Linn.], *fronte plano-concavâ, lamellis molarium arcuatis undatis.*

Espèces qu'on ne connôit que fossiles.

Elephas mammonteus [Cuv. = *Elephas primigenius* Blum.], *maxillâ obtusiore, lamellis molarium tenuibus rectis.*

Elephas americanus [Kerr = *Mastodon americanus* of the present Memoir], *molaribus multi-cuspidibus, lamellis post detritionem quadri-lobatis.*"



A Fig. 1. Fig. 11 F.

L'éléphant à crâne allongé, à front concave, à très-longues alvéoles des défenses, à mâchoire inférieure obtuse, à mâchelières plus larges, parallèles, marquées de rubans plus serrés, que nous nommons *éléphant fossile* (*elephas primigenius*, Blumenb.), est le *mammont* des Russes.

B Fig. 2. Fig. 9. I.

L'éléphant à crâne allongé, à front concave, à petites oreilles, à mâchelières marquées de rubans ondoyans que nous appelons *éléphant des Indes* (*elephas indicus*), est un quadrupède qu'on n'a observé d'une manière certaine qu'au-delà de l'Indus.

C Fig. 3. Fig. 10. A.

L'éléphant à crâne arrondi, à larges oreilles, à mâchelières marquées de losanges sur leur couronne, que nous appelons éléphant d'Afrique (*elephas africanus*), est un quadrupède dont la seule patrie connue est jusqu'à présent l'Afrique.

Fig. 992. Comparison of crania of *Elephas* [*Mammonteus*] *primigenius*, *E. indicus*, and *E.* [*Loxodonta*] *africanus*, after Cuvier, 1806.1, Pl. 39 (II), figs. 1, 2, 3, and Pl. 41 (IV), figs. 9.I, 10.A, and 11.F. One thirty-seventh to one-twentieth natural size.

Figures 1 above and 11.F below are two views of the same skull (Messerschmidt, see Fig. 991), first figured by John Philip Breyne (1741.1, Pl. I), subsequently figured by Cuvier (1806.1, Pl. 39, fig. 1, and Pl. 41, fig. 11.F), and finally made the type of *Elephas giganteus* by Brandt (1833.1,[1] p. XII).

The descriptive captions at the right are taken from Cuvier (*op. cit.*, 1806.1, p. 262 (*E. africanus*), p. 263 (*E. indicus*), and p. 264 (*E. primigenius*).

Cuvier's designations were: "le Mammouth" (Review, Cuvier, an 3 [1795], p. 90'); *Elephas mammonteus* Cuvier, 1796, MS., published 1799, Fructidor, an VII [August-September, 1799], p. 21; not until 1806 did he adopt the specific name of *Elephas primigenius* Blumenbach.

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[1] [See footnote on page 1136 regarding the date of description as 1832.—Editor.]

1799 *Elephas primigenius* Blumenbach ("Handbuch der Naturgeschichte," Sechste auflage, p. 697).[1]

3) Von einem ungeheuer grossen Elephanten (*Elephas primigenius?*) [die vermeinten Riesenknochen** unsrer ehrlichen Alten]; unter andern auch in Menge in Deutschland***). So z. B. das berüchtigte Elephantengerippe das 1695 bey Burg-Tonna im Gothaischen ausgegraben worden etc.

**s. Voigts Magazin. V. B. I. St S. 16 u. f.

***(Kriegsr. Merk) *lettres sur les os fossiles d'elephans et de rhinoceros qui se trouvent en Allemagne &c.* I-III. St. Darmst. 1783 u. f. 4.

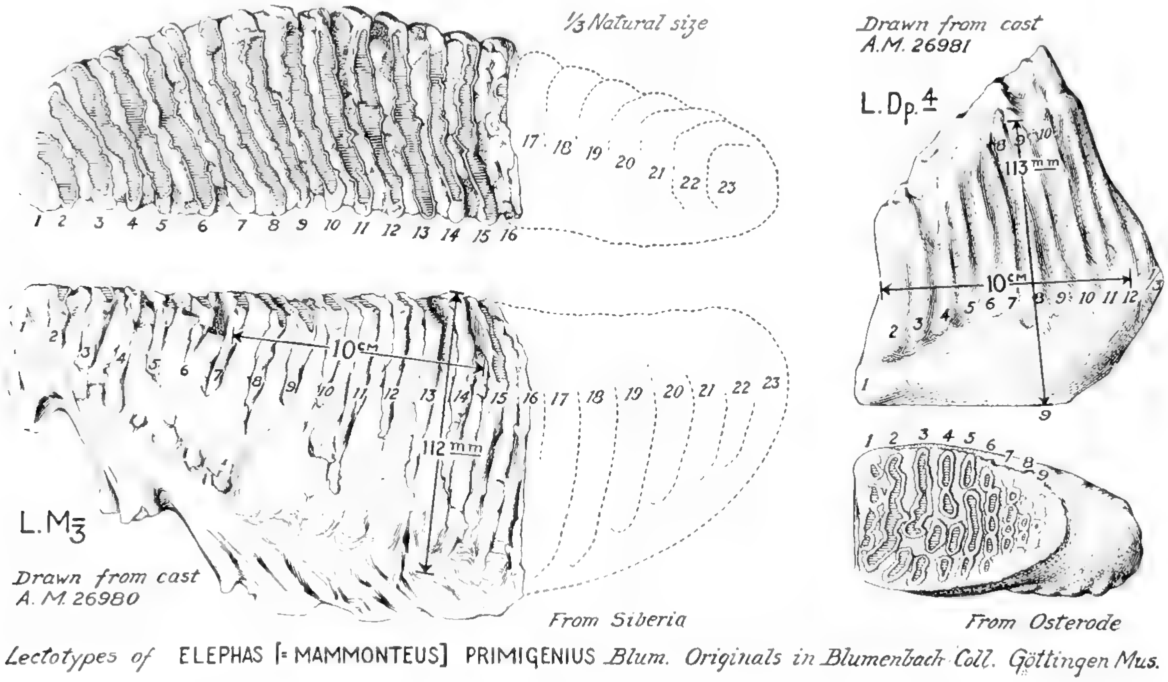

Fig. 993. Lectotypes of Elephas [Mammonteus] primigenius Blumenbach
After casts furnished by Director R. W. Hoffmann, Zoologische Institut der Universität Göttingen

(Left) Siberian lectotype (l.M$_3$) from the Blumenbach Collection of the Zoological Institute of the University, Göttingen (cast Amer. Mus. 26980). Described by Dietrich (letter, July 4, 1930) as follows: "Es handelt sich bei dem Zahn aus Sibirien M$_3$ sin., dist. nähere Provenienz und Acquisition unbekannt."

Interpreted by Osborn as a portion of a third inferior molar of the left side, namely, l.M$_3$, with 16 of the anterior ridge-plates preserved, of which at least 15 are more or less fully worn; 8 posterior ridge-plates are missing; 7½ ridge-plates in 100 mm. on the convex internal side. Height of 14th ridge-plate (tallest) 112 mm. Drawn in crown and internal aspects.

(Right) Osterode lectotype (l.Dp^4) from the Blumenbach Collection of the Zoological Institute of the University, Göttingen (cast Amer. Mus. 26981). Determined by Dietrich (letter, July 4, 1930) as follows: "Der Zahn aus Osterode ist ein dritter oberer Milchmolar (m^3 [sin.]); er ist Kurz beschrieben in Annalen der Physik, hersg. v. Gilbert 15, [45], 1813, p. 427/28. Er ist typisch für unsere spätglacialen Mammute. Blumenbach dürfte ihn vor dem sibirischen Zahn erworben haben, so dass dieser m^3 aus Osterode als Type specimen des *Elephas primigenius* Blumenbach, 1799, zu betrachten ist, wenn man nicht vorzieht, das Adams-Tilesius'sche Skelet zum Typus der Spezies zu machen."

Interpreted by Osborn as belonging on the left side, namely, as an l.Dp^4, with 12⅓ ridge-plates; 10–11 ridge-plates on the convex external side in 100 mm.

The above passage in which Blumenbach, the pioneer of mammalian palæontology in Europe, refers to the discovery near "Burg-Tonna" in the year 1695, is regarded as the type description of *Elephas primigenius* Blum.; unfortunately the "Burg-Tonna" skeleton, now in the Gotha Museum, belongs to '*Elephas antiquus*.' On the advice of Dietrich (1930),[2] we may select as *lectotypes* of *E. primigenius*: (1) A grinder from Siberia in the Blumen-

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[1] The priority of publication of Blumenbach's species *Elephas primigenius* (spring of 1799) is established over Cuvier's *Elephas mammonteus* (August-September, 1799). Sherborn writes (letter, May 16, 1930): "It is rare that one finds so perfectly clear a statement in these old reviews. This comes from Göttingische Anzeiger von gelehrten Sachen, 18 Dec. 1799, p. 2057. . . . 'Von dem Blumenbachischen Handbuch der Naturgeschichte ist schon vorige Ostern die 6te Auflage auf 708 S. herausgekommen.'"

[2] See letter of February 8, 1930, from W. O. Dietrich, Geologisch-Paläontologisches Institut und Museum der Universität Berlin: "Das zoologische Institut der Universität Göttingen besitzt nach Auskunft durch den Direktor Prof. Dr. R. W. Hoffmann nur zwei Stücke fossiler Elefanten aus der Zeit Blumenbachs 1. Einen Molar mit der Bezeichnung *Elephas primigenius.* Diluvium, Sibirien. Coll. Blum. 2. Einen Molar mit der Bezeichnung Osterode (Harz) 1808."

bach Collection of the Göttingen Museum, cast Amer. Mus. 26980; also (2) a molar from Osterode (Harz), Germany, original in same Museum; cast Amer. Mus. 26981 (see Fig. 993 on opposite page.)

Blumenbach's type description is in a rare document; no figure accompanies it; the sixth edition (1799) of his "Handbuch der Naturgeschichte," in which the above type description appears, attracted the attention of the French naturalist Soulange Artaud, who visited Blumenbach and translated it under the title "Manuel d'Histoire Naturelle," 1803. In the manuscript of the French volume, Blumenbach inserted the name and definition of *Elephas primigenius*, consequently the species *Elephas primigenius* is of date 1799, 1803.

1799 *Elephas mammonteus* Cuvier (MS., 1796, published August-September, 1799).

> (Letter, Messieurs Emile Picard and A. Lacroix, April 15, 1930): "Nous n'avons pas trouvé trace d'une telle publication, mais il est évident que le mémoire était écrit avant le 21 janvier 1796. . . . Ce mémoire a été lu à la classe des sciences de l'Institut national, le pluviôse, an IV (21 janvier 1796). Cette lecture est mentionnée au procès-verbal de la séance (Procès-verbaux des séances de l'Académie tenues depuis la fondation de l'Institut jusqu'au mois d'août 1835, t.I page 6). Réservé pour être imprimé, il a été publié dans le tome II des Mémoires de l'Institut national, en Fructidor, an VII (août-septembre 1799)."
>
> Cited by Tilesius (1815, p. 470).

1806–1834 *Elephas primigenius* Blum., Cuvier ("Oss. Fos.").
1807 *Elephas primævus* Blumenbach (in M. Adams; translation (1808) from the French by Sir Joseph Banks, Phil Mag., XXIX, London, p. 152; cited by Tilesius, 1815, p. 452.
1807 *Elephas Mammouth* Link, Beschr. Nat. Samml. Univ. Rostock (4) 1807,3 (*fide* Sherborn, 1928, Pt. XV, p. 3845).
1815 *Elephas primordialis* Blumenbach (in Tilesius, 1815, p. 470).
1820 *Elephas jubatus* Schlotheim.
1829 *Elephas mammonteus* Fischer de Waldheim.
1829 *Elephas paniscus* Fischer de Waldheim.
1829 *Elephas periboletes* Fischer de Waldheim.
1829 *Elephas pygmaeus* Fischer de Waldheim.
1829 *Elephas campylotes* Fischer de Waldheim.
1829 *Elephas Kamenskii* Fischer de Waldheim.
1830 *Mammuthus Borealis* Burnett.
1832 *Mammut Sibiricum* (in von Meyer, Palaeologica, p. 64).
1832 *Elephas brachyramphus* Brandt ('Adams skeleton').
1832 [*Elephas*] *homotaphrus* Brandt.
1832 *Elephas giganteus* Brandt.
1832 *Elephas commutatus* Brandt.
1832 *Elephas stenotoechus* Brandt.
1832 *Elephas platytaphrus* Brandt.
1832 *Elephas affinis* Brandt.
1834 *Elephas macrorynchus* Morren.
1835 *Elephas odontotyrannus* Eichwald.
1837 Dicyclotherium E. Geoffroy St. Hilaire, Compte Rend. Acad. Sci., IV., No. 4, pp. 119, 120, fig. 1.
1839–1864 *E.* [*Elephas*] *primigenius sibiricus* de Blainville (Atlas, "Ostéographie," Pl. iii, 1845), also Depéret and Mayet, 1923, pp. 183–201.
1839–1864 *E.* [*Elephas*] *primigenius germanicus* de Blainville (Atlas, "Ostéographie," Pl. iii, 1845).
1848 Cheirolites von Meyer (in Bronn's Handb. einer Gesch. d. Natur., III, Index Pal., p. 286).
1850 Synodontherium Costa, "Palæont. del Regno di Napoli," Atti Acad. Pontaniana, V, Pt. I, p. 271, Tav. iii, figs. 1–4.
1885 Polydiskodonten Pohlig, p. 1027.
1888 Polydiskodon Pohlig, Nova Acta K. Leop.-Carol. Deutsch. Akad., LIII, p. 252.
1913 *Elephas primigenius comune* Issel, 1879 (in Zuffardi, 1913, p. 136)[1].

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[1] [Zuffardi (1913, p. 136) attributes this subspecies to Issel (1879) who, in describing two molars from Camporosso near Ventimiglia, in the region of S. Andrea, Italy, states (p. 160) that these two teeth belong to the "comune *Elephas primigenius*," using comune in the adjectival sense.—Editor.]

Out of this host of names, barbaric, semibarbaric, non-technically Latinized or technically Latinized, applied to the northern mammoth between the years 1696 and 1888, the species *Elephas primigenius* of Blumenbach alone survives and is accepted in the scientific literature of the entire world.

As to the genus, nearly a century and a half of research since 1799, when Blumenbach assigned the name *Elephas primigenius*, demonstrates that the woolly mammoth belongs not to *Elephas*, but to a genus of its own, distinct by all the canons of nomenclature from the true modern *Elephas*. Technically the choice of a generic name rests between the inappropriate *Dicyclotherium* Geoffroy, 1837, *Cheirolites* von Meyer, 1848, *Synodontherium* Costa, 1850, and the first really appropriate generic name *Polydiskodon* Pohlig, 1885–1888. As Linnæus chose many of his generic names, i.e., from those previously ill defined or not technically proposed, so in the present Memoir we may go back to the eminently appropriate and distinctive generic term *Mammonteum*, 1788[1] (changing the orthography to *Mammonteus*).

NATIVE SIBERIAN ORIGIN OF THE WORD MAMMUT

IDES, 1706.—The following is cited (pp. 25, 26) from the book of travels "Three Years Travels from Moscow over-land to China: thro' Great Ustiga, Siriania, Permia, Sibiria, Daour, Great Tartary &c. to Peking" of Eberhard Ysbrant Ides, who was sent ("by the most Serene and most Potent Soveraign Czar, and Great Prince, Peter Alexewitz") on an embassy to the King of China in 1692, returning in the year 1695.

> Amongst the Hills which are situate North-East of, and not far from hence [village of Makofskoi near the river Keta], the *Mammuts Tongues and Legs are found*: as they are also particularly on the Shoars of the Rivers *Jenize, Trugan, Mongamsea, Lena,* and near *Jakutskoi,* to as far as the Frozen Sea. In the Spring when the Ice of this River breaks, it is driven in such vast quantities, and with such force by the high swollen Waters, that it frequently carries very high Banks before it, and breaks off the tops of Hills, which falling down, discover these Animals whole, or their Teeth only, almost frozen to the Earth, which thaw by degrees. I had a Person with me to *China,* who annually went out in search of these Bones; he told me as a certain truth, that he and his Companions found a Head of one of these Animals, which was discovered by the fall of such a frozen piece of Earth. As soon as he opened it he found the greatest part of the Flesh rotten, but it was not without difficulty that they broke out his Teeth, which were placed before his Mouth as those of the Elephants are; they also took some Bones out of his head, and afterwards came to his Fore-foot, which they cut off, and carried part of it to the City of *Trugan,* the Circumference of it being as large as that of the wast of an ordinary Man. The Bones of the Head appeared somewhat red, as tho' they were tinctured with Blood.
>
> Concerning this Animal there are very different reports. The Heathens of *Jakuti, Tungust,* and *Ostiacki,* say that they continually, or at least by reason of the very hard Frosts, mostly live under ground, where they go backwards and forwards; to confirm which they tell us, That they have often seen the Earth heaved up when one of these Beasts was on the March, and after he was past the place sink in, and thereby make a deep Pit. They further believe, that if this Animal comes so near to the surface of the frozen Earth as to smell or discern the Air, he immediately dies, which they say is the reason that several of them are found dead, on the high Banks of the River, where they unawares came out of the Ground. This is the Opinion of the Infidels concerning these Beasts, which are never seen.
>
> But the old *Siberian Russians* affirm that the *Mammuth* is very like the *Elephant*; with this only difference, that the Teeth of the former are firmer, and not so straight as those of the latter. They also are of Opinion, that there were Elephants in this Country before the Deluge, when this Climate was warmer, and that their drowned bodies floating on the surface of the Water of that Flood, were at last wash'd and forced into Subterranean Cavities: But that after this *Noachian* Deluge, the Air which was before warm was changed to cold, and that these bones have lain frozen in the Earth ever since, and so are preserved from putrefaction till they thaw, and come to light; which is no very unreasonable conjecture. Tho' it is not absolutely necessary that this Climate should have been warmer before the Flood, since the Carkasses of the drowned *Elephants* were very likely to float from other places several hundred Miles distant, to this Country, in the great Deluge which covered the surface of the whole Earth. Some of these Teeth, which doubtless have lain the whole Summer on the Shoar, are intirely black and broken, and can never be restored to their former condition; but those which are found in good case, are as good as

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[1] [See footnote on page 1117 above regarding the doubtful validity of the genus *Mammonteus*.—Editor].

Ivory, and are accordingly transported to all parts of *Muscovy*, when they are used to make *Combs*, and all other such like things, instead of *Ivory*. The above mentioned Person also told me, that he once found two Teeth in one Head that weighed above 12 *Russian Pounds*, which amount to 400 *German Pounds*; So that these Animals must of necessity be very large, tho' a great many lesser Teeth are found. By all that I could gather from the Heathens, there's no Person ever saw one of these Beasts alive, or can give any account of it's shape; so that the most that is said on this subject arises from bare conjecture only.

HOWORTH, 1882.1, PP. 30-32.—Howorth has given an excellent account of the name "Mammoth" in his article of 1882 in "The Field Naturalist," page 30, from which we quote the following:

In the year 1666, a learned Dutchman, named Cornelius Witzen, who became burgomaster of Amsterdam, visited Moscow. From the materials he there collected, and from various other sources, he compiled a famous work which he afterwards published at Amsterdam, entitled *Noord en Oost Tatarye* [Witsen, Nicolaes, 1692.1]. . . . It has never been translated into any other western language, and remains still buried to a large part of the scientific world in the original Dutch.

In this work *the name* Mammoth appears for the first time, and is there written Mammout. Witzen describes how numbers of elephants' teeth are found on the banks of the Siberian rivers, and says 'by the Inlanders,' *i. e.* the Russian settlers in Siberia, 'these teeth are called Mammouttekoos, while the animal itself is called Mammout.'—(*Op. cit.* ed. 1785, 742). In the *Grammatica Russica* of Ludolf, published in 1696, p. 96, these bones are called Mammotovoi Kost. Among the Russians the name is invariably written Mamont—Bull. St. Pet. Acad. x. 258. The insertion of the *n* in this form is no doubt a corruption, although an old corruption, since Captain J. B. Müller, in 1716, says 'the inhabitants (*i. e.* the Russians) call the beast Mamant.' Schiefier explains it as due to a confusion made by the peasants between the name Mammoth and that of Saint Mamas, called Mamant by the Russians, to whom the second of September is dedicated in the Russian calendar—(*id. note* 2). Pallas derived Mammoth from the word Mama, which he says means earth in the Tartar tongue, but as Baer says, in the great Polyglot, edited by Pallas himself, in which the various dialects of Tartar are illustrated, no such name as Mama occurs as a synonym for earth. Baer himself suggests that the name is derived from ma, which means the earth in various Fin dialects, while mut or muit is the name by which the mole is still known to the Esthonians, whence he explains Mammoth as meaning the earth-mole—(Bull. St. Pet. Acad. x. 258). Not only is this an inconsequential etymology, since all moles live under ground, but the notion of finding an explanation of the name among a people so far removed from Siberia as the Esthonians is quite fanciful. Klaproth was told by the Buriat and Mongol Lamas whom he consulted in 1806, that the name was of Tibetan origin. This again is a most unlikely quarter to go to for our etymology. A much more reasonable explanation of the name was given long ago by the Swedish exile to Siberia, Strahlenberg, who wrote his well-known description of the north and eastern parts of Europe at the beginning of the last century. In the 13th chapter of this work, under the heading Mamatova Kost, we read 'As to the name it doubtless had its origin from the *Hebrew* and *Arabick*; this word denoting *Behemot*, of which *Job* speaks (in the xi. chapter), and which the *Arabs* pronounce *Mehemot***** This is certain, that they (*i. e.* the Arabs) brought the word into Great Tartary; for the *Ostiacks* near the river *Oby* call the *Mammuth Khosar*, and the Tartars call it *Khir*; and although the *Arabian* name of an *elephant* is *Fyhl*, yet if very large they add the adjective *Mehemodi* to it; and these Arabs coming into Tartary, and finding there the relicks of some monstrous great beasts, not certain of what kind they might be, they called these teeth *Mehemot*, which afterwards became a Proper Name among the *Tartars*, and by the *Russians* is corruptly pronounced *Mammoth*.*** The *Russian Mammoth* certainly came from the word *Behemot*; in which opinion I am confirmed by the testimony of an ancient *Russian* Priest, *Gregory* by name, Father-Confessor to Princess *Sophia*, who was many years an exile in *Siberia*, from whom I was told, that formerly the name for these bones in *Siberia* was not *Mammoth*, but *Memoth*, and that the *Russian* dialect had made that *alteration*.'—(*Strahlenberg Eng. ed.* 403). This view is curiously confirmed by the fact that Father Avril, a Jesuit, who went overland to China in 1685, and who is quoted by Witzen in the notices he gives of the Mammoth, never calls it Mammoth, but always Behemot.—(*Avril's Travels, Eng. ed.*, 175, 177). Witzen himself also says that these teeth belong to the beast *Behemoth*, called Mammout, otherwise Mammona by the *Russians*.—(*Op. cit.*, 742). The Turkish dialects habitually interchange the letters B and M, which are, in fact, used indifferently by them, so that the change from Behemoth to Mehemoth is perfectly regular and natural, and we can hardly doubt that Mammoth is in fact a mere form of Behemoth. At first it looks strange that the Arabs should have given a name to this beast which has become current all over the world; but this is easily explained when we remember the immense enterprise and energy of the Arabs in the ninth and two succeeding centuries, when, as we know, their traders and emissaries frequented the borderlands of Siberia, and probably first initiated the trade in fossil ivory in the west. . . . Father Avril's narrative shows that this trade still survived in his day, and he tells us the Persians and Turks put a great value on elephants' teeth from Siberia, and preferred a scimitar or a dagger haft made of this precious ivory before a handle of massy gold or silver. There is, therefore, every reason to believe that the name Mammoth, as well as Mammoth ivory itself, were first introduced to the notice of the western world as an article of commerce by the Arabs, who were familiar with it probably as early as the ninth century.

Fig. 994. Restoration of the migrating woolly mammoth (*Elephas* [*Mammonteus*] *primigenius* Blum.) as it appeared on the river Somme, northern France. Details after the Upper Palæolithic etchings and paintings of Magdalenian time, especially in the caverns of Font-de-Gaume and Combarelles. Painted in 1919 by Charles R. Knight, under the direction of Henry Fairfield Osborn, for the Hall of the Age of Man, American Museum of Natural History.

II. CHARACTERS OF THE SUBFAMILY MAMMONTINÆ, INCLUDING THE GENUS MAMMONTEUS

SUPERFAMILY: ELEPHANTOIDEA Osborn, 1921
FAMILY: ELEPHANTIDÆ Gray, 1821
SUBFAMILY: MAMMONTINÆ Osborn, 1921 (as defined above in Chapter XVI, *Archidiskodon*)

GENUS: **MAMMONTEUS** Camper, 1788[1]

Original reference: Camper, 1788, pp. 251,259; Osborn, 1924.633, p. 2.

Pleistocene of Europe, northern Asia, and North America.

Syn. (partial list): *Dicyclotherium* Geoffroy, 1837; *Cheirolites* von Meyer, 1848; *Synodontherium* Costa, 1850: *Polydiskodonten* Pohlig, 1885, *Polydiskodon* Pohlig, 1888.

MAMMONTEUM CAMPER, 1788, P. 251.—". . . os humanum petrifactum, aut fossile, etiamsi Mammonteorum, Elephantorum, . . . Adserere ex eodem principio audeo Mammonteum animal extinctum non modo esse, sed nullam omnino habuisse cum Elephanto similitudinem!"

GENERIC CHARACTERS IN CRANIUM AND TEETH (OSBORN, 1928).—The *Mammonteum* of Camper, 1788 [*Mammonteus* of Osborn, 1924], includes *Elephas primigenius* Blum., also *Elephas americanus* DeKay, *Elephas primigenius astensis* Depéret and Mayet, *Elephas primigenius fraasi* Dietrich, and *Mammonteus primigenius compressus* Osborn.[2] (1) Cranium related to that of *Archidiskodon* and of *Parelephas*, but extremely acrocephalic, hypsicephalic, bathycephalic. Frontals concave, occipital crest greatly elevated, occiput slightly convex. (2) Molars, in Upper Pliocene to Upper Pleistocene stages, with relatively numerous ridge-plates; Upper Pliocene stage, *M. primigenius astensis*, M 3 $\frac{19\text{-}20}{19\text{-}20}$; typical Upper Pleistocene stage, *Mammonteus primigenius*, M 3 $\frac{24}{24}$; final progressive stage, *M. primigenius compressus*, M 3 $\frac{27}{(?)27}$. Ridge-plates compressed in typical superior molars to 10–11–12 in 100

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[1] [See footnote on page 1117 above for remarks on the doubtful validity of the genus *Mammonteus*.—Editor.]

[2] [To these should be added *Mammonteus primigenius alaskensis* described below (pp. 1159–1161), this chapter.—Editor.]

mm., in highly progressive superior molars 13 in 100 mm.; in progressive inferior molars 8–9–10 in 100 mm. Molar crowns broad, M^3 extremely short with enamel ridge-plates of minimum thickness, ridge-plates more or less crimped or sinuous. (3) Manus pentadactyl with five digital nails (*fide* Herz, 1902), manus and pes tetradactyl, not pentadactyl (*fide* Salensky, 1904, p. 86—see citation from Salensky[1] on page 1129 below); four digits (*fide* Pfizenmayer, 1926, p. 239), total phalanges in each foot reduced to nine in number, e.g., $\begin{array}{cccccl} 0 & 2 & 3 & 2 & 2 & \text{Phalanges.} \\ \hline 0 & \mathrm{II} & \mathrm{III} & \mathrm{IV} & \mathrm{V} & \text{Digits.} \end{array}$ (4) Dietrich (1912) records five digits in the manus and pes of the large and more primitive Upper(?) Pleistocene *M. primigenius fraasi.* (5) Tail abbreviate, caudals 21. (6) Habitat, northern tundras and steppes, grassy meadows; summer diet chiefly of grasses.

All authors have included *E. primigenius* within the genus *Elephas*, the genotypic species of which is *Elephas indicus* Linnæus, 1754 (= *Elephas maximus* Linnæus, 1758). It has now been demonstrated that the true northern mammoth (*Elephas primigenius*) is one of the final members of a long series of species and of ascending mutations extending back through the entire period of Pleistocene time and first recognized in the Upper Pliocene of Italy as *Elephas primigenius* mut. *astensis*, described by Depéret and Mayet in 1923. Throughout this long geologic period these ascending mutations and species exhibit fundamental dental or cranial characters and proportions which clearly distinguish them from *Elephas indicus*; consequently we have to do with a distinct generic phylum, comparable to the phyla of *Archidiskodon* and of *Parelephas.* For this 'northern' or 'woolly' mammoth the appropriate name *Mammonteum* Camper (= *Mammonteus*) was revived by the present author in 1924 (Osborn, 1924.633, p. 2).

1. EXTERNAL CHARACTERS AND FEEDING HABITS

The true Mammoth is the only extinct proboscidean of which the characters of the soft parts and of the hairy and woolly covering, as well as the nature of the food both of the Mammoth and Mastodon, are fully known. The student is referred to the reports of Herz (1902) on the mammoth discovered on the Beresowka River; also to Salensky[1] (1903) who described in the greatest detail the external characters of the same individual. The most recent descriptions, however, are those of Quackenbush (1909) noting the discovery in 1907 at "Historic Bluff," Eschscholtz Bay, Alaska, of part of a skeleton of the Mammoth, together with some skin and hair (Amer. Mus. 13749—paratype of *M. primigenius compressus*), and of Felix (1912) in his "Das Mammuth von Borna," from which we may cite by translation:

Summer Food of Grasses (Felix, 1912, p. 11). On uncovering the skull a portion of the animal's food was found in the form of a wad lying between the upper and lower teeth. Its death, therefore, must have been so sudden that it did not have time to swallow this food. In addition, the entire stomach was discovered containing about 12 kilograms (24 lbs.) of undigested food. On examination this material proved to contain a flora of no great variety, but of exceeding interest, because it consisted of plants that are still native to the place, i.e., Beresowka River, northern Siberia. They are *almost exclusively grasses.* The needles of conifers occur very rarely. Here is the list:

1. Alopecurus alpinus Sm. [= alpine foxtail grass].
2. Hordeum jubatum L. [= squirrel-tail grass].
3. Agrostis borealis Hartm. [= red bent-grass].
4. Atropis distans Griseb. [= sweet-grass].
5. Beckmannia crucæformis Host. [= slough-grass].
6. Carex glareosa Wg. [= clustered sedge].
7. Carex incurva Lightf. [= curved sedge].
8. Thymus serpyllum L. [= wild thyme].
9. Oxytropis campestris DC. [= field oxytrope].
10. Papaver alpinum L. [= alpine poppy].
11. Ranunculus acer L. var. borealis [= common buttercup].

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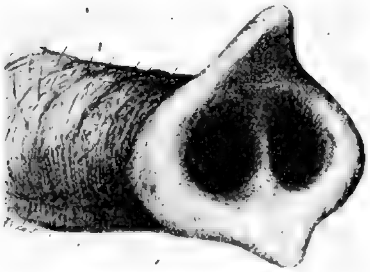
[1] [See Zalensky, Vladimir Vladimirovich, in Bibliography of Volume I of the present Memoir.—Editor.]

(*Op. cit.*, p. 12): All these kinds of plants are found in the same locality at the present day and form a characteristic meadow flora. With the exception of Alopecurus alpinus Sm. and Papaver alpinum L. which are also found in the tundra, there were no typical tundra plants. From other discoveries we know that the mammoth fed also on: (1) Betula nana L. [=dwarfed birch]; (2) Salix polaris Wahlnbrg. [=arctic willow]; (3) Cladonia rangiferina Hoffm. [=reindeer moss].

In addition to these the mammoth ate (probably in winter) the bark and twigs of conifers, chiefly larches.

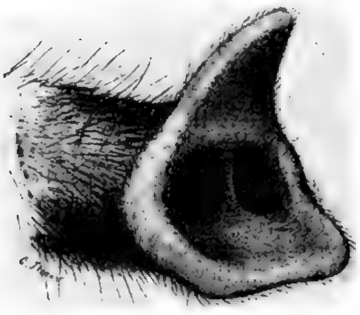
Proportions.—(Felix, 1913, pp. 13, 14, translation): (1) This discovery not only gave us complete knowledge of the skeleton of *E. primigenius* but showed conclusively the proper position of the tusk in the jaw, and its inclination. (2) As to the animal's outward appearance, it involved a number of corrections in even the best reconstructions that had been made. (3) The proportion of the *length of skull* and trunk in the mammoth is quite different from that of existing elephants. The length of the mammoth's skull is more than half that of the trunk while the elephant's skull [*E. indicus*] is always less than half the trunk length. The mammoth's head, therefore, was larger in proportion to the body than that of the recent elephants, and in consequence the tusks could attain enormous proportions. The largest of the tusks in the St. Petersburg Museum measures no less than 4, 17 m. (13′8″) and in the Franzens-Museum of Brünn there is a tusk that actually exceeds 5 m. (16′5″) in length!



Mammonteus primigenius

Reconstruction

Elephas indicus



Loxodonta africana

Comparison of the Tip of the Trunk of the Mammoth (Mammonteus primigenius) with that of the Indian elephant (Elephas indicus) and of the African elephant (Loxodonta africana)

After Flerov, 1931, Figs. 1, 2, and 3

Fig. 995. The following is cited from Doctor Flerov's interesting description (1931, pp. 863 and 869) of the first discovery of the tip of a mammoth's trunk:

In 1924 a well preserved mammoth trunk was found by an unknown Tungus in the everfrozen soil on the banks of the Bolshaya Baranikha River in the Kolyma district. This region is very distant from any inhabited place, devoid of regular means of communication and peopled with half-wild tribes. Five years elapsed before the news of a discovery, so exceptionally interesting for the Science, reached by a good chance some of our geologists working in the Kolyma district. The trunk in this time passed from person to person, its tip was cut off, then dried and the rest was thrown away and lost. Only in 1929 the dried tip of the trunk was handed over by Mrs. Kondratiev, a resident of Sredne-Kolymsk, a little town on the Kolyma River, to Mr. K. J. Pjatovsky, a geologist, who sent it to the Zoological Museum of the Academy of Sciences through Mr. M. J. Tkatchenko, an assistant of the Yakutsk Museum.

Table of Measurements
(Cf. op. cit., p. 869)

	mm		mm
Length of the tip of trunk on the external side	280	Length of the 'lip' on the exterior border	36
Maximal width	114	Width of the right nasal opening	23
Width above the base of the 'lip'	74	Width of the left nasal opening	17
Width of the 'lip'	71	Thickness of the wall dividing both nasal openings	6
Length of the finger-like process	95	Thickness of the skin on the exterior side	2
Width of the finger-like process on the base	57	Thickness of the skin on the interior side	0.5

The *trunk* of the Beresowka mammoth was entirely missing, but probably differed little from that of recent elephants. The many representations of the mammoth found in the Palæolithic caves of France all show a strongly developed trunk. The ear was somewhat smaller than that of the Indian elephant. Its length was 38 cm. (15″), its breadth, 17 cm. (6¾″). The ears, as well as the whole body, were covered with a thick coat consisting of short wool and longer hair. The massive body, rather short in proportion to its height, is joined to the mighty head by a short neck which seems still shorter on account of the great muscles.

The *tail*—almost unknown until this discovery—is (1) conical in form, sharply pointed at the end and about 36 cm. (14″) broad at the root. It ended in a bunch of bristles. (2) Salensky[1] gives the length—measured from the back—as 60 cm. (23½″). Pfizenmayer writes [1905, pp. 524, 525]: 'The tail of this specimen – measured from the under side—is 35 cm. long, decidedly shorter than that of living elephants. The number of [caudal] vertebræ is only 21.' (3) It would appear from this that the older reconstructions make it much too long. The difference in the measurement of Salensky and of Pfizenmayer can hardly be attributed to the mode of measurement. Probably Salensky included the bunch of bristles at the end in his length, while Pfizenmayer did not.

The *skin* was extraordinarily thick and underneath it was a layer of fat from 1 to 9 cm. (⅖–3½ in.) deep. The whole body was thickly covered with hair, even the legs down to the horny ends of the toes. The mammoth was thus particularly well fitted to withstand cold, while its outward appearance was quite different from that of its living relatives. The covering of the body consisted of three elements: (1) Fine, soft, woolly hair about an inch (20–25 mm.) long, in color varying from faded blond to yellow brown, and covering the entire body; (2) coarser and longer hair up to 20 inches (50 cm.) in length, of a dark rust colored brown, covering the entire neck and trunk (of the body) perhaps forming a fringe of hair still heavier and thicker from the cheeks along the shoulders and sides to the rump, similar to that of the yak. (3) "Bristles"—so called on account of their stiffness—from 8 to 14 inches (20–35 cm.) in length, much darker than the other kinds of hair, found only in the "brush" at the end of the tail.

2. SKELETAL CHARACTERS OF MAMMONTEUS PRIMIGENIUS

These authors do not give a complete description of the osteological characters of the Beresowka mammoth. The most important note is that of Salensky[1] (1903, p. 86): "An osteological study of the Beresowka mammoth led to the unexpected conclusion that considerable differences exist between the *Elephas primigenius* and the recent elephants [*E. indicus*], notably in the foot, which is tetradactyl and not pentadactyl. These differences absolutely exclude the possibility of the direct descent of the elephant from the mammoth."

One of the fullest comparative discussions of the mammoth skeleton is that of Dietrich (1912), in which the vertebral formula, covering our whole knowledge, is summarized below.

Abbreviated Vertebral Column.—Since the abbreviated backbone shares the extreme fore-and-aft compression of the cranium, *E. primigenius* has relatively the shortest vertebral column of any of the Proboscidea. The reader is here referred to pages 930, 931, Chapter XV for a full treatment of vertebral distinctions in the genera of the Proboscidea. This abbreviation is indicated, however, in the *shortening* of the vertebral centra as well as in the *number* of dorso-lumbar vertebræ (dorso-lumbars 24–23 in *Elephas indicus*, 23 in *Loxodonta africana*, 22–24 in

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[1] See footnote on page 1127 above.

Skeletons of Mammonteus primigenius Mounted in the Museums of Russia, Germany, and Belgium

Mounted skeletons of Kolyma-Beresowka, of Borna, of Steinheim, and of Lierre. Reduced to a uniform scale of about one-fiftieth natural size

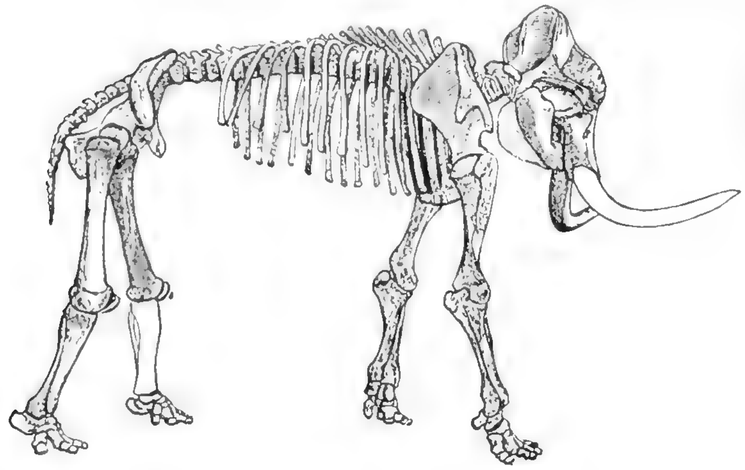

Fig. 996. Skeleton of *Mammonteus primigenius* from the Kolyma-Beresowka River, Siberia, as mounted in the Museum at Leningrad, Russia. After Abel, 1925, p. 56, fig. 36, as reconstructed by W. Salensky [see footnote, p. 1127 above].

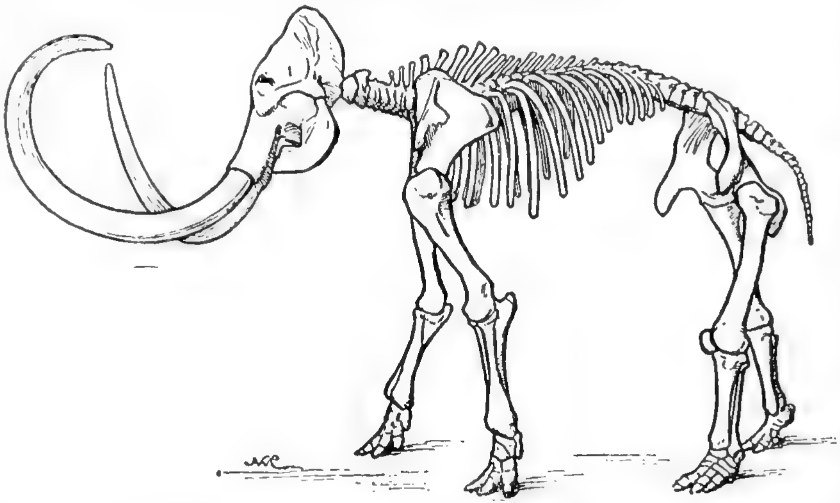

Fig. 998. Skeleton of *Mammonteus primigenius* from Borna, Germany, as mounted in the Museum für Völkerkunde, Leipzig (Grassi-Museum). After Abel, 1925, p. 279, fig. 204 (see Felix, 1912, Taf. VIII, for original).

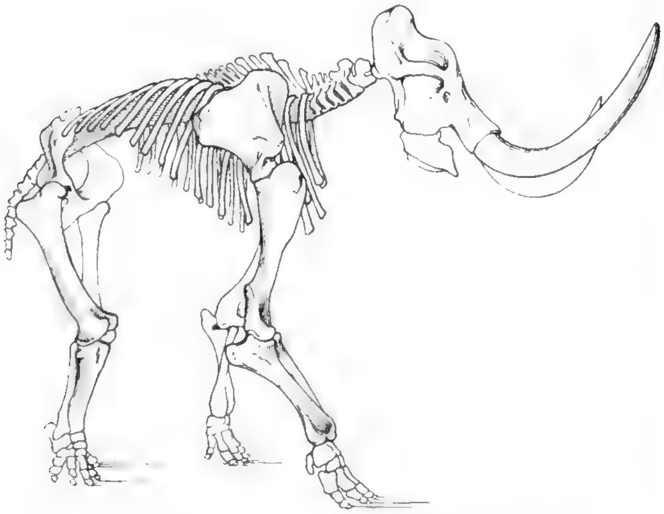

Fig. 997. Skeleton of *Mammonteus primigenius* (=*Elephas* [*Mammonteus*] *primigenius fraasi* Dietrich, 1912) from Steinheim on the Murr, Württemberg, Germany, as mounted in the Stuttgarter Naturalienkabinett. After Abel, 1925, p. 57, fig. 37, as reconstructed by E. Fraas and W. O. Dietrich. About one-fiftieth natural size.

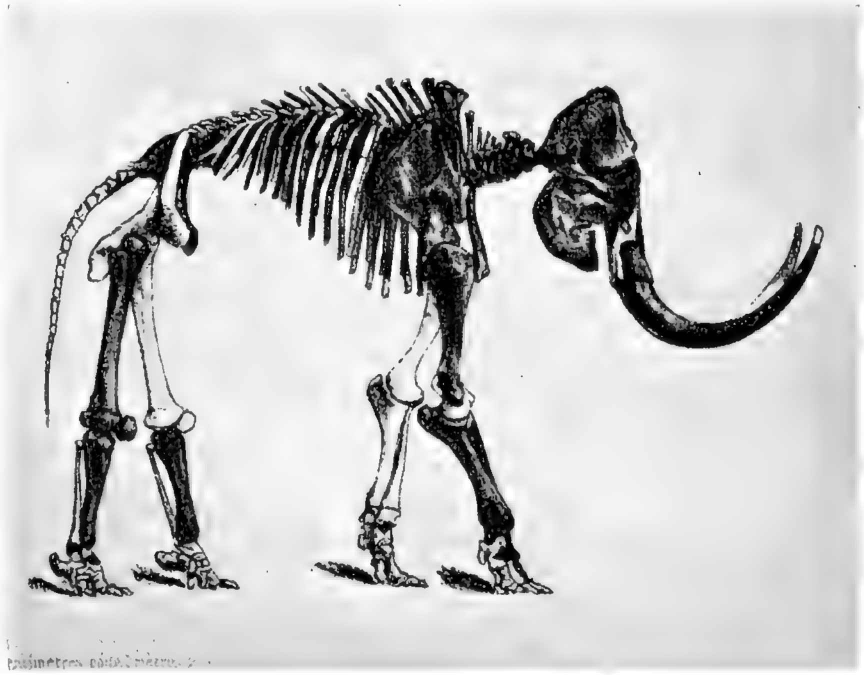

Fig. 999. Mammouth du Musée de Bruxelles découvert a Lierre (Province d'Anvers) en 1860. After Dupont "L'Homme pendant les Ages de La Pierre dans les Environs de Dinant-sur-Meuse," Brussels, 1873, Pl. II. One-fiftieth natural size.

It will be observed that the acrocephalic, hypsicephalic, and bathycephalic proportions of the cranium and the harmonic abbreviation of the vertebral column are manifest in each of these reconstructions. The sharp notch behind the peaked skull in the Combarelles restoration (Fig. 1000) is a feature of every drawing of Palæolithic age. Compare figure 994.

'Adams Skeleton,' 1807 (see Fig. 1014).—The first complete remains, known as the 'Adams skeleton' as mounted (Fig. 1014) in the Zoological Museum of the Academy of Sciences of the U. S. S. R., Leningrad, were discovered in 1799 on the banks of the Lena River at the threshold of the Polar Sea (cf. Lang, 1925, p. 28):

"Imbedded in ice, as it had been for thousands of years, its meat was still in such condition as to be eagerly devoured by polar bears, wolves, and other carnivores attracted from great distances. As time went on every warm season bared more of the body; only the natives contested the booty by securing some of the meat for their dogs through the following years of exposure. It was then that the intrepid explorer and botanist Adams happened to arrive in the neighborhood and, hearing of the famed monster, lost no time in reaching it. Most of the soft parts were gone, one limb had been carried away, and a native had sawed off both tusks and sold them for about fifty rubles. Through Adams' energy and foresight practically all remaining bones were collected. He also took to Petrograd a piece of the hide with the hair in place. It was from the still frozen side upon which the mammoth lay, and so heavy as to tax the strength of ten men to drag it along the shore. A large amount of loose, coarse hair, evidently trampled into the snow by feasting polar bears, was long enough to be considered as having formed a mane." This 'Adams skeleton' as described and figured by Tilesius in 1815 was further described by Cuvier as cited below (see Fig. 1014). [Made by Brandt (1832, pp. XI, XII) the type of *Elephas brachyramphus*.—Editor.]

Mammonteus primigenius, and 23 in *Parelephas jeffersonii*), as shown in the following comparative table—see also Chapters XV and XIX:

	Loxodonta africana		*Elephas indicus*	*Parelephas jeffersonii*	*Mammonteus primigenius*			
	Flower, 1885	"Jumbo" Amer. Mus. Dept. Mam. 3283	Flower, 1885	Type Amer. Mus. 9950	Falconer and Amer. Mus. 14559 (*M. p. compressus*)	Felix, 1912	'Adams Mammoth,' Tilesius 1815	Beresowka Mammoth Pfizenmayer in Dietrich 1912
Cervicals	7	7	7	7	7	7	7	7
Dorsals	19	20	19–20	19	18–19	19	17–19?	18
Pairs of ribs	....	..	..	19	18–19	19	17–19?	..
Lumbars	4	3	5–3	4	4–3	5	4?	5
Sacrals	5	4	4	5	4–3	4		4
Caudals	24+	21	24–30+	12+	21	21 (Salensky)[1]	8+	21

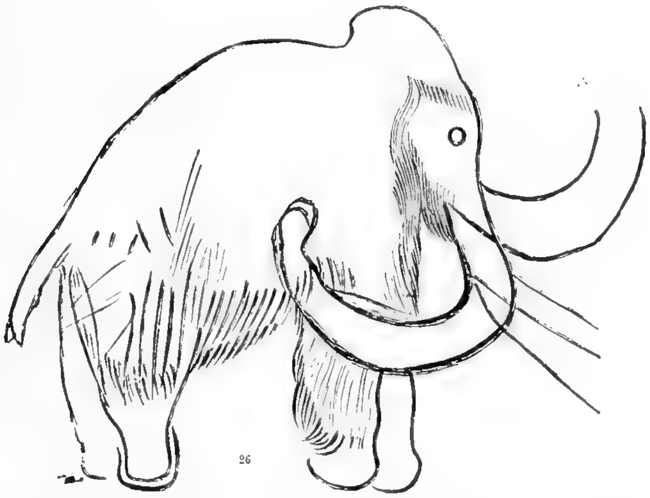

Fig. 1000. Restoration of the woolly mammoth sketched on the wall of the cavern of Les Combarelles aux Eyzies (Dordogne), France. After Capitan, Breuil, and Peyrony, 1924, p. 137, fig. 121. Observe the very small feet, the short tail, the drooping hind quarters, the upcurved backbone, and the neck sharply incurved behind the summit of the occiput, characters which agree closely with those of the skeletons of Steinheim (Fig. 997) and of Borna (Fig. 998).

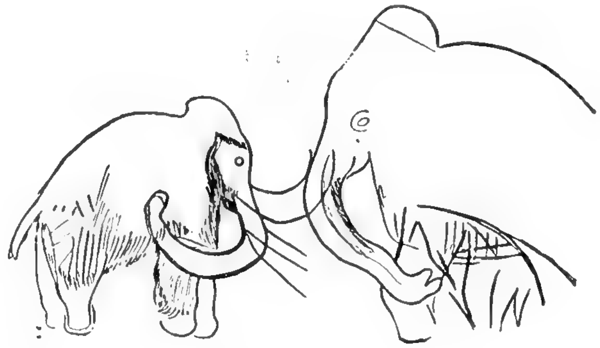

Fig. 1001. The above outlines of the woolly mammoth are from the Grotto of Combarelles, in which representations of the mammoth are next in order of frequency to those of the horse. Compare Capitan, Breuil, and Peyrony, 1924, pp. 136, 137, figs. 120, 121. MacCurdy (1924.1, p. 275) records twenty or more caverns in France, Spain, and Germany in which drawings of the mammoth occur, mostly in outline, while the famous painted murals of Font-de-Gaume are of a dark brownish tint. The mammoth was the only member of the elephant family in northern Europe during the period of the Fourth Glaciation or close of the Stone Age. In Spain, however, the straight-tusked *Elephas* [*Hesperoloxodon*] *antiquus* lingered to the very end of the Stone Age and its outline in the Cavern of Pindal, northern Spain, is shown in figure 1047 of the present Memoir (Chap. XIX, the Loxodontinæ).

Pfizenmayer, 1926, p. 239.—While the skeleton of manus and pes in elephants has five digits, that of the mammoth has only four in both fore- and hindfeet [cf. Herz, 1920, five digits in manus]. The first digit is completely lacking, and the other digits even in older animals show three phalanges only in the third digit, while digits II, IV and V have but two phalanges in fore- and hindfeet.

All four extremities (feet) of the Beresowka mammoth were complete, and the left hindfoot from the knee joint down was preserved in alcohol with the skin and soft parts. This formula of four digits for the Siberian mammoth was demonstrated when three extremities of the Beresowka mammoth were macerated by Professor Salensky,[1] director of the Museum, and myself as his assistant. There can be no doubt about this fact, as we also proved it to be the case in three older fore- and hindfeet which had been preserved with the soft parts intact. They belonged to the Maydell mammoth (1869) in the St. Petersburg Museum collection, and showed the same feature. Also the perfectly preserved fore- and hindfeet of the mammoth of Sanga-jurach agreed with the former

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[1] See footnote on page 1127 above.

discoveries in this respect. The phalangeal formula of the adult Siberian mammoth for both manus and pes is therefore $\frac{0\;\;2\;\;3\;\;2\;\;2\;\;\text{Phalanges.}}{0\;\;\mathrm{II}\;\;\mathrm{III}\;\;\mathrm{IV}\;\;\mathrm{V}\;\;\text{Digits}}$

Restoration.—It will be observed in the Palæolithic restoration (Fig. 1002) that the apex of the cranium is extremely short and pointed (cyrtocephalic, acrocephalic), while the facial profile of the cranium (Fig. 1000) is rounded, a feature probably due to the storage of fat during the winter beneath the woolly dome. All these drawings indicate also a sharp depression between the head and the back, due to the extremely sharp elevation of the cranium; they also indicate the rapid downward slope (usually exaggerated) of the back toward the pelvis. Consequently the drawings fully confirm the evidence afforded by the fossilized skeletons, that the mammoth was wholly different in bodily contour from either of the existing elephants, *Elephas indicus* or *Loxodonta africana*.

Another characteristic is the rapidly sloping hind quarters, as observed in all the numerous drawings and paintings of *Mammonteus primigenius* by the Cro-Magnon artists of Upper Palæolithic age, the most striking and

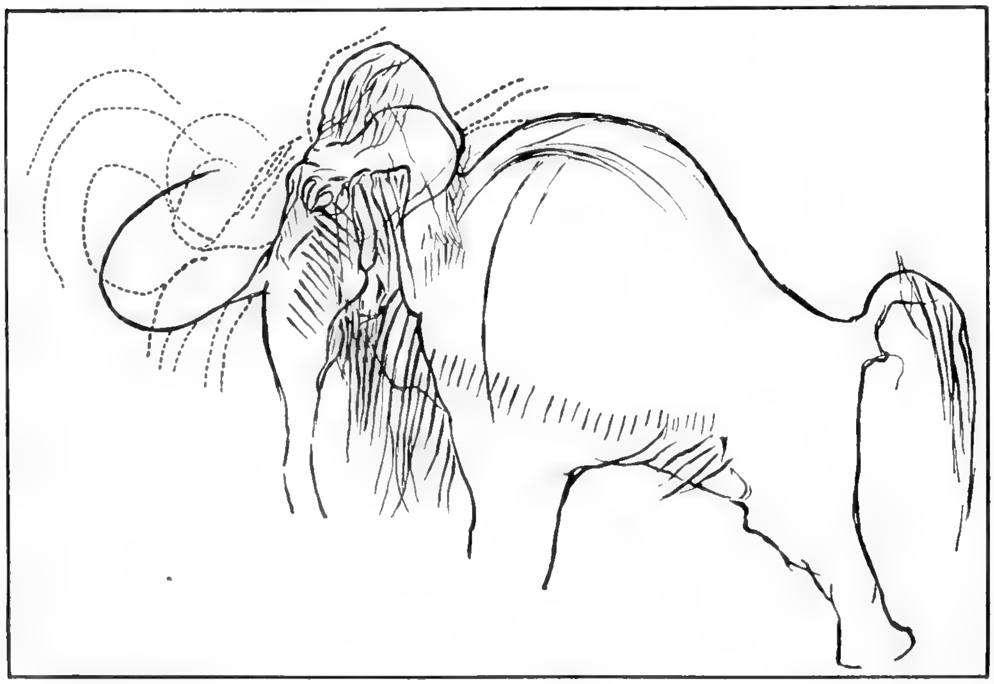


Fig. 1002. Charging mammoth incised on a tusk of *Elephas primigenius* discovered in 1865 in the Magdalenian cultural level of the great rock shelter of La Madeleine (Dordogne), France, and first described by Lartet in the Comptes Rendus des Séances de l'Académie des Sciences, Vol. LXI, 1865, pp. 309-311, subsequently figured by Lartet and Christy in the Reliquiæ Aquitanicæ, 1875, B. Pl. xxviii, and amplified by them in the Descriptions of the Plates, p. 168, as follows:

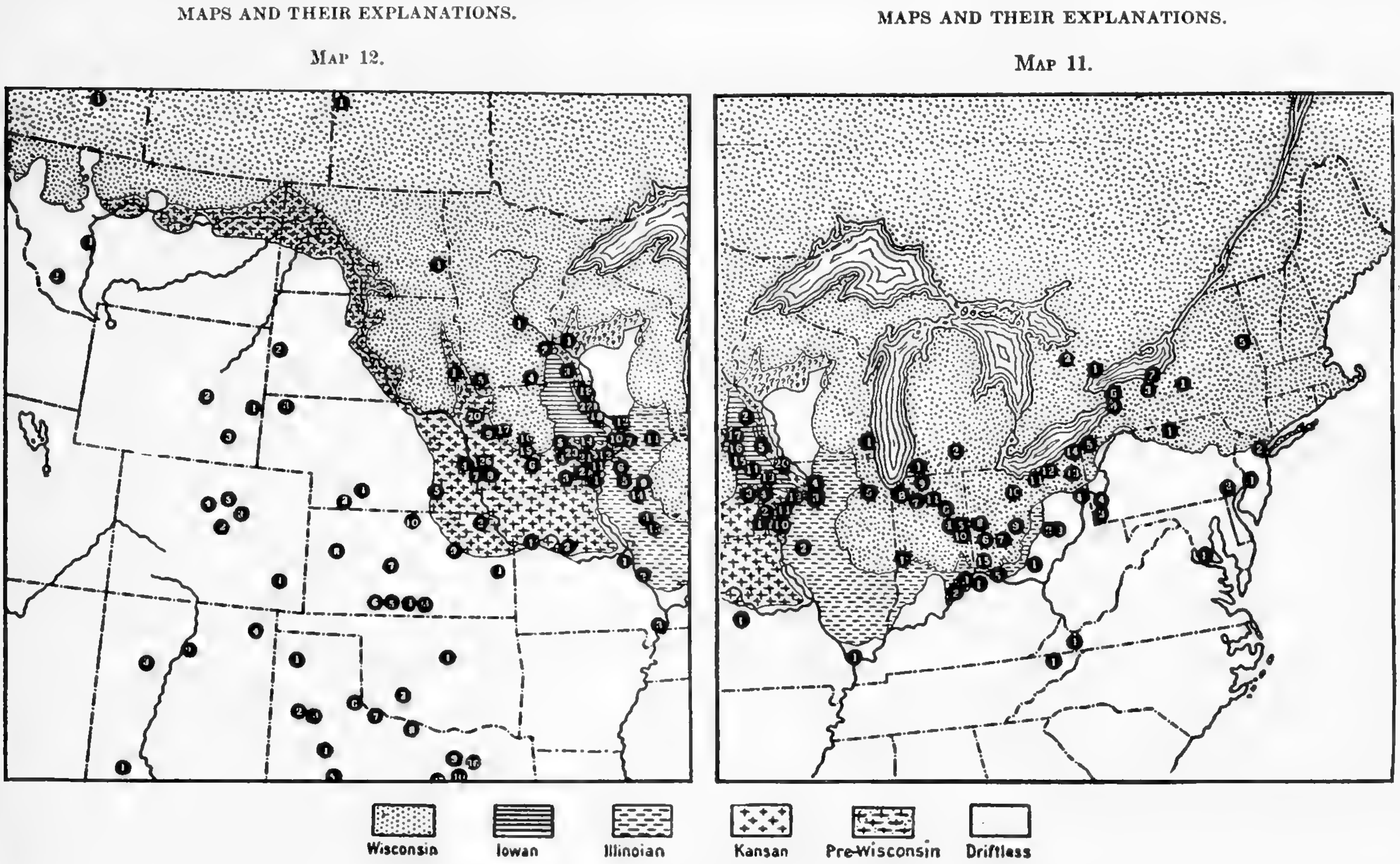
"It is a thin oblong piece, convex from side to side with the roundness of the tusk, and somewhat concave in the longitudinal direction, owing to its curvature. The outer surface presents what at first appears to be a medley of faintly scratched lines; but, on closer and more careful inspection, they resolve themselves into a characteristic outline of a hairy Elephant, with some of the lines doubled and redoubled apparently by the old artist's repeated attempts to sketch out the main features of his subject. The lofty skull and hollow forehead are recognizable as striking features, characteristic of the Siberian Mammoth at St. Petersburg [Footnote: 'See Le Hon's "L'Homme fossile," 1867, p. 70, woodcut.'], of the skull of the Mammoth from Ilford, Essex, preserved in the British Museum [Footnote: 'Much modern information on the features, distribution, and general natural history of the Mammoth, together with references to other authors, will be found in the Memoirs by Mr. Henry Woodward, F.R.S., of the British Museum, in the Geological Magazine, 1864, vol. i. p. 241, and woodcut; 1868, vol. v. p. 540, plates 22 and 23; 1869, vol. vi. p. 58; and 1871, vol. viii. p. 193, pl. 4.'], and of the Belgian Mammoth at Brussels [Footnote: 'See Dr. E. Dupont's "L'Homme pendant les âges de la Pierre dans les Environs de Dinant-sur-Meuse" (pl. 2), 8vo, 2nd edit. 1872.']. The small eye and long trunk of the Elephant, and the great curved tusks and shaggy hair peculiar to the Mammoth, are easily recognized. The upper and more convex sketch-lines of the back agree with the high withers of the Mammoth; and the lower and sloping dorsal lines probably had reference, in the draughtsman's mind, to some special attitude of the animal, with which also the outstretched portion of the hind leg, and the elevated tail, may be associated.

"Mr. H. Woodward, F.R.S., F.G.S., has kindly communicated the interesting suggestion that the attitude of the animal, together with the vertical position of the trunk, would well accord with the idea of one of a herd of Elephants coming down by moonlight to drink, and that the confusing *double lines* might then be explained as an attempt, on the part of the artist, to represent the rest of the herd. In running, or when alarmed, the trunk of the Elephant is always raised. And he adds that there can be little or no doubt that the sketch, rude as it is, was the result of a *life-study* of the animal, and is consequently of the highest importance as attesting the actual presence of the living Mammoth in France when the Caves of Périgord were occupied by Man."

In the present figure the other outlines, probably designed to indicate a charging herd of mammoths, are represented by dotted lines only (cf. Osborn's "Men of the Old Stone Age," p. 384, and Fig. 199): This classic engraving, now preserved in the Museum d'Histoire Naturelle, Paris, is one of the most realistic pieces of Palæolithic engraving which has ever been found; observe especially the outline of the ear, the elevation of the highly peaked (acrocepahlic) head, also the remarkably lifelike action of the limbs and body. There are indications that the artist used this relatively small piece of ivory for the representation of three mammoths; the tusks and trunks of two other elephants appear in the distance.

probably the most accurate representation of the mammoth being the famous charging mammoth as engraved on an ivory tusk (Fig. 1002), the original of which is now in the Museum d'Histoire Naturelle, Paris.

Geographic Distribution.—(1) The geographic distribution of *Mammonteus primigenius* in the United States, in the recent valuable memoirs by Hay (1923, 1924), is unfortunately marred by the fact that many of the recorded specimens attributed by him to "*Elephas primigenius*" really belong to the animal described in the present Memoir as *Parelephas jeffersonii.* (2) The same confusion of the remains of *Parelephas* with those of *Mammonteus* doubtless applies to the plotted distribution[1] by Osborn (Fig. 1005) in the Northern Hemisphere, designed to show the former distribution of the true mammoth; the European plotting (solid black) is largely after Boule and certainly includes both the '*Elephas primigenius*' and the '*Elephas trogontherii*' range. (3) The Asiatic plotting (deep bars) is largely conjectural, and the same doubt exists as to the distinction between the '*E. primigenius*' and the '*E. trogontherii.*' The American plotting (solid black) is also after Hay and, as above noted, doubtless includes the range of species of both *Mammonteus* and *Parelephas.* (4) The distribution of



Geographic Distribution of Mammonteus and Parelephas. After Hay

Fig. 1003. Geographic distribution of *Mammonteus primigenius* in the central (left) and eastern (right) regions of North America, after plotting by O. P. Hay: (Left) Hay, 1924, map 12, pp. 340, 341; (right) 1923, map 11, pp. 428, 429. A point of great significance is this indubitable occurrence of *Mammonteus primigenius* in the Wisconsin and pre-Wisconsin 'drift' (IV Glacial), in the areas of the 'middle drift' (Illinoian, III Glacial), and Iowan?, IV Glacial), and in the 'old drift' (Kansan, II Glacial). See Plate viii opposite page 348 of Volume I of the present Memoir.

This plotting by Hay (1924) also includes finds of *Parelephas jeffersonii* and of *P. progressus* (listed under the names '*Elephas boreus*,' 1924, pp. 47–56, and '*Elephas columbi*,' 1924, pp. 57–84). As shown in the present Memoir, the crania and grinding teeth of the various species of *Mammonteus* and *Parelephas*, after years of confusion by all palæontologists including the present author, are now readily distinguishable.

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[1] [The plotted distribution (Fig. 1005) is entirely out of date (1938); it is now superseded by figure 795 in Chapter XV above, in which the range of the southern 'trogontherians' and northern 'mammoths' is theoretically plotted.—Editor.]

Pleistocene life in the very important geographic area of Alaska, on the confines of North America and Asia, has been treated in recent years by Maddren (1905), by Gilmore (1908), by Quackenbush (1909), by Osborn (1910. 346), and by Frick (1930). A synthesis of their observations is recorded in the accompanying map of 1930 (Fig. 1004.)

Alaska, broadly connected with the Asiatic mainland, was a peninsula for free migration between Eurasia and America; the fossil fauna thus far discovered, chiefly of Pleistocene times, is of boreal or circumpolar character but includes mammals of the north temperate latitude, such as the horse, the bison, a single foot bone of

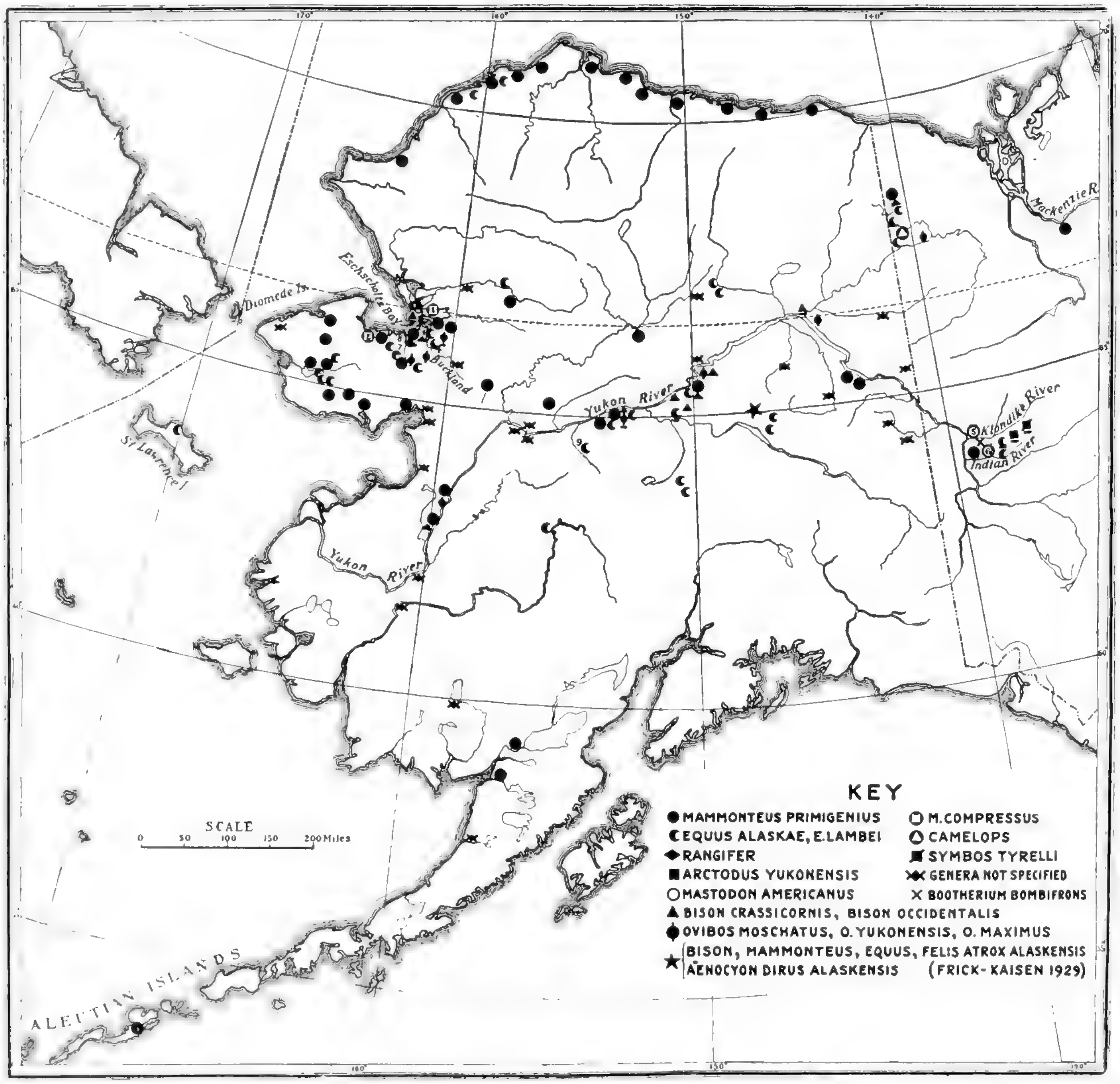


Fig. 1004. Fossil mammalian fauna of Alaska-Yukon and location of principal discoveries to the year 1929. Modified after Quackenbush (1909, see full bibliography, pp. 128-130, and map), including discoveries and records of Maddren (1905) and identifications of Gerrit S. Miller, Gidley, Hay, Lambe, also of Frick (1930).

As shown by the symbols, *Mammonteus primigenius* was extremely abundant; *M. prim. compressus*, represented by the single paratype specimen from Eschscholtz Bay; *Equus* surprisingly abundant, there being recorded thirty-three localities, including (Wainwright) the north coast; *Mastodon americanus* very rare,[1] being recorded only in the upper Canadian Yukon, on the Indian River, Long. 140, Lat. 64; and six records of *Ovibos*. In the very rich explorations, made through the coöperation of the Fairbanks Exploration Company, Frick, Bunnell, and Kaisen (1929) discovered the two new types *Felis atrox alaskensis* and *Ænocyon dirus alaskensis*, resembling like forms from the Rancho La Brea, southern California, intermingled with very numerous remains of *Bison crassicornis, Equus, Mammonteus*,[2] etc.

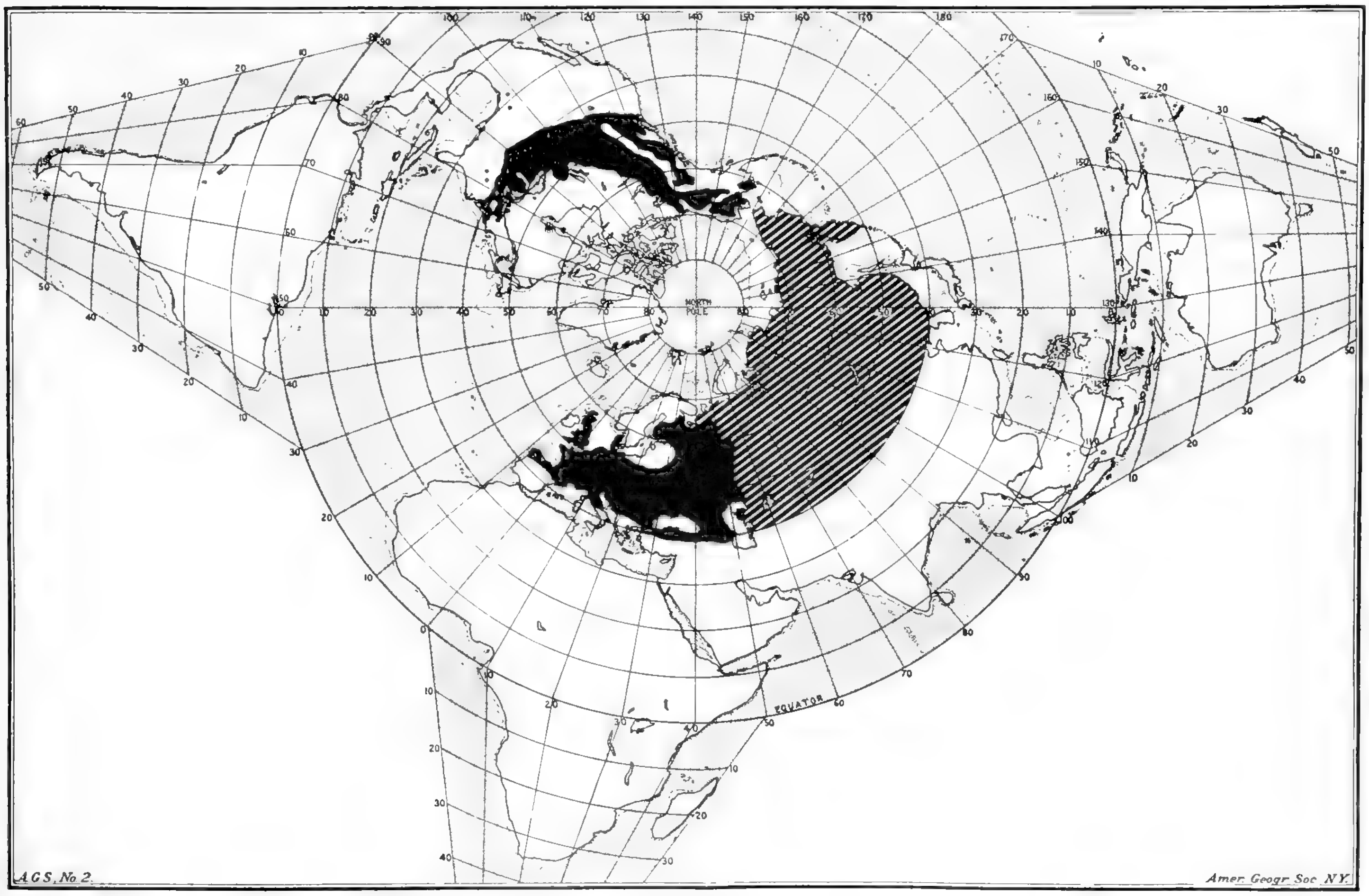
[1] [Compare *Mastodon americanus alaskensis* Frick, 1933, on page 176 of Volume I of the present Memoir.—Editor.]

[2] [*Mammonteus* equals *Mammonteus primigenius alaskensis* sp. nov., from near Fairbanks (Long. 148.10 W., Lat. 64.59 N.) the description of which will be found on page 1159 below.—Editor.]

a camel, and the recently discovered lion[1] or tiger (*Felis atrox alaskensis* Frick). Alaska was free from glaciers, except in its central mountainous belt. Scattered remains of mammals occur: (1) In the frozen tundras along the northern coast, (2) in the black muck accumulated in gulches and valleys of the smaller streams, (3) in the fine elevated clays of the 'Yukon silts' and the 'Kowak clays,' (4) in the more recent fluvial and alluvial deposits. In the northerly clays of Kotzebue Sound, Eschscholtz Bay (1907–1908), Quackenbush discovered a female mammoth skeleton (Amer. Mus. 13749) with portions of hair and wool perfectly preserved. Recent stripping operations of the U. S. Smelting and Mining Company, on Gold Stream and Clery Creek near Fairbanks (Fig. 1004), yielded the following (Frick, 1930, p. 73): ". . . during the four summer months some twenty-eight large cases of skulls, jaws, and bones—rare and important evidence on the prehistory of Alaska which otherwise would have been lost to science. The great percentage of this material, interestingly enough, came from three restricted areas, 'bone pits,' scattered between several widely separated operations of the Company, the remainder of the worked areas being, for the purposes of the bone hunter, nearly barren."

PRE-TUNDRA OR FOSSIL FAUNA OF ALASKA-YUKON

Mammonteus primigenius Blum.
Mammonteus primigenius compressus Osb.
Mastodon americanus Kerr
Rangifer sp.
Bison crassicornis Rich.
Symbos tyrelli Osgood
Boötherium sargenti Gidley
Ovibos yukonensis Gidley
Ovibos moschatus Zimm.
Bison alleni Marsh
Ovis sp.
Oreamnos sp.
Equus alaskæ Hay
Equus lambei Hay
Camelops sp. Gidley
Arctodus yukonensis Lambe
Ænocyon dirus alaskensis Frick
Felis atrox alaskensis Frick



GEOGRAPHIC RANGE OF MAMMONTEUS AND OF PARELEPHAS

Superseded by figure 795, Chapter XV, above

Fig. 1005. This diagram shows that these two mammoths, confused in all previous descriptions, were north temperate and circumpolar in distribution. Closest to the Pole and to the northern ice-sheets during the Fourth Glaciation (Wisconsin-Würm) was doubtless the range of *Mammonteus primigenius*; closest to the 40th parallel was doubtless the chief range of *Parelephas trogontherii*, *P. intermedius*, and *P. jeffersonii*. It is possible that *Parelephas trogontherii* and its successor *P. intermedius* migrated (diagonal) at the close of *1st* or *2d Interglacial* time across northern Asia, thence across Bering Strait into Alaska and southward to the 40th parallel of the United States.

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[1] According to Frick's researches (letter, March, 1930), the cranium of *Felis atrox alaskensis* resembles that of the lion (*Felis leo*) rather than that of the tiger (*Felis tigris*).

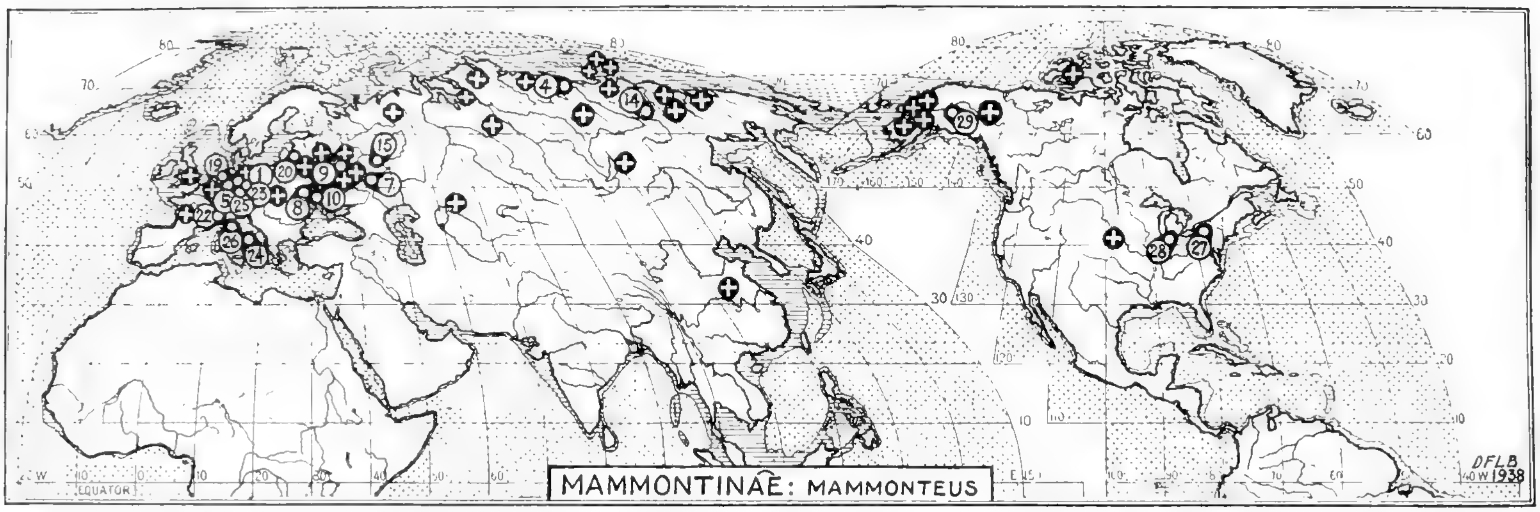

Fig. 1006. Geographic distribution of the principal species of *Mammonteus*. The white dots within the black areas represent the approximate localities where the types of these twenty-nine species and subspecies were discovered. The white crosses represent referred specimens.

3. HISTORICAL ORDER OF NAMING OF SPECIES OF MAMMONTEUS EXCLUSIVE OF SPECIES WHICH ARE NOW KNOWN TO BELONG TO PARELEPHAS TROGONTHERII, ETC.

See Figure 1006

SPECIES AS NAMED IN EUROPE AND ASIA

Late Pleistocene	**1.**	1799	*Elephas primigenius* Blumenbach, Osterode (Harz), Germany, and Siberia	=*Mammonteus primigenius*
	2.	1799	*Elephas mammonteus* Cuvier (1796 MS.), Siberia, etc.	=*Mammonteus primigenius*
	3.	1807	*Elephas mammouth* Link (*fide* Sherborn, 1928, Pt. XV, p. 3845)	=*Mammonteus primigenius*
	4.	1807	*Elephas primævus* Blumenbach (in Adams, p. 152), near mouth of the Lena River, Siberia	=*Mammonteus primigenius*
	1.	1815	*Elephas primordialis* Blumenbach (in Tilesius, p. 470)	=*Mammonteus primigenius*
	5.	1820	*Elephas jubatus* Schlotheim, Düsseldorf, Germany	=*Mammonteus primigenius*
	6.	1829	*Elephas mammonteus* Fischer de Waldheim, Russia	=*Mammonteus primigenius*
	7.	1829	*Elephas paniscus* Fischer de Waldheim, Volga, Russia	=*Mammonteus primigenius*
	8.	1829	*Elephas periboletes* Fischer de Waldheim, Podolia, Russia	=*Mammonteus primigenius*
	9.	1829	*Elephas pygmaeus* Fischer de Waldheim, district of Calomna and of Zwenigorod, Russia	=*Mammonteus primigenius*
	10.	1829	*Elephas campylotes* Fischer de Waldheim, borders of the Bug, Russia	=*Mammonteus primigenius*
	11.	1829	*Elephas Kamenskii* Fischer de Waldheim, Siberia	=*Mammonteus primigenius*
	1.	1830	*Mammuthus Borealis* Burnett (name only)	[=*Mammonteus primigenius*]
	12.	1832	*Mammut Sibiricum* von Meyer (p. 64)	=*Mammonteus primigenius*
	4.	1832[1]	*Elephas brachyramphus* Brandt (pp. XI, XII), near mouth of the Lena River, Siberia. Type: 'Adams skeleton'	=*Mammonteus primigenius*
	13.	1832	[*Elephas*] *homotaphrus* Brandt	[*Nomen nudum*]
	14.	1832	*Elephas giganteus* Brandt, Indigirka River, Siberia. Type: Skull discovered by Messerschmidt (see Fig. 991 above)	=*Mammonteus primigenius*
	15.	1832	*Elephas commutatus* Brandt, Volga River, Russia	=*Mammonteus primigenius*
	16.	1832	*Elephas stenotoechus* Brandt, Russia	=*Mammonteus primigenius*
	17.	1832	*Elephas platytaphrus* Brandt, Russia	=*Mammonteus primigenius*
	18.	1832	*Elephas affinis* Brandt, St. Petersburg, Russia	
	19.	1834	*Elephas macrorynchus* Morren, Tamise, Belgium	=*Mammonteus primigenius*

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[1] [In the Bibliography (Vol. I, p. 766, of the present Memoir) the following species described by Brandt (nos. 4, 13–18 inc.) are given as of date 1833. It has been found since this Bibliography was compiled that a separate publication, containing these names and descriptions, appeared in 1832; hence the adoption of this date. Editor.]

	20.	1835	*Elephas odontotyrannus* Eichwald, banks of the Nieman, dist. of Novogrodek, gouv. Vilna, Russia	=*Mammonteus primigenius*
	21.	1845	*E.* [*Elephas*] *primigenius sibiricus*[1] de Blainville (Atlas, "Ostéographie," Pl. III)	=*Mammonteus primigenius*
	22.	1879	*Elephas primigenius comune* Issel [in Zuffardi, 1913, p. 136], Camporosso, near Ventimiglia, Italy	=*Mammonteus primigenius* (*fide* Issel, 1879, p. 160)
Upper to Lower Pleistocene	**23.**	1888	*Elephas* (*primigenius*) *Leith-Adamsi* Pohlig, Dornap (Fuhlrott), Thuringia, Germany	=*Mammonteus* (?) *primigenius leith-adamsi*
	24.	1891	*Elephas primigenius* Blum. var. *hydruntinus* Botti, Otranto, Italy	=*Mammonteus primigenius hydruntinus*
	25.	1912	*Elephas primigenius Fraasi* Dietrich, Steinheim, Germany	=*Mammonteus primigenius fraasi*
		1913	*Elephas primigenius* Blum. var. *trogontherii* Pohl. Zuffardi	=*Mammonteus primigenius* mutation *astensis* (see No. 26 below)
Upper Pliocene[2]	**26.**	1923	*Elephas primigenius* mutation *astensis* Depéret and Mayet, San Paolo de Villafranca, Italy	=*Mammonteus primigenius astensis*

2. SPECIES AS NAMED IN NORTH AMERICA

Upper Pleistocene	**27.**	1842	*Elephas americanus* DeKay, Monroe County, near Rochester, New York	=*Mammonteus primigenius americanus*
	28.	1924	*Mammonteus primigenius compressus* Osborn, Rochester, Indiana	=*Mammonteus primigenius compressus*
	29.	1933	*Elephas primigenius alaskensis* Osborn (in Frick, *nomen nudum*), vicinity of Fairbanks, Alaska	=*Mammonteus primigenius alaskensis* sp. nov.

Possibly twenty or more of the above species are synonyms of *Mammonteus primigenius* and probably belong to the Upper Pleistocene drift and Postglacial deposits of the Fourth Glaciation. Four of the above, more primitive, of greater geologic age, and with probably lower ridge formulæ, are as follows:

1888 *Elephas primigenius* (?) *Leith-Adamsi* Pohlig, Nova Acta Leop. Carol., LIII, Nr. 1, pp. 229, 232.

1891 *Elephas primigenius* var. *hydruntinus* Botti, Bol. Soc. geol. Ital., IX, p. 709.

1912 *Elephas primigenius fraasi* Dietrich, Jahresh. Ver. vaterl. Naturk. Württemberg, LXVIII. This species is fully annotated below.

1923 *Elephas primigenius* mut. *astensis* Depéret and Mayet, "Les Éléphants Pliocènes," Deuxième Partie, pp. 183, 184. This species is fully annotated below.

4. GEOLOGIC AND PROVISIONALLY ASCENDING PHYLETIC ORDER OF SPECIES AND SUBSPECIES OF MAMMONTEUS. EURASIA AND NORTH AMERICA

Falconer and Hay have referred to *Elephas primigenius* the American specimens of the true woolly mammoth, the ridge formulæ of which remain to be more precisely determined. Falconer attributed to the American specimens the same ridge formula, namely, M 3 $\frac{24}{24}$, but remarked that the ridge-plates were more compressed or closer together; this compression reaches the highest possible stage in *Mammonteus primigenius compressus*, in which

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[1] [See footnote on p. 1391 below where it is stated that *E. primigenius sibiricus* and other subspecies "perhaps may be regarded as geographic designations rather than as subspecies."—Editor.]

[2] [Possibly Lower Pleistocene (see footnote 1 on p. 1049 above).—Editor.]

the ridge-plates increase to M 3 $\frac{27}{27}$. Altogether, including Upper to Lower Pleistocene and Upper Pliocene stages, six[1] species and subspecies have been described as follows:

Upper Pleistocene IV GLACIAL and Postglacial	Alaska, Indiana	*Mammonteus primigenius compressus* Osborn	= The most extreme or progressive subspecies known M $3\frac{27}{(?)27}$
Upper Pleistocene IV GLACIAL and Postglacial	Alaska and the United States	*Mammonteus primigenius americanus* DeKay	= Slightly progressive American stages M $3\frac{26e}{24e}$
Upper Pleistocene IV GLACIAL and Postglacial	Siberia and western Europe	*Mammonteus primigenius primigenius* Blumenbach	= Typical or true mammoth M 3 $\frac{24}{24}$
3d(?) Interglacial	Western Europe	*Mammonteus primigenius fraasi* Dietrich	= Ancestral Upper(?) Pleistocene subspecies of *Mammonteus primigenius* M 3 $\frac{}{22}$
3d(?) Interglacial	Thuringia, Germany	*Mammonteus primigenius Leith-Adamsi* Pohlig	= Small primitive branch of the main stem of *Mammonteus primigenius*
Lower Pleistocene	Forest Bed, East Anglia	*Mammonteus primigenius astensis* (?) ref. Depéret and Mayet	= (Cf. Falconer, 1868, II, p. 170): Small "slightly thick" . . . *pre-glacial* variety of *Elephas primigenius* from the Norwich coast (cf. Fig. 1020).
Upper Pliocene[2]	Italy	*Mammonteus primigenius astensis* type Depéret and Mayet	= Ridge formula: M 3 $\frac{19-20}{19-20}$ (cf. Fig. 1019)

As shown above, the typical or true mammoth was found in Siberia long before it was recognized in western Europe. Blumenbach had in mind both Siberian and North German specimens in defining *Elephas primigenius* in 1799 (1799.1, p. 697), also Cuvier had the Siberian mammoth in mind in defining *Elephas mammonteus in* 1796 (MS., published in 1799). Unfortunately Blumenbach in his type description mentioned as an example the Burgtonna skeleton, which we now know belongs to '*Elephas antiquus*' and is not the type. The exact evolutionary stage of '*Elephas primigenius*' was finally defined and determined by Falconer in 1863 (pp. 64,65), with a typical ridge formula of M 3 $\frac{24}{24}$. Attributed, or referred, to the typical species *Elephas primigenius* have been all the Pleistocene mammoths of western Europe and North America including, as we have seen, all the species of *Parelephas* also all the primitive and geologically ancient species and subspecies of the true mammoth. The American subspecies *Mammonteus primigenius americanus* has the same ridge formula but the plates are more compressed (*fide* Falconer). Consequently the recognition of the geologically ancient forms with relatively low ridge formulæ, as listed above, is a matter of the utmost importance and interest.

We regard it as somewhat problematic whether the Upper Pliocene *Mammonteus primigenius astensis* Depéret and Mayet, 1923, is ancestral to *Mammonteus*; certainly it shares characters of *Mammonteus* and of *Parelephas*; its ridge formula of M 3 $\frac{19-20}{19-20}$ is higher than that of the contemporary *Parelephas* species *P. trogontherioides*.

The Forest Bed stage, previously determined by all authors as the true *Mammonteus primigenius*, more probably belongs to a primitive stage with fewer ridge-plates, perhaps M 3 $\frac{19-20}{19-20}$, similar to *M. primigenius astensis*. From among the considerable number of Forest Bed specimens probably a correct ridge-plate count can be made.

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[1] [To these should be added the new subspecies *Mammonteus primigenius alaskensis* (see pp. 1159 to 1161 of this chapter for description).—Editor.]

[2] [See footnote 1 on page 1049.—Editor.]

Aurignacian Mammoth Hunters of Moravia.—The following passages may be freely cited from Doctor Absolon's recent description in the Illustrated London News (Nov. 23, 1929) of his remarkable discoveries in the years 1924–1929 of mammoth-hunting stations of Moravia:

> Of these stations we now know about one hundred in Moravia, but only a small part of their area is explored as yet. . . . It is because Moravia was a kind of passage, by way of which the fossil mankind of the increasing Aurignacian tribe penetrated from Asia through Russia to the West of Europe. . . . They are: Věstonice, Předmostí, Petřkovice, Pekárna, and Ondratice. Pekárna is a cave (Fig. 1); the rest of them are in loess on the slopes of hills. Pekárna is the most important, Věstonice the largest of them. . . . This was the first culture of the Old Aurignacian invasion of mammoth-hunters coming frcm Asia, the cradle of mankind. . . .
>
> One thing is certain—namely, that the mammoth-hunters killed these huge pachyderms in hundreds, and that in diluvial Moravia, a great tragedy, like the destruction of elephants in Africa, took place. . . .
>
> In the refuse-heap discovered in 1925, no tusks were found in the whole area of 45 square metres; but in that encountered in 1926, on the other hand, three heaps of tusks were piled one over another, between which was left a narrow path (Figure 13). In the same year an imposing sight opened before our astonished eyes, when we discovered a field of huge pelvic bones (Fig. 14) of adult mammoths. The skulls are usually broken to pieces, because mammoth-brain was appreciated by primitive hunters as a delicacy. Nevertheless, we found an intact skull of strikingly large proportions in 1928 (Figure 15). Long bones (femurs, tibiæ) were found also in strange position forming a half-circle, so that their broken ends all pointed in one direction: evidently the fire was kept alight by the fat which flowed out of the ends of the burning bones into the flames. . . .
>
> Lower jaw-bones lie generally apart, and the teeth have often keen knocked out and piled up in heaps. In 1927 we found at Předmostí a jaw-bone within which was a red-painted stone club (Fig. 9) which might have been used for striking out the teeth from the jaw-bones—a unique discovery. From 1924 to 1929 we counted as many as sixty mammoths, all of them caught and killed by man, on the area of 1600 square metres.
>
> There cannot be the least doubt that the hunters did not attack these powerful animals 'face to face,' but caught them by cunning, enticing or driving them into large pitfalls. The picture (Figure 16) shows a stratum dipping abruptly downwards. It must have been purposely made; dug in diluvial times. We intend to try to open this pitfall, for such I take it to be. Mammoths trapped and caught were killed by large stones, trimmed to serve such a purpose. These stones might have been suspended in strong leather straps and thus let down on the animals by the united efforts of several men, in the same way that navvies drive piles into river-beds by means of rams. I have found one such stone, trimmed like a big pear, or bomb, 1 metre long, and weighing over 120 pounds (Fig. 11). [See Fig. 1037, this chapter.—Editor.]

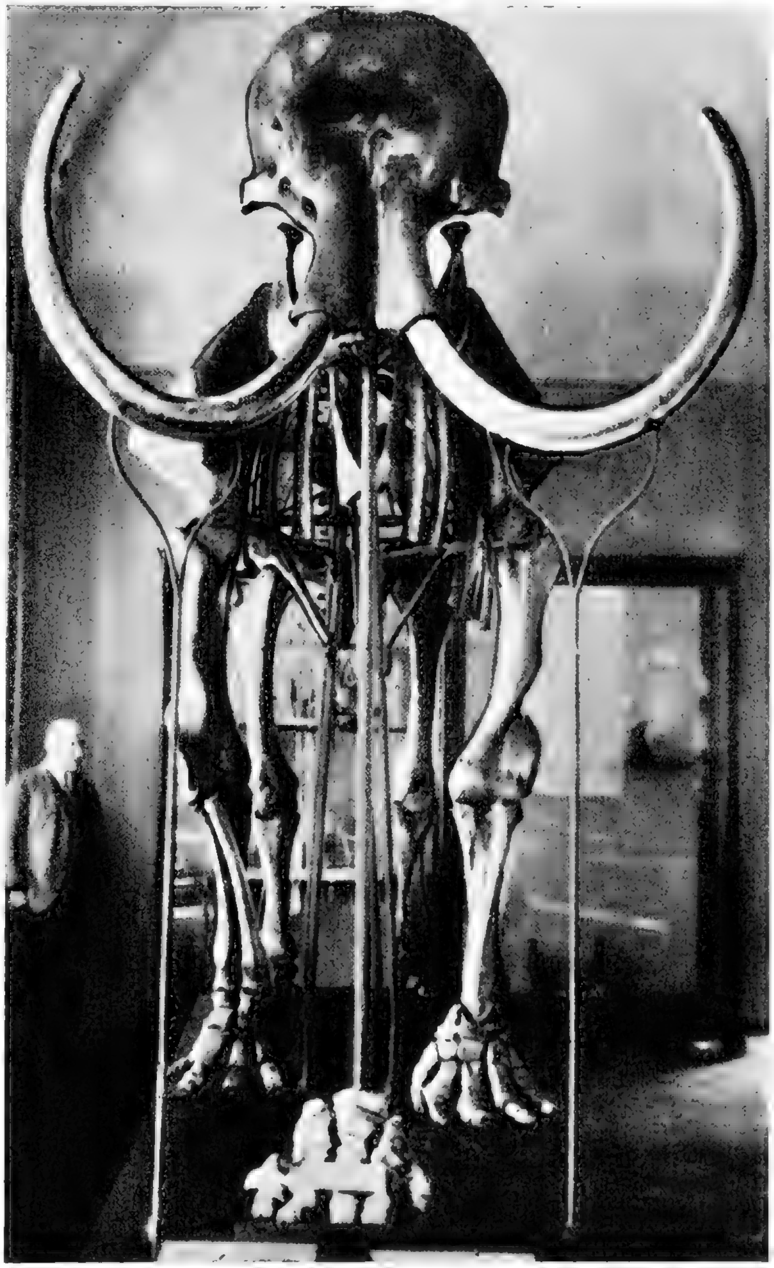


Fig. 1007. Skeleton of the Mammoth (*Mammonteus primigenius*) from the diluvium of Moravia, now in the Moravian Government Museum of Brno (Brünn), Czechoslovakia. After photograph furnished by Prof. Karel Absolon of the University of Prague and Curator of the Museum at Brünn. This skeleton was found nearly complete at Piedmont in Moravia, whereas all the skeletons in the kitchen-middens of the mammoth hunters of Moravia were scattered and partly destroyed for a food supply. It measures 3 m. or 9 ft. 10 in. in height and 4.42 m. or 14 ft. 6 in. in length.

III. SYSTEMATIC DESCRIPTION OF SPECIES OF MAMMONTEUS

Specific Revision.—(1) All the earlier writers even up to the time of Lydekker's "Catalogue of the Fossil Mammalia in the British Museum" (1886.2) included within the typical species *Elephas* [=*Mammonteus*] *primigenius* all the progressive and primitive mammoths with fine-plated molars discovered in Pleistocene deposits, from the typical horizon of the Fourth Glaciation downwards to the Forest Bed stages of the Lower Pleistocene. (2) They also included within *E. primigenius*, as we have seen above in the *Parelephas* chapter, many stages properly belonging to *Parelephas trogontherii* and its ascending and descending mutations. (3) Within the last half century, however, Pohlig (1888) and Dietrich (1912) have separated the stages of *2d* and *3d Interglacial* times in Germany as *Elephas primigenius leith-adamsi* Pohlig, 1888, and as *Elephas primigenius fraasi* Dietrich, 1912; (4) also Depéret and Mayet (1923) believe they have recognized an Upper Pliocene (Villafranchian) stage, to which they have given the name *Elephas primigenius* mut. *astensis*. Thus there have been four great steps in specific revision, concluding with the present revision by Osborn.

As shown in the table above, the highly specialized *Mammonteus* conforms with the principle of ridge-plate addition as we pass from Upper Pliocene to the close of Pleistocene times, so beautifully manifested in the two more generalized mammontines *Archidiskodon* and *Parelephas*. We may select the third superior and inferior molars to show this parallel ridge-plate progression of M 3 in two of these three great lines of ascent.

	Mammonteus		*Parelephas*	
Final Pleistocene	*M. primigenius compressus*:	M 3 $\frac{27}{(?)27}$	*P. progressus*:	M 3 $\frac{30}{26}$
?Postglacial	*M. primigenius americanus*:	M 3 $\frac{26^{\circ}}{24^{\circ}}$	*P. jeffersonii*:	M 3 $\frac{25}{24}$
IV Glacial or typical	*M. primigenius primigenius*:	M 3 $\frac{24}{24}$	*P. columbi*:	M 3 $\frac{18-19}{15-16+}$
Upper Pleistocene to Upper Pliocene	*M. primigenius fraasi*:	M 3 $\frac{}{22}$	*P. intermedius*:	M 3 $\frac{20}{20-21}$
	M. primigenius leith-adamsi:	M 3 $\frac{19-20}{19-20}$	*P. trogontherii*:	M 3 $\frac{15+}{16+}$
	M. primigenius astensis:	M 3 $\frac{19-20}{19-20}$	*P. trogontherioides*:	M 3 $\frac{\frac{1}{2}-14-\frac{1}{2}}{\frac{1}{2}-14-\frac{1}{2}}$

We observe that: (1) *Mammonteus* even in Lower Pleistocene time has a much higher ridge-plate formula than *Parelephas*; (2) but that *Parelephas* finally surpasses *Mammonteus* in the species *P. progressus*; (3) in *Parelephas* the ridge-plates are added more rapidly in the superior than in the inferior molars, a case of imperfect parallelism.

Much further research is necessary to verify the ancestral relationships of these supposed early geologic stages to the typical *Mammonteus primigenius primigenius*. Also further research is essential to complete and verify the ridge formulæ of *M. prim. fraasi* and *M. prim. leith-adamsi*. In the meantime we may present the conclusions independently reached by Pohlig, Dietrich, and Depéret and Mayet that true ancestral stages of *Elephas primigenius* are to be found in the early Pleistocene and Upper Pliocene and that the ridge formulæ conform with the general law of ridge-plate progression through the very long period of Pleistocene time, now estimated at not less than 1,000,000 years.

1. TYPICAL PROGRESSIVE EURASIATIC STAGES OF MAMMONTEUS

There can be no doubt that during late Pleistocene (IV Glacial and Postglacial) time there existed all over northern Eurasia a single species of mammoth to which the name *Mammonteus primigenius* has been assigned, since it furnished the type to which the earliest as well as the original and later descriptions were applicable.

SYSTEMATIC DESCRIPTION OF SPECIES

Mammonteus primigenius Blumenbach, 1799, 1803

Figures 794, 816, 818, 865, 934, 937, 962, 990–999, 1000–1002, 1007–1014, 1032–1034, 1042, 1062, 1084, 1226, Pl. XXII

Upper Pleistocene, IV Glacial drift(?), Siberia and northern Germany. For synonyms, see page 1136.

Type Description of Elephas primigenius, 1799.—(Blumenbach, 1799, p. 697): "3) Von einem ungeheuer grossen Elephanten (Elephas *primigenius?*) [die vermeinten Riesenknochen** unsrer ehrlichen Alten]; unter andern auch in Menge in Deutschland***). So z. B. das berüchtigte Elephantengerippe das 1695 bey Burg-Tonna im Gothaischen ausgegraben worden etc."

Lectotypes.—Blumenbach's type description (1799, p. 697) is in a rare document; no type figure accompanies it. Blumenbach had the Siberian and German mammoth in mind. The 'Elephantengerippe' of Burgtonna is not the type. Dietrich and Osborn select (1930) as *lectotypes*: (1) A Siberian grinder in the Blumenbach Collection of the Zoological Institute of the University of Göttingen, and (2) a molar from Osterode (Harz), Germany. The sixth edition of his "Handbuch der Naturgeschichte," in which the type description appears, attracted the attention of the French naturalist Soulange Artaud, who visited Blumenbach and translated his "Handbuch" into French under the title "Manuel d'Histoire Naturelle." In the manuscript of the French volume of 1803, Blumenbach inserted the name and definition of *Elephas primigenius*, consequently the species *Elephas primigenius* is of date 1799, 1803.

Second Description, 1803 (Blumenbach-Artaud).—Many authorities, namely, Trouessart (1897, p. 711), Lydekker (1886.2, p. 175), and Hay (1902, p. 713), erroneously cite 1803 as the date of the type description of this species, i.e., "Manuel d'Histoire Naturelle, traduit de l'Allemand, de J. Fr. Blumenbach, . . . par Soulange Artaud," 1803, Vol. II. The explanation of the definition of a new species in the translation is found in the "Préface du Traducteur," p. xvi: *"C'est que j'ai travaillé sous les yeux de M.* Blumenbach *lui-même; qu'il a eu la complaisance de revoir mon manuscrit, et qu'ainsi je puis presque répondre de la fidélité de la traduction."* This shows that Blumenbach inserted the name and definition of *E. primigenius* in Artaud's MS.

In Volume II, p. 407, of Artaud, we find the following definition: "3.° D'un *éléphant* énormément grand (*elephas primigenius*) (ce sont les prétendus os de géants de nos bons aïeux); il se trouve des os fossiles de cet animal, en grande quantité, en Allemagne . . . (Le squelette d'éléphant, par exemple, qui a été trouvé, en 1695, près de Burgtonna, dans le pays de Gotha)."

In Artaud's translation no figure of *Elephas primigenius* occurs, although in the explanation of the figures appears the American Mastodon designated as "28. Fossile Ohio incognitum" and on page 408 designated as "le mammouth de l'Ohio (*mammout Ohioticum*)," also the "Table Alphabétique des Noms Latins, de Genres et d'Espèces" of Artaud's translation, p. 443, gives the orthography as "Mammut Ohioticum."

Trouessart (1904–1905).—Trouessart (Quinquennale Supplementum, 1904–1905, p. 600) remarks: "Le nom barbare de '*Mammout*,' basé, par Blumenbach, sur une erreur grossière (l'identité du *Mastodonte de l'Ohio* avec *l'Elephas primigenius*), n'a aucun droit, malgré sa priorité, a être substitué à celui de 'Mastodon,' genre bien caractérisé par Cuvier."

Osborn, 1924: The above paragraphs from the quaint writings of Blumenbach and of Artaud firmly establish the specific name *Elephas primigenius* as of date 1799, 1803; they show that Blumenbach erroneously selected the Burgtonna skeleton[1] as an example of *E. primigenius*; they show that there was no type figure. Finally, as pointed out by Trouessart, Blumenbach applied the barbaric name "*Mammut*" to the American Mastodon of Ohio under the erroneous idea that the latter was related to *Elephas primigenius*.

TYPICAL UNIFORM RIDGE FORMULA OF MAMMONTEUS PRIMIGENIUS OF EUROPE

(Falconer, 1863).—As to the ridge formula of the mammoth, Falconer (1863, p. 64) remarks that in the European and American specimens the characters are constant, as defined by Cuvier and as witnessed in the British Museum collections from Siberia and in the American collections from Eschscholtz Bay. He concludes (*op. cit.*, p. 65): "They all present, in the main, the same characters: a uniform ridge-formula; the same obtuse form of the lower jaw, and the same broad crowned molars, composed of closely compressed colliculi, with numerous digitations and attenuated uncrimped enamel-plates. . . . One of the most essential points, is to determine the *constancy of the ridge-formula* [italics Osborn], which, after the examination of a very large quantity of materials, I believe in the Mammoth to be thus:

$$[\mathrm{Dp}\ 2]\ \tfrac{4}{4},\ [\mathrm{Dp}\ 3]\ \tfrac{8}{8},\ [\mathrm{Dp}\ 4]\ \tfrac{12}{12},\ [\mathrm{M}\ 1]\ \tfrac{12}{12},\ [\mathrm{M}\ 2]\ \tfrac{16}{16},\ [\mathrm{M}\ 3]\ \tfrac{24}{24}.\text{"}$$

Of this ridge formula he observes (*op. cit.*, p. 65): "The plates advance by quaternary increments in each series, bearing in mind, that the first true molar, although of larger dimensions, commonly repeats the number of ridges presented by the last milk-molar, and that the last true molar in all the Elephants and Mastodons is more composite than the others. . . . The formula in the North American Mammoth is identical with that of the Siberian and European forms. Exceptions are occasionally met, in which an unusual number of plates is presented."

Comparison with Elephas (Euelephas) indicus.—Falconer (1863) considers and repeatedly states that the ridge formula of *E. primigenius* is closely similar to that of the subgeneric group as typified by *E.* (*Euelephas*) *indicus* in which he corrects his formula of 1857, p. 315, and substitutes (*op. cit.*, p. 65) for *E. indicus* the following collective formula:

$$\mathrm{Dp}\ 2\ \tfrac{4}{4},\ \mathrm{Dp}\ 3\ \tfrac{8}{8},\ \mathrm{Dp}\ 4\ \tfrac{12}{12},\ \mathrm{M}\ 1\ \tfrac{12}{12},\ \mathrm{M}\ 2\ \tfrac{16}{16},\ \mathrm{M}\ 3\ \tfrac{24}{24\text{-}27}.$$

**f. Voigts Magazin. V. B. I. St S. 16 u. f.

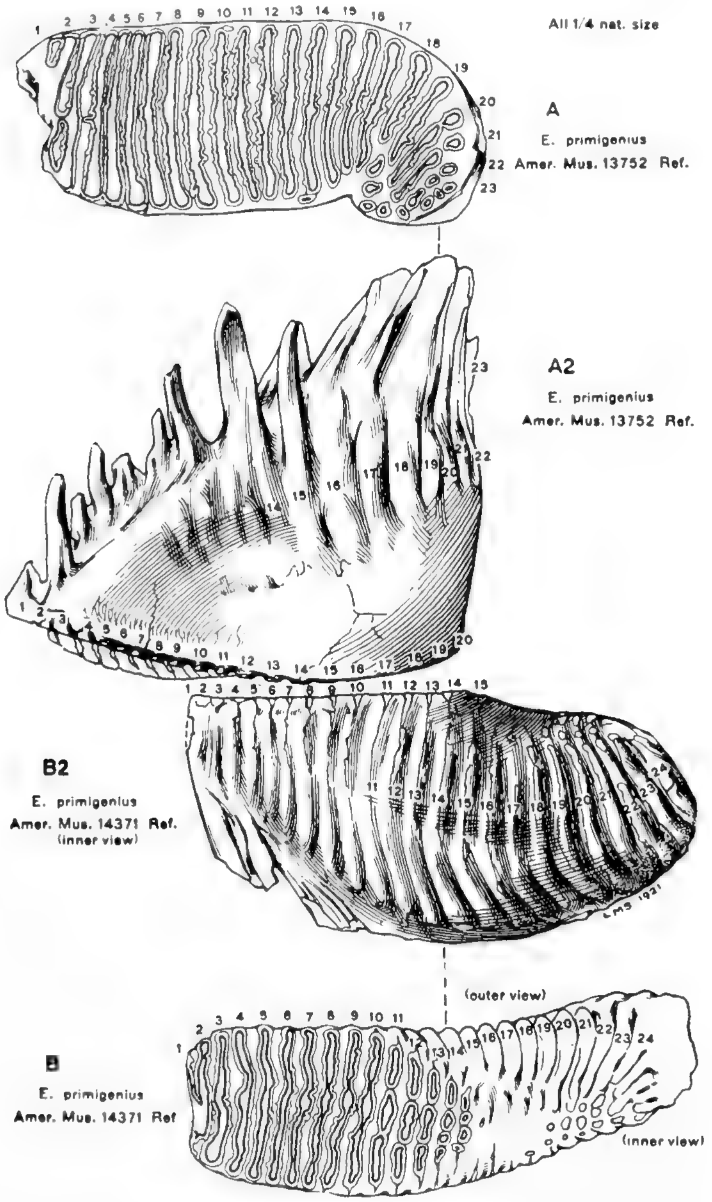
***(Kriegsr. Merk) *lettres sur les os fossiles d'elephans et de rhinoceros qui se trouvent en Allemagne &c.* I–III. St. Darmst. 1783 u. f. 4.

[1] See footnote 2 on page 1118.

Errors of Leith Adams, Lydekker, Hay.—Falconer, with unerring eye and logical mind, dwelt upon the *constancy* of the dental and cranial characters of *Elephas primigenius.* He did not confuse with this true species of mammoth (*E. primigenius*) the ridge formulæ of other species of elephants, as was done by subsequent writers, i.e., Leith Adams, Lydekker, Felix, Soergel, and Hay, who assigned to *E. primigenius* the *collective* ridge formula derived from a considerable number of species belonging, as shown in this Memoir, to two distinct phyla, namely, to *Mammonteus* and to *Parelephas.* As to the ridge formula of *Elephas primigenius*, Felix (1912) erroneously follows Leith Adams in giving the ridge formula of *E. primigenius* as $M\,3\,\frac{18-27}{18-27\,(?29)}$. This erroneous collective ridge formula first appears in Leith Adams (1879),[1] then in Lydekker (1886.2, p. 175), and finally reappears in Hay (1914, p. 395), as follows:

Collective ridge formula: $Dp\,2\,\frac{4}{4}\;Dp\,3\,\frac{6-9}{6-9}\;Dp\,4\,\frac{9-12}{9-12}\;M\,1\,\frac{9-15}{9-15}\;M\,2\,\frac{14-16}{14-16}\;M\,3\,\frac{18-27}{18-27}$.

The above partly erroneous formula is undoubtedly based on the ridge-plate formulæ of species of *Parelephas* combined with the ridge-plate formulæ of species of *Mammonteus.* This confusion throughout Hay's observations on the grinding teeth of *Elephas primigenius* (1914, pp. 395–410) unfortunately renders his observations of little systematic or phylogenetic value. Hay's observations had been summarized for extensive citation in the present Memoir, but for the reasons given we are obliged to omit them.



Referred Mammontfus primigenius Molars of Alaska with Typical M. primigenius Ridge Formula

Fig. 1008. Third superior and inferior molars (twenty-three to twenty-four ridge-plates) of *Mammonteus primigenius*, Alaska, of less compressed type (Amer. Mus. 13752, 14371). After Osborn, 1922.555, p. 10, fig. 9. The ridge formula of these typical specimens of *M. primigenius* corresponds very closely with that given by Falconer (1863) as characteristic of western Europe, namely, $\overline{M\,3}\,\frac{23+}{21}$.

A, Crown view, left M^3, twenty-three ridge-plates. A 2, Outer view of same tooth. It is apparent that one or possibly two of the anterior ridge-plates have been worn off, consequently the formula should be written: $M\,3\,\frac{23+}{24}$.

B 2, Inner view of right M_3 of another individual, twenty-four ridge-plates. B, Crown view of same.

Osborn's Observations (1922–1924) on American Museum Specimens Referred to Mammonteus primigenius

Osborn (1922) supports Falconer's observations of 1863.

Compare Osborn, 1922.555, pp. 7–11.—*Elephas primigenius* is the name assigned to a series of species which ranged through the entire Pleistocene epoch, from the Lower Pleistocene Forest Bed[2] deposits of East Anglia to the southerly range of this animal in the middle United States. It is a collective species embracing an undoubted progressive evolution and intensification of specific characters extending over a very long period of time. It exhibits various extremes of fore-and-aft compression of the cranium with related fore-and-aft compression of the grinding teeth (*hypsicephaly* and *bathycephaly*). The cranium is high, pointed at the summit, relatively narrow, and relatively deep. The forehead from the peak of the cranium to the extremity of the nasals is relatively elongate and slightly concave.

Ridge-plate Compression.—As compared with *E. columbi* and *E. imperator*, 10 ridge-plates of *M. primigenius* are compressed into a line 100 mm. in length in the typical *M. primigenius* of Germany; the most highly compressed tooth observed by Osborn is an M^3 from Alaska (Amer. Mus. 13749 [paratype of *M. primigenius compressus*]) in which 13 ridge-plates are compressed into a line 100 mm. in length (Fig. 1024); a similar condition prevails in a female skull from Indiana (Amer. Mus. 14559 [since made the type of *M. primigenius compressus*]), in which 13 ridge-plates are compressed into a 100 mm. space, the total number of ridge-plates rising to 27 (Fig. 1022).

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[1] See Bibliography of the present Memoir, Vol. I, p. 762, under Leith Adams, 1877-1881.

[2] The Forest Bed *Mammonteus primigenius astensis*(?) is diagrammatically figured (Fig. 871, *Archidiskodon*, Chapter XVI, the present Chapter, Fig. 1020) in comparison with the contemporaneous molars of *Parelephas* (C, D) and with *Archidiskodon* (E–H). This figure by the author shows (A) the thin, fine-plated or "slightly thick" (*fide* Falconer, 1868, Vol. II, p. 170) enamel characteristic of *Mammonteus* at the beginning of Pleistocene time.

The prevailing condition, however, is of the kind shown in figure 1008, namely, Amer. Mus. 13752, from Alaska, in which the ridge formula is M 3 $\frac{23+}{}$, here figured with a lower molar (Amer. Mus. 14371), in which the ridge formula is M 3 $\frac{}{24}$; in these specimens there are 10 plates in a 100 mm. line; these less compressed molars are arcuate, thus the count of the ridge-plates is greater on the concave side of the tooth and smaller on the convex side.

For example, in a superior molar, M^3 (Amer. Mus. 10656), from Germany, the compression is as follows:

M^3 10 ridge-plates in 100 mm. on the external convex surface,
11 ridge-plates on the horizontal mid-coronal surface,
12 ridge-plates on the internal concave surface.

In the lower molars, these M^3 conditions are reversed in counting the ridge-plates in which the external surface is concave and the internal surface is convex. For example, in an M_3 from Alaska (Amer. Mus. 14343) the count is as follows:

M_3 10 ridge-plates in 100 mm. on the external concave surface,
10 ridge-plates in 100 mm. on the horizontal mid-coronal surface,
8–9 ridge-plates in 100 mm. on the internal convex surface.

In the *highly compressed* superior tooth, M^3 (Amer. Mus. 13749 [paratype of *M. primigenius compressus*]), from Alaska (Fig. 1024), the count on all three measurements is the same, namely:

M^3 13 ridge-plates in 100 mm. on the external convex surface,
13 ridge-plates in 100 mm. on the horizontal mid-coronal surface,
13 ridge-plates in 100 mm. on the internal concave surface.

It follows from the above observations that the horizontal mid-coronal section gives, as a rule, an average between the internal and external sides; the average in *M. primigenius* is 10 ridge-plates in 100 mm., the minimum observed is 8 in 100 mm., the maximum observed is 13 in 100 mm.[1] This variation in compression applies to fifteen specimens ranging through England, Germany, Siberia, Alaska, Ohio, and Indiana, and characterizes the *typical M. primigenius* M^3 of Thuringia, Germany (cf. Soergel, 1912.2, Tab. VII, VIII).

The worn mid-coronal surface is sometimes fully horizontal, i.e., at right angles to the perpendicular ridge-plates; in such case it registers the exact distance between the plates. In other cases the wear is obliquely horizontal; in which case it increases the actual distance between the plates. It is important to note also that the ridge-plates are arcuate and more closely compressed towards their summits; thus more ridge-plates may be counted in 100 mm. at the summit of the crown than at the base of the crown, and *as a rule the ridge-plate count should be taken midway between the summit and the base, both on the internal and external sides.*

COMPARISON WITH PARELEPHAS AND MAMMONTEUS PRIMIGENIUS COMPRESSUS

By the above observations of Osborn, the *typical* ridge formula of M 3 of *Mammonteus primigenius* agrees precisely with that established by Falconer in 1863, namely: M 3 $\frac{24}{24}$. This relatively low ridge formula agrees approximately with that of *Parelephas jeffersonii*, namely, M 3 $\frac{25}{24}$, but the M^3 of *M. primigenius* is relatively shorter and deeper than the M^3 of *P. jeffersonii*; consequently the ridge-plate compression is much closer in *M. primigenius.* The ridge-plate compression is still closer in *Mammonteus primigenius compressus*, in which M 3 is the broadest and deepest proboscidean molar known, the formula being M 3 $\frac{27}{(?)27}$, the ridge-plate compression rising to 13 in 100 mm. Undoubtedly intermediate ascending mutations will be found between these two stages of ridge-plate evolution; meanwhile they may be distinguished as follows:

Typical *Mammonteus primigenius primigenius* of northern Europe, Alaska, and the United States: ridge formula M 3 $\frac{24}{24}$; ridge-plate compression in the superior molars 10–11–12 in 100 mm.

Mammonteus primigenius compressus of Alaska and Indiana: ridge formula M 3 $\frac{27}{(?)27}$; ridge-plate compression 13 in 100 mm.

A fresh survey of the true *Mammonteus primigenius* grinding teeth, of Alaska and the northern United States, will probably reveal a series of intermediate *ascending mutations* between these two extremes. When the grinding teeth which have been erroneously referred to *Mammonteus primigenius* are eliminated, namely, all of those molars actually belonging to *Parelephas*, we shall probably discover these transitional mutations.

SKULLS AND JAWS OF MAMMONTEUS PRIMIGENIUS

Compare Figures 865, 962, 1009, 1010, 1023

The true cranium of *Mammonteus primigenius* (Figs. 865, 962 C, C^1) is readily distinguishable from that of *Parelephas trogontherii* (Fig. 865) and of *P. jeffersonii* (Fig. 962 A) with which it has been confused except by Pohlig. The jaws of *M. primigenius* (Fig. 962 C, C^1, and Fig. 1011 C, B, A) are also clearly distinguishable. In this connection observe the characters pointed out by Falconer, Leith Adams, Pohlig, and others enumerated above.

Cranial Materials Figured Herewith (Figure 962).—Crania of the true *Mammonteus primigenius*, as distinguished from crania of *Parelephas jeffersonii*, are very rare in the United States. Fortunately there is a finely preserved cranium from Siberia in the United States National Museum (Nat. Mus. 8580), photographs of which are reproduced in figure 962; the lateral aspect of this cranium (Fig. 962 C) is perfect, but the frontal aspect (Fig. 962 C^1) is foreshortened and thus gives an erroneous impression of the *height* of this cranium.

Cranial Characters.—All the distinctive characters of the true *Mammonteus primigenius* skull arise from the maximum *fore-and-aft compression*, resulting in bathycephaly and hypsicephaly, which exceeds by far that of any other proboscidean or other mammalian skull thus far known. (1) This compression brings the anterior rim of the orbits much closer to the occipital condyles (Fig. 962 C^1) than in either *P. jeffersonii* (Fig. 962 A), or *P. washingtonii* (B); (2) it elevates the occipital crest, which is relatively higher, more elevated, and more pointed, i.e., acrocephalic, in *M.*

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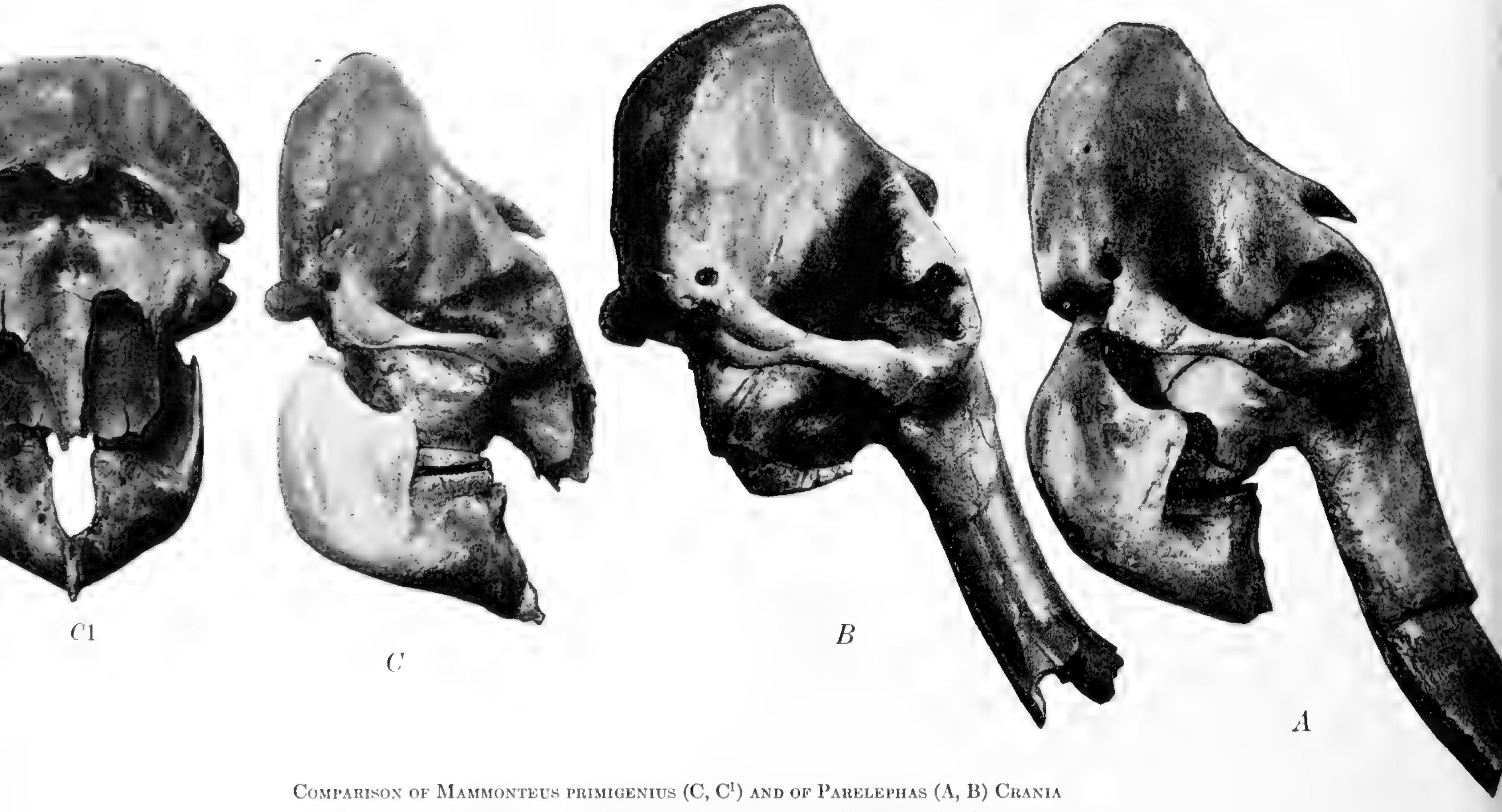
[1] [In *Mammonteus primigenius compressus* Osborn.—Editor.]



COMPARISON OF MAMMONTEUS PRIMIGENIUS (C, C^1) AND OF PARELEPHAS (A, B) CRANIA
See also comparative figure (Fig. 865) of the European Crania

Fig. 1009. Profile views of type and referred skulls of *Parelephas jeffersonii* (A), *P. washingtonii* (B), and *Mammonteus primigenius* (C) in the American Museum and United States National Museum, also front view of *M. primigenius* (C^1). All figures one-twelfth natural size.

A, Type of *Parelephas jeffersonii* (Amer. Mus. 9950), reversed. An aged individual. Main portion of the tusks not included. From Jonesboro, Indiana.

B, Referred skull of *Parelephas washingtonii* (Amer. Mus. Cope Coll. 8681). From Whitman County, Washington.

C, Referred skull of *Mammonteus primigenius* (Nat. Mus. 8580), from Siberia, with jaws belonging to another individual (Nat. Mus. 8579), from Alaska.

C^1, Front view of same skull and jaws.

primigenius (Fig. 962 C) than it is in *P. jeffersonii* (Fig. 962 A) or *P. washingtonii* (Fig. 962 B). (3) This fore-and-aft compression brings the auditory foramen of *M. primigenius* close to the occipital condyles; it increases the *hypsicephaly*, whereby the apex of the occipital crest is raised relatively higher above the grinding surface of M^3; and (4) it accounts for the extreme hypsodonty of M^3, which is the highest and the shortest of all proboscidean molar teeth. (5) This compression or bathycephaly extends to the lower jaw which has an excessively short, deeply depressed ramus, terminating in a deflected and extremely narrow rostrum (Fig. 962 C, C^1). (6) This vertical compression or hypsicephaly extends to the vertically placed tubular maxillo-premaxillary insertions of the incisor tusks (Fig. 1023), which are relatively longer, narrower, and deeper than those of any species of *Parelephas*. (7) The frontal or facial aspect of *Mammonteus primigenius compressus* (Fig. 1023) is quite distinct from the frontal or facial aspect of *Parelephas* (Fig. 961); the arches supporting the orbits appear relatively broader, because the frontals above and the maxillaries below are laterally compressed.

Figures 865, 934, 937.—Comparison with crania referable to the typical *M. primigenius* of western Europe is afforded in figure 865, especially the frontal view (No. 2) inscribed " *E. primigenius* Ref., Falc., 1847, Pl. XLIII, Fig. XXIV"; this west European cranium may be considered a "typical *Mammonteus primigenius.*" As far as we can judge from Falconer's figure (1847, Pl. XLIII, fig. XXIV) this cranium shows exactly the same characters throughout as the crania above described from Alaska and from Indiana; we observe especially the small anterior nares, the tubular tusk insertions, the extremely elevated occiput.

Another "typical *Mammonteus primigenius*" cranium (Figs. 865, 934) is that figured after Pohlig (Pohlig, 1891, p. 384, fig. 120—reversed); this cranium in profile view may be compared with that of the female skull (*Mammonteus primigenius compressus*) from Indiana (Fig. 1023) in its extreme acrocephaly, hypsicephaly, fore-and-aft compression, deep M^3 insertion, and relatively plano-frontal and occipital surfaces. In brief, the west European crania of the true *M. primigenius* exhibit precisely the same characters as the true *M. primigenius* crania of Alaska and of Indiana. They completely confirm the specific and generic separation of the cranium of *Mammonteus* from the cranium of *Parelephas* and still more from the cranium of *Elephas*. Doubtless other true crania of *M. primigenius* will be discovered in the United States and in Alaska; it is of the utmost importance that these should be carefully exhumed and that they should find their way permanently to some museum.

Figure 1010.—It is through the courtesy of Charles W. Gilmore of the United States National Museum that we reproduce herewith (Fig. 1010) a superb cranium and tusks of *M. primigenius* discovered in the Yukon Territory, Canada, and described by Gilmore (1908, Pl. VII); it is difficult to determine from the photograph whether this cranium belongs to the true *Mammonteus* or to *Parelephas*; we are inclined to relate it to *Mammonteus*. A profile photograph of this fine skull would at once determine the question of its affinity.

CRANIUM OF MALE MAMMONTEUS PRIMIGENIUS OF THE YUKON

Fig. 1010. Male skull and tusks probably referable to *Mammonteus primigenius*, found in gravel 42 feet below the surface on Quartz Creek, near Dawson, Yukon Territory, Canada, March, 1904. After photograph by Gilmore appearing in his important paper entitled, "Smithsonian Exploration in Alaska in 1907 in Search of Pleistocene Fossil Vertebrates, Second Expedition," 1908, Pl. VII.

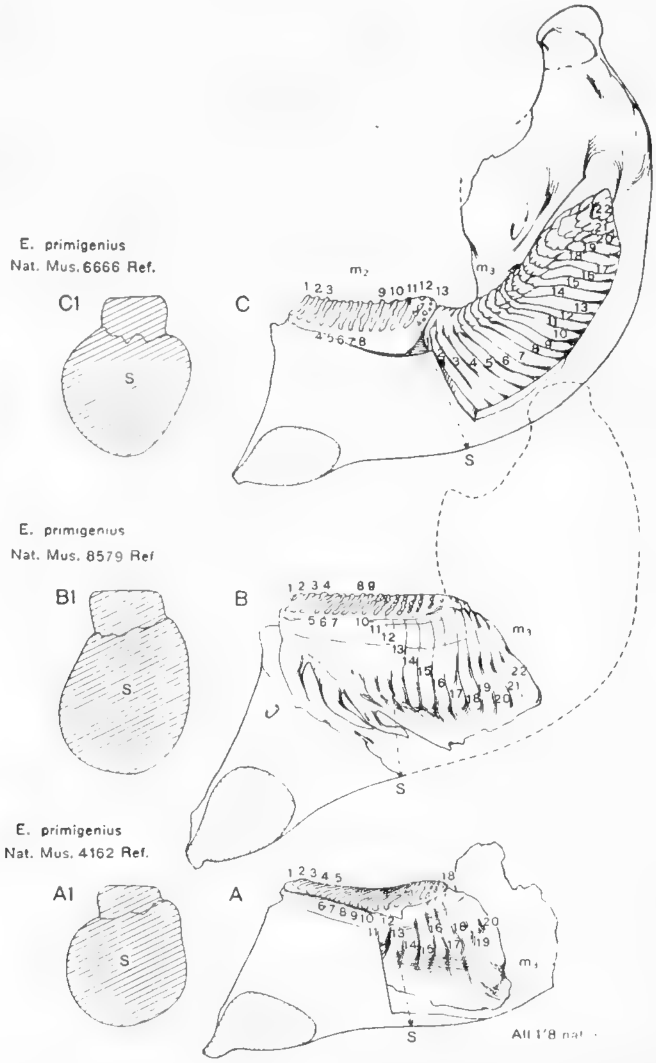
As observed in the text, the generic and specific reference of this skull is somewhat uncertain; the very prominent antorbital tuberosities resemble those in the type female skull of *Mammonteus primigenius compressus of* Indiana.

Figure 1023.—Fortunate also is the preservation of the skull of a female mammoth (*M. primigenius compressus* type) in the American Museum (Amer. Mus. 14559) from Rochester, Indiana, which more correctly shows the frontal plane of the true *Mammonteus primigenius* cranial type.

JAWS OF THE TRUE MAMMONTEUS PRIMIGENIUS

We have enumerated above (pp. 1141–1144) the chief observations of Falconer, Leith Adams, Pohlig, Soergel, and other writers on the jaws of the European specimens of the true *Mammonteus primigenius*. The characters observed in the American specimens are as follows:

The first jaw (Nat. Mus. 6666—shown in Fig. 1011 C) is from Alaska, twenty-five miles north of Anvik. The second jaw (Nat. Mus. 8579—Fig. 1011 B) is also from Alaska, and indicates twenty-four ridge-plates; the third jaw (Nat. Mus. 4162—Fig. 1101 A) is from Elephant Point, Alaska. We owe to Gidley exact information regarding the American crania and jaws referred to *Mammonteus primigenius* in the present Memoir.



GROWTH STAGES IN THE JAWS AND TEETH OF MAMMONTEUS PRIMIGENIUS

Fig. 1011. Internal aspect of three jaws of typical *Mammonteus primigenius* from Alaska, in the United States National Museum. All one-eighth natural size. Sections C1, B1, A1.

C, Juvenile jaw of *Mammonteus primigenius* (Nat. Mus. 6666) from Alaska, twenty-five miles above Anvik. Ridge formula: M 2 $\frac{}{13+}$, M 3 $\frac{}{22+}$. In M_2 at least one plate is missing in front of the alveolus of the anterior root, therefore there may be four or more plates missing; total preserved thirteen, maximum seventeen ridge-plates in M_2. In M_3 no ridge-plates in use; 22+ ridge-plates developed out of the typical twenty-four ridge-plates characteristic of this species.

B, Adult *Mammonteus primigenius* jaw (Nat. Mus. 8579) from Alaska, showing M_3 *in situ*; seventeen plates in use, five additional plates, total twenty-two plates; apparently the two anterior ridge-plates of the typical number twenty-four have been worn off in this adult jaw.

A, Aged *Mammonteus primigenius* (Nat. Mus. 4162), from Elephant Point, Alaska, M_3 *in situ*; seventeen to eighteen plates in use, two additional plates unworn, nineteen to twenty plates present, apparently four anterior ridge-plates worn off out of the maximum twenty-four characteristic of this species.

Jaw Characters.—As in the case of the skull, the jaws of the true *Mammonteus primigenius* have doubtless been partly confused by Falconer and by all subsequent writers with those properly belonging to *Parelephas* both in Eurasia and in North America.

As shown in figures 962 and 1011 of this Memoir, the true *Mammonteus* jaws, with their true *Mammonteus* inferior grinding teeth, are harmonic with the extreme *hypsicephaly* and *bathycephaly* of the cranium. In proportion they are shorter anteroposteriorly, and deeper from the mandibular condyle to the symphysis of the mandibuli; the rostrum is deeper and more deflected; the section of the ramus is more rounded.

These hypsicephalic proportions of the jaw are clearly displayed in the referred *adult* jaw of *Mammonteus primigenius* (Nat. Mus. 8579) from Alaska, which is shown in side view in figure 962C and in mid-section in figure 1011 B1; this adult jaw, both in external aspect (Fig. 962) and in section (Fig. 1011 B, B1) displays the deeply *depressed rostrum*, also the relatively abbreviated third inferior molar, M_3.

In the young *M. primigenius* jaw (Nat. Mus. 6666) the rostrum is less depressed and as a whole is relatively longer and partakes more of the character of the young jaw of *Elephas indicus*; in fact, all young jaws of *Elephas*, of *Mammonteus*, and of *Loxodonta* are relatively elongate, and the deep, hypsicephalic proportion is acquired only in the adult.

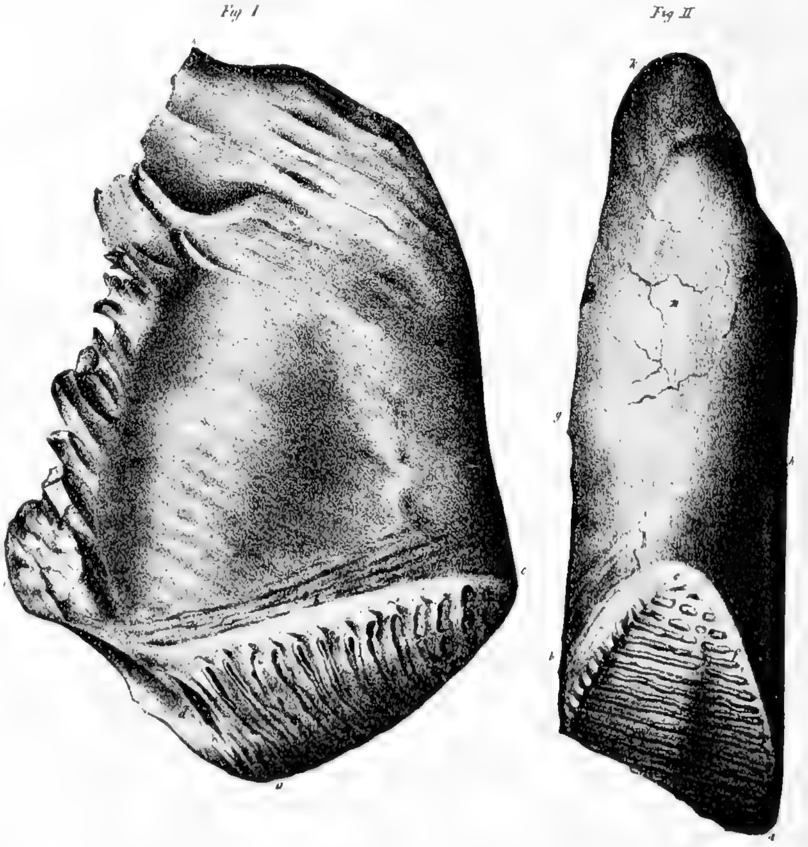
Fortunately three growth stages of the typical *Mammonteus primigenius* jaws are well displayed (Fig. 1011) in three specimens in the United States National Museum, as carefully drawn to a uniform one-eighth scale.

Comparison of Mammonteus with Parelephas and Archidiskodon.—Exactly similar mid-sections of the jaws of *Archidiskodon* and of *Parelephas* are shown in figures 892 and 893, by which it appears that the adult jaw of *Mammonteus primigenius* may readily be distinguished from adult jaws of *Archidiskodon* and of *Parelephas* in mid-section; also from the adult jaw of *Elephas indicus* (Fig. 893, D, D1) by the following bathycephalic characters: (1) Depression of the rostrum; (2) elevation of the coronoid and of the mandibular condyle; (3) narrowness of the space between the anterior border of the condyle and the posterior border of the angle; (4) relative abbreviation and depth of M_3, which is compressed into a much smaller, shorter space anteroposteriorly than that of *Parelephas jeffersonii* or of *Archidiskodon imperator*. This confirms the statement above, that the jaws and inferior grinders of the true *Mammonteus* are shorter, deeper, that is, more bathycephalic, in proportion, than the jaws of *Elephas*, *Parelephas*, or *Archidiskodon*.

Fischer de Waldheim, 1829.1, p. 285.—"C'est à Mr. le Baron Cuvier que nous devons le développement des caractères anatomiques qui font distinguer le *Mammont* ou l'espèce fossile d'Eléphant, de celles qui existent encore. Je me suis porté longtemps avec l'idée, que j'ai énoncée dans ma Zoognosie [Footnote: 'Fischer, Zoognosia tabulis synopticis illustrata. Mosquae. Vol. III, p. 320.'], que parmi les ossemens fossiles d'Eléphant pourraient être cachées plusieurs espèces, que nous confondons dans une seule, savoir celle du Mammont. La forme de la mâchoire inférieure, surtout celle des dents molaires et de leur lames nous conduisent à des différences, qu'on ne saurait admettre dans une et la même espèce. Voici le résultat de mes recherches sur beaucoup de dents molaires que j'ai pu examiner et qui me fait distinguer les espèces suivantes:

1. *Elephas mammonteus,* dentibus molaribus rectis, laminis numerosis angustis, parum elevatis, anguste fimbriatis.
2. *Elephas paniscus,* dentibus molaribus rectis, laminis latis elevatis, parum fimbriatis, latere longe distinctis.
3. *Elephas periboletes,* dentibus molaribus rectis, laminis elevatis, profunde fimbriatis, oblique projectis.
4. *Elephas pygmaeus,* dentibus molaribus similibus mammonteo; sed magnitudine, plus quam dimidio minoribus.
5. *Elephas campylotes,* dentibus molaribus subarcuatis, laminis angustis, numerosis, arcuatis, parum elevatis.

Later in the same year in a Bulletin of the Société Impériale des Naturalistes de Moscou, Fischer (1829.2) reviews the above five species to which he adds a sixth (p. 276) under the designation of *Elephas Kamenskii,* as follows: "D'aprés cette manière de voir, il faudrait nécessairement indiquer comme espèce distincte celle,



A Typical Third Superior Molar of Mammonteus primigenius

Fig. 1012. Type of *Elephas odontotyrannus* Eichwald, 1835, Pl. lxiii, figs. 1 and 2. One-third natural size. Last superior molar of the "right" [left] side, l.M³. From Russia.

à la quelle a appartenue la mâchoire inférieure de Siberie que nous devons à S. E. Mr. Bantich-Kamensky."

> "6. *Elephas Kamenskii*, molaribus subarcuatis utrinque attenuatis; laminis parum elevatis, numerosis, medio annulatis."

History and Synonymy.—Following the early descriptions of Ludolf (1696) and of Ides (1706), the mammoth waited nearly a century for the generic name *Mammonteus* Camper (1788)[1] and another decade (1799) for the specific name *primigenius* Blumenbach, after which it was fairly deluged with the host of generic and specific names listed above, which rank with those applied to the *Mastodon* among the curiosities of scientific literature. Cuvier (1806.1) traces the discovery of fossil elephants back to Theophrastus (born 372 B. C., died 287 B. C.), a pupil of Aristotle, and follows (*op. cit.*, pp. 4, 5) with discoveries in Greece, Crete, and North Africa, continuing with a long account of the introduction of the domestication of the recent elephant in Europe and Africa and closing with a summing up of all the previous fossil discoveries of elephants of Upper Pliocene and Miocene times in all parts of Europe and northern Asia, as well as of the *Mastodon* in America. In the first and all subsequent editions of the "Ossemens Fossiles" he recognizes only three species of elephants, living and fossil, namely, *Elephas africanus*, *Elephas indicus*, and *Elephas primigenius*, which he clearly separates by cranial and dental characters, as cited above (caption to Fig. 992).

Adams (1807), Tilesius (1815).—Adams described the animal as the mammoth; he states on page 152 that Blumenbach actually called the animal *Elephas primævus.* Cuvier assigned the name *Elephas mammonteus* to the northern Mammoth (1799). Brandt named it *Elephas brachyramphus* (read 1831, published 1832). From the time of Camper (1788) and of Cuvier to the time of Tilesius (1815) a classical feature of the various descriptions is the constant use of "mammonteum," "mammonteus," and "mammonteo" as the Latin designation of the mammoth, first as an adjective and then as a specific name, i.e., *Elephas mammonteus* Cuvier, as compared with *Elephas indicus* Linnæus.

Among the outstanding points in Tilesius' 100-page description in Latin of the 'Adams skeleton' are the measurements given in "pedum anglicum" [=about 9 inches] and "pollicum anglicum" [=about 1 inch]. Tilesius gives the entire length of the skeleton, from the curvature of the tusks to the tip of the tail, as "viginti pedum" [=about 15 feet in our measurement]. The vertebral column, according to the Adams-Tilesius descriptions of 1807, 1815 (written immediately on Adams' return from the field), includes 28–30 presacrals, that is, from the first cervical to the last lumbar, as follows:

Cervicals	7
Dorsals	17–19?
Lumbars	4?
Caudals	8+

Only the eight anterior caudals are preserved [see Tilesius' figure reproduced herewith (Fig. 1014), which includes 7 cervicals, 17–19? rib-bearing dorsals, and 4 lumbars, or 28–30 presacral vertebræ].

Adams, in describing this specimen, used the quaint measurements and language of the time (Adams, 1807, "Relation d'un Voyage à la Mer Glaciale et Découverte des restes d'un Mammouth," Journ. du Nord, St. Petersburg, translated by Sir Joseph Banks, Philosophical Magazine, 1808, Vol. XXIX, p. 148): "The parts least damaged are a fore foot and a hind one; they are covered with skin, and have still the sole attached. According to the assertion of the Toungouse chief, the animal had been so large and well fed, that its belly hung down below the knee joints. This mammoth is a male, with a long mane at his neck, but it has no tail and no trunk. The skin, three-fourths of which are in my possession, is of a deep gray, and covered with a reddish hair and black bristles. The humidity of the soil where the animal has lain so long, has made the bristles lose some part of their elasticity. The entire carcase, the bones of which I collected upon the spot, is 4 archines and a half high by 7 long, from the tip

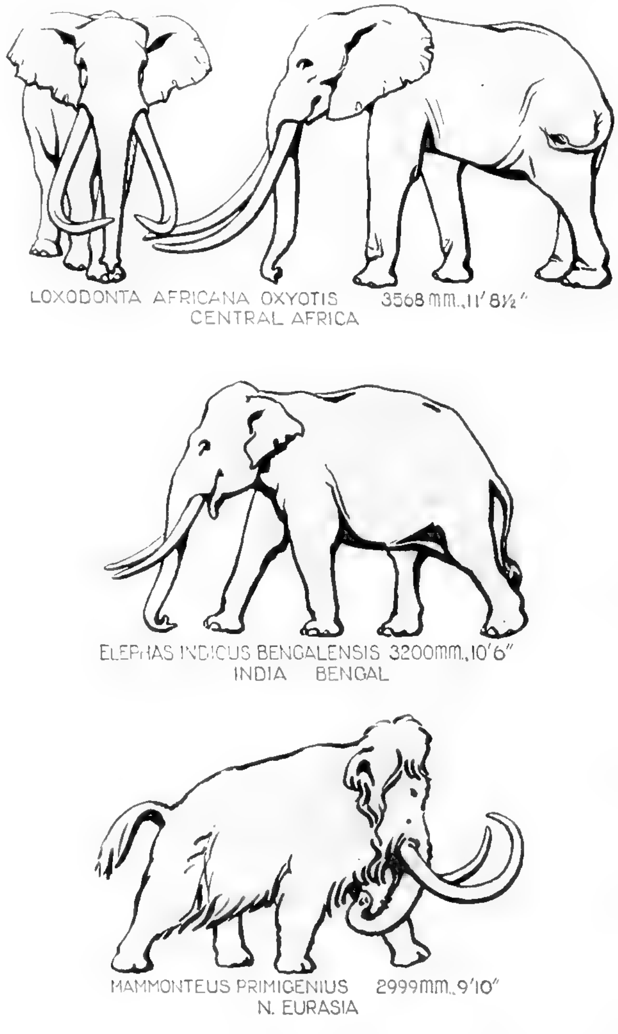


Fig. 1013. Restorations by Margret Flinsch Buba, under the direction of Henry Fairfield Osborn, of *Loxodonta africana oxyotis*, *Elephas indicus bengalensis*, and *Mammonteus primigenius*. All figures to a one one-hundredth scale.

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[1] [See footnote on page 1117 above regarding the validity of the genus *Mammonteus*.—Editor.]

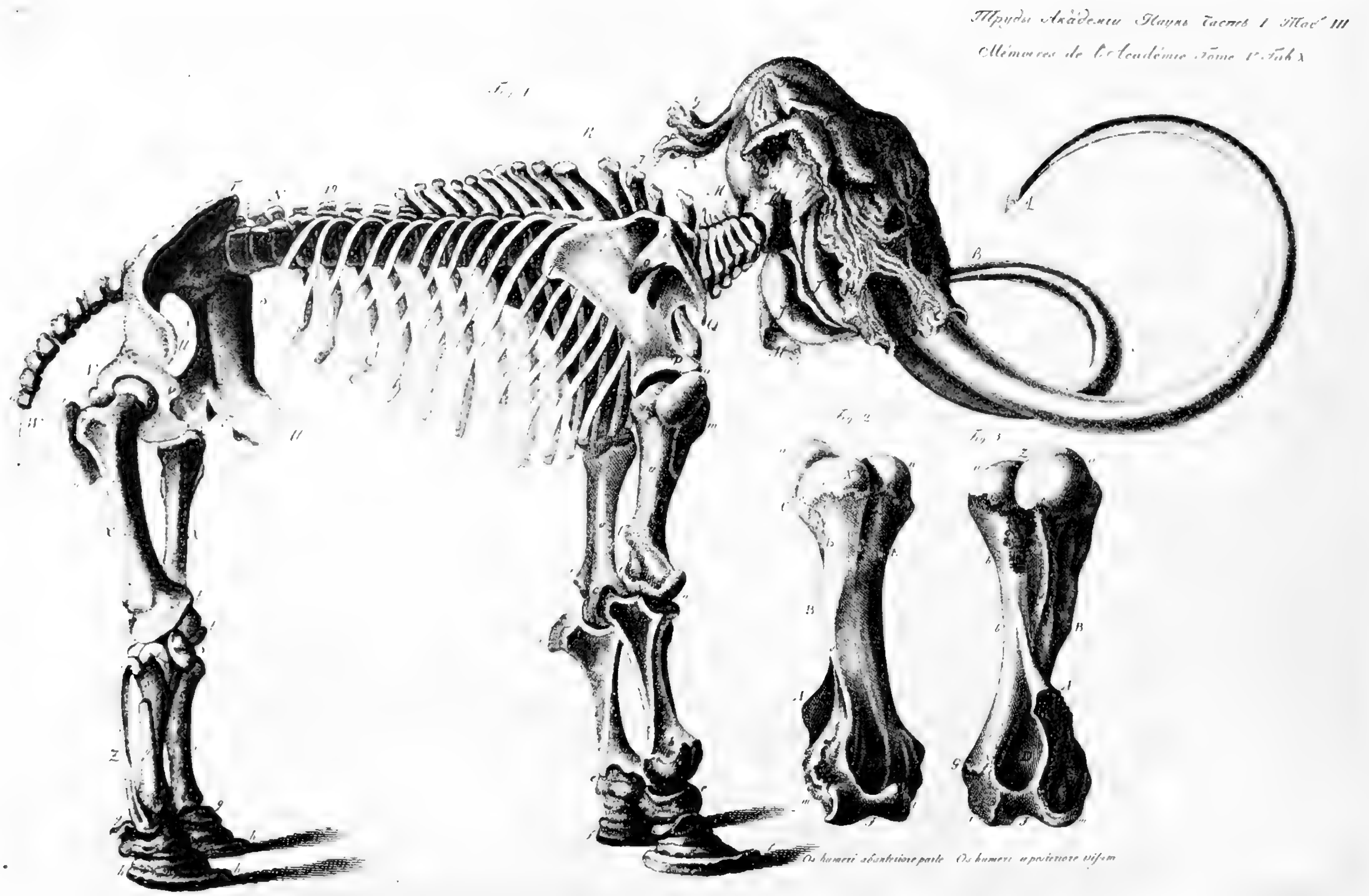

Fig. 1014. 'Adams skeleton' of *Elephas primigenius* Blum. in the Zoological Museum of the Academy of Sciences of the U. S. S. R., Leningrad, Russia. Reproduced after Tilesius, 1815, Tab. x. About one twenty-sixth natural size. This was also reproduced by Cuvier in his "Recherches sur les Ossemens Fossiles," Quatrième Edition, Atlas, 1836, Pl. 17 (xi), one-fiftieth natural size. (Cf. Cuvier, *op. cit.*, 1836, Explanation of Plates, p. 9): "Planche 17. Éléphans. Pl. xi. *Fig.* 1. Squelette entier d'éléphant fossile, rapporté par M. Adams de la mer Glaciale et copié d'après Tilésius. L'oreille *a b* a conservé quelques parties molles, et les pieds sont encore couverts de peau, et garnis de leurs semelles."

of the nose to the coccyx [Footnote: 'An archine is a little more than two feet English measure.']; without however comprehending the two horns, each of which is a toise and a half long, and both together weigh 10 pouds [Footnote: 'A poud is 40 pounds.']. The head alone weighs eleven pouds and a half."

Length of vertebral column	12–14 "pedum anglicum"	[=9–10 feet]
Neck short	17 "pollicum anglicum"	[=17 inches]
Entire length of skeleton, from forward arch of tusks to tuberosities of ischium	20 "pedum anglicum"	[=15 feet]
Height of skeleton	4 "archines" and a half	[=about 9 ft. 3 in.[1]]
Length of tusks	1½ "toise"	[=about 9 feet]
Length of humerus	40 "pollicum anglicum"	[=about 3 ft. 4 in.]
Length of cubitus or ulna	35 "pollicum anglicum"	[=about 2 ft. 11 in.]
Length of femur	46½ "pollicum anglicum"	[=about 3 ft. 10½ in.]
Length of tibia	28 "pollicum anglicum"	[=about 2 ft. 4 in.]
Height of scapula	29 "pollicum anglicum"	[=about 2 ft. 5 in.]

CUVIER (OP. CIT., 1834, VOL. II, PP. 131, 133, 204, 208, 231).—Cuvier describes this famous skeleton as follows: "La deuxième est celle de l'éléphant rapporté à Pétersbourg par M. Adams, et dont la conservation allait presque jusqu'au merveilleux. Le fait fut annoncé d'abord en octobre 1807, dans le Journal du Nord,

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[1] [Lang in his article in Zoologica (1925.1, p. 28) gives a height of 9 ft. 11 in. at the shoulder, as mounted in the Leningrad Museum.—Editor.]

recueil imprimé à Pétersbourg, n° xxx, et ce morceau, qui a reparu depuis en divers journaux allemands, a été réimprimé en 1815, dans le tome V^{e} des Mémoires de l'Académie de Pétersbourg. Nous en tirons les détails qui suivent. En 1799, un pêcheur Tongouse remarqua sur les bords de la mer Glaciale, près de l'embouchure de la Léna, au milieu des glaçons, un bloc informe qu'il ne put reconnaître. L'année d'après il s'aperçut que cette masses était un peu plus dégagée, mais ne devinait point encore ce que ce pouvait être. Vers la fin de l'été suivant, le flanc tout entier de l'animal et une des défenses étaient distinctement sortis des glaçons. Ce ne fut que la cinquième année que les glaces ayant fondu plus vite que de coutume, cette masse énorme vint échouer à la côte sur un banc de sable. Au mois de mars 1804, le pêcheur enleva les défenses, dont il se défit pour une valeur de cinquante roubles. On exécuta, à cette occasion, un dessin grossier de l'animal, dont j'ai une copie que je dois à l'amité de M. Blumenbach. . . . L'animal était mâle; ses défenses étaient longues de plus de neuf pieds en suivant les courbures, et sa tête, sans les défenses, pesait plus de quatre cents livres. . . . [p. 204] Encore plus récemment j'ai retrouvé ces longs alvéoles dans le crâne des bords du Volga, gravé par M. Tilésius, et dont je donne une copie pl. 15, fig. 7. Il est vrai que ce caractère ne se montre pas sur le grand squelette de M. Adams, mais M. Tilésius nous dit expressément que les Tongouses avaient mutilé les bords des alvéoles lorsqu'ils en arrachèrent les défenses, et qu'ensuite M. Adams, pour les y rajuster, fit encore rogner et égaliser ces bords [Footnote: Mém. de l'Acad. de Pétersb., t. v. (1815), p. 511.]."

Measurements
(Compare *op. cit.*, p. 208)

	Crâne de Messerschmidt, Transact. philos., vol. xl, pl. I. Pl. 8, fig. I [Fig. 991]	Crâne du squelette de M. Adams, Pl. 17, [Fig. 1014]
Depuis le sommet jusqu'au bord des alvéoles	1,178	1,300
Depuis le sommet jusqu'aux condyles occipitaux	0,663	0,770
Des condyles aux bords alvéolaires		0,946

(Cuvier, *op. cit.*, p. 231): "La peau est semblable à celle de l'éléphant vivant, mais on n'y distingue pas les points bruns qu'on remarque dans l'espèce des Indes. M. Adams assure que la peau dont il avait conservé les trois quarts était d'un gris foncé. . . . [p. 232] M. Adams nous dit qu'une des oreilles de son individu était bien conservée et garnie d'une touffe de crins; mais dans son état actuel, comme on peut le voir, pl. 17 *ab*, fig.I, elle est fort altérée et n'a plus aucun poil. Les pieds du squelette de Pétersbourg sont encore couverts de peau et garnis de leurs semelles. M. Tilésius dit que ces semelles sont arrondies, et comme dilatées et foulées par le poids du corps; en sorte qu'elles remontent sur les bords du pied et les recouvrent. Il y avait quelque chose de semblable dans l'éléphant de la ménagerie de Versailles, décrit par Perrault. Ni M. Adams, ni M. Tilésius ne nous parlent du nombre des ongles."

2. PRIMITIVE EUROPEAN STAGES OF MAMMONTEUS PRIMIGENIUS

As listed above (pp. 1136–1138), European stages of dwarfed dimensions, or supposedly more primitive than the typical *Mammonteus primigenius* of late Glacial and Postglacial times, were described in the following order:

1888 *Mammonteus primigenius leith-adamsi* Pohlig, a dwarfed *3d*(?) *Interglacial* race of Thuringia, Germany.
1891 *Mammonteus primigenius hydruntinus* Botti, a dwarfed race of the cavern of Cardamone, Otranto, southeastern Italy.
1912 *Mammonteus primigenius fraasi* Dietrich, an Upper(?) Pleistocene stage of Steinheim on the Murr, central Germany.
1923 *Mammonteus primigenius astensis* Depéret and Mayet, an Upper Pliocene stage of Piedmont, northern Italy.

Between the typical *Mammonteus primigenius* Blum. of northern Germany and the Upper Pliocene[1] *M. primigenius astensis* of northern Italy there are doubtless numerous intermediate *ascending mutations* which only by very close monographic research can be clearly distinguished from each other. It must be remembered, however, that *Mammonteus* was not a permanent resident like the members of the *Hesperoloxodon antiquus* or *Parelephas trogontherii* phyla, but a southerly and northerly migrant during the advances and retreats of the four great glaciations. Pohlig regards his subspecies *leith-adamsi* (Fig. 1015) as a diminutive variety of *3d*(?) *Interglacial* time in the forests of Thuringia, while Botti describes also as a dwarfed subspecies his *hydruntinus*[2] (Fig. 1016) from the caverns bordering the Otranto Straits, southeastern Italy. Dietrich clearly distinguishes his subspecies *fraasi* (Fig. 1017) as a full-sized race, with pentadactyl manus and pes, of Middle [Upper?] Pleistocene time, living on the

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[1] [Possibly Lower Pleistocene (see footnote 1 on p. 1049 above).—Editor.]

[2] Bearing on the presence of *Mammonteus primigenius hydruntinus* in southeastern Italy is the unique note of James Smith (Proc. Geol. Soc., London, 1847, p. 52): "The fragment which accompanied the specimen was given to Mr. Smith by Mr. St. John of Valetta, who stated that he found it, encrusted with stalagmite and adherent to the rock, in the island of Gozo. According to Dr. Falconer, it consists of two plates of a young grinder of the true *Elephas primigenius*. The occurrence of so large an animal in a locality of such limited extent seems to point to a period when it was connected with a continent."

borderland between the forests and steppes of central Germany. Of great phyletic significance, if confirmed, is the very primitive stage *M. primigenius astensis* (Fig. 1019) of the Upper Pliocene of northern Italy, described by Depéret and Mayet, and also observed in the Forest Bed, Lower Pleistocene, of Anglia (Fig. 1020); this primitive *M. p. astensis* is distinguishable by its thicker enamel and fewer ridge-plates (M 3 $\frac{14}{14\text{-}15}$) as compared with M 3 $\frac{24}{24}$ of the typical Upper Pleistocene *M. primigenius*. The supposed phyletic order of descent of these primitive species is given above on page 1138; the following are the type descriptions and figures in chronological order.

Mammonteus primigenius leith-adamsi Pohlig, 1888

Figure 1015

3d(?) *Interglacial* Travertines of Thuringia, Dornap (Fuhlrott).

In 1888, Pohlig described this diminutive variety of *Mammonteus primigenius* as a branch of the main stem of the true *Mammonteus primigenius*. It was found in Thuringian deposits of *3d*(?) *Interglacial* time and is consequently more *ancient* than the typical *Mammonteus primigenius*, which belongs to IV GLACIAL and Postglacial times.[1]

E. [*Elephas*] (*primigenius*) *Leith-Adamsi* Pohlig, 1888. "Dentition und Kranologie des Elephas antiquus Falc. mit Beiträgen über Elephas primigenius Blum. und Elephas meridionalis Nesti," Nova Acta Leop. Carol., LIII, Nr. 1, pp. 229, 232. TYPE.—Third left inferior molar, l.M_3. Original in Bonn. HORIZON AND LOCALITY.—*3d*(?) *Interglacial* travertines of Thuringia, Dornap (Fuhlrott), Germany. TYPE FIGURE.—*Op. cit.*, p. 229, fig. 101, *c*, *d*.

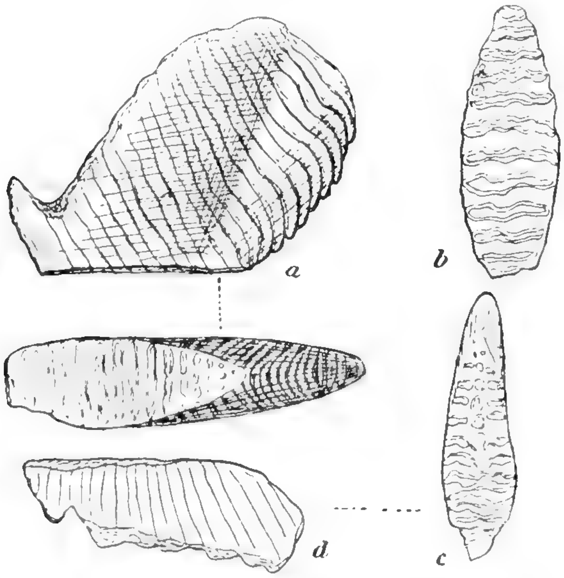

Fig. 101. Ein maxillarer und zwei mandibulare letzte Molaren von *Elephas primigenius* (in c—d von *E. pr. Leith-Adamsi*). Originale in Bonn ($^1/_6$).

Fig. 1015. Type figure (*c,d*) of *E.* (*primigenius*) *Leith-Adamsi*. After Pohlig, 1888, p. 229, fig. 101.

TYPE DESCRIPTION—*Op. cit.*, p. 232: ". . . Noch fremdartiger ist ein pachyganaler Mandibelzahn aus den Steinbrüchen von Dornap (Fuhlrott), welcher—15 x in mindestens 0,22 ca. × 0,08 m aufweist; . . . Den vorstehend angeführten Belegen der typischen, der angusticoronaten und der pachyganalen rheinischen Mammuthform reihen sich in Folgendem einige höchst bemerkenswerthe Beispiele der *diminutiven Primigeniusvarietät* in den Bonner Sammlungen an; es mag geeignet sein, dieses Zwergmammuth durch eine besondere Bezeichnung, etwa *E.* (*primigenius*) *Leith-Adamsi* n.f. von der Stammform zu unterscheiden."

Trouessart (1897) cites *Elephas* (*primigenius*) *Leith-Adamsi* as a subspecies of *primigenius*. His citation is as follows (*op. cit.*, p. 711): "*d.—Leith-Adamsi*, Pohlig (Var. minor), *loc. cit.*, 1889." Pohlig's letter (Sept. 10, 1924) does not authenticate var. *minor* as a subspecific term. Following the original description of the species in 1888, Pohlig in 1892 refers again to this species as perhaps one of the dwarf elephants which found its way to the mainland (*op. cit.*, 1892.1, pp. 260, 261): "Es ergibt sich also der interessante Schluss, dass gleich dem Zwergmammuth, *Elephas Leith-Adamsi*, auch der mediterran insulare Zwerg-Urelephant *Elephas Melitæ* stellenweise wieder mit dem Festland communiciren konnte; —dieser jedoch offenbar, nach der grossen Seltenheit seiner Ueberreste daselbst zu schliessen, nur auf ganz kurze Zeit."[2]

Mammonteus primigenius hydruntinus Botti, 1891

Figure 1016

La Grotta Ossifera di Cardamone in Terra d'Otranto, Italy.

This subspecies is based upon a twelve ridge-plated first superior molar of the left side, l.M^1 (Fig. 1016); the validity of this subspecies is dependent upon its geologic age.

The title of Botti's paper is "La Grotta Ossifera di Cardamone in Terra d'Otranto" and consists of descriptions of fossil bones found in this cave, including a molar and other portions of an elephant to which he assigned the name *E. primigenius* Blum. var. *hydruntinus*. The specific reference and type description are as follows:

E. primigenius Blum. var. *hydruntinus* Botti, "La Grotta Ossifera di Cardamone in Terra d'Otranto," Boll. Soc. geol. Ital., Vol. IX, 1891, p. 709, Tav. XXVI.

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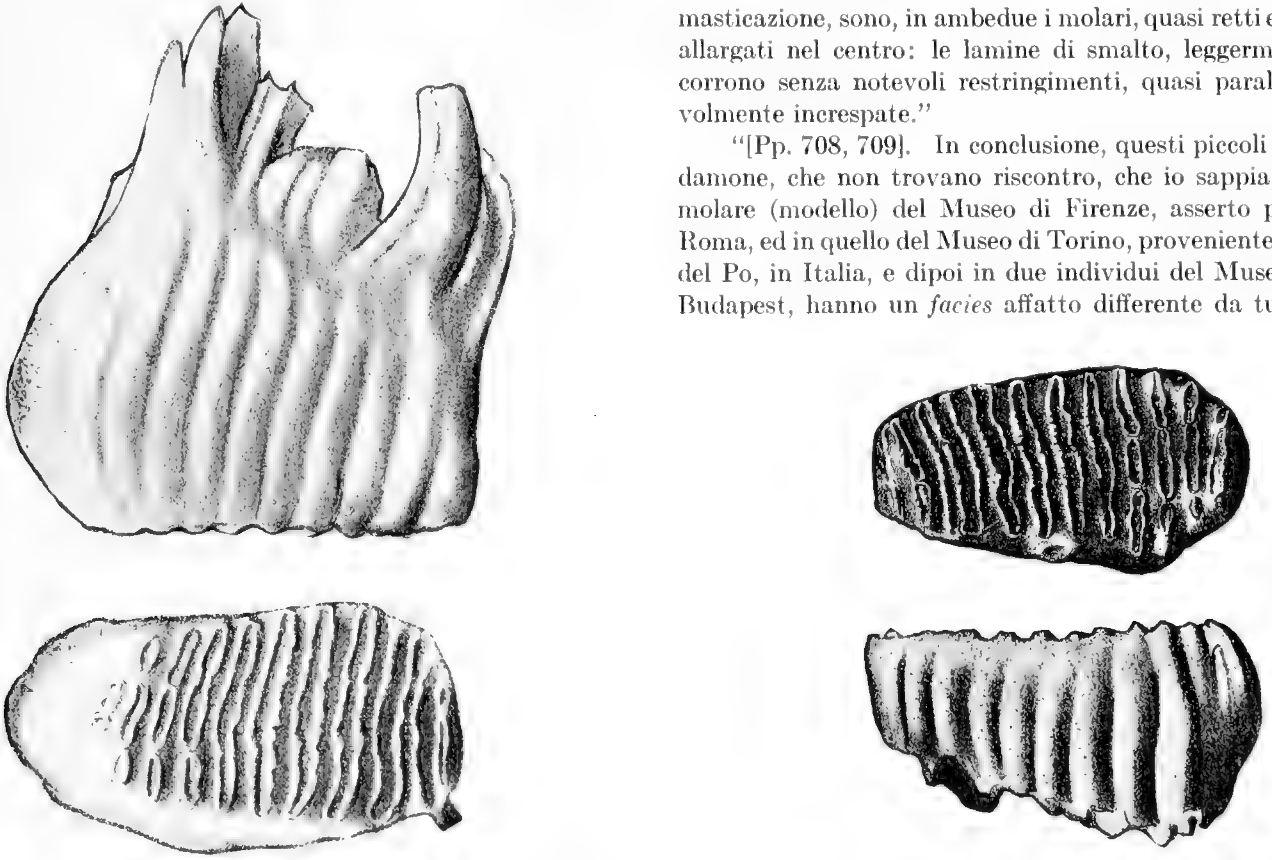
[1] The type figure (Fig. 1015*c*, *d*) and description of the type third left inferior molar do not convince Osborn (1930) that this tooth belongs in the true *Mammonteus primigenius* phylum. It appears too long and narrow, the ridge-plates are too widely separated, and the enamel is too thick. A reëxamination of the type would settle this question.

[2] As noted above, the type third left inferior molar of '*E.* (*primigenius*) *Leith-Adamsi*' in the Bonn Museum does not appear to clearly establish its relationship to the *Mammonteus* phylum.

Type Description.—(Botti, *op. cit.*, p. 705): "Uno di questi, un 1° molare vero, superiore, sinistro (tav. xxvi, fig. 1, 1a) presenta una corona alta 90^{mm} e la lunghezza di 122^{mm}; la superficie triturante, l'estremità posteriore non essendo ancora scoperta, si riduce alla lunghezza di 105^{mm}, la sua larghezza massima, misurata nel terzo anteriore 60^{mm}; questa superficie inclina leggermente verso l'interno, ma non è convessa, bensì piana, particolarità che ricordo avere osservata in tutti gli altri molari superiori di Cardamone, la quale, sebbene oppugnata da coloro che vogliono i molari superiori a superficie convessa, concorda coll'assioma dato da Falconer: '*Constant character of mammoth's molars of all ages and regions: worn surface nearly flat*' [Footnote: 'Falconer H. *Paleontological Memoirs and Notes.* Vol. II, p. 285.']."



Type of Mammonteus hydruntinus

Fig. 1016. Type l.M^1 of *Elephas primigenius* Blum. var. *hydruntinus* Botti, 1891, Tav. xxvi, figs. 1, 1a, 2, 2a. From the Grotta Cardamone near Otranto, Italy. Scale (left figure) one-half natural size, height of crown 90 mm., length 122 mm.; (right figure) a milk tooth, height 55 mm., length 97 mm., breadth 46 mm.

"Ed infatti undici lame in uso, le ultime quattro a piccoli dischi non ancora divenuti confluenti, ed una non ancora scoperta mi fanno ritenere per questo dente la formula di 12 lame, non compreso il tallone, formula appartenente all'ultimo dente di latte (secondo Owen e Falconer) o premolare (secondo Blainville) ovvero ad un antepenultimo (ossia primo) molare vero di *E. primigenius* Blum."

"Mi fanno inclinare a quest'ultima opinione la forma massiccia del dente e la presenza di robuste radici, sebbene troncate nell'esemplare in esame, in specie di una anteriore, isolata dalle successive, che sono fra loro saldate, la quale sostiene le due prime lamine anteriori. Di tallone anteriore non scorgo traccia, sebbene una certa depressione, la quale potrebbe dipendere dal contatto del dente che lo precedeva nella serie."

"[P. 706] L'altro, molto consumato dall'uso, alto 55^{mm}, (tav. xxvi, fig. 2, 2*a*), ha la superficie triturante lunga 97^{mm}, la quale presenta la maggior larghezza di 46^{mm} nel terzo posteriore, concava dal davanti all'indietro, leggermente inclinata verso il lato interno. Ha parimenti dodici lame, manca affatto di radici e ritengo essere l'ultimo molare di latte o premolare, inferiore, sinistro, della stessa sunnominata specie."

"I dischi resultanti dal consumo delle lamine per effetto della masticazione, sono, in ambedue i molari, quasi retti e stretti, niente allargati nel centro: le lamine di smalto, leggermente flessuose, corrono senza notevoli restringimenti, quasi parallele, ma notevolmente increspate."

"[Pp. 708, 709]. In conclusione, questi piccoli molari di Cardamone, che non trovano riscontro, che io sappia, se non in un molare (modello) del Museo di Firenze, asserto proveniente da Roma, ed in quello del Museo di Torino, proveniente dalle alluvioni del Po, in Italia, e dipoi in due individui del Museo nazionale di Budapest, hanno un *facies* affatto differente da tutti gli altri in grandissimo numero esistenti nei Musei colla determinazione di *E. primigenius* Blum.; hanno lo smalto più fino e più finamente increspato, le lame più serrate e più avvicinate, le dimensioni della metà più moderate."

"Nuove specie furono create con minor divario di forme e l'elefante di Cardamone differisce certamente dal *primigenius* tipico più di quello che il *primigenius* differisca dall'*indicus*; ma considerando che il molare di Roma e quello delle alluvioni del Po, non che quelli di Budapest, furono raccolti prima di quelli di Cardamone e nessuno pensò a separarli dalla specie primigenia, e riflettendo che in sostanza e poi un solo e medesimo piano di struttura che si sviluppa, sebbene in grado diverso, nell' *E. primigenius* Blum. e negli elefanti di Cardamone, così stimo miglior partito di lasciar questi ultimi nella specie primigenia, tutt'al più proponendo di distinguerli, poichè sono in fatto distinti, in ragione della dimensione di una metà minore e della più sensibile ristrettezza dei loro elementi, come una varietà, che potrebbe chiamarsi, dalla regione di provenienza:

E. primigenius Blum var. *hydruntinus.*"

"Questa distinzione d'altronde non mi appartiene del tutto."

"Già fino dal 1873, faceva notare Leith Adams alla Zoological Society considerevoli discrepanze nei molari a lame ordinariamente sottili del Mammuth, ed allegava una autorità altamente competente, quella di M. Davies del British Museum, il quale, dall'esame di numerosi molari di *Elephas primigenius,* trovati in Inghilterra ed altrove, era da assai tempo venuto nella opinione che esistano due distinte varietà, facili a riconoscere, i molari dell'una essendo formati di lame sottili separate da ristretti strati di comento interposti, l'altra composta di lame più dense con intervalli più larghi, soggiungendo quest'ultima forma essere più frequente dell'altra [Footnote: 'Leith Adams A. *op. cit.* p. 6, 7.']."

Mammonteus primigenius fraasi Dietrich, 1912

Figures 1017, 1018

"Mitteldiluvialen Schottern in Steinheim a.d. Murr," Germany.

This subspecies, named in honor of Eberhard Fraas by Professor Dietrich in 1912, is based on a type skeleton mounted under the direction of Professor Fraas in 1911 in the Museum of Stuttgart. As displayed in the type figure (1912, Taf. I, II), it appears to represent a Middle [Upper?] Pleistocene race or subspecies of *Elephas primigenius* clearly characterized by its large size, fewer ridge-plates in lower molars, and five digits in the manus and pes, probably a typical phalangeal formula.

Elephas primigenius Fraasi Dietrich, 1912. "Elephas primigenius Fraasi, eine schwäbische Mammutrasse." Jahresh. Ver. f. vaterl. Naturk. in Württemberg, Jahrg. LXVIII, pp. 42–106. Type.—Skeleton, adult male. Mounted under the direction of Professor Fraas in the K. Naturalienkabinett, Stuttgart (No. 12837). Horizon and Locality.—Found in 1910 in "Mitteldiluvialen Schottern in Steinheim a. d. Murr." Type Figure.—*Op. cit.,* Taf. I and II, also text figs. 2, 4, 11–14, 16–21, 24–26.

Type Description.—(*Op. cit.,* pp. 105, 106): "*E. primigenius Fraasi,* wie ich die neue Rasse Herrn Professor Fraas zu Ehren nenne, ist also keineswegs synonym mit der eben erwähnten Bezeichnung, worunter lediglich eine Anzahl bestimmter Molarenformen zu einer Mutationsreihe zusammengefasst werden. *E. primigenius Fraasi* ist vielmehr innerhalb dieser Reihe eine distinkte, osteologisch vollständig bekannte Form, in deren Skelett eine Reihe von Merkmalen vereinigt sind wie es bisher an keinem anderen Mammut beobachtet ist. Ausserdem ist der *E. primigenius Fraasi* eine charakteristische Lokalform, denn die Steinheimer Funde zeigen immer wieder das gleiche gewaltige Ausmass der Glieder."

Observe the relatively primitive structure of M_3 (cf. Dietrich, 1912, p. 76):

M_3 max. sin. Fig. 12. Lamellenformel x 22 x [Footnote: 'Die 13. Lamelle ist nur an der Labialseite entwickelt.'] in 27 cm Länge, 22 cm Höhe [Footnote: 'An der 16. Lamelle.'], 10,4 cm Breite, Abkauungsgrad x—17. Lamelle. . . . Distanz der Lamellen 4—8 mm., Länge der Lamellen 7—8 mm (an der labialen Seite), Form des Lamellenumrisses, nach unten verschmälert, Dicke des Schmelzes 1, 4—1, 5 mm (starke Kräuselung), Typus der Verschmelzungsfigur der Lamellen, median lamellär, lateral annulär.

(P. 106): "Diagnose: Grosse hochbeinige, fünfzehige Mammutrasse mit kurzem und schlankem Rumpf. Im Schädel und den Molaren mit primitiven Merkmalen. Schädel verhältnismässig niedrig, Molaren weitlammelliger als bei den jüngsten Mammuten.

Fig. 1017. Type cranium of the subspecies *Elephas primigenius fraasi* Dietrich, 1912, Taf. II, figs. 1 and 2 [=*Mammonteus primigenius fraasi* of the present Memoir].

This cranium, associated with the skeleton now mounted in the K. Naturalienkabinett in Stuttgart (No. 12837) illustrates the extreme hypsicephaly and acrocephaly, fore-and-aft compression, of the profile of the fronto-occipital region and the marked concavity of the frontals, agreeing closely with the cranial characters of all species of *Mammonteus* and differing widely from the cranial profile of *Parelephas.*

Carpus und Tarsus hochentwickelt, der erste aussen rein serial, innen nahezu serial. Die Männchen gehören zu den Riesenformen; sie tragen starke, gebogene, aber nur wenig spiral gedrehte Stosszähne, deren Wachstum einer Hemmung unterliegt. Die Stosszähne werden gebraucht."

"Typus: Das Skelett No. 12837 (♂ adult) im K. Naturalienkabinett zu Stuttgart."

HABITS OF ELEPHAS [MAMMONTEUS] PRIMIGENIUS FRAASI (cf. DIETRICH, 1912, P. 42).—In *E.* [*Mammonteus*] *primigenius* the enamel folds barely rise above the cement, affording a relatively even surface which is admirably designed for the comminution of the finer grasses. The mammoth is thus chiefly a grass-eater, a fact which is also attested by the contents of the stomach. It also is an open country animal, but we cannot of course deduce from the structure of its teeth whether this country was warm or cold, for while it is occasionally found mingled with an arctic fauna this is not invariably the case. The remains at Steinheim prove that it lived on the borderland between the forests and the steppes because it is found in association with *E.* [*Hesperoloxodon*] *antiquus.*

Fig. 1018. Mounted skeleton of *Mammonteus primigenius fraasi* (Naturalienkabinett, Stuttgart, No. 12837), after photograph kindly forwarded to the present author by Dr. W. O. Dietrich. Compare Dietrich, 1912.1, Taf. I. The skeletal height, from the sole of the foot to the top of the cranium, is at least 4 m. or 13 ft. 1½ in. (see Dietrich, *op. cit.*, p. 64).

Mammonteus primigenius astensis

Depéret and Mayet, 1923

Figures 871, 1019, 1020

Upper Pliocene (Villafranchian stage),[1] San Paolo de Villafranca, northern Italy.

If confirmed by more material, the recognition by Depéret and Mayet of an Upper Pliocene stage in the evolution of the genus *Mammonteus* is a step of the utmost importance in the phylogeny of the Proboscidea and especially in the phylogeny of the genus *Mammonteus*. The type grinders (Fig. 1019) appear to Osborn to be relatively narrower than we should expect. If, however, we may depend upon the highly trained and acute observations of Charles Depéret and Lucien Mayet then *Elephas primigenius* mut. *astensis* actually belongs in the *Mammonteus* phylum and is quite separate from what these authors have named "Groupe des *Elephas Trogontherii*."

Fig. 1019. Type and Paratype Grinders of Mammonteus primigenius astensis

(Left) Type of *Elephas primigenius astensis* from San Paolo de Villafranca. After Depéret and Mayet, 1923, Pl. xi, fig. 5, p. 221: "Fig. 5.—*Elephas primigenius*, mut. *astensis* de San Paolo de Villafranca. M³ droite. (Voir p. 184). Musée du Palais Carignan, à Turin, figurée par Zuffardi, 1913, pl. vi, fig. 2a [as *Elephas primigenius* Blum. var. *trogontherii* Pohl.]." Less than one-half natural size; actual length 216 mm., breadth 94 mm., height 186 mm.; nineteen ridge-plates present.

(Right) Paratype of *Elephas primigenius astensis*. After Depéret and Mayet, 1923, Pl. xi, fig. 6, p. 221: "Fig. 6.—*Elephas primigenius*, mut. *astensis*. Pliocène fluvio-lacustre de l'Astesan, à San Paolo. M_3 droite. (Voir p. 185). Pièce du Musée géologique de Turin, n° 15, figurée par Zuffardi, 1913, pl. v, fig. 8a [as *Elephas primigenius* Blum. var. *trogontherii* Pohl.]." Less than one-third natural size; length 280 mm., breadth 84 mm., height 138 mm.; nineteen ridge-plates plus talon.

E. [*Elephas*] *primigenius* mutation *astensis* Depéret and Mayet. "Les Éléphants Pliocènes," Deuxième Partie, 1923, pp. 183, 184. Type.—Right third superior molar, r.M³. Musée du Palais Carignan, à Turin. Horizon and Locality.—San Paolo de Villafranca. Type Figure.—*Op. cit.*, Pl. xi, fig. 5, p. 221; figured by Zuffardi, 1913, Tav. xii [vi], fig. 2*a*, as *Elephas primigenius* Blum. var. *trogontherii* Pohl.

Description of Type.—(*Op. cit.*, p. 184): "*Molaire supérieure* M³.—Il existe au Musée de Turin les deux M³ d'un même sujet. Nous figurons (pl. xi, fig. 5) la dent du côté droit qui est la mieux conservée. L'animal était déjà assez âgé, car la couronne est très arasée en avant par la mastication et ne compte plus que 19 lames présentes, il doit en manquer quelques-unes, 2 ou 3 peut-être. La longueur conservée de la couronne est de 216 millimètres et on peut estimer la longueur totale probable à 249 millimètres. La largeur de la couronne est de 94 millimètres et la hauteur au milieu atteint le chiffre considérable de 186 millimètres. Ces dimensions sont celles de M³ d'un sujet de petite taille d'*E. primigenius*, M³ dont la longueur moyenne est, d'après Pohlig, de 300 millimètres et atteint parfois 385 millimètres. La fréquence laminaire est de près de 8 lames pour 10 centimètres de couronne; c'est le chiffre normal de l'*E. primigenius*. Les bandes d'émail sont très minces, bien plus que chez l'*E. trogontherii* du même gisement; elles sont tout aussi onduleuses, mais *beaucoup moins plissées*, l'émail étant presque uni d'un bout à l'autre des bandes, sauf quelques plis dans les lames antérieures très unies. Il n'existe aucune trace du sinus loxodonte."

Falconer, 1868. Vol. II, p. 170.—Falconer described as follows a perfect l.M³ "of the *pre-glacial* variety of *Elephas primigenius*. . . . The matrix is indisputably of the *forest-bed* of the Norfolk Coast." Length 11.5 in. (292 mm.), breadth 4.1 in. (104 mm.), height 7 in. (178 mm.); ridge-plates 18+, fourteen in a space of 7½ in. (190 mm.); enamel slightly thick. This l.M³ is either of *Mammonteus primigenius* or of *Parelephas trogontherii* (cf. Fig. 1020).

Paratype.—(*Op. cit.*, Depéret and Mayet, p. 185): "Les M_3 figurées par Zufiardi (1913, pl. v, fig. 8–9) ont une couronne relativement étroite et fortement arquée comme dans la dernière molaire inférieure des Eléphants. Nous figurons (pl. xi, fig. 6) la dent du côté droit qui est la mieux conservée. La longueur de la couronne est de 280 millimètres mesurée en ligne droite pour une largeur de 84 millimètres et une hauteur de 138 millimètres. On compte 19 lames plus le talon et des traces de quelques lames usées à la partie antérieure. La fréquence laminaire est de 7, 5 à 8 comme chez l'*E. primigenius*. Les caractères de l'émail sont identiques à ceux des molaires précédentes: émail mince, uni et non plissé, sans sinus loxodontes."

Osborn, 1924: The relatively high ridge formula, $M\,3\,\frac{19\text{-}20}{19\text{-}20}$, is what we should expect in an ancestral stage of the phylum *Mammonteus*, which in *M. primigenius*, at the close of the Pleistocene

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[1] [Possibly Lower Pleistocene (see footnote 1 on p. 1049 above).—Editor.]

age, rises to M 3 $\frac{24}{24}$, and finally in M. *primigenius compressus* to M 3 $\frac{27}{(?)27}$. From the above very accurate description and admirable figures may be deduced the ridge formula of *Mammonteus primigenius astensis*: M 3 $\frac{19\text{-}20}{19\text{-}20}$. This is a much higher ridge formula than that of the typical *Parelephas trogontherii* of Pohlig, namely, M 3 $\frac{15+}{16+}$, although the type of *P. trogontherii* belongs to a more recent geologic stage than the type of *M. primigenius astensis.* The ridge formula of *M. primigenius astensis* is thus higher than that of any contemporary species of mammoth or elephant, much exceeding the contemporary ridge formulæ of species of *Archidiskodon* and of *Parelephas* (see Fig. 1020).

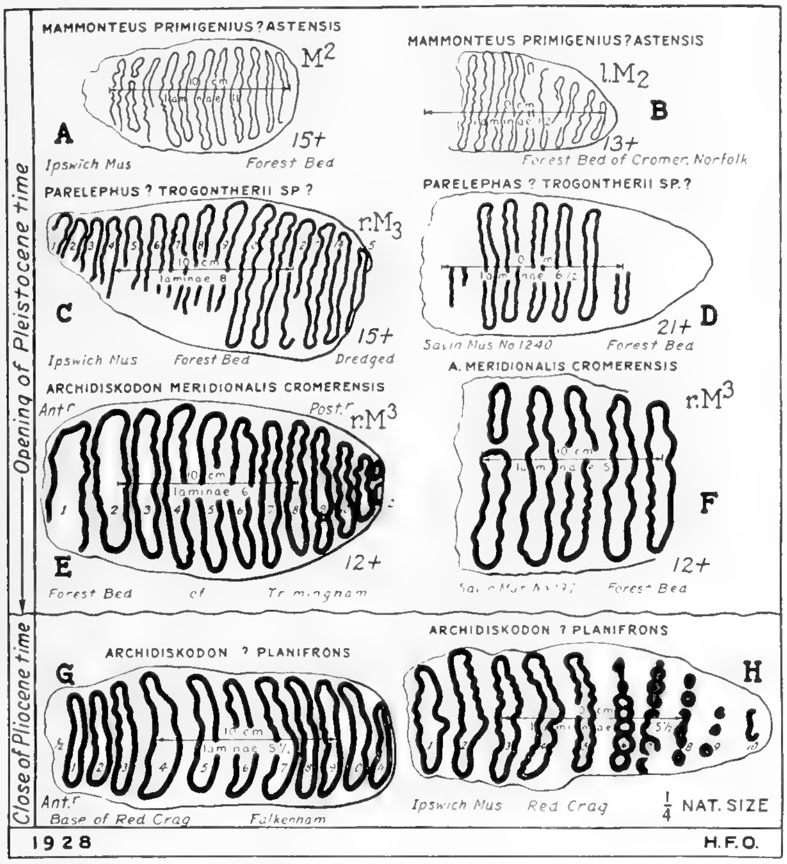

Fig. 1020. *Mammonteus primigenius* (?)*astensis* (A, B). Crowns of referred superior (M^2) and inferior (M_2) molars, from the Forest Bed of Cromer, Norfolk, England, compared with (?) *Parelephas* (C, D), *Archidiskodon* (E, F), and *Archidiskodon* or *Hesperoloxodon* (G, H) molars. All figures one-fourth natural size, reproduced from direct scale tracings by the author. For details see figure 871, Chapter XVI.

Mammonteus primigenius (?)astensis, Forest Bed, England (Osborn, 1922, 1924).—The Cromer Forest Bed of England includes a sub-arctic faunal phase of the northern latitude of East Anglia, Lat. 53, during the period of the first Scandinavian glaciation, which has no parallel in southern France or in northern Italy, Lat. 44–46. The Forest Bed contains two distinct faunas, namely:

I. *Survivals.*—Upper Pliocene Red and Norwich Crags *warm* types which *survived* in the Forest Bed and belong to the *1st Interglcaial* stage.

II. *Arrivals.*—Pleistocene *cold* types which *first appear* in the Forest Bed and *may* belong to the I Glacial stage.

From the studies of Geikie, Prestwich, Clement Reid, and from the collections of A. C. Savin, Osborn in 1922 (1922.563, p. 439) summarized these two faunas as given below.

In brackets are indicated the possible references of the Forest Bed proboscideans to the north Italian species, but to determine the exact specific and subspecific references of the Forest Bed proboscideans, namely, "*Elephas meridionalis,*" "*Elephas antiquus,*" and "*Elephas primigenius,*" very close examination and comparison will be required:

(1) The "*Elephas primigenius*" listed below may prove to correspond in its ridge formula with that of the *Elephas primigenius* mut. *astensis* Depéret and Mayet (M 3 $\frac{19\text{-}20}{19\text{-}20}$), of Asti, northern Italy. (2) It is also possible that the "*Elephas antiquus Nestii* type" of the Forest Bed may prove to correspond with members of the *Parelephas trogontherii* phylum.[1]

FOREST BED, OR CROMERIAN, FAUNA OF EAST ANGLIA

I. Survivals

Warm Upper Pliocene Red Crag and Norwich Crag Types which *Survive* in the Forest Bed of Cromer

Elephas [*Archidiskodon*] *meridionalis* [*cromerensis?*] type
Elephas antiquus Nestii type [=*Parelephas*(?) *trogontherii nestii*]
Elephas [*Hesperoloxodon*] *antiquus* (typical)
Hyæna striata
Hyæna antiqua
Rhinoceros etruscus
Equus stenonis
Cervus carnutorum
Machærodus sp.?
Trogontherium Cuvieri
Macacus sp.?
Rhinoceros megarhinus
Hippopotamus amphibius

II. Arrivals

Cold and northern Pleistocene Types which *First Appear* in the Forest Bed of Cromer

Elephas [*Mammonteus*] *primigenius* [=*astensis?*]
Equus caballus fossilis
Sus scrofa
Bison bonasus
Caprovis Savinii
Ovibos moschatus
Alces latifrons
Capreolus capreolus
Cervus elaphus
Ursus spelæus
Felis spelæa
Varied forest rodent fauna
Northern forest small Carnivora

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[1] [After this text was written, Professor Osborn referred '*Elephas*' *antiguus Nestii* Pohlig, cotypes, to *Parelephas*(?) *trogontherii nestii* (see Chap. XVII, above, p. 1059.—Editor.]

3. AMERICAN STAGES OF MAMMONTEUS

In the full description and discussion above of the typical species *Mammonteus primigenius,* with a ridge-plate formula of M 3 $\frac{24}{24}$, as determined by Falconer, this species appears to range completely across Eurasia into Alaska, with the same ridge-plate formula. In Alaska also occurs[1] the much more progressive species *Mammonteus primigenius compressus* (M 3 $\frac{27}{(?)27}$), which ranges southward into Indiana, probably subsequent to the time of the appearance of the typical *M. primigenius.* Unfortunately the type of *M. primigenius americanus* DeKay, Upper Pleistocene of New York, has been lost and further research is necessary to determine precisely the ridge formula of this stage, which is estimated in the present Memoir as M 3 $\frac{26}{24}$.

Owing to the confusion by Hay and others of species of the true *Mammonteus* with species of *Parelephas jeffersonii,* in which the ridge-plate formula ranges from M 3 $\frac{25}{24}$ to $\frac{30}{26}$, much careful research remains to be done in connection with the revision and determination of the species and subspecies of *Mammonteus* characteristic of the northern regions of North America. The tentative arrangement is as follows:

Mammonteus primigenius:	M 3 $\frac{24}{24}$, typical of Alaska and ranging southward.
Mammonteus primigenius americanus:	M 3 $\frac{26e}{24e}$, typical of New York.
Mammonteus primigenius compressus:	M 3 $\frac{27}{(?)27}$, occurring in Alaska, also ranging southward into Indiana (typical).

So far as our present evidence goes, *Mammonteus primigenius* reached its final and most progressive stages of evolution in North America, probably in Postglacial time.

Mammonteus primigenius americanus DeKay, 1842

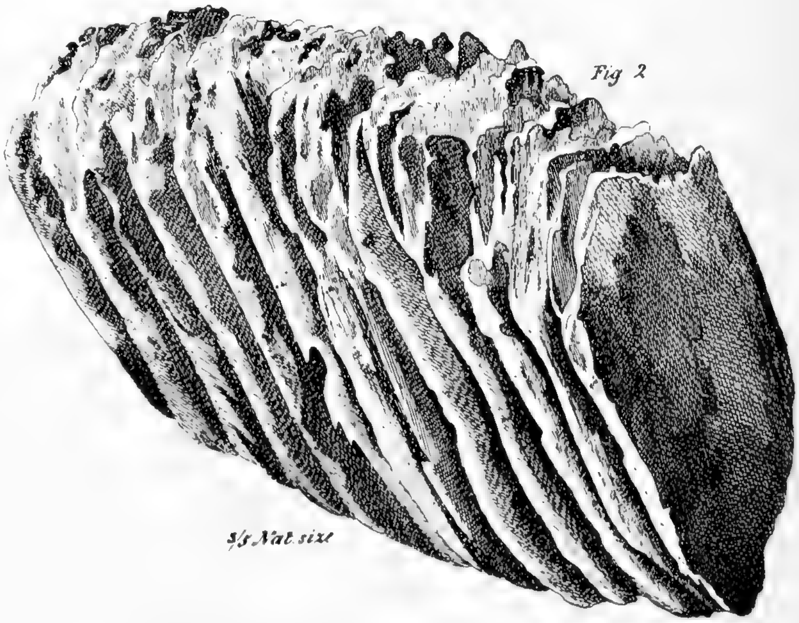
Figure 1021

Upper Pleistocene, IV GLACIAL (Wisconsin diluvium), Irondiquoit River, Monroe County, near Rochester, New York.

The type of this species was in the Cabinet of the Lyceum of Natural History, New York, which was destroyed by fire. The name was alluded to by Leidy (1858.2, p. 29), also by Adams, Cope, and Pohlig. As DeKay mentions thirteen plates in five inches (= 126 mm.), and also gives an excellent figure, it seems desirable to retain this subspecific name as *Mammonteus primigenius americanus* DeKay.

E. [*Elephas*] *americanus* DeKay, 1842. "Natural History of New York. Part I. Zoology: Zoology of New York, or the New York Fauna," 1842, p. 101. TYPE.—Portion of an upper molar tooth with thirteen ridge-plates. HORIZON AND LOCALITY.—Irondiquoit River, Monroe County, near Rochester, New York. TYPE FIGURE.—*Op. cit.*, Pl. XXXII, fig. 2.

TYPE DESCRIPTION.—"It is with some hesitation that I venture to designate, under a new name, a species founded on specimens of teeth, which appear to differ widely from any hitherto met in this country. . . . The specimens above alluded to were found in a diluvial formation near the Irondiquoit river in Monroe county, ten miles east of the city of Rochester. According to a writer in the American Journal, Vol. 32, p. 377, these remains consisted of a tusk and two molars, one of which is in the Cabinet of the



TYPE OF MAMMONTEUS PRIMIGENIUS AMERICANUS

Fig. 1021. Type of *Elephas americanus* De Kay, 1842, Pl. XXXII, fig. 2, three-fifths natural size. Portion of an upper molar tooth with thirteen ridge-plates. From near the Irondiquoit River, Monroe County, in the vicinity of Rochester, New York. Type formerly in the Cabinet of the Lyceum of Natural History, New York, destroyed by fire.

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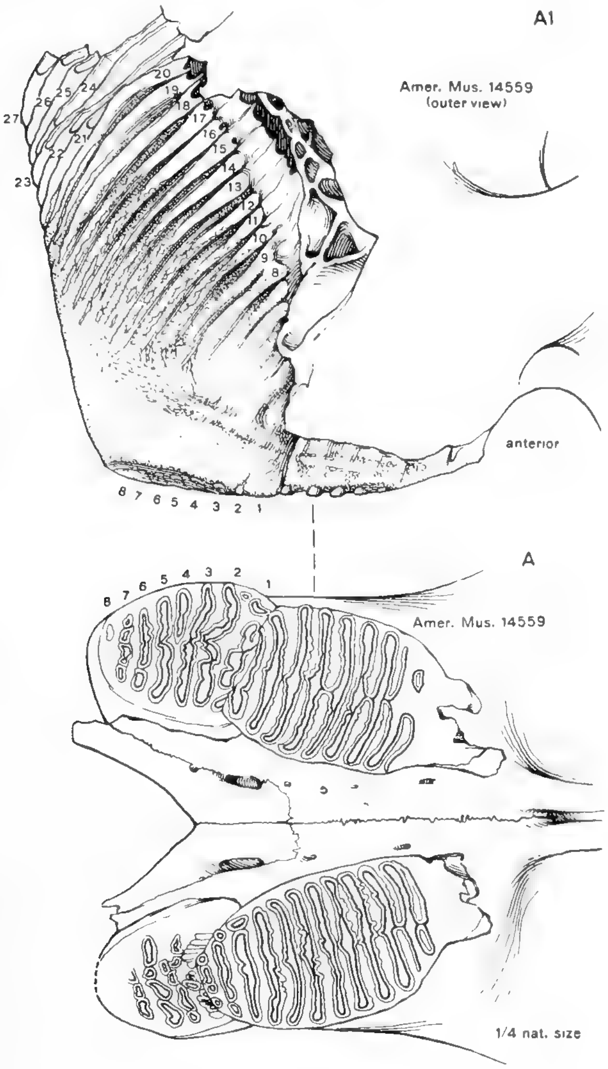
[1] [See new subspecies *Mammonteus primigenius alaskensis* from near Fairbanks, Alaska (pp. 1159 to 1161 of the present chapter).—Editor.]

Lyceum, and is that figured in the plate. This is six inches in its greatest depth; and, as nearly as can be conjectured from the part which remains, it must have been about eight inches long, and three in breadth on its grinding surface, which is, however, too much injured to exhibit the ends of the enamel. There are thirteen plates in a space of five inches, and they are more compressed than in any fossil species with which I am acquainted, being almost in contact, with very little interstitial substance. It is altogether different from any fossil elephant hitherto described, and merits the distinct appellation of *E. americanus*."

FALCONER (1863).—*Elephas primigenius* [*americanus*]. Falconer observed (1863, p. 66) that a constant character of the North American mammoth is that the ridges and their constituent elements are more attenuated and condensed. Thus, one tooth with 14 ridges shows an average of .36 in.; another presents 17 discs with an average of .46 in. Taken singly, the difference between the higher ridge condensation in American as distinguished from European specimens seems inconsiderable, but when it extends over a length of crown comprising 16 or 24 ridges, it is perceptible at a glance. It gives a certain amount of distinctive physiognomy to the molars of the North American mammoth. Falconer, however, does not regard this as indicating more than a slight geographical variety, as the other characters remain constant to the true mammoth type.



MAMMONTEUS PRIMIGENIUS COMPRESSUS. TYPE. FROM INDIANA

Fig. 1022. Type second and third superior molars of female *Mammonteus primigenius compressus* (Amer. Mus. 14559), from Indiana, one-fourth natural size. The teeth (A1) belong on the right side of the beautiful female skull also represented in figure 1023. After Osborn, 1924.633, p. 6, fig. 2 (originally figured as *Elephas primigenius*, see Osborn, 1922.555, p. 8, fig. 8). Ridge formula: M 3 $\frac{27}{(?)27}$.

A 1, External view showing *twenty-seven* ridge-plates of M^3.

A, Crown view showing M^3 with eight ridge-plates in use, closely compressed to M^2 with eight ridge-plates in use.

Osborn, 1924: Falconer's observation that a constant character of the North American mammoth is that the ridges and their constituent elements are *more attenuated and condensed* conforms with De Kay's type description that "there are thirteen plates in a space of five inches, and they are more compressed than in any fossil species with which I am acquainted, being almost in contact, with very little interstitial substance." Assuming that De Kay's measurement of thirteen plates in a space of five inches was accurately made, we find that the ridge-plate compression of the type of *Mammonteus primigenius americanus* is as follows: 10+ ridge-plates in 100 mm. This would relate this subspecies more closely to the typical *Mammonteus primigenius* than to *M. primigenius compressus*, but while De Kay's specific name may be retained, we can hardly consider that this can be raised to a higher rank than a subspecies, namely, *Mammonteus primigenius americanus*.

Mammonteus primigenius compressus Osborn, 1924

Figures 806, 819, 1022–1024

Type from Rochester, Indiana; paratype from Alaska. Probably of the Postglacial or retreat period, IV (Wisconsin) GLACIAL.

This subspecies is typified by the female skull (Amer. Mus. 14559), from Rochester, Indiana, and the paratype from Alaska (Amer. Mus. 13749), fully figured and described in this Memoir. It is readily distinguished from the typical *Mammonteus primigenius* of Eurasia (M 3 $\frac{24}{24}$) by the very high compression of its dental ridge-plates, namely, M 3 $\frac{27}{(?)27}$. The original description by Osborn (1924.633) is as follows:

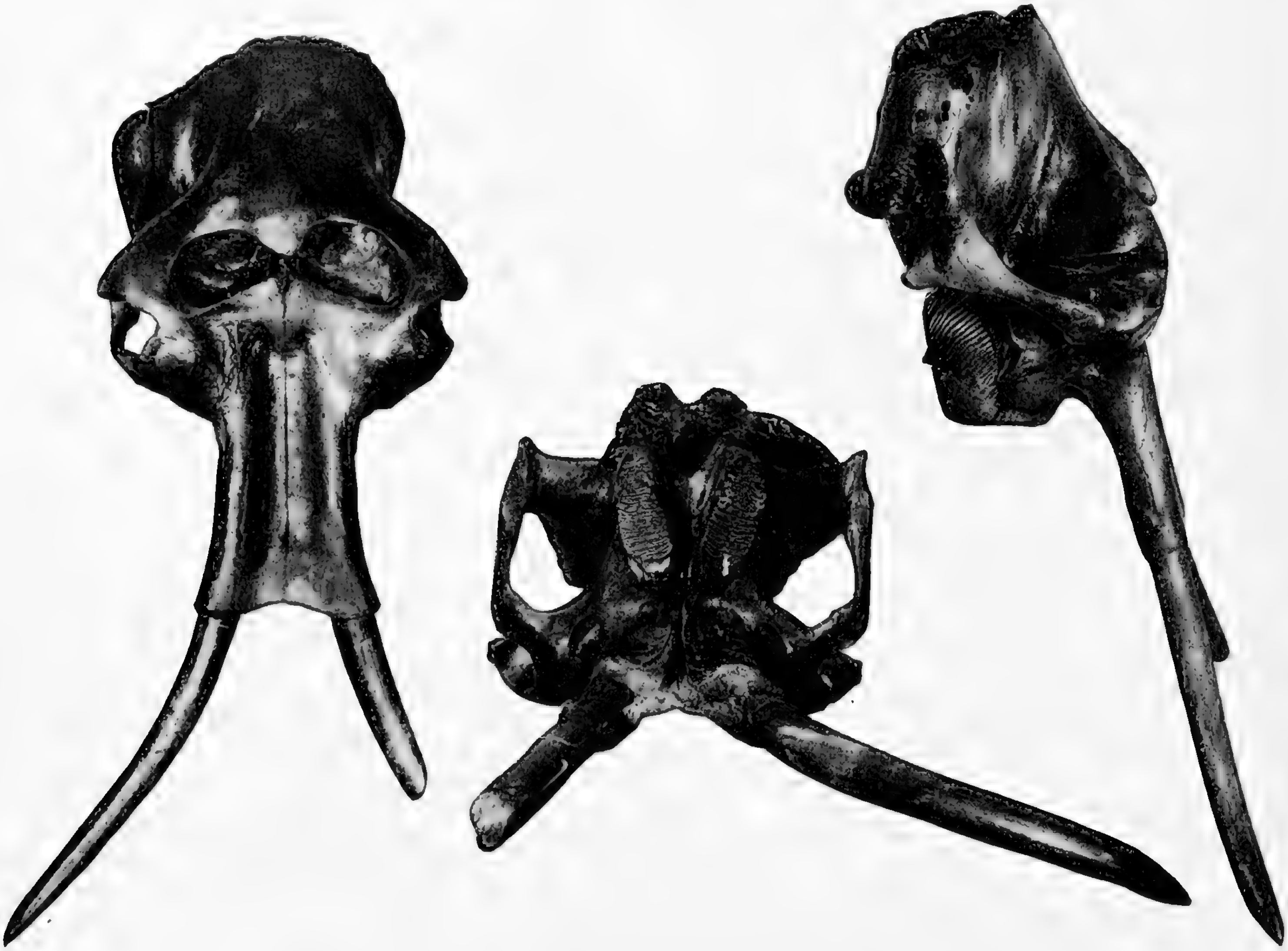
Mammonteus primigenius compressus Osborn, 1924. "*Parelephas* in Relation to Phyla and Genera of the Family Elephantidæ." Amer. Mus. Novitates No. 152, Dec. 20, 1924, pp. 5–7. TYPE.—Skull of a female mammoth including both tusks, also superior grinding teeth. HORIZON AND LOCALITY.—Rochester, Indiana; Upper Pleistocene of Alaska and of the Central United States. TYPE FIGURE.—*Op. cit.*, 1924.633, fig. 2, p. 6; and figure 1023 of the present Memoir. PARATYPE.—A third right superior molar, r.M^3, from Alaska (Amer. Mus. 13749). PARATYPE FIGURE.—See Osborn, 1922.555, p. 7, fig. 7 (Fig. 1024 of the present Memoir).

TYPE DESCRIPTION (OSBORN, 1924.633, PP. 5–7).—The original description of this subspecies is in part as follows: "(1) Extreme fore-and-aft compression and vertical elevation (hypsicephaly, bathycephaly), correlated with extreme hypsodonty and fore-and-aft compression of the twenty-seven ridge-plates which compose M^3. (2) Measurement across outside of orbits, 262 mm.; from top of skull to bottom of premaxillaries, 393 mm."

"After careful and prolonged examination of the specimens and the descriptions of Falconer (1863), we conclude that the typical *Mammonteus primigenius* of Eurasia and of North America displays a very constant ridge formula, as especially observed by Falconer, namely:

$$\mathrm{Dp}\ 2\tfrac{4}{4}\ \ \mathrm{Dp}\ 3\tfrac{8}{8}\ \ \mathrm{Dp}\ 4\tfrac{12}{12}\ \ \mathrm{M}\ 1\ \tfrac{12}{12}\ \ \mathrm{M}\ 2\ \tfrac{16}{16}\ \ \mathrm{M}\ 3\ \tfrac{24}{24}.$$

Falconer himself remarked that while American specimens of the true *E. primigenius* display a similar formula, namely, M 3 $\frac{24}{24}$, the grinding teeth in general show more closely compacted ridges."



Mammonteus primigenius compressus. Type Female Skull from Indiana

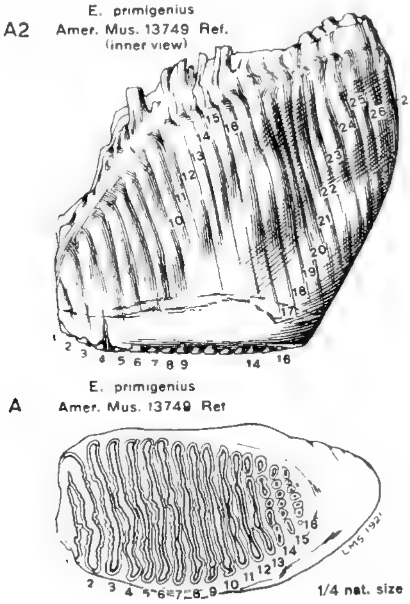
Fig. 1023. Type skull of female mammoth (*Mammonteus primigenius compressus*), Amer. Mus. 14559, from Rochester, Indiana, acquired by purchase in 1921. See occipitofrontal section of same skull (Fig. 806); also teeth of same skull (Fig. 1022). This skull is the *type* of the species *Mammonteus primigenius compressus* Osborn. One-twelfth natural size.

Observe in the three aspects of the skull, frontal, palatal, and lateral, the following important points: (1) The extreme fore-and-aft compression (cyrtocephaly, hypsicephaly or acrocephaly) correlated with the extreme compression of the twenty-seven ridge-plates which compose M^3 and are displayed in detail in figure 1022; (2) the slender parallel female tusk insertions and deep extension of the incisive alveolar plates; (3) this is the most extreme fore-and-aft compression of the skull, grinding teeth, and alveolar processes thus far recorded; (4) the measurement across outside of orbits is 262 mm.; from top of skull to bottom of premaxillaries 393 mm.

The cranium of this type, as beautifully displayed in the figure at the right, exhibits the utmost extreme of vertical elevation (hypsicephaly) of the occiput and of vertical depression (bathycephaly) of the grinding teeth. In harmony with the almost straight vertical line of the forehead and of the condylar processes are the maxillæ and the sharply downturned tusks. The apex of the skull, half complete, would terminate in a sharp peak (acrocephaly). This harmonious fore-and aft compression and deepening of the entire cranium, which brings the occipital condyles relatively close to the nares, apparently exhibits the absolutely finest stage in the evolution of the *Mammonteus* cranium and dentition. Certainly this remarkable foreshortening, doubtless initiated in the *M. primigenius astensis* of the Upper Pliocene [Lower Pleistocene?], could go no farther and we may regard this species as the final stage in the evolution of the phylum *Mammonteus*.

"It is owing to the excessively high compression (hypsodonty) and multiplication of the plates (polydiskodonty), amounting to M 3 $\frac{27}{(?)27}$, that the new subspecific name *Mammonteus primigenius compressus* is now defined and illustrated by figure 2 [Fig. 1022 of the present Memoir]."

The type and paratype superior grinding teeth are clearly illustrated in figures 1022 and 1024 of the present Memoir, and the cranial characters of the type are also shown in figure 1023, a female cranium in which the summit of the occiput is unfortunately broken away. We do not at present know of any jaw in which the grinders display this extreme stage of compression. Consequently the ridge formula of the lower teeth is not certainly known. The ridge formula of M 3 is probably $\frac{27}{(?)27}$.



MAMMONTEUS PRIMIGENIUS COMPRESSUS. PARATYPE. FROM ALASKA

Fig. 1024. Paratype figure of right third superior molar, r.M^3, of *Mammonteus primigenius compressus* (Amer. Mus. 13749), from "Historic Bluff," Eschscholtz Bay, Alaska, showing the maximum compression of the ridge-plates; ridge-formula M 3 $\frac{27}{(?)27}$. One-fourth natural size. After Osborn, 1922.555, p. 7, fig. 7.

Mammonteus primigenius alaskensis sp. nov.[1]

Figures 1025, 1026

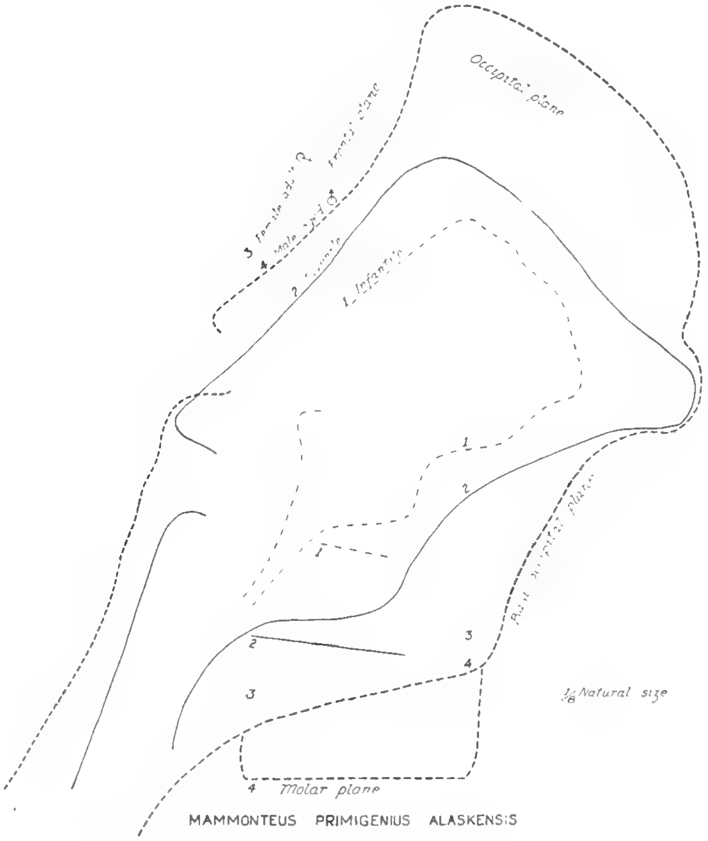
From vicinity of Fairbanks, Alaska. Pleistocene.

[In anticipation of Professor Osborn's description of a series of crania of the northern Mammoth, discovered in 1929 near Fairbanks, Alaska, Mr. Childs Frick, who generously accorded Professor Osborn the privilege of first description, used (1933.1, pp. 506, 632) the manuscript name *Elephas primigenius alaskensis*. Mr. Frick not only listed the proboscidean material collected in the Fairbanks region by the joint Alaska College-Frick American Museum parties, but he figured (Pl. 12A) a palatal specimen (A. C.—F: A. M. 27010) which he referred to this subspecies.

While it was Professor Osborn's intention to describe in Novitates this new ascending mutational stage, prior to the article by Mr. Frick in the Bulletin of the American Museum of Natural History, the text was never completed; in order, however, that such portion of it as he had prepared may be recorded, we are inserting it herewith, including certain essential additions.—Editor.]

Elephas primigenius alaskensis Osborn (in Frick, 1933). "New Remains of Trilophodont-Tetrabelodont Mastodons," Bull. Amer. Mus. Nat. Hist., LIX, pp. 506, 632. COTYPES.—Four crania (infantile, with deciduous dentition, A. C.—F: A. M. 26991; juvenile, with deciduous dentition, A. C.—F: A. M. 26990; adult female, with left maxillary tusk, A. C.—F: A. M. 26989; and aged male, Alaska College). HORIZON AND LOCALITY.—"Bone pits" scattered between several widely separated stripping operations of the U. S. Smelting and Mining Company, vicinity of Fairbanks and the Tanana River, Alaska. Pleistocene. COTYPE FIGURES.—Figures 1025 and 1026 of the present Memoir. Referred figure, see Frick, 1933.1, Pl. 12A.

FRICK, 1933.1, p. 632.—"*Elephas primigenius alaskensis* Osborn. Among the twenty-six tusks secured of the Northern Mammoth there is one of unusual size, the same weighing in the neighborhood of 300 pounds. The average number of laminæ in the normal m^3 is twenty-five and the length of the crown in use varies between 157–207 mm. A mandible of an aged cow is remarkable in that the last molars have been extruded and the alveoli healed over. Another mandible exhibits a somewhat produced symphysis."



COTYPE CRANIA OF MAMMONTEUS PRIMIGENIUS ALASKENSIS. MIDCRANIAL SECTION

All one-eighth natural size

Fig. 1025. Superposed cranial outlines: (1) Infantile, (2) juvenile, (3) adult female, and (4) aged male showing relations to *molar plane* (attrition). This superposition reveals the growth phases in the four chief cranial planes, namely, *molar plane, basi-occipital plane, occipital plane, frontal plane*, which culminate in the lofty occiput and depressed palate (bathycephaly), in the foreshortened occiput to anterior nares (brachycephaly), and in the concave frontal plane characteristic of all the adult Mammontinæ.

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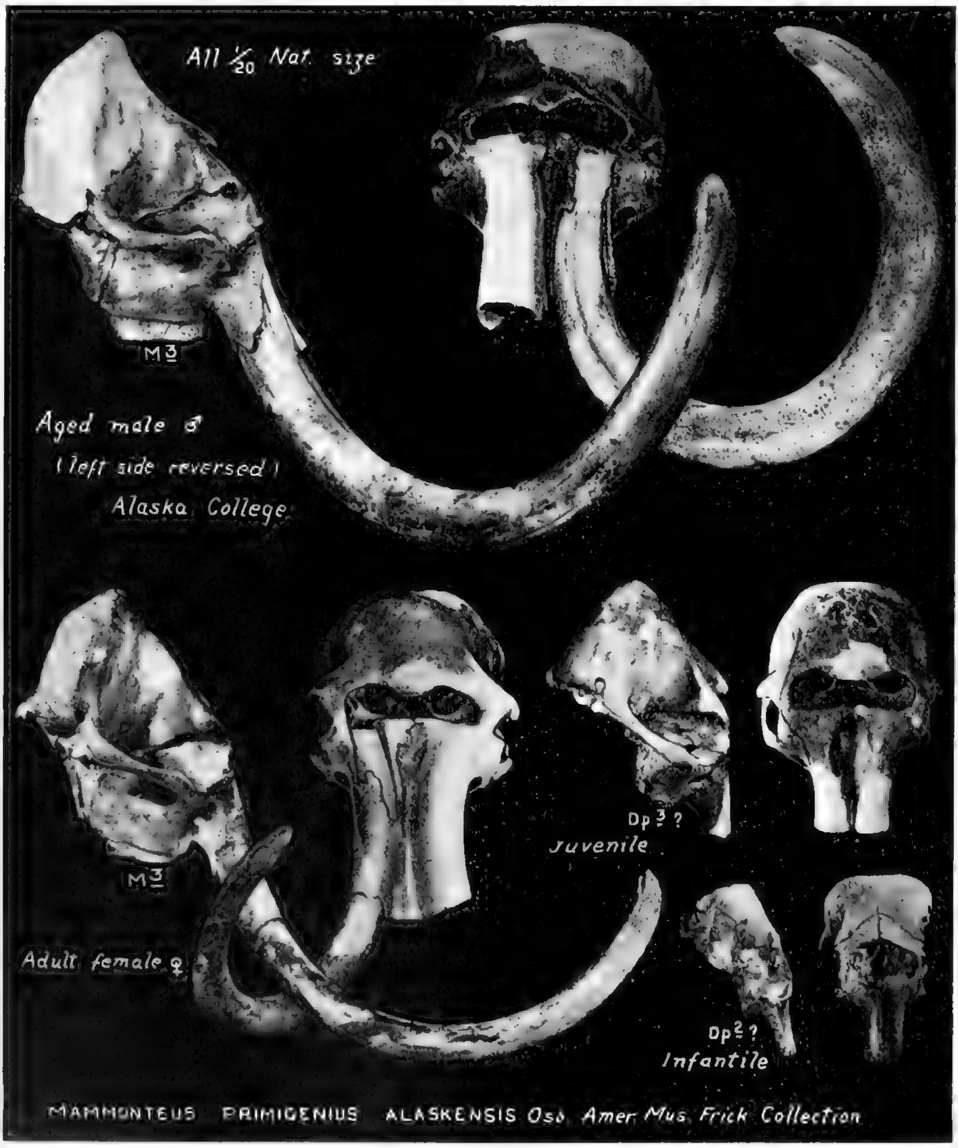
[1] [Inasmuch as Mr. Frick in 1933, pp. 506, 632, quoted the name *Elephas primigenius alaskensis* from Osborn's manuscript, without diagnosis or designation of type, this subspecific name in Frick is essentially a *nomen nudum* and its unequivocal establishment dates from the present Memoir. (Note by Dr. George Gaylord Simpson, 1939).—Editor.]

"LIST OF MATERIAL FROM THE VICINITY OF FAIRBANKS, ALASKA

- 26 tusks (largest, on curve 12 ft. 10 in., base circumference 24 in.)
- Large bull skull with m^3s and tusk (9 ft. 8 in. x 18.5 in.), Alaska College Collection
- Large cow skull with m^3s and tusk (6 ft. 5 in. x 13 in.)
- 4 smaller skulls, including 2 of calves
- 6 partial palates
- Some 24 mandibles or partial mandibles
- 204 detached molars or partial molars
- 31 partial scapulæ
- 7 complete and 5 partial humeri (largest 98 cm., smallest 75 cm.)
- 16 complete and 5 partial ulnæ
- 2 complete and 12 partial radii (largest 61 cm., smallest 56 cm.)
- 8 complete and 8 partial femurs (largest 113 cm., smallest 96.5 cm.)
- 12 complete and 14 partial tibiæ (largest 68 cm., smallest 44 cm.)
- 3 complete and 2 partial fibulæ
- 37 metapodials
- 17 astragali
- 16 calcanea
- 60 carpal or tarsal bones
- 6 patellæ
- Numerous vertebræ
- Several ribs, partial ilia"



COTYPE CRANIA OF MAMMONTEUS PRIMIGENIUS ALASKENSIS

All one-twentieth natural size

Fig. 1026. Cotype crania of *Elephas* [*Mammonteus*] *primigenius alaskensis*: (1) Infantile (A. C.–F:A. M. 26991); juvenile (A.C.–F:A.M. 26990); adult female (A.C.–F:A.M. 26989); aged male (Alaska College, through the courtesy of President Charles E. Bunnell). Compare figure 1023 above.

ASSOCIATED FAUNA

(cf. Frick, 1930.1, p. 79):

PRE-TUNDRA FAUNA OF ALASKA-YUKON

Large herds of the super-bison, *Bison crassicornis* Rich, ref.
A new Alaskan lion, *Felis atrox alaskensis*, Frick
A new wolf, *Aenocyon dirus alaskensis*, Frick
An arctothere, *Arctodus yukonensis* Lambe, ref.
A camel, *Camelops* (?)
Three species of musk-oxen, *Ovibos*, *Symbos tyrelli* Osgood, and *Boötherium sargenti* Gidley
A horse, *Equus alaskæ* Hay, ref.
A mastodon, *Mastodon americanus* Kerr, ref.
A Mammoth, *Mammonteus primigenius alaskensis*

The association of these mammals points to a Pleistocene phase which Frick inclines to compare with the Sheridan fauna of the Aftonian or *1st Interglacial* stage of Nebraska.

OSBORN'S MANUSCRIPT (1931).—The chief result of intensive researches on the genus *Mammonteus* is to establish in the evolution of the genus a number of successive ascending mutations ancestral to, or descending from, a typical '*Elephas primigenius* Blum.' (1799) of Siberia and north Germany to which Falconer (1863.1, p. 65) rightly attributed a very constant ridge formula, namely: $\mathrm{Dp}\,2\,\frac{4}{4}\ \mathrm{Dp}\,3\frac{8}{8}\ \mathrm{Dp}\,4\,\frac{12}{12}\ \mathrm{M}\,1\,\frac{12}{12}\ \mathrm{M}\,2\,\frac{16}{16}\ \mathrm{M}\,3\,\frac{24}{24}$

In 1924 Osborn described (1924.633, p. 5) the most progressive form *Mammonteus primigenius compressus*: $\mathrm{M}\,3\,\frac{27}{(?)27}$. Recent explorations in Alaska have revealed to President Charles E. Bunnell of the Alaska Agricultural College and School of Mines and to Mr. Childs Frick a more primitive ascending mutation to which the name *Mammonteus primigenius alaskensis* may be assigned.

The Alaska College and the American Museum are indebted to the United States Smelting and Mining Company for the privilege of making a very careful survey of the fossils revealed during the recent stripping operations of the company on Gold Stream and Clery Creek near Fairbanks; the survey was conducted under the supervision of Mr. Peter Kaisen during the seasons of 1929 and 1930. On this material Frick (1930.1, p. 73) reports as follows: ". . . the joint Museum and College party succeeded in harvesting during the four summer months some twenty-eight large cases of skulls, jaws, and bones—rare and important evidence on the prehistory of Alaska which otherwise would have been lost to science. The great percentage of this material, interestingly enough, came from three restricted areas, 'bone pits,' scattered between several widely separated operations of the Company, the remainder of the worked areas being, for the purposes of the bone hunter, nearly barren."

TABLE XV. CRANIAL AND DENTAL MEASUREMENTS

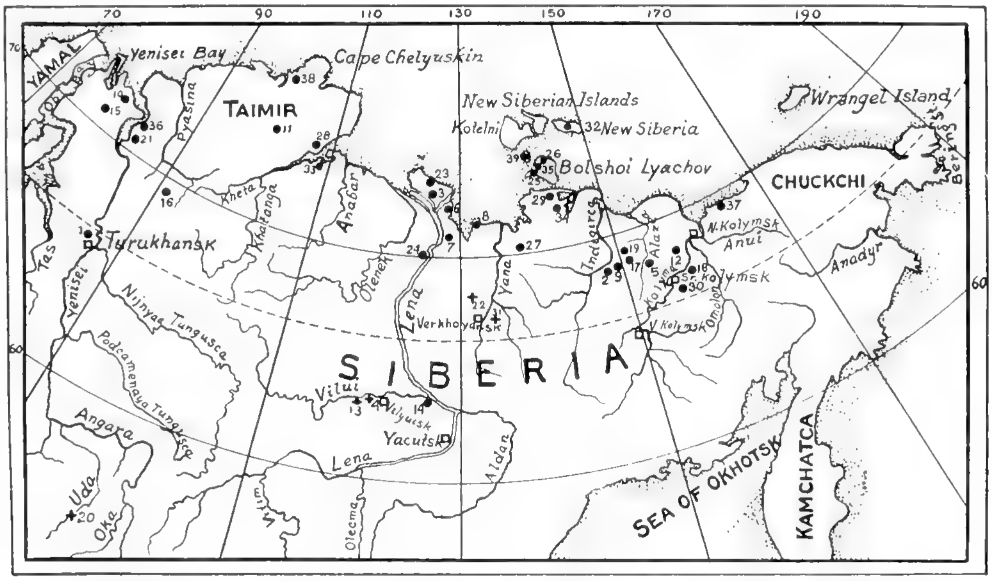
	Infantile (1) (A.C.-F:A.M. 26991)	Juvenile (2) (A.C.-F:A.M. 26990)	Female-adult (3) (A.C.-F:A.M. 26989)	Male-aged (4) (Alaska College)
Occipital condyle to front of orbit (cyrtocephaly, brachycephaly)	340e	515	550	600
Occipital summit to attritional molar plane (bathycephaly, hypsicephaly)	357	618	705	815
Width across summit of parietals (brachycephaly)	287	453e	548	650
Incisive premaxillary alveoli, length (bathycephaly)	×	320e	550	520e
" " " width (hypsicephaly)	×	195	318	380e
Glenoidal breadth (brachycephaly)	280e	410e	465	540
Incisive tusk, length on outer curve	×	×	1960	2945
" " maximum diameter	×	×	110	163
" " maximum circumference	×	×	315	485
Third superior molar, M^3, length, anteroposterior	×	[Dp^3? 86e]	180+	245
" " " " breadth, transverse	×	[Dp^3? 64e]	99	104
" " " " height, vertical (*e.*)	×	×	200e	215e

4. THE FROZEN MAMMOTH OF SIBERIA

Recent studies by Herbert Lang (1925) and by I. P. Tolmachoff (1928, 1929) add greatly to our knowledge of the habits, structure, distribution, and causes of extinction of the mammoth and form a fitting conclusion to the present chapter.

The 'Adams mammoth,' located by a Tungusian fisherman in 1799 on the banks of the Lena River, served Tilesius (1815) as the basis of the first description of a complete skeleton, measuring 9 ft. 3 in. at the shoulder.[1] This was followed by successive discoveries, described by Lang and in greater detail by Tolmachoff (1929).

The distinctive external characteristics besides those already mentioned above include its much shorter and more massive body, its large bulky head, the relatively small size of the trunk, the closely spiraled tusks, the small ears, the small size of the feet, the two-fingered tip of the trunk, the long fan-shaped, bristled tassel of the tail, the layer of fat three or four inches in thickness on the under side of the belly, and the winter layer of fat on the concave face of the cranium.



DISCOVERY SITES OF FROZEN CARCASSES OF THE WOOLLY MAMMOTH AND RHINOCEROS

Fig. 1027. The discovery sites of the woolly mammoth are indicated by black dots (•) and those of the woolly rhinoceros by crosses (+). (After Tolmachoff, 1929.) For explanation of numbers 1–39 appearing on this map, see caption by Tomachoff on page 20 of his Memoir.

Tolmachoff (1928) attributes the extinction of the mammoth to over-specialization (*op. cit.*, p. 1137), as seen in the extreme complexity of the grinding teeth, the peculiar spiral tusks, and the four-toed feet. Invaluable is Tolmachoff's Memoir of 1929, with its map and list of not less than thirty-nine localities where frozen carcasses (including five of the woolly rhinoceros) have been found, beginning with Ysbrant Ides (1692) and ending with Andrews (1923). The author gives due credit to the works of Basset Digby (1926) and of Pfizenmayer (1926). He also gives a most detailed and interesting history of the progress of discovery of *Elephas primigenius* and of *Rhinoceros antiquitatis*.

The ivory industry of Siberia, dating back to very ancient times, furnishes a very good idea of the immense former number of mammoths, as discovered (or still buried) in the frozen ground of Siberia, estimated by Middendorf (1885) at 20,000 during the past two centuries and by Nordenskiöld (1882) at a very much higher figure. The highest estimate is 46,750 animals discovered during the last two and a half centuries; a corresponding estimate is that 250 specimens were discovered annually. The average weight of the ivory tusks is 288 lbs.

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[1] [See footnote on page 1148 above, where a height of 9 ft. 11 in. is given.—Editor.]

SUMMARY OF THE DISCOVERY AND NATURAL HISTORY OF THE WOOLLY MAMMOTH

Compare Osborn's "The Romance of the Woolly Mammoth" in Natural History, Vol. XXX, No. 3, 1930, May-June, pp. 227-241

Since 1907, when the explorations and researches for the present Memoir were begun, our knowledge of the classification and palæontology of the woolly mammoth has not only been greatly extended by exploration and discovery but greatly modified by intensive and very laborious research. Especially surprising, perhaps, is the evidence presented for the first time in this Memoir that *Mammonteus* is probably a branch of the same primary stock as that which gave rise to the intermediate mammoth *Parelephas* and to the southern mammoth *Archidiskodon.* This subfamily interrelationship may not be absolutely demonstrated, but the evidence for it seems to be very strong in the unique structure of the tusks, which are entirely relieved in later years of the mechanical function of procuring food, with a corresponding feeble structure of the backbone. If this relationship between the Mammontines proves to be the true one, it is certainly a paradox that the grinding teeth of the relatively primitive *Archidiskodon* are so widely separated in character from those of the most highly specialized *Mammonteus,* while *Parelephas* is intermediate.

A recent popular summary of these contrasts (cf. Osborn, 1930.824) may appropriately conclude our previous systematic and formal presentation of this subject.

The woolly mammoth is the classic of palæontology; it is the first extinct mammal to be found by man; it is the first to be used as proof of a universal deluge; it is the first to be used as proof of the existence of a long extinct world of mammalian life antecedent to the deluge; it is the first to receive a scientific description in the Latin language; it is the first to receive a scientific name—*Elephas primigenius* or 'the first of all, or original, elephant.' It took nearly two centuries thus to baptize the woolly mammoth as the honored primate of the fossil mammalian world and to usher in the elaborate and intricate science of mammalian palæontology through which we now decipher the prehistory of the earth for the past thirty million years almost as clearly as if we were able to project ourselves back into these long corridors of time.

. The romance of the woolly mammoth stretches back for thousands—perhaps for hundreds of thousands—of years to the time when the men of the Old Stone Age discovered that the ivory of the tusk of the mammoth and of other elephants was superior to bone for several utilitarian purposes, as well as for the expression of man's sculptural instinct. At all times, from the very beginning of the Age of Man or close of the Pliocene period when, on the authority of Charles Depéret, its ancestors first appeared in the warm forests of Italy, the woolly mammoth has kept its beautiful, brightly shining tusks sharpened at the tips, both for prowess in combat for the mastery of the female herd, and to further the efforts of the young mothers to ward off the many enemies that might surround and attack the baby mammoths straying for a moment from the sheltering maternal side. It is only when the old bull mammoths retire from their paternal duties to a quiet, bucolic life on the northern tundras that the ivory tusks begin to curl inward, even to the crossing point, thus rendering them useless both for purposes of combat and for herd protection. This is true also of the Jeffersonian [*Parelephas*] and the imperial [*Archidiskodon*] mammoths of North America.

Similar tusks glisten today in the African and Indian elephant, their beautiful 'ivory-white' contrasting with the somber gray sides of these animals, just as during the million-year Stone Age they contrasted with the hairy and woolly covering of the mammoth of the North.

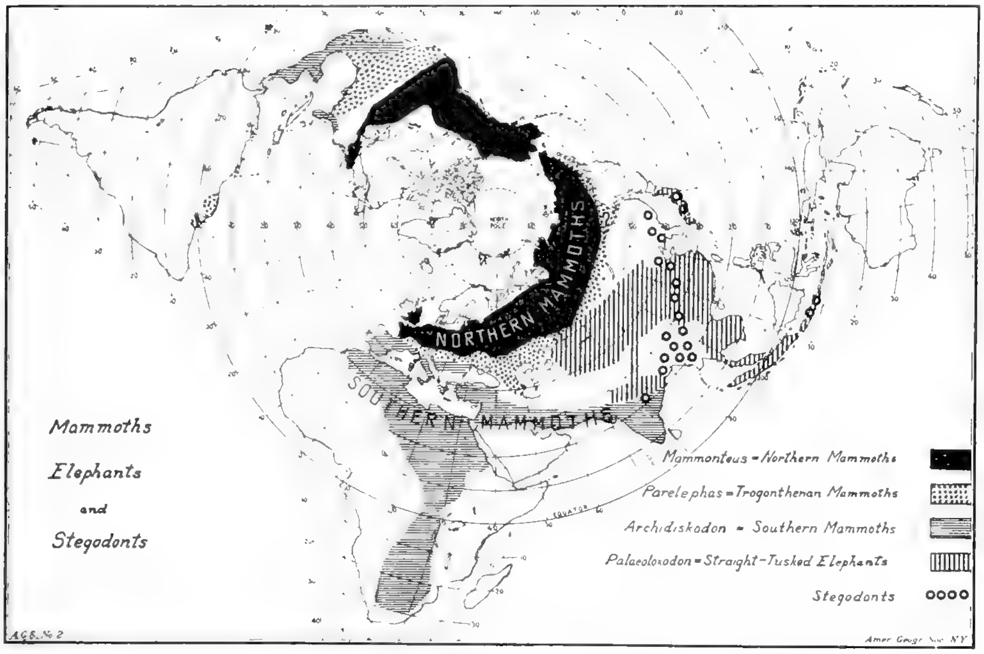
Upon close observation, however, a very important difference between all the mammoths and the living African and Indian elephants is thus revealed in the curvature and uses of the tusks, namely, the tusks of the mammoth, while emerging from the upper jaw closely side by side, soon begin to spread apart and then, slowly rotating on their axes, turn inwards toward each other to finally form a huge ivory circle with tips actually crossing.

A similar ivory circle around the large proboscis is also observed in the related extinct elephants to which for this and other reasons the name 'mammoth' may be applied. The Jeffersonian mammoth, *Parelephas jeffersonii,* was probably a hairy type lacking the heavy undercoating of wool of its northern relative, which roamed from the north temperate region to about N. Lat. 40° over France through Germany to the United States. The imperial mammoth, *Archidiskodon imperator* [Fig. 1030] was probably hairless, with great incurved ivory tusks that attained a gigantic size in its antecedents of the more southerly latitudes of Europe and Asia. As shown on the map below, these three mammoths—the 'woolly,' the 'Jeffersonian,' the 'imperial'—formed three great mammoth belts around the Northern Hemisphere which were as sharply demarcated as are the reindeer, the moose, and the stag, or wapiti, belts today.

We know that Stone Age man hunted the bone of the elephant and mastodon for a million years, for we find that the Piltdown Man of Upper Tertiary time fashioned one of the long bones of the mastodon for a tool; it is not improbable that he tried to fashion the ivory tusks as well, although we have no proof of this until ivory carvings are discovered toward the close of the Old Stone Age. Certainly ivory has been treasured by man for thousands of years. Primitive traders carried ivory from point to point. It is not surprising, therefore, that man knew about ivory long before he knew about its source.

Thus, again, in the early and wide-spread quest of ivory by man for utilitarian and artistic purposes it is not surprising that the word 'ivory' is the actual source of the scientific name *Elephas*, a Greek term of vague linguistic origin, subsequently Latinized. Homer used this Greek term not in reference to the elephant itself but to its tusks or 'ivory.' With both Homer and Hesiod the word *Elephas* means ivory. Aristotle (384–322 B.C.) in his *History of Animals*[1] used ἐλέφας in its modern generic sense as applying to the elephant of India, in referring to its courage in combat:

"... Elephants also fight fiercely with each other, and strike with their tusks; the conquered submits entirely, and cannot endure the voice of the victor: and elephants differ much in the courage they exhibit."



Geographic Distribution of Mammoths in Upper Pliocene and Pleistocene Times

Fig. 1028. Partly theoretic geographic distribution (1930) of the southern, intermediate, and northern mammoths. See figure 795 for distribution map of 1938.

Southern mammoths: *Archidiskodon planifrons, A. meridionalis, A. imperator.*

Intermediate mammoths: *Parelephas trogontherii, P. jeffersonii.*

Northern mammoths: *Mammonteus primigenius, M. primigenius compressus, M. primigenius alaskensis.*

Relatives of the southern imperial mammoth, *Archidiskodon imperator*, are now known to have ranged from South Africa to India and from Nebraska to Mexico. [Since this was written, a specimen referable to *Archidiskodon* cf. *planifrons* has been described from Shansi, China, by Dr. Arthur Tindell Hopwood (1935.1, pp. 87–90), who states as follows: "It is clear that there is a wide gap in the known distribution of the genus, and that the forms from the Old and New Worlds are separated by most of Asia. Hitherto no species of *Archidiskodon* has been described from the Far East, and the specimen described below is the first evidence that this gap may be expected to close with the march of knowledge."—Editor.] The temperate Trogontherian and Jeffersonian mammoths of the genus *Parelephas* ranged along the 40th parallel from southern France to central United States. The northern mammoth, of the genus *Mammonteus*, ranged about the Arctic Circle from western Europe to eastern North America.

The word 'mammoth' has a similar non-classic and indirect origin. In allusion to the fact that the Tatars of Siberia first discovered the ivory tusks by digging in the earth, the word 'mammoth' is certainly derived from the alleged Tatar word *mamma*, signifying 'earth.' As early as 1696 this was combined with another Tatar word *kost*, signifying 'ivory,' and the two words were Latinized by Ludolf into *Mammotovoi Kost.* The buried tusks were sometimes mistaken for horns; Cuvier alludes to these words of Tatar origin as follows: "C'est sous le nom de *cornes de mammont, mammontova-kost*, qu'ils désignent les défenses." Thus in the Latinization of the Tatar word *mamma* into the Gallic *mammont* there was assigned by Camper in 1788 the name *Mammonteus*, which is now applied by Osborn to the woolly mammoth as a genus distinguished in many external and internal characters from the genus *Elephas* which is typified by the elephant of India.

Thus, as cited in full above (p. 1124) from Ides, originated the word 'mammoth,' variously spelled in different languages *mammot, mamant* (Russian), *mammouth* (French), *mammuth* (German), from the Tatar *mamma* because the remains of these animals were found imbedded in the earth, the natives therefore believing that the animals burrowed like moles. Undoubtedly the woolly mammoth was in its time the colossus of living mammals of northern or western Europe; in consequence the word 'mammoth' has become a convenient adjective to signify gigantic, immense, of great comparative size. As a matter of fact, the woolly mammoth is a dwarf in comparison with its relatives, the Jeffersonian and imperial elephants, as is shown in the illustrations by Knight which have been brought to a relatively uniform scale (Figs. 1029, 1030, 1034).

Long before the elephant was known in Europe, Phœnician traders brought ivory from the South to Greece; in the North ivory was also procured in the tusks, the average weight of which was 288 pounds, of the more or less fresh or partly frozen bodies of the woolly mammoths. This northern source of the primitive ivory trade was summarized by Herbert Lang (1925); it has been thoroughly studied in recent years by Basset Digby (1926), Pfizenmayer (1926), and Tolmachoff (1929). In Tolmachoff's recent and comprehensive memoir (1929) is found a map (Fig. 1027 above) and a list of not less than thirty-nine localities where frozen carcasses have been found, beginning with Ysbrant Ides (1692) and ending with Andrews' discovery of 1923. The author gives due credit to the works of Basset Digby and of Pfizenmayer. He also gives a most detailed and interesting history of the progress of discovery of the woolly mammoth, *Elephas primigenius*, and of its woolly companion, *Rhinoceros antiquitatis*, the 'rhinoceros of antiquity.' The export ivory industry of Siberia, dating back

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[1] Translation by Richard Cresswell, London, 1887, p. 234.

to very ancient times, furnishes a very good idea of the immense number of mammoths that have been discovered by exploring parties in the frozen ground of Siberia, estimated by Middendorf (1885) at 20,000 during the past two centuries and by Nordenskiöld (1882) at a very much higher figure. The highest estimate is 46,750 for the last two and a half centuries, although one estimate even puts the number at 250 specimens annually, a total of 62,500 for the two hundred fifty years. The northern ivory trade to China is now traced back as far as 500 B.C. Doubtless the value of northern ivory rose as the Chinese gradually exterminated their own native or imported breeds of elephants from India.

Herbert Lang (*op. cit.*, 1925) notes that Ides, the famous Dutch traveler and ambassador to China, seems to have been the earliest to gather first-hand information regarding the frozen Siberian mammoths.[1] In traversing northern Siberia between the years 1692 and 1695, Ides learned that many of the Yakuts, Tunguses, and Ostyaks steadfastly believed that these huge monsters spent their lives deep underground, moving about easily in spacious tunnels even though the earth was thoroughly frozen. Should they become particularly active, the whole ground might rise above them, caving in later as they passed on; but should they come to the surface and breathe the warm air, they instantly died.

Imperial Mammoth of Nebraska. About one fifty-fifth Natural Size

Fig. 1030. This superb animal, first named *Elephas imperator* by Leidy, stands fully 13 feet at the shoulder—4 feet taller than the woolly mammoth but with similar curved tusks and sloping hind quarters. The best skeleton is in the Nebraska State Museum (*Archidiskodon imperator maibeni*); the finest cranium is in the Geological Institute of the City of Mexico (Fig. 902 of present Memoir). The animal ranged from Nebraska to Mexico. Like the Indian elephant, it probably had little hair and no wool.

Jeffersonian Mammoth of Indiana. About one forty-fifth Natural Size

Fig. 1029. The Jeffersonian mammoth was probably hairy, with a fine undercoating of wool in the winter season. Its tusks are incurved exactly as in the remotely related woolly and imperial species. Its concave forehead is quite distinct from that of the modern elephant. As found in Indiana, it measured 10½ feet at the shoulder.

It seems as if the very gradual recognition of the woolly mammoth as actually an extinct elephant extended well over a whole century; in 1696 the Russian explorer Ludolf described the mammoth of Siberia under the name *Mammotovoi kost*; two years later the German scholar Tentzelius defended against all sceptics the discovery of a really fossil elephant at Burg-Tonna near Gotha, but this classic skeleton has recently proved to belong not to the mammoth family but to the straight-tusked elephant family known as the 'elephant of antiquity'; in 1728 Sir Hans Sloane confirmed the finding of Tentzelius by reference to the discovery; seven years later (1735) John Phil. Breyne wrote to the Royal Society as follows:

> ". . . I was busied . . . to prove, that the extraordinary large Teeth and Bones found under Ground, and digged up in several Places of *Siberia*, by the name of *Mammoth's* or *Mammut's*, Teeth and Bones, were,
>
> I. True Bones and Teeth of some large Animals once living; and,
>
> II. That those Animals were *Elephants*, by the Analogy of the Teeth and Bones, with the known ones of *Elephants*.
>
> III. That they were brought and left there by the universal Deluge. I made likewise several useful Inferences about this matter."

The first finely etched figure of the cranium of the mammoth brought by Messerschmidt from Siberia was published

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[1] [See also Witsen, Nicolaes, 1692.—Editor.]

by Doctor Breyne in 1737 [1741?]. Thus step by step the way was prepared for Blumenbach to name the animal in 1799 and for the great Cuvier to thoroughly describe it in a series of memoirs between 1796 and 1834. Since that time our knowledge has advanced by leaps and bounds. The first bones of the mastodon found on the banks of the Hudson River in 1705 and of the Ohio River in 1739 were naturally confused in Europe with those of the mammoth when Blumenbach first labeled them *Ohio incognitum* and then *Mammut*. A century later, in 1842, DeKay described his *Elephas americanus*, a fossil mammoth tooth found in Monroe County near Rochester, New York. Finally, in 1924, the present author described his *Mammonteus primigenius compressus*, the most highly specialized and perfected mammoth thus far found, as known both near Rochester, Indiana, and in Alaska (see p. 1157 above).

Arched Tusks of the African Elephant

Fig. 1031. Giant arched tusks of the African elephant, 11 feet in length, presented by Charles D. Barney to the Heads and Horns Collection of the New York Zoological Park.

Skull and Tusks of the Woolly Mammoth

Fig. 1032. Skull and half-grown tusks of a middle-aged male specimen of *Mammonteus primigenius* found on the Yukon River, Alaska. With advancing age these tusks would curve inward and cross in the middle line.

Circular Tusks of the Woolly Mammoth of Siberia

Fig. 1033. Contrast these circle-shaped tusks, 8 feet in length, of the male woolly mammoth of Siberia with the arched tusks of the African elephant shown in opposite figure.

Beginning with the discovery of a complete frozen mammoth skeleton—known as the Adams' mammoth—near the mouth of the

Woolly Mammoth, Somme River, France
One-fiftieth Natural Size

Fig. 1034. This mammoth is a little more than 9 feet at the shoulder, whereas the Jeffersonian mammoth is 10½ feet and the imperial mammoth 13 feet. The painting closely follows the drawings in the cavern of Combarelles (p. 1169, tailpiece). The rapidly sloping hind quarters of the animal serve as a watershed for rain and sleet.

Lena River in 1799, other complete skeletons were unearthed and mounted in the museums of St. Petersburg, Leipsic, Stuttgart, and Brussels, all closely similar in size, in the wheel-like curvature of the great tusks, in the extraordinary foreshortening of the skull (p. 1158 above), in the rapid falling away or sloping of the hind quarters, in the shortness of the backbone and of the tail, in the reduction or complete loss of one of the digits of the hand—briefly, in the truly marvelous adaptation, in every part of the skeleton as well as in the teeth, to the very severe conditions of boreal life. In 1912 Felix described a mammoth found near Borna, whose death must have been so sudden that the animal did not have time to swallow a mouthful of food which lay in the form of a wad between the upper and lower teeth; in the stomach of this animal were about twenty-four pounds of undigested plant food, exceedingly interesting because it consisted of plants that are still native to the place (Beresowka River, northern Siberia), the tundra flora which the mammoths stored up during the short summer season for the long winter. These plants are *almost exclusively grasses* and form the characteristic meadow flora; the needles of conifers occur very rarely. From other discoveries we know that the mammoth fed during the winter on the arctic willow, *Salix polaris* of *Wahlenberg*, and on other northerly dwarf plants.

The description by Felix not only gives us complete knowledge of the skeleton of *Elephas primigenius* but shows conclusively the proper position of the tusk in the jaw and also its inclination. As to the animal's outward appearance, it involved a number of corrections in even the best reconstructions that had been made; the proportion of the length of skull and trunk in the mammoth is quite different from that of existing elephants: in the mammoth the skull is more than half the trunk length, in the elephant (*E. indicus*) it is always less than half. The mammoth's head, therefore, was higher in proportion to the body than that of recent elephants and in consequence the tusks could attain enormous proportions. The largest of the tusks in the Leningrad Museum measures no less than 13 ft. 8 in. and in the Franzens-Museum of Brünn there is a tusk that actually exceeds 16 ft. 5 in. in length, including the long basal portion of the tusk which was incased within the exceptionally long tube-like premaxillary bones shown in our figure (p. 1158) of the female mammoth skull of Indiana, the type of Osborn's *M. primigenius compressus*.

The trunk of the mammoth was extremely well developed. The ear was somewhat smaller than that of the Indian elephant, being about 15 in. in length and 6.7 in. in breadth, and, like the rest of the body, was covered with a thick coat consisting of short wool and longer hair. The tail is conical in form, about 14 in. broad at the root, sharply pointed at the end where it terminates in a bunch of bristles. The skin was extraordinarily thick and underneath it was a layer of fat up to 3½ in. deep. The whole body was thickly covered with fine soft hair about an inch long, varying in color from faded blond to yellow brown; coarser and longer hair, sometimes 20 in. in length, of a dark, rust-colored brown, covered the entire neck and trunk, perhaps forming a fringe of hair still heavier and thicker from the cheeks along the shoulders and sides to the rump.

The above details regarding the external appearance of the mammoth are given very fully because they enhance the reputation of the Old Stone Age artists not only as close observers but as portrayers with marvelous fidelity of the external appearance of the woolly mammoth. Among the very numerous etchings, drawings, and paintings there is one which possesses high artistic merit as truthfully depicting the characteristics of the charging mammoth (p. 1132 above). The majority of these etchings and sculptures, as fully enumerated[1] in MacCurdy's encyclopedic volumes, are of the modern comic supplement order; they give the impression that our Stone Age ancestors were struck only with the humorous side of the mammoth as he appeared in the full panoply of his winter coat. But our increasing knowledge of these animals, derived from study of the frozen skeletons of Siberia and from the extremely close studies made by the present author in the preparation of this memoir on the Proboscidea, assures us that even the crude outlines on the walls of the cavern of Combarelles (p. 1169 tailpiece) are not of the comic supplement order but are very truthful portrayals of the woolly mammoth as he actually appeared during the winter season, rounded out with his huge thickness of fat (three and a half inches in places) over the entire body and with a woolly covering extending down to his very hoofs and masking the muscular outlines of the limbs beneath. His extremely elevated head was followed by a deep nick or indenture of the neck, then by the rising hump of the back which sloped rapidly downward into the depressed region of the pelvis and terminated suddenly in a short, blunt tail.

Thus the apparent caricatures of the Stone Age artists are realities; the mammoth in his winter pelage was even more disguised than the yak of Tibet. The sloping hind quarters served admirably as a watershed for the torrents of sleet and rain and the whirlwinds of snow that raged during the northern blizzards. Not only this, but the apparently weak and sloping hind quarters were all that the mammoth needed for the forward propulsion of his body, since, unlike all modern elephants, he never used his tusks for digging or uprooting purposes; consequently the hind limbs were not propellers of the body as they are in the African and Indian elephants of today. Another important feature is the bulbous or well-rounded forehead, which rises like a sloping dome at the top of the otherwise pointed head; this swollen forehead, we are sure, was a food reservoir for the winter season which disappeared as winter advanced into spring, when the deep fatty covering all over the body was exhausted and the animal began to assume the normal outlines and proportions of other elephants.

This interpretation is to our mind absolutely demonstrated by the contrast between the comic outlines of the Combarelles mammoths of midwinter and the wonderfully spirited charging mammoth of midsummer engraved on a section of mammoth ivory tusk discovered beneath the Magdalenian shelter of La Madeleine along the Vézère River (p. 1132 above). Here we see that the round fatty outlines of winter give place to those which conform very closely to the lean profile of the summer season; the high, peaked skull especially, with its characteristic concave forehead, affords us a view of the actual summer profile of the mammoth which corresponds with that of the Indiana mammoth shown on page 1158. The classic Magdalenian engraving is one of the most realistic

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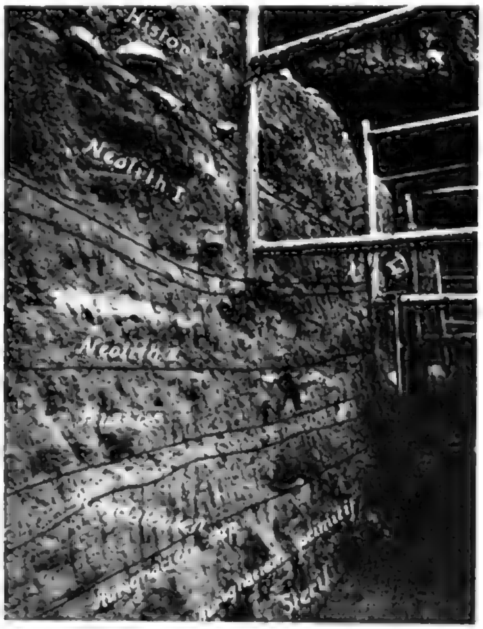
[1] "George Grant MacCurdy: Human Origins. Vol. I, 1924, p. 265."

pieces of Palæolithic art that has ever been found; there are indications that the artist used the relatively small piece of ivory for the representation of three mammoths, for the tusks and trunks of two other elephants appear in the distance. Observe especially the outline of the ear, the elevation of the highly peaked, acrocephalic head, and the remarkably lifelike action of the limbs and body.

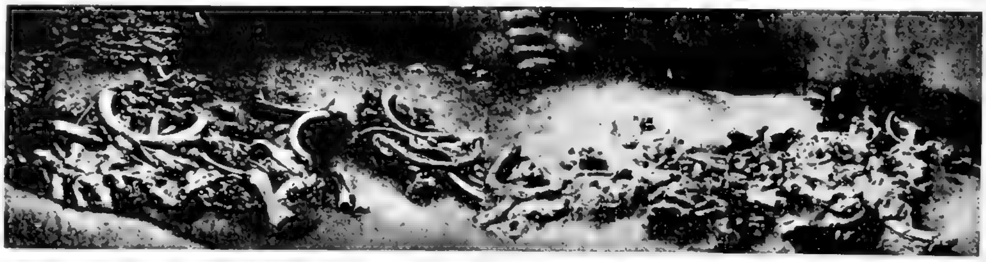
Toward the close of the Old Stone Age there began the wide-spread custom of the ceremonial burial of the dead to which we owe our really remarkable knowledge of the great hunting races that swarmed over central and western Europe during closing glacial time, succeeding the last of the Neanderthal race which seems to have had full possession of the river shores and caverns at the height of the fourth or last descent of the Scandinavian glaciers. Largely known by their flint implements found in the burials of hunters and warriors of Neanderthal time, we know little of their prowess; the Neanderthal flint implements are relatively small and clumsy and it would appear that the Neanderthal hunters were not equipped to pursue the large and formidable woolly mammoths of their time.

Succeeding the Neanderthals, however, was another race, probably from the Far East of central Asia, first found buried in the cavern of Aurignac and hence known as man of the Aurignacian stone culture. This race is known as the Brünn or Předmost; they are long-headed, with a narrow, short face and rather prominent brow ridges, and with brain development inferior to the broad-faced, artistic Cro-Magnons who drew and painted the mammoth. The Brünn people were apparently more interested in eating the mammoth than in depicting it, but they have left some sculptures in bone and ivory of both animal and human figures. This was one phase of the Brünn Aurignacian culture, but their culture is more largely known by their stone implements adapted to the making of clothing and to the killing of smaller kinds of animals—none of the Aurignacian implements so far found in western Europe was adapted to the chase of larger game. Evidence of the killing and consumption for food of a great number of the wild horses of the period has recently been found near Solutré in southern France, but, so far as I know, without the accompaniment of very large flint implements of the chase.



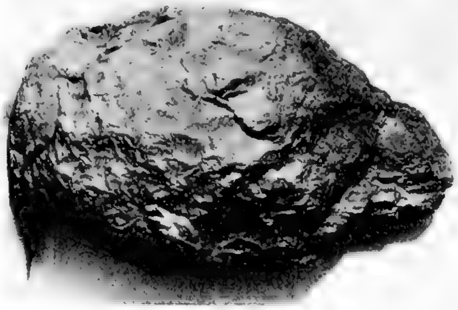
Strata of the Pekárna Cave, Moravia

Fig. 1035. New and Old Stone Age strata, from historic time downward to Lower Aurignacian—altogether ten distinct layers, representing a period which Doctor Absolon believes extended over 100,000 years. The mammoth layer is contemporaneous with the Lower Aurignacian. (After photograph by Doctor Absolon.)



The Mammoth Pit of Věstonice, Moravia

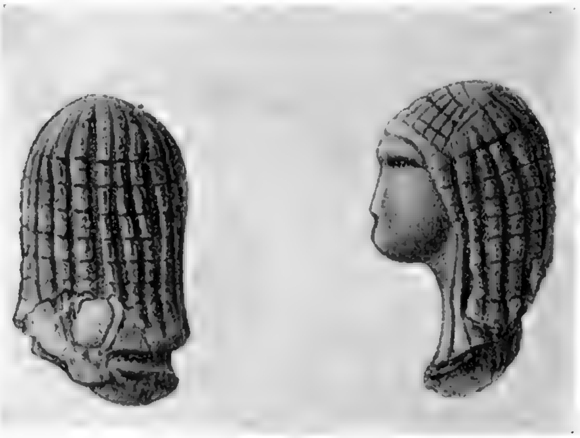
Fig. 1036. View of the mammoth pit of Věstonice. Mammoth skeletons are strewn over the floor. (Photograph by Doctor Absolon.)



Giant Killing Stone of the Moravian Hunters

Fig. 1037. Doctor Absolon interprets the large stones found in the cave as the weapons with which the mammoths were killed after being trapped. Photograph by Doctor Absolon.

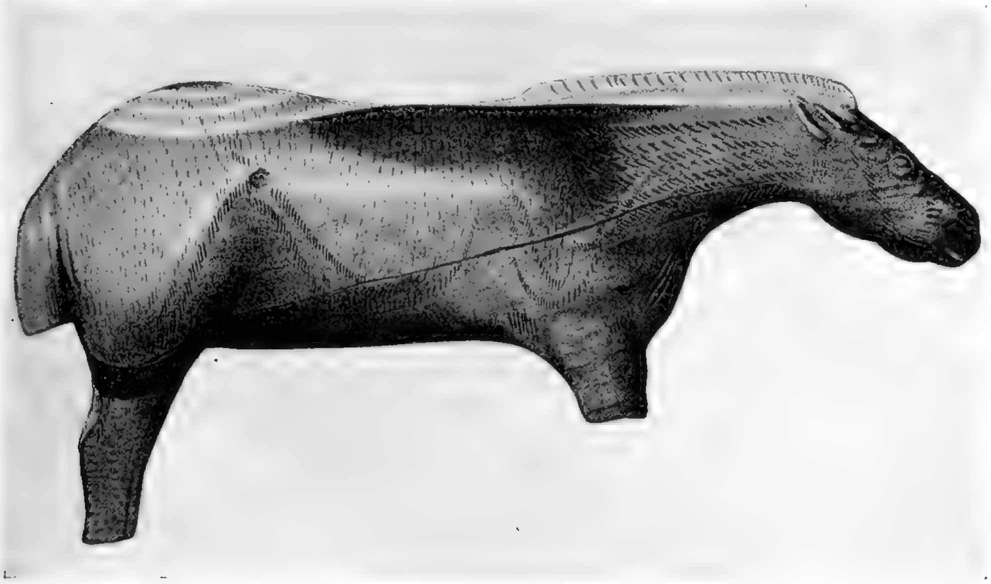
The discovery of giant killing flints by Dr. Karel Absolon of



Ivory Figurine from Brassempouy

Fig. 1038. Back and profile views of a woman's head carved on ivory. (After J. Pilloy in Edouard Piette's *L'Art pendant L'Age du Renne*, 1907.)

the University of Prague and the Museum of Brünn, one of the most distinguished archæologists of central Europe, is therefore a revelation not only of the pursuit of the woolly mammoth for purposes of food, but of the killing methods employed, whereby the animals were driven into great pits and then felled by giant stones let down by their captors. These stones appear (Fig. 1037) like greatly magnified *coups de poings* of the long bygone Chellean and Acheulean age. Citations from the description of his remarkable discoveries in the years 1924–1929 of mammoth-hunting stations of Moravia are given on page 1139 above.



Equine Ivory Statuette from Lourdes

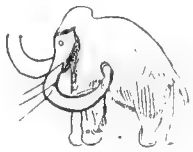
Fig. 1039. This statuette, found in the Grotte des Espélugues at Lourdes, is carved from mammoth ivory. Twice natural size. (After J. Pilloy in Edouard Piette's *L'Art pendant L'Age du Renne*, 1907).

The woolly mammoth appears to have ranged almost exclusively north of the 40th parallel; it loved the borders of the retreating glaciers of the close of the Glacial Age both in Europe and North America. In Alaska it was extremely abundant and was occasionally found in frozen form along the ancient shores of Eschscholtz Bay. Alaska, broadly connected with the Asiatic mainland by a great isthmus bounded on the south by the present mountain peaks of the Aleutian Islands, yields abundant remains not only of the true woolly mammoth closely similar to the *E. primigenius* of Blumenbach, but also an extremely rare and highly specialized grinder (Fig. 1022) to which the specific terminal *compressus* was recently applied by Osborn in descriptive relation to the exclusively compressed and fine-plated grinding teeth which attain the very high number of 27 compressed ridge-plates above and below, in comparison with the 24 ridge-plates above and below in *E. primigenius* of Siberia and western Europe. This proves that the marvelous adaptability of the mammoth did not cease when he entered the continent of America but reached even a higher point of specialization in his essential grinding tooth mechanism, just as we Americans pride ourselves today on our mechanical achievements.

This grinding tooth is a perfect marvel of adaptation and it is lodged below the very highly peaked cranium with a correspondingly deep depression and foreshortening of the jaw and approximation of the front and back planes of the skull which are so extreme as to appear almost artificial. It is this high, narrow, and deep skull to which the Greek adjectives hypsicephaly, acrocephaly and bathycephaly especially apply as absolutely unique in the animal kingdom [See Fig. 1023 above]; in adaptation to grassy diet it is the extreme antithesis to the long and relatively flatheaded cranium of the American mastodon which was the contemporaneous forest dweller of Alaska and as far south as Florida.

The woolly mammoth, however, like the polar bear, arctic fox, ptarmigan, and arctic reindeer, was at its best when in the severe climate of the far North, defying with its woolly covering the coldest arctic blasts. During the summer season it lost not a moment's time in laying in its grassy hoard for the coming winter, in comparison with its less hardy relative, the Jeffersonian mammoth of the mid-temperate region, and its subtropical and more remote relative, the imperial mammoth of the south temperate zone.

Like many other fossil mammals the mammoths appear to have become rather suddenly extinct after the climax of the Old Stone Age, namely, during the slow northward recession of the final great glaciers of Scandinavia and North America. The cause of their disappearance at the very moment when they reached the highest degree of specialization and perfection of their grinding teeth (Fig. 1022) is a mystery; it is attributed by Tolmachoff to further specialization and by Howorth to the universal flooding which accompanied the sullen northward retreat of the great glaciers. A more likely explanation is that during this unfavorable period the herds may have become numerically reduced by underfeeding through lack of grassy food during the summer season. During these decades the underfed mothers were probably unable to protect their young from the attacks of wolves and other carnivorous mammals. Fortunately for us, during the height of their supremacy in western Europe they had been superbly drawn, modeled, and painted by the artists of the closing period of the Old Stone Age. In fact, it was not very long after the recognition of the woolly mammoth as a true fossil that man was also discovered in the fossil state.



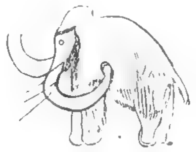


Fig. 1040. A young adult bull elephant (*Loxodonta africana*) in the bush of the Lake Paradise region, east Central Africa, as photographed by Mr. and Mrs. Martin Johnson in 1923-1924, and shown in the film "Simba." Reproduced through the courtesy of Mr. Daniel E. Pomeroy.

Chapter XIX

THE GENERA LOXODONTA, PALÆOLOXODON, AND HESPEROLOXODON OF THE SUPERFAMILY ELEPHANTOIDEA, SUBFAMILY LOXODONTINÆ

Loxodonta, palæoloxodon, and hesperoloxodon, united in the subfamily loxodontinæ by similar cranial and dental characters. Similar especially in the broad premaxillary rostrum and the widely spreading superior incisive tusks with uprooting functions to the end of life. Also relatively simple grinding teeth and more or less pronounced mesial 'loxodont sinus' adapted to browsing rather than to grazing. Of exclusive African, Mediterranean, and Eurasiatic distribution. Surviving in the existing loxodonta africana.

I. Classification and History of Discovery of the Loxodontinæ.
  1. Difficulties of generic nomenclature.
  2. History of discovery and separation of European, Indian, Mediterranean, African, Japanese, and Javanese species.
  3. Order of discovery and description of the fifty-three type species of the extinct Loxodontinæ.

II. Systematic Revision of the Loxodontinæ.
  Subfamily characters.
  Loxodonta: Generic characters.
    1. Order of description of eighteen living African species and subspecies.
    2. Systematic description of species of *Loxodonta*: *Loxodonta africana*, *L. cornaliae*.

III. Eurasiatic Species of Palæoloxodon and Hesperoloxodon.
  Palæoloxodon: Generic characters.
    Palæoloxodon namadicus.
  Hesperoloxodon: Generic characters.
    Hesperoloxodon antiquus.
      Upnor elephant (*H. antiquus*)
    Hesperoloxodon antiquus nanus.
    Hesperoloxodon antiquus platyrhynchus.
    Hesperoloxodon antiquus ausonius.
    Hesperoloxodon antiquus germanicus of Rumania.
    Hesperoloxodon antiquus italicus.
    Hesperoloxodon antiquus germanicus of Steinheim.

IV. Extinct Dwarfed Species of the Mediterranean Islands.
  Palæoloxodon melitensis.
  Palæoloxodon falconeri.
  Palæoloxodon mnaidriensis.
  Palæoloxodon lamarmorae.
  Palæoloxodon cypriotes.
  Palæoloxodon creticus.

V. Les Éléphants Nains des Iles Méditerranéennes et la Question des Isthmes Pléistocènes (Vaufrey, 1929).

VI. Ancestral Stages of Palæoloxodon in Africa.
  Palæoloxodon atlanticus.
  Palæoloxodon jolensis.
  Palæoloxodon recki.

VII. Palæoloxodon and Loxodonta of South Africa.
  ?*Palæoloxodon andrewsi*.
  Palæoloxodon hanekomi.
  Palæoloxodon yorki.
  Palæoloxodon wilmani.
  Palæoloxodon kuhni.
  Palæoloxodon archidiskodontoides.
  Palæoloxodon transvaalensis.
  Palæoloxodon sheppardi.
  Loxodonta zulu.
  Loxodonta prima.
  Loxodonta africana var. *obliqua*.
  Loxodonta subantiqua.

VIII. Loxodontines of Japan and Java.
  Palæoloxodon namadicus naumanni.
  Palæoloxodon namadicus namadi.
  Palæoloxodon protomammonteus.
  Palæoloxodon tokunagai.
  Palæoloxodon protomammonteus proximus.
  Palæoloxodon namadicus yabei.
  Palæoloxodon tokunagai junior mut.
  Parelephas protomammonteus matsumotoi.
  Palæoloxodon yokohamanus.
  Palæoloxodon hysudrindicus, Java.

IX. Summary of Geographic Distribution along the Eastern Coast of Asia.

The cranial, dental, and incisive tusk resemblances of members of the Loxodontinæ to each other and the profound distinctions in cranial profiles, sections, and proportions from the Mammontinæ (*Archidiskodon*, *Parelephas*, *Mammonteus*) types are fully set forth in Chapter XV and synoptically in figure 1041, which illustrates the profile and frontal aspects of the chief specimens known of *Palæoloxodon namadicus and Hesperoloxodon antiquus* in comparison with *Loxodonta africana*. The typical species of *Palæoloxodon* exhibits the broadly diver-

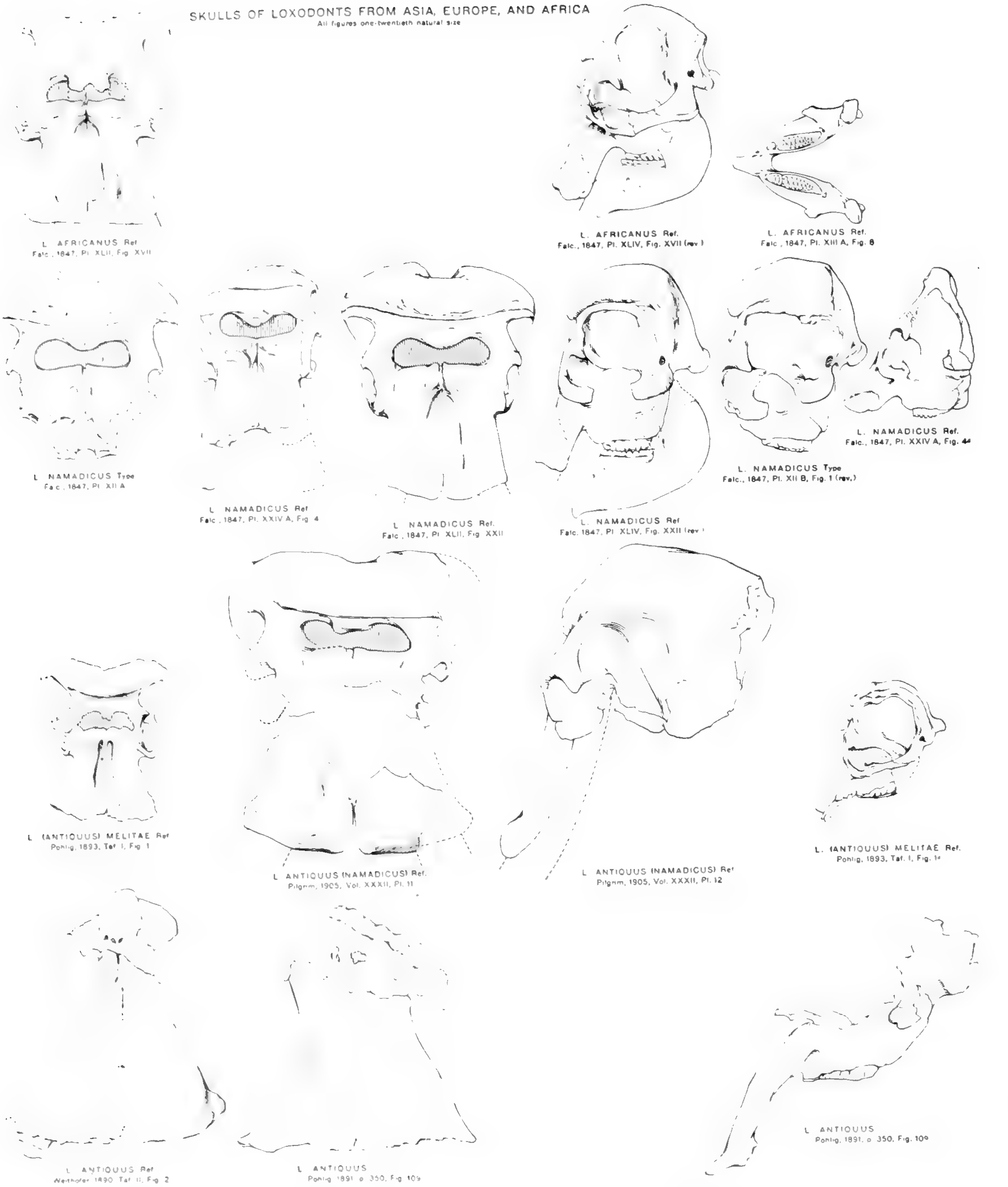


Fig. 1041. Crania of Loxodonta africana, Palæoloxodon namadicus, and Hesperoloxodon antiquus

All to the same scale, one-twentieth natural size. Assembled in the year 1922. Compare figure 1069 of the year 1929

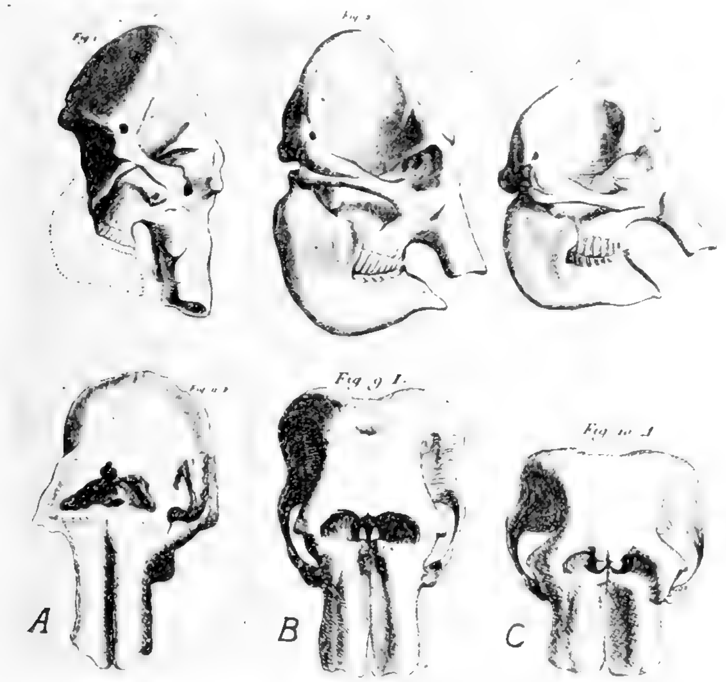
Upper Row. *Loxodonta africana*, after Falconer and Cautley, 1847, Pls. xlii, xliv, xiii.a.

Second Row. *Palæoloxodon namadicus* Falconer and Cautley, type, 1847, Pls. xii.a, xii.b, front and side views. Two referred skulls of *P. namadicus* in front and side views, after Falconer and Cautley, Pls. xxiv.a, xlii, xliv.

Third Row. Referred skulls of *Palæoloxodon melitensis*, after Pohlig, 1893, front and side views, island of Sicily, and of *P. namadicus*, after Pilgrim, 1905, front and side views.

Fourth Row. (Left) Referred rostrum of *Hesperoloxodon antiquus ausonius*?, after Weithofer, 1890. (Middle and right) Rostrum of *H. antiquus ausonius* erroneously referred by Pohlig (1891, p. 350, fig. 109) to *Elephus (antiquus) Nestii*. Recorded as of Upper Pliocene age.

gent premaxillary rostrum similar to that of *Loxodonta africana* but differs very widely in the broadly rugose parietofrontal crest which extends like a Phrygian cap down over the frontals almost to the nasals; this is seen even in the dwarfed species *L.* (*antiquus*) *melitæ*[1] [= *Palæoloxodon melitensis*]. It is obvious that in *Palæoloxodon* the cranium is somewhat more hypsicephalic and bathycephalic than in *Loxodonta*, but this cannot be shown in longitudinal section at present. The function of the gigantic rugose Phrygian cap is doubtless for the support and retraction of enormous divergent tusks and a greatly broadened and enlarged proboscis.



A Fig. 1. Fig. 11 F.

L'éléphant à crâne allongé, à front concave, à très-longues alvéoles des défenses, à mâchoire inférieure obtuse, à mâchelières plus larges, parallèles, marquées de rubans plus serrés, que nous nommons *éléphant fossile* (*elephas primigenius*, Blumenb.), est le *mammont* des Russes.

B Fig. 2. Fig. 9. I.

L'éléphant à crâne allongé, à front concave, à petites oreilles, à mâchelières marquées de rubans ondoyans que nous appelons *éléphant des Indes* (*elephas indicus*), est un quadrupède qu'on n'a observé d'une manière certaine qu'au-delà de l'Indus.

C Fig. 3. Fig. 10. A.

L'éléphant à crâne arrondi, à larges oreilles, à mâchelières marquées de losanges sur leur couronne, que nous appelons éléphant d'Afrique (*elephas africanus*), est un quadrupède dont la seule patrie connue est jusqu'à présent l'Afrique.

Fig. 1042. Cuvier's figures and definitions of *Elephas primigenius* (Messerschmidt's cranium, cf. Fig. 991), *E. indicus*, and *E. africanus*. After Cuvier 1806.1, Pl. 39 (II), figs. 1, 2, 3, and Pl. 41 (IV), figs. 9.I, 10.A, and 11.F. One thirty-seventh to one-twentieth natural size. See also figure 992 above.

I. CLASSIFICATION AND HISTORY OF DISCOVERY OF THE LOXODONTINÆ

(Continued from Chapter II, p. 32, of Vol. I, and Chapter XV of the present Volume)

As repeatedly observed in the present Memoir (e.g., Chap. I, p. 5, Chap. II, pp. 17, 18), it is impracticable in *palæontology* to apply all the principles of nomenclature established in *zoology* and botany, because the classification of the imperfectly known fossil forms is ever changing with our increasing knowledge of *origins, adaptive radiations, and phyletic successions*. Such mutability does not disturb the nomenclature of living animals and plants, in which priority of adequate description, figure, and definition is the chief concern of systematists.

Zoological principles of classification, as in the classic works of Cuvier and of Falconer, must therefore surrender to phylogenetic principles of classification (cf. Chap. II, pp. 5–13) and names and classifications of the dawn period of palæontology must be reworded and rearranged on modern principles and knowledge (cf. Chap. XV, pp. 911, 912). Even certain technical rules of nomenclature, of orthography, and of priority, as revised by zoologists,[2] must give way to palæontologic standards; otherwise we find ourselves repeatedly compelled to

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[1] [The lettering in figure 1041 was executed at a time when all these species were united in the single genus *Loxodonta*, that is, before Professor Osborn had adopted *Palæoloxodon* Matsumoto (1924) for members of the *namadicus* group and had created the new genus *Hesperoloxodon* for certain other species.—Editor.]

[2] The International Commission on Zoological Nomenclature, Congress held at Monaco in 1910.

sacrifice the spirit to the letter and to bury as *nomina nuda* the classic terms of vertebrate palæontology proposed by such great founders as Blumenbach,[1] Cuvier, and Falconer. In no subfamily is this historic recognition and common-sense spirit more essential than in the Loxodontinæ, as shown in the following revision.

1. DIFFICULTIES OF GENERIC NOMENCLATURE

The generic nomenclature of the Loxodontinæ is full of confusion, which can only be cleared up by a common-sense interpretation and reëxamination of the original definitions and types. The history of nomenclature is as follows:

LOXODONTE, F. CUVIER.—Frédéric Cuvier (1825) was the first to apply the appropriate term "Loxodonte" (signifying slanting toothed) to distinguish the African from the Indian elephants, but despite the profound differences in dental and cranial characters and in geographic distribution, the generic term *Elephas* continued to be widely used as late as 1886, e.g., Lydekker, '*Elephas africanus*,' and even in 1928, Andrews, Forster Cooper, and Bather adhered to the generic term *Elephas* in describing the Upnor elephant as '*Elephas antiquus*.'

In the case of the term "Mastodonte" of G. Cuvier, 1806, it was not until 1817 that G. Cuvier adopted the Linnæan classic system of generic orthography: (1) Accordingly F. Cuvier's original term of 1825 was "Loxodonte," as G. Cuvier's original term of 1806 was "Mastodonte."[2] (2) In an unsigned review of F. Cuvier's description in the Zoological Journal of London (1827, 1828, Vol. III, p. 140), the generic term *Loxodonta* was substituted for his "Loxodonte" of 1825; therefore the generic term *Loxodonta* should be credited to F. Cuvier as the generic term *Mastodon* should be credited to G. Cuvier. (3) In 1843, p. 184, Gray, in his "List of the Specimens of Mammalia in the Collection of the British Museum," employed the Latin spelling, as appears from the following citation:

> The African Elephant. Loxodonta Africana. Elephas Africanus, *Blumenb. Abbild.* t. 19. f. c. E. maximus, part, *Linn. Mam. Lithog.* t. *Harris, W. A. Afric.* t. 22. *Cuvier, Oss. Fos.* I. t. 2 to 8.

Again in 1869, p. 359, in his "Catalogue of Carnivorous, Pachydermatous, and Edentate Mammalia in the British Museum," Gray employs the same spelling:

> 2. Loxodonta.
>
> Lamina of the teeth with lozenge-shaped crown. Skull subglobular, forehead shelving, crown rounded; front of lower jaw acute, produced. Trunk conical, thick at the base. Ears very large.
> Loxodonta, *F. Cuvier, Dents Mamm.* [1825,1827.]
>
> Loxodonta africana. (African Elephant.) B.M.
> Loxodonta africana, Gray, *List Mamm. B.M.* 1843; *Gerrard, Cat. Bones B.M.*
> Elephas africanus, *Blumenb. Abbild.* t. 19. f.c.; *Kirk, P.Z.S.* 1864, p. 654; *Giebel, Säugeth.* p. 159; *Blainv. Ostéogr.* Gravigrades, t. 3 (skull), t. 7 & 9 (teeth).
> Elephas maximus (part.), *Linn.*

(4) Falconer and Cautley ("Fauna Antiqua Sivalensis," 1847, Pl. XLII) and Falconer (Quart. Journ. Geol. Soc. London, 1857, pp. 315, 318) employed the shorter masculine term *Loxodon* [preoccupied], which Falconer (1857, p. 315) defined as follows:

> For this subgeneric group, the name of *Loxodon* [Footnote: 'From λοξός *obliquus*, and ὀδούς *dens*, having reference to the rhomb-shaped discs of the worn molars; an adaptation of the term '*Loxodonta*' proposed by Fred. Cuvier, Hist. Naturelle des Mammifères, tom iii., "Article Éléphant d'Afrique." 1835 [1825].'], first indicated by Frederick Cuvier, has been adopted. It comprises both extinct and living species.

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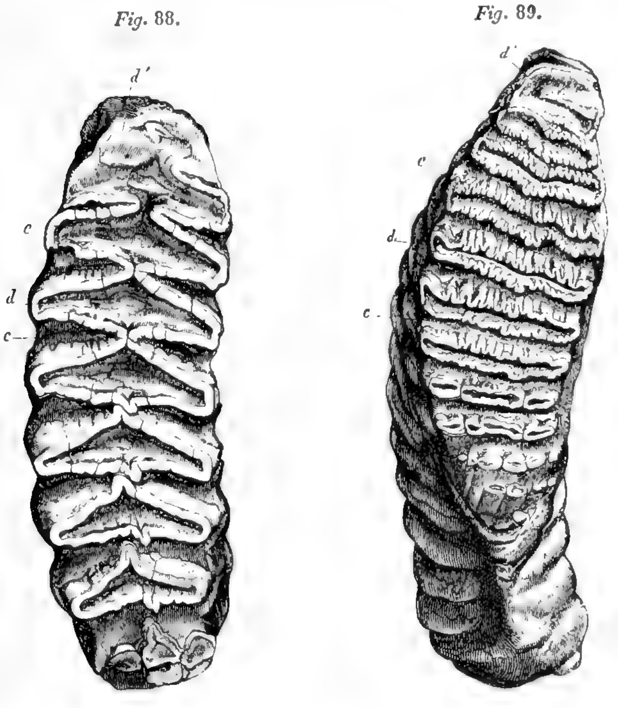
[1] Blumenbach's original description (1799, p. 697) of *Elephas primigenius* cites as an example the Burgtonna (Gotha) skeleton, which certainly belongs to '*Elephas antiquus*,' as fully explained in Chapter XVIII above; see also the present chapter (p. 1181 below).

[2] Compare Chap. V, p. 119, Chap. VI, pp. 135, 165, and Chap. XXI, pp. 1363 and 1372, for the history of the term Mastodonte.

This most appropriate term, however, is preoccupied by *Loxodon* Müller and Henle, 1841, for a genus of sharks, e.g., *Loxodon macrorhinus*; consequently Osborn adheres to the orthography *Loxodonta* (F. Cuvier, 1825, 1827; Gray, 1843), although it involves the feminine termination of the species referable to this great genus. (5) Lydekker (Ency. Brit. 11th Ed.) never admitted the generic distinction of the genotypic and other species of African elephants, but adhered to *Elephas africanus*. (6) Heller and Roosevelt (1914, p. 739) erroneously employed the trinomial *Loxodonta africana africana*, as listed under the existing African species below.

ELASMODON FALC. (PREOCCUPIED) AND EUELEPHAS FALC. (NOMEN NUDUM).—(1) In 1846, Falconer and Cautley first named (p. 45), and figured (1847, Pls. XII.A, XII.B) a new Upper Siwalik species as '*Elephas namadicus*,' the specific name referring to the Nerbudda [or Narbada] River, the Namadus River of Ptolemy. (2) A year later (Fauna Antiqua Sivalensis, 1847, caption to Pl. XLII, figs. XIX–XXIV), they proposed the new subgeneric term *Elasmodon* [in allusion to the waving enamel ridges], to include the six species *E. antiquus*, *E. hysudricus*, *E. meridionalis* [not figured], *E. namadicus*, *E. indicus* (Dauntela var., Mukna var., and young), and *E. primigenius*; these six heterogeneous species are the 'genotypes' of *Elasmodon* and of its substitute *Euelephas*. (3) In this same caption they erroneously applied the generic name *Loxodon* to *E. planifrons*, grouping it with *E. africanus*. (4) In 1857, learning that the name *Elasmodus* had been used for a series of fossil fish, Falconer (p. 315) substituted the generic term *Euelephas* for *Elasmodon*: "For this subgeneric group we propose the term of *Euelephas* [Footnote, 'From εὖ *bene*, and ἐλέφας, having reference to the typical Elephants most familiarly known.']." (5) W. L. Sclater (1900, p. 317) was in error in making *Elephas planifrons* the genotypic species of *Euelephas*, because this species was not included in the original definition of *Elasmodon* referred to above. (6) Palmer (1904, p. 275)

THIRD (INFERIOR) AND SECOND SUPERIOR MOLARS OF THE AFRICAN (LOXODONTA) AND ASIATIC (ELEPHAS) ELEPHANTS.



African Elephant. ⅓ nat. size. Asiatic Elephant.

Fig. 1043. Crown view of the third inferior molar of the right side of: Fig. 88, *Loxodonta africana*; Fig. 89, *Elephas indicus*, one-third natural size. Compare Owen, "History of British Fossil Mammals, and Birds," 1846, pp. 230–232, figs. 88, 89.

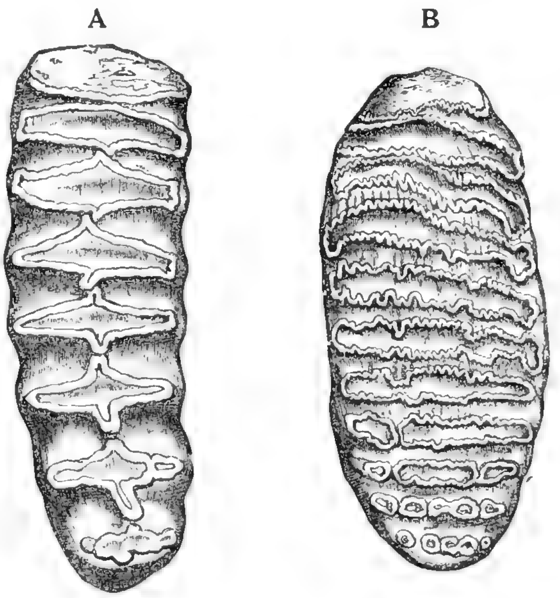
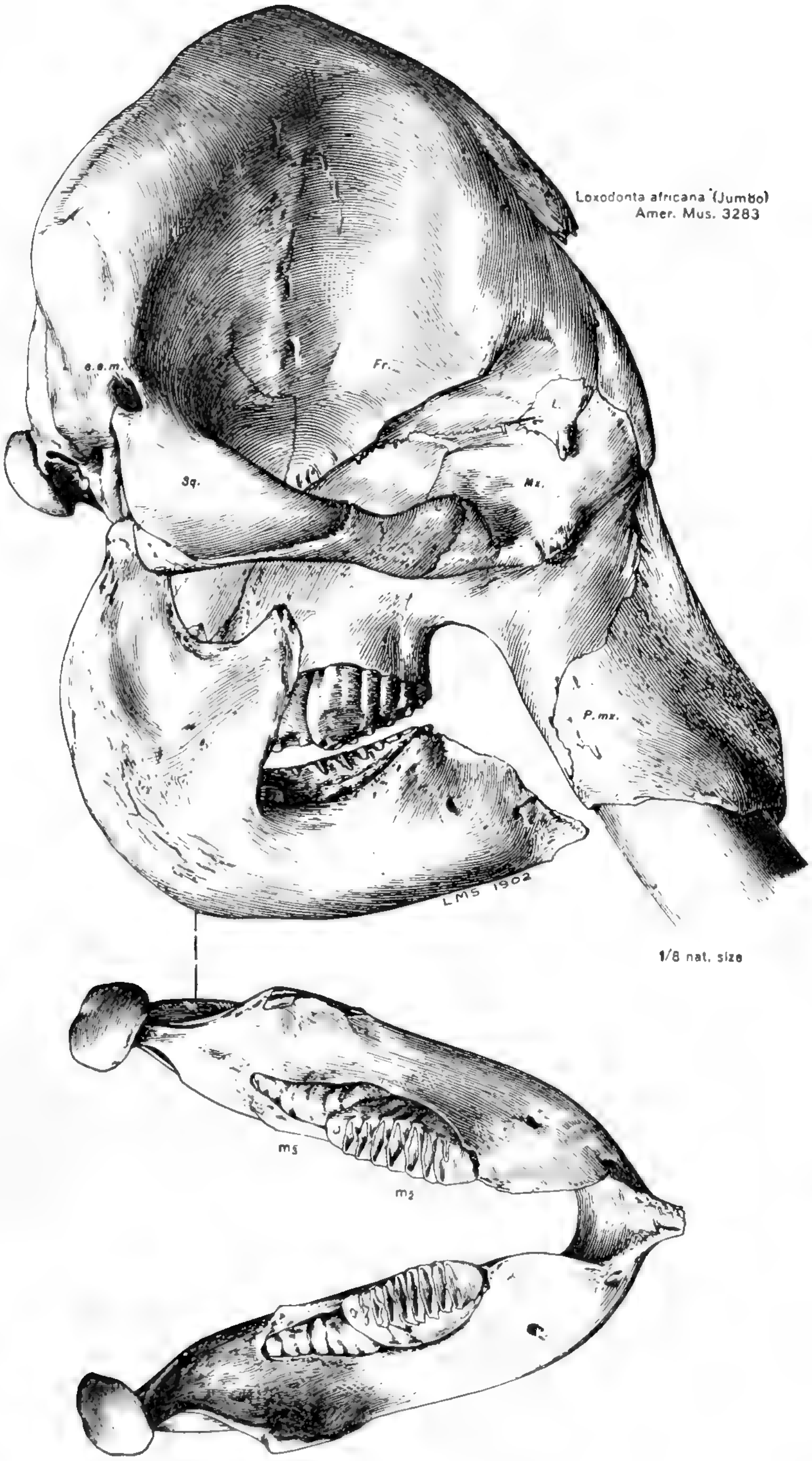


Fig. 1044. Crown view of: (A) second right superior molar of *Loxodonta africana*, with eight lozenge-shaped ridge-plates; (B) second right (?) superior molar of *Elephas indicus*, exhibiting eleven worn ridge plates. After Lydekker, "Catalogue of the Ungulate Mammals in the British Museum (Natural History)," Vol. V, 1916, p. 80, fig. 22.



CRANIA OF AFRICAN (LEFT) AND OF NERBUDDA, INDIA (RIGHT), ELEPHANTS

Both one-eighth natural size

LOXODONTA (MALE)

Fig. 1045. Cranium and jaws of the typical African elephant of the Sudanese or Abyssinian subspecies *Loxodonta africana oxyotis*. In the jaw observe the extremely lozenge-shaped or centrally expanding molar ridge-plates characteristic of all species of the genus *Loxodonta*. Compare figure 1043.

PALÆOLOXODON (FEMALE)

Fig. 1046. Cranium of the type of *Palæoloxodon namadicus*. In the palate observe the closely parallel and relatively compressed molar ridge-plates characteristic of all species of *Palæoloxodon*. Compare figure 1070, also figure 1072.

simply quoted Sclater's erroneous statement. (7) Falconer in his Memoir of 1857 (p. 318) defined in Latin the collective genus *Elephas* (Linn.), on the basis of premolar and molar tooth structure, as embracing three subgenera, namely:

Subgen. 1. STEGODON.—Dentium molarium 3 utrinque intermediorum coronis complicata colliculis hypisomeris (*e.g.* 7+7+8), mammillatis, tectiformibus. Præmolares nondum observati.

Subgen. 2. LOXODON.—Dent. molar. 3 utrinque intermedior. coronis lamellosa colliculis hypisomeris (*e.g.* 7+7+8), cuneiformibus. Præmolares raro utrinque 2.

Subgen. 3. EUELEPHAS.—Dent. molar. 3 utrinque intermedior. coronis lamellosa colliculis deinceps numero auctis, anisomeris (*e.g.* 12+14+18), attenuatis, compressis. Præmolares nulli.

(8) In Falconer's classification (1847) *Elephas* [*Archidiskodon*] *meridionalis* was erroneously grouped with *Elasmodon* (=*Euelephas*), while the closely related *E.* [*Arch.*] *planifrons* was grouped with *Loxodon*; this obvious discrepancy was corrected in 1857 (Synop. Tab. opp. p. 319), but Falconer fell into a fresh error by uniting *E.* (*Loxod.*) *planifrons* and *E.* (*Loxod.*) *meridionalis* in the same group with the African elephant, *Elephas* (*Loxod.*) *africanus*, because of the possession of 'digitated' ridge-plates.

(9) From the above historic analysis it is clear that '*Elasmodon*' Falc. is preoccupied and that the substitute name '*Euelephas*' Falc. is an invalid and unusable *nomen nudum*, because it was based on an *artificial and heterogeneous assemblage of six species*, which, as shown in the present Memoir, belong to five or six entirely distinct generic phyla, namely:

Elephas antiquus =*Hesperoloxodon*[1]
Elephas namadicus =*Palæoloxodon* (Syn.: *Sivalikia, Pilgrimia*)[2]
Elephas hysudricus =*Hypselephas*
Elephas indicus =*Elephas*
Elephas meridionalis =*Archidiskodon*
Elephas primigenius =*Mammonteus*[3]

(10) These criticisms imply no disrespect of Falconer's genius, but rather the insuperable difficulties under which he labored in disregarding cranial characters and in defining from ridge-plate characters only, as pointed out above in Chapter XV, "Classification of the Elephantoidea." As repeatedly shown in the present Memoir, the arrangement of the ridge-plates, whether separated ("colliculi grossè digitati") or compressed ("colliculi approximati") is an unreliable and misleading basis of phyletic and generic distinction, because it is subject to parallelism or convergence; Cuvier (1806–1836) used both cranial and dental characters in separating the only three species recognized by him, viz., *Elephas africanus, E. indicus,* and *E. primigenius,* as shown above in Cuvier's legends beneath figure 1042.

Falconer's reliance, for identification and definition of genera, on ridge-plate formulæ is shown in the entirely unnatural arrangement of genera in his Note Book for August 25, 1862 (Pal. Mem., 1868, II, p. 176) as follows:

[Falconer, 1862,1868]	Milk	True	[Totals]	[Present Memoir]
Dinotherium	1+2+ 3	3+ 2+ 2	=13	*Deinotherium giganteum*
Trilophodon Ohioticus	1+2+ 3	3+ 3+ 4	=16	*Mastodon americanus*
Tetralophodon Arvernensis	2+3+ 4	4+ 4+ 5	=22	*Anancus arvernensis*
Pentalophodon	3+4+ 3	5+ 5+ 6	=28[26]	*Pentalophodon sivalensis*
Stegodon insignis	2+5+ 7	7+ 8+10–11	=40	*Stegodon insignis-ganesa*
Loxodon meridionalis	3+6+ 8	8+ 9+12	=46	*Archidiskodon meridionalis*
Euelephas antiquus	3+6+10	10+12+16	=57	*Hesperoloxodon antiquus*
" primigenius	4+8+12	12+16+24	=76	*Mammonteus primigenius*
" indicus	4+8+12	12+16+24	=76	*Elephas indicus*

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[1] [See p. 1217 below for definition of *Hesperoloxodon*.—Editor.]

[2] [See explanation on p. 1179 below.—Editor.]

[3] [For doubtful validity of the genus *Mammonteus*, see footnote on p. 1117 above.—Editor.]

SEPARATION OF ANTIQUUS (III) AND AFRICANA (V) LINES.—Depéret and Mayet (1923, table, pp. 204 and 205) in their phyletic arrangement of the Proboscidea distinguished five absolutely separate phyla or lines of elephants, all of which, however, they included within the genus *Elephas*.

GENUS ELEPHAS
I. Primigenius line: *astensis, primigenius, trogontherii, sibiricus.*
II. Meridionalis line: *planifrons, hysudricus, meridionalis* mut. *cromerensis.*
III. Antiquus line: *ausonius, antiquus: melitensis, creticus, cypriotes, atlanticus.*
IV. Indicus line: *indicus, namadicus.*
V. Africanus line: *africanus* [= *Loxodonta* F. Cuvier].

In the following year Matsumoto (1924.2, Sept. 20) raised Depéret's 'III. Antiquus line' into a subgenus of the genus *Loxodonta*, namely, *Palæoloxodon*, cited below.

FALCONER, 1857, OSBORN, 1918. Falconer himself was the first to recognize the mutual resemblances of his British Pleistocene species *Elephas antiquus* to his Siwalik species *E. namadicus* (1857, Synop. Tab. opp. p. 319), because they both exhibited "colliculi approximati"; he did not perceive, however, their phyletic resemblance in cranial characters to the African elephant (*Loxodonta africana*), but only the difference in the ridge-plates ("colliculi dilatati") of the latter. It remained for several subsequent writers (Pohlig, Pilgrim) to perceive this very close resemblance, and Osborn (1918.468, table opp. p. 134) finally placed *Elephas africanus, E. antiquus,* and *E. namadicus* in the generic phylum *Loxodonta*, subfamily Loxodontinæ.

Osborn six years later (1924.633, p. 2, Dec. 20) selected *Elephas namadicus* Falc. and Caut. as the genotype of his new genus *Sivalikia*, to embrace also *E. antiquus*, both distinguished from *Loxodonta* by more numerous and more compressed ridge-plates (i.e., "colliculi approximati").

> *Sivalikia*, new genus. Typified by *Loxodonta namadica* Falconer, type species, and distinguished by broad grinding teeth, numerous ridge-plates, and absence of 'loxodont sinus.' Unfortunately the name *Falconeria* is preoccupied for a genus of reptiles, consequently the name *Sivalikia* is proposed in honor of Dr. Hugh Falconer's great work on the Siwalik fauna.

In the same paper (1924) he proposed the genus *Pilgrimia*, typified by the narrow-toothed *Elephas falconeri* of the Mediterranean Islands (Osborn, 1924.633, p. 2) as follows:

> *Pilgrimia*, new genus. Typified by *Elephas falconeri* Busk, type species, *E. melitensis* Falconer, *E. mnaidræ* Adams, and *E. antiquus Recki* Dietrich; distinguished by narrow grinding teeth, numerous ridge-plates, 'loxodont sinus' vestigial or absent. The name *Pilgrimia* is given in honor of Dr. Guy E. Pilgrim of the Geological Survey of India, to whom palæontology is indebted for the complete solution of the stratigraphy of the Siwaliks and of other mammaliferous horizons of India and Burma.

PALÆOLOXODON MATSUMOTO, 1924.[1]—Independently of Osborn's proposal of the genus *Sivalikia*, and at a somewhat earlier date (Sept. 20) in the same year (1924), Matsumoto (pp. 256, 260) selected a subspecies of *Elephas namadicus*, namely, *E. namadicus naumanni* Makiyama (1924), as the type of a new subgenus *Palæoloxodon*, a name which now proves applicable to the narrow- to broad-toothed[2] loxodonts of Japan and the East Indies as well as to similar loxodonts of Eurasia and Africa. An abstract of Matsumoto's paper is as follows (pp. 257, 260):

> *Palæoloxodon* corresponds to Depéret's group of *E. antiquus*, with molars consisting of a small number of ridge-plates, others with numerous ridge-plates. When worn the molars show clearly the rhombic form [loxodont sinus] and the enamel folds are almost parallel in the anterior and posterior portions of the unworn teeth. The molars vary in width, some being narrow, others wide. This subgenus is divided into two lines (a) *E. melitensis-atlanticus* and (b) *E. antiquus-namadicus*, according to the classification of Depéret. *E. antiquus* is not extremely narrow, and the number of the ridges is rather numerous. The species of this group belong to a later period, and the ridge-plates of the molars are less rhombic in form; easily confused with *E. trogontherii*. *E. ausonius* equals the Calabrian in Europe, *E. antiquus* the middle and lower Diluvian in Europe, *E. namadicus naumanni* the lower Diluvian in Japan, *E. namadicus* the middle Diluvian in Japan and India.

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[1] Unfortunately this article of 1924 did not reach the present author until much of the text of this Memoir had been prepared. The original was probably lost in transmission to America.

[2] In all elephantine phyla the primitive grinders are relatively *narrow*; they become progressively *broad* as the cranium shortens, broadens, and deepens. Hence the *narrow to broad or wide* adaptation.

Osborn, 1924.—During these years Osborn was engaged in a very close comparison of the crania and dentition of the loxodonts of Asia, Europe, and Africa, the results of which are fully set forth in the present chapter, finally describing the entire structure of all the known Loxodontinæ. Unaware of Matsumoto's publication of September 20, 1924, he independently separated the genus *Sivalikia*, based upon the genotypic species '*Elephas namadicus*' Falc. and Caut., publishing the same on December 20 of the same year (1924), three months later than Matsumoto's publication. In the present Memoir it is shown that the *E. namadicus naumanni* of Makiyama (genotype[1] of *Palæoloxodon*) is very close in character to the '*Elephas namadicus*' of Falconer and Cautley (genotype of *Sivalikia*). Although Matsumoto proposed the name *Palæoloxodon* as a subgenus of *Loxodonta*, and Osborn proposed the name *Sivalikia* as a genus entirely distinct from *Loxodonta*, Dr. T. S. Palmer (letter of March 12, 1929) rules that even if incorrectly conceived and defined, the subgeneric name *Palæoloxodon* (Sept. 20, 1924) preoccupies and anticipates the full generic name *Sivalikia* (Dec. 20, 1924). Osborn accordingly accepts Palmer's ruling, although it appears to do injustice to his four years of research, in which his conclusions quite differ from those of Matsumoto. Meanwhile the generic name *Sivalikia* runs throughout the text and many of the illustrations; the reader, therefore, should make the following substitution: *Palæoloxodon* (syn. *Sivalikia*, *Pilgrimia*).

Original Definition of Genera (1825–1924)

These four generic lines were originally separated and defined by the characters of the subgenera and species grouped within them, as follows:

I. Genus: *Loxodonta* F. Cuvier, 1825, 1827.	II. Subgenus: *Palæoloxodon* Matsumoto, September 20, 1924.	III. Genus: *Sivalikia*[3] Osborn, December 20, 1924.	IV. Genus: *Pilgrimia*[3] Osborn December 20, 1924.
Genotypic species: *Elephas africanus* Blumenbach.	Genotypic species: *Elephas namadicus naumanni* Makiyama.[1]	Genotypic species: *Elephas namadicus* Falconer and Cautley.	Genotypic species: *Elephas falconeri* Busk.
Relatively narrow grinding teeth with relatively few ridge-plates: M 3 $\frac{10}{11\text{-}12}$	Ridge-plates expanded somewhat mesially, 'loxodont sinus' rudimentary, vestigial, or absent, enamel typically plicate; relatively narrow grinding teeth, with numerous ridge-plates: Max.: M 3 $\frac{19}{17}$.	Relatively *broad* grinding teeth with numerous ridge-plates: Max.: M 3 $\frac{16\frac{1}{2}-17}{16\frac{1}{2}-17}$	Very long and *narrow* grinding teeth, with numerous and closely compressed ridge-plates: Max.: ?M 3 $\frac{13}{14}$.
Conservative in cranial and grinding tooth structure. Distinguished by very broad 'loxodont sinus'; enamel nonplicate, or smooth.		Progressive in cranial and grinding tooth structure. 'Loxodont sinus' absent or rudimentary; enamel plicate.	Dwarfed elephants of the Mediterranean Islands. 'Loxodont sinus' vestigial or absent.
Descended from unknown ancestors[2] to the modern *Loxodonta africana*.	Large elephants of Japan.	Including animals of gigantic size.	Including animals of diminutive size.
Premaxillaries broad.	Premaxillaries broad.	Premaxillaries very broad. Incisive tusks widely divergent.	Premaxillaries broad.
Parietofrontal cranial vertex rounded, subacrocephalic.	Cranium [of genotype] unknown. [Cf. *P. namadicus* figured by Falconer and by Pilgrim (Fig. 1041).—Editor.]	Parietofrontal cranial vertex broadly expanded, with prominent frontal crest.	Parietofrontal vertex expanded, with frontal crest.
The genus *Loxodonta* is readily distinguished by its primitive cranium, primitive ridge-plate formula, and specialized lozenge-shaped or 'loxodont sinus.'	The subgenus *Palæoloxodon* Matsumoto, 1924, founded on the species '*Elephas namadicus naumanni*' Makiyama, 1924, is also characterized as relatively narrow toothed.	The genus *Sivalikia*, typified by '*Elephas namadicus*,' is distinguished by its relatively broad grinding teeth, numerous parallel ridge-plates, and the absence of a 'loxodont sinus.' It proves to be the same as the subgenus *Palæoloxodon* Mats.	The genus *Pilgrimia*, founded on the narrow-toothed, dwarfed species '*Elephas falconeri*,' with less numerous ridge-plates, may prove to be ancestral to the subgenus *Palæoloxodon* of Matsumoto, 1924.[3]

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[1] [See footnote by Dr. E. H. Colbert on page 1247 below.—Editor.]

[2] [Compare *Loxodonta prima* and *L. africana* var. *obliqua* of Dart, 1929, on page 1287, below.—Editor.]

[3] [*Sivalikia* and *Pilgrimia* finally determined by Professor Osborn as synonyms of *Palæoloxodon* Matsumoto.—Editor.]

DEFINITIONS AND DISTINCTIONS BY OSBORN OF THE TWO GENERA

There can be no question of the clear generic distinction of *Palæoloxodon*[1] (synonyms *Sivalikia* and *Pilgrimia*) from *Loxodonta*. Subsequent research may reveal more than one generic phylum within the genus *Palæoloxodon*, but at present it would appear, as explained in the following paragraphs of this chapter, that the phylum *Palæoloxodon* originated in Africa, migrated northward into Europe, possibly developing into the '*Elephas antiquus*' group, also northeastward through the Mediterranean Islands, leaving dwarfed descendants resembling either the '*E. antiquus*' group or the '*E. namadicus*' group, finally arriving in southern and southeastern Asia, developing into the '*Elephas namadicus*' group.

Meanwhile the animals composing the great generic phyla *Palæoloxodon* and *Hesperoloxodon*, as in parallel species of *Archidiskodon*, increased in size and multiplied their molar ridge-plates from the minimum, M 3 $\frac{12\text{-}14}{12\text{-}14}$ (*Palæoloxodon atlanticus*), to the maximum, M 3 $\frac{19}{17}$ (*P. namadicus naumanni*), and from the minimum, M 3 $\frac{16\frac{1}{2}\text{-}17}{16\frac{1}{2}\text{-}17}$ (*Hesperoloxodon antiquus typicus*), to M 3 $\frac{17\text{-}19}{+18+}$ (*H. antiquus germanicus*), to M 3 $\frac{20}{18+}$ (*H. antiquus italicus*).

The species in these two great phyla are progressively distinguished by the successive addition of ridge-plates, by the increasing hypsodonty of the grinding teeth, by the absence (in the typical '*E.* [*Hesperoloxodon*] *antiquus*' group) of the transverse bony ridge above the orbits, or by the presence (*E. mnaidriensis, E. melitensis, E. namadicus* [=*Palæoloxodon*]) of this broad bony ridge above the orbits. Consequently according to this interpretation the subfamily Loxodontinæ contains three chief generic phyla, as follows:

I. Genus: *Loxodonta* F. Cuvier, 1825, 1827.	II. Genus (subgenus): *Palæoloxodon* Matsumoto, 1924; Subgen. or syn.: *Sivalikia* Osborn, 1924. *Pilgrimia* Osborn, 1924.	III.[2] Genus: *Hesperoloxodon* Osborn, 1931.
Genotypic species: *Elephas africanus* Blumenbach.	Genotypic species *Elephas namadicus naumanni* Makiyama.	Genotypic species *Palæoloxodon antiquus italicus* Osborn.[3]
Relatively conservative and primitive in cranial and grinding tooth structure.	Relatively progressive in cranial and grinding tooth structure.	Cranium domelike with flattened forehead, more hypsicephalic and bathycephalic than that of *Palæoloxodon*.
Grinders distinguished by broadly open 'loxodont sinus' (lozenge shaped), on wear; enamel non-plicate or smooth.	Grinders distinguished by rudimentary, vestigial, or absent 'loxodont sinus'; enamel typically plicate.	Grinders hypsodont, 'loxodont sinus' vestigial or absent.
Grinders relatively narrow, low crowned, with comparatively few ridge-plates: Max.: M 3 $\frac{10}{11\text{-}12}$.	Primitive grinders relatively narrow, with increasingly numerous ridge-plates: Min.: M 3 $\frac{12\text{-}14}{12\text{-}14}$ Max.: M 3 $\frac{19}{17}$.	Ridge-plate formula: Min.: M 3 $\frac{16\frac{1}{2}\text{-}17}{16\frac{1}{2}\text{-}17}$ Max.: M 3 $\frac{20}{18+}$
Premaxillaries broad with widely divergent incisive tusks, elongate, slightly incurved.	Premaxillaries extremely broad, incisive tusks widely divergent, straight or slightly incurved.	Premaxillaries extremely broad, incisive tusks widely divergent, slightly upcurved and incurved.
Parietofrontal cranial vertex low, rounded, subacrocephalic, of persistent primitive form.	Parietofrontal cranial vertex somewhat more progressive, acrocephalic, with smooth or with prominent frontal ridge-crest for attachment of the muscles of the trunk.	Lacking prominent parietofrontal crest so distinctive of *Palæoloxodon namadicus*.

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[1] [Subsequently (1931) Professor Osborn's researches on the skull of *Palæoloxodon antiquus italicus* led him to the conclusion that this subspecies belonged in a quite distinct phylum from that containing '*Elephas' namadicus*; consequently he provisionally assigned to it and to other members of the '*E. antiquus*' group the new generic name *Hesperoloxodon* (see Osborn, 1931.846, p. 21), retaining the name *Palæoloxodon* for members of the '*E. namadicus*' group.—Editor.]

[2] [Compiled from statements in the text.—Editor.]

[3] [See footnote by Dr. E. H. Colbert on page 1247 below.—Editor.]

2. HISTORY OF DISCOVERY AND SEPARATION OF EUROPEAN, INDIAN, MEDITERRANEAN, AFRICAN, JAPANESE, AND JAVANESE SPECIES

Europe: Sceleto Elephantino Tonnæ, 1695 (Tentzelius, 1698).—In 1695 occurred the discovery near Gotha, northern Germany, of the classic 'Burg-Tonna skeleton,' followed by the first scientific descriptions, as fully set forth in Chapter XVIII above, pp. 1118–1119; this famous skeleton, which aroused the interest of all the savants of western Europe, was referred to by Blumenbach (1799) in his type description of *Elephas primigenius* (also cited in Chapter XVIII, p. 1141), but it now proves to belong to the '*Elephas antiquus*' phylum, judging by the few parts that remain of this originally fine specimen.

As shown above in Chapter XVIII (footnote, p. 1119) of the present Memoir, parts of the Burgtonna skeleton were presented by Tentzelius to the Royal Society through Sir Hans Sloane and are now lost. Other parts are still preserved in the Gotha Museum. Dietrich writes (April 14, 1930) that there is no doubt that the classic Burgtonna skeleton belongs to *Elephas antiquus*; its geological horizon is the travertine sands of the last Interglacial Period, that is, it belongs to the same deposits as those of Weimar-Taubach-Ehringsdorf, a more recent phase of the last Interglacial. Amthor of Gotha confirms the fact that the skeleton, incisors, tusks, etc., are present in the Gotha Museum, but illustrations are not available.

Other European remains now known to belong to '*E. antiquus*' were for a long period confused with those of the southern mammoth, '*Elephas meridionalis.*' It is also a singular and generally unnoticed fact that the generically related '*Elephas namadicus*' of India was described by Falconer and Cautley in 1846, a year before they figured (1847) the '*Elephas antiquus*' of Europe, as shown in the following history of nomenclature.

In the present Memoir are reproduced the type figures of all the species of *Loxodonta, Palæoloxodon* (syn.: *Sivalikia, Pilgrimia*), and *Hesperoloxodon* so far as published by the authors, also so far as the type specimens have been available.

India: Elephas namadicus Falc. and Caut. (1846).—It was a long time before the relationship of the Indian species *Elephas namadicus* to the African genus *Loxodonta* rather than to the Asiatic *Elephas indicus* was recognized. In 1846 Falconer and Cautley (1846, p. 45) observed:

> Another extinct Indian species *E. Namadicus* (to be described in the sequel), which is closely allied to the existing Indian form [i.e., *Elephas indicus*], comes between it and *E. Hysudricus*, together with a European fossil species [probably referring to the as yet unnamed *Elephas antiquus* Falconer and Cautley, 1847], which we believe to be distinct from the Mammoth [i.e., *Elephas primigenius* Blum.]; and the gap between the existing African Elephant and *E. planifrons* is filled up by another well-marked European fossil species, *E. priscus* (?), pl. 13, fig. 7, which is closely allied to the former.

The type of '*E. namadicus*' (Fig. 1070) was designated (Falconer, 1867, p. 15; 1868, Vol. I, p. 435) as from the "valley of the Nerbudda. Probably a female, from small size of tusks." Falconer writes (*op. cit.*, pp. 15 and 435): "I have named the species *E. Namadicus*, after the Nerbudda river, the Namadus of Ptolemy."

Falconer and Cautley, 1847.—Falconer became impressed with the close resemblance between this Middle [to Upper] Pleistocene species of India, which he named *E. Namadicus* in 1846, and the British Lower Pleistocene proboscidean, which he named *Elephas antiquus* in 1847.

Great Britain: Elephas antiquus Falconer (1847).—Up to 1844 all the British fossil elephants had been referred to '*Elephas primigenius.*' At that time Falconer was arranging and describing his rich collections from the sub-Himalaya and river deposits of central India, which had been aided by the contributions of Sir Proby T. Cautley, Mr. Fraser, and others. The superb plates of the "Fauna Antiqua Sivalensis," beginning in 1845, display Falconer's confusion of the *Elephas meridionalis* of Nesti with the animal which he first erroneously named '*Elephas priscus*' [after Goldfuss = *Loxodonta africana*] and finally in 1857 clearly distinguished in his mind as *Elephas antiquus.*

The first figure of '*Elephas antiquus,*' published in 1847, Pl. XII.D, fig. 4 (Brit. Mus. M.2006), may be taken as Osborn's lectotype, although designated in the plate as "*Elephas meridionalis,*" but corrected by Falconer in a copy of the "Fauna Antiqua Sivalensis" belonging to the British Museum. Falconer's first[1] printed description of *E. antiquus* is that published by Murchison in 1867, p. 18, in the legend of figures 4, 4*a*, of Pl. XII.D; this description applies to a first true molar (M_2, *fide* Lydekker, 1886, p. 130) with twelve to thirteen ridges. On a subsequent page (*op. cit.*, 1867, p. 21) he described (Pl. XIV, fig. 7), as '*Elephas priscus,*' an unmistakable specimen of *E. antiquus* from Gray's Thurrock (Brit. Mus. 39,370), designating it as a "last lower molar, left side, containing eight ridges, heel inclusive" [$l.M_3$, see Fig. 1076 below]. He adds: "Besides the great expansion, this tooth differs from all true *E. antiquus* specimens in the lowness of the crown ridges. . . . If not a separate species, [it] is a very marked variety."

Leith Adams (1877–1881, p. 47) erroneously determined the ridge formula of the typical *Elephas antiquus* as:

$$\text{Dp 2 } \frac{+2\text{-}3+}{+3+\text{-}?} \quad \text{Dp 3 } \frac{+5\text{-}7+}{+6\text{-}8+} \quad \text{Dp 4 } \frac{+9\text{-}10+}{+9\text{-}11+} \quad \text{M 1 } \frac{+9\text{-}12+}{+11\text{-}12+} \quad \text{M 2 } \frac{+12\text{-}13+}{+12\text{-}13+} \quad \text{M 3 } \frac{+15\text{-}20+}{+16\text{-}19+}.$$

MEDITERRANEAN ISLANDS: MALTA, SARDINIA, AND SICILY (1862–1907)

The existence of pigmy elephants on the island of Malta (*Elephas melitensis* Falc.), as first announced at the Cambridge meeting of the British Association, October 6, 1862, astounded the palæontologists. Besides two dwarfed species (*E. melitensis* Falc., 1862, 1868, and *E. falconeri* Busk, 1867), both found in the Zebbug Cave of Malta, there were traces of a third elephant of nearly normal size referred to *Elephas antiquus*.

In addition to reviewing this important discovery, Leith Adams (1870, p. 224) added a third species (*E. mnaidræ*), a name amended by its author to *E. mnaidriensis* in 1874, p. 116). "This species [Lydekker, 1886, p. 138] is considered to have averaged between six and seven feet in height and to have been allied to the narrow-crowned race of *E. antiquus* and also to *E. africanus*. The ridge-formula is given by Leith Adams [Footnote: 'Trans. Zool. Soc. vol. ix. p. 112.'] (exclusive of talons) as":

$$\text{'}\textit{Elephas mnaidræ}\text{': Dp 2 } \tfrac{3}{3} \text{ Dp 3 } \tfrac{6}{6} \text{ Dp 4 } \frac{8\text{-}9}{8\text{-}9} \text{ M 1 } \frac{8\text{-}9}{8\text{-}9} \text{ M 2 } \tfrac{10}{10} \text{ M 3 } \frac{12\text{-}13}{12\text{-}13}.$$

This formula is much lower than that of *Hesperoloxodon antiquus*, as cited from Leith Adams above; it is actually lower than that of *H. antiquus* as now determined, namely, M 3 $\frac{16\frac{1}{2}\text{-}17}{16\frac{1}{2}\text{-}17}$; but it is higher than that of *Loxodonta africana*, namely, M 3 $\frac{10}{11\text{-}12}$.

SICILY.—The fossil elephants discovered from early times in Sicily included forms which Falconer considered identical with the full-sized '*Elephas antiquus*' and with '*E. melitensis,*' a dwarfed form. Pohlig (1893, p. 81) described the latter, from the Elephant Cave of Carini near Syracuse, as *Elephas* (*antiquus*) *Melitæ* Falc. Soergel (1912.2, p. 1) applies the term *El. antiquus* var. *insularis* to the Sicilian stage from Carini. According to our record no new species have been described from Sicily, in which large island also the nearly full-sized elephant recorded as '*Elephas antiquus*' prevailed at a certain period before it became dwarfed.

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[1] Compare Preface by F. A. Bather to Memoir by Andrews and Cooper "On a Specimen of *Elephas antiquus* from Upnor," 1928, p. iii.

Ramiro Fabiani (1928, p. 34) records the distribution of the dwarfed elephants of Sicily as follows:

> *Elephas* (*antiquus*) *mnaidriensis* Leith Adams.—Grotte di S. Ciro, Olivella, Benfratelli, Billiemi, *S. Elia*, dei Puntali, *Maccagnone?*, S. Teodoro. Corso Vittorio Emanuele, Teatro Massimo, Giardino Inglese, Cappuccini, Acqua dei Corsari, Fossa della Garofala (Palermo), Presso *Case Capizzi* (Monreale). Montelepre, Alcamo, Marianopoli, regione 'La Romana' presso Sciacca, Siracusa, *Tabuna* di Ragusa.
>
> *Elephas* (*antiquus*) *melitensis* Falconer (incluso l'*E. Falconeri* Busk).—Grotte S. Ciro, Addaura, *Luparello* e *Stazione* di Boccadifalco, *Cava dell' Arena*, Carburanceli, *Cava Muletta* (Capaci), S. Teodoro, della Santa (Siracusa). Montelepre, *Tabuna* di Ragusa.

SARDINIA.—In 1883 Forsyth Major described the dwarfed species, *Elephas Lamarmorae*, from this island.

EASTERN MEDITERRANEAN.—In 1903 Dorothea Bate described the diminutive form *Elephas cypriotes* from the island of Cyprus. In 1907 the same author described the diminutive form *Elephas creticus* from the island of Crete.

The dwarfed elephants of the Mediterranean Islands were long considered as subspecies of '*Elephas antiquus*,' but the cranium of '*E. melitensis*,' as figured by Pohlig (Fig. 1121), more closely resembles that of *E.* [*Palæoloxodon*] *namadicus* of India.

In October of 1929 appeared Raymond Vaufrey's admirable Memoir "Les Éléphants Nains des Iles Méditerranéennes" (Arch. Inst. Pal. Humaine, Mem. VI). This Memoir, with its invaluable observations and detailed studies, has been briefly abstracted and annotated in Section V of the present chapter. Osborn accepts many of Vaufrey's conclusions but gives his reasons for hesitating or declining to accept others.

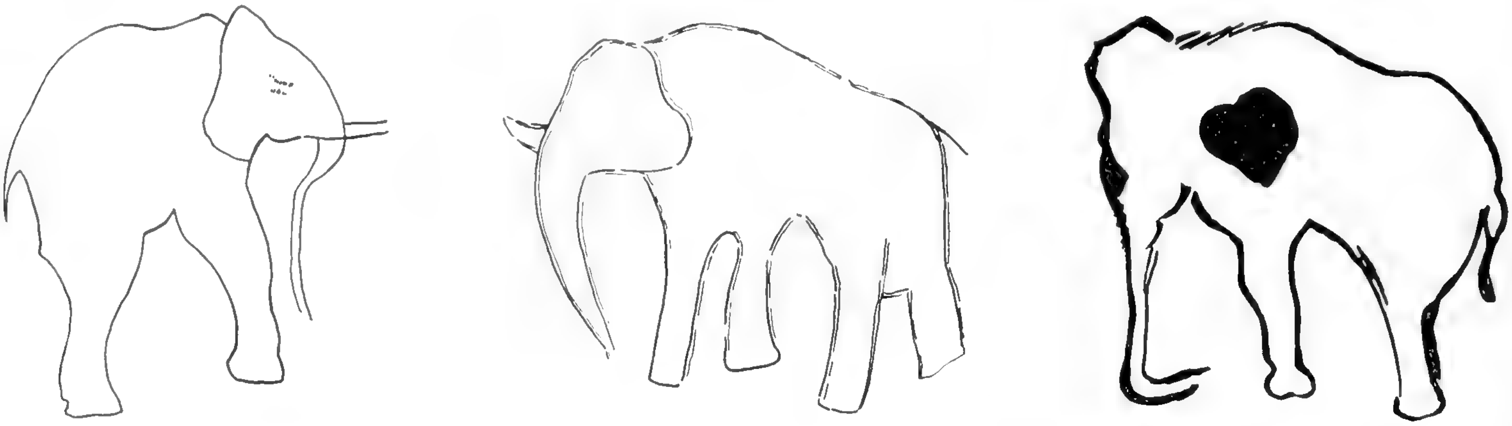
EXTINCT AFRICAN SPECIES AND SUBSPECIES, DISCOVERY AND DESCRIPTION (1875–1929)

About 1875 discoveries began in the Pleistocene of North Africa. The first fossil species described, *Elephas atlanticus* Pomel, 1879, proves to be a primitive loxodont and in the present Memoir is treated as *Palæoloxodon atlanticus*. To the same species may be assigned *Elephas africanus foss.* of Thomas, named in 1884. In 1895 Pomel also described another form from Algeria, namely, *Elephas jolensis*, which is also a loxodont and is here treated as *Palæoloxodon jolensis*.

Ancestral forms of the true '*Elephas africanus*' (cf. Pomel, 1895, pp. 66, 67, Pls. I-III) suddenly occur in the more recent Quaternary deposits of North Africa, as excellently described and figured by Pomel, who in his "Résumé Général Stratigraphique" distinguishes the Quaternary Proboscidea of the North African littoral as follows:

> MOST RECENT
>
> *Elephas africanus* [=*Loxodonta africana*] not included in any of the prehistoric drawings of more recent age. Certainly living in Barbary at a prehistoric period, but not figured. Found in the geologic horizons of least antiquity. Ridge-plate and dental formulæ corresponding with Falconer's formulæ of *Loxodonta africana*.
>
> ELEVATED MARINE LITTORAL, PLEISTOCENE
>
> *Elephas* [*Palæoloxodon*] *atlanticus* Pomel most characteristic and abundant of this period, affording a complete dental formula. More primitive than *Elephas* [*Hesperoloxodon*] *antiquus*, a contemporary of *Bubalus antiquus* in southern Oran; figured in wall drawings by contemporary prehistoric men, who showed the difference from the African species by the conformation of the ears (cf. Fig. 1047).
>
> *Elephas* [*Palæoloxodon*] *melitensis*(?) Falc. ref. Quaternary of Ternifine.
>
> *Elephas* [=*Palæoloxodon*] *jolensis* Pomel, of Jol ou Julia casarœa, Cherchel, related to *antiquus* and to *mnaidriensis* of the island of Malta, but with less numerous ridge-plates.
>
> PLIOCENE SERIES
>
> *Mastodon* [=*Zygolophodon*] *borsoni* ref.
>
> *Elephas* [=*Archidiskodon*] *meridionalis* ref., possibly referable to *Archidiskodon planifrons*.

It is to these six species of proboscideans that Pomel's Memoir of 1895, "Les Éléphants Quaternaires," is devoted.



Palæoloxodon and Hesperoloxodon as Depicted by the Cave Men of North Africa and Spain. With small ears

The left-hand figure, after Pomel, probably relates to *Palæoloxodon atlanticus*; the right-hand and middle figures, after Breuil, probably relate to *Hesperoloxodon antiquus platyrhynchus*

Fig. 1047. The left-hand figure is designated by Pomel (1895, Explanation of Pl. xiv, fig. 4) as follows: "Éléphant atlantique de Guebar-Rechim." Algeria.

The right-hand and middle figures are designated by Breuil (1911, p. 61, text fig. 57, and p. 239, text fig. 245) as follows: (Right figure) "Éléphant tracé en rouge (largeur o^m 44) et signes formés de lignes rouges verticales en faisceau." Cavern of Pindal, province of Asturias, northern Spain. Middle figure) "Figures d'Éléphants gravés dans le Sud Oranais .... d'après Flamand." Algeria.

Observe that these figures, although drawn by different artists, present a striking general agreement, that is, in the general body profile, the elevation of the limbs, the slight concavity of the forehead, the shortness of the inferior abdominal region, and especially, as noted by Pomel, in the contour of the relatively small and depressed ears, which entirely differ from those of the living African elephant or even from those of the pigmy variety (*Loxodonta africana pumilio*). Consequently these figures are used in the preparation of our restorations of the Upnor elephant (Fig. 1074) and other representatives of *Hesperoloxodon antiquus*. The contour of the ear resembles that of the Indian elephant (Fig. 1120) rather than that of the African elephant (Fig. 1052).

The first fossil elephant to be described from South Africa was Scott's *Elephas* (*Loxodon*) *zulu*, 1907, which we refer to *Loxodonta zulu* (see Osborn, 1934.925, p. 2).

This was followed in 1916 by Dietrich's description of *Elephas antiquus Recki* of northern Tanganyika Territory, referred in the present Memoir to *Palæoloxodon recki*.

The supposed *Loxodonta griqua* of Haughton, from South Africa, described in 1922, proves to belong to the more ancient genus *Archidiskodon*, namely, *A. griqua*.[1]

Germany and Rumania

In 1924 Sabba Stefănescu described the two subspecies *Elephas antiquus rumanus* from Tulucesti, Rumania, and *E. antiquus germanicus* from Tanganu (Ilfov) Rumania, horizon of Taubach and Weimar, Germany, as well as a referred *E. antiquus ausonius* and a referred *E. antiquus germanicus* also from Ilfov, Rumania. It is somewhat doubtful whether these moderately broad-plated types (Figs. 857 and 1089) are truly referable to the *Elephas* [*Hesperoloxodon*] *antiquus* group or to the extremely broad-plated *Archidiskodon planifrons*. Judging from Stefănescu's figures it would appear that:

Elephas antiquus rumanus S. Stef., of Rumania = *Archidiskodon planifrons rumanus*. Upper Pliocene of Rumania.

Elephas antiquus germanicus S. Stef., of Germany and Rumania = *Hesperoloxodon antiquus germanicus*. Upper Pleistocene of Germany and Rumania.

Elephas antiquus ausonius ref., of Ilfov, Rumania = *Hesperoloxodon antiquus ausonius*. ?Upper Pliocene.

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[1] [Professor Osborn in 1934 (1934.925, p. 12) made *Loxodonta griqua* the type of a new genus, namely, *Metarchidiskodon* (see Chap. XVI, p. 994).—Editor.]

Japan and Java

(Compare abstract of Matsumoto's articles, also letters of July 14 and November 20, 1924, pp. 901-908, Chap. XIV)

JAPAN.—For a long period Japan constituted the extreme eastern portion of the continent of Asia, and, as described in recent papers and memoirs by Matsumoto and others, contained a stegodont and elephant fauna closely related to that of Burma and India. Beginning in the year 1924 Matsumoto has given a complete synopsis of this mastodont, stegodont, and elephantine fauna, which is summarized above (Chap. XIV, pp. 901–908). In the present chapter it is shown that all the elephants described by Matsumoto under different generic and specific names probably belong to the Loxodontinæ and are more or less closely related to *Palæoloxodon* (syn. *Sivalikia*) *namadicus*; none of them appears to be related to the genus *Loxodonta* or to the genus *Parelephas* as Matsumoto supposed. In the order of description, these Japanese species are as follows:

Original Name, Matsumoto, Makiyama	Specific Reference in Present Memoir
Elephas namadicus naumanni Makiyama (English description: June 30, 1924, p. 264) Made the genotypic species of *Palæoloxodon* Matsumoto (Sept. 20, 1924, p. 257) from an admirable type which is fully described and refigured on pp. 1294–1296 of the present Memoir.	= *Palæoloxodon namadicus naumanni*
Elephas namadicus namadi Makiyama (English description: June 30, 1924, p. 264)	= *Palæoloxodon namadicus namadi*[1]
Loxodonta Cuvier Type *Elephas africanus.* Subgenus. *Palæoloxodon*, n. Matsumoto (Sept. 20, 1924, pp. 257, 260) = *E. antiquus-namadicus* group	= Genus PALÆOLOXODON
Euelephas protomammonteus, sp. n. Matsumoto (Sept. 20, 1924, p. 262)	= *Palæoloxodon protomammonteus*
Loxodonta (*Palæoloxodon*) *tokunagai*, sp. n. Matsumoto (Sept. 20, 1924, p. 267)	= *Palæoloxodon tokunagai*
Loxodonta (*Palæoloxodon*) *namadicus naumanni* (Mak.), Matsumoto (Sept. 20, 1924, p. 268)	= *Palæoloxodon namadicus naumanni*
Loxodonta (*Palæoloxodon*) *namadicus* Falc. and Caut. (typicus), Matsumoto (Sept. 20, 1924, p. 269)	= *Palæoloxodon namadicus*
Parelephas protomammonteus proximus Matsumoto (1926.2, pp. 48–50)	= *Palæoloxodon protomammonteus proximus*
Loxodonta (*Palæoloxodon*) *namadica* (*Yabei*) Matsumoto, 1929, p. 4	= *Palæoloxodon namadicus yabei*
Loxodonta (*Palæoloxodon*) *Tokunagai junior* mut. Matsumoto, 1929, p. 10	= *Palæoloxodon tokunagai* mut. *junior*

Of the above species six type figures have been published which are available for reproduction in the present Memoir, namely, (1) Makiyama's type figures of *Elephas namadicus Naumanni* (here reproduced as Fig. 1152 below) and (2) of *Elephas namadicus namadi* (Fig. 1153); (3) Matsumoto's type figures of *Euelephas* (*Parelephas*) *protomammonteus* (Fig. 1154) and (4) of *Parelephas protomammonteus proximus* (Fig. 1155); also (5) of *Loxodonta* (*Palæoloxodon*) *namadica* (*Yabei*) (Fig. 1156), and (6) of *Loxodonta* (*Palæoloxodon*) *Tokunagai junior* mut. (Fig. 1157).

In 1924 (Sept. 20) Matsumoto published in the Journal of the Geological Society of Tokyo, Vol. XXXI, his article "Preliminary Note on Fossil Elephants in Japan" (pp. 255–261), in which were listed the species named in the column above, with the exception of the subspecies mentioned in the preceding paragraph, namely, Nos. 2, 4, 5, and 6. This Japanese paper was not received by the present author until February, 1929; if sent, the first copy was lost in transmission.

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[1] [See "1924 *Elephas namadicus namadi* Makiyama," Chap. XXI, p. 1409, of the present Memoir.—Editor.]

In 1926 (Matsumoto, 1926.1) the same treatment was repeated in the English language and the same series of species was listed with the localities in which each was found, as reproduced in Chapter XIV, pp. 901–908, of the present Memoir. This list includes the following (cf. Chapter XIV, pp. 906–908, for full citations from Matsumoto's printed and written synopses):

9. *Euelephas protomammonteus* Matsumoto, 1924, p. 262. Smaller than *E. trogontherii.* Of Calabrian age.
10. *Euelephas trogontherii* (Pohlig), 1924, p. 265. Of Cromerian age.
11. *Elephas indicus* Linn., 1924, p. 266. Probably of Post-Monastirian and Pre-Neolithic age.
12. *Loxodonta* (*Palæoloxodon*) *tokunagai* Matsumoto, 1924, p. 267. Possibly older Pleistocene.
13. *Loxodonta* (*Palæoloxodon*) *namadica naumanni* (Makiyama), 1924, p. 264. Of Cromerian [Lower Pleistocene] age.
14. *Loxodonta* (*Palæoloxodon*) *namadica* (Falc. and Caut.), 1924, p. 269. Of Milazzian-Tyrrhenian age.

As stated above the specific and generic reference of these elephants awaits further study and comparison. With the possible exception of the specimen identified as *Elephas indicus*, Osborn is inclined to regard them all as belonging to the *Palæoloxodon* (syn. *Sivalikia*) phylum.

Java.—In 1908 Dubois described from the Kendeng formation, Pithecanthropus zone, Lower or Middle Pleistocene of Java, *Elephas hysudrindicus* as standing near the *Elephas hysudricus* Falconer of the Siwaliks, but still more close to *Elephas indicus*, accordingly naming it *hysudrindicus*. Stremme (1911) related this species more closely to '*Elephas antiquus*.' Accompanying the publication of figure 1160, this species may confidently be placed with *Palæoloxodon* as *P. hysudrindicus*.

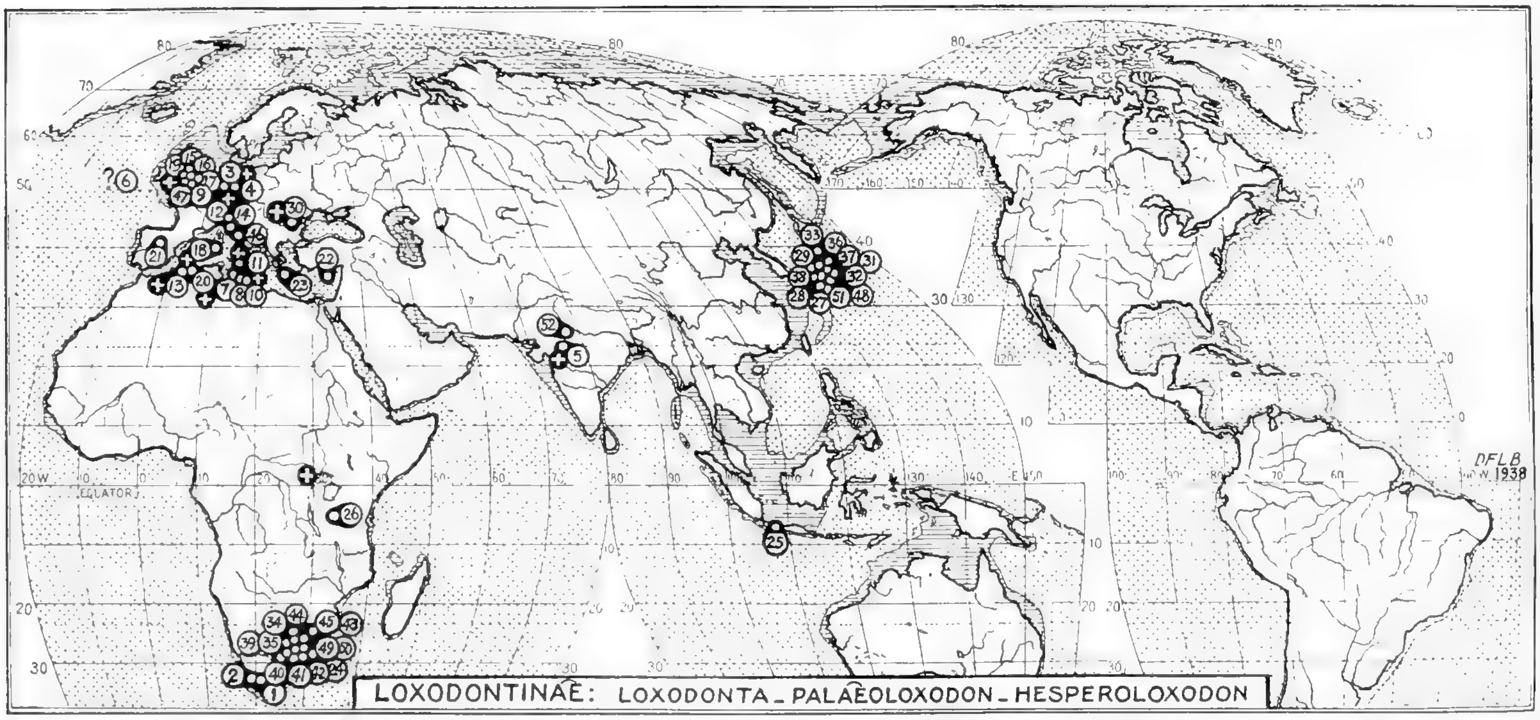


Fig. 1048. Geographic distribution (according to the numbers in the following list, which represent the chronologic sequence of type description) of the principal species of the Loxodontinæ. See also figure 1055, map of distribution of existing African elephants.

3. ORDER OF DISCOVERY AND DESCRIPTION OF THE FIFTY-THREE TYPE SPECIES OF THE EXTINCT LOXODONTINÆ

See Figure 1048

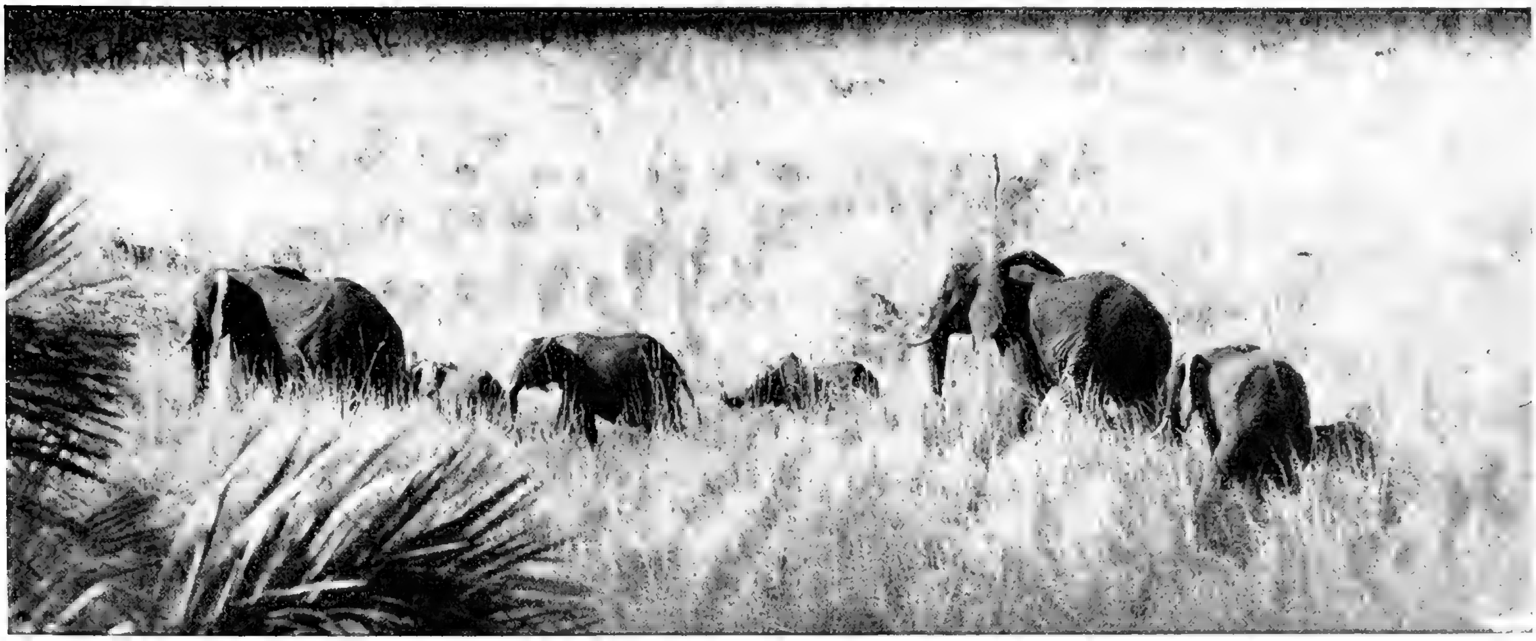
1.	1797	South Africa	*Elephas africanus* Blumenbach. Probably Cape region; exact locality unknown	=*Loxodonta africana*
2.	1798	South Africa	*Elephas capensis* G. Cuvier, Cape of Good Hope	=*Loxodonta africana capensis*
3.	1821	Germany	*Elephas priscus* Goldfuss, near (?) Cologne	=*Loxodonta africana*
4.	1823	Germany	*Elephas antiquitatis* Krüger, Thiede, Thuringia	=*Hesperoloxodon antiquus germanicus*
5.	1846	India	*Elephas namadicus* Falconer and Cautley, Nerbudda Valley	=*Palæoloxodon namadicus*
	1846, 1847	England	*E.* [*Elephas*] *priscus*? Falconer and Cautley, Gray's Thurrock—see E. (Loxod.) priscus (*Goldf.*) Falconer, 1857, below, this list.	
6.	1847	Europe	*Elephas antiquus* Falconer and Cautley, locality unrecorded	=*Hesperoloxodon antiquus*
	1857	Europe	E. (Eueleph.) antiquus Falconer	=*Hesperoloxodon antiquus*
	1857	England	E. (Loxod.) priscus (*Goldf.*) Falconer—see Elephas (Loxod.) priscus Falconer, 1868, below, this list	
7.	1862, 1868	Malta	*Elephas Melitensis* Falconer, Zebbug Cave	=*Palæoloxodon melitensis*
8.	1867	Malta	*Elephas falconeri* Busk, Zebbug Cave	=*Palæoloxodon falconeri*
9.	1868	England (Gray's Thurrock)	*E.* (*Loxod.*) *priscus* Falconer	=*Hesperoloxodon antiquus*
10.	1870	Malta	*Elephas mnaidrae* Adams, Mnaidra Gap	=*Palæoloxodon mnaidriensis*
11.	1870	Sicily (Catania)	*Elephas Cornaliae* Aradas	=*Loxodonta cornaliae*
12.	1875–1886, 1923	Italy	*Elephas ausonius* Major (MS., 1875), in Verri, 1886 (name only), Depéret and Mayet, 1923, San Romano, Val d'Arno inferior	=*Hesperoloxodon antiquus ausonius*
13.	1879	North Africa	*Elephas atlanticus* Pomel, Ternifine, Algeria	=*Palæoloxodon atlanticus*
14.	1880	Northern Italy	*Elephas antiquus nana* Acconci, near Monti Pisani, Cucigliana, Tuscany	=*Hesperoloxodon antiquus nanus*
15.	1883	England (Norwich)	*Leptodon minor* Gunn	=*Hesperoloxodon antiquus*
16.	1883	England (Norwich)	*Leptodon giganteus* Gunn	=*Hesperoloxodon antiquus*
17.	1883	England (Forest Bed, Norfolk)	*E. Gunnii* Lartet	=*Hesperoloxodon antiquus*
18.	1883	Sardinia	*Elephas Lamarmorae* Major, near Gonnesa	=*Palæoloxodon lamarmorae*
	1884	North Africa	*Elephas africanus fossilis* Thomas	=*Palæoloxodon atlanticus*
	[1888	Germany	*Elephas* (*primigenius*) *Leith-Adamsi* Pohlig	See *Mammonteus*? (Chap. XVIII)]
	[1889	Germany	*Elephas* (*primigenius*) *Leith-Adamsi minor* Pohlig	See *Mammonteus*? (Chap. XVIII)]
	[1891	England (Forest Bed, Norfolk)	*Elephas antiquus Nestii* Pohlig	See *Parelephas* (Chap. XVII)]
19.	1891, 1902	England (Forest Bed, Norfolk)	*E. giganteus intermedius* Gunn	=*Hesperoloxodon antiquus*
20.	1895	Algeria	*Elephas jolensis* Pomel, Algerian seacoast, below Kromer-Roubia	=*Palæoloxodon jolensis*
21.	1897	Spain	*Elephas platyrhynchus* Graells, San Isidro del Campo, near Madrid	=*Hesperoloxodon antiquus platyrhynchus*
22.	1903	Cyprus	*Elephas cypriotes* Bate, Kerynia Hills	=*Palæoloxodon cypriotes*
23.	1907	Crete	*Elephas creticus* Bate, near Cape Maleka	=*Palæoloxodon creticus*
24.	1907	South Africa	*Elephas* (*Loxodon*) *zulu* Scott, Zululand	=*Loxodonta zulu*
25.	1908	Java	*Elephas hysudrindicus* Dubois, Kendeng-Schichten	=*Palæoloxodon hysudrindicus*
	1912	Sicily	*Elephas antiquus* var. *insularis* Soergel (name only), Carini	*Nomen nudum*
26.	1916	Tanganyika Territory	*Elephas antiquus Recki* Dietrich, Oldoway-Tuffe, Serengetisteppe, northern Tanganyika Territory	=*Palæoloxodon recki*
	[1922	South Africa	*Loxodonta griqua* Haughton	See *Metarchidiskodon* (Chap. XVI)]
27.	1924	Japan	*Elephas namadicus Naumanni* Makiyama, Sahamma, Tôtômi Province	=*Palæoloxodon namadicus naumanni*
28.	1924	Japan	*Elephas namadicus namadi* Makiyama, island of Shôdo, Sanuki Province	=*Palæoloxodon namadicus namadi*

29.	1924	Japan	*Loxodonta* (*Palæoloxodon*) *Tokunagai* Matsumoto, Soyama, Gokayama, Hira-mura, Higashi-Tonami District, Province of Etchû	= *Palæoloxodon tokunagai*
	[1924	Rumania	*Elephas antiquus rumanus* S. Stefănescu	See *Archidiskodon* (Chap. XVI)]
30.	1924	Rumania	*Elephas antiquus germanicus* S. Stefănescu, Tanganu (Ilfov), horizon of Taubach and Weimar	= *Hesperoloxodon antiquus germanicus*
	1924	Japan	*Euelephas protomammonteus* Matsumoto. See below under *Parelephas protomammonteus* Matsumoto, 1926	
31.	1926	Japan	*Parelephas protomammonteus* (Matsumoto) *typicus* Matsumoto, Nagahama, Kimitsu District, Province of Kazusa	= *Palæoloxodon protomammonteus*
32.	1926	Japan	*Parelephas protomammonteus proximus* mut. Matsumoto, Isone, Kokubo, Onuki-mura, Kimitsu District, Province of Kazusa	= *Palæoloxodon protomammonteus proximus*
33.	1927	Japan	*Elephas indicus Buski* Matsumoto, Ninohe District, Province of Mutsu	= ?*Palæoloxodon buski* (See Chap. XX, p. 1333, for description and figure)
34.	1927	South Africa	*Archidiskodon transvaalensis* Dart, near Bloemhof, Vaal River	= *Palæoloxodon transvaalensis*
35.	1927	South Africa	*Archidiskodon sheppardi* Dart, near Bloemhof, Vaal River	= *Palæoloxodon sheppardi*
36.	1929	Japan	*Loxodonta* (*Palæoloxodon*) *namadica* (*Yabei*) Matsumoto, Inland Sea	= *Palæoloxodon namadicus yabei*
37.	1929	Japan	*Lox.* (*Pal.*) *Tokunagai junior*, mut. Matsumoto. Exact locality unknown	= *Palæoloxodon* (?*Archidiskodon*) *tokunagai* mut. *junior*
38.	1929	Japan	*Elephas* (*Palæoloxodon*) *namadicus setoensis* Makiyama, Seto	[Not determined by the present author]
39.	1929	South Africa	*Archidiskodon andrewsi* Dart, Gong-Gong, Vaal River	= ?*Palæoloxodon andrewsi*
40.	1929	South Africa	*Archidiskodon hanekomi* Dart, Delport's Hope, Vaal River	= *Palæoloxodon hanekomi*
41.	1929	South Africa	*Pilgrimia yorki* Dart, below Christiana, Vaal River	= *Palæoloxodon yorki*
42.	1929	South Africa	*Pilgrimia wilmani* Dart, below Christiana, Vaal River	= *Palæoloxodon wilmani*
43.	1929	South Africa	*Pilgrimia kuhni* Dart, Pniel Estate, Vaal River	= *Palæoloxodon kuhni*
44.	1929	South Africa	*Loxodonta prima* Dart, Pilandsberg, Limpopo River	= *Loxodonta prima*
45.	1929	South Africa	*Loxodonta africana* var. *obliqua* Dart, Kranzkloof farm, Steelport River	= *Loxodonta africana* var. *obliqua*
46.	1931	Southern Italy	*Palæoloxodon antiquus italicus* Osborn, Pignataro Interamna, near Naples	= *Hesperoloxodon antiquus italicus*
47.	1931	England	*Palæoloxodon antiquus* (*andrewsi*?) Osborn, Upnor, Kent	= *Hesperoloxodon antiquus*
48.	1931	Japan	*Parelephas protomammonteus* (Matsumoto) *matsumotoi* Saheki, Mishima, Kimitsu District, Province of Kazusa	[Not determined by the present author]
49.	1932	South Africa	*Pilgrimia archidiskodontoides* Haughton, Sydney-on-Vaal Breakwater	= *Palæoloxodon archidiskodontoides*
50.	1932	South Africa	*Pilgrimia subantiqua* Haughton, Delport's Hope, Vaal River	= *Loxodonta subantiqua*
51.	1934	Japan	*Palæoloxodon yokohamanus* Tokunaga, Yokohama	[= *Palæoloxodon yokohamanus*]
52.	1935 1937	India	*Palæoloxodon priscus* var. *bosei* Chakravarti, Jammu, Siwaliks	[Not determined by the present author]
53.	1939	Africa	*Palaeoloxodon darti* Cooke and Clark, Victoria Falls, northern Rhodesia	[Not determined by the present author]

Habitat of the African Elephant (Loxodonta)
Forest and savanna of the Uasin Gishu Plateau, Kenya Colony, near the 'Nzoi River. After photographs by Kermit Roosevelt (right) and Carl E. Akeley (left)

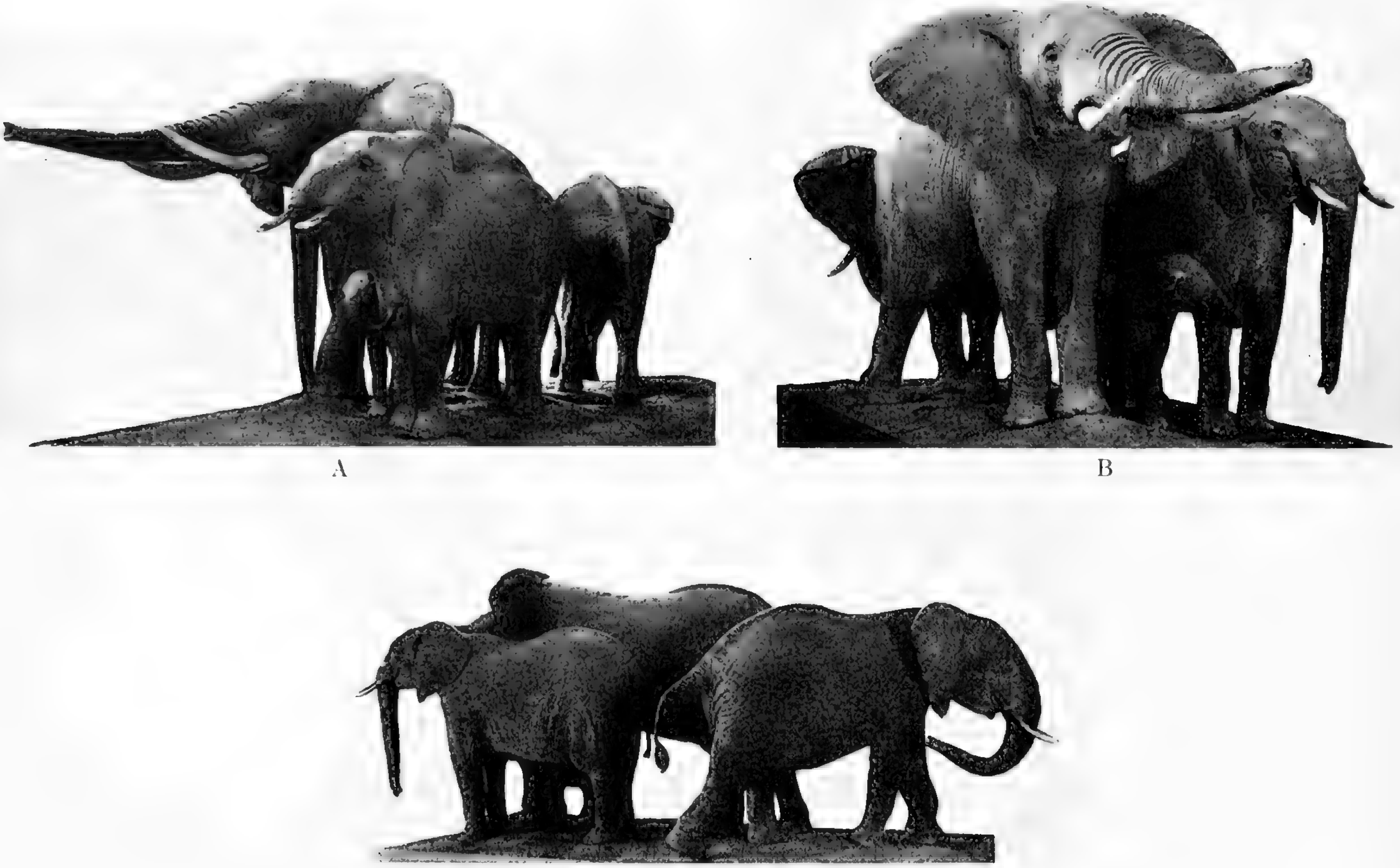
Fig. 1049. Calf of old female charging elephant. Open savanna country. Photograph by Carl E. Akeley.

Fig. 1050. Females and young bulls in forest. Photograph by Kermit Roosevelt.



Last of the African Elephant (Loxodonta)

Fig. 1051. A small herd of elephants, containing two bulls, two cows with calves, and one young bull in the center, passing through the grassy meadows of an open savanna country in British East Africa. After a film photograph taken by Martin Johnson in the year 1923.



A

B

C

Akeley Group of African Elephants in the American Museum

Fig. 1052. A special expedition of the American Museum of Natural History was sent out in 1909 under Carl E. Akeley to collect materials for this group of African elephants, male, female, and young, for the African Hall of the Museum. The cow elephant was shot by ex-President Theodore Roosevelt, and the calf by Kermit Roosevelt, in 1909, on the Uasin Gishu Plateau where the Roosevelt and Akeley expeditions met. The large bull was shot by Mr. Akeley.

The composition (A, B) shows the bull scenting danger, silently feeling fer scent with his trunk, ears fully extended to catch the least sound, for he does not see the source of disturbance. The attitude of the cow indicates that she has seen the intruder and has "frozen," ears back, trunk pendant, prepared for any move she may decide on, whether attack or retreat. The calf, conscious of the alarm, is snuggling up to its mother for protection. The young bull to the right (C), startled, has started forward to swing around and face the danger, his trunk thrown back to catch the scent, and his ears forward to catch the sounds.

Measurements in Millimeters of Adult and Young

	Amer. Mus. 32727 Calf	Amer. Mus. 32732 Female	Amer. Mus. 32734 Small Bull	Amer. Mus. 54085 Large Bull
Height of shoulder	1358.9	2590.8	2711.45	3251.2 = 10 ft. 8 in.
Height to top of head	1409.7	2679.7	2628.9	3403.6 = 11 ft. $2\frac{1}{2}$
Circumference of forefoot	651.05	1174.75	1352.55	1473.2 = 4 ft. 10
Height above pelvis	1346.2	2451.1	2489.2	3048. = 10 ft.
Total spread of ears	1066.8	2400.3	2870.2	3149.6 = 10 ft. $2\frac{1}{2}$
Exposed length of tusks:				
(a) left	38.1	508	635.	1422.4 = 4 ft. 8
(b) right	44.45	508	660.4	1447.8 = 4 ft. $8\frac{7}{8}$

Geographic Data of the Four African Elephants in the Group

1. The large bull (*Loxodonta africana albertensis*).
   Locality: Budongo Forest, east of Lake Albert, Unyoro, northern Uganda.
   Amer. Mus. Dept. Mam. 54085.
   (According to condition of molars about middle-age.)
2. The small bull (*Loxodonta africana albertensis*).
   Locality: Budongo Forest, east of Lake Albert, Unyoro, northern Uganda.
   Amer. Mus. Dept. Mam. 32734.
   (According to condition of molars rather older, but certainly not younger than the large bull No. 54085.)
3. The old female (*Loxodonta africana peeli*).
   Locality: Near 'Nzoi River, Uasin Gishu Plateau, Kenya Colony. Shot by Colonel Theodore Roosevelt.
   Amer. Mus. Dept. Mam. 32732.
   (According to condition of molars approaches senile condition.)
4. The bull calf (*Loxodonta africana peeli*).
   Locality: Near 'Nzoi River, Uasin Gishu Plateau, Kenya Colony. Shot by Captain Kermit Roosevelt.
   Amer. Mus. Dept. Mam. 32727.

II. SYSTEMATIC REVISION OF THE LOXODONTINÆ

SUPERFAMILY: ELEPHANTOIDEA Osborn, 1921

FAMILY: ELEPHANTIDÆ Gray, 1821

SUBFAMILY: **LOXODONTINÆ** Osborn, 1918

Original reference: Osborn, Bull. Geol. Soc. Amer., XXIX, table (opp. p. 134), p. 136 (Osborn, 1918.468); Amer. Mus. Novitates, No. 1, 1921, p. 15 (Osborn, 1921.515).

Compare Pohlig, 1885–1888, Loxodonten, Loxo (disko) donten, Loxo (disko) don (*Elephas africanus, E. priscus, E. antiquus*).

SUBFAMILY CHARACTERS.—United by the common dental and cranial characters of *Loxodonta*, *Palæoloxodon*, and *Hesperoloxodon*. Cranium relatively primitive, platycephalic, brachycephalic (*Loxodonta*); somewhat more elevated or hypsicephalic in *Palæoloxodon* and *Hesperoloxodon*. Premaxillary rostrum broadened for insertion of widely divergent incisive tusks. Tusks relatively straight or slightly incurved, continuously serving in uprooting habits, chiefly in forests. Grinding teeth moderately hypsodont, typically narrow to broad; lozenge shaped (*Loxodonta*) or with 'loxodont sinus' rudimentary or absent (*Palæoloxodon, Hesperoloxodon*). Habits chiefly browsing, crushing of coarse leafage, herbage, and wood fiber. Ridge formula progressive from M 3 $\frac{10}{11-12}$ (*Loxodonta*), to M 3 $\frac{19}{17}$ (*Palæoloxodon*), to M 3 $\frac{20}{18+}$ (*Hesperoloxodon*).

The grinding teeth of *Palæoloxodon*, as shown in *P. namadicus*, with "colliculi approximati" of Falconer (Figs. 1070 and 1189), certainly display no resemblance to the lozenge-shaped grinders of the existing species of *Loxodonta*, all of which are of the typical 'losange' form (Figs. 1043, 1058) first observed by F. Cuvier. Of somewhat intermediate ridge pattern are many of the species of *Hesperoloxodon*, such as are shown in figure 1076 in the '*Elephas priscus*' of Falconer and Cautley, but less distinctly in the lectotype specimen *Elephas* [*Hesperoloxodon*] *antiquus* (Fig. 1075). This narrow 'loxodont sinus,' although but a rudiment, is characteristic of many of the species of *Palæoloxodon* in the Mediterranean Islands and in Africa; it is also observed in primitive *Archidiskodon* molars.

From the resemblances and contrasts enumerated above in the comparative figures and definition of *Loxodonta, Palæoloxodon*, and *Hesperoloxodon*, it is certain that we have to do with three distinct generic phyla, the descent lines of which begin to be known only in Upper Pliocene and Lower Pleistocene times. One of the strongest proofs of this profound phyletic cleavage is seen in the fact that all the modern living species of *Loxodonta* have a more primitive cranial structure and a more primitive ridge formula, namely, M 3 $\frac{10}{11-12}$ (*Loxodonta africana*), whereas the long extinct *Palæoloxodon namadicus* exhibits M 3 $\frac{15}{16}$ and the typical *Hesperoloxodon antiquus* M 3 $\frac{16\frac{1}{2}-17}{16\frac{1}{2}-17}$.

In brief, in all cranial and dental characters the surviving species and subspecies of *Loxodonta africana* are more primitive than any of the known fossil species or subspecies of *Palæoloxodon namadicus* or of *Hesperoloxodon antiquus*.

GENUS: **LOXODONTA** F. Cuvier, 1825, 1827

Compare *Loxodonte* F. Cuvier, 1825; unsigned *Loxodonta*, 1827; *Loxodonta* Gray, 1843; *Loxodon* Falconer, 1847–1857.

The South African form *Elephas africanus* Blumenbach, 1797, is probably the genotypic species. It is important to note that in 1798 G. Cuvier distinguished the extreme South African form as *Elephas capensis*.

GENERIC CHARACTERS.—Ridge-plates of grinding teeth expanding into broad 'losange' or 'lozenge-shaped' median sinus. Relatively narrow superior and inferior grinding teeth, with relatively few ridge-plates; total permanent ridges Dp 4—M 3: $\frac{32}{35}$. Enamel borders thick and simple without foldings or plications. Superior tusks widely divergent as they issue from the broadened premaxillaries; relatively straight, slightly upcurved (Fig. 1059) and incurved (Fig. 1063); marked sexual disparity in the tusks of females (Fig. 1063). Typical ridge formula:

$$\text{Dp } 2\,\tfrac{3}{3}\ \text{Dp } 3\,\tfrac{6}{6}\ \text{Dp } 4\,\tfrac{7}{7}\ \text{M } 1\,\tfrac{7}{7}\ \text{M } 2\,\tfrac{8}{8-9}\ \text{M } 3\,\tfrac{10}{11-12}.$$

Premaxillaries broadened; parietofrontal cranial vertex rounded, platycephalic to subacrocephalic. Cranial profile and section much more primitive, less hypsicephalic and bathycephalic than in the Mammontinæ (cf. pp. 921–925) or Elephantinæ (cf. p. 921). Vertebral formula: Cervicals 7, dorsals 20–21, lumbars 3, sacrals 4, caudals 26–31.

Adaptation of the grinding teeth (cf. Falconer, p. 927 above). The grinders of the African elephant are relatively primitive in construction; the aggregate series of upper ridge-plates (Dp^4—M^3) amounts to only 32 as compared to 48 in '*Elephas antiquus*' and 64 in *Elephas indicus*. The molars are shorter, narrower, and of less elevation than in *E.* [*Hesperoloxodon*] *antiquus* or *E. indicus*. In *E.* [*H.*] *antiquus* the numerous and closely set ridge-plates, without mesial expansion, indicate feeding habits similar to those of *E. indicus*. In *Loxodonta africana* the discs of wear exhibit the well-known rhomboidal expansion or 'losange' characteristic of all the species. These low grinding teeth are best adapted to squeezing and crushing leaves and succulent stems or roots. Besides browsing on the foliage of the Mimosas and Acacias, these African elephants used their tusks like a crow-bar to tear up the trees of certain species by the roots.

In *Elephas* [*Hesperoloxodon*] *antiquus* the numerous narrow transverse ridge-plates of Dp 4—M 3, totaling 48, form a perfect triturating mechanism like that of the Indian elephant. This food adaptation alone, in Falconer's opinion of 1868, would entitle his *Elephas* [*Palæoloxodon*] *namadicus* to subgeneric distinction from his '*Loxodon*'; he accordingly grouped it under the unusable generic names of *Elasmodon* (preoccupied) and *Euelephas* (invalid).

GENERIC DESCRIPTION, 1825–1827.—Cuvier, Frédéric, et Geoffroy Saint-Hilaire, Étienne, 1824–1829, "Histoire Naturelle des Mammifères," Vol. III, Livr. LI, LII, 1825, p. 2 (Loxodonte):

> Je proposerai pour nom générique de cette espèce, le mot de *Loxodonte*, qui peut rappeler le caractère de ses dents, les losanges qu'on apercoit sur leur coupe.

A review (unsigned) of this work appeared in the Zoological Journal, London, 1827, 1828, III, p. 140, noticing the:

> dismemberment of the genus *Elephas*, for the purpose of establishing a new one under the name of LOXODONTA. . . . For the Elephant of Asia he [Cuvier] retains the original generic name *Elephas*. The surfaces of its molar teeth present fasciæ of enamel irregularly festooned; while in those of the African Elephant, the type of the new genus LOXODONTA, the enamel is disposed in lozenges. In addition to this striking distinction derived from the dentary system, M. F. Cuvier also enumerates the other characters which have hitherto been regarded as specific. The smaller, more elongated, and less irregular head of the African animal when compared with the Asiatic; the rounded forehead of the former, strongly contrasted with the deep depression in the middle of that of the latter; the ear of the former also twice the extent, while the tail is only half the length, &c.

1. ORDER OF DESCRIPTION OF EIGHTEEN LIVING AFRICAN SPECIES AND SUSBPECIES[1]

Osborn does not express any opinion as to the validity of all these eighteen African geographic species and subspecies, as listed below with the aid of Mr. Herbert Lang and Dr. Paul Matschie, but furnishes this geographic-varietal list as a real contribution to palæontology and as a picture of past conditions, namely: *In past time each extinct collective species, by local and continental adaptive radiation, doubtless embraced numerous geographic subspecies and varieties adapted to local conditions and as clearly distinguishable from each other in external and internal characters as are the eighteen living African species and subspecies.*

From Blumenbach's first notice in 1797 to Roosevelt and Heller's work[2] in 1914 and finally Frade's articles of 1924 and 1928[2], eighteen species and subspecies have been proposed led by the *Elephas capensis* of G. Cuvier, a name which is probably a synonym of *Loxodonta africana*. This list is extremely valuable to the palæontologist as demonstrating the *very wide range of geographic-varietal* characters in existing loxodonts of a single continent. Undoubtedly a similar range of geographic-varietal characters distinguished the great herds of elephants belonging

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[1] Prepared with the coöperation of Mr. Herbert Lang of the American Museum and of Dr. Paul Matschie of the Berlin Museum. Chronological list of the eighteen names proposed for the living African elephants, with the name as the author originally described it (to the left) and the present proposed name (to the right), together with references to the type figures, locality of the type specimens, and the museums in which they are to be found.

[2] Roosevelt, Theodore, and Heller, Edmund. 1914. "Life-Histories of African Game Animals," Vols. I, II, New York. Also Frade, Fernando, 1924, "Notes de Mammalogie Africaine," Pt. 2—Les Eléphants du Jardin Zoologique de Lisbonne, Bull. Soc. Portugaise Sci. Nat., Tome IX, Fasc. 3, pp. 130–135, text figs. 1–6, and 1928, "Títulos e trabalhos cientificos (Curriculum vitae)," pp. 15, 16, Lisboa.

to the genera *Archidiskodon*, *Parelephas*, *Mammonteus*, and *Elephas*. A similar range of geographic-varietal characters is now observed in the four to five living species and subspecies of the true genus *Elephas*, as described below (Chap. XX).

According to different observers, the vertebral formulæ, as given in detail on pages 930 and 931 of the present Memoir, undoubtedly differ among these numerous subspecies and geographic varieties. The food of the African elephant, as observed by Falconer (p. 927), also probably differs in the various regions of Africa.

	SUBSPECIES
Elephas africanus Blumenbach, 1797, No. 19, fig. C. Type loc.: South Africa; according to Matschie (letter, 1921) probably from the Cape. [Location of type molar unknown.—Editor.]	=*Loxodonta africana africana*[1]
Elephas capensis G. Cuvier, 1798, p. 149. Type loc.: ?Upper Orange River, eastern S. Africa. Type fig.: skull, in Cuvier, 1799, pp. 1–22. Type probably in Museum, Paris	=*Loxodonta africana capensis*
Elephas cyclotis Matschie, 1900, p. 194. Type loc.: Mwelle district northeast of Yaunde on the left bank of the Sanaga, east of the Nachtigall Falls, S. Cameroon. Type fig.: Heck, 1899, p. 116, Pl. CXLVI (live animal from the Berlin Zoological Garden). Type (skull) in Berlin Museum	=*Loxodonta africana cyclotis*[2]
Elephas (*Loxodonta*) *oxyotis* Matschie, 1900, p. 196. Type loc.: Upper Atbara, Sudan. Type not specified; species founded on numerous examples brought back from the Upper Atbara region, Sudan, by Casanova, Hagenbeck and Menges; according to Matschie (letter, 1921) a skull, undoubtedly similar to *oxyotis*, is in the Berlin Museum.	=*Loxodonta africana oxyotis*
Elephas (*Loxodonta*) *knochenhaueri* Matschie, 1900, p. 197. Type loc.: Barikiwa, Tanganyika Territory. Type (skull) in Berlin Museum	=*Loxodonta africana knochenhaueri*
Elephas africanus albertensis Lydekker, 1906, p. 1089. Type loc.: South end of Lake Albert. Type fig.: Lydekker, 1907.1, text fig. 121 (skull). Type in British Museum (Natural History)	=*Loxodonta africana albertensis*
Elephas africanus pumilio Noack, 1906, p. 631. Type loc.: French Congo. Type fig.: Hornaday, 1905, pp. 237, 238 (photographs of live animal). Type in the American Museum of Natural History (Amer. Mus. 35591)	=*Loxodonta africana pumilio*
Elephas africanus toxotis Lydekker, 1907, pp. 385, 388. Type loc.: Mossel Bay, western Cape Colony. Type fig.: 1907.1, text fig. 106 (head). Type (mounted female) in South African Museum at Capetown	=*Loxodonta africana toxotis*
Elephas africanus selousi Lydekker, 1907, pp. 387–389. Type loc.: Mashonaland, southern Rhodesia. Type fig.: 1907.1, text fig. 108 (head). Type in Imperial Institute, London	=*Loxodonta africana selousi*
Elephas africanus peeli Lydekker, 1907, pp. 393, 394. Type loc.: Aberdare Mts., Kenya Colony. Type fig.: Lydekker, 1907.1, text fig. 114 (mounted head). Lectotype in private collection of Mr. C. V. A. Peel, 12 Woodstock Road, Oxford. Cotype in Mr. Rothschild's Museum at Tring	=*Loxodonta africana peeli*
Elephas africanus cavendishi Lydekker, 1907, p. 395. Type loc.: Lake Rudolf district. Type fig.: Lydekker, 1907.1, text fig. 115 (mounted head). Type in British Museum (Natural History)	=*Loxodonta africana cavendishi*
Elephas africanus orleansi Lydekker, 1907, p. 398. Type loc.: North Somaliland. Type fig.: Lydekker, 1907.1, text fig. 118 (dried right ear). Type in collection of Duc d'Orléans at Wood Norton	=*Loxodonta africana orleansi*
Elephas africanus rothschildi Lydekker, 1907, p. 399. Type loc.: French Sudan ("probably southward of Lake Chad"). Type fig.: Lydekker, 1907.1, text fig. 119 (head from life). Type (skeleton) in the American Museum of Natural History. Lydekker states that he takes as type the statuette of "Jumbo" in the British Museum	=*Loxodonta africana rothschildi*[3]
Elephas africanus cottoni Lydekker, 1907 (1907.2), p. 783. Type loc.: Northeastern Congo. Type fig.: Lydekker, 1907.1, text fig. 111 (ear). Type probably in Powell-Cotton's private collection	=*Loxodonta africana cottoni*
Elephas africanus Fransseni Schouteden, 1914, p. 396. Type loc.: M'Paa near Bongo, northwest of Lake Leopold II. Type fig.: Schouteden, 1914, Pl. XI, figs. 1, 2 (dead animal). Type (skin and skull) in Tervueren Museum	=*Loxodonta africana fransseni*
Elephas africanus moçambicus Frade, 1924, pp. 131, 133. Type loc.: Maputo, Mozambique. Type fig.: Frade, 1924, text fig. 5. Type: Female living at the time of description in the Jardin de Zoologique de Lisbonne	=*Loxodonta africana moçambica*
Loxodonta africana Zukowskyi (Strand in Zukowsky, 1924), p. 68. Type loc.: Kaoko District, southwest Africa.	=*Loxodonta africana zukowskyi*
Loxodonta africana angolensis Frade, 1928, p. 15. Type loc.: Region of Cunene, southern Angola; at the time of description, living in the Jardin de Zoologique de Lisbonne	=*Loxodonta africana angolensis*

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[1] *Loxodonta africana africana* Roosevelt and Heller, 1914, Vol. II, p. 739. Type loc.: near Albert Nyanza. The typical *L. africana africana* is believed to be Blumenbach's type from the Cape Colony region. Consequently the Roosevelt and Heller name cannot be used for the subspecies from the Albert Nyanza = *Loxodonta africana* ?subsp.

[2] [Compare, however, "Captive pigmy elephants in America," Journ. Mam., 1934, Vol. XV, p. 248, by C. Emerson Brown.—Editor.]

[3] [Professor Osborn referred "Jumbo" to the subspecies *Loxodonta africana oxyotis* (Osborn, 1931.846, p. 21), which would make *rothschildi* a synonym of *oxyotis*.—Editor.]

Osborn, 1929: In the present Memoir the skull and skeleton of "Jumbo" (Amer. Mus. Dept. Mam. 3283) are referred to the subspecies *Loxodonta africana oxyotis* rather than to *L. a. rothschildi* Lydekker. The eighteen subspecies listed above are partly distinguished by size, partly by geographic distribution, and partly by the shape of the ears. The names adopted were listed by Matschie and Lang, with the exception of *Loxodonta africana moçambica* Frade, *Loxodonta africana zukowskyi* Strand, and *Loxodonta africana angolensis* Frade.

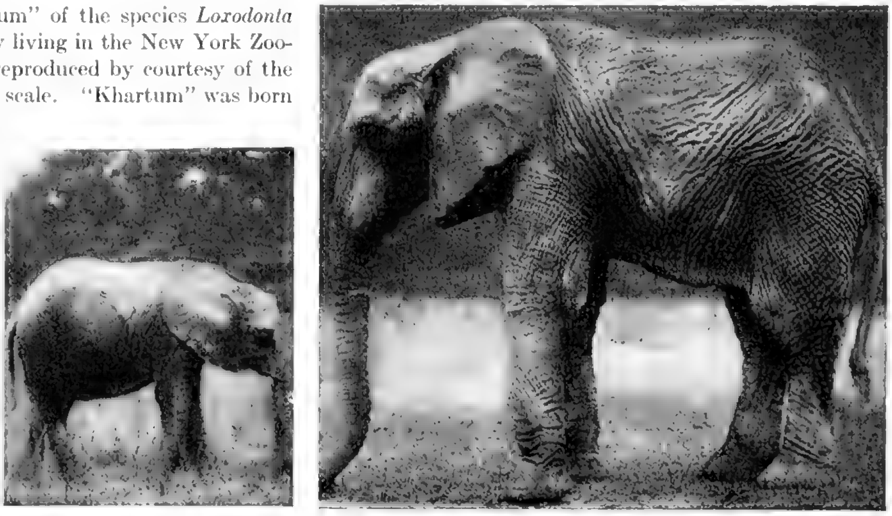


Fig. 1053. Two growth stages in the Sudanese elephant "Khartum" of the species *Loxodonta africana oxyotis* Matschie, from the Upper Atbara, Sudan, formerly living in the New York Zoological Park. Both photographs taken by Elwin R. Sanborn and reproduced by courtesy of the New York Zoological Society. Reduced to a uniform one-fiftieth scale. "Khartum" was born about 1903 and was captured on the Blue Nile in 1906; collected by Capt. Stanley S. Flower, Director of the Government Zoological Gardens, Egypt.

(Left) Young "Khartum" photographed in 1908 at the age of 5 years and measuring 5 ft. 1¾ in. or 1567 mm.

(Right) Young adult "Khartum" photographed in 1930 at the age of 27 years and measuring 10 ft. 8¼ in. or 3257 mm.

The measurements of the successive heights of this elephant, abundantly fed on a varied diet, indicate a growth at the shoulder of 2007 mm. or 6 ft. 7 in., in twenty-four years elapsing between October, 1906, and January, 1930, namely, an increase from 1250 mm. (4 ft. 1¼ in.) to 3257 mm. (10 ft. 8¼ in.), or an annual growth of 83.6 mm. (3¼ in.). The rate of growth is very rapid until the fifth year, then it slows down gradually to 2 in., and finally to ¾ in. a year, namely, from January, 1929 (10 ft. 7½ in.) to January, 1930 (10 ft. 8¼ in.).

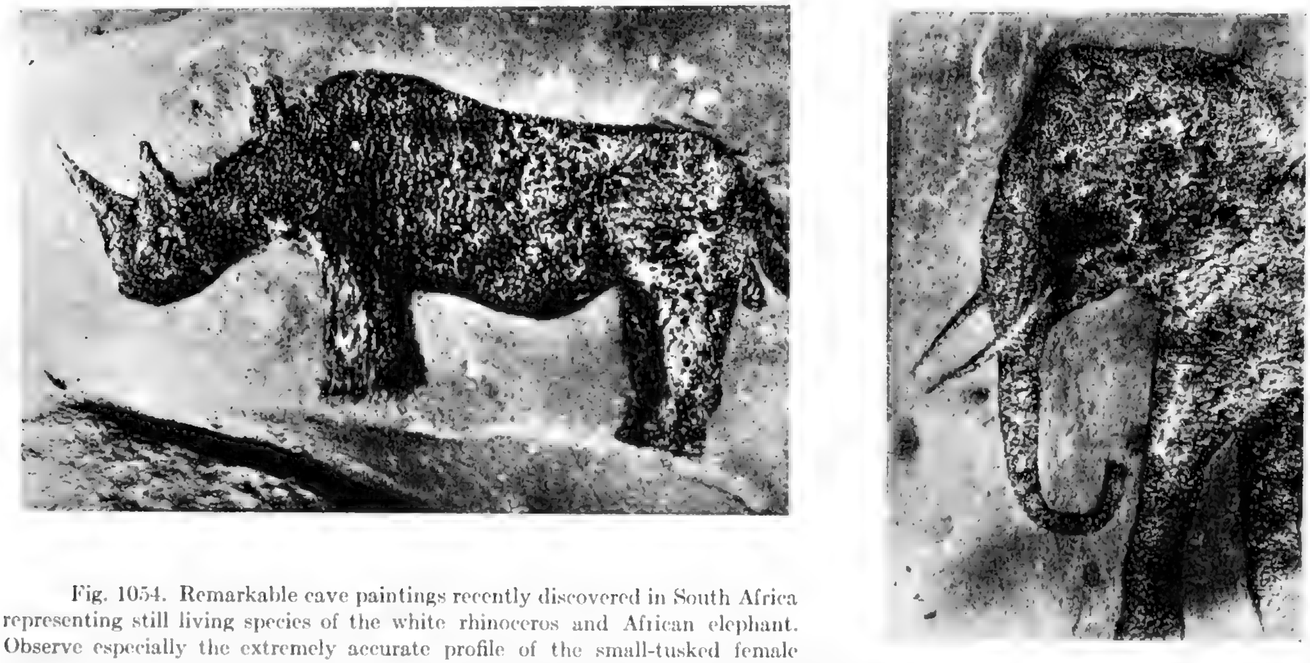


Fig. 1054. Remarkable cave paintings recently discovered in South Africa representing still living species of the white rhinoceros and African elephant. Observe especially the extremely accurate profile of the small-tusked female elephant, herewith reproduced one thirty-seventh natural size; also the correct proportions of the long-headed white rhinoceros reproduced to the same one thirty-seventh scale; both by courtesy of the London Illustrated News.

In the great area north of the dotted line (Fig. 1055), comprising the Atlas Mts., the desert of the Sahara, and the more or less mountainous and formerly forested regions bordering the Mediterranean Sea, other subspecies of the African elephant formerly ranged in large numbers, as recorded by Pomel and as summarized by

Sir Harry Johnston from various classical historians. Pomel (1895) also records '*Elephas africanus*' in the Upper Pleistocene of Oran, northern Africa.

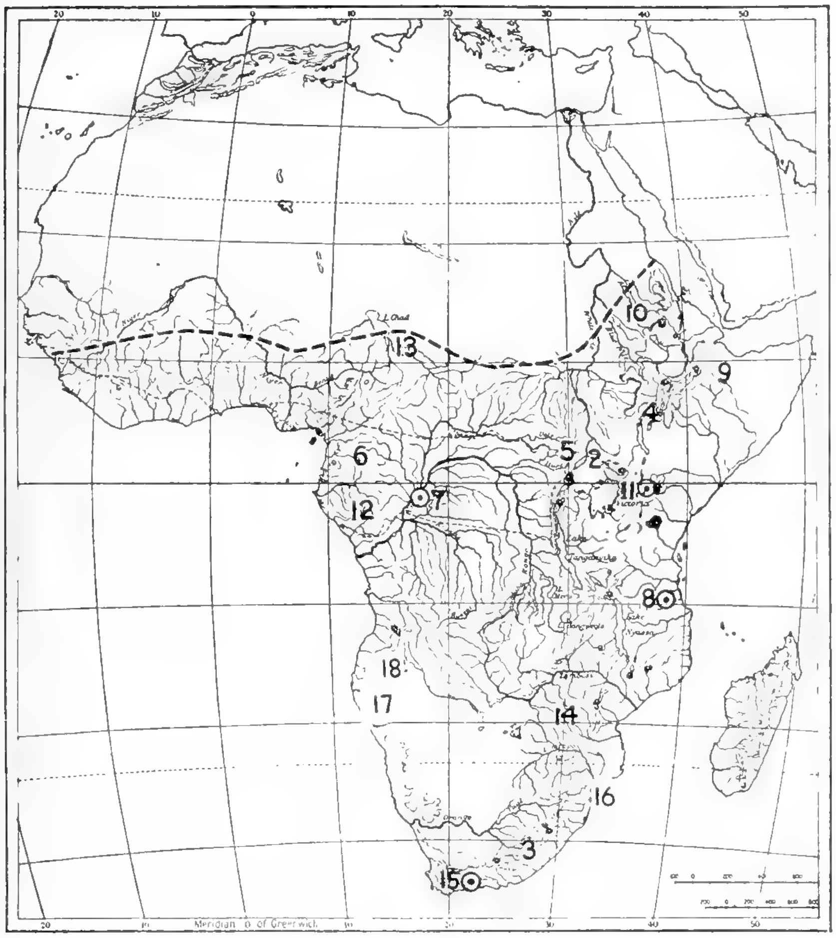


Fig. 1055. Distribution of the existing African elephant (*Loxodonta*); location of the proposed species and subspecies as indicated by various authors. The four known type localities are marked by a circle. The northern limit of distribution has been indicated by an interrupted line.

1. *L. africana* Blumenbach. Range unknown, probably South Africa.
2. *L. africana albertensis* Lydekker. Lake Albert region.
3. *L. capensis* G. Cuvier. Upper Orange River District.
4. *L. africana cavendishi* Lydekker. Galla Country.
5. *L. africana cottoni* Lydekker. Congo.
6. *L. capensis cyclotis* Matschie. Southern Cameroon.
7. *L. africana fransseni* Schouteden. M'Paa near Bongo, region of Lake Leopold II.
8. *L. africana knochenhaueri* Matschie. Barikiwa, Tanganyika Territory.
9. *L. africana orleansi* Lydekker. North Somaliland.
10. *L. africana oxyotis* Matschie. Upper Atbara, Sudan.
11. *L. africana peeli* Lydekker. Aberdare Mts., Kenya Colony.
12. *L. africana pumilio* Noack. French Congo.
13. *L. africana rothschildi* Lydekker. French Sudan.
14. *L. africana selousi* Lydekker. Mashonaland, southern Rhodesia.
15. *L. africana toxotis* Lydekker. Mossel Bay, western Cape Colony.
16. *L. africana moçambica* Frade. Maputo, Mozambique.
17. *L. africana zukowskyi* (Strand in Zukowsky), Kaoko District, southwest Africa.
18. *L. africana angolensis* Frade. Cunene, Angola.

From Sir Harry Johnston's "A History of the Colonization of Africa by Alien Races," 1905, pp. 6, 7: "This Punic explorer [Hanno the Carthaginian] started from Carthage some time in the sixth century before Christ (perhaps about 520 B.C.) . . . on a voyage of discovery mainly. . . . In the account given of the journey it is stated that after passing the Straits of Hercules, and stopping at the site of the modern Sebu, they rounded Cape Cantin and came to a marsh in which a large number of elephants were disporting themselves [Footnote: 'This is an interesting observation. Not only does the statement repeatedly occur in the writings of ancient Greek and Roman geographers that the African elephant was found wild in Mauretania in these times, but this animal is pictured in the remarkable rock sculptures in the Sus country in the extreme south of Morocco, and in the Roman mosaics and frescos found in the interior of Tunis, and now to be seen at the Bardo Museum near Tunis. (See for this the travels of the Moroccan Jewish Rabbi, Mordokhai.)'] . . . The Carthaginians do not seem to have tamed the indigenous African elephant (which was certainly still found in Mauretania), but they introduced and used the Indian elephant."

From Sir Harry Johnston's "The Opening Up of Africa," 1911, pp. 103–105: "Jugurtha [King of Numidia (134 B.C.)] adopted a plan of fighting learnt from the Carthaginian armies. He had war elephants of the African species, which he placed in the van of his attack; but somehow they did not make much impression on the dogged Roman infantry. After the Roman conquest the African elephant disappears from the annals of North Africa and, no doubt, became extinct everywhere north of the Sahara except in Morocco, where—in the country near the High Atlas—it seems to have lingered till the arrival of the Arabs. The camel had been introduced into North Africa from Egypt about 200 B.C., and was rapidly adopted by the nomad races of Mauretania as an animal very useful in war. . . . About 45 A.D. another general of British fame, Suetonius Paulinus, marched up the valley of the Muluya river in Morocco and reached the High Atlas range. He ascended these mountains to the snows, and descended to the southern side of them into the valley of the Gir stream, and gave a vivid description of the burnt-looking rocks of the desert and the swarms of elephants in the Atlas forests."

[The question having arisen as to the existence in the same forest of the South Cameroon elephant and the "pygmy" elephant, recourse was had to the article of Dr. Glover M. Allen on the "Zoological Results of the George Vanderbilt African Expedition of 1934. . . . The Forest Elephant of Africa" (Proc. Acad. Nat. Sci. Phila., LXXXVIII, 1936, pp. 15–44), in which he comes to the following conclusion. The African elephants are represented by two general types—the large, more or less typical Bush elephant of the eastern and southern plains, and the smaller Forest elephant of the Congo forests. The former is *Loxodonta africana* and its several (?)subspecies or (?)varieties; the latter is *L. cyclotis* or *L. africana cyclotis*, type from the South Cameroons (syn. *L. pumilio*, etc.). He also provisionally relegates both *cottoni* and *fransseni* of the Congo region to the synonymy of *cyclotis*, giving his reasons therefor on pages 21–24. Furthermore he regards the term "pygmy" for the Forest Elephant as a misnomer—it is a small variety or a small species if one wishes to so designate it, which may reach a shoulder height of 9½ feet as compared with perhaps 11½ feet in the largest Bush Elephants. Thus there is no tremendous disparity in size between the two. In the closing paragraph (p. 41) of his article, Doctor Allen remarks as follows: "Very probably the Forest Elephant represents more nearly the older original stock from which the larger Bush Elephants have been derived. The evolutionary development of the latter has doubtless taken place slowly and over a long period of time with intergradation and interbreeding of long duration before they became sufficiently differentiated to maintain complete segregation, in the absence of physical barriers. . . For this reason, and because of the slight but apparently constant differences in carriage, form of ears, and size, the Forest Elephant is given tentatively the rank of a separate species. Nor is there any ground as yet for believing that it breaks up further into geographical races within its rather limited range in the rain forest."—Editor.]

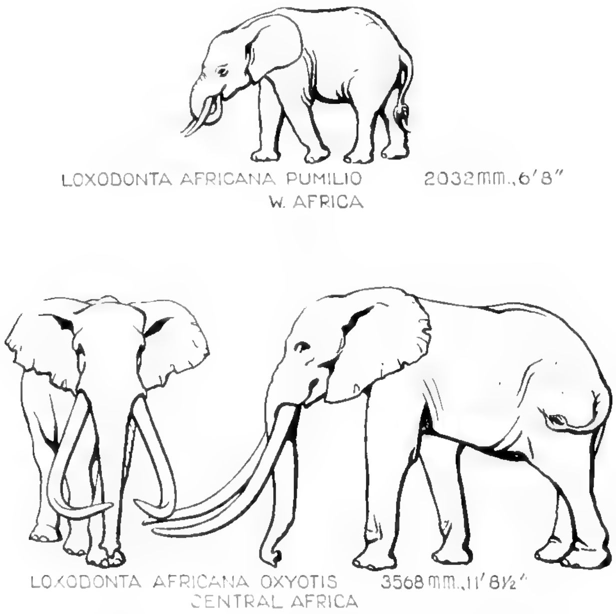


Fig. 1056. Restorations by Margret Flinsch Buba, under the direction of Henry Fairfield Osborn. One one-hundredth natural size.

The tusks of *Loxodonta africana oxyotis* were restored after the longest (Fig. 1062) and heaviest (Fig. 1065) pairs of tusks recorded. See caption to figure 1093, this chapter.

2. SYSTEMATIC DESCRIPTION OF SPECIES OF LOXODONTA

Loxodonta africana Blumenbach, 1797

Figures 794, 805, 806, 810–814, 816, 893, 908, 912, 992, 995, 1013, 1031, 1040–1045, 1049–1054, 1056–1065, 1067, 1081, 1093, 1107–1109, 1112, 1120, 1167, 1190–1192, 1226, 1234, Pl. XXIII

Elephas africanus Blumenbach, 1797.

Syn.: *Elephas capensis* Cuvier, 1798: *Elephas priscus* Goldfuss, 1821.

Type locality: Probably Cape Colony, South Africa. Eighteen living or recently extinct subspecies described from various parts of Africa south of the equator. Extinct forms of the true '*Elephas africanus*' described by Pomel (1895) from the Upper Pleistocene of northern Africa. Range of the species, formerly abundant, the North African coast and Atlas Mountains in the time of Hannibal. See caption to figure 1055.

Elephas africanus, 1797. Blumenbach's paper (1797.1), in which the name *Elephas africanus* was first used, was accessible to the present author by photostat only, through the courtesy of the British Museum. The chief references are as follows: 1. (Matschie, letter, 1921): "Not in the edition of the 'Handbuch der Naturgeschichte' of 1779 [First Edition] but in the Fifth Edition (1797); in 'Abbild. Naturhist. Gegenstände,' Heft 2, No. 19, fig. C, the name is also used. . . . The arrangement of the lamellæ would indicate its Cape origin. It can only be a question of the Cape Colony and the Congo, perhaps the French Congo. The confluence of the anterior lamellæ is peculiar." 2. (Andrews, C. W., and Bather, F. A., June 6, 1922): "Handbuch der Naturgeschichte." Fifth Edition. *Elephas asiaticus*, p. 124. *Elephas africanus*, p. 125. Mammontovaiakost, p. 703. 3. (Sherborn, "Index Animalium," 1902): Sherborn lists *E. africanus* in the Fifth Edition of the "Handbuch," but reference is not made to a figure in this edition.

TYPE MOLAR, R. M_2.—Blumenbach's *type figure* (Fig. 1057), probably a second right inferior molar, r.M_2, serves to characterize clearly the species with very prominent lozenge-shaped ridge-plates to which also the generic name *Loxodonta* applies so aptly; this was the feature which commanded the attention of F. Cuvier in applying the descriptive generic term 'Loxodonte.' TYPE LOCALITY.—Matschie (1900, p. 190) states that no exact locality is known for the type of *E. africanus* Blumenbach. It is probable that the type came from the Cape region of South Africa, because at the time the Central African elephants were inaccessible to European naturalists, whereas the South African mammal fauna was comparatively well known. Consequently it is probable that the type of *Elephas africanus* Blumenbach came from the same region as the type of *Elephas capensis* Cuvier (see note under *E. capensis* below).

In 1797 Blumenbach clearly defined these teeth, as in the legend of his type (Fig. 1057). In 1846 Owen summed up the distinction between these teeth and those of the Indian elephant (Owen, 1846, pp. 230–232—see Fig. 1043 of the present Memoir): "Thus in the African Elephant, (fig. 88,) in which the lozenge-shaped plates are always much fewer and thicker than the flattened ones in the Asiatic species, the variation which can be detected in any number of the grinders of the same size is very slight. . . . In the molars of the Asiatic Elephant, (fig. 89,) which, besides the difference in the shape of the plates, have always thinner and more numerous plates than those of the African species, a greater amount of variation in both these characters obtains; . . . and the like caution is still more requisite in the comparison of the molars of the Mammoth (*Elephas primigenius*), which, having normally more numerous and thinner plates than in the existing Asiatic Elephant, present a much greater range of variety."

Elephas capensis Cuvier, 1798, "Tableau Élémentaire de l'Histoire Naturelle des Animaux," p. 149. TYPE.—(Matschie, letter, 1921): "Cuvier had at his disposal one skeleton from the Senegal and one skull from the Cape [Cap de Bonne-Espérance, Cuvier, Mém. Inst. (de France) National des Sciences et Arts, sometimes called the Académie des Sciences, Vol. II, année 7, (1799)]." FIGURE.—Cuvier, 1799, Pls. III, IV, fig. 2. TYPE LOCALITY.—Cape of Good Hope, South Africa.

THE EXPANDING 'LOXODONT SINUS' OF THE AFRICAN MOLAR CROWN (LOXODONTA AFRICANA)

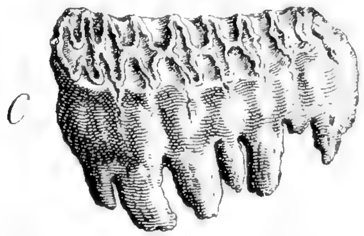


Fig. 1057. Type r.M_2 unworn crown of *Elephas africanus* Blumenbach, 1797. After Blumenbach, 1797.2, No. 19: "C. vom *Africanischen*. . . . . Nur bilden jene beym *Elephas asiaticus* geschlängelte an beiden Enden paarweis zusammenlaufende Linien; hingegen beym *africanus* rautenförmige Leisten. Diese Zähne der beiderlei Elephanten sind nach Originalen im hiesigen academischen Museum gezeichnet."

[According to Pohle (see Dr. Glover Allen, 1936, p. 16) the present location of the original tooth of *Elephas africanus* is unknown: "The molar tooth on which Blumenbach founded his *Elephas africanus* is not now known to be in existence, although Pohle (1926) searched for it in recent years among the collections of the Zoological Museum and of the Anatomical Institute of the University at Göttingen."—Editor.]

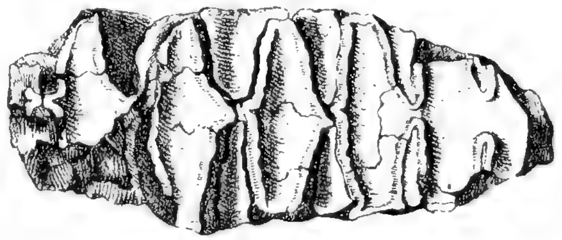


Fig. 1058. Type of *Elephas priscus* Goldfuss, 1821, Pl. XLIV, one-half natural size. Type of a worn molar tooth said to have been found in the neighborhood of Cologne described by the author as follows: (*op. cit.*, p. 485) "Beschreibung eines fossilen Backenzahns vom afrikanischen Elephanten. . . . Daher verdient ein unbezweifelt fossiler Backenzahn, dessen Rhomben auf der Kaufläche denen des afrikanischen Elephanten entsprechen, welchen das Museum der hiesigen Universität kürzlich als ein schätzbares Geschenk empfing, die Aufmerksamkeit der Naturforscher . . . und es ist daher zu vermuthen, dass auch dieses seltene Stück in der Gegend von Cöln gefunden worden sey."

(1) According to the above note, the type of *Elephas capensis* is probably a skull from the Cape of Good Hope. Lydekker (1907.1, p. 384) states that *Elephas capensis* may "really be inseparable from Blumenbach's *E. africanus typicus* [= *Loxodonta africana africana*], based on teeth from a locality unknown." (2) Matschie (1900, p. 190) states that if it were possible to prove that the elephant in different parts of Africa shows certain distinctive characteristics, i.e., occurs as different subspecies, one must not readily synonymize *E. capensis* Cuvier with *E. africanus* Blumenbach; it would then be necessary to distinguish *E. capensis* as the elephant of the Orange River District and *E. africanus* as some other subspecies." (3) Osborn, 1924: In the list, as fully cited above, *Elephas capensis* appears as follows: "*Elephas capensis* G. Cuvier, 1798, p. 149. Type loc.: ?Upper Orange River, eastern S. Africa. Type fig.: skull, in Cuvier, 1799, pp. 1–22. Type probably in Museum, Paris = *Loxodonta africana capensis*."

Elephas priscus Goldfuss, 1821, 1823. The same lozenge-shaped ridge-plates are observed in the type of *Elephas priscus* Goldfuss, 1821. This type undoubtedly belongs to the living species of *Loxodonta africana*, but it misled Goldfuss into the impression that he was describing a fossil tooth, as shown in the legend to figure 1058. Cuvier considered the Goldfuss type as belonging to a recent African elephant. Falconer remarks (1868, Vol. II, p. 95): "In the autumn of 1847 I had an opportunity of examining the specimens above referred to, in company with Dr. Goldfuss. . . the fracture and texture of the ivory yielded the . . . appearance characteristic of recent teeth, and conveyed to my mind a corresponding impression that the molar was probably of modern origin." Nevertheless Falconer employed the name *Elephas* (*Loxod.*) *priscus* for undoubted Pleistocene fossil teeth from Gray's Thurrock and elsewhere. Subsequently (cf. Leith Adams, 1877–1881, pp. 1, 2) Falconer abandoned the name *Elephas priscus* Goldfuss, and it is now considered (*fide* Pohlig) as a synonym of *Loxodonta africana*.

Pomel, 1895, p. 20, revives the name, after a very careful review: *Elephas africanus priscus*, Goldfuss. He says that the teeth of the *africanus priscus* type are found in Europe and certainly in northern Africa. In Plate II, figure 1, he refers the latter, from the mountains of l'Oued Bourkika, to *E. africanus*.

CONSTANT RIDGE FORMULA OF LOXODONTA AFRICANA AS OBSERVED BY VARIOUS AUTHORS

De Blainville (1839–1864, *fide* Falconer, 1865, p. 264): $\mathrm{Dp}\ 2\ \frac{4}{4}\ \mathrm{Dp}\ 3\ \frac{7}{7}\ \mathrm{Dp}\ 4\ \frac{6}{?}\ \mathrm{M}\ 1\ \frac{7}{?}\ \mathrm{M}\ 2\ \frac{9-10}{8-9}\ \mathrm{M}\ 3\ \frac{10}{10-12}$.

Owen ("Odontography," 1840–1845, p. 638): $\mathrm{Dp}\ 2\ \frac{4}{4}\ \mathrm{Dp}\ 3\ \frac{7}{7}\ \mathrm{Dp}\ 4\ \frac{7}{7}\ \mathrm{M}\ 1\ \frac{7}{7}\ \mathrm{M}\ 2\ \frac{}{8-9}\ \mathrm{M}\ 3\ \frac{}{10-12}$.

Falconer (1865, p. 265) on De Blainville's and Owen's materials, "excluding the two talons": $\mathrm{Dp}\ 2\ \frac{3}{3}\ \mathrm{Dp}\ 3\ \frac{6}{6}\ \mathrm{Dp}\ 4\ \frac{7}{7}\ \mathrm{M}\ 1\ \frac{7}{7}\ \mathrm{M}\ 2\ \frac{8}{8-9}\ \mathrm{M}\ 3\ \frac{10}{11}$.

Falconer (1865, p. 265) observes that a left M^3, eleven inches in length, from Cape Colony [region typical of *Loxodonta africana capensis* Cuv.], exhibits thirteen plates, "*i.e.*, eleven principal ridges, besides front and back talons," namely, $\mathrm{M}\ 3\ \frac{\frac{1}{2}-11-\frac{1}{2}}{}$.

Falconer, 1857–1868.—Although Falconer did not adopt the term *Loxodon* as of full generic value, he referred to these animals as *Loxodon*, a subgenus of *Elephas*. In his "Palæontological Memoirs" of 1868, and in the plates accompanying that work, after most precise study, he gave a description of the lower ridge formula, including the half ridge-crests or "talons," as follows: (Falconer, "Palæontological Memoirs," Vol. I, 1868, pp. 422, 440, 441, Plates II, XIII.A, XIV):

Elephas africanus. Plate II, fig. 4a, M_2 with 9½ ridges; fig. 4b, M_2 with 9 ridges. Plate XIII.A, fig. 8, lower jaw with Dp_4, M_1; M_1 with ½–7–½ ridges. Plate XIV, fig. 4, lower jaw, r.Dp_3 with 6½ ridges; figs. 5, 5*a*, r.M_2 with 8½ ridges. From the above may be deduced Falconer's lower ridge-plate formula of referred *Elephas africanus*, namely:

$$\mathrm{Dp}\ 3\ \frac{}{6\frac{1}{2}}\ \mathrm{M}\ 1\ \frac{}{\frac{1}{2}-7-\frac{1}{2}}\ \mathrm{M}\ 2\ \frac{}{8\frac{1}{2}-9-9\frac{1}{2}}\ [\mathrm{M}\ 3\ \frac{}{10-11}].$$

Leith Adams, 1879–1881, p. 48.—Leith Adams gives the ridge formula of *Loxodonta africana* as follows:

$$\mathrm{Dp}\ 2\ \frac{2-3}{2-3}\ \mathrm{Dp}\ 3\ \frac{5-6}{5-6}\ \mathrm{Dp}\ 4\ \frac{4-7}{4-7}\ \mathrm{M}\ 1\ \frac{7}{7}\ \mathrm{M}\ 2\ \frac{8}{8-9}\ \mathrm{M}\ 3\ \frac{10+}{10-12}.$$

Felix, 1912, p. 17.—Felix gives the following ridge formula of *Loxodonta africana*:

$$\mathrm{Dp}\ 2\ \frac{3}{3}\ \mathrm{Dp}\ 3\ \frac{6}{6}\ \mathrm{Dp}\ 4\ \frac{7}{7}\ \mathrm{M}\ 1\ \frac{7}{7}\ \mathrm{M}\ 2\ \frac{8}{8-9}\ \mathrm{M}\ 3\ \frac{10}{11}.$$

Fig. 1059. Photograph of the dome-shaped skull and of the tusks (Amer. Mus. Dept. Mam. 21889) of adult male *Loxodonta africana peeli* ref., reduced to about one-twentieth natural size. Represents the cranium characteristic of elephants of eastern equatorial Africa. Specimen collected in 1911 by Mrs. Carl E. Akeley on southern slopes of Mt. Kenya. Tusks measure 8 ft. 5½ in. and 8 ft. 9½ in. respectively and weigh 112 and 115 lbs. each.

Now exhibited in the Age of Man Hall, American Museum, beside the skull of *Hesperoloxodon antiquus italicus.* Compare figure 1107 of the same crania.

Constant Ridge Formula.—According to the above, the ridge formula of *Loxodonta africana is constant and very conservative,* since the M 3 ridge formula of the living African elephant closely corresponds with that of the primitive Upper Pliocene *Archidiskodon planifrons.*

The constancy of the ridge formula in the two existing species of elephants, *Loxodonta africana* and *Elephas indicus,* is a very important fact in its bearing on the probable constancy of ridge formulæ in extinct species of elephants of a single geologic time period, for example, in *Mammonteus primigenius* of Upper Pleistocene time, as observed both by Falconer and Osborn.

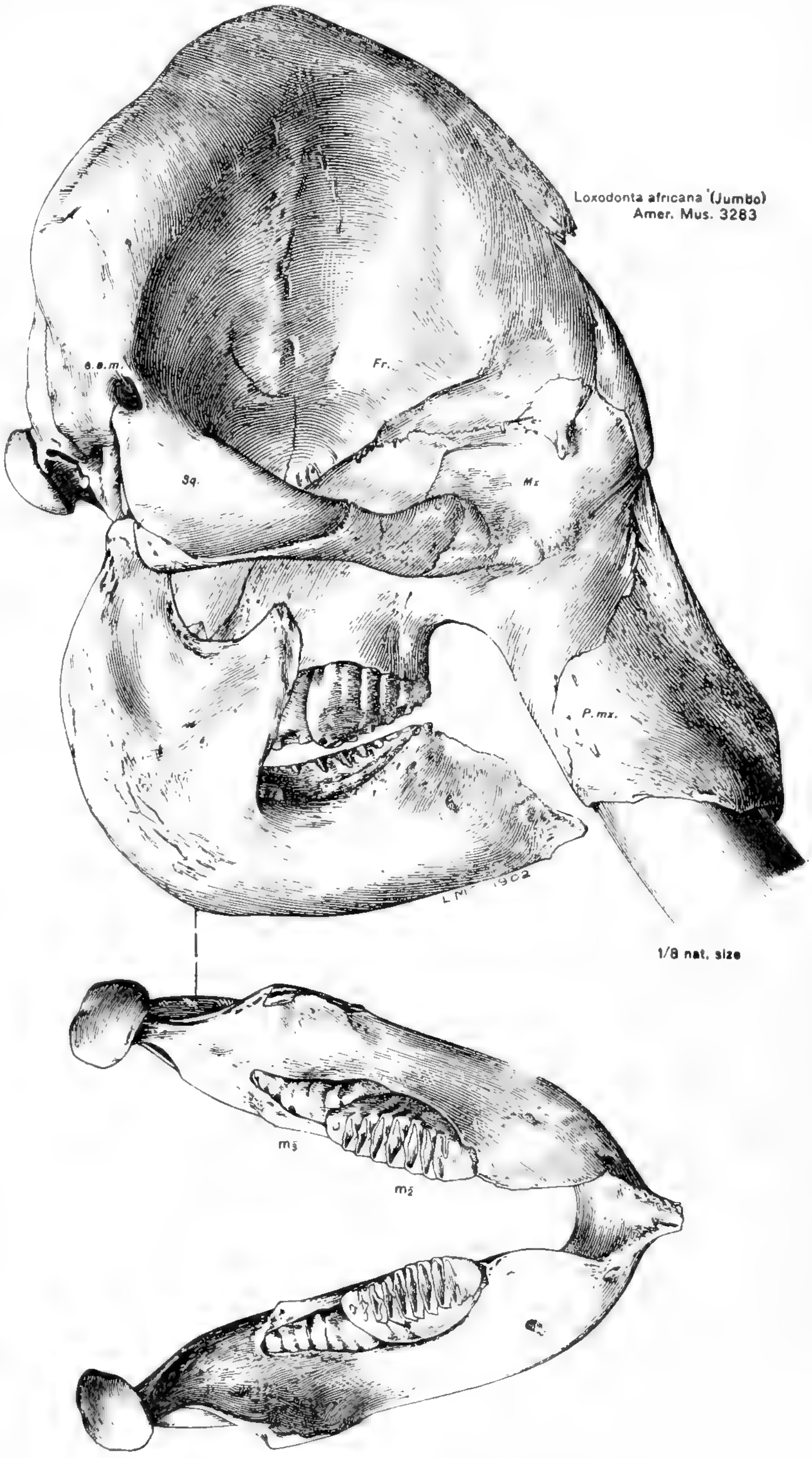
CRANIAL CHARACTERS AND TUSKS OF LOXODONTA AFRICANA

(Continued from Chapter XV, pp. 915–927)

Cranial Axis.—The profound characters of the platycephalic cranial axis of *Loxodonta africana* in comparison with the hypsicephalic *Elephas indicus* and *Archidiskodon imperator* are clearly shown in figure 805, also in figures 806, 812, 811, 810, and 813. In Chapter XV, the introductory section on the cranium of the Elephantoidea, these profound differences between the cranium of *Loxodonta* and the crania of other genera of elephants are much more apparent than the superficial differences which are displayed in the accompanying figures (Figs. 1041, 1059, 1060, 1061, 1062).

The summary of the sectional or axial characters of the *Loxodonta africana* skull is as follows: (1) Occipital plane, perpendicular to basis cranii, extremely long; (2) frontal plane extremely short, convex anteroposteriorly and transversely; (3) nasals broad and rounded; (4) occipitohorizontal section extremely broad with deep pit for ligamentum nuchæ; (5) cranial dome, i. e., occipitohorizontal contour, uniformly rounded; (6) cranium more platycephalic and brachycephalic and less hypsicephalic and bathycephalic than that of *Mammonteus,* of *Archidiskodon,* or of *Parelephas.*

These primitive characters of low, rounded cranial dome and of relatively mesocephalic profile contour are best displayed in figure 1059 and in figure 1060. The latter illustrates the classic middle-aged skull of "Jumbo," a Sudanese subspecies. We observe: (1) That in the fully adult skull the dome is continuously rounded from the occipital condyles to the broad extremities of the nasals, presenting the widest contrast to the profiles of *Archidiskodon,* of *Parelephas,* of *Mammonteus,* and of *Elephas*; (2) that while actually *brachycephalic,* the cranium of *Loxodonta* is also comparatively *mesocephalic* or elongate (shown in the relatively long mandibular ramus, Fig. 1060), as compared with the deeply depressed mandibular ramus of *Elephas indicus,* or with the extremely bathycephalic and abbreviate mandibular ramus of *Mammonteus primigenius*; (3) that since both superior and inferior molars, M^3, M_3, are shorter and less hypsodont, the maxillary and mandibular dental cavities are much less deep, thus accounting for the less hypsicephalic proportions of this part of the skull; (4) the superior aspect of the mandibular rami (Fig. 1060) also displays the relative prominence and horizontal distinction of the rostrum, again presenting a very wide contrast to the deep, hypsicephalic rostrum of the Mammontinæ and of the Elephantinæ; (5) the superior or frontal aspect of the cranium is beautifully displayed in figure 1061A, showing (a) the short frontal bones, (b) the massive orbital prominences, (c) the broad narial openings, (d) the widely separate maxillo-premaxillary sockets for the enormous incisive tusks, similar to those in *Palæoloxodon namadicus* and *Hesperoloxodon antiquus*; (6) the *palatal* aspect of the *Loxodonta* cranium should be examined side by side with the palatal aspect of the *Elephas*

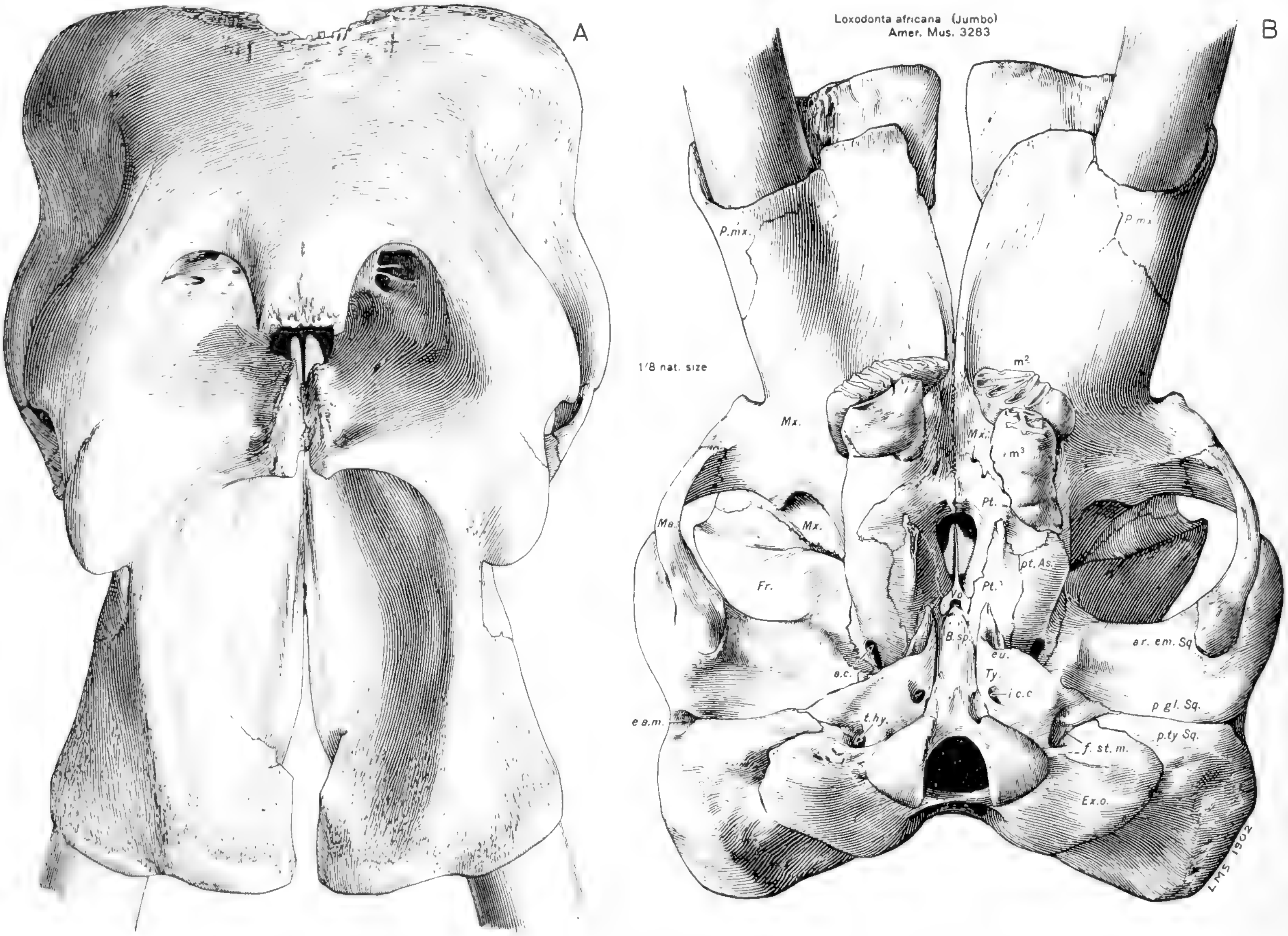


African Elephant Cranium at the Age of Twenty-four, M^2, M_2 in Use

Fig. 1060. Middle-aged skull of the Sudanese or Abyssinian subspecies, *Loxodonta africana oxyotis* (Amer. Mus. Dept. Mam. 3283) with nine-plated M_2 in use and an unworn M_3 still embedded in the jaw. One-eighth natural size. Observe the angular vertex. For full details, see legend to figure 1061.

This is the famous individual, named "Jumbo," purchased in 1883 by P. T. Barnum, the American showman, from the London Zoological Society. "Jumbo" died Sept. 15, 1885; skin at Tufts College, Medford, Massachusetts; skeleton in the American Museum.

indicus cranium (Fig. 800). It will be observed that the *Loxodonta* skull (1061 B) is relatively broader, more *brachycephalic* in all its dimensions. Compare the measurements from the occipital condyles to the extremities of the premaxillaries in *Loxodonta africana* (Fig. 1061 B) with the measurements in *Elephas indicus* (Fig. 800); compare also the zygomatic breadth of *Loxodonta africana* with the zygomatic breadth of *Elephas indicus*. The comparison shows that what the *Loxodonta* skull loses in length it gains in breadth, i.e., in brachycephaly, and in platycephaly. It also shows that while relatively narrow and long, the skull of *Elephas indicus* gains greatly in vertical depth; it is more hypsicephalic, more acrocephalic.



African Elephant Cranium at the Age of Twenty-four. Same Cranium as in Figure 1060

Fig. 1061. Superior and palatal views of cranium of "Jumbo" (*Loxodonta africana oxyotis*), Amer. Mus. Dept. Mam. 3283; same skull as that shown in figure 1045. One-eighth natural size. Compare B with similar views of *Elephas indicus* (Fig. 800).

A middle-aged male (twenty-four years) taken in 1861 at the Setit River, northwestern Abyssinia; famous in history as having lived three years in the Jardin des Plantes, Paris, and then transferred to the London Zoological Society, which, doubtful of his temper, accepted in 1882 an offer of $10,000 made by the celebrated circus proprietor, P. T. Barnum, of the United States. Jumbo is supposed to have been twenty-four years of age at the time of his death.

W. K. Gregory on E. africanus (Jumbo Skull).—The remarkable foreshortening (cyrtocephaly) and deepening (bathycephaly) of the African elephant cranium, while less extreme than that of other elephants, is nevertheless far more advanced than in any species of mastodont. (1) Note extreme compression of the hinder part of the palate, correlated with the very backward extension and great vertical depth [bathycephaly] of the maxillary alveoli containing M^2, M^3. (2) Note anterior position of suture separating malar from maxillary portion of zygoma. In the primitive mastodont *Trilophodon* the malar extends forward over the maxillary to form the postorbital process; very primitive. (3) Note extremely robust [brachycephaly] buccal portion of zygoma.

(4) Note confluence of anterior palatine canals and wide divergence of incisive alveoli. (5) Note reduction in size of auditory bulla which is squeezed down close against the basis cranii; the anterior prolongation under the eustachian tube is less prominent. (6) Note reduction in size and in-sinking of foramen for carotid artery in the bulla.

External Characters and Tusks of Loxodonta africana (Figs. 1062, 1052 A, B, C).—The external characters of the male and female and young African elephant are beautifully displayed in the great group (Fig. 1052 A) which includes two subspecies of *Loxodonta africana* (*peeli* and *albertensis*) collected and mounted by Carl E. Akeley between the years 1909 and 1922 for the African Hall of the American Museum of Natural History. The bull is a typical example of the male African elephant, as carefully observed and measured by Mr. Akeley in the field; it attains a shoulder height of 10 ft. 8 in. [as mounted, height of head 11 ft. 2½ in.]; the expanse of the ears is 10 ft. 2½ in.

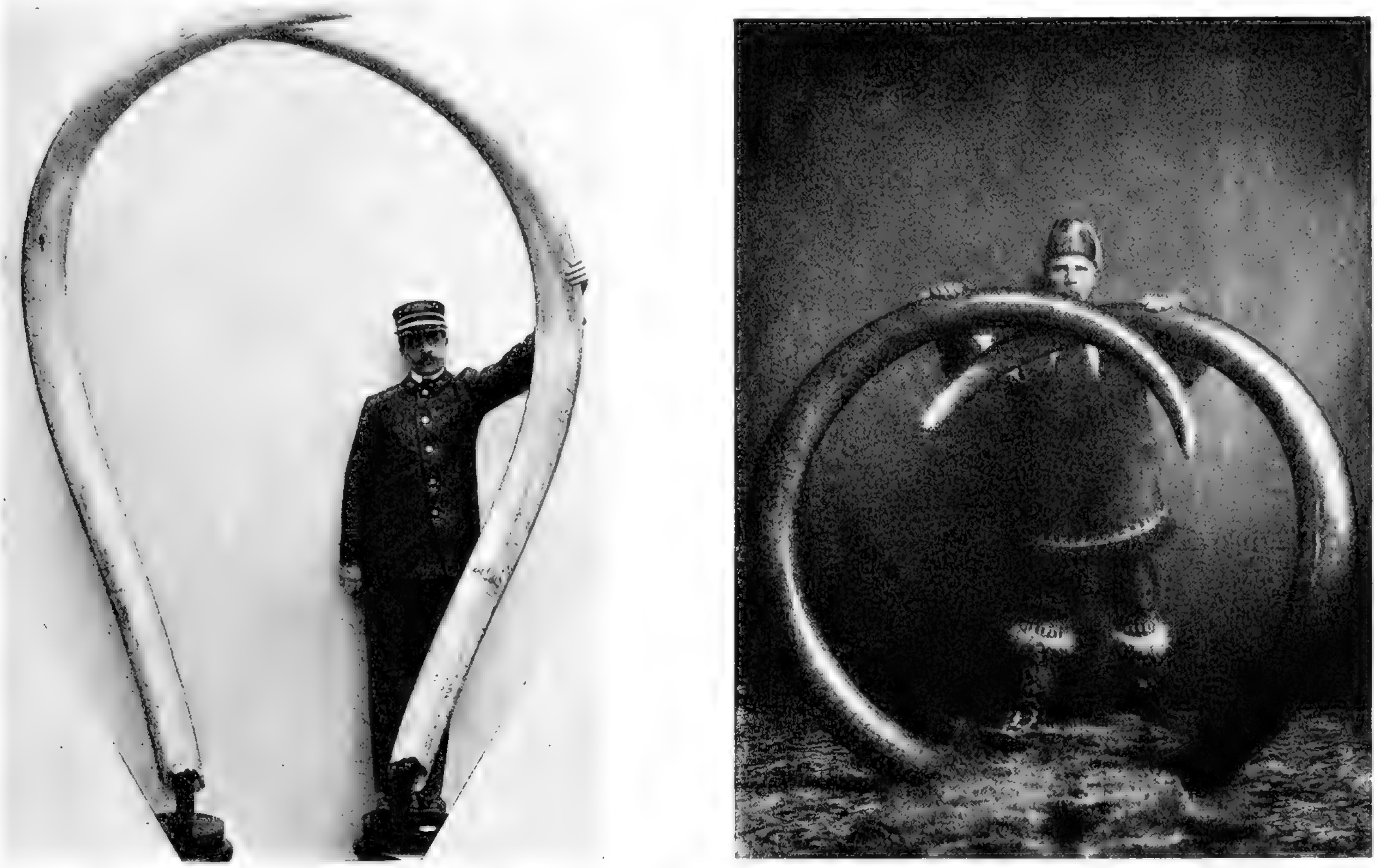


Fig. 1062. Comparison of Tusks of Loxodonta and of Mammonteus

(Left). Tusks of *Loxodonta africana oxyotis* in the New York Zoological Society collection, one twenty-fourth natural size. Right tusk 11 ft. 5½ in. on outer curve; left tusk 11 ft. Circumference of right tusk 18½ in.; of left tusk 18⅛ in. Weight of the pair 293 lbs. The locality record of these tusks is East Africa; it is reported that they were recently owned by King Menelek of Abyssinia who presented them to a European political officer, eventually they were offered for sale in London, were purchased by Rowland Ward, and finally were presented to the New York Zoological Society by Mr. Charles T. Barney.

(Right). Tusks of *Mammonteus primigenius* from Alaska, showing the circular curvature and crossing in *Mammonteus* as compared with the lyre-shaped arrangement in *Loxodonta*. From original photograph brought from Alaska. One twenty-fourth natural size.

The different views of the head of this full-grown male elephant, as displayed in figures 1063, 1052 A,B,C, all show the same depressed, relatively flattened or platycephalic profile, corresponding with the short space between the eyes and the top of the head, due to the lesser development of the frontal sinuses, as compared with *Elephas indicus* or with the extreme acrocephaly and hypsicephaly of *Archidiskodon* and of *Mammonteus*.

Male and Female Crania.—The wide disparity between male and female crania and tusks in species of *Loxodonta* is shown in the accompanying figure (Fig. 1063) of two mounted heads from east central Africa. The male is the great bull collected and mounted by Carl E. Akeley; the geographic locality is northern Uganda; the specific reference is *Loxodonta africana albertensis* Lydekker. The female is a specimen collected by Paul Rainey north of Mt. Kenya; the species is *Loxodonta africana peeli*.

These two heads display the following generic and sexual characters: (1) Uniform elongation or mesocephaly of the cranium, as compared with that of *Elephas indicus*; (2) the male and female crania are substantially of the same elongate, mesocephalic proportions; (3) the gigantic ears are relatively of the same size; (4) there is a great disparity in size of the female as compared with the male cranium; (5) the female tusks are extremely slender as compared with the male tusks, yet they constitute formidable weapons for the defense of the young; (6) this sexual disparity of size is equally apparent in extinct species (e.g., *Hesperoloxodon antiquus*, cf. Fig. 1090), and it is important to note that there should be observed a very marked difference in the development of the fronto-occipital crest in the male as compared with the female cranium. (7) Similar disparity, between male and female tusks, to that shown in figures 1063, 1090, and 1106, is displayed in all the known members of the Elephantidæ or true elephants. The disparity in the known members of the Mastodontidæ is somewhat less extreme between the male and female tusks.

FŒTAL SKELETON OF LOXODONTA AFRICANA (?)COTTONI

Eales, 1926–1929.—The fœtal cranium, jaw, and milk dentition of *Loxodonta africana* (?)*cottoni* (Fig. 1064), as fully described

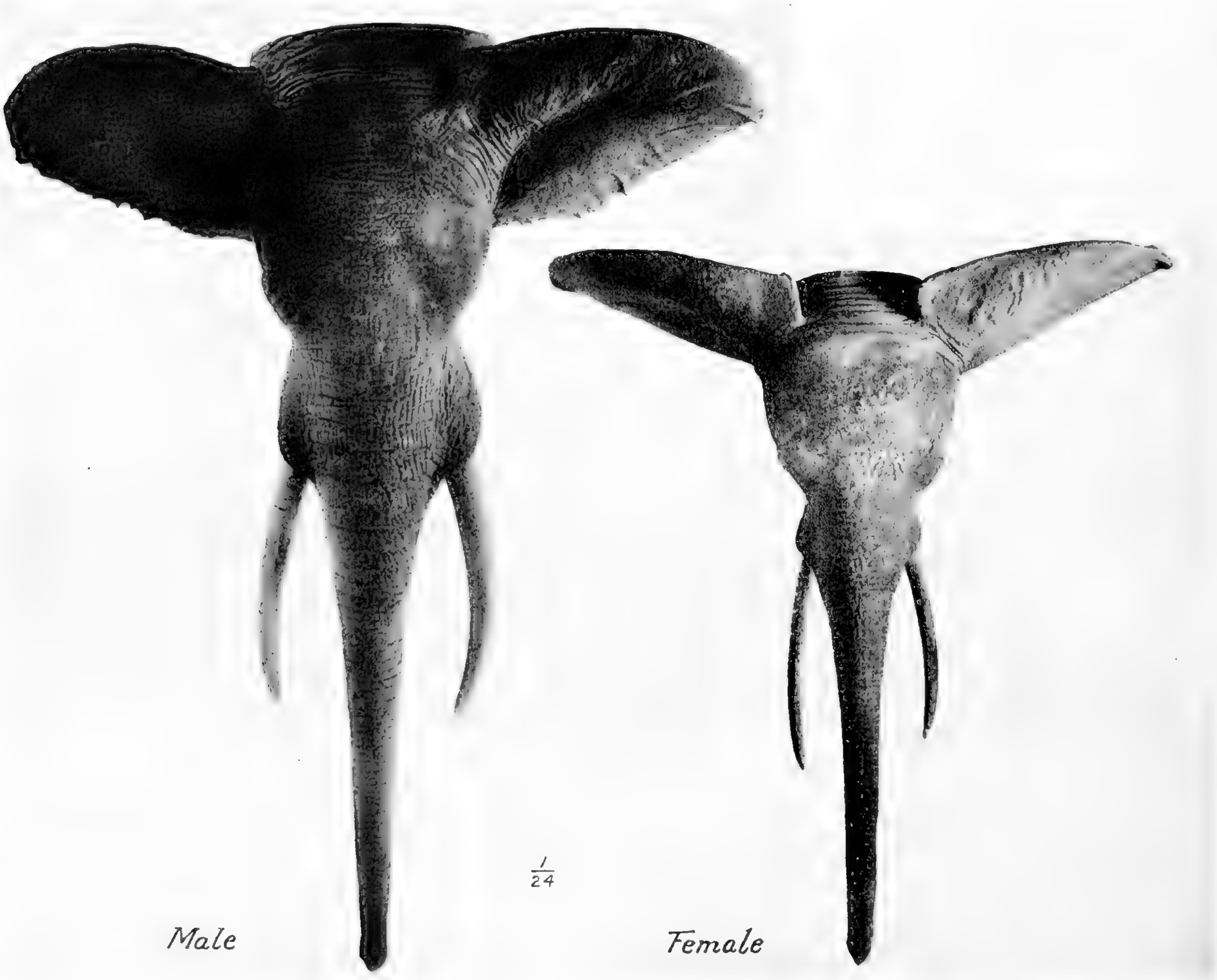


Fig. 1063. Head of Adult Male and Female Loxodonta africana

Compare figure 1090, male and female tusks of *Elephas* [*Hesperoloxodon*] *antiquus* [*germanicus*?], after Pohlig, 1888, Taf. I, figs. 1, 1*a*, 1*b*, 2, 2*a*.

Full-grown male head of *Loxodonta africana albertensis* (Amer. Mus. Dept. Mam. 54085), from the Budongo Forest, east of Lake Albert, northern Uganda, as mounted by Carl E. Akeley in the American Museum, 1922.

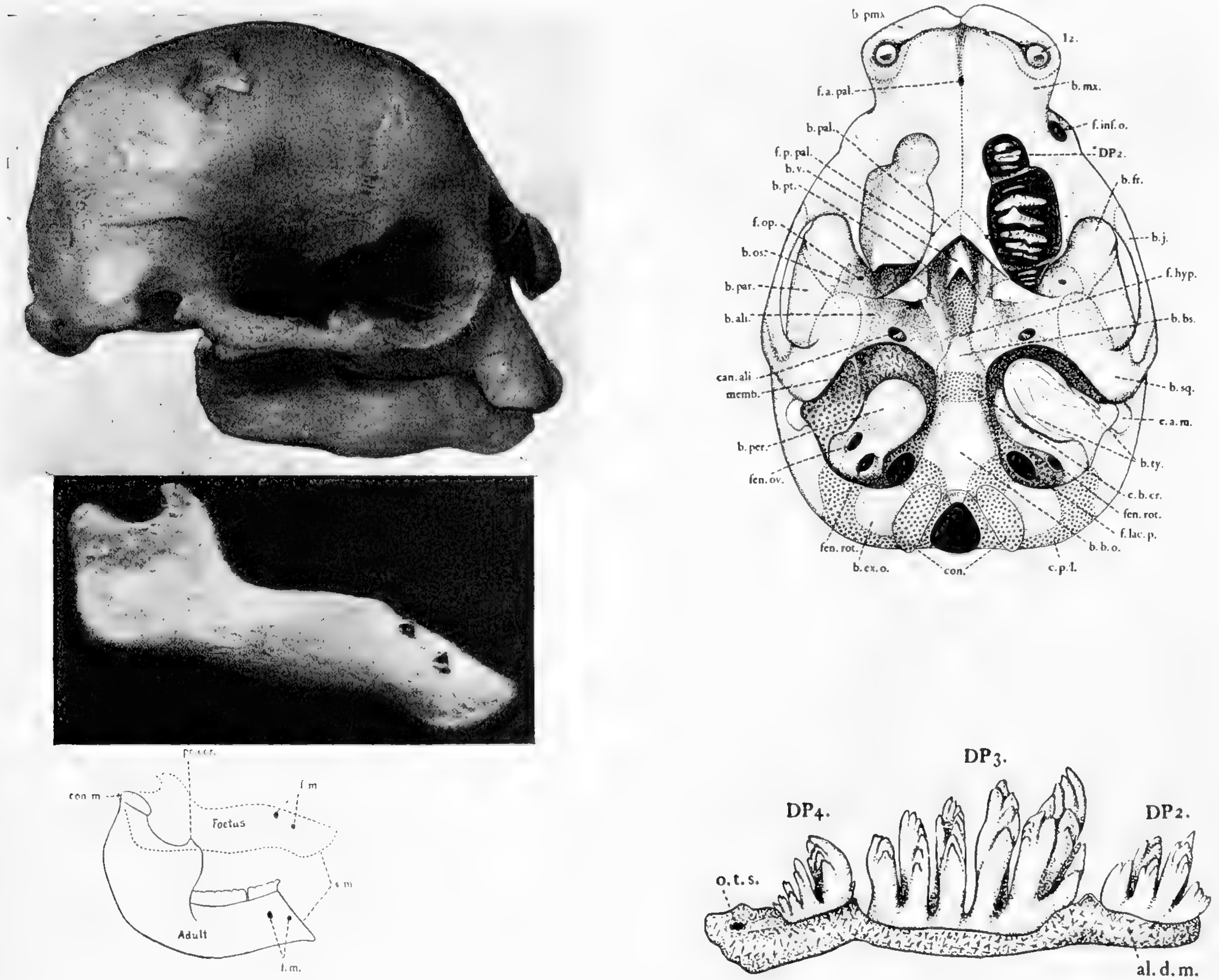
Full-grown female head of *Loxodonta africana peeli* collected north of Mt. Kenya by Paul Rainey and mounted under the direction of Carl E. Akeley. It is now in the private collection of Mr. Percy Madeira of Philadelphia.

in Miss Nellie B. Eales's Memoir of 1926–1929, should be compared with the juvenile stages of the cranium of *Mastodon americanus* (Chap. VI, Fig. 131B, Vol. I), also with the juvenile cranium of *Elephas indicus* (Chap. XV, pp. 915–918, Figs. 796, 797). The cranial contours and the elongated jaw, the occipital condyle on the same plane as the dentition, the budding incisors with delicate tips, the primitively plated crowns of the lower milk molars, Dp_{2-4}, contain no forecast of the tremendous transformation which this fœtal cranium is destined to undergo into the typical African elephant skull, such as appears in figures 1060 and 1061.

No trace of the permanent premolars is found, as might be expected in so young a specimen; the ridge formula, as shown in figure 1064, is:

$$\mathrm{Dp}\ 2\tfrac{3}{5}\quad \mathrm{Dp}\ 3\tfrac{6}{7}\quad \mathrm{Dp}\ 4\tfrac{5}{4+}$$

the posterior plates in Dp 4 not being calcified; this formula agrees with that of Owen, Flower, and Lydekker.



Primitive Form of the Loxodontine Cranium and Dentition, after Eales

Fig. 1064. Fœtal cranium, jaw, and milk dentition of *Loxodonta africana* (?)*cottoni* of the Belgian Congo, locality not given. After photographs kindly sent the present author by Miss Nellie B. Eales. Compare Eales on "The Anatomy of a Fœtal African Elephant, Elephas africanus (Loxodonta africana)," Trans. Roy. Soc. Edinburgh, Vol. LIV, Pt. III (No. 11), 1926, Pl. IX, fig. 29, Pl. X, figs. 32 and 34 on the "Anatomy of the Head," etc.; see also Vol. LV, Pt. III (No. 25), 1928, on the "Body Muscles," and Vol. LVI, Pt. 1 (No. 11), 1929, on the "Contents of the Thorax and Abdomen and the Skeleton." In Vol. LVI, Pt. 1 (No. 11), 1929, of this invaluable Memoir, the author's conclusions as to the phylogenetic relationships of *Loxodonta* are fully set forth.

Fig. 1065. Tusks of the African elephant, believed to be the heaviest (combined weight 461 lbs.) in the world, shown in front of a typical Arab door at Zanzibar. From Kilimanjaro, East Africa, purchased in Zanzibar in 1900 and exhibited for some time by Tiffany & Company of New York. The length of the larger tusk is given as 10 ft. 1 in. on outer curve, circumference 23¾ in. at hollow end. One of these tusks is now in the British Museum (weight 226 lbs.). Reproduced after "Ivory and the Elephant in Art, in Archaeology, and in Science," 1916, p. 411, by Dr. George F. Kunz, through the courtesy of the Executors of his Estate.

Loxodonta cornaliae Aradas, 1870

Figure 1066

From Catania, near the monastery of Santa Chiara, Sicily. Quaternary or Post-Pliocene.

Elephas Cornaliae Aradas, 1870. "Sopra un Molare Elefantino Fossile Riferibile a Specie Distinta dalle Conosciute." Atti Accad. Gioenia sci. nat. Catania, (3), IV, pp. 233–235. Type.—Superior molar of the right side. Horizon and Locality.—From Catania, near the monastery of Santa Chiara, Sicily. Quaternary or Post-Pliocene. Type Figure.—*Op. cit.*, figs. 1, 2.

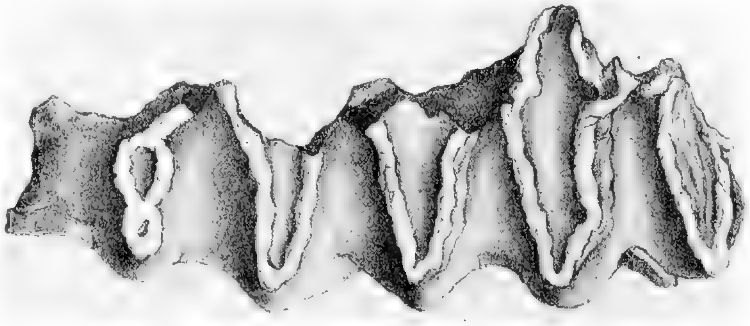
Type Description.—(Aradas, *op. cit.*, pp. 233–235): "Esso è un molare vero, superiore, destro; è rotto in mezzo quasi e per lungo, talchè manca di poco meno della metà; manca pure del tallone anteriore e del posteriore, e conseguentemente della estrema lamina anteriore, non che della posteriore; le radici si conservano in ottimo stato, meno quelle che dovevano spettare alle lamine mancanti. Sulla sua superficie triturante, qualora stato fosse intiero, si avrebbero potuto contare otto a nove lamine. I dischi di logoramento sono romboidali, in forma di losanghe; le lamine leggermente increspate, non molto avvicinate. Le digitazioni della corona dal lato esteriore son quasi perpendicolari alla superficie triturante e regolarmente arrotondite."

"Or, se fossero questi soltanto i caratteri che il molare in esame presenta, certamente potrebbe per la configurazione dei dischi di logoramento, come si è detto, romboidali, riferirsi all' Elephas africanus di Blumenbach. Ma è da considerare, che gli angoli mediani delle losanghe son poco approssimati a quelli delle contigue, e che se la specie africana offre da 9 a 10 lamine in esercizio sopra 0, ″20 o 0, ″24 di superficie triturante in lunghezza secondo Lartet, nel nostro molare, come si disse, non più di 7 o 8 se ne possono contare sopra 0, ″24 di superficie triturante."

"Oltre a ciò è da notarsi, che la corona del molare, che descriviamo, calcolandola nella sua totalità, cioè, comprendendovi ciò che manca, presenta tale proporzione tra la lunghezza e la larghezza, da non trovarsi in altri l'uguale, essendo, a meglio spiegarci, assai più largo proporzionalmente degli altri molari conosciuti."

"Pure si potrebbe, non ostante le premesse considerazioni, e qualora non si volesse tener conto di altri caratteri del descritto molare, riconoscere in esso una certa affinità coll'Elephas africanus. Però, confrontandolo coi molari riferiti a questa specie, ben descritti e figurati nella eccellente monografia degli Elefanti siciliani del prof. Gemmellaro e del Barone Anca, saremmo forzati a dire, o che il nostro spetti veramente all'africano e quelli dei sullodati autori appartenenti a specie distinta, oppure tutto al contrario, essendo che la configurazione dei loro dischi di logoramento e le altre proporzioni fra loro apertamente differiscono."

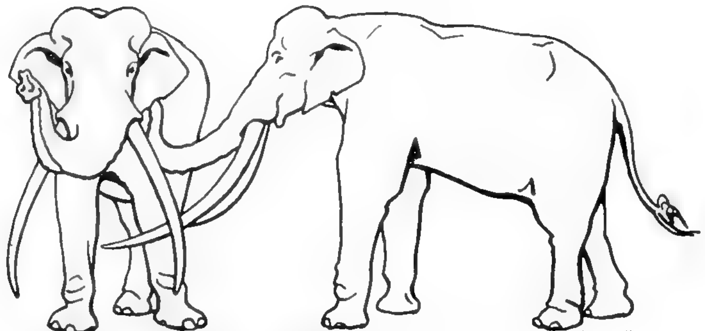
"Ma tutte queste riflessioni debbon cedere e cadere a fronte di un carattere singolare, che il nostro molare appresenta, e che in alcun altro non si osserva, ed il quale basterebbe solo a far riguardare come una specie distinta l'Elefante cui esso appartenne. Le lamine sono tra loro separate da solchi lati e profondi, molto levigati, i quali a mò di semi-coniche escavazioni, vanno elevandosi man mano dagli orli esterni, laterali e ad archi interrotti della corona sino ai punti nei quali si pongono in avvicinamento gli angoli mediani delle lamine. Questi solchi, che le figure possono assai meglio mostrare di qualsiasi descrizione, non sono da attribuirsi a cause accidentali, per esser tutti regolarmente architettati, senza che si possa rilevare alcuna alterazione nella materia che la corona esternamente compone, nè a dislocamento delle lamine, perchè, oltre che questo sarebbe un fatto senza alcuno stento riconoscibile, gli abbassamenti sarebbero solo di un lato ed in modo di dare alle lamine una disposizione scalariforme. Questi solchi, che, come abbiamo detto, formano un carattere nuovo e molto singolare, a nostro modo di vedere, potrebbero significare il passaggio degli Elefanti ai Mastodonti. Per noi il descritto molare dee appartenere ad una specie nuova, che, ove fosse per tale riconosciuta dai dotti che saranno per giudicare la nostra opinione, vorremmo portasse il nome dell'egregio Prof. Cav. Emilio Cornalia, che sui vertebrati ha fatto studii positivi ed utili alla scienza, chiamandolo *Elephas Cornaliae.*"



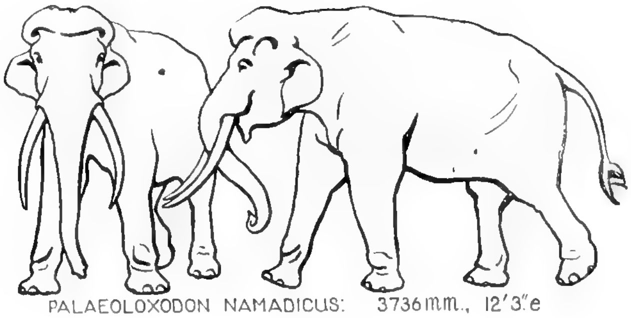
Type of Loxodonta cornaliae

Fig. 1066. Type superior molar of the right side of *Elephas Cornaliae* Aradas, 1870, fig. 2 of plate, two-thirds natural size. From Catania, Sicily.

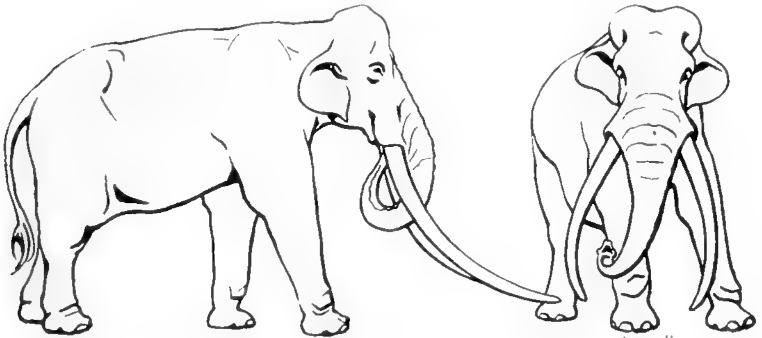
Fig. 1067. Young Addobush Elephant (*Loxodonta*) from Cape Colony. Probably six months old, with a height at shoulder of about three feet. Reproduced through the courtesy of Mr. Henry C. Raven, who took the photograph in 1919.



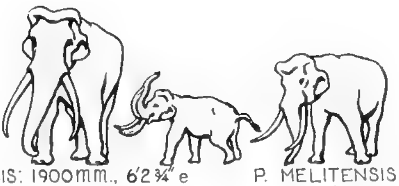
HESPEROLOXODON ANTIQUUS GERMANICUS 4074mm., 13' 4 3/8"e
NORTH GERMANY



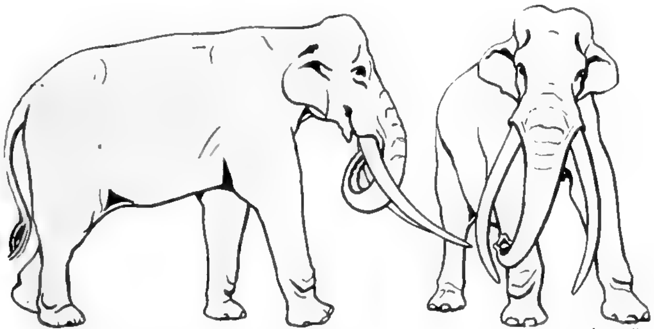
PALAEOLOXODON NAMADICUS: 3736mm., 12'3"e
INDIA



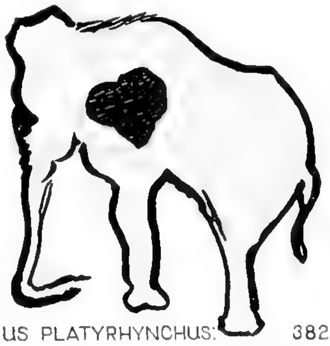
HESPEROLOXODON ANTIQUUS ITALICUS: 4068mm., 13' 4 1/8"e
ROME



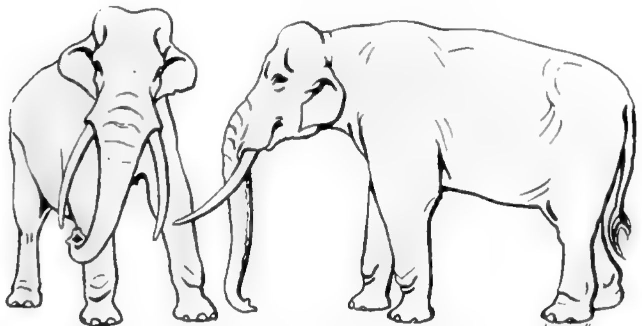
P. MNAIDRIENSIS: 1900mm., 6'2 3/4" e P. MELITENSIS: 1400mm., 4'7 1/8"e
P. FALCONERI: 900mm., 2'11 1/2"e



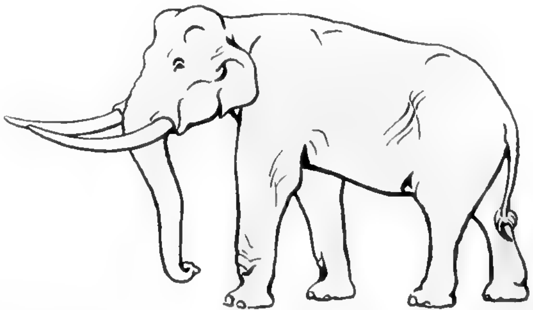
HESPEROLOXODON ANTIQUUS ITALICUS: 3905mm, 12'9 3/4"e
PIGNATARO



HESPEROLOXODON
ANTIQUUS PLATYRHYNCHUS: 3828mm, 12'6 3/4"e
PINDAL N. SPAIN



HESPEROLOXODON ANTIQUUS: 3934mm., 12'10 7/8"
UPNOR



HESPEROLOXODON ANTIQUUS PLATYRHYNCHUS: 3828mm., 12'6 3/4"e
N SPAIN

Fig. 1068. Restorations by Margret Flinsch Buba (1931), under the direction of Henry Fairfield Osborn, of species of Hesperoloxodon of Europe and of Palæoloxodon of India and of the Mediterranean Islands, in comparison with a drawing of Hesperoloxodon by the Cave Men of Northern Spain. One one-hundredth natural size.

III. EURASIATIC SPECIES OF PALÆOLOXODON AND HESPEROLOXODON

Superfamily: ELEPHANTOIDEA Osborn, 1921
Family: ELEPHANTIDÆ Gray, 1821
Subfamily: Loxodontinæ Osborn, 1918

Genus: **PALÆOLOXODON** Matsumoto, 1924

Original reference: Matsumoto, Journ. Geol. Soc. Tokyo, 1924, XXXI, No. 371, pp. 257, 260 (Matsumoto, 1924.2). Compare *Elephas namadicus* Falc. and Caut., 1846. Genotypic species *Elephas namadicus naumanni* Makiyama, 1924. Syn.: *Elasmodon* (preoc.) Falconer, 1847 (in part); *Euelephas* Falc., 1857 (in part). *Sivalikia* Osborn, 1924, and *Pilgrimia* Osborn, 1924 (in part). Subgenus *Palæoloxodon* = '*E. antiquus-namadicus* group' of Matsumoto (1924–1926).

Generic Characters.—Ridge-plates of grinding teeth parallel, closely compressed, waving or plicate. 'Loxodont sinus' rudimentary or absent. Progressively narrow to broad superior grinding teeth, with numerous ridge-plates composed of thin, plicate enamel foldings; twelve ridge-plates in 10 cm.; total number of ridge-plates in lower grinding series (Dp 4–M 3) fifty-one. Ridge-plate formula progressive from:

P. melitensis, $\frac{12}{11\text{-}12}$, to *P. atlanticus*, M 3 $\frac{12\text{-}?14}{12\text{-}?14}$, to *P. namadicus* $\frac{15}{16}$, to *P. namadicus naumanni*, $\frac{19}{17}$.

Correlated with more hypsodont and numerous ridge-plated grinding teeth, cranium more hypsicephalic and bathycephalic than that of *Loxodonta*; broad, rugose parietofrontal crest (*P. namadicus*) overlapping the forehead, adapted to muscular insertion of the very broad proboscis. Premaxillaries (Fig. 1069) broadening inferiorly for the insertion of widely divergent superior incisive tusks. Tusks relatively straight, slightly upcurved and incurved toward the extremities.

The genotype of *Palæoloxodon* Matsumoto is '*Elephas namadicus naumanni*' Makiyama, 1924. The genotypic species of *Sivalikia* Osborn is '*Elephas namadicus*' Falconer and Cautley, as fully explained in the historical introduction to the present chapter; it is also shown that the generic name *Sivalikia* Osborn (Dec. 20, 1924) is technically preoccupied by the subgeneric name *Palæoloxodon* Matsumoto (Sept. 20, 1924).

In 1924 (MS.) Osborn observed: "The gigantic elephants typified by the *Elephas namadicus* of Falconer are believed by Osborn to constitute a distinct generic phylum, to which the name *Sivalikia* is applied in honor of Dr. Hugh Falconer's great work on the Siwalik fauna. They agree with *Loxodonta* in certain characters of the cranium, especially in the low occiput and the distally broadened premaxillaries; they differ from *Loxodonta* in the compressed ridge-plates lacking the 'loxodont sinus,' also in the breadth of the grinding teeth. This generic phylum may spring from the giant species of North Africa, e.g., *Loxodonta atlantica* [*Palæoloxodon atlanticus*], but it is certainly distinct from the typical *Loxodonta africana* group."

Historic Period.—It is not impossible that some elephants of the *Palæoloxodon* type survived into early historic times, but it is an open question whether the elephants described from Mesopotamia were of the ancient 'loxodontine' or of the modern 'elephantine' type, probably the latter; drawings and inscriptions will probably be found some day which will determine these relations.

(Letter, A. H. Godbey, July 19, 1927): Assyrian Royal Inscriptions mention *elephant* hunting in northern Syria, Mesopotamia, etc. But no *reliefs*, so far, *portray* the elephant. Have you any information as to the *species* that once existed there?—any skeletal evidence? . . . Also, Josephus mentions monster bones exhibited as 'giant's bones' in Palestine. Benjamin of Tudela, A.D. 1173, was shown a 'giant's rib' at Damascus, 9 cubits long. (Letter, Godbey, April 5, 1928): "*Hunting* elephants on upper Euphrates is a notable achievement of Assyrian kings. The *only portrayal* so far is on Black Obelisk Shalmaneser, small ears like Indian type, tusks project up from lower jaw; like a boar's, or 'Babyroussa.' It may be an artist's blunder.—The ideogram for elephant is 'Big-Horned Bison' ('Mountain Ox'), compare *Bos Lucas*, from Lucania, the 'boot-toe' of Italy.

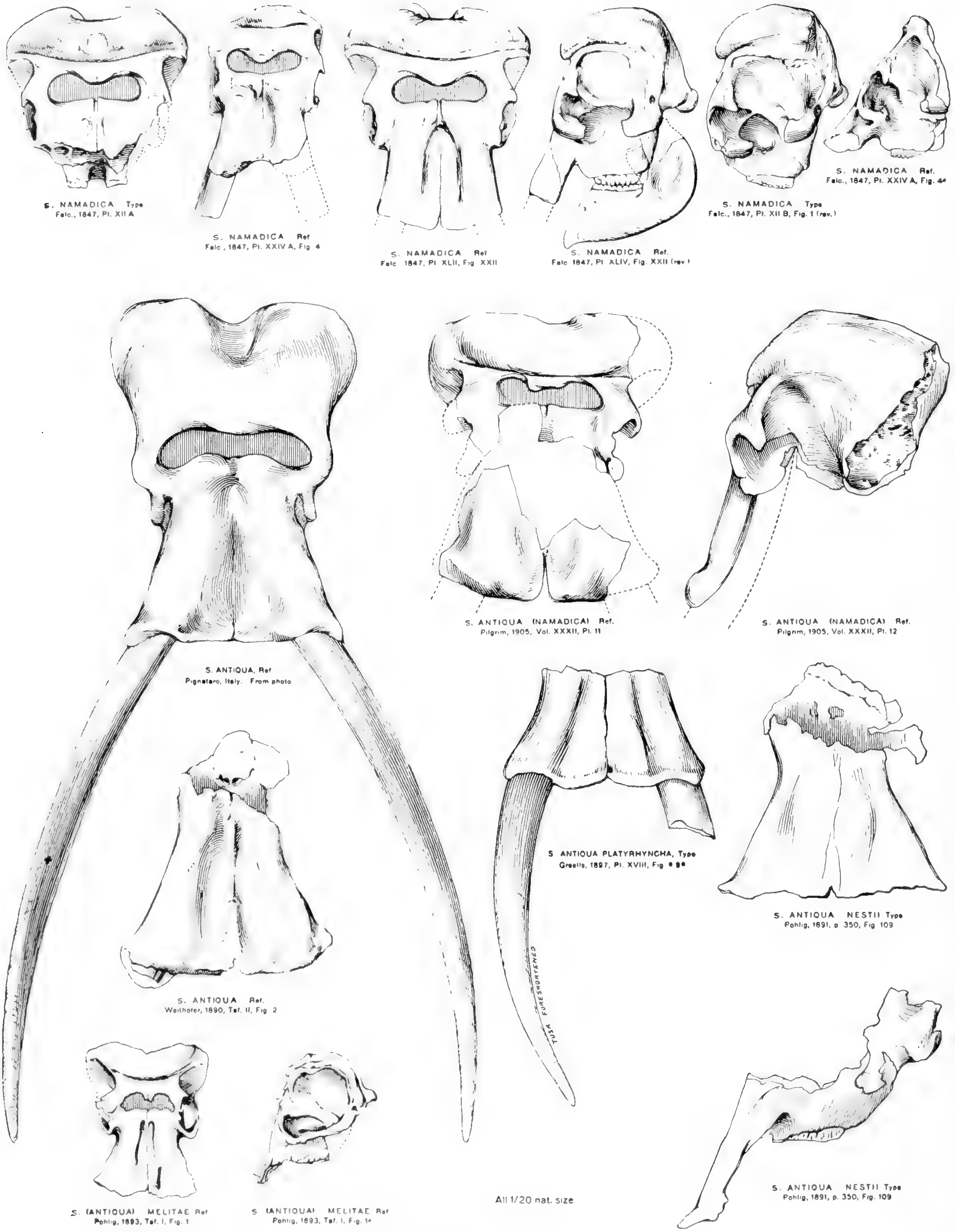


Fig. 1069. See explanatory legend on opposite page.

As shown below (Chap. XX) in comments of Murray on the etymology of the word *Elephas*, signifying ivory, it would seem that the animal first became known from trade in its tusks originating in Africa, as mentioned by Homer, Hesiod, and Heroditus, whereas Aristotle treats only of *Elephas indicus*. From this it does not appear that the Mesopotamian elephants were known to the Greeks.

CRANIAL CHARACTERS OF PALÆOLOXODON NAMADICUS AND HESPEROLOXODON ANTIQUUS COMPARED WITH LOXODONTA AFRICANA.—In figure 1041 above the cranial characters of the recent *Loxodonta africana* are shown in comparison with those of the fossil Indian species *Palæoloxodon namadicus* and those of the European species *Hesperoloxodon antiquus*. The relatively low, brachycephalic, platycephalic, and mesocephalic form of the *Loxodonta* cranium, as compared with the hypsicephalic crania of *Elephas*, of *Parelephas*, and of *Mammonteus*, is more clearly shown in the preceding figures (Chap. XV, pp. 915–926) relating to the comparative structure of the crania in these genera.

In the present comparison (Figs. 1041, 1069) of the crania of *Loxodonta africana*, *Palæoloxodon namadicus*, and *Hesperoloxodon antiquus*, we are especially struck by the short and extremely broad rostrum and by other characters, as follows: (1) Rostrum short and extremely broad, the premaxillaries diverging to the point where the tusks issue from the skull; (2) thus the bases of the tusks are very far apart instead of being close together as in *Mammonteus primigenius* or relatively close as in *E. indicus*; (3) whereas the premaxillary sockets are relatively of the same length in all three species, the divergence of the sockets in *P. namadicus* is about the same as in *L. africana*; (4) the premaxillary sockets are relatively longer and diverge still more widely in *H. antiquus*; (5) the crania of both *P. namadicus* and *H. antiquus* are distingushed from the cranium of *L. africana* by the greater development of the fronto-occipital crest which in *P. namadicus* engulfs the frontal bones so that there is a very short space between the lower border of this crest and the extremities of the nasals and the narial openings; (6) the narial openings are extremely broad and shallow, they exhibit approximately the same hour-glass-shaped form in *L. africana*, *P. namadicus*, and *H. antiquus*; (7) the skull of *P. namadicus*, moreover, is relatively broader and more flattened or platycephalic than the skull of *L. africana*; (8) this broadening and flattening of the summit of the cranium reaches an extreme in the gigantic *P. namadicus* cranium.

The phyletic affinities of these three types of crania, namely, *Loxodonta africana*, *Palæoloxodon namadicus*, and *Hesperoloxodon antiquus*, to each other are obvious, while there is a wide separation from the cranial type of *Elephas* and a still wider separation from the cranial type of *Archidiskodon* and of *Mammonteus*, which represent the opposite extreme of hypsicephaly.

Fig. 1069. COMPARISON OF CRANIA OF PALÆOLOXODON NAMADICUS, HESPEROLOXODON ANTIQUUS ITALICUS, H. ANT. AUSONIUS, AND H. ANT. PLATYRHYNCHUS

All to the same one-twentieth scale. Compare figures 1041, 1121, 1096, 1105, 1106

[At the time this figure was prepared Professor Osborn was not aware that Matsumoto had preceded him by three months in the description of *Palæoloxodon*, thereby rendering his own genus *Sivalikia* a synonym. Consequently the reader should disregard the letter "S" in this figure (=*Sivalikia*) and substitute Matsumoto's genus *Palæoloxodon* and Osborn's *Hesperoloxodon* (a subsequent determination for the *antiquus* group), as indicated in the following caption.—Editor.]

(Upper row) *Palæoloxodon namadicus*: One juvenile and two adult crania, front and side views. After Falconer and Cautley, 1846 [1847].

(Second row) *Hesperoloxodon antiquus italicus* (left), excavated at Pignataro Interamna, Italy, about fifty miles north of Naples. Drawn after photograph of specimen as it lay in the quarry (Fig. 1096); subject to modification after restoration of the cranium (Fig. 1098 and especially Fig. 1106, an orthogonal drawing from the mount). (Right) Aged *Palæoloxodon namadicus*, after Pilgrim, 1905, front and side views.

(Third row) *Hesperoloxodon antiquus ausonius*? (left), from the Val d'Arno of Italy, after Weithofer, 1890; *H. antiquus platyrhynchus* (middle), from San Isidro, Spain, after Graells, 1897; *H. antiquus ausonius* (right), from the Val d'Arno of Italy, after Pohlig, 1891, erroneously referred to *Elephas (antiquus) Nestii*.

(Lower row) *Palæoloxodon melitensis* (left), from the island of Sicily, front and side views, after Pohlig, 1893; *Hesperoloxodon antiquus ausonius* (right), from the Val d'Arno of Italy, after Pohlig, 1891, erroneously referred to *Elephas (antiquus) Nestii*.

Geologic and Geographic Distribution of the Loxodontinæ.—Originally described by Falconer from deposits now determined as of the Upper Pleistocene of India (*Palæoloxodon namadicus*) and the Lower(?) Pleistocene of England (*Hesperoloxodon antiquus*), the geologic range has been extended from the relatively small Upper Pliocene[1] *H. ausonius* to the great ascending Upper Pleistocene mutations (i.e., *H. antiquus* in Germany = *H. antiquus germanicus*), also throughout western Europe, to the progressive *Palæoloxodon namadicus* of the Middle to Upper Pleistocene of India, to smaller subspecies or varieties of *Palæoloxodon* in Japan, described by Matsumoto, and in Java, described by Dubois, to the *P. atlanticus* of northern Africa and a long series of probably antecedent species in central and southern Africa, as well as to larger and smaller varieties in the Mediterranean Islands.

The straight-tusked elephants of western and southern Europe have been treated, in succession to Falconer, by Leith Adams in Italy, by Pohlig, Weithofer, Soergel, and Berckhemer in Germany and Italy, by Forsyth Major and Depéret and Mayet in the Pliocene of Italy and of England, by Andrews and Forster Cooper in the description of the Upnor elephant (*Hesperoloxodon antiquus*) of England, and finally by Osborn in his description of *Palæoloxodon* [*Hesperoloxodon*] *antiquus italicus* of Italy.

As the whole Pleistocene period is now estimated at approximately 1,000,000 years, the straight-tusked elephant *Hesperoloxodon antiquus* lived in western Europe for an enormously long period of time, it survived many climatic phases, it doubtless passed through many ascending mutations which will be determined by final monographic comparison and description. First appearing in Upper Pliocene time, it survived three successive glaciations of northern Europe, but perished toward the close of the *3d Interglacial*. Throughout this long period its companions in southwestern Europe were the *Parelephas trogontherii*, the hippopotami and the rhinoceroses (*Rhinoceros etruscus* and *R. merckii*). The provisional geologic succession and companionship of these four types may be presented in the table after Osborn and Reeds, 1922-1929 (Pl. xxiv).

Osborn, 1929: Pilgrim (1905) first notes that *Elephas namadicus* is entirely absent from all the Pliocene Siwalik strata, in which there is no ancestral type from which it might arise; this suggests the probability that the genus *Palæoloxodon* originated in Africa, migrated north into Europe, thence to India and the Oriental regions. As soon as we begin to examine the Pleistocene deposits of the Godávari, the Nerbudda, and the Ganges, *Palæoloxodon namadicus* occurs in great abundance; it is also found *sparingly* in Burma, China, Java, and Japan, as described by Owen, Martin, Koken, Schlosser, Naumann, Makiyama, and Matsumoto.

SYSTEMATIC DESCRIPTION OF SPECIES OF PALÆOLOXODON AND HESPEROLOXODON

The present revision by Osborn makes no attempt at finality, but is devoted to the establishment of the characters and geologic age of the principal generic and specific types, awaiting fuller monographic revision based only upon close comparison and measurement of the rich materials which the museums of western Europe and of India afford. To the writer's knowledge, no complete cranium of *Hesperoloxodon antiquus* has been figured, and it is accordingly of interest to reproduce the photograph of a cranium[2] recently discovered at Pignataro Interamna, in Valle del Liri, near Cassino, Italy, between Naples and Rome, which appears to be exceptionally complete (see Figs. 1096, 1098, and 1101 below).

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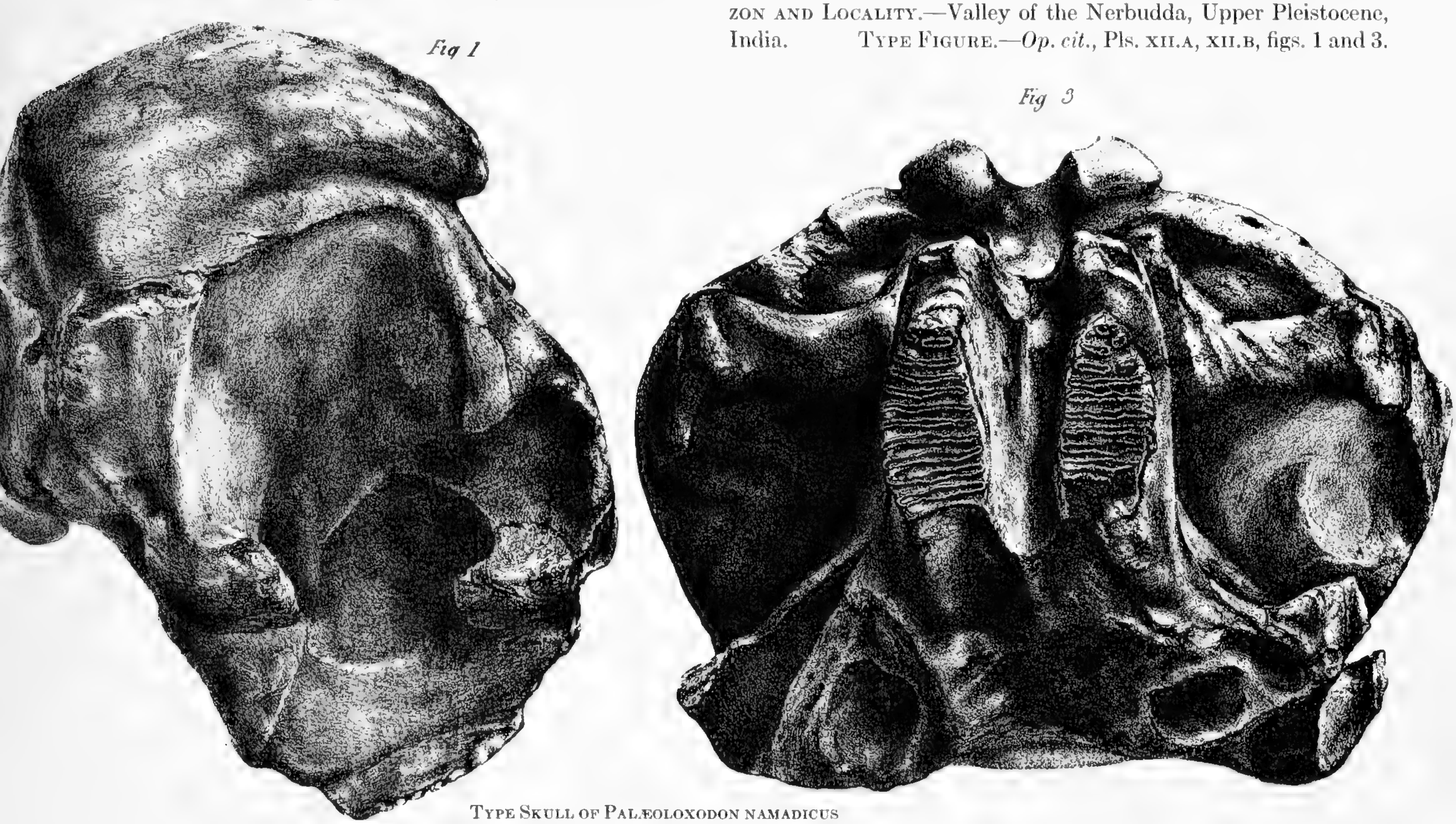
[1] [See footnote 1 on p. 1049 regarding the possible Lower Pleistocene age of the Villafranchian.—Editor.]

[2] This cranium was presented (May, 1929) by the author to the American Museum of Natural History and bears the number Amer. Mus. 22634. When discovered it was in perfect condition (as shown in Figs. 1096 and 1069), but it was seriously damaged in removal and in attempts to repair it by the owner. Full description and figures are given below in the present chapter.

Palæoloxodon namadicus Falconer and Cautley, 1846, 1847

Figures 1041, 1046, 1068–1070, 1072, 1073, 1108, 1110

Type locality: Valley of the Nerbudda (or Narbada), Godávari formation (see Fig. 729). Narbada Alluvium horizon, compare '*Elephas antiquus* (*namadicus*)' Pilgrim, 1905, containing also referred *Stegodon insignis*, *S. ganesa*, and *Rhinoceros unicornis*. Upper Pleistocene.



Type Skull of Palæoloxodon namadicus

Fig. 1070. (?)Female type cranium of *Elephas Namadicus* Falconer and Cautley, 1846 [1847, Pl. xii.b, figs. 1 and 3]; lateral and palatal views of the skull, showing portions of the third true molar of either side; ten and a half ridge-plates remain (there were possibly three or four anterior to these, making fourteen or fifteen). One-sixth natural size. Brit. Mus. M.3092; cast Amer. Mus. Warren Coll. 10381. Valley of the Nerbudda (or Narbada), India (see (Fig. 729).

Specific Characters.—Transverse occipitofrontal rugosity very prominent in males and females. Typical ridge formula as below (p. 1212). Third superior molars with an estimated total of fifteen ridge-plates; 8e ridge-plates in 10 cm.; maximum breadth 101 mm. Breadth of M_2 84 mm.; estimated length of M_2 264 mm. Ridge-plates broad, close set, entirely lacking 'loxodont sinus'; enamel borders thin. Skeleton of gigantic size, height estimated at 12–13 feet (cf. Fig. 1068).

In 1846, Falconer and Cautley in the "Fauna Antiqua Sivalensis," p. 45, first named the Upper Pleistocene species of the "Valley of the Nerbudda," India, *Elephas Namadicus*, but did not figure the species until 1847 (Pls. xii.a and b of the "Fauna Antiqua Sivalensis"). Subsequently, in the year 1847 (*op. cit.*, Pl. xii.d), they figured and named the Lower Pleistocene species of western Europe *Elephas antiquus*. Consequently the name *Elephas namadicus* Falc. and Caut. antedates the name *Elephas antiquus* Falc. and Caut. by nearly a year. Later Falconer clearly recognized and pointed out that his species *E. namadicus* of India most closely resembled his species *E. antiquus* of western Europe. Meanwhile he gave his usual thorough description and characterization of this very important Indian species. The systematic references are as follows:

E. [*Elephas*] *Namadicus* Falconer and Cautley, 1846, 1847. "Fauna Antiqua Sivalensis," 1846, p. 45, and Atlas, 1847. (*Op. cit.*, p. 45): "Another extinct Indian species *E. Namadicus* (to be described in the sequel)." Type.—Skull showing portions of the third true molar of either side (Brit. Mus. M.3092). Horizon and Locality.—Valley of the Nerbudda, Upper Pleistocene, India. Type Figure.—*Op. cit.*, Pls. xii.a, xii.b, figs. 1 and 3.

Type Description.—(Falconer in Murchison, 1867, p. 15, Pls. xii.a and xii.b: "From the valley of the Nerbudda. Probably a female, from small size of tusks. . . . It was chiselled out by Dr. Falconer, and determined by him to be a new species. In a letter to Lieut.-Colonel Ousely, Dr. F. writes thus: 'It is probably the most perfect specimen of a fossil elephant's cranium in Europe. The species is especially interesting from the form of the cranium, which is so grotesquely constructed that it looks the caricature of an elephant's head in a periwig. I have named the species *E. Namadicus*, after the Nerbudda river, the Namadus of Ptolemy.' There is a very similar specimen in the Museum of the Asiatic Society of Bengal. . . . Length of remaining portion left molar, 7.5 in. [12e ridge-plates in 7.5 in. or 191 mm.]. Width of remaining portion left molar, 3.7 in. N.B.—Twelve plates in this extent. Width of palate in front (between molars), 2.8 in. Width behind, 4.1 in." Falconer gives full measurements (*op. cit.*, pp. 15 and 16) and comparison with *E. indicus*, *E. hysudricus*, and *E. primigenius.*

Falconer (1868) Materials and Ridge Formula.—The ridge formula of *Palæoloxodon namadicus* may be derived by Falconer's careful examination and comparison of the type skull (Fig. 1070) containing M^3, an imperfect tooth, also of referred upper jaws (Pl. XIII) and of several referred lower jaws (Pl. XII.C, XII.D), as annotated herewith:

Falconer, "Palæontological Memoirs," 1868, Vol. I, pp. 435–438. Type skull: Plates XII.A,B,C,D and XIII, ridge-plates $\text{M}\,3^{14\text{-}15}$. Referred Upper Jaws.—Plate XIII, figs. 1, 1*a*, 1*b*, upper jaw, M^3, ridge-plates 11+. Referred Lower Jaws.—Plate XII.C, figs. 3, 3*a*, lower jaw, Dp_4, ridge-plates 10½; figs. 4, 4*a*, lower jaw, M_3, ridge-plates 20½; Plate XII.D, figs. 1, 1*a*, lower jaw, M_1, ridge-plates ½–13–½, 15 in all; figs. 2, 2*a*, lower jaw, M_1, ridge-plates 13; figs. 3, 3*a*, lower jaw, M_2, about 15 ridge-plates.

Falconer's type and referred ridge formula of *Elephas* [= *Palæoloxodon*] *namadicus* is:

$$\text{Dp } 4\ \frac{}{10\tfrac{1}{2}}\ \text{M } 1\ \frac{}{\tfrac{1}{2}\text{-}13\text{-}\tfrac{1}{2}}\ \text{M } 2\ \frac{}{?15}\ \text{M } 3\ \frac{14\text{-}15}{15\text{-}16}.$$

Lydekker (1886.2).—Lydekker does not give the complete ridge formula of *Palæoloxodon namadicus* but states (p. 169) that the third lower molar in specimens referred to *Elephas namadicus* from Japan has but sixteen ridge-plates. He characterizes the grinding teeth of *E. namadicus* as follows (p. 167): "The cheek-teeth of this species appear frequently almost or quite indistinguishable from those of the broad-toothed variety of *E. antiquus,* although the ridge-formula is, on the whole, rather higher and the ridges themselves are somewhat taller; some teeth, however, especially those from Burma, China, and Japan, show excessive plication of the enamel, and thereby approximate to *E. indicus,* although with a lower ridge-formula. . . . The adult cranium is characterized by the presence of a bold, overlapping, transverse ridge on the frontals. . . . which appears to be wanting in *E. antiquus*. . . . In India the species occurs in the Pleistocene of the Narbada valley, and it is probable that the other specimens are from strata of equivalent age."

China.—From China is recorded a 9½+ ridge-plated third superior molar (Brit. Mus. 29007); length 166 mm., breadth 101 mm., height 180 mm.; laminar frequency 6 in 100 mm. (*fide* Hopwood, letter, August 9, 1928).

Osborn, 1928: It is important to observe: (1) That the type ridge formula of *Palæoloxodon namadicus,* as deduced above from Falconer's observations, greatly exceeds the constant ridge formula of *Loxodonta africana*; (2) while Falconer also includes an M_3 with twenty ridge-plates, it is probably an erroneous generic reference, the true M 3 formula appears to be $\text{M } 3\ \frac{14\text{-}15}{15\text{-}16}$; (3) in *P. namadicus* the ridge-plates are relatively broader, more numerous, more closely compressed, and entirely *lacking* the *loxodont sinus* character. (4) In 1868 (Vol. II, p. 261) Falconer observes: "In the fossil *E. antiquus* of Europe, the dentition of which I have been able to determine with precision, the formula for the three intermediate molars, and the last true molar, above and below, is 10: 10, 12, 16, being nearly intermediate between the Indian and African Elephants."

COMPARISON OF PALÆOLOXODON NAMADICUS AND HESPEROLOXODON ANTIQUUS

Pilgrim (1905) on the Godávari Specimens of Palæoloxodon namadicus.—The fullest and most recent treatment of the species *Palæoloxodon namadicus* is that of Pilgrim (1905): (1) He erroneously adopts Pohlig's opinion that *Elephas namadicus* and *E. antiquus* are closely related if not identical species.[1] (2) Consequently he describes the Nerbudda species as "*Elephas antiquus* (*namadicus*)," giving *namadicus* the rank of a subspecies; inasmuch, however, as Falconer named the species *E. namadicus* prior to naming the species *E. antiquus,* this usage (Pilgrim) cannot be adopted; nor are these species identical. (3) He regards the Godávari river gravels (Lat. 20° 1′, Long. 74° 11′) as of the same Lower [Upper] Pleistocene age as the typical Nerbudda deposits in which the type of *E. namadicus* was discovered, containing alike *E. namadicus*, *Stegodon insignis* ref., *S. ganesa* ref., *Equus namadicus*, *Hippopotamus palæindicus*, *H. tetraprotodon*, also *Rhinoceros unicornis*. He regards *E. namadicus* as abundant also in the Pliocene of Burma, of China, of Java, and of Japan.

Pilgrim's description of the skull and skeleton of *Elephas namadicus* may be freely cited as follows (Pilgrim, 1905, pp. 203-206): "The cranium and bones, which I am describing, and which represent the species *Elephas antiquus* (*namadicus*) Falc. et Cautl., belonged to an individual of remarkable size. It cannot have stood much less than 16 feet at the shoulder. The cranium, as found, is larger than any hitherto recorded. . . . The cranium either on one or both sides possesses all the essential features of the portion above the maxillaries and the foramen magnum. . . . The accompanying plates exhibit all the more important characters of the present cranium, and the most casual inspection of it can leave no doubt as to its identity with the crania from the Narbada beds, figured by Falconer in the *Antiqua Fauna Sivalensis,* Plates 12A, 12B, figs. 1–3, and Plate 24A, figs. 4, 4*a*, as *Elephas namadicus.* These are the two most complete crania which have been known up to now, and are preserved in the British Museum. One of them has small tusks and probably belonged to an adult female. . . . The present skull is that of a fully grown male. It seems that the supra-orbital ridge grew forward with age, so that in young skulls there is a considerable interval between its margin and the extreme tip of the nasal process; in the large female skull in the British Museum this interval is sensibly diminished, while in this latest specimen, which represents the largest and presumably the most aged type with which we are acquainted, the supra-orbital ridge almost overhangs the nasal fossa, and the interval is reduced to its smallest dimensions. . . . Considering only the teeth and mandible of *E. antiquus* and of *E. namadicus,* Leith Adams . . . remarked that they seemed to him to be indistinguishable. This opinion of Leith Adams has been endorsed by many subsequent writers, among whom I need only mention Naumann, Weithofer, Pohlig,

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[1] [Professor Osborn (1931.846, p. 21) provisionally made his subspecies *Palæoloxodon antiquus italicus* the genotype of a new genus *Hesperoloxodon,* as distinct from *Palæoloxodon,* to include also other members of the *antiquus* group (see Fig. 1068 of the present Memoir), which he finally adopted (Osborn, 1934.926, p. 285, 1935.937, fig. 2, p. 407, and Pl. XI, Vol. I of the present Memoir).—Editor.]

Fig. 1071. Channel of the Godávari near Nandúr Madméshwar, India, in which region the referred skull of *Palæoloxodon namadicus* described by Pilgrim in 1905 (see pp. 1212, 1214 of present Memoir, figs. 1041, 1110 and 1108) was found. Reproduced after Pilgrim, 1905.1, Pl. IX.

and Lydekker. . . . So far is this from being the case, however, that all the skulls of the dwarf forms which Pohlig . . . has figured from the Grotto di Pontale von Carini in Sicily bear a striking resemblance to *Elephas namadicus*, and leave us no excuse for separating the two forms specifically. The accompanying text figure, taken from one of Pohlig's plates [Fig. 1041], brings out these resemblances in a remarkable degree. There is no doubt that future discoveries will prove that the original *E. antiquus* of Europe possesses the same craniological peculiarities as its Indian variety."[1]

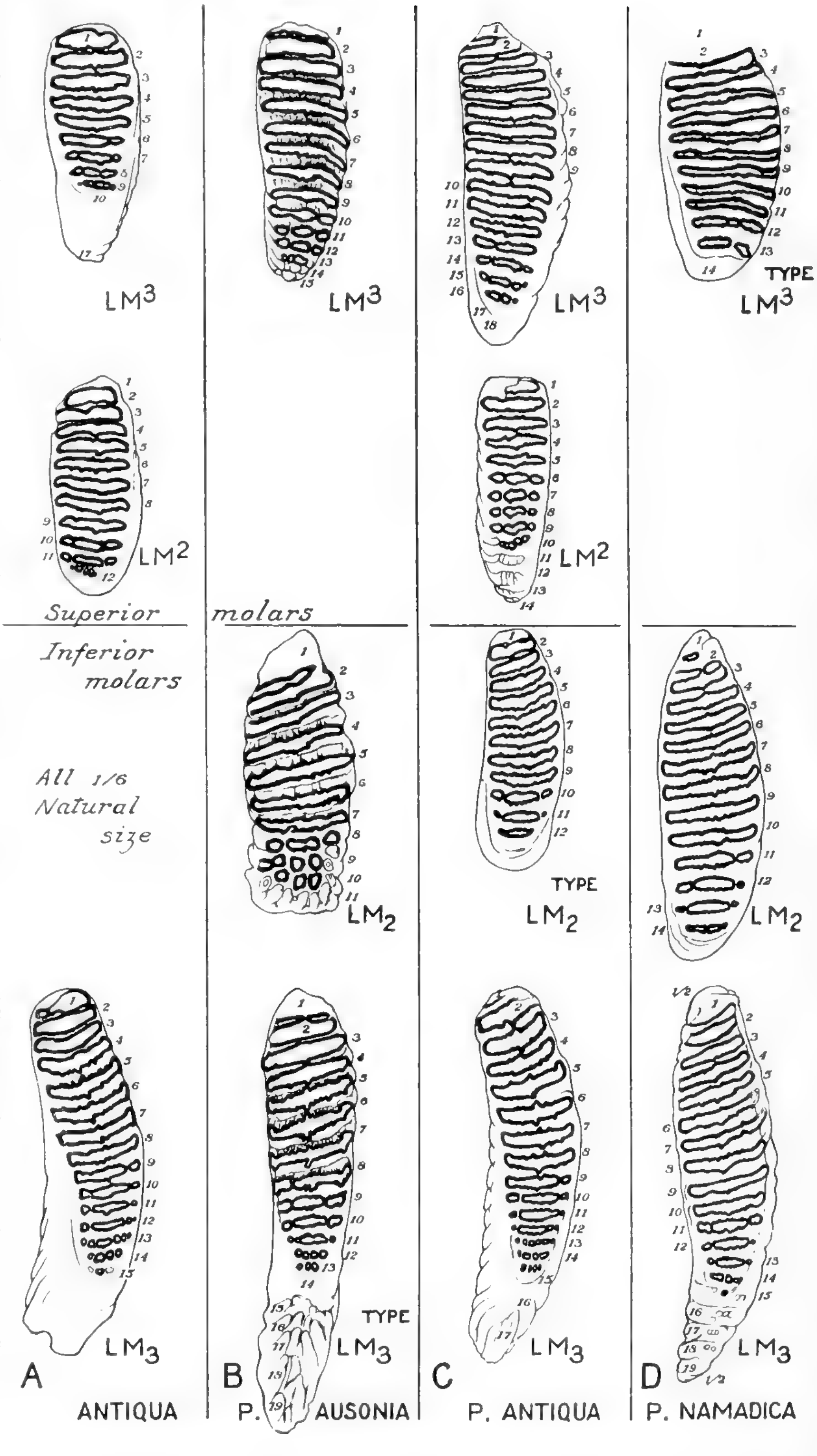

Fig. 1072. Comparison of Hesperoloxodon and Palæoloxodon (syn. Sivalikia) Superior and Inferior Molars

Drawn to the same one-sixth scale. Compare figures 1073 and 1152

A, *Hesperoloxodon antiquus* after Forster Cooper, 1924, Pls. IX, X. Left M^3, 17 ridge-plates; left M^2, 12 ridge-plates; left M_3, 15 ridge-plates. Lower Pleistocene. From Barrington, England.

B, *Hesperoloxodon ausonius* after Depéret and Mayet, 1923, Pls. X, XI. Left M^3, 15 ridge-plates; left M_2, 11 ridge-plates; left M_3, type, 19 ridge-plates. Upper Pliocene [Lower Pleistocene?]. San Romano. Val d'Arno inf., Italy.

C, *Hesperoloxodon antiquus* Falc. and Caut., 1847, Pls. XII.D, XIV.A, and Leith Adams, 1877–1881, Pl. IV. Left M^3, 18 ridge-plates; left M^2, 14 ridge-plates; left M_2, type, 12+ ridge-plates; left M_3, 17 ridge-plates. Lower Pleistocene. From England.

D, *Palæoloxodon namadicus* Falc. and Caut., 1847, Pls. XII.B, D, C. Left M_3, type, 14+ ridge-plates; left M_2, 14 ridge-plates; left M_3, 19½ ridge-plates. Upper Pleistocene. Nerbudda Valley, India.

Observe the progressive *increase in breadth* both of the superior and inferior molars and the corresponding *decrease in length*. The superior and inferior molars of *Hesperoloxodon ausonius* are relatively the *longest* and the *narrowest*; the grinders of *H. antiquus* (A, C) are intermediate in width and length; the grinders of *Palæoloxodon namadicus* are relatively the *shortest* and the *broadest*, also the most elevated or hypsodont. This change of proportions from the extremely long and narrow type, *H. ausonius*, to the relatively short and broad type, *P. namadicus*, is correlated with the progressive hypsicephaly, bathycephaly, and brachycephaly of the cranium. The same principle of the relative *shortening* and *broadening* of the grinders is displayed in figure 1073.

Pilgrim (*op. cit.*, pp. 208, 209) gives detailed comparative measurements of the crania of *Elephas antiquus* (*namadicus*), *E. antiquus*, and *E. antiquus melitensis* in the museums of Calcutta, London, Florence, and Palermo, and concludes (p. 210): "*E. antiquus* [*Hesperoloxodon antiquus*] approaches nearest to *E. africanus* [*Loxodonta africana*] in the flattened shape of the vertex, in the shortness and breadth of brow, in the form of the temporal fossa and of the interjugal space, and in the obtusely angled junction between the frontal and occipital surfaces. It differs in the slope of the occipital surface, in the greater length and shallowness of the intermaxillary median fossa, in the convexity of the occiput, in the higher position of the maxillary zygomatic process, and in the shorter length and greater width of the sub-orbital foramen."

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[1] [Professor Osborn regarded *E. antiquus* as referable to his genus *Hesperoloxodon* (see footnote 1 on p. 1180 above).—Editor.]

GENERIC CHARACTERISTICS OF PALÆOLOXODON NAMADICUS CRANIUM

(Compare Figs. 1069 and 1041)

(Pilgrim, 1905, pp. 206, 207): "The crania of *E.* [=*Hesperoloxodon*] *antiquus* (stem. sp.), imperfect as they are, show the following points in common with the Indian variety [*namadicus*] and the pygmy types which serve to distinguish them from all other elephants:— 1. The extreme divergence of the incisive alveoli and the broad shallow depression which occupies their centre. 2. The great distance of the occipital fossa from the foramen magnum and the basal breadth and extreme depth of the fossa. 3. The strong convexity of the occiput in a horizontal direction, which pushes the zygomatic process of the temporal to the front in an unusual degree. The crania of the Sicilian and of the Narbada elephants exhibit in addition the following points of likeness:— 4. The shortness and breadth of the brow and the widening out of the cranium from below upward. 5. The rhomboidal outline of the temporal fossa and its sharply-cut, acute-angled upper margin. 6. The presence of protuberances on either side of the occipital fossa. 7. The almost rectangular bend by which the occipital passes into the parietal, and the obtusely-angled junction between the parietal and frontal surfaces. 8. The well-marked frontal projection [*namadicus*] of the crown, which must have given an exceedingly beetling aspect to the living animal. 9. The approximately transversely oval contour of the cranium, when viewed in a direction at right angles to the plane of the occiput. It is much broader than high. [10.] *E. africanus* also approaches them to some extent in regard to the 1st, 4th, 5th, and 9th of the above characters."

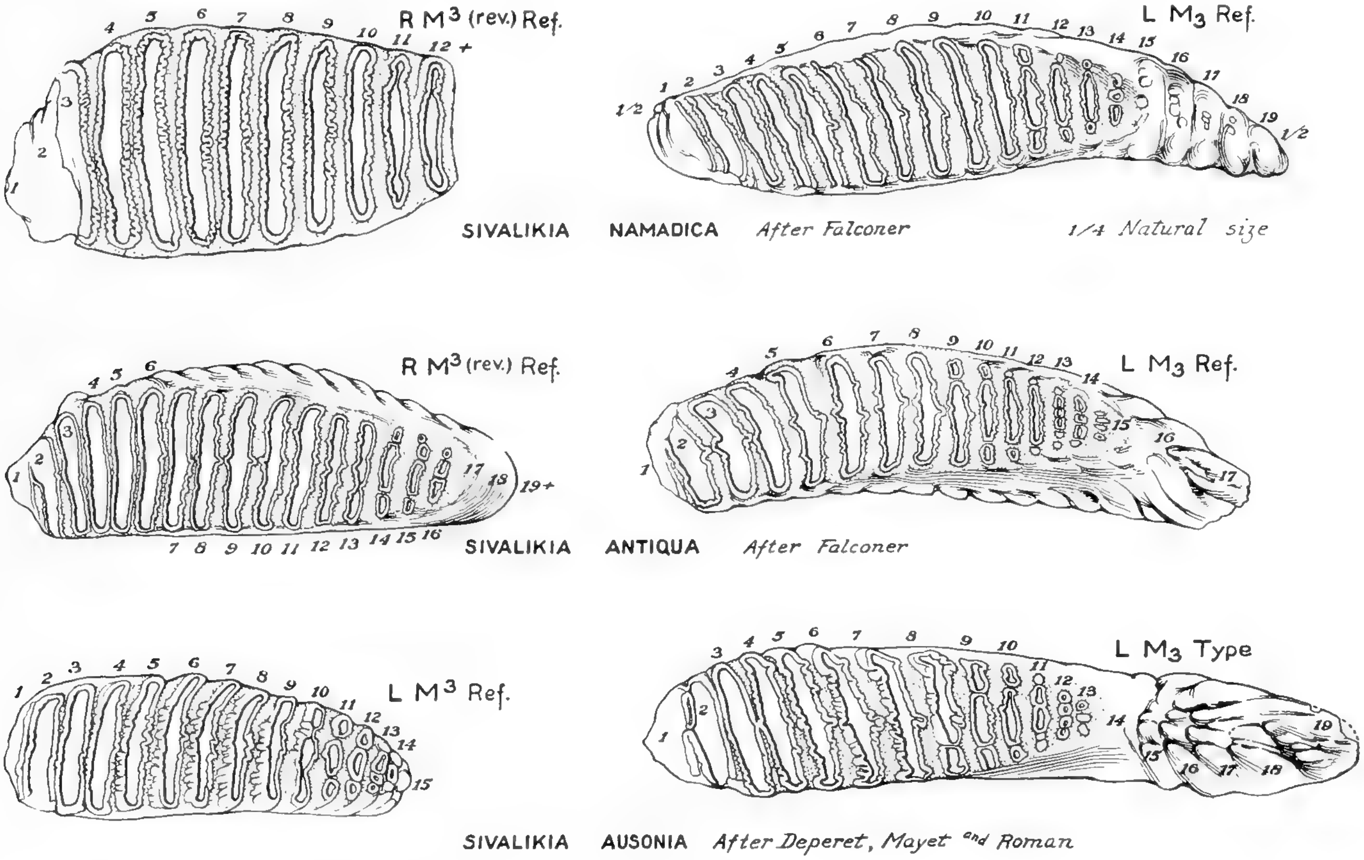


Fig. 1073. Three Progressive Broadening Stages in the Palæoloxodon (syn. Sivalikia) and Hesperoloxodon Superior Grinding Teeth. All to the same one-fourth scale.

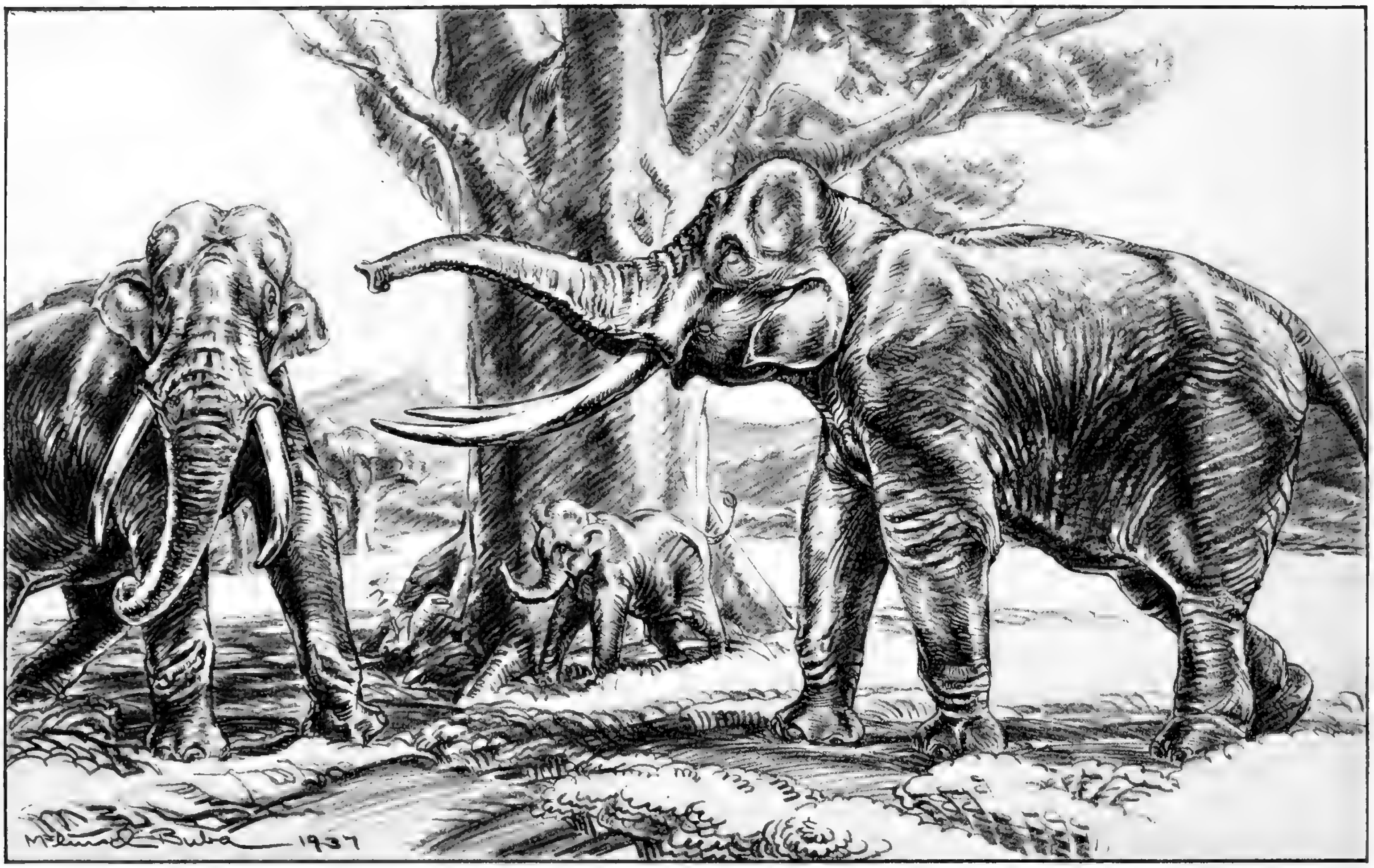
Compare Figures 1072, 1152, 1075, 1078

(Upper) *Palæoloxodon* (*syn. Sivalikia*) *namadicus*. Right M^3, 12+ ridge-plates; left M_3, 19½ ridge-plates, after Falconer and Cautley, 1847, Pl. XIII, fig. 1*a*, and Pl. XII.C, fig. 4, respectively.

(Middle) *Hesperoloxodon antiquus*. Right M^3, 19+ ridge-plates, after Falconer and Cautley, 1847, Pl. XII.D, fig. 5, Kent, England (Canterbury Mus.); left M_3, 17 ridge-plates, Pl. XIV.A, fig. 11, Saffron Walden, England. Of intermediate length and width.

(Lower) *Hesperoloxodon ausonius*. Left M^3, 15e ridge-plates, after Depéret and Mayet, 1923, Pl. x, fig. 3, Malafrasca (Val d'Arno sup.), Italy; left M_3, type, 19 ridge-plates; Pl. x, fig. 1, San Romano (Val d'Arno inf.). Both in the Inst. Géol., Florence. Relatively long and narrow grinders.

Observe as in figure 1072 the progressive *broadening* and *shortening* of the third superior and inferior grinders. Also observe as in figure 871 that the superior ridge-plates are concave *posteriorly*, the inferior ridge-plates concave *anteriorly*. Cement areas dotted.



Straight-tusked Elephant of Upnor (Hesperoloxodon antiquus) in the British Museum. Restoration, under the direction of Henry Fairfield Osborn, by Margret Flinsch Buba (1935) to a one-fiftieth scale (Bulls) and a one-sixtieth scale (Calf)

Skeleton and growth stage based upon the Upnor elephant (Fig. 1079); head or cranium based upon the Pignataro Interamna elephant (Fig. 1098); the one fragmentary tusk found at Upnor furnishes the length of the ivories in the restoration; ears based upon the cave drawings of Africa and Spain (Fig. 1047). Several months' research and all the studies involved in the preparation of figures 1079, 1080, 1084, 1083, and 1081 were also preliminary to the execution of this restoration.

Fig. 1074. This giant straight-tusked elephant, which formerly ranged over western Europe, is here shown in its relatively early Pleistocene stage of evolution and in a stage of growth which corresponds to the twenty-fifth year of living African and Indian elephants, namely, in which the second superior and inferior molars are still in use, while the third superior and inferior molars have not come into use (cf. Fig. 1061 of *Loxodonta africana*).

In other words, the Upnor straight-tusked elephant in the British Museum was about 25 to 30 years of age; it had not attained the full height characteristic of this species nor the maximum length of the tusks; yet it was a giant in life, measuring from the summit of the scapula to the ground, as originally estimated by Andrews and Forster Cooper, 12 ft. $1\frac{1}{2}$ in. (3700 mm.), and, as estimated by Osborn, 12 ft. $10\frac{7}{8}$ in. (3934 mm.) in the flesh.

The views of the skull and tusks, drawn directly from the Pignataro skull (Amer. Mus. 22634), are extremely accurate and characteristic, with great breadth between the tusks and correspondingly broad proboscis. The relatively level vertebral contour lacks the marked mid-depression and elevation above the pelvis which are characteristic of the African elephant (Fig. 1084). The relatively small, low-set ears are restored from the admirable cave drawings reproduced from Pomel (1895) and Breuil (1911) in figure 1047 above. As observed in the legend of that figure, the ears resemble those of the Indian (Fig. 1120) rather than the enormously enlarged and elevated ears of the African elephant (Fig. 1052).

GENUS: **HESPEROLOXODON** Osborn, 1931

Original reference: Amer. Mus. Novitates, No. 460, 1931, p. 21.
Genotypic species: *Palæoloxodon antiquus italicus* Osborn, 1931.846, p. 21.[1]

[The genus *Hesperoloxodon* was provisionally proposed by Professor Osborn in his article entitled, "*Palæoloxodon antiquus italicus* Sp. Nov., Final Stage in the 'Elephas antiquus' Phylum" (see Osborn, 1931.846, p. 21), to include *Palæoloxodon antiquus italicus* from Pignataro Interamna, Italy. Subsequently in various ways he indicated his opinion that the typical '*Elephas antiquus*' and other members of the *antiquus* group should be referred to his genus *Hesperoloxodon*, and finally in 1934 (Osborn, 1934.926, p. 285) the name appears as follows: "*Hesperoloxodon* Osborn, a Loxodontine of western Eurasia and Africa, never reaching America." Also the name appears on a chart between *Loxodonta* and *Palæoloxodon* (see Osborn, 1935.937, p. 407, fig. 2), and on page 12 as well as on Plate XI of Volume I of the present Memoir.

The accompanying definition, therefore, has been compiled from several sources and embodies, as far as can be determined, the distinctive characters on which Professor Osborn separated *Hesperoloxodon* from *Palæoloxodon* Matsumoto.

> GENERIC DEFINITION.—(Osborn, 1931.846, p. 21): "Comparison [of the cranium of *Palæoloxodon antiquus italicus*] with the cranium of '*Elephas namadicus*' shows a strong resemblance in the breadth of the premaxillary rostrum but an extreme difference in the summit of the cranium, which in '*E. namadicus*' is relatively low and reinforced by the overhanging parieto-frontal crest. This points to *Pal. ant. italicus* as a member of a phylum quite distinct from that of the Siwalik '*E. namadicus*,' a phylum which if supported by other cranial and skeletal differences might well constitute a new genus to which the name HESPEROLOXODON, or 'loxodont of the west,' might be applied. This name is provisionally proposed, as I would not like to be forestalled a second time, as in the case of *Palæoloxodon*, a generic name assigned to '*E. namadicus naumanni*' by Matsumoto but a few weeks prior to my description of *Sivalikia*."

Supposed diagnostic characters of *Hesperoloxodon* compiled from statements in the present Memoir: Cranium domelike with flattened forehead, more hypsicephalic and bathycephalic than that of *Palæoloxodon*; the prominent frontoparietal crest or "bold overlapping transverse ridge on the frontals" as mentioned by Lydekker in his description of *E.* [*Palæoloxodon*] *namadicus* (1886.2, p. 167) is lacking. Occiput relatively narrow and high (broad and low in *namadicus*). Grinders hypsodont, 'loxodont sinus' vestigial or absent; ridge formulæ: M $3\frac{16\frac{1}{2}-17}{16\frac{1}{2}-17}$ (typical), to M $3\ \frac{17-19}{+18+}$ (*germanicus*), to M $3\ \frac{20}{18+}$ (*italicus*). Premaxillaries extremely broad, incisive tusks widely divergent, slightly upcurved and incurved.—Editor.]

Hesperoloxodon antiquus Falconer and Cautley, 1847, 1857

Figures 794, 871, 1068, 1072–1084, 1088, 1109, Pl. XXIII

Type locality: Not recorded, probably Lower Pleistocene. Also very numerous referred specimens of Lower and Middle Pleistocene age (see Falconer, "Palæontological Memoirs," Vol. II, pp. 176–188).

Syn.: '*Elephas priscus*' Falconer and Cautley, 1847; *Elephas* (*Loxod.*) *priscus* Falconer, 1857.

GEOLOGIC AGE.—While the locality of Falconer's type specimen (Brit. Mus. M.2006) is not recorded, Falconer's referred specimen, *Elephas* (*Loxod.*) *priscus*, is from Gray's Thurrock (Essex); the same locality yields six of the British Museum specimens described by Leith Adams (1877-1881), while one specimen comes from Clacton (Essex) and another from Cromer (Forest Bed, Norfolk). All these beds probably belong to the Lower Pleistocene, *1st Interglacial* stage, and are geologically older than the *2d Interglacial* beds of Mosbach, etc., Germany, which contain larger and more progressive stages of *Hesperoloxodon antiquus*, as published by Pohlig. They are much older than the beds of Taubach and Weimar containing *H. antiquus germanicus*.

HISTORY.—As noted above, the "Sceleto Elephantino Tonnæ of Tentzelius (1698) is the first scientific description of the '*Elephas antiquus*' of Europe; Blumenbach confused this skeleton with that of '*E. primigenius*' of Europe. The species '*E. antiquus*' was then confused even by Falconer until 1847 with '*E. meridionalis*,' owing to the wide separation of the ridge-plates.

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[2] [See footnote on p. 1247 below.—Editor.]

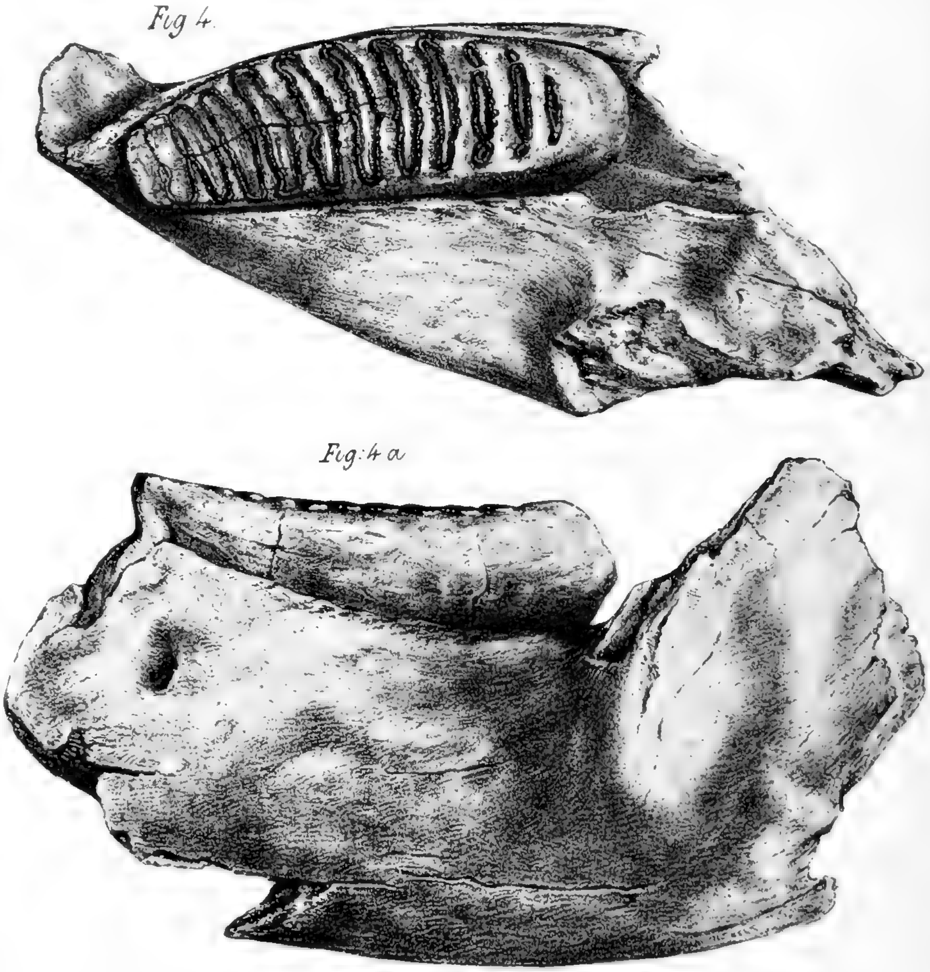
Specific Characters.—Prominent transverse fronto-occipital crest known to be lacking. Typical ridge formula of *Hesperoloxodon antiquus* somewhat greater than that of *Palæoloxodon namadicus*, namely;

$$\mathrm{Dp\,2}\,\tfrac{3}{3}\ \mathrm{Dp\,3}\,\tfrac{6}{6}\ \mathrm{Dp\,4}\,\tfrac{10}{10}\ \mathrm{M\,1}\,\tfrac{10-12}{12}\ \mathrm{M\,2}\,\tfrac{12}{12}\ \mathrm{M\,3}\,\tfrac{16\frac{1}{2}-17}{16\frac{1}{2}-17}.$$

Grinding teeth relatively longer and narrower than in *P. namadicus*; height more than double the width of the crown (Falc.). 'Loxodont sinus' absent in the type (Fig. 1075); absent or vestigial in other specimens (Fig. 1076); "mesial rhomboidal expansion of the discs of wear" (Falc., 1868, II, p. 176). Inferior ridge-plates concave anteriorly; superior ridge-plates concave posteriorly; crowns with thicker cement and relatively thicker and less plicate enamel than in *P. namadicus*; "great crimping of the enamel-plates" (*op. cit.*, Falconer, 1868, p. 176). Extremely narrow 'loxodont sinus' indicated in worn ridge-plates of *Hesperoloxodon antiquus* and *P. namadicus* (Fig. 1072). See also characters noted under *H. antiquus italicus* and *H. antiquus germanicus* below (pp. 1238–1256).

The above specific characters, including Falconer's final definition ("Palæontological Memoirs," 1868, Vol. II, p.176) doubtless apply to a *collective species* embracing many ascending mutations from Upper Pliocene to Middle Pleistocene time, but the typical *Hesperoloxodon antiquus* is probably of Lower Pleistocene age.

Falconer and Cautley named this species of straight-tusked elephant in 1847, a year after naming the Indian species *Elephas namadicus* in 1846; consequently if the two species are identical, as alleged by Pohlig and by Pilgrim, the name *Elephas namadicus* has the technical priority. There are many reasons, however, for treating the great straight-tusked elephant of southern Europe as a species distinct from, although nearly allied to, its Indian relative *Elephas namadicus.* All authors agree as to the relationship of these two animals and there is little doubt as to their affinity, but it is important to observe that in Falconer's *type* of *Elephas namadicus* (Fig. 1070) the grinding teeth are much *broader* than in Falconer's *type* of *Elephas antiquus* (Fig. 1075), which are relatively narrow. Consequently *E. antiquus* cannot be the same species as *E. namadicus*, however much these animals resemble each other in cranial characters.[1]



Lectotype Second Left Inferior Molar of Hesperoloxodon (syn. Sivalikia) antiquus Falconer and Cautley

One-third natural size

Fig. 1075. Lectotype, l.M_2, of *Elephas antiquus*, first figured as "*E. meridionalis*" (Falconer and Cautley, 1847, Pl. xii.d, figs. 4, 4*a*); Brit. Mus. M. 2006, locality unrecorded. One-third natural size. Named E. (Eueleph.) antiquus (Falconer, 1857, Synop. Tab. opp. p. 319), defined by Falconer, 1867, p. 18, and 1868, Vol. I, p. 438, as follows: "*Elephas antiquus.* . . . Lower jaw, left side, with first [?] true molar. This tooth is a beautiful specimen; shows twelve to thirteen ridges, with front ridge and heel. It narrows excessively in front and behind, like fig. 3 of *E. Namadicus!* The crimping, &c, are also exactly alike.—B. M. [Brit. Mus. M. 2006]. Length of molar, 8. in. Width at middle, 2.6 in. Width in front, 1.3 in."

CONFUSED HISTORY OF NAME AND TYPE

Elephas antiquus Falconer and Cautley, 1847. "Fauna Antiqua Sivalensis," 1847, Atlas, figs. 4, 4*a* of Pl. xii.d, figured as "*E. meridionalis*" but corrected by Dr. Falconer in copy of "Fauna Antiqua Sivalensis" belonging to British Museum; also Pl. xiv.b (the first time the name was published).[2] E. (Eueleph.) antiquus Falconer. "On the Species of Mastodon and Elephant occurring in the fossil state in Great Britain," Quart. Journ. Geol. Soc. London, 1857, Vol. XIII, table opposite page 319. Type.—Lower jaw with second lower molar, M_2, of the left side (Brit. Mus. M.2006). Type Locality.—Unnkown, undoubtedly England, probably of Lower Pleistocene age. Type Figure.—Falconer and Cautley, 1847, Pl. xii.d, figs. 4, 4*a*.

Falconer's Type.—There can be no question that this second inferior molar (Fig. 1075) should be regarded as Falconer's type.

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[1] [In 1931 Professor Osborn proposed the genus *Hesperoloxodon* to embrace members of the '*Elephas*' *antiquus* group, retaining Matsumoto's genus *Palæoloxodon*, 1924, for members of the '*E.*' *namadicus* group (see pp. 1212 and 1217 of this chapter).—Editor.]

[2] [Compare Bather, in Andrews and Cooper, 1928.1, p. iii; also for descriptive legend, see Falconer, 1867.1, pp. 18 and 23, and 1868.1, II, pp. 438, 441, and 443.—Editor.]

(Osborn, 1924): This twelve-plated M_2, of the left jaw, may be regarded as the *type*, since it was the first specimen figured and named (1847), and first described in 1867 by Falconer. Lydekker (1886.2, p. 130) designated it as follows: "M.2006. Part of the left ramus of the mandible, containing the half-worn $\frac{\quad}{\text{m. 2}}$; locality unknown. Figured by Falconer and Cautley in the 'Fauna Antiqua Sivalensis,' pl. xii.D, fig. 4, 4*a*. *No history.*" At the time, unfortunately, Falconer was misled by the spurious fossil type of *Elephas priscus* Goldfuss, for in the same table (Falconer, 1857, opp. p. 319) he cites "E. (Loxod.) priscus (Goldf.) . . . Pliocene . . . England; Lombardy . . . Imperfectly known. Fossil remains rare." This citation agrees entirely with his previous reference (Falconer, 1846, p. 15), in which he recognizes *E. priscus* Goldfuss, 1821, as a valid fossil type, although disputed by Cuvier. We must therefore regard the tooth described as *E.* (*Loxod.*) *priscus*, and reproduced in this Memoir (Fig. 1076), as referable to the true *Elephas* [*Hesperoloxodon*] *antiquus* of Falconer.

E. (LOXOD.) PRISCUS (GOLDF.) OF FALCONER, 1857 = HESPEROLOXODON ANTIQUUS

E. (*Loxod.*) *priscus* (Goldf.) Falconer, 1857. "On the Species of Mastodon and Elephant occurring in the fossil state in Great Britain," Quart. Journ. Geol. Soc., London, Vol. XIII, pp. 345, 346, and table opposite page 319. TYPE.—A second lower molar of the left side. HORIZON AND LOCALITY.—Gray's Thurrock, England, Pleistocene. FIGURE.—Falconer and Cautley, 1847, Pl. XIV, figs. 7, 7*a*, 7*b*, under the name *E. priscus?* (Brit. Mus. 39370).

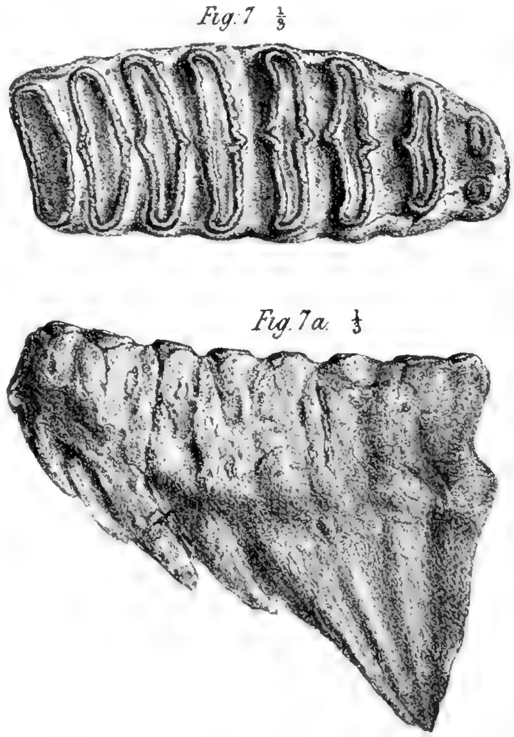
Falconer's type tooth of *E. antiquus* (Fig. 1075) and the tooth designated as *E.* (*Loxod.*) *priscus* (Fig. 1076) supplement each other in the fact that the *loxodont* character is more evident in the *priscus* variety. This is the eight-crested grinding tooth from the brick earth of Gray's Thurrock, Pleistocene, to which Falconer applied (1865, pp. 276, 277) the preoccupied name *Elephas* (*Loxod.*) *priscus*, in allusion to the lozenge-shaped crests, which remotely suggest those of the type of *Elephas priscus* Goldfuss (= *Loxodonta africana*). Falconer described this tooth (1865, pp. 270, and 1868, p. 96) as a "last molar [an error], left side, of the lower jaw." Lydekker described the tooth (1886.2, p. 133) as a "second left lower true molar." In the same publication, Lydekker (p. 122) treats it under *Elephas antiquus* as follows: "Syn. *Elephas* (*Loxodon*) *priscus*, Falconer and Cautley."

ELEPHAS ANTIQUUS AND E. NAMADICUS, FALCONER'S NOTES OF 1867 AND 1868 RELATING TO SPECIMENS FIGURED IN THE PLATES OF THE "FAUNA ANTIQUA SIVALENSIS," 1845–1847

Osborn, 1923: Future research will probably distinguish between the lectotype ridge formula of *Elephas antiquus* from Essex, Norfolk, etc., and the *collective* ridge formula of specimens from other localities.

COLLECTIVE RIDGE FORMULA.—Falconer's conception of the dental characters of *Elephas antiquus* and their points of similarity to the molars of *Elephas namadicus* are to be found in the beautiful plates and legends of the "Fauna Antiqua Sivalensis" and in the "Palæontological Memoirs" of 1868, as follows:

Falconer, "Palæontological Memoirs," Vol. I, 1868, pp. 438–440, 442, 443, 447, legends to Plates XII.D, XIII.A, XIV, XIV.A, XIV.B. *Elephas antiquus.* LECTOTYPE. Plate XII.D, figs. 4, 4*a*, M_1 [M_2] with 12–13 ridge-plates, and front ridge and heel, closely similar to *E. namadicus*, crimping, etc., exactly alike. UPPER JAWS.—Plate XII.D, figs. 5, 5*a*, M^3?, with 16½ ridge-plates [19+]. Plate XIV, figs. 2, 2*a*, 2*b*, Dp^3, ridge-plates 6½. Plate XIV.A, figs. 1, 1*a*, Dp^3, ridge-plates 5; figs. 2, 2*a*, Dp^4, ridge-plates 10; figs. 3, 3*a*, Dp^4, ridge-plates 10½, figs, 4, 4*a*, M^1, ridge-plates 8; figs. 5, 5*a*, r.M^3, ridge-plates 14½ [16½]. Plate XIV.B, figs. 16, 16*a*, entire upper molar, M^3, ridge-plates 16–17, length 11 in. = 280 mm. LOWER JAWS.—Plate XIII.A, fig. 4, lower jaw, M_2, ridge-plates 6+, M_3, ridge-plates 17; fig. 5, lower jaw, M_1, ridge-plates 12½. Plate XIV, figs. 1, 1*a*, 1*b*, lower jaw, Dp_3, ridge-plates ½–6–½, from Grays, Essex. Plate XIV.A, figs. 8, 8*a*, r.M_1, ridge-plates 12; figs. 10, 10*a*, lower jaw, r.M_2, ridge-plates 12½; figs. 11, 11*a*, l.M_3, ridge-plates 15–16½.



REFERRED HESPEROLOXODON ANTIQUUS

Fig. 1076. Aged second molar of the left side, l.M_2, from Gray's Thurrock (Essex), figured as *E.* [*Elephas*] *priscus?* by Falconer and Cautley, 1847, Pl. XIV, figs. 7, 7*a*, and as *Elephas* (*Loxod.*) *priscus* by Falconer, 1868, Vol. II, Pl. VII, fig. 1. One-third natural size. Brit. Mus. 39370.

Falconer's type and referred ridge formula of *E. antiquus*:

$$\text{Dp 3}\ \frac{5\text{-}6\tfrac{1}{2}}{\tfrac{1}{2}\text{-}6\text{-}\tfrac{1}{2}}\ \text{Dp 4}\ \frac{10\text{-}10\tfrac{1}{2}}{\quad}\ \text{M 1}\ \frac{8+}{12\text{-}12\tfrac{1}{2}\text{-}13}\ \text{M 2}\ \frac{\quad}{6\text{-}12\tfrac{1}{2}}\ \text{M 3}\ \frac{14\text{-}16\text{-}16\tfrac{1}{2}\text{-}17}{15\text{-}16\tfrac{1}{2}\text{-}17}.$$

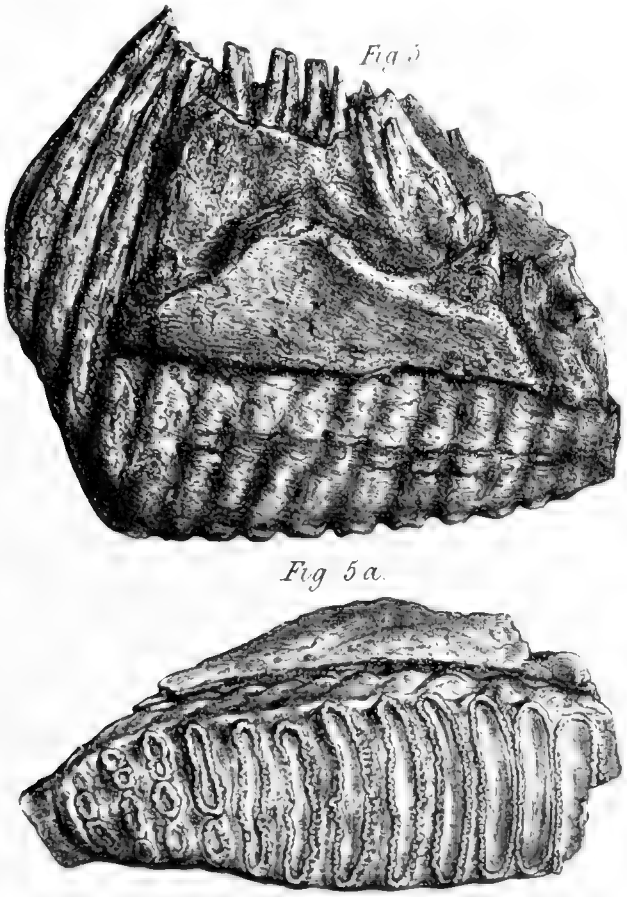
The above observations of Falconer (1867, 1868) and on Falconer's plates (by Osborn) are consistent with Falconer's less detailed formula of 1863. We may regard the following as his collective ridge formula of *Elephas* [= *Hesperoloxodon*] *antiquus*:

$$\text{Dp 3}\ \frac{6}{6}\quad \text{Dp 4}\ \frac{10}{10}\quad \text{M 1}\ \frac{12}{12}\quad \text{M 2}\ \frac{12}{12}\quad \text{M 3}\ \frac{16\tfrac{1}{2}\text{-}17}{16\tfrac{1}{2}\text{-}17}.$$

FALCONER'S OBSERVATIONS SUMMARIZED BY MURCHISON

"Palæontological Memoirs," 1868, Vol. II, pp. 176–188

We owe to Murchison ("Palæontological Memoirs," 1868, Vol. II, pp. 176–188) the complete enumeration of the numerous specimens regarded by Falconer as belonging to the above species, as observed in the museums of England, Italy, and Sicily; they doubtless belong to many successive geologic horizons. Falconer himself observed many variations in the 'loxodont sinus' or loop, the thickness of the enamel, the width and length of the crown, and the greater or less crimping or undulation of the ridge-plates. The typical '*Elephas antiquus*' of Falconer appears to have been of Lower Pleistocene, or Cromer Forest Bed age, as shown by the fact that the collective ridge formula cited above agrees precisely with that assigned to Cromer Forest Bed superior and inferior molars as cited below by Osborn.



Third Right Superior Molar of Hesperoloxodon antiquus

Compare diagrammatic figure 1088

Fig. 1077. Referred 16½ ridge-plated molar, r.M^3, of *Elephas antiquus*, after Falconer and Cautley, 1846 [1847, Pl. XIV.A, figs. 5, 5a]. Erroneously designated on Falconer's plate (XIV.A) as '*Elephas meridionalis*,' but corrected in his handwriting in copy of the "Fauna Antiqua Sivalensis" belonging to the British Museum. Falconer defined this specimen as follows (1867, p. 22, 1868, Vol. I, p. 442, Pl. XIV.A): "Figs. 5 and 5a.- Last true molar, upper jaw, right side. Has [+] fourteen plates and a heel, well crimped. From forest bed, Ostend, Norfolk. Green collection.—No. 16,229 B.M. Length, 10. in. Width, 3.4 in. Height, 6.5 in." One-third natural size. Compare with the type of *Elephas* [*Hesperoloxodon*] *antiquus* (Fig. 1075).

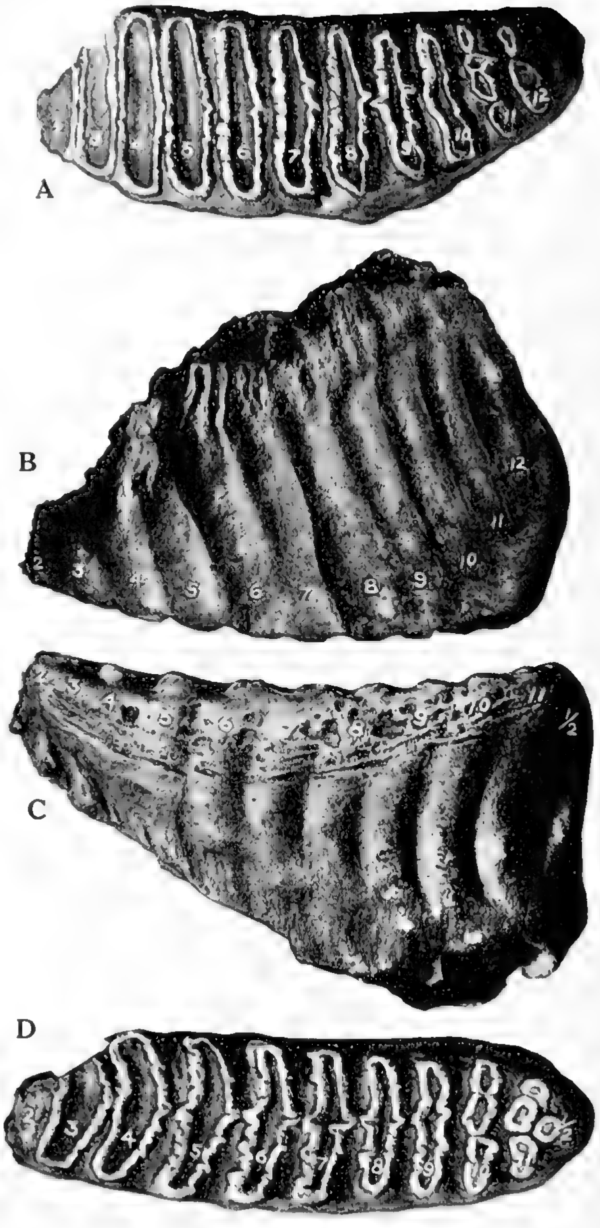


Fig. 1078. Upnor Elephant (Hesperoloxodon antiquus). Second Superior and Inferior Molars of Skeleton described below

One-third natural size

A, Crown view of twelve ridge-plated second right superior molar, r.M^2.

B, External view of twelve ridge-plated second left superior molar, l.M^2; anterior ridges partly worn.

C, Lateral view of second right inferior molar, r.M_2, retaining ridge-plates 2 11½.

D, Crown view of second right inferior molar, r.M_2, retaining ridge-plates 2–11½ estimated.

After retouched original photographs by C. Forster Cooper.

Observe that these molars were identified as second superior and inferior molars by Andrews (1915, p. 11), as third superior and inferior molars by Forster Cooper (1928, pp. 23, 24). The two upper molars, r.M^2, l.M^2, show twelve remaining ridge-plates with a posterior talon; they measure +221 mm. in length, 83 mm. in breadth, 150 mm. in maximum depth; laminar frequency 5 ridge-plates in 10 cm. The lower molar, r.M_2, measures +231 mm. in length, 70 mm. in breadth, 123 mm. in depth; laminar frequency 5 in 10 cm. Loxodont sinus rudimentary. This r.M_2 compares closely with Falconer's type l.M_2 (Fig. 1075).

Falconer found no trace of successional premolars such as are observed in *Archidiskodon planifrons* nor of the first lower milk molar. The other priceless observations contained in Falconer's Note-book of 1862 are summarized by Murchison (*op. cit.*, Pal. Mem., 1868, p. 176) as follows:

"4. *Elephas* (*Euelephas*) *antiquus*. . . . compiled from entries in Dr. Falconer's Note-books.—[Ed.]

The distinctive characters of the teeth of *Elephas antiquus* may be expressed in the following terms.—

1. Narrowness of the tooth in proportion to its length and height.
2. Great height of the plates. The height is more than double the width of the crown.
3. Mesial rhomboidal expansion of the discs of wear.
4. Great crimping of the enamel-plates.

The dental formula of *E. antiquus* is as follows:

Milk Molars.	True Molars.
$\frac{3+6+10}{3+6+10}$	$\frac{10+12+16}{10+12+16}$ "

The comparative enumeration of the ridge-plate totals and of the characteristic formulæ was also commented upon in Falconer's posthumous Memoir of 1865. Observe throughout his notes that the:

First upper milk molar = Dp^2 of the present Memoir.
Second upper milk molar = Dp^3 of the present Memoir.
Third upper milk molar = Dp^4 of the present Memoir.

CONFUSION WITH PARELEPHAS MOLARS, BY ADAMS, LYDEKKER, AND MATSUMOTO

Leith Adams (1877–1881, p. 47), after careful consideration of Falconer's work and ridge formulæ, concludes as follows: "From the foregoing details it seems to me that the ridge formula of *Elephas antiquus*, as far as British specimens in particular demonstrate, is, . . . [without talons], in upper and lower jaws, as follows:

$$\text{Dp 2}\,\frac{2-3}{3-?}\ \ \text{Dp 3}\,\frac{5-7}{6-8}\ \ \text{Dp 4}\,\frac{8-10}{9-11}\ \ \text{M 1}\,\frac{9-12}{11-12}\ \ \text{M 2}\,\frac{12-13}{12-13}\ \ \text{M 3}\,\frac{15-20}{16-19}.$$

Leith Adams' error arose from his confusing the '*E. antiquus*' molars with those of the contemporary *Parelephas*.

Distinction from Parelephas trogontherii.—Lydekker (1886.2, p. 122), although making use of the same materials as Falconer, erroneously assigns to *E. antiquus* a higher ridge formula; because, like Leith Adams, he includes within the narrow-plated *E. antiquus* the 'broad-plated' molars belonging to *Parelephas trongontherii*. He observes: "The ridge-formula [Footnote: 'Slightly modified from Leith-Adams, "British Fossil Elephants" (Mon. Pal. Soc.), p. 176. If the talons be included the formula will be higher, see Leith-Adams, *op. cit.*, p. 231.'], excluding talons, may be represented as:

$$\text{Mm. [Dp 2]}\,\frac{(2-3)}{3}\ \ \text{[Dp 3]}\,\frac{(5-7)}{(6-8)}\ \ \text{[Dp 4]}\,\frac{(8-10)}{(9-11)}\ \ \text{M.[M 1]}\,\frac{(9-12)}{(11-12)}$$
$$\text{[M 2]}\,\frac{(12-13)}{(12-13)}\ \ \ \text{[M 3]}\,\frac{(15-20)}{(16-21)}\text{"}$$

The higher numerals in this Leith Adams and Lydekker formula probably pertain to *Parelephas trogontherii*, namely:

$$\text{M 1}\,\frac{12}{12}\quad \text{M 2}\,\frac{13}{13}\quad \text{M 3}\,\frac{20}{21}.$$

Similarly Matsumoto (1924–1926) erroneously considered that the *Palæoloxodon* phylum represented by his '*Parelephas protomammonteus*' was ancestral through the *Parelephas trogontherii* phylum to the *Elephas* [=*Mammonteus*] *primigenius* phylum, as indicated by his choice of the specific name '*protomammonteus*' (cf. p. 1297 below).

PRIMITIVE AND PROGRESSIVE RIDGE–PLATE FORMULÆ

Research to the end of the year 1929, aided by the cranium from Pignataro Interamna, Italy (the type of *Palæoloxodon* [=*Hesperoloxodon*] *antiquus italicus*), reveals (Fig. 1088) a progressive hypsodonty and ridge-plate addition from the Upper Pliocene to the *3d Interglacial* stage, when *H. antiquus germanicus* and *H. antiquus italicus* mark the extinction of this phylum in western Europe.

Progressive Ridge Formulæ.—The progression from the typical Lower Pleistocene M 3 $\frac{17}{17}$ cited above, to the progressive ridge formulæ given by Zuffardi, Depéret, Soergel, and others, namely M 3 $\frac{20}{21}$ cited below, does not represent contemporary variations; it represents rather progressive or *ascending mutations*. As shown in the Osborn-Reeds diagram (Pl. xxiv), *Hesperoloxodon antiquus* lived for an enormously long period of time, perhaps hundreds of thousands of years, during which ridge-plates were constantly being added. During the same long geologic period, as shown in figures 1072 and 1073, the ridge-plates were constantly broadening.

Forster Cooper cites the primitive and progressive ridge formulæ (1924, p. 117), as given by more recent authorities, as follows:

$$\left.\begin{array}{lll} \text{Zuffardi, 1913:} & \text{M 2}\,\frac{12/13}{} & \text{M 3}\,\frac{15/20}{16/21} \\ \text{Depéret, 1923:} & \text{M 2}\,\frac{10/14}{11/15} & \text{M 3}\,\frac{15/20+}{16/21} \\ \text{Soergel, 1912:} & \text{M 2}\,\frac{10/13}{} & \text{M 3}\,\frac{14/19}{15/20} \end{array}\right\}\left.\begin{array}{l} \textit{Elephas antiquus} \\ \quad[=\textit{germanicus}],\ \text{M 2}\,\frac{9/12}{10/13}\quad \text{M 3}\,\frac{13/16}{14/18} \\ \quad\text{mid-Pleistocene} \end{array}\right\}\textit{Elephas antiquus}\ \text{mut.}\ \textit{ausonius}$$

He adds the following characters:

Elephas antiquus: "Thick, much folded plates regular rhombic or rectangular [S].
Fairly thick, always folded. Loxodont sinuses always well marked [D].
Folding not particularly noticeable, lozenges marked, a considerable difference in size between upper and lower molars [Z].
Long straight high crowns [Z]."

Elephas antiquus mut. *ausonius*: As *antiquus* but more deeply folded, and with folds more numerous, a very regular feature.
Loxodont sinuses variable but on the whole stronger and more prominent [D].
Elongated straight crowns about ½ smaller than *antiquus* from Clacton, Saffron Walden, etc. [D]."

Osborn, 1930: The ridge formulæ cited by Forster Cooper (1924, p. 117) and the specific references and identifications are superseded by the more precise ridge formulæ and specific identifications in the present Memoir; the unique '*Elephas ausonius*' (M 3 $\frac{19}{20}$) does not occur in the Forest Bed, the mut. *ausonius* is probably '*Parelephas trogontherii nestii*'; the higher ridge formulæ attributed to Zuffardi, Depéret, and Soergel belong only with the mid-Pleistocene [Upper Pleistocene] progressive *E.* [*Hesperoloxodan*] *antiquus germanicus*, as shown in figure 1088.

Primitive Ridge-Plate Formulæ and Measurements

	Ridge-plates		Length	Breadth	Height
Cromer Forest Bed	R. M^3	16–17	280 mm. = 11 in.	90 mm. = 3.50 in.	175 mm. = 6.80 in.
Happisburgh (Forest Bed)	R. M_3	+11	267 mm. = 10.5 in.	88 mm. = 3.40 in.	146 mm. = 5.70 in.
Upnor Elephant (after Forster Cooper)	R. M^2	12½	221 mm. = 8.7 in.	83 mm. = 3.25 in.	150 mm. = 5.90 in.
	R. M_2	12½ est.	231 mm. = 9.1 in.	70 mm. = 2.75 in.	123 mm. = 4.76 in.
E. antiquus type	L. M_2	12	204 mm. = 8 in.	66 mm. = 2.60 in.	

THE HESPEROLOXODON ANTIQUUS SKELETON OF UPNOR, KENT, ENGLAND[1]

Illustrated by figures 1078–1084, 1074

One of the most fortunate events in the recent history of mammalian palæontology is the discovery and restoration of a nearly complete skeleton of an elephant (lacking only the skull). This skeleton was discovered in 1911-1912 in a trench near Upnor on the banks of the Medway, opposite Chatham Dockyard, in Kent, England. A trench was unwittingly cut through the great skeleton and destroyed a large number of bones and a tusk. The remaining skeleton was excavated in 1915 under the supervision of Dr. Charles W. Andrews and Mr. L. E. Parsons; it was restored and reconstructed under the direction of Dr. Andrews and Mr. Forster Cooper; the restoration and mounting (made possible through the generosity of Mr. Rushton Parker) was completed July 23, 1927, after twelve years of research and reconstruction, as shown in figures 1079, 1080, and 1083. The following is cited from Doctor Bather's description of 1927, p. 104:

> "No complete skeleton [of *Elephas antiquus*] has ever been obtained, and ours, incomplete though it be, is far nearer perfection than any other yet known. The highest point of the backbone is 12 ft. 7 in. from the ground, and the top of the shoulder-blade reaches 12 ft. 1½ in. The pelvis has an actual width of six ft. less ⅛ in., but, since its edges have been much broken and eaten away, it may well have exceeded this by 6 in., or 20 in. more than the width of the pelvis of the largest mammoth. The safest comparison is based on the well-preserved upper arm-bone (humerus), which has a length of 4 ft. 1 in., as compared with 3 ft. 1 in. in the biggest Indian elephant (*E. maximus*) in the Museum. Visualizing the animal in the flesh, one must add several inches of muscle and skin to the height, which may safely be estimated at a full 13 ft."

Unfortunately Dr. Charles Williams Andrews died on May 25, 1924. The Memoir begun by him and completed by Mr. C. Forster Cooper in 1928, namely, "On a Specimen of *Elephas antiquus* from Upnor," contains the following remarks by Dr. F. A. Bather in the Preface (p. iii):

> Dr. Andrews' account of the specimen runs from page 1 to page 18, and contains, just as left by him, the description of all the skeleton except the vertebral column, pelvis, and teeth. Those portions are described by Mr. Forster Cooper. The black-

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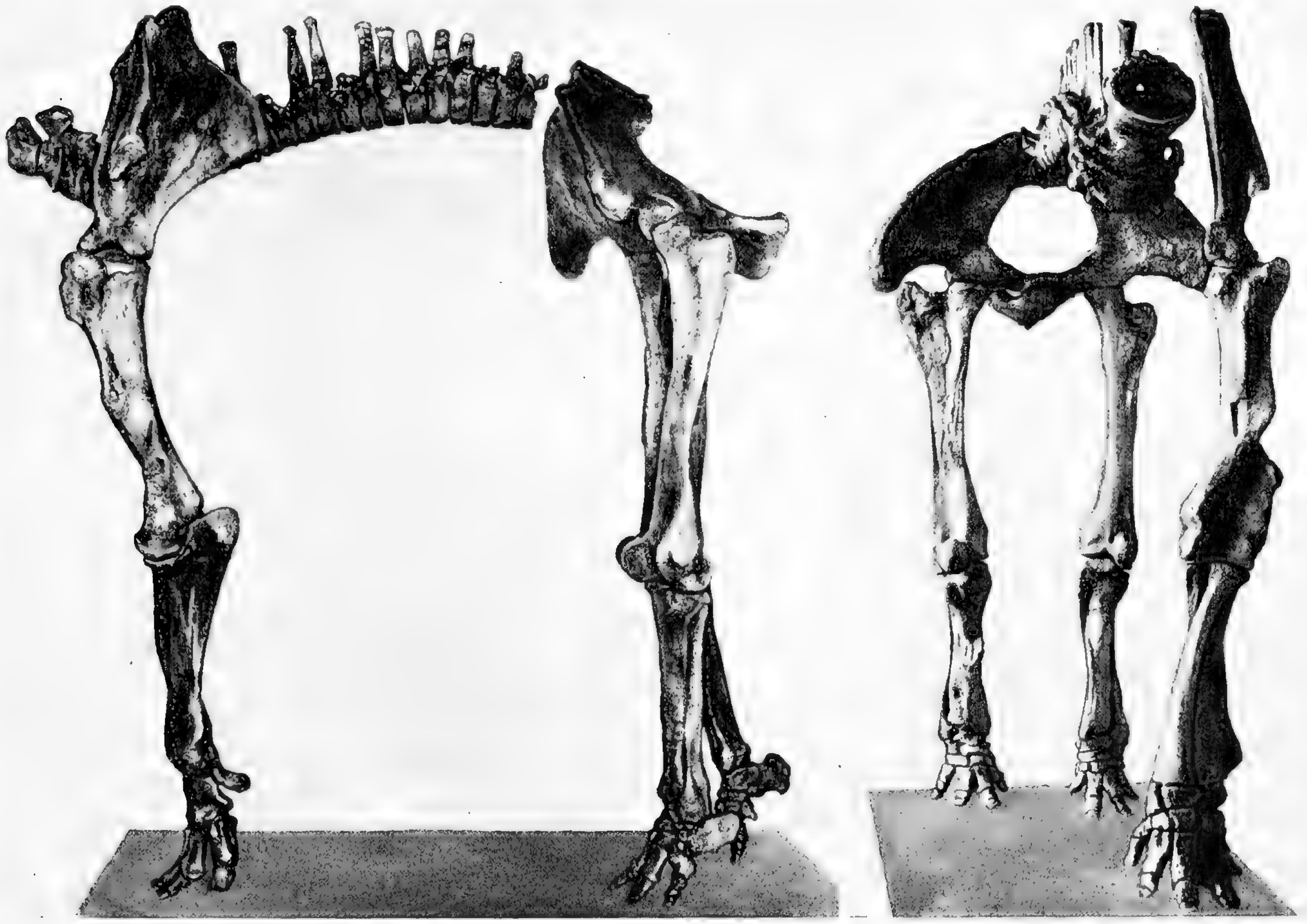
[1] [In 1931, in an article entitled "*Palæoloxodon antiquus italicus* Sp. Nov., Final Stage in the 'Elephas antiquus' Phylum" (Osborn, 1931.846, pp. 1, 19, 21, 23), Professor Osborn provisionally assigned the name *Pal. ant.* (*andrewsi?*) to this Upnor specimen, a name which also appeared in his unrevised manuscript of the present Memoir, evidently in response to the suggestion of Prof. C. Forster Cooper (see quotation from Cooper, 1924, bottom of p. 1226 below, this chapter). Inasmuch, however, as Professor Osborn failed to validate this subspecies by the necessary description, the Upnor elephant is treated in the present Memoir as *Hesperoloxodon antiquus*. (This note was prepared by Dr. George Gaylord Simpson after a careful study of the subject.)—Editor.]

and-white illustrations to Dr. Andrews' section are by Miss Gertrude M. Woodward; Mr. Forster Cooper has made the drawings for his own contributions.

From this Memoir the following citations (Andrews) may be paraphrased (pp. 2 and 3):

> The fore-limbs are represented by a left scapula; a left humerus, wanting most of the head, the tuberosities and the front of the upper part of the shaft; the upper articular end of the right humerus; the left ulna, wanting part of the shaft; a complete right radius and the greater part of the left; and most of the bones of the fore-foot on one side or the other except the cuneiform and unciform.
>
> [Comparison with African (Loxodonta africana) and Indian (Elephas indicus = maximus) Skeletons]
>
> The *scapula* is preserved on the left side only. It is much crushed, the spine being bent backwards over the post-scapular fossa. The upper angle is not quite complete, and a considerable portion of the posterior angle is wanting. The form of the glenoid surface is most nearly like that of *E. africanus*; the coracoid tuberosity is rather more developed than in that species, but less than in *E. maximus*; it is much as in *E. primigenius.* Between this tuberosity and the anterior border of the glenoid cavity there is a deep pit, such as also occurs in *E. africanus.* A similar pit is also seen in the glenoid portion of a large scapula (B.M. Geol. Dept. 21680) from Grays, probably belonging to *E. antiquus.* . . . The *humerus* is an enormously massive bone,



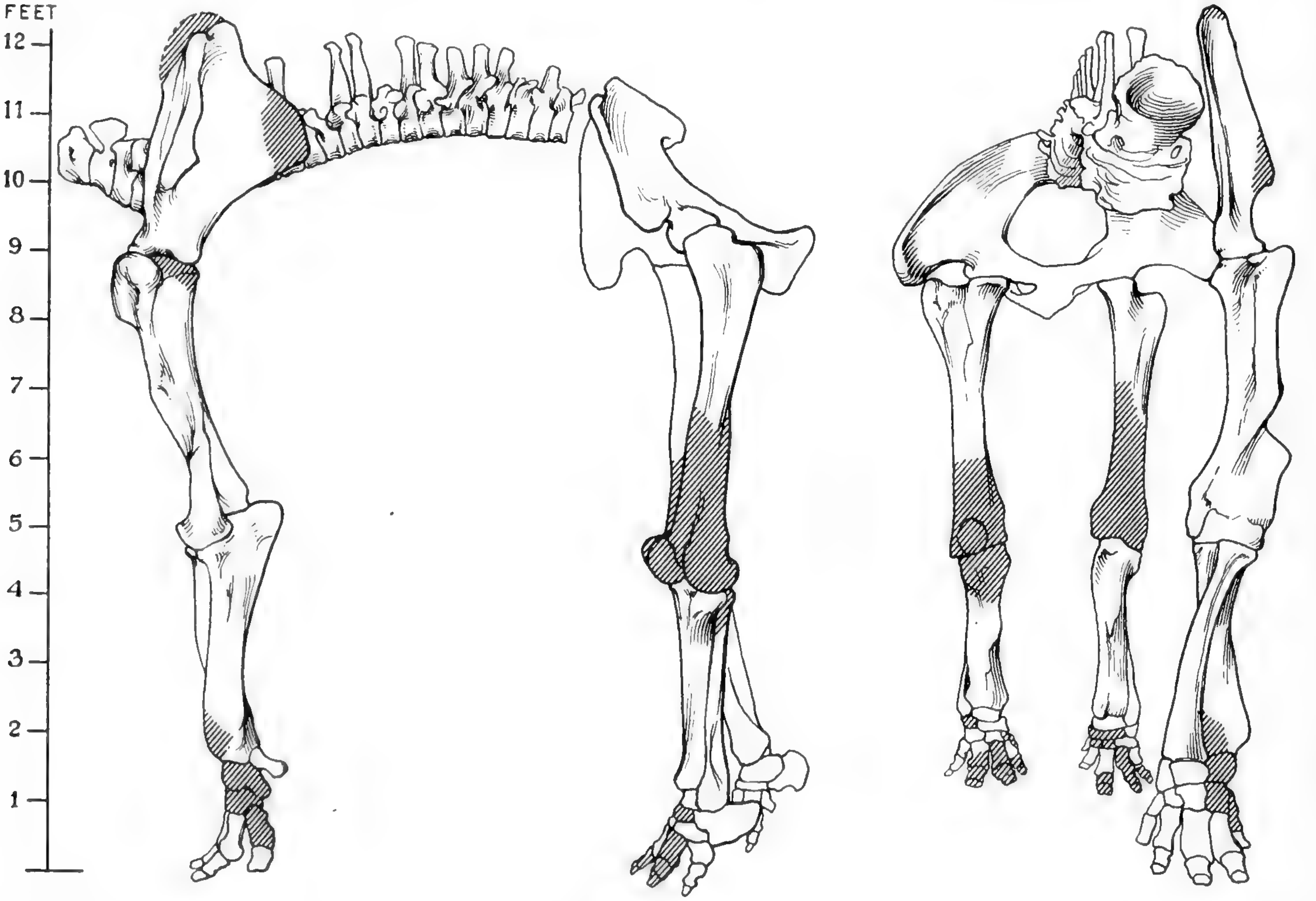
The Upnor Straight-tusked Elephant, Hesperoloxodon antiquus, of the British Museum, as Mounted in 1927

After photographs kindly furnished by the British Museum (Natural History)

Fig. 1079. This skeleton was discovered in 1911–1912 in a trench near Upnor on the banks of the Medway in Kent, England; it was excavated in 1915 under the supervision of Dr. C. W. Andrews and Mr. L. E. Parsons; the restoration and mounting under the direction of Doctor Andrews and Mr. C. Forster Cooper (made possible through the generosity of Mr. Rushton Parker) were completed July 23, 1927. The above figures (side and front views) are reproduced, one-thirtieth natural size, from original photographs kindly sent the present author by Mr. Cooper (cf. Cooper and Andrews, 1928, frontispiece and Pl. I).

The restored backbone (as shown in Fig. 1084) is complete except for two vertebræ; the radius of the left fore leg is restored in plaster, the right radius is complete; this radius, with some of the bones of the right foot, one of the tusks (too shattered for restoration), and a few grinding teeth are exhibited in a case adjacent to this mount in the British Museum. Compare figures 1080, 1081, 1082, and 1084, also text pages 1222–1228 of the present Memoir.

being apparently stouter in proportion to its length than in *E. maximus*, *E. africanus*, and *E. primigenius*; . . . The upper end of the *radius* is much like that of the radius of *E. maximus*; its anterior border is nearly straight, and the outer end of the humeral surface terminates in a point on the outer edge of the outer lobe of the humeral surface of the ulna. . . . Only the left *ulna* was found. This was nearly complete, wanting only a portion of the shaft immediately above the distal articulation, part of which is likewise missing. . . . Falconer and Leith Adams have both commented on the relative stoutness of the limbs of *Elephas antiquus*; probably it is the natural result of the enormous bulk attained by this species. . . . On the whole, the radius and ulna together are very similar to those of *E. africanus* and also to those of *E. antiquus recki*. . . . The collection at the British Museum includes the upper half of an ulna from Grays as large as that now under description. . . . Of the *fore-foot* the following bones are preserved; scaphoid (right and left), lunar (right and left), pisiform (left), trapezium (right and left), trapezoid (right and left), metacarpal I (right and left), metacarpal II (right), metacarpal III (right and left), metacarpal IV (left and part of right), phalanges and sesamoids. . . . In the *scaphoid* the radial facet is nearly flat. . . . and is more like the corresponding surface in *E. africanus*. . . In the *lunar* the facet for the radius (right) occupies nearly the whole upper surface; it is concave from before backwards posteriorly and concave in the same direction in front. . . The *magnum* is preserved on both sides. Its upper articular surface is almost exactly as in *E. africanus*. . . . The surfaces for articulation with the trapezoid and unciform are almost exactly like those occurring in *E. africanus*, but the distal (metacarpal) surface is peculiar. . . . The *metacarpals* are extraordinarily stout and massive. . . . The third metacarpal is the largest; it is preserved on both sides. . . . On the whole, the third and fourth metacarpals are very like those of the African elephant. . . . Only the proximal halves of the two *femora* are preserved, the remainder having been destroyed in digging the original trench. The head of the bone is nearly hemispherical, and the neck is very short. . . . There seems to be no trace of the lesser trochanter, and in this our specimen resembles the femur of *E. africanus* rather than that of *E. maximus*. . . . The left *tibia* is nearly complete, but the



UPNOR STRAIGHT-TUSKED ELEPHANT, HESPEROLOXODON ANTIQUUS, OF THE BRITISH MUSEUM, REDRAWN TO SHOW THE ORIGINAL AND RESTORED PARTS (OBLIQUE SHADING)

Fig. 1080. The scale of the skeletal height to top of scapula (3700 mm. = 12 ft. 1$\frac{5}{8}$ in.) agrees with the estimates of Bather, Andrews, and Cooper. The oblique shading indicates the restored portions of the scapula, humerus, radius, carpals, tarsals, and metatarsals, and both femora. For a new restoration of the vertebral column by Osborn, see figure 1084, *Hesperoloxodon antiquus* of Upnor. For a new reconstruction of the skeleton and outline of the flesh of the Upnor elephant, see figure 1083. For a new restoration of the Upnor straight-tusked elephant, see figure 1074. For comparative details of the vertebræ, scapulæ, and backbones, see figures 1082, 1081, and 1084. One-thirtieth natural size.

right is represented only by the lower end, which is much cracked and distorted.... The astragalar surface is wider from before backwards than in any specimen with which comparison has been made, but it comes nearest to what occurs in *E. africanus*.... The *fibula* of the left side is complete except for two or three inches towards the upper end of the shaft;... The form of these surfaces is much as in *E. africanus*... The *astragalus*... is very low and broad as in *E. antiquus recki*; the tibial facet is scarcely perceptibly concave from side to side. On the whole, the bone is much like that of *E. maximus* and *E. primigenius*, and differs from the astragalus of *E. africanus* in the greater development of what may be called the neck, which carries the facet for the navicular;... The *calcaneum* is preserved on both sides; it is a very heavily built and massive bone.... On the whole, our specimen most nearly resembles the calcaneum of *E. africanus*, except that the fibular facet is smaller.... The *navicular* is preserved on the right side only. It differs only in detail from the navicular of *E. africanus*;... The navicular of *E. antiquus recki* is very similar to that of the Upnor specimen, but the astragalar facet is wider from side to side in proportion to its antero-posterior diameter.... The first *metatarsal* is not preserved on either side, but judging from the distal facet on the ectocuneiform it must have been of fairly large size.... The third metatarsal is considerably larger than the second, being especially wider at its upper end. The proximal surface has a considerable area of contact with the mesocuneiform; in *E. africanus* this contact is very small, and in *E. maximus* is wanting altogether.... In *E. antiquus recki* the third metacarpal is said to have a distinct facet for contact with the mesocuneiform, and as in the Upnor specimen the fourth metatarsal has a considerable articulation with the ectocuneiform. It thus appears that in that form, as in our specimen, there is a considerable degree of alternation between the distal row of tarsals and the metatarsals; this alternation exists in a lesser degree in *E. africanus*, but is not present in *E. maximus*.

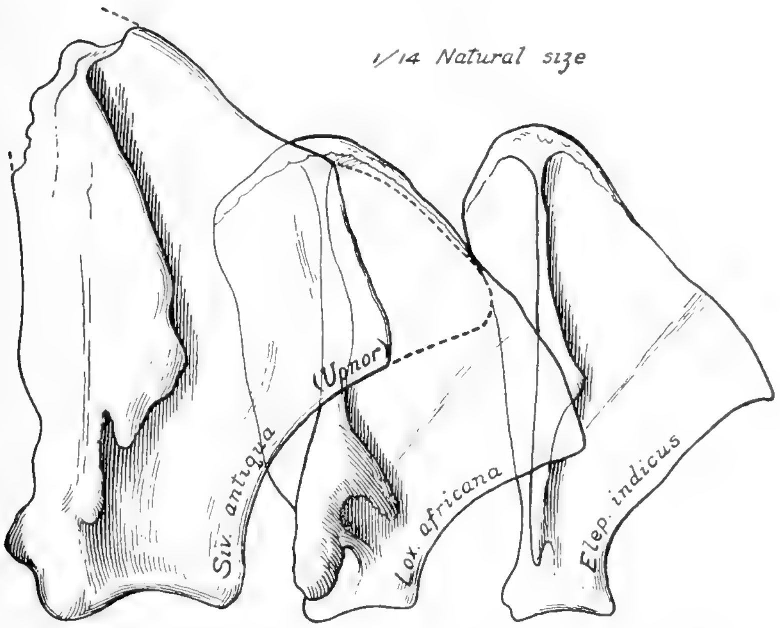


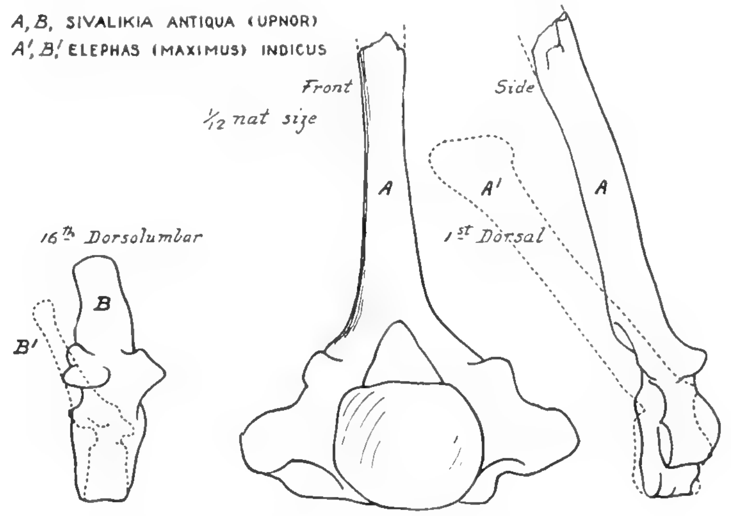
Fig. 1081. Comparative Views of the Scapulæ of Hesperoloxodon (syn. Sivalikia), of Loxodonta, and of Elephas

After Andrews and Cooper, 1928, figs. 1 and 2

Hesperoloxodon antiquus of Upnor. Very large, broadly triangular, greatly exceeding in size the scapula of 'Jumbo.'

Loxodonta africana ('Jumbo') of the Sudan (Abyssinia). Of smaller size and of very similar proportions to the scapula of *Hesperoloxodon antiquus* of Upnor.

Elephas indicus. Scapula elevated with relatively small pre- and post-scapular fossæ; much less broadly triangular than either *Loxodonta* or *Hesperoloxodon*.



Hesperoloxodon antiquus of Upnor

Fig. 1082. Front and lateral aspects of (A) erect first dorsal vertebra, of (B) sixteenth dorsolumbar vertebra of *Hesperoloxodon antiquus*, to the same scale as (A') first dorsal and (B') sixteenth dorsolumbar of *Elephas indicus* (= *maximus*), one-twelfth natural size. Compare Forster Cooper (1928, fig. 4).

Forster Cooper's Observations (1928, pp. 19–24).—In general contour and proportions the *pelvis* is similar to that of *Elephas africanus*, except for its considerably greater size. The principal measurements of the pelvis as restored are:

	mm.
Extreme width across the ilia at right angles to the vertebral axis	1830
Greatest width of ilium	1100
Width between the acetabula	945
Greatest diameter of acetabulum	250
Approximate length of symphysis	570

> The *vertebral column* was found practically complete, but much weathered. . . . The number of dorsal vertebrae actually found was twenty; the specimen has been mounted so as to leave space for two more. The series runs in order from the atlas to the twentieth dorso-lumbar, the missing ones belong, therefore, to the vertebral column just in front of the sacrum. [Dorso-lumbars of *E. africanus* = 23–24, of *E. indicus* (= *maximus*) = 22–23.] . . . The *atlas* . . . . which lacks the wing on each side, has a somewhat low spine on the neural arch, whose pedicel on each side is pierced by a foramen through which the vertebral artery was transmitted. . . . The *axis* . . . which likewise may be compared with a specimen belonging to *E. meridionalis* (B. M. 27872, . . .), shows again a slight difference in proportions, and, of the two, has a rather more slender neural arch. While both the atlas and axis are each of them a little larger than the corresponding bones of *E. meridionalis,* they are not so to the extent that might be expected in an animal of such remarkable size in the rest of its skeleton. . . . Of the other vertebrae the most striking point is the unusual angle at which the neural spines are placed, both in respect to the individual vertebra and to the backbone itself. There is, in various species, some variation in the curve along the back that is formed by the tips of the neural spines. Dietrich has illustrated diagrammatically these curves for *E. africanus, E. primigenius,* and *E. maximus.* From lack of sufficient material the curve for *E. antiquus* has been so far unknown, nor does the present skeleton, owing to damage, yield absolutely definite information, but, as far as can be seen, it is not unlike that of *E. maximus,* where the top of the spine of the first dorsal vertebra reaches approximately the same height as the top of the scapula, and from this point the spines gradually rise in height to a maximum in the region of the eleventh or twelfth dorsal vertebrae, and thereafter fall away in height gradually down to that of the sacral vertebrae. The Upnor specimen, however, shows one great difference, not only from *E. maximus,* but apparently from other elephants, in that the neural spines of all the dorso-lumbar vertebrae stand bolt upright at right angles to the longitudinal plane of the vertebra. In other elephants all the dorso-lumbar spines except the most anterior slope backwards at a considerable angle. The condition here is undoubtedly natural, is not due to postmortem changes, and appears to have no parallel. The spines of the vertebrae in this region also show another peculiarity, in that those of the posterior lumbar vertebrae are broad right up to the top (as seen in side view) instead of dwindling down to a point, which is the more usual condition.

In the measurements and comparisons below of the Upnor skeleton assembled by Andrews (pp. 1–18) and by Forster Cooper (pp. 19–25) there is repeatedly pointed out: (1) The resemblance of the parts of the Upnor specimen observed and measured to certain of the referred specimens from Grays Thurrock, from Happisburg, and from other Lower Pleistocene localities; also to similar parts referred by Dietrich to *Elephas* [*Palæoloxodon*] *recki,* from which it appears that we have to do in all these British specimens with a Lower Pleistocene phase of *Hesperoloxodon antiquus*; (2) in comparison by Andrews and Forster Cooper, the resemblances of the scapula, humerus, and other parts are in general observed to be closer to the African elephant (*L. africana*) than to the Indian elephant (*E. indicus* = *maximus*): (Cooper, p. 24) "the Upnor specimen shows, when compared with other forms, a great mixture of specific characters. The femur, for example, 'resembles *E. africanus* more than *E. maximus*' (p. 13), while the astragalus 'on the whole is much like that of *E. maximus* and *E. primigenius,* and differs from the astragalus of *E. africanus*' (p. 15), and so on. The general result of Andrews' detailed investigation is that in some characters the specimen resembles one form and other forms in other characters, with the result that a clear diagnosis is not possible. . . . The absence of any definite standard of comparison as well as the absence of any complete specimen of *E. antiquus* prevents us therefore from estimating the true value of the two outstanding features of this Upnor specimen, namely the curious and apparently unique upright position of the spines of the vertebral column, and the unexpectedly small size of the teeth in relation to the great bulk of the body. Should examination of further material eventually show that this form differs from the type [of *Elephas antiquus*] so far as to warrant the erection of a sub-species, then it is to be hoped that the present specimen will be taken as the holotype, and that the sub-species will be named after Dr. Charles W. Andrews, who did so much to elucidate the early history of the Proboscidea."

The vertebral measurements of *Hesperoloxodon antiquus* somewhat exceed those of *Archidiskodon meridionalis.* The mass of the atlas and axis about equals that of *A. meridionalis,* while the entire vertebral column greatly exceeds that of *E. indicus* (= *maximus*). Forster Cooper's descriptions and figures (*op. cit.,* 1928, pp. 19–25) show that the vertebral column of *H. antiquus* is unique. It differs widely from both *Loxodonta africana* and *Elephas indicus* (=*maximus*). As illustrated in our new comparative figure 1084, it differs still more widely from the backbone of the two mammontines *Parelephas jeffersonii* and *Mammonteus primigenius.* The following are Gaudry's (1893.1, p. 19) measurements of *A. meridionalis* of Durfort:

	Durfort (*meridionalis*), Gaudry	Upnor (*antiquus*), Cooper
Ground to top of head	4150 mm.	
Ground to withers [scapula]	3830	3700 est.
Length from tusks to drop of tail	6800	
Length without tusks	5450	
Humerus	1220	1290
Cubitus	1080	
Femur	1360	
Tibia	820	1020
Third metacarpal	250	
Third metatarsal	170	

COMPARISON OF VERTEBRAL CHARACTERS OF HESPEROLOXODON ANTIQUUS OF UPNOR WITH LOXODONTA AFRICANA, ELEPHAS INDICUS (=MAXIMUS), PARELEPHAS JEFFERSONII, AND MAMMONTEUS PRIMIGENIUS (FIG. 1084)

(Compare pp. 930–931 of the present Memoir on Vertebral Distinctions of *Elephas*, *Loxodonta*, *Mammonteus*, and *Parelephas*)

COMPARISON OF VERTEBRAL COLUMN IN THE LOXODONTINÆ, MAMMONTINÆ, AND ELEPHANTINÆ.—The vertebral columns of these five types of living and extinct proboscideans are carefully redrawn in figure 1084 from original materials; they exhibit very significant resemblances between *Hesperoloxodon* and *Loxodonta* (= Loxodontinæ), also between *Parelephas jeffersonii* and *Mammonteus primigenius* (= Mammontinæ), but the Elephantinæ (*Elephas indicus*) differ widely both from the Loxodontinæ and Mammontinæ in the construction of the vertebral column.

Hesperoloxodon antiquus of Upnor: Cervicals 1–7, dorsals 1–20, lumbars 1–3 est.; all dorso-vertebral spines vertically placed, very much elevated. Orthogonal drawing after photographs and data by C. Forster Cooper.

Loxodonta africana: Cervicals 1–7, dorsals 1–20, lumbars 1–3; vertebral spines oblique, expansive; post-dorsal and lumbar spines elevated. After 'Jumbo' (*Loxodonta africana oxyotis*), from the Setit River, Abyssinia.

Elephas indicus, Asiatic elephant: Cervicals 1–7, dorsals 1–19, lumbars 1–3. Based on the mounted skeleton in the American Museum (Amer. Mus. Dept. Mam. 39082, known as "Samson" when alive) but enlarged to the record size of the Indian elephant.

Mammonteus primigenius, the woolly mammoth: Cervicals 1–7, dorsals 1–19, lumbars 1–4. Drawn after the *Elephas primigenius* of Borna, Germany, as mounted by Felix, 1912, Pl. VIII.

Parelephas jeffersonii, the Jeffersonian mammoth: Cervicals 1–7, dorsals 1–19, lumbars 1–4. Drawn after mounted type skeleton in the American Museum (Amer. Mus. 9950).

Observe in *Parelephas* the marked resemblance to *Mammonteus primigenius* in the extremely oblique and recumbent vertebral spines, the rapid decrease in size as we pass from the posterior dorso-lumbar region, in wide contrast to the Loxodontinæ. Observe also the general resemblance between *Hesperoloxodon* (the straight-tusked elephant of Upnor) and the typical African elephant of Abyssinia, as well as the marked resemblances between the vertebral columns both in the formulæ and the recumbent spines of *Parelephas* and *Mammonteus*. For the vertebral formulæ of the different genera, species, and subspecies of elephants, compare Chapter XV, pp. 930, 931. The formulæ shown above may be summarized as follows:

	CERVICALS	DORSALS	LUMBARS	TOTAL DORSO-LUMBARS	SACRALS	CAUDALS
Hesperoloxodon (straight-tusked elephant of Upnor)	7	20	3 est.	23	Unknown	21
Loxodonta africana, 'Jumbo' (Amer. Mus. Dept. Mam. 3283)	7	20	3	23	4	21
Elephas indicus (Asiatic elephant)	7	19	3	22	4	24–30+
Mammonteus primigenius (mammoth of Borna)	7	18–19	4–5	23–24	4	21
Parelephas jeffersonii (Jeffersonian mammoth)	7	19	4	23	5	12+

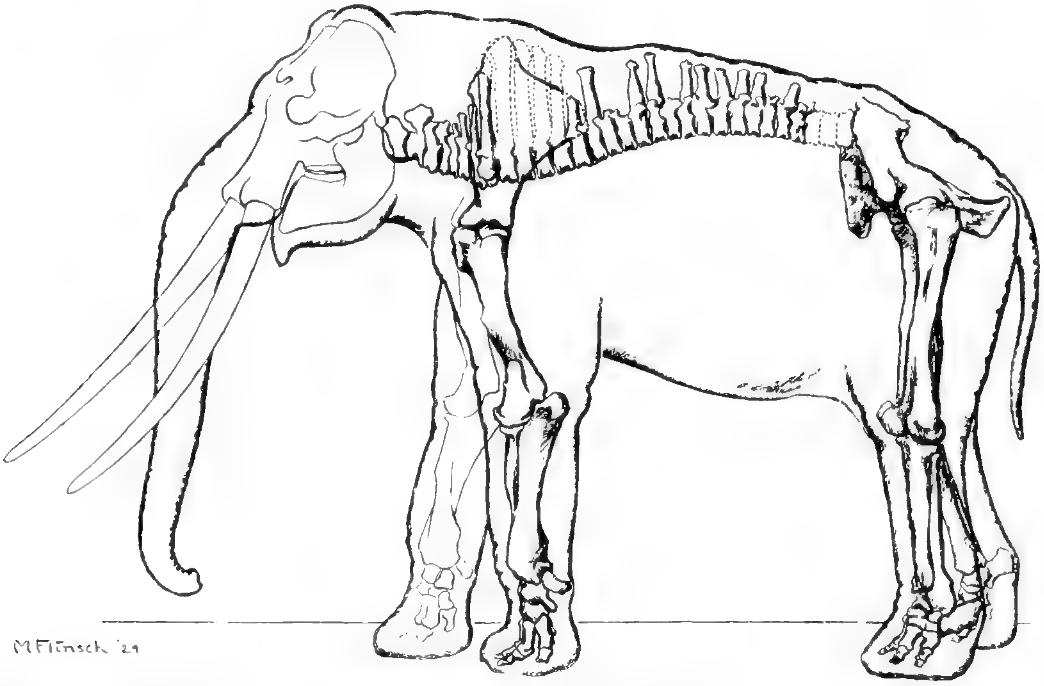


Fig. 1083. Partly restored skeleton and flesh outlines of the Upnor elephant, with modifications in the vertebral column more fully illustrated in figure 1084. After British Museum mount (Fig. 1079). Outline of cranium from the recently found Pignataro Interamna specimen of Italy (Figs. 1096, 1098, 1101, 1103, 1105, 1106). Approximately one forty-eighth natural size.

COADAPTATION OF THE VERTEBRAL COLUMN WITH THE SUPERIOR INCISIVE TUSKS OF THE ELEPHANTS

WITH NOTES BY ROBERT T. HATT, 1931

As shown in figure 1084 there are very striking divergencies in the neural spines of the Elephantidæ. A glance at figures 1084 and 868 shows that in the Mammontinæ (including *Archidiskodon meridionalis* of Durfort, *Parelephas jeffersonii*, and *Mammonteus primigenius*) the spines are relatively low and backwardly inclined, diminishing rapidly in size toward the pelvis, in wide contrast (as shown in Fig. 1084) to the Loxodontinæ, in which the spines are relatively large and less backwardly inclined. In *Loxodonta africana* the posterior dorsals (D^{20}) rise to the same height as the anterior dorsals (D^1); in the remotely related *Hesperoloxodon antiquus* of Upnor the dorsal spines are even larger and absolutely erect, as first observed by Forster Cooper. Between these two extremes (in the Elephantinæ) we observe *Elephas indicus* in which the spines are intermediate in size and elevated in the mid-dorsal region into a decided mid-hump, conspicuous in aged Indian elephants.

It proves that this is a case of *coadaptation of the neural spines with the divergent functions of the superior incisive tusks*: (1)In *Loxodonta* the tusks are constantly used for digging and uprooting purposes; (2) in *Elephas indicus* they are less frequently used; (3) in *Mammonteus* and *Parelephas* they are not used at all for uprooting purposes, because they soon become incurved and actually cross each other in old age; thus the only strain put upon the incisive tusks is the weight of the ivory or dentine which they carry, whereas in the Loxodontines the ivory tusks not only have an enormous weight but are subject to tremendous strains in uprooting large trees.

This interesting functional divergence has been analyzed by Dr. Robert T. Hatt as follows:

> The spinal columns of the elephantoid Proboscidea differ chiefly in their height and in the horizontal or oblique angulation of their neural spines. These spinal columns present three main patterns, which are:
>
> (1) SUBFAM. MAMMONTINÆ.—Spines of the interscapular region long and backwardly inclined. Caudad to this the length of spines decreasing markedly to the middle of the back where and beyond which they are insignificant in size (*Mammonteus*).
>
> (2) SUBFAM. ELEPHANTINÆ.—Spines of the interscapular region long but less inclined than in the first type. Caudad to the interscapular region the spines gradually decrease in length into the sacral region. The spines of the lumbar region are of greater length and strength than those of the lumbar region of the Mammontinæ. (*Elephas indicus.*)
>
> (3) SUBFAM. LOXODONTINÆ.—Spines of the interscapular region nearly or quite vertical. The spines decreasing in length to a minimum height near the middle of the back. Caudad to this the spines again become longer, reaching a secondary summit on the latter third of the dorsal vertebræ (*Loxodonta africana*). The skeleton of the African elephant, "Jumbo," being very badly mounted, the spinal column of this individual is in consequence misleading as to the spinal curvature in the African elephant; this error is corrected in figure 1084.
>
> [*Hesperoloxodon* is evidently nearer to the *Loxodonta* type than to any of the others, but differs in the great vertical development of the mid-dorsal spines.—Editor.]

The following deductions by Dr. Hatt, concerning the observed differences in the spines with relation to muscular strains, are drawn from a consideration of the mechanical differences that accompany such changed proportions.

> (1) The height and massiveness of the spines in the scapular region are determined by the magnitude of the force acting upon these bodies; this is in large part an age and sex difference, for strain increases with increased size of head, tusks, forelimbs, etc., and balanced or diminished strains in the caudad, pelvic, and hindlimb region.
>
> (2) The inclination of these interscapular spines is dependent upon the development of the spines on the caudal third of the dorsal vertebræ. Those animals with low spines in this region presumably have weak *spinalis* muscles. As a result the strain imposed on the interscapular spines by head pull is not counteracted by equal muscular pull from the rear, and the spines are inclined in order to throw the strain near the long axis of the spine rather than perpendicular to this axis. Such conformation occurs in *Archidiskodon, Parelephas,* and *Mammonteus.* It is probable that the woolly mammoths (*Mammonteus primigenius*) were incapable of raising both forefeet from the ground simultaneously, for their skeletons present evidence that the chief extensor muscles of the back were weak.
>
> (3) The modern elephants on the contrary have strong *spinalis* muscles. Strain upon the interscapular spines, as produced by head pull, is counteracted by contraction of the *spinalis* muscles to the rear. These opposing muscular forces are best met by vertical spines intercepting the forces at right angles.

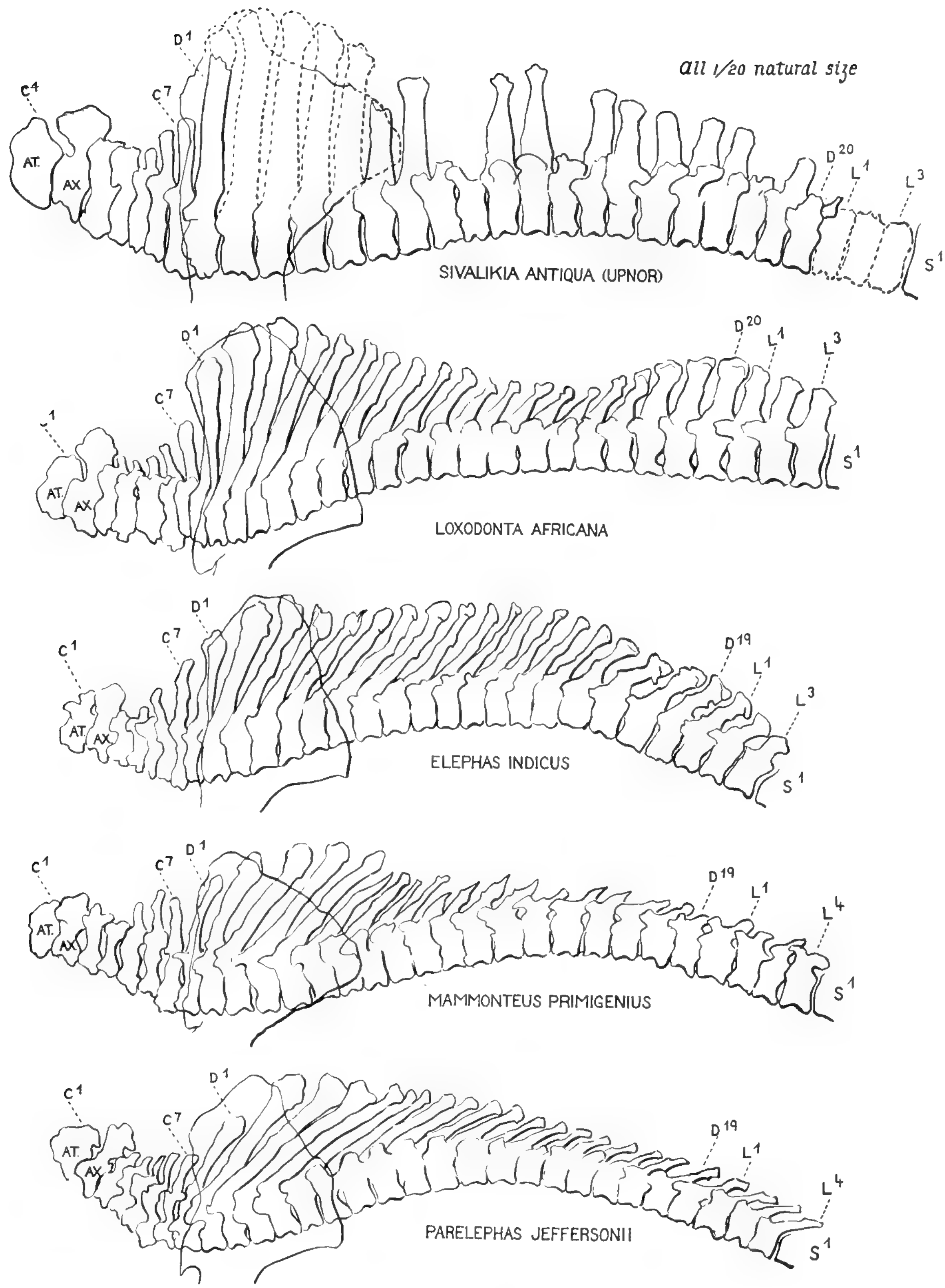


Fig. 1084. Vertebral columns of *Hesperoloxodon antiquus*, *Loxodonta africana*, *Elephas indicus*, *Mammonteus primigenius*, and *Parelephas jeffersonii*, drawn to a uniform one-twentieth scale.

Hesperoloxodon antiquus of Upnor, modified after Forster Cooper, 1928, and from photographs and data subsequently forwarded to the present author.

Loxodonta africana oxyotis ("Jumbo"), after original in the American Museum (Amer. Mus. Dept. Mam. 3283).

Elephas indicus, after original in the American Museum (Amer. Mus. Dept. Mam. 39082).

Mammonteus primigenius, after Felix, 1912, Pl. VIII. Original in the Leipzig Museum.

Parelephas jeffersonii, after original type skeleton in the American Museum (Amer. Mus. 9950).

Observe the very marked differences in the curvatures of the back, indicated by the heights of the dorsal spines, which correspond closely with profile photographs of the living *Loxodonta* and *Elephas* in the cave drawings and with our own restorations of *Hesperoloxodon antiquus* and *Parelephas jeffersonii*.

Comparison of the Upnor and San Isidro Skeletons of Hesperoloxodon antiquus with the African and Indian Elephant Skeletons

	Hesperoloxodon antiquus of Upnor, after Andrews and Cooper	*Hesperoloxodon antiquus platyrhynchus* of San Isidro, after Graells	*Loxodonta africana oxyotis*, full-grown African elephant "Jumbo," after Osborn	*Elephas indicus* (= *maximus*), after Andrews and Cooper
Maximum height:				
Scapula to top of spine (vertical)	1170	1020	925	
Length:				
Humerus to top of articular head	1290	1170	1078	940
Radius	990	980 (ulna)	830	790
Third median metacarpal	246		190	
Femora	not preserved	1440	1246	1140
Left tibia	1020	1070	760	660
Fibula	930		764	
Extreme width across ilia	1830	2350 [1350][1]	1340	
Extreme width between acetabula	945		392	
Total height of forelimb, excluding scapula	2750 = 9 ft. ¼ in.		2230 = 7 ft. 3¾ in.	2090 = 6 ft. 10¼ in.
Total height of hindlimb	2890 = 9 ft. 5¾ in.		2223 = 7 ft. 3½ in.	2050 = 6 ft. 8¾ in.
Height from top of scapula to ground	3700 = 12 ft. 1⅝ in.	[3670e]	3194 = 10 ft. 5¾ in.	2890 = 9 ft. 5¾ in.
Estimated height from summit of ilium to ground	3580 = 11 ft. 9 in.		2753 = 9 ft. ⅜ in.	2750 = 9 ft. ¼ in.
Height from ground to top of spine of 11th dorsal vertebra	3840 = 12 ft. 7¼ in.		2880 = 9 ft. 5⅝ in. (III D. 3120 mm.)	

Hesperoloxodon antiquus nanus Acconci, 1880

Figure 1085

From a Cavern near Monti Pisani, Cucigliana, Tuscany, Italy.

Specific Characters.—Supposedly a dwarfed subspecies living in northern Italy, of unknown geologic age. Type a left second superior molar, estimated 12½ ridge-plates of which the posterior 9½ are preserved; length 52 mm., breadth 46 mm., height 49 mm.

In a full account of the cavern fauna near Monti Pisani, Acconci describes in detail, with figures (1880, pp. 146–150, Tav. iv, figs. 6, 7) a diminutive loxodont, represented by a tooth identified as a third superior molar. He compares it in size with the Maltese species referred to *Elephas melitensis* by Busk, and in dental characters with the *Elephas antiquus* of Falconer. He concludes by naming this species *Elephas* (*Euelephas*) *antiquus* var. *nana*.

Elephas (*Euelephas*) *antiquus* var. *nana* Acconci, 1880. "Sopra una Caverna Fossilifera Scoperta a Cucigliana (Monti Pisani)." Atti Soc. Toscana Sci. Nat., Vol. V, pp. 146–150. Type.—Second superior molar of the left side, l.M^2. Horizon and Locality.—Cavern near Monti Pisani, Cucigliana, Tuscany, Italy. Type Figure.—*Op. cit.*, Tav. iv, figs. 6, 7.

Type Description.—(*Op. cit.*, pp. 147 and 150): "In questi denti (Tav. iv, fig. 6 e 7) sono disgraziatamente rotte le radici: la corona però è ben conservata ed alla sua faccia laterale si vedono dei solchi longitudinali ben marcati, che limitano tanti rilievi, quante sono le lamine che costituiscono la massa totale del dente. . . . La corona del terzo molare . . . consta di undici o tredici lamine (*plates*) di smalto, le quali consumandosi sulla superficie formano delle creste rilevate (*ridges*): ha due radici, una anteriore piccola ed una posteriore molto sviluppata. Comincia a spuntare al disopra della gengiva verso la fine del secondo anno, è completo nel suo massimo esercizio durante il sesto, quindi logorato e mutato alla fine del nono anno. . . . Queste ragioni mi hanno indotto a ritenere i resti di questi Elefanti come appartenenti all' *E. antiquus* e considerare come una varietà di questa stessa specie l'essere di

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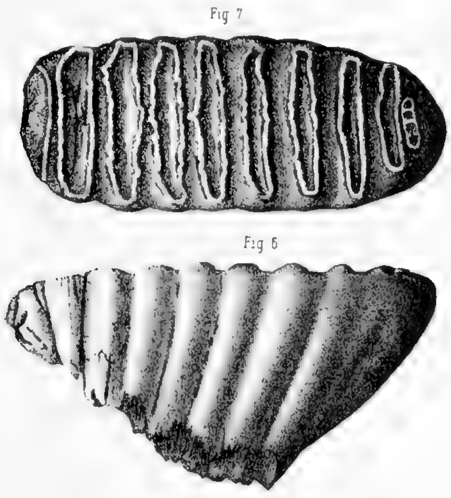
[1] The measurement given by the author (2350 mm. = 7 ft. 8½ in.) is obviously an error, although it appears in both the original text (p. 569) and plate (Lám. xviii) of Graells.

così piccola mole; quindi propongo per essa la denominazione di *Elephas* (*Euelephas*) *antiquus* var. *nana*.



Type of Hesperoloxodon antiquus nanus

Fig. 1085. Type figure of *Elephas* (*Euelephas*) *antiquus* var. *nana* Acconci, 1880, Tav. iv, figs. 6 and 7. Described by the author as "La corona del terzo molare." One-half natural size. This appears to be the posterior portion of a 12½ ridge-plated second superior molar of the left side, l.M^2, with the three anterior ridge-plates worn off.

Larghezza massima della corona....	Mill[1] 52	[Length 2.1 in.
Altezza massima della medesima...	" 49	Height 1.9 "
Diametro massimo della superficie triturante della corona.........	" 46	Width 1.7 "]

The associated fauna includes referred specimens of *Bos primigenius, Canis lupus, Meles taxus, Ursus spelæus.*

Hesperoloxodon antiquus platyrhynchus

Graells, 1897

Figures 1047, 1068, 1069, 1086, Pl. xxiii

(?) Lower or Middle Pleistocene. San Isidro del Campo, near Madrid, Spain.

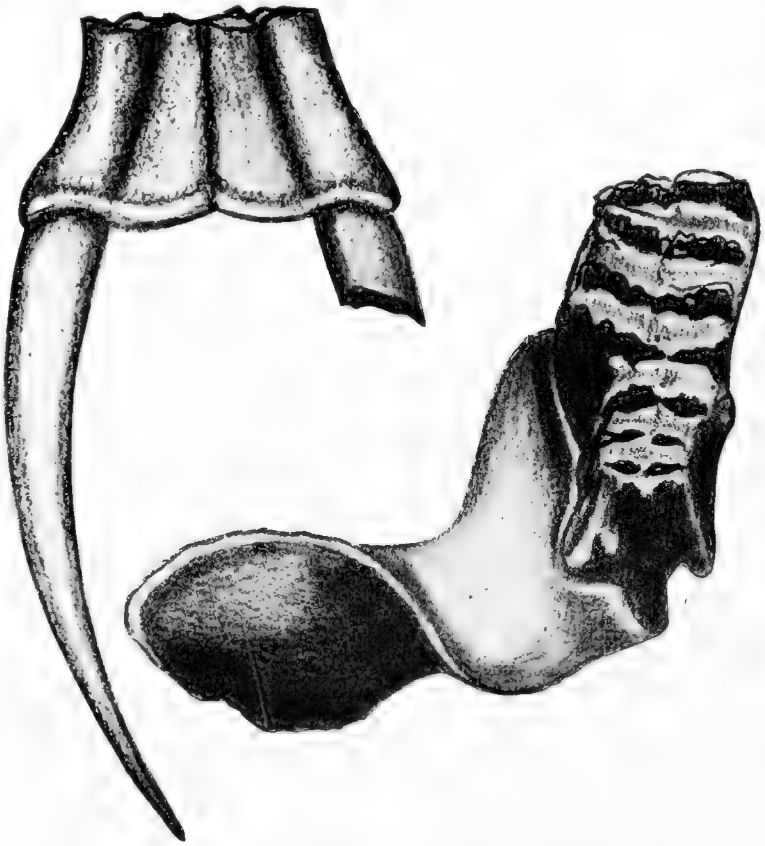
The type of '*Elephas platyrhynchus*' does not deserve specific rank but is possibly a subspecies or geographic variety of the typical *Hesperoloxodon antiquus*, as shown by the comparison of its extremely broad premaxillary rostrum (Fig. 1086) with the rostrums (Figs. 1069, 1105) of *H. antiquus* of Germany and Italy.

Elephas platyrhynchus Graells, 1897. "Fauna Mastodológica Ibérica." Mem. Real. Acad. Cien. Exactas, Fis. Nat., Madrid, Tome XVII, pp. 558–572. Type.—A portion of the superior maxillary with molar *in situ*, right tusk, complete pelvis, humerus, tibia, etc. Horizon and Locality.—Probably Lower or Middle Pleistocene. San Isidro del Campo, near Madrid, Spain. Type Figure.—Graells, *op. cit.*, Lám. xviii—see figure 1086 of the present Memoir.

The following are the measurements obtained from the author's description (*op. cit.*, p. 569):

Length of exposed incisive tusks, tapering, pointed, and somewhat curved inwards towards the extremities...	2350 mm.	7 ft.	8½ in.
Transverse breadth across premaxillaries [as compared with 857 mm. (2 ft. 9¾ in.) in *Hesperoloxodon antiquus italicus* of Pignataro Interamna (Fig. 1098)]....................	[860e]	2	10
Measurements of associated skeleton:			
Maximum height of the scapula...	1020 mm.	3 ft.	4¼ in.
Maximum length of humerus.....	1170	3	10
Maximum length of ulna........	980	3	2½
Maximum length of right and left femora....................	1440	4	8¾
Maximum transverse width across the iliac bones of the pelvis....	2350 [1350][1]	7 [4]	8½ [5⅛]
Estimated height of the body in the flesh (Graells)..............	3900	12	9½
Estimated shoulder height in the flesh (Osborn)..............	3828	12	6¾e

The combined vertical height of the scapula, humerus, and ulna (3170 mm.) is somewhat inferior to that of the combined



Type of Hesperoloxodon antiquus platyrhynchus

Compare *Hesperoloxodon antiquus* of Upnor (Figs. 1079, 1080, 1083, 1081, 1074)

Fig. 1086. Type premaxillary rostrum with tusk, and portion of right superior maxillary with M^2 *in situ*, of *Elephas platyrhynchus* Graells, 1897, Lám. xviii, figs. 9*a* and 10, one-sixteenth and one-fifth natural size respectively.

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[1] See footnote on page 1230.

scapula, humerus, and radius of the Upnor elephant (3450 mm.).

The specific name *platyrhynchus* is fittingly derived from the Greek πλᾰτύς, broad, and ῥύγχος, snout. *Hesperoloxodon platyrhynchus* is exceeded in width by the Pignataro Interamna specimen (Fig. 1098).

This type was probably found in Lower Pleistocene levels of San Isidro overlying older beds of Middle Miocene age, to which the horizon name San Isidro is applied; it is fully described by Graells on pages 558 to 572 and figured in Lám. XVIII. In the greatly broadened and flattened structure of its premaxillaries (see Lám. XVIII, figs. 8*a*. 9*a*) this animal is apparently related to *Hesperoloxodon antiquus*, as shown in comparison with figure 1106. Somewhat against this reference is the strong curvature of the superior tusks; in favor of this reference is the conclusion of Graells (p. 568) that this species from the heights of San Isidro del Campo is either a synonym of *antiquus* or represents an independent species.

Hesperoloxodon antiquus ausonius Major (MS.), 1875, Verri, 1886, Depéret and Mayet, 1923

Figures 1041, 1069, 1072, 1073, 1087

Upper Pliocene of Italy, Villafranchian stage,[1] San Romano, Val d'Arno inférieur, also San Paolo de Villafranca.

Compare Upper Pliocene molars referred by Falconer to *Elephas antiquus*, by Pohlig to *Elephas* (*antiquus*) *Nestii*, by Sabba Stefănescu to *Elephas antiquus ausonius* from Colintina (Ilfov), Rumania, not to be confused with the referred *E. antiquus ausonius* of the Forest Bed, England.

The extremely narrow nineteen to twenty ridge-plated type molar (Fig. 1087) of this Upper Pliocene species is very distinct from the sixteen and a half to seventeen ridge-plated *typical* lower molars of the Lower Pleistocene '*Elephas antiquus*' of Falconer, as fully defined above. It has been erroneously confused with the doubtful Lower Pleistocene subspecies '*Elephas* (*antiquus*) *nestii*' from which it is also quite distinct [=*Parelephas*? *trogontherii nestii*]. Falconer's observations of 1868 and Major's observations of 1875 on the distinctness of this Upper Pliocene stage were confirmed and extended by Depéret and Mayet in 1923, who adopted Major's manuscript name of *ausonius*.

SPECIFIC CHARACTERS (OSBORN, 1928).—An Upper Pliocene stage of Italy, distinguished from *Hesperoloxodon antiquus* by its smaller size and extremely long and narrow third inferior molars with a large number of ridge-plates, namely, $M\,3\,\frac{19}{19-20}$. The comparative measurements of the type M_3 in millimeters are as follows:

	H. ausonius Type M_3 Villafranchian	*H. antiquus* (*typicus*) M^3 Forest Bed
Length of crown	240	254
Width of crown	74	85
Height	160	166–174

Laminar frequency of 5–6 in 100 mm. Enamel coarse and numerously crimped. Loxodont sinus generally strong.

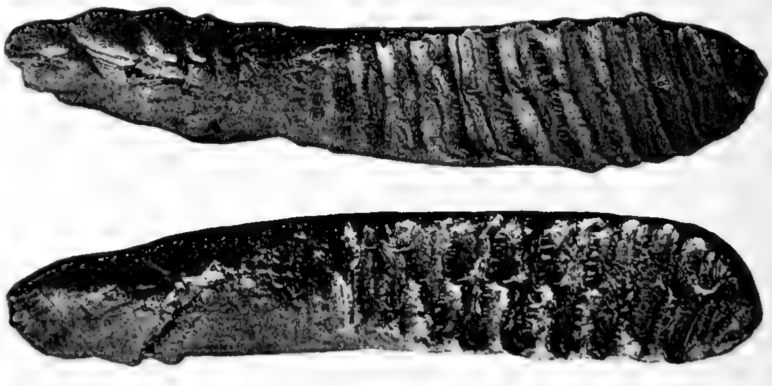
The specific ridge formula ($M\,3\,\frac{19}{19-20}$) agrees with that of a referred specimen of *Palæoloxodon namadicus* (Fig. 1072D) from the Nerbudda, India, namely, l.M 3 $\frac{}{19\frac{1}{2}}$. This ridge formula *exceeds* that typical of the Lower Pleistocene *Hesperoloxodon antiquus* (Fig. 1072A), namely, l.M 3 $\frac{}{15}$. Thus the type of *Hesperoloxodon antiquus ausonius* exhibits an exceptionally high ridge formula ($M\,3\,\frac{19}{19-20}$) for an Upper Pliocene[1] stage.

HISTORY.—In 1875, Forsyth Major (following Falconer, 1868) discovered in the Upper Pliocene[1] of Italy extremely long molar teeth, supposedly related to *E.* [*Hesperoloxodon*] *antiquus* but specifically distinct, to which he gave the manuscript name of *Elephas ausonius*. Similarly in 1891, Pohlig observed teeth (in the Upper Pliocene[1] of Italy) which he erroneously *referred* to his Forest Bed species *Elephas* (*antiquus*) *Nestii*.

This renders it certain that in the Upper Pliocene[1] of Italy there was a relatively small narrow-toothed variety of the larger *Hesperoloxodon antiquus* of the Forest Bed level, clearly distinguished by the name of *Elephas* [=*Hesperoloxodon*] *ausonius*; with the greater ridge formula:

$$\textit{`Elephas ausonius'}\text{: } M\,3\,\frac{19}{19-20}$$

GEOLOGIC LEVEL.—Depéret and Mayet (1923, p. 162) and Falconer (1868, Vol. II, p. 187) also describe *Elephas antiquus* as found in the marine Pliocene of Rignano and in the lacustrine Pliocene of Astésan, at San Paolo de Villafranca: ". . . two last upper and two last lower molars, also from St. Paolo: . . . Each of the upper teeth consists of nineteen plates, the rear part being broken off. . . . Of the lower molars, the right shows twenty plates, and is very narrow for its height."



TYPE OF HESPEROLOXODON ANTIQUUS AUSONIUS

Fig. 1087. Type of *Elephas ausonius* Major. After Depéret and Mayet, 1923, Pl. x, figs. 1 and 2, p. 220: "Fig. 1 et 2.—*Elephas ausonius*, de San Romano (Val d'Arno inférieur), pièces types de l'espèce. M_3 droite et gauche. (Voir p. 166.) Institut géologique de Florence. Photographie du professeur Stefanini." Third lower molars of the right and left side. About one-fourth natural size.

Forsyth Major (1875) first observed in the upper layers of the Val d'Arno inférieur at San Romano teeth related to *E. antiquus* but sufficiently distinct to be separated under the manuscript name of "*Elephas ausonius.*" Depéret and Mayet note that F. Major's manuscript name, cited by Weithofer (1891 [1890], p. 194), quoted by Verri (1886) from labels in different museums, deserves to be revived and retained. Pohlig (1891, pp. 303, 350), while also clearly discerning the differences between the Upper Pliocene form and the

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[1] [See footnote 1 on page 1049 above regarding the possible Lower Pleistocene age of the Villafranchian.—Editor.]

true *E. antiquus*, erroneously refers an Upper Pliocene[1] skull (Fig. 1041 of the present Memoir) to his "special race," namely, *Elephas* (*antiquus*) *Nestii*; this skull is probably a referred *Hesperoloxodon antiquus ausonius*. Consequently the type and referred specimens of this true Upper Pliocene *H. ausonius* appear in the previous literature under various names as follows:

1868	Vol. II, p. 187	*Elephas antiquus* ref., Falconer.
1868	Vol. II, p. 250	*Elephas armeniacus* ref., Falconer.
1875		*Elephas ausonius* F. Major MS. in collection labels.
1886	p. 453	*Elephas ausonius* F. Major, in Verri.
1890	p. 194	*Elephas antiquus* ref., Weithofer.
1891	p. 303	*Elephas* (ant.) *Nestii* ref., Pohlig.
1923	pp. 162–166	*Elephas ausonius* type, Depéret and Mayet.

Elephas ausonius F. Major, MS. in collection labels, 1875; in Verri (1886, Soc. Geol. Boll. [Ital.], V, p. 453); in Depéret and Mayet "Les Éléphants Pliocènes," 1923, p. 162. TYPE.—Third lower molars of the right and left side. HORIZON AND LOCALITY.—San Romano, Upper Pliocene[1] of Italy. TYPE FIGURE.—Not figured by Forsyth Major; Depéret and Mayet chose the same types as those described by Major (Depéret and Mayet, 1923, Pl. x, figs. 1 and 2). Originals in the Geological Institute of Florence.

TYPE DESCRIPTION.—(Depéret and Mayet, 1923, p. 166): "Le Musée de Florence contient, de cette localité, deux belles M_3 du même sujet, qui ont été déterminées par F. Major et doivent être regardées comme les *pièces types de l'espèce*; nous les figurons pl. x, fig. 1 et 2. Leur couronne est remarquablement étroite et allongée. La dent gauche, la mieux conservée, comprend 13 lames en action, plus 7 autres lames intactes à l'état de colonnettes isolées, soit en tout 20 lames, plus les talons. Du côté droit, on voit 13 lames déjà entamées, plus un nombre indéterminé de lames non encore dégagées de l'alvéole. La fréquence laminaire est à peu près de 5, comme dans le crâne de Florence. L'émail est finement et assez régulièrement plissé; il existe de forts sinus loxodontes en arrière dans les lames moyennement usées; ces sinus disparaissent en avant par l'usure. Longueur de la couronne, 240 millimètres, avec une largeur maximum de 74."

CHARACTERS OF HESPEROLOXODON ANTIQUUS AUSONIUS.—According to Depéret and Mayet, the two type inferior molars, selected by F. Major for his manuscript name *Elephas ausonius* and revived by them, exhibit the following ridge formula and size; $M\,3\,\frac{}{20}$; length of crown 240 mm.; width of same 74 mm. Consequently Depéret and Mayet describe and figure the same type lower molars as those named *Elephas ausonius* in manuscript by Forsyth Major.

These type molars are shown in the accompanying figure 1087 after photographs furnished the authors, Depéret and Mayet, by Professor Stefanini. Pohlig (1891, p. 303) erroneously applied the name *E. Nestii* to the rostrum of the cranium described by Nesti as *E. meridionalis*, Crâne B; this piece is shown in our figure 1041, lower row, after Pohlig, 1891, p. 350, fig. 109. It is the same rostrum as that figured by Weithofer, 1890, Taf. II, fig. 2, as *E. antiquus*. Consequently it is now demonstrated clearly that the type of the species *E. ausonius* Major-Depéret-Mayet does not belong to the same race as the type of the subspecies *Elephas* (*antiquus*) *nestii* [=*Parelephas*? *trogontherii nestii*] Pohlig, from the Forest Bed of Norfolk.

RELATION TO E. ANTIQUUS.—Depéret and Mayet (1923, pp. 163–170) give a detailed description of similar Upper Pliocene[1] stages from specimens in the museums of Florence, Rome, Bologna, and Norwich, derived from various Upper Pliocene beds of Villafranchian age, and conclude that the species *E. ausonius* is without doubt a *direct ancestral form or Pliocene mutation* of the Pleistocene species *Elephas antiquus*. In free translation: *Elephas ausonius* is a Pliocene mutation of the typical Quaternary *Elephas antiquus*. (1) Its molars are one-third smaller than those of the typical Lower Pleistocene stage of Grays Thurrock (Essex). (2) The crowns of the molars, especially of M_3, are relatively longer than those of the Quaternary *E. antiquus* and equally narrow. (3) The ridge-crests are less elevated, the height ranges from 75 mm. to 160 mm. (in the type M_3 of San Romano), whereas in *E. antiquus* the ridge-plates range from 175 mm. to 240 mm. (in the tooth from Taubach). (4) The ridge formula does not vary greatly from that of *E. antiquus* but in the type M_3 of San Romano there are twenty ridge-plates, while in general the ridge-plate formula is from fifteen to sixteen. (5) The laminar frequency is from five to six laminæ in 100 mm. (6) In *E. ausonius* the enamel thickness is equal to that of *E. antiquus*; it is more largely and more numerously crimped. (7) The loxodont sinus is generally strong and more striking in *E. ausonius*, but there are notable individual variations. (8) The most constant and most important character is the inferior dimensions of the molars of *E. ausonius*, the length of M 3 not exceeding 220 mm. in the superior teeth and 240 mm. in the inferior teeth; whereas Pohlig assigns to *E. antiquus* of the Middle [Upper] Pleistocene of Germany 380 mm. for M^3 and 480 mm. for M_3.

Osborn, 1929: Depéret's conclusion that '*Elephas*' *ausonius* is *directly ancestral* to '*E.*' *antiquus* is contrary to our present knowledge of the ridge-plate formulæ in these two species, namely:

Typical Lower Pleistocene *Hesperoloxodon antiquus*: $M\,3\,\frac{16\frac{1}{2}-17}{16\frac{1}{2}-17}$

Typical Upper Pliocene[1] *Hesperoloxodon ausonius*: $M\,3\,\frac{19}{19-20}$.

Despite its smaller size and narrower molars, *Hesperoloxodon ausonius* is more progressive in the addition of three posterior ridge-plates. While very primitive in its long, narrow proportions, it has a higher ridge-plate formula than either the Mediterranean dwarfed species or the North African species [of *Palæoloxodon*], as shown in the comparative ridge-plate formulæ below; it exceeds the typical *Palæoloxodon namadicus* ($M\,3\,\frac{15}{16}$) and equals the progressive *P. namadicus* illustrated in figure 1073; the typical *Hesperoloxodon ausonius* exceeds that of *H. antiquus* ($M\,3\,\frac{16\frac{1}{2}-17}{16\frac{1}{2}-17}$).

Hesperoloxodon antiquus germanicus S. Stefănescu, 1924

Figures 1068, 1088–1091, 1114–1116, 1152, Pl. XXIII

Type level: Geologic horizon of Weimar and Taubach, Germany. Type from Tanganu (Ilfov), Rumania. Upper Pleistocene. Now amplified by crania discovered at Steinheim (see p. 1253 below).

Osborn, 1930: For the progressive Upper Pleistocene stage of '*Elephas antiquus*' we may adopt the subspecific name *germanicus* Stefănescu, 1924, and amplify the characters of this stage from

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[1] [See footnote 1 on p. 1049 above, regarding the possible Lower Pleistocene age of the Villafranchian.—Editor.]

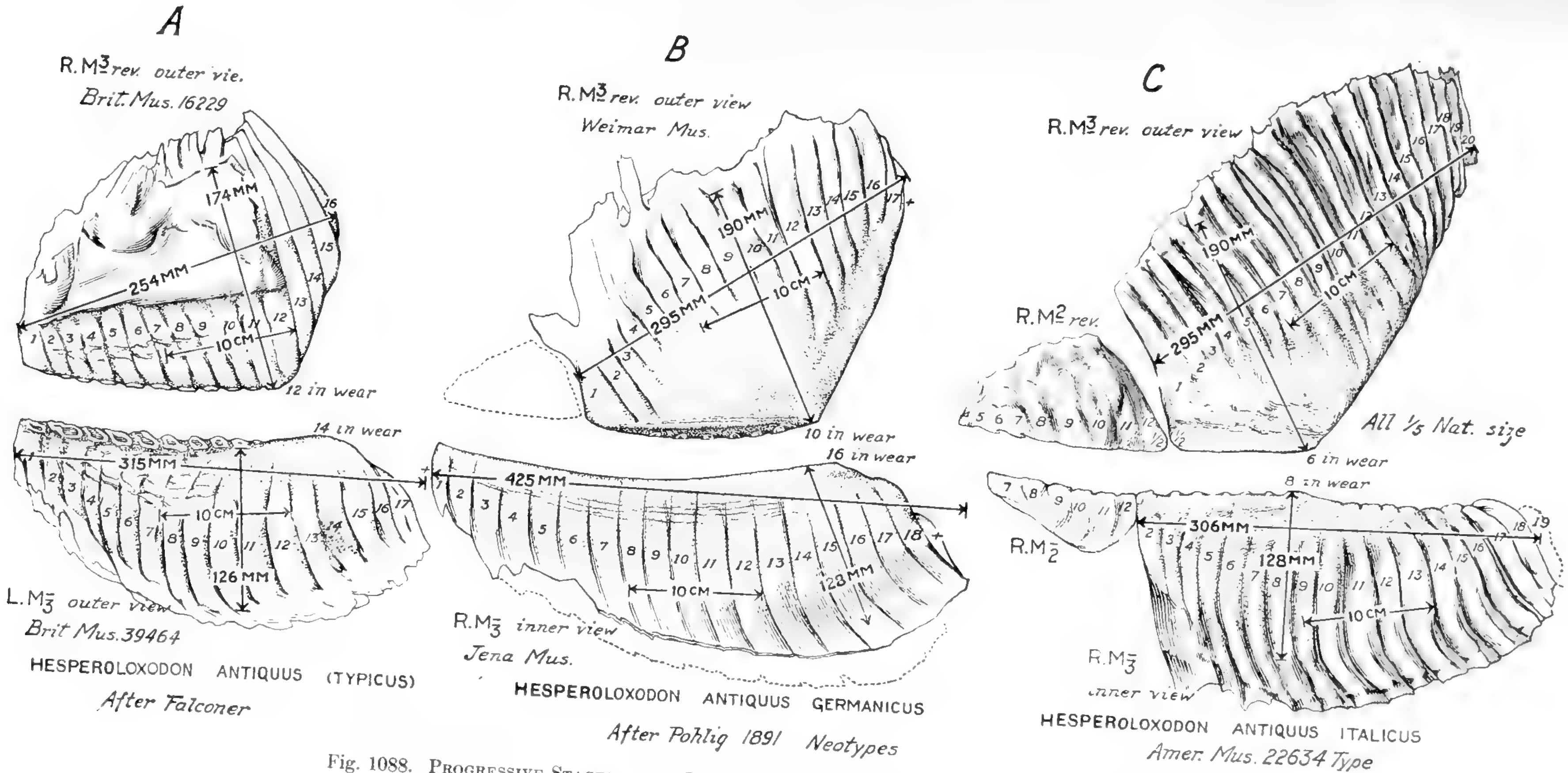


Fig. 1088. Progressive Stages in the Evolution of Hesperoloxodon antiquus Grinding Teeth

All figures to the same scale, one-fifth natural size

Referred

Hesperoloxodon antiquus (typicus) third superior and inferior molars, r.M³, l.M₃.

R.M³, from the Forest Bed, Ostend (Norfolk), England. Brit. Mus. 16229, Green Collection. Length 10 in. = 254 mm., breadth 3.4 in. = 85 mm., height 6.5 in. = 166 mm. [Tallest ridge-plate 174 mm., 5½ ridge-plates in 10 cm., total ridge-plates 16]. After Falconer, 1846 [1847, Pl. xiv.a, fig. 5]. Compare figure 1077, which shows another anterior plate, i.e., 16½ ridge-plates.

L.M₃, from Saffron Walden (Essex), England. Brit. Mus. 39464. Bowerbank Collection. Length 12.3 in. = 315 mm., breadth 3 in. = 77 mm., height 5 in. = 126 mm. [Tallest ridge-plate 126 mm., 5⅛ ridge-plates in 10 cm., total ridge-plates 17.] After Falconer, 1846 [1847, Pl. xiv.a, fig. 11*a*].

Neotypes

Hesperoloxodon antiquus germanicus. Upper Pleistocene, *3d Interglacial* stage of Taubach and Weimar.

R.M³, external view (reversed), with 17+ ridge-plates, of which 10 are worn. Length 295 mm. (max. 315 mm.), breadth 80 mm., height 210 mm. (max. 235 mm.), [height of tallest ridge-plate 190 mm.], 6 ridge-plates (i.e., 7–12) in 10 cm. After Pohlig, 1891, Taf. iii bis, fig. 7*a*. Original in Weimar Museum. Molar from Taubach.

R.M₃, external view, diagrammatic drawing, with 18½ ridge-plates, 20+ est. Total length of crown (actual 425 mm., estimated 480 mm.), breadth 85 mm., height 170 mm. [Height of tallest ridge-plate 128–130 mm., 4½ ridge-plates in 10 cm.] After Pohlig, 1888, Taf. vi, fig. 1¹. Original in Jena Museum. From the great Taubach skeleton.

Type

Hesperoloxodon antiquus italicus, progressive stage from southern Italy. Right second and third superior and inferior molars, original diagrammatic drawing after Amer. Mus. 22634, type.

R.M³ with 20 ridge-plates, height of tallest ridge-plate 190 mm., 6 ridge-plates (i.e., 7–12) in 10 cm., 8 ridge-plates in greatly worn r.M². Length 295 mm., breadth 82 mm.

R.M₃ with 18+ ridge-plates, height of tallest ridge-plate 128 mm., 4⅓ (i.e., 9–13) ridge-plates in 10 cm. In front is the greatly worn r.M₂, with 6 ridge-plates. Total ridge-plates in use above (M², M³) 12½; total ridge-plates in use below (M₂, M₃) 13.

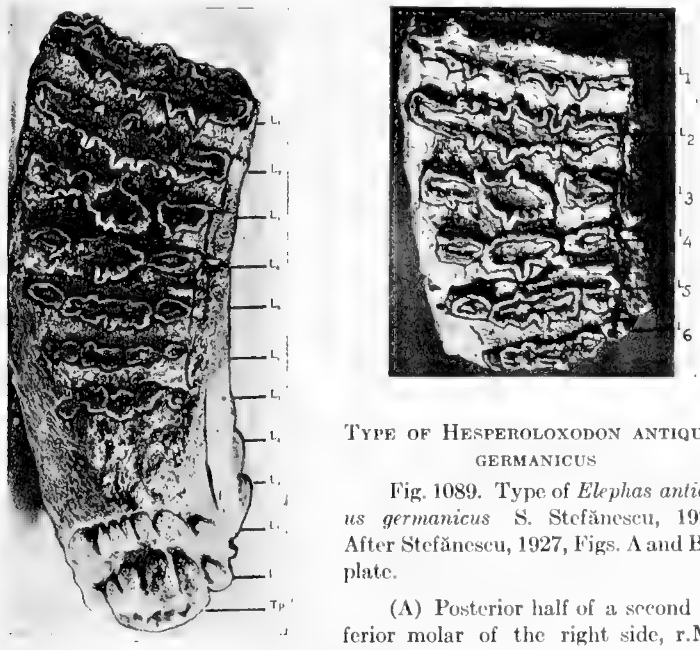
These molars are placed in their natural position as found in the jaw and skull of the type of *Hesperoloxodon antiquus italicus* of Pignataro Interamna, Italy.

Pohlig's monographic descriptions of Taubach grinding teeth, selecting the most characteristic specimens he has described and figured (Fig. 1088) as *neotypes* of *Elephas* [=*Hesperoloxodon*] *antiquus germanicus.*

In brief, Stefănescu designated as '*Elephas antiquus germanicus*' the Upper Pleistocene mutation of Weimar and Taubach. He designated Weimar and Taubach (Allemagne) as corresponding with the geological horizon of the type. The type itself, however, comes from Tanganu (Ilfov), Rumania (Fig. 1089). In the same notice Stefănescu characterized this subspecies as follows:

Elephas antiquus germanicus S. Stefănescu, 1924. "Sur la présence de l'*Elephas planifrons* et de trois mutations de l'*Elephas antiquus* dans les couches géologiques de Roumanie." Compt. Rend. Acad. Sci., Paris, Tome 179, p. 1418, December 15, 1924. Type.—Fractured crown of a second inferior molar of the right side, r.M_2, in the Laboratory of Geology, University of Bucharest. Horizon and Locality.—Type from Tanganu (Ilfov), Rumania. Upper Pleistocene horizon of Weimar and Taubach, Germany. Type Figure.—S. Stefănescu, 1927.

Type Description.—(Sabba Stefănescu, 1924, p. 1418, also 1927): The brief description of the subspecies *germanicus* is quoted with the context under *Archidiskodon planifrons rumanus* in Chapter XVI, pp. 968, 969; it is also fully embodied in the following sentence: "Je n'insiste pas pour le moment sur les caractères de cette mutation qui, à mon avis, est la plus rapprochée de l'origine mastodontide de l'espèce *antiquus.* J'ajoute seulement que la mutation *ausonius* de l'Italie lui succède et que la mutation de Weimar et Taubach (Allemagne), que je désigne sous le nom *germanicus,* est la plus récente."



Type of Hesperoloxodon antiquus germanicus

Fig. 1089. Type of *Elephas antiquus germanicus* S. Stefănescu, 1924. After Stefănescu, 1927, Figs. A and B of plate.

(A) Posterior half of a second inferior molar of the right side, r.M_2, exposing 11 posterior ridge-plates (L. 1-11); 7-8 anterior ridge-plates wanting.

(B) Six intermediate ridge-plates of the same inferior molar, r.M_2: "Face trituratrice de la couronne de M^2 [M_2] d'*Elephas antiquus germanicus* (A) et de ses six lames antérieures (L_1-L_6) détachées (B): talon postérieur (Tp), deux lames (L_{11}-L_{10}) depouillées de cément, deux lames (L_9-L_8) enveloppées de cément, sept lames (L_7-L_1) entamées par l'érosion."

Specific Characters.—Comparing this type specimen with third superior and other molars of '*Elephas antiquus*' of Taubach and Weimar figured by Pohlig (1888–1891, Taf. III bis, fig. 7a (explanation of plate, p. 272), and Taf. VI, fig. 1^1—Fig. 1088) we record the following dimensions, after Pohlig and Osborn, of the *neotypes* of *germanicus.*

	Length	Breadth	Height	Ridge-plates
Right M^3	295–315	80	190–235	17+–18½
Right M_3	375–425	85	128–170	18+

Explanation of Figure 1088.—As shown in the partly diagrammatic figure: (1) The progressive *height* of the upper ridge-plates (174–190 mm.) is measured on the *enameled* portions only and does not include the roots lacking enamel; (2) the progressive *length* of the superior molars (254–295, 315 mm. max.) is measured directly across the ridge-plates, as indicated by the oblique arrow; (3) the progressive inferior molars (315–425 mm.) are measured horizontally directly across the ridge-plates; (4) the height of the lower ridge-plates (126–128 mm.) represents the enameled portion of the tallest ridge-plate.

Neotype Characters of Hesperoloxodon ant. germanicus (Pohlig, 1888–1891, pp. 183–185, 298).—In Pohlig's great Memoir he described a number of third superior and inferior grinding teeth from Taubach and Weimar, of which two especially typical examples from Taubach, as shown in figure 1088, are selected as neotypes. (1) Of the giant specimens from Taubach ("Theile des grossen Taubacher Skelettes") are figured and described the superior and inferior molars of one individual (Taf. VI, figs. 1–6); the inferior molar (left), with 18+ ridge-plates, has a total length of 375 mm., the inferior molar (right) has an actual count of 18+ ridge-plates, total length 425 mm., estimated 20+ ridge-plates, total estimated length 480 mm. (or nearly 20 inches), breadth 85 mm., height 170 mm. (see Taf. VI, figs. 1, 1^1. (2) Of the same Taubach skeleton are gigantic maxillary grinders in the Jena Museum (Pohlig, *op. cit.*, Taf. VI, figs. 2, 2a), namely, an r.M^3, with 18½ ridge-plates (length 340 mm., breadth 98 mm., height 240 mm.), and an l.M^3, with 17+ ridge-plates (length 320 mm., greatest breadth 98 mm., according to Pohlig, probably due to pressure). (3) Also from Taubach, in the Weimar Museum, an r.M^3, with 17+ ridge-plates (Pohlig, *op. cit.*, Taf. III bis, fig. 7*a*); length 295 mm., (max. 315 mm.), breadth 80 mm., height 210 mm. (4) Another highly typical example of gigantic length is an l.M_3 from Weimar, in the Halle Museum (Pohlig, *op. cit.*, Taf. VI, figs. 11, 11a), with ?16+ ridge-plates in 330 mm.; length 410 mm., breadth 90 mm., height 180 mm.

Erroneous Reference.—In 1924 the veteran palæontologist of Hungary, Dr. Sabba Stefănescu, also described '*Elephas antiquus rumanus*,' a mutation from the Pliocene of Tulucesti, as an ancestral mutation of '*Elephas antiquus*'; this specimen is referred by Osborn (p. 968) to *Archidiskodon planifrons rumanus* and is not regarded as ancestral to '*E. antiquus.*' Stefănescu adds that all three mutations are found in Rumania, namely, *rumanus,* i.e., *Archidiskodon planifrons rumanus,* from Tulucesti (Covurlui), *ausonius,* i.e., *Hesperoloxodon antiquus ausonius,* from Colintina (Ilfov), and *germanicus,* i.e., *H. antiquus germanicus,* from Tanganu (Ilfov).

TUSK OF HESPEROLOXODON ANTIQUUS GERMANICUS IN FIELD MUSEUM OF NATURAL HISTORY, CHICAGO

[A decade ago Dr. Henry Field acquired by purchase for Field Museum of Natural History an *'Elephas antiquus'* tusk [= *Hesperoloxodon antiquus germanicus*], found at Steinheim on the Murr, Germany, which at that time was supposed to be the largest of the *antiquus* species in existence. While this tusk measures 2925 mm. or 9 ft. 7⅛ in. in length, it is slightly smaller in size than a male tusk from Tonna, Germany, preserved in the Gotha Museum, which, according to Dr. Hans Pohlig (1888, p. 49, Taf. 1—Fig. 1090 of the present Memoir), measures 2950 mm. in length or 9 ft. 8⅛ in. Furthermore, Dr. Fritz Berckhemer mentions (1930.1, Abb. 4) an isolated tusk in the Stuttgart Museum of even larger proportions, namely, 3390 mm. or 11 ft.

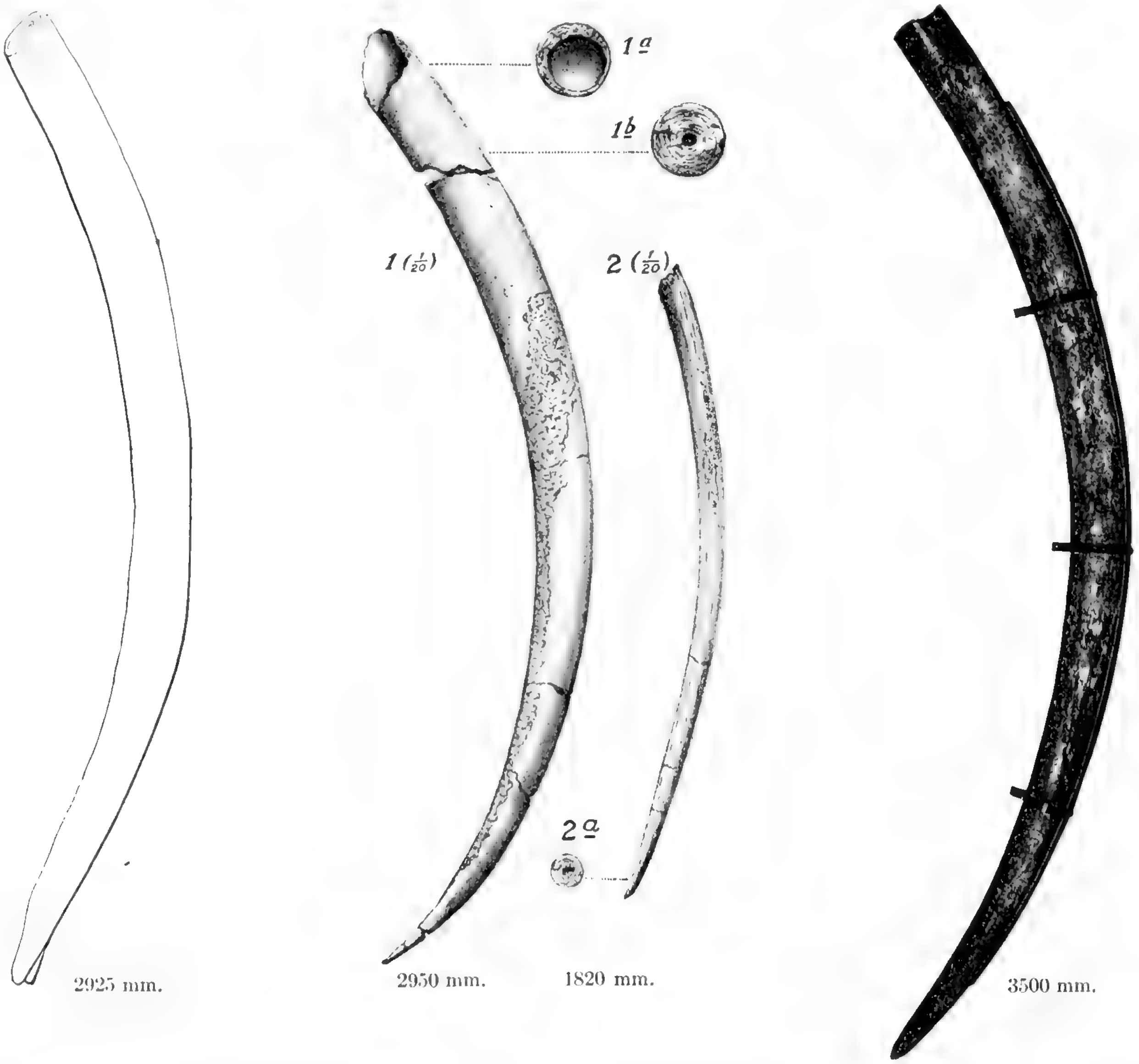


Fig. 1090. Male and Female Tusks of Hesperoloxodon antiquus germanicus

All figures one-twentieth natural size. Compare figure 1106, *Hesperoloxodon antiquus italicus*, one twenty-fourth natural size

(Left) Right tusk (Field Mus. Nat. Hist. 201616) excavated at Steinheim on the Murr, Germany. Length on inner curve 2770 mm. or 9 ft. 1 in., on outer curve 2925 mm. or 9 ft. 7⅛ in. Diagrammatic sketch furnished through the courtesy of Dr. Henry Field of Field Museum of Natural History, Chicago.

(Center) Male and female tusks unearthed at Tonna, Germany, preserved in the Museum of Gotha. After Pohlig, 1888, Taf. I, figs. 1*a*, 1*b*, 2, 2*a*. Compare figure 1063 (*Loxodonta africana*). The male tusk (Taf. I, fig. 1) measures 2950 mm. or 9 ft. 8⅛ in.; the female tusk (Fig. 2) 1820 mm. or 5 ft. 11½ in.

(Right) Right male tusk (Stuttgart Mus. 16274) found in 1929 at Steinheim on the Murr, Germany, measuring 3500 mm. or 11 ft. 5¾ in. Photograph kindly sent by Dr. Fritz Berckhemer.

Doctor Berckhemer writes (letter, May 15, 1937) that the largest tusk of *'Elephas antiquus'* in the Stuttgart Museum collections measures about 3750 mm. or 12 ft. 3⅝ in.; the longest tusk recorded by Pohlig (*op. cit.*, p. 51), excavated from the "schottern" (rubble) of the ancient river Arno at the Porta S. Lorenzo, is in the University of Rome and measures nearly 3900 mm. or 12 ft. 9½ in. [= *Hesperoloxodon antiquus italicus* of Rome—see Fig. 1068 above]. The male tusks of *Hesperoloxodon antiquus italicus* (Fig. 1106) measure 3070e mm. or 10 ft. ⅞ in., within the alveolus 840–845 mm., free length beyond alveolus 2230–2270 mm., a total of about 10 ft.

5¾ in., and in a letter of May 15, 1937, he states that the largest tusk in the collection found at Steinheim measures about 3750 mm. or 12 ft. 3⅝ in.

Doctor Field very generously offered Professor Osborn the privilege of first description in the present Memoir of the Field Museum specimen, an opportunity of which he intended to avail himself, but, as in other instances, his regrettable death prevented the consummation of his plan. The following description has been prepared with the kind assistance of Doctor Field, supplemented by the diagrammatic sketch of the tusk (Fig. 1091).—Editor.]

Right Tusk of Hesperoloxodon antiquus germanicus in the Collections of Field Museum of Natural History, Chicago

F.M.N.H. specimen No. 201616. Right tusk excavated at Steinheim on the Murr, Württemberg, by the late Professor E. Fraas, Stuttgart, from interglacial river-sands associated with *Rhinoceros merckii* and *Bison priscus*. This specimen was purchased by Dr. Henry Field, leader of the Marshall Field Archæological Expedition to Western Europe (1927–1928), from Dr. F. Krantz, Herwarthstrasse 36, Bonn, Germany, who very kindly supplied the above information.

The length of the tusk on the inner curve is 2770 mm. or 9 ft. 1 in., on the outer curve 2925 mm. or 9 ft. 7⅛ in., along the projection of the base 2850 mm. or 9 ft. 4¼ in., and the maximum circumference is 520 mm. or 1 ft. 8½ in. The curvature of the tusk is clearly shown in the accompanying sketch, which is reproduced herewith one-twentieth natural size; "the dotted lines indicate the probable terminal extension and the depth of the pulp cavity." The alveolar portion cannot be determined. The ivory is in fair condition, although the tusk was broken into four sections.

The tusk has been repaired by Mr. L. L. Pray (who also made the diagrammatic sketch, reversed in this figure) and is now on exhibition in the Hall of the Stone Age of the Old World (Hall C) in Field Museum of Natural History.

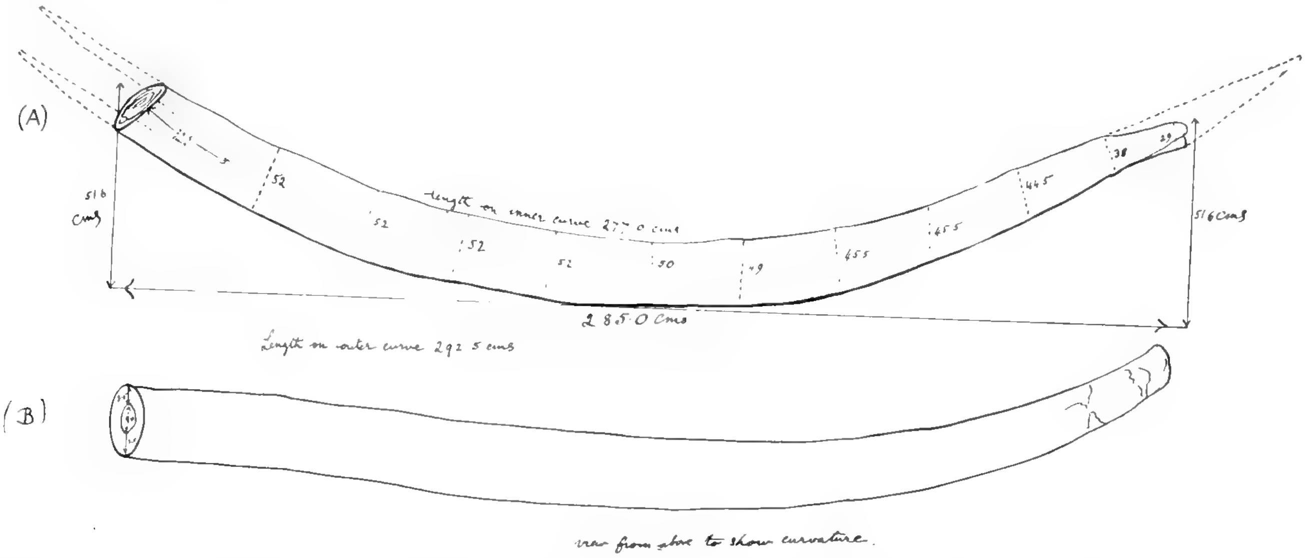
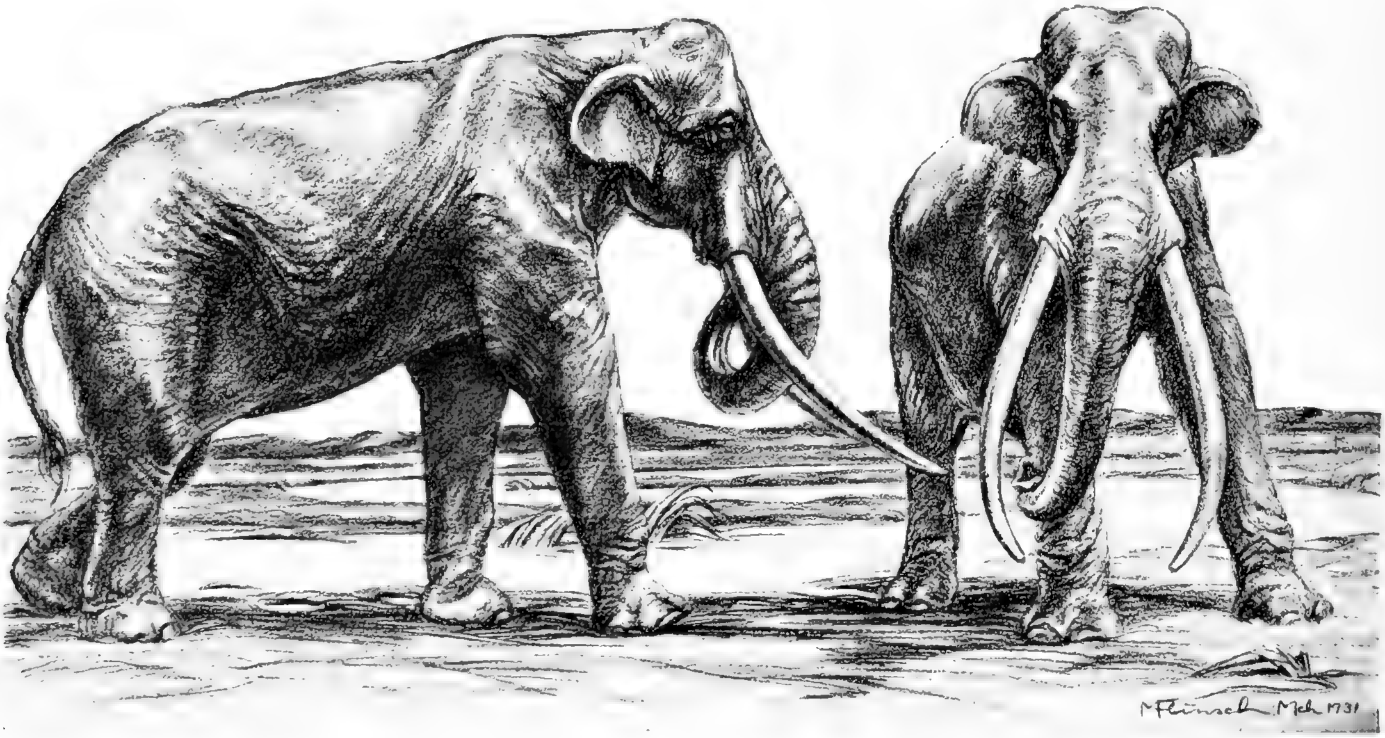


Fig. 1091. Lateral and vertical views of right tusk of *Elephas antiquus* [=*Hesperoloxodon antiquus germanicus*] exacavated at Steinheim on the Murr, Württemberg, by the late Professor E. Fraas, Stuttgart, from interglacial river sands, associated with *Rhinoceros merckii* and *Bison priscus*. One-twentieth natural size. Compare figure 1090 (left). Sketch by Mr. L. L. Pray, reproduced through the courtesy of Dr. Henry Field.

HESPEROLOXODON ANTIQUUS ITALICUS OF SOUTHERN ITALY AND HESPEROLOXODON ANTIQUUS GERMANICUS OF NORTH CENTRAL GERMANY

A flood of light on the cranial structure of the 'ancient' or 'straight-tusked' elephant of Europe has resulted from the discovery in 1911–1912 at Pignataro Interamna, near Cassino, Italy, of the skull and jaws herein described as *Palæoloxodon* [=*Hesperoloxodon*] *antiquus italicus*, a subspecies of the classic '*Elephas antiquus*' of Falconer.

During the years 1926 and 1928 excavation in the region of Steinheim a.d. Murr, Germany, yielded to the Stuttgart Museum one exceptionally perfect cranium and another less perfect cranium which were finally restored and reconstructed by Dr. Fritz Berckhemer in 1929–1930, and herein referred to *Hesperoloxodon antiquus germanicus* of Stefănescu and Pohlig.

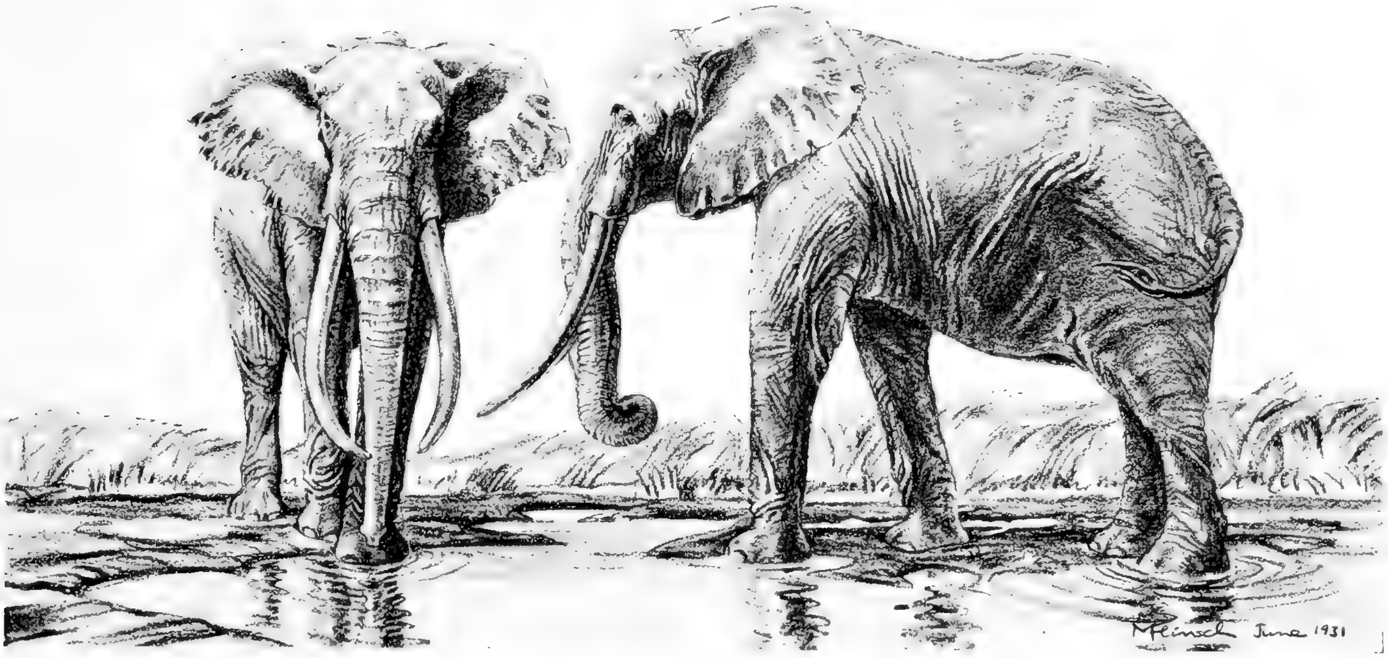


RESTORATION OF HESPEROLOXODON ANTIQUUS ITALICUS

Adult but not full grown. Shoulder height (fully adult) estimated at 13 ft. 6 in. (cf. p. 1250 below). One-fiftieth natural size.

Fig. 1092. This restoration of *Palæoloxodon* [=*Hesperoloxodon*] *antiquus italicus* is based entirely on the type cranium (Amer. Mus. 22634) combined with the skeletal characters of the Upnor 'straight-tusked' elephant *Elephas* [*Hesperoloxodon*] *antiquus*. Compare figures 1079, 1080, 1096, 1098, 1105, 1099, 1100, and 1083 of the present Memoir, with accompanying skeletal measurements and comparisons (pp. 1245–1252). The relatively small ears are drawn from outlines by Palæolithic artists of North Africa and of Spain represented in figure 1047. Both in frontal and lateral aspects this 'straight-tusked' elephant is widely different from the recent African elephant. After crayon drawings by Margret Flinsch, 1931.

Thus within a period of twenty-years (1911–1931) there came a most welcome mass of new cranial knowledge with a very important bearing on the evolutionary history and relationships of Falconer's species '*Elephas antiquus*.' As shown in the preceding pages of this chapter, the 'ancient' or 'straight-tusked' elephant has previously been known by isolated portions of the cranium, jaws, grinding teeth, and tusks, which can now be considered in their mutual mechanical relations, especially in the Italian specimen.



Loxodonta africana albertensis, after drawing by Margret Flinsch, under direction of author. One-fiftieth natural size

Fig. 1093. This combination drawing of a Central African elephant is based upon the bull elephant in the Carl E. Akeley group (Amer. Mus. Dept. Mam. 54085—see Fig. 1052 above) collected in 1909 by Mr. Akeley in the Budongo Forest, east of Lake Albert, Unyoro, Northern Uganda, also upon the Sudanese elephant "Khartum" (*Loxodonta africana oxyotis*—Fig. 1053), formerly living in the New York Zoological Park, and upon a photograph by Marius Maxwell showing an elephant drinking at the river border.

The tusks (measuring 8 ft. 5½ in. and 8 ft. 9½ in. respectively and weighing 112 and 115 lbs. each) of a bull shot by Mrs. Akeley on the slopes of Mt. Kenya (*Loxodonta africana peeli*—Fig. 1059) furnished the basis for those in the present restoration. The longest tusks of the African elephant on record are the lyre-shaped pair in the Heads and Horns Collection of the New York Zoological Park (*L. a. oxyotis*—Fig. 1062), which measure 11 ft. 5½ in., circumference 18½ in. (right), 18⅛ in. (left), with a combined weight of 293 lbs. The heaviest pair (although not the longest) recorded may be seen in our figure 1065, with a combined weight of 461 lbs. The tusks of *L. a. oxyotis* (Fig. 1056) were restored after these two record pairs.

The large ears are drawn in extended position for contrast with the relatively small, low-set ears of *Hesperoloxodon antiquus italicus* (Fig. 1092).

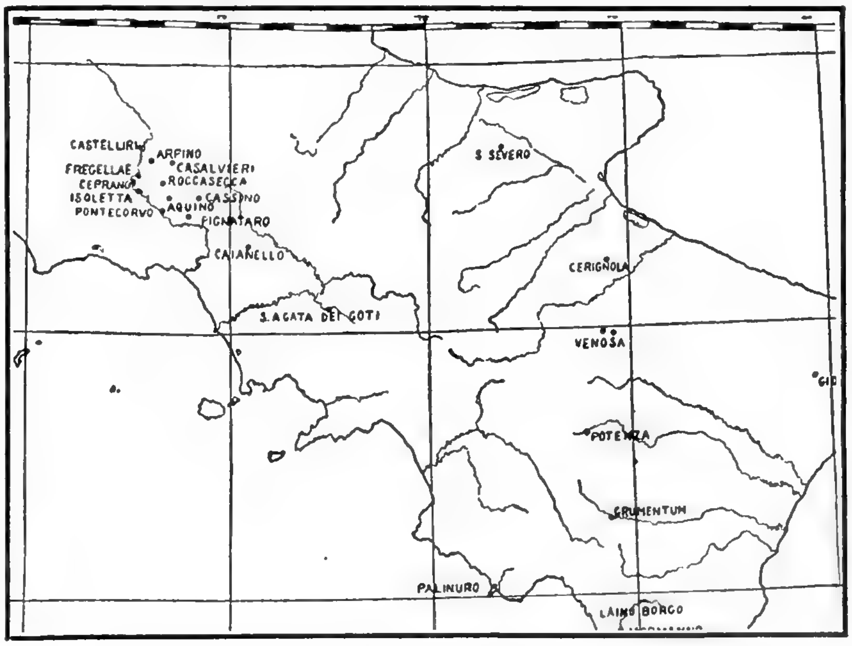
The height at the shoulder in the flesh, namely, 11 ft. 6½ in. or 3520 mm., is after Ward's skeletal record (1928) of 10 ft. 9½ in. or 3290 mm. (cf. caption to Fig. 912, Chap. XVI, above).

HESPEROLOXODON ANTIQUUS ITALICUS OF SOUTHERN ITALY

Twelve localities have been recorded in which discoveries by Italian palæontologists of more or less perfect remains have been made in this region since the first note by Oronzio Costa in June, 1864.

In July, 1926, the cranium and jaws of the 'Pignataro Interamna' elephant were discovered and exposed by a farmer, Saverio Tiseo, while excavating for building purposes, in the extraordinarily perfect condition shown in figure 1096 and most fortunately reported to Professor Giuseppe De Lorenzo, Director of the Institute of Geology of the University of Naples and a member of the R. Accademia Nazionale dei Lincei. Professor De Lorenzo promptly made a preliminary communication (1926) on this most important discovery, and in the following year (1927) published, with the coöperation of Professor Geremia D'Erasmo, also of the University of Naples, a superb memoir entitled "L'Elephas antiquus nell'Italia Meridionale"; this memoir (pp. 1–35) affords a valuable review of the discoveries previously made in the valley of the river Liri (see Fig. 1094) in the following localities:

Castelliri
Arpino
Fregellae
Ceprano
Casalvieri
Roccasecca
Cassino (grotto)
Aquino
Isoletta
Pontecorvo
Pignataro Interamna
Caianello



Upper Pleistocene Horizon of Hesperoloxodon antiquus italicus

Compare Osborn, 1931.846, p. 4, fig. 3, also figure 1097 of the present Memoir.

Fig. 1094. Valley of the Liri River displaying the principal exposures along the eastern and western banks and slopes of the bordering hills, varying from 60 to 70 meters above the present sea level, of a thickness of about 50 meters, where the remains of *Hesperoloxodon antiquus italicus*, of *Hippopotamus*, of *Cervus*, and of other Pleistocene animals have been found. After De Lorenzo and D'Erasmo, 1927, p. 7, fig. 1. Upper portion only. Scale 1:3,000,000.

Geologic Age.—According to recent estimates of Pleistocene time, a 500,000-year interval elapsed between the typical Lower

Pleistocene *'Elephas antiquus'* Falconer and the new subspecies herein described, which is even somewhat more progressive than the *'Elephas germanicus'* Pohlig of Taubach-Weimar. The more or less fragmentary mammalian remains found in proximity to the *type* include the following (see Fig. 1095):

(1) *Cervus elaphus* Linn.: (a) Three antlers from the left side, (b) two antlers from the right side, and (c) right astragalus. Stag.

(2) *Bos primigenius* Boj.: (a) Portion of left M_1 and (b) fragment of mandible. Primitive ox.

(3) *Palæoloxodon* [*Hesperoloxodon*] *antiquus italicus*: (a) Fragment of r.M_2, (b) symphysis of mandible, (c) a nearly complete female tusk, (d) right scapula (probably belonging to the *type*), and (e) central portion of a right humerus. Ancient elephant.

(4) *Hippopotamus amphibius* Linn. (Pleist. = *H. major* Cuvier): (a) Complete mandible, (b) cervical 5, (c) left metatarsal IV, and (d) left femur (juvenile). African hippopotamus.

(5) *Rhinoceros merckii* Kaup: (a) Right radius and (b) cervical 7. Merck's rhinoceros.

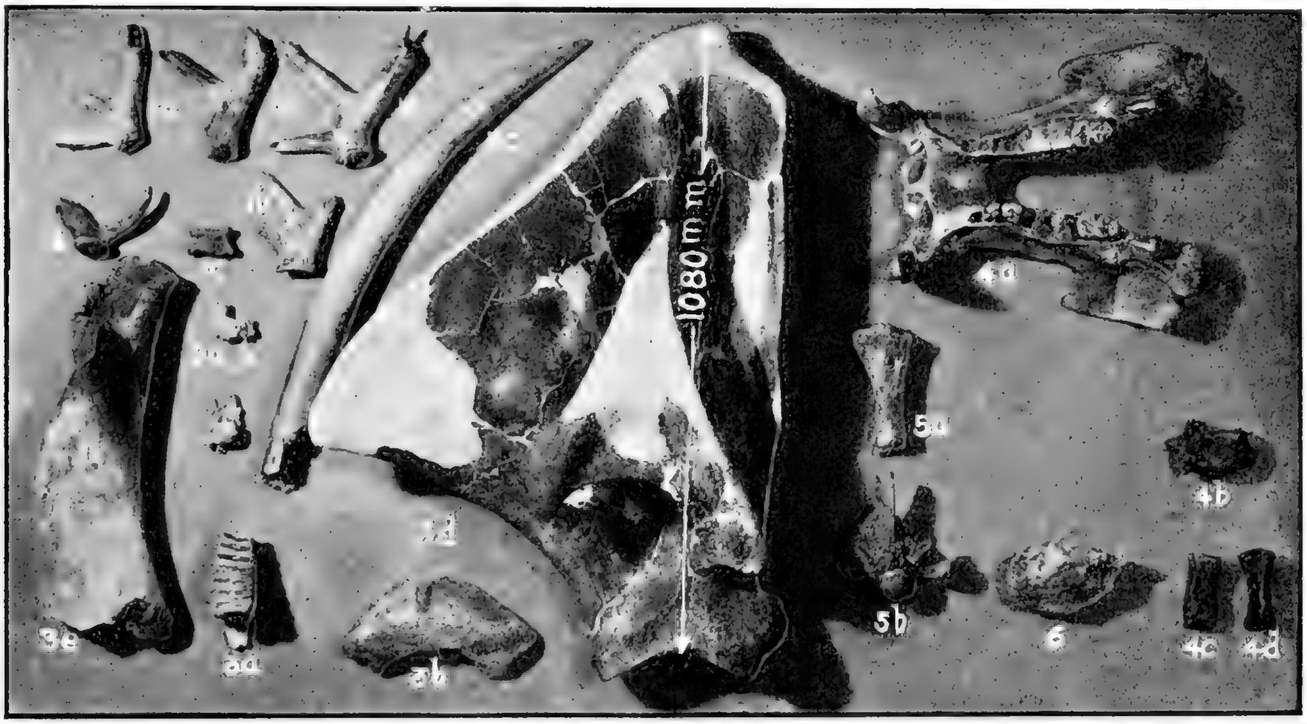
(6) Associated with the mammal fauna was the imperfect shell of a freshwater mollusc, referable to the genus *Unio*, of the family Unionidæ.

DESCRIPTION BY DE LORENZO AND D'ERASMO

De Lorenzo and D'Erasmo (1926, 1927).—On pages 35 to 39 (see also Tav. I) of the De Lorenzo and D'Erasmo Memoir of 1927 is given a complete description of this superb cranium in its original state (as cited in full from De Lorenzo's original contribution of 1926, pp. 185–188), of which the following is a literal translation in part[1]:

"In the past month of July [1926], the farmer Saverio Tiseo, of Pignataro Interamna near Cassino, excavating, for building purposes, a piece of ground on his farm situated on the southern slope of the hill which borders the village and is really in Fontanarosa, found, at a depth of about 8 metres, a large cranium of a mammifer."

"The locality in which the fossil in question was found forms, with the hill of Pignataro Interamna, part of this whole system of gently rolling hills, which extend from Aquino and Pontecorvo along the left bank of the Liri as far as the river Rapido below Cassino, and which are made up of large alluvial deposits of the early quaternary, deposited first among the chain of the Aurunci and that of the Mainarde, later moulded by backwaters, defluents in lesser volume of the present and more confined course of the river Liri, which still today, as in the day of Orazio, continues with its calm waters the taciturn corrosion of its plains."



Mammalian Fossils Associated with the Type Cranium of Hesperoloxodon antiquus italicus
About one-thirteenth natural size
After Osborn, 1931.846, p. 14, fig. 11

Fig. 1095. Type right scapula (3*d*) of *Palæoloxodon* [*Hesperoloxodon*] *antiquus italicus*.

(3*a*, *b*, *c*, *e*) Fragment of right second inferior molar (r.M_2), symphysis of mandible, nearly complete female tusk, and central portion of right humerus of *Palæoloxodon* [=*Hesperoloxodon*] *antiquus italicus*, (3*d*) right scapula (probably belonging to type).

(4*a*, *b*, *c*, *d*) Mandible, 5th cervical, Mts. IV, juvenile femur of *Hippopotamus amphibius major* ref.

(5*a*, *b*) Right radius and 7th cervical of *Rhinoceros merckii* ref.

(2*a*, *b*) Portion of left inferior molar (M_1) and fragment of mandible of *Bos primigenius*.

(1*a*, *b*, *c*) Portions of three antlers from the left side, two antlers from the right side, also right astragalus of the stag *Cervus elaphus*.

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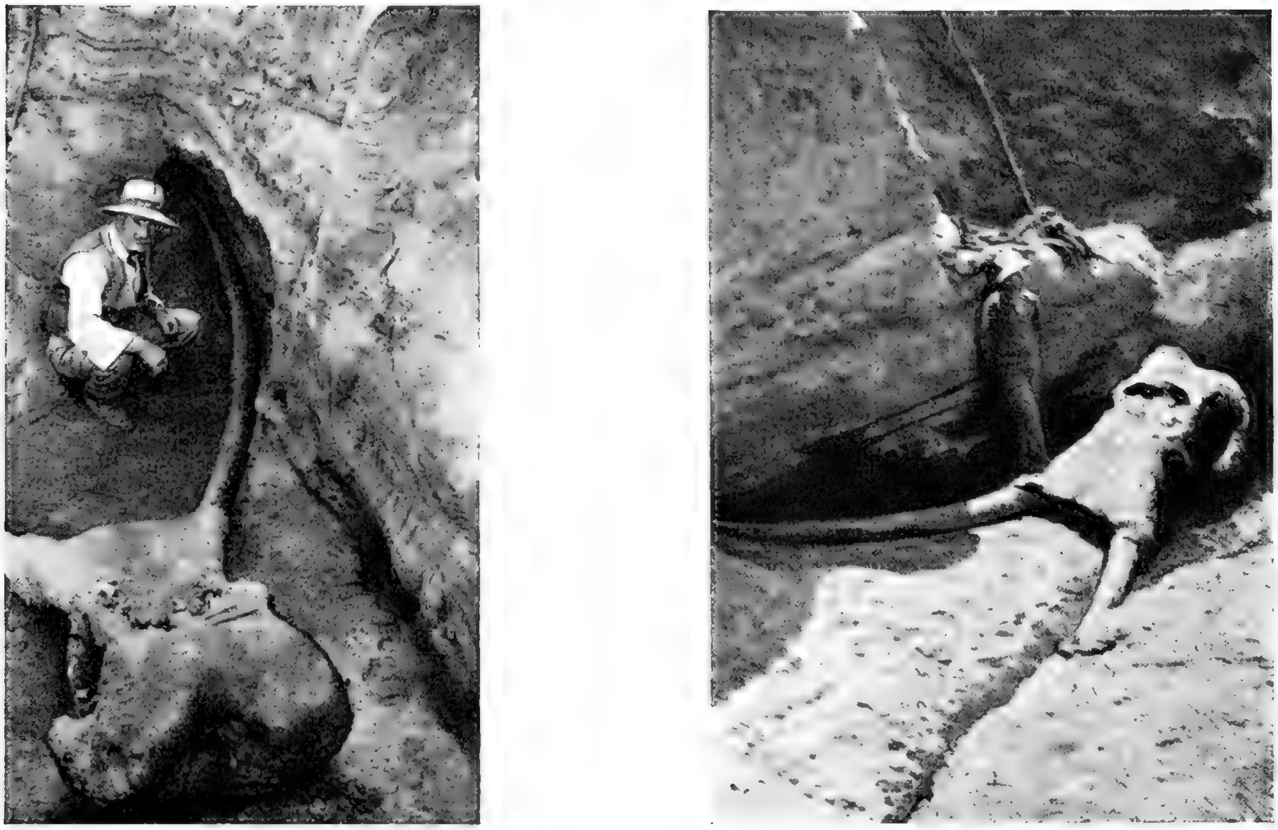
[1] Kindly prepared by Miss Francesca LaMonte of the Department of Ichthyology of the American Museum of Natural History.



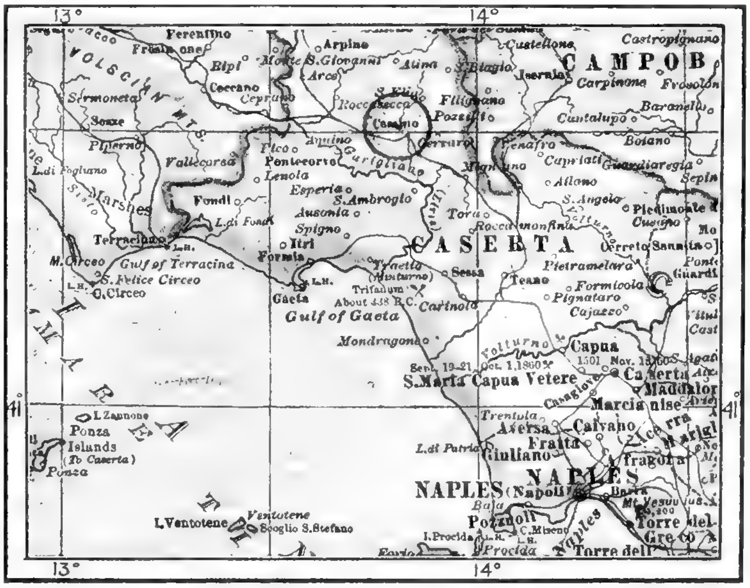
Pignataro Interamna Cranium (Type) before removal, showing (left) the Original Owner Saverio Tiseo

After Osborn 1931.846, p. 2, fig. 1

Fig. 1096. Type cranium *in situ* of *Palæoloxodon* [*Hesperoloxodon*] *antiquus italicus* (Amer. Mus. 22634) as found and exposed by Saverio Tiseo at Pignataro Interamna, near Cassino, Italy, and measured and described by Giuseppe De Lorenzo in 1926 and 1927. Compare Tav. I, figs. 1 and 2, of the Memoir of 1927 by De Lorenzo and D'Erasmo.

"The present plains, formed in recent times by the Liri, extend below Pignataro Interamna to about twenty metres above sea level; while the hills mentioned above, formed by the early quaternary diluvium, vary between 60 and 70 metres, thus giving a thickness of about 50 metres to the uncovered Pleistocene ground. This territory, prevalently clayish in the lower parts, becomes on top sandy,—yellowish sand and gravel interspersed with layers of clay and mud, and, on top, volcanic cinders."

"In this early quaternary district some time ago there were already found remains of fossil mammifers, especially elephants. These have been preserved in part in the Museum of Geology and Palæontology of the University of Naples. Oronzio Costa first noted them in the Rendiconti della Reale Accademia di Scienze fis. e mat. di Napoli for June, 1864. They were fully described by Giustiniano Nicolucci in his memoir *Su gli elefanti fossili della Valle del Liri* [Concerning the fossil elephants of the Valle del Liri] (Memorie della Soc. ital. delle Scienze, detta dei XL, vol. IV, 1882). Cacciamali contributes further to this in the Bollettino della Società geologica italiana, 1890, describing some molars of the elephants of Val di Comino and of Aquino. Finally, they are mentioned by Antonio Weithofer in his memoir on the fossil Proboscideans of Valdarno (a memoir which serves as the descriptive matter for a geologic atlas of Italy, vol. IV, part 2, Firenze, 1893). Hans Pohlig also speaks of this in his big monograph on *Elephas antiquus*, published in the Nova Acta Academiae Caes.



Upper Pleistocene Horizon of Hesperoloxodon antiquus italicus

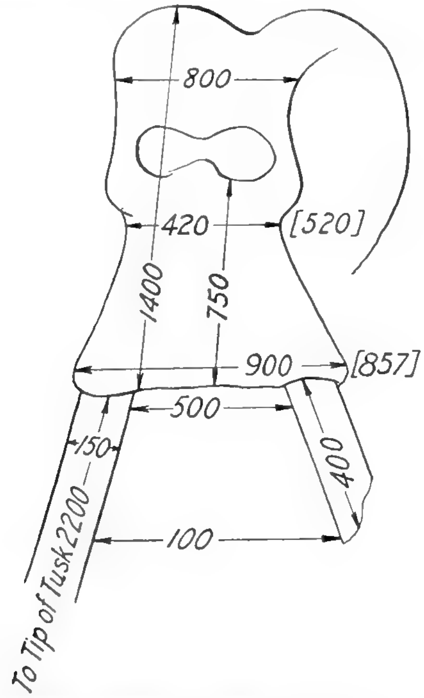
Compare Osborn, 1931.846, p. 3, fig. 2, also figure 1094 for details

Fig. 1097. Pignataro Interamna is near Cassino (circle), southwestern Italy, about fifty miles north of Naples. Region of the Valley of the Liri (Liris) occupied in Pleistocene time by large herds of the 'ancient' or 'straight-tusked' elephant now known as *Hesperoloxodon antiquus italicus*, also by *Hippopotamus*, *Cervus*, *Bos*, *Dicerorhinus*, and other species of *3d Interglacial* time. After Pl. 94 of the Century Atlas, edition of 1913.

Leopold. Carol. Germanicae naturae curiosorum, vol. 53, Halle, 1889, and vol. 57, Halle, 1892."

"My own and the observations of others are gathered together in my 'Geologia e Geografia fisica dell'Italia meridionale,' Bari (Laterza), 1904. On page 157 I spoke of the certain existence of *Elephas* (*Euelephas*) *antiquus* Falc. in the early quaternary deposits of the Valle del Liri."

"The fact that remains of fossil elephants already existed in the Valle del Liri does not diminish the importance of the present discoveries at Pignataro Interamna; of really exceptional importance because of the completeness of the exhumed cranium and because of its position, a position which leads to the deduction that it was found in its original posture, not a secondary one caused by transportation, and this leads to the hope that it may be connected with the rest of the animal's skeleton."



De Lorenzo's Original Sketch and Measurements of the Type Cranium of Hesperoloxodon antiquus italicus

Compare Osborn, 1931.846, p. 8, fig. 7

Fig. 1098.—Diagrammatic sketch, prepared in the American Museum to aid in the eighteen months' process of reconstruction. Cranium of *Palæoloxodon* [*Hesperoloxodon*] *antiquus italicus* (Amer. Mus. 22634), based upon original photographs (Fig. 1096), showing the exact measurements recorded in De Lorenzo's contribution of 1926 and fully quoted in his Memoir of 1927. The American Museum reconstruction, completed November, 1930, in front view accords exactly with the 1926–1927 measurements of De Lorenzo, except as to width of rostrum [857 mm., 520 mm.], as follows:

Apex of right tusk to vertex of cranium	3500 mm.	11 ft.	5¾ in.
Vertex of right tusk to border of premaxillary socket	2200	7	2⅝
Lower border of premaxillary socket to vertex of cranium	1400	4	7⅛
Diameter of incisive tusk at exit from socket	150		5⅞
Transverse breadth across premaxillary sockets	900 [857]	2	11⅜ [9¾]
Space between inner sides of incisive tusks	500	1	7⅝
Transverse space across rostrum just below orbits	420 [520]	1	4½ [8½]
Midline of premaxillary rostrum to midline of nasal opening	750	2	5½
Transverse across narrowest portion of frontals	800	2	7½

THE CRANIUM AND TUSKS

"The enormous head rests with its longitudinal axis, which measures not less than 3.50 metres from the frontal protuberance to the apex of the tusks, in an almost perfect horizontal position (Pl. I, figs. 1 and 2) in such a way as to lead one to suppose that the animal, descending to bathe in a muddy and richly vegetated brook, sank in the sand and mud, and, unable to swim, tried to keep its head and proboscis above in order to breathe as long as possible, until it sank altogether, and a lower alluvial deposit than that of its prey covered and surrounded the creature. This hypothesis is strengthened by the fact that in close proximity to the head and interspersed among the yellow gravel is a soft black layer, muddy and agreeing with the herbaceous vegetation of the bottom of the swamp in which the elephant probably sank. For these reasons it is anticipated that probably behind the head, still *in situ*, there is to be discoveed all the skeleton of the elephant, which can therefore be dug out, given the opportunity."

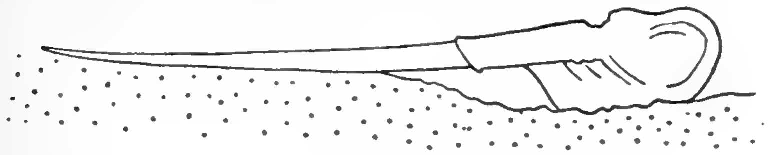
"But the excavation is not easy, not so much because of the depth as because of the easily shattered nature of the skeleton itself. The bones excavated up to now, that is, those of the head, as well as being petrified are, as it were, decalcified, in such a way that to isolate and gather them, there is need of great delicacy and accuracy."

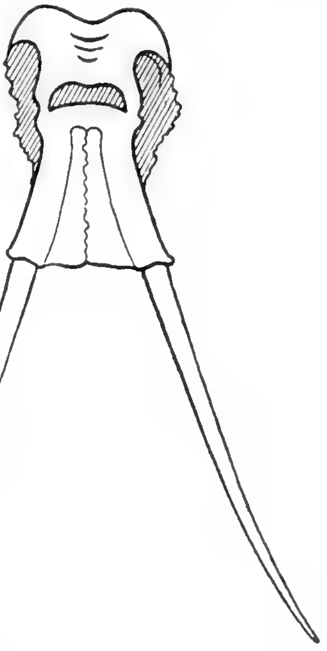
"In this formation and in such conditions now lies the cranium of the elephant, truly imposing in its silent grandeur. From the peak of the cranial protuberance [vertex of cranium] to the distal border of the intermaxillaries it is 1.40 metres long, its width on the frontal line between the parietals is 0.80 metres. Characteristic is the fan-shape of the two intermaxillaries, which together, below the nasal cavity, measure 0.42 metres [520 mm.]wide, while on the anterior border, concave and circular, they widen to 0.90 m. [857 mm.], keeping in the free internal space between the two incisive tusks a width of 0.50 m. and having a total length, along the median suture, of 0.75 m. The two incisive tusks, 0.15 m. in diameter at the exit of the sockets and 2.20 m. long, very beautifully and perfectly formed and gently and elegantly curved both on the inner and outer curves, diverge widely, following the external line of the intermaxillaries in such a way that 0.45 m. from the exit of the sockets they are already a metre apart, and the two apices more than two metres from each other."

"The mandible is so closely adherent to the upper maxillary that its symphysis appears to be almost soldered to the internal surface of the intermaxillaries. The symphysis is wide, near the condyles, about 0.60 m., with as much again in measurement on the bisettrice [midline?]. On detaching the cranium, the plates of the upper molars, devoid, as we have said, of cement, and deprived of support, fell at once. The lower molars of the mandible stayed in place; especially on the right arc of the mandible one can see plainly the traces of the abrasion of the first (or second) molar, 0.10 m. long, 0.07 m. wide, with six residual plates, and the second (or third) molar, 0.17 m. long, 0.07 m. wide, with 10 plates."

"All these characters, and especially the length of the cranium, the prominence of the protuberance and of the occipital fossa (see Pl. I, fig. 1), the enormous divergence of the intermaxillaries and of the incisive tusks (Pl. I, fig. 2 and interpolated figs. 10 and 11), the frontal depression, the narrowness of the plates of the molars in proportion to their height and to the length of the molars themselves, the form of the *difese* [framework?], show clearly that the cranium from Pignataro Interamna belongs to the species *Elephas* (*Euelephas*) *antiquus* Falconer, characteristic of the interglacial phases of the early quaternary and the largest of the few species of elephants which have inhabited the earth. The fortunate discovery of this complete cranium further shows that, contrary to what Pohlig wrote, Falconer was right in maintaining that his *Elephas antiquus* was closely allied to the living Indian elephant, *Euelephas indicus*."

The above citation from G. De Lorenzo and G. D'Erasmo (1927), pages 35–39, figures 10 and 11, and plate I, figures 1 and 2, affords invaluable information as to the Pignataro Interamna cranium in its original undisturbed condition partly buried in the matrix. These drawings and photographs demonstrate the superb condition of the cranium and tusks when first exposed and our knowledge is fortunately amplified by two photographs (reproduced in our Fig. 1096) subsequently taken by Saverio Tiseo before he attempted to remove this priceless fossil from its original bed in the matrix. The precise knowledge of the specimen in its original condition afforded by these four photographs, also by the measurements and outline sketches by De Lorenzo reproduced in our figures 1099 and 1100, is in close accord with the measurements in De Lorenzo's original paper of 1926, pages 187 and 188, as reproduced in our diagram (Fig. 1098). Had it not been for these priceless measurements, sketches, and figures, we should find ourselves obliged to record one of the most tragic losses in the history of vertebrate palæontology, namely, the characters of the cranium, jaws, and tusks of an adult *Elephas antiquus* in a perfect condition of preservation.





De Lorenzo's Original Sketches of the Type Cranium of Hesperoloxodon italicus

One-fortieth natural size

Fig. 1099. Pignataro Interamna cranium (Amer. Mus. 22634) *in situ*. After De Lorenzo and D'Erasmo, 1927, p. 37, fig. 11: "Cranio dell '*El. antiquus* di Pignataro Interamna, visto di fianco, ancora parzialmente immerso nella sabbia (1/40 della grand. nat.)." Reproduced same size. Compare Osborn, 1931.846, p. 5, fig. 5.

Fig. 1100. Front view of the Pignataro Interamna cranium (Amer. Mus. 22634) *in situ*. After De Lorenzo and D'Erasmo, 1927, p. 36, fig. 10: "Cranio dell '*El. antiquus* di Pignataro Interamna, visto di fronte(1/40 della grand. nat.)." Reproduced same size. Compare Osborn, 1931.846, p. 5, fig. 4.

ACQUISITION BY THE AMERICAN MUSEUM IN THE YEAR 1929

In the hope that the excavations would be continued and the precious remains would become a part of the collection of the State, Professor De Lorenzo, as Director of the Institute of Geology of the University of Naples, made every effort (1927, p. 39) to secure the specimen for the Naples Museum, but without success.

During the following year (September 4, 1928), the American Museum of Natural History was informed of the desire of Saverio Tiseo to dispose of the specimen and began negotiations (November, 1928) on condition that no step would be taken without due permission from the authorities of the Italian Government. On December 3, 1928, these terms were formulated in detail, and in May, 1929, the specimen was received in the American Museum. The total cost to the American Museum, including the donation of $1,000.00 by Henry Fairfield Osborn, mounted step by step to $4,375.34, almost nine times the amount originally set aside for the purpose.

On opening the boxes containing the fossil, the extremely painful discovery was made that between 1927, when the negotiations of Tiseo with De Lorenzo were concluded, and 1929, the owner Saverio Tiseo had irretrievably damaged the entire upper portion of the cranium by attempting to remove it for purposes of exhibition. Thus the superb and unique cranium shown in Professor De Lorenzo's description and in the figures and photographs above mentioned and reproduced in the present text no longer existed. The remaining parts of the specimen, namely, the rostrum, tusks, palate, jaws, and the lower portion of the occiput were also seriously damaged, while the entire upper portion was irrevocably lost to science with the exception of three small pieces extricated with great difficulty from the hard cement in which Tiseo had attempted to repair the terrible injury which he had inflicted on this priceless specimen. At first the reconstruction of the skull appeared hopeless, and the present author, who had donated it to the American Museum collection on the basis of the excellent photographs showing the specimen in its original condition, was not even allowed to see it in the laboratory. After eighteen months of arduous labor on the part of Mr. Jeremiah Walsh, under the direction of preparator Charles Lang, and of Curator Barnum Brown, and finally of Honorary Curator-in-Chief Osborn, the reconstruction entered its final stages in which the precise measurements, figures, and photographs secured by Professor De Lorenzo of the cranium in its original unfractured condition were of in-

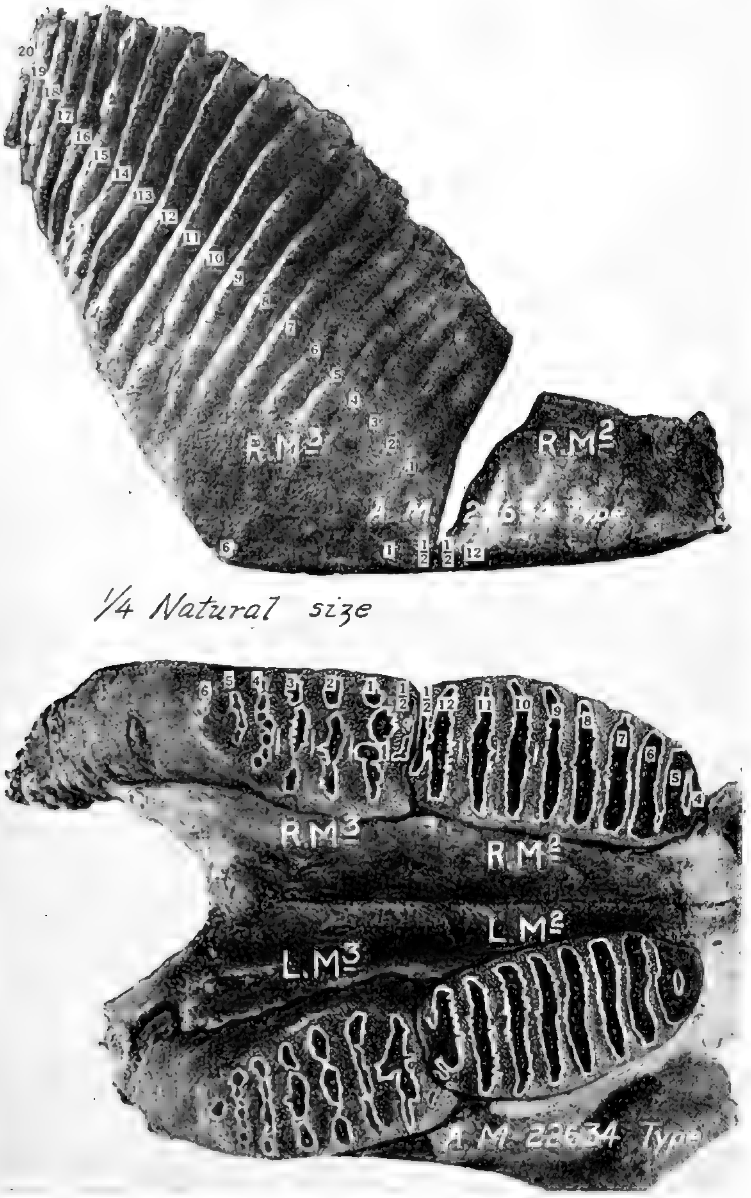


Fig. 1101. Type superior grinders of *Hesperoloxodon antiquus italicus* (Amer. Mus. 22634). One-fourth natural size. After original photographs, retouched and numbered, displaying ridge-plates 1 to 20 in r.M^3, ridge-plates 4 to 12 in r.M^2. Compare Osborn, 1931.846, p. 10, fig. 8.

(Upper) Second and third right superior molars, r.M^2, r.M^3.

(Lower) Palate exhibiting right and left superior molars, M^2, M^3.

calculable value and importance. Thus, after almost continuous and very expensive labor between May, 1929, and November, 1930, the specimen was ready for complete description and exhibition, although not open to the public until January 1, 1931.

Despite all these drawbacks and scientific disappointments, the restored cranium and tusks, jaws, and scapula still afford a wealth of new knowledge regarding the relationships of the classic '*Elephas antiquus*,' which, added to the equally priceless Upnor skeleton, also the Steinheim crania (*Elephas* [*Hesperoloxodon*] *antiquus germanicus*), remove this great branch of the family Elephantidæ from its previous obscurity and uncertainty and enable us to rank it as among the best known of the fossil elephants of Eurasia.

Whereas *Elephas* [*Hesperoloxodon*] *antiquus* belongs in the Lower Pleistocene, or *1st Interglacial*, the present specimen belongs in the upper Middle Pleistocene,[1] or *3d Interglacial*; it is somewhat more progressive than the *H. antiquus germanicus* of Weimar.

Hesperoloxodon antiquus italicus is far superior in size to *Palæoloxodon namadicus* and greatly surpasses *H. antiquus typicus* both in the number and height of the ridge-plates (see Figs. 1102 and 1088). It is a very progressive ascending mutation, equaling in size, but exceeding in the number of its superior ridge-plates, the most progressive *H. antiquus germanicus* of Weimar. However, from close comparison with all the numerous specimens described from Lower Pleistocene deposits in England (by Falconer and others) to *3d Interglacial* deposits in Weimar (by Pohlig and Soergel), *H. antiquus italicus* appears to be the largest and most progressive member of the '*Elephas antiquus*' phylum thus far discovered.

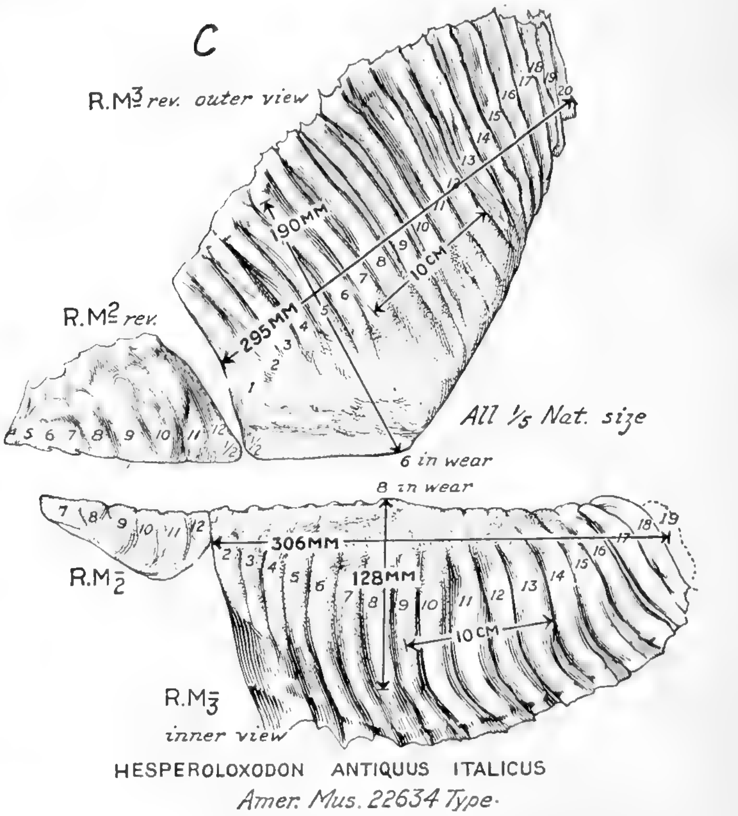


Fig. 1102.—Type right superior and inferior grinders, M 2, M 3, of *Hesperoloxodon antiquus italicus* (Amer. Mus. 22634). Diagrammatic key to the superior and inferior ridge-plates:

M 2 $\frac{12\frac{1}{2}}{12}$ M 3 $\frac{20}{18+}$.

The principal measurements of r.M^3 are: Length of 20 ridge-plates 295 mm.; height of 5th ridge-plate 190 mm.; 6 ridge-plates in 10 cm. The principal measurements of r.M_3 are: Length 306 mm., height of 8th ridge-plate 128 mm., 4½ ridge-plates in 10 cm.

After Osborn, 1931.846, p. 13, fig. 10.

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[1] [Careful consideration of the several statements by Professor Osborn in the present Memoir, as well as the general opinion today of geologists and palæontologists, has led to the conclusion that Professor Osborn would have placed the *3rd Interglacial* in the Upper Pleistocene; hence throughout it will be observed that this determination has been adopted.—Editor.]

Fig. 1103.—Type mandible, right lateral and superior aspects, of *Hesperoloxodon antiquus italicus*, one-sixth natural size.

A, Right lateral view, with second and third superior teeth, M^2, M^3, superposed on corresponding inferior teeth, M_2, M_3. After Osborn, 1931.846, p. 16, fig. 12.

B, Superior view, with second inferior molar, M_2, exhibiting ridge-plates 7–12, third inferior molar, M_3, exhibiting ridge-plates 1–8. After original photograph.

Fortunately the second and third superior and inferior molars of both sides were preserved *in situ* and their characters are very clearly displayed in the accompanying type figures, in which all the ridge-plates are shown both in crown and lateral view, with clear enumeration of the ridge-plate numbers in figures 1101, 1103, and 1104, and in the diagrammatic figure 1102. Very important is figure 1011 (lower) in which 15 ridge-plates are shown in simultaneous use, namely, r.M^2, ridge-plates 4 to 12½, plus r.M^3, ridge-plates ½–1 to 6. This stage of attrition represents a young adult male, corresponding with the attrition of *Elephas indicus* estimated to be about forty years of age. To the 20 ridge-plates actually observed in r.M^3 (Fig. 1101) there may possibly be added ridge-plates 21 and 22; whereas in a much older individual of the typical *Hesperoloxodon antiquus* only 16½–17 ridge-plates are shown.

SUBSPECIFIC DESCRIPTION

Compare Osborn, 1931.846, pp. 17-24

Hesperoloxodon antiquus italicus Osborn, 1931

Figures 1068, 1069, 1088, 1092, 1095, 1096, 1098–1108, 1111, 1112, Pl. xxiii

Pignataro Interamna, near Cassino, Italy. Upper Pleistocene river gravels of *3d Interglacial* time.

Palæoloxodon antiquus italicus Osborn, 1931. "*Palæoloxodon antiquus italicus* sp. nov., Final Stage in the '*Elephas antiquus*' Phylum." Amer. Mus. Novitates, No. 460, pp. 1–24. Type.—Cranium and jaws with superior and inferior dentition (M 2–M 3) of a young adult male; also right scapula (Amer. Mus. 22634). Locality and Horizon.—"Pignataro Interamna, near Cassino, Italy. Found in upper Middle[1] Pleistocene river gravels, of *3d Interglacial* time, equivalent to, or slightly more recent in geologic age than, the *3d Interglacial* stage of Taubach-Weimar of the Ilm River valley, Saxe-Weimar, Thuringia, northern Germany, 40 kilometers east and a little south of Burgtonna, north of Gotha, where the first skeleton of '*Elephas antiquus*' (cited by Blumenbach as *Elephas primigenius*) was discovered in 1695." Type Figure.—*Op. cit.*, figs. 1, 4–16.

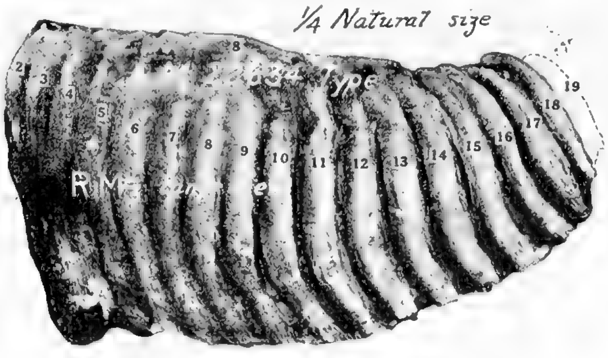

Fig. 1104.—Type of *Hesperoloxodon antiquus italicus* (Amer. Mus. 22634). Inner view of third right inferior molar, r.M_3, exhibiting +18+ ridge-plates. One-fourth natural size. After Osborn, 1931.846, p. 12, fig. 9.

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[1] [See footnote on opposite page.—Editor.]

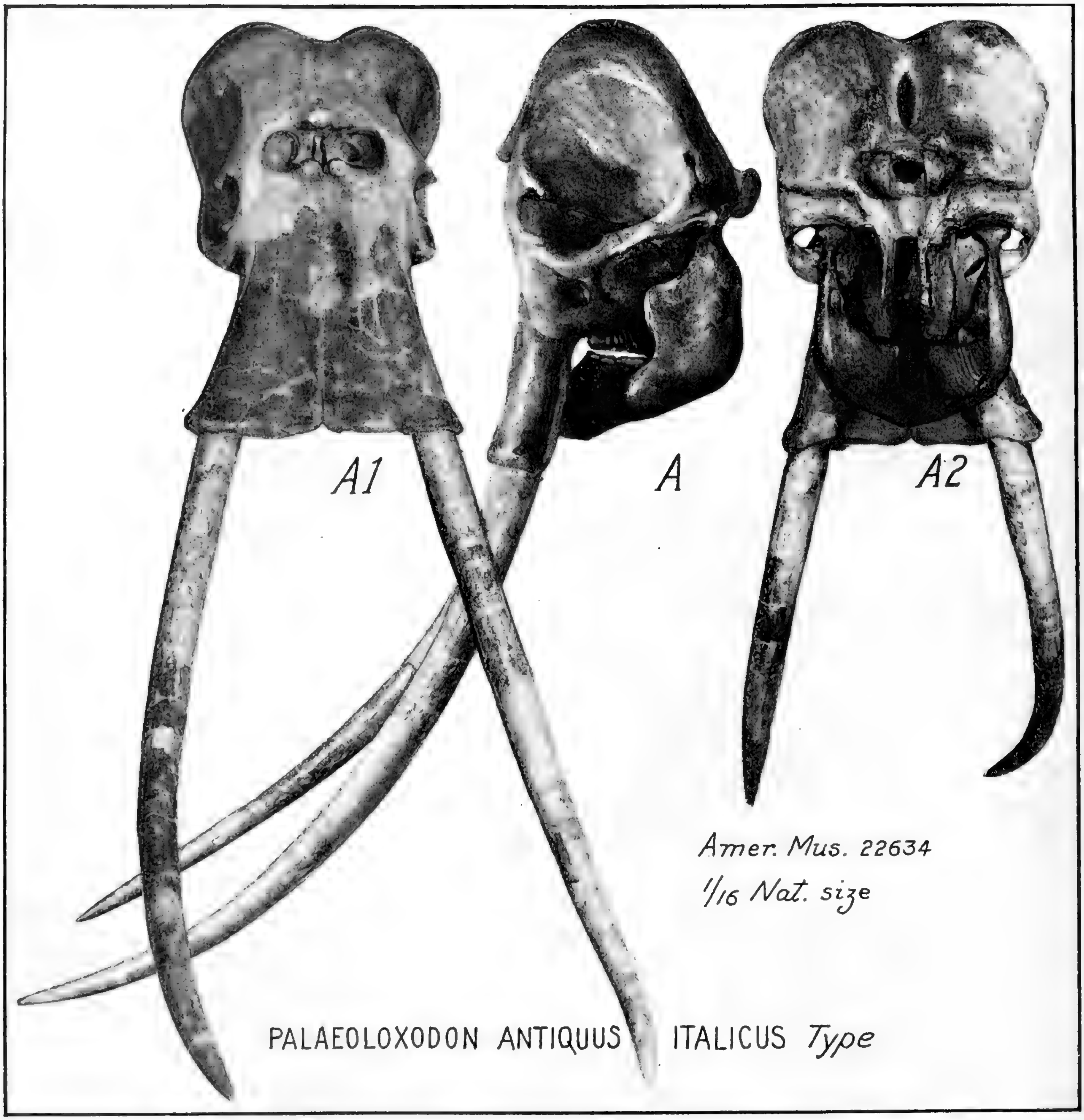


Fig. 1105. HESPEROLOXODON ANTIQUUS ITALICUS TYPE, OF PIGNATARO INTERAMNA, ITALY, VALLEY OF THE LIRI, IN THE AMERICAN MUSEUM OF NATURAL HISTORY (AMER. MUS. 22634)

After photographs and indicated measurements (March 10, 1931) by the present author. Reduced to a uniform scale of one-sixteenth natural size. See also *type* figure 1106.

A, Left lateral view of cranium.

A1, Anterior view of cranium, exhibiting upturned portions of tusks in slight perspective.

A2, Posterior view of cranium and jaws, exhibiting exposed lower grinding teeth of the right side, tusks in strong receding perspective.

Observe the relatively high, narrow occiput exceeding in height that of *Hesperoloxodon antiquus germanicus*. The adult cranium (A) is about equal in depth or bathycephaly (990c mm.) to that of *H. ant. germanicus* (980 mm.—Fig. 1114, B); this is owing to the greater depression of the tritural surface of M^3 below the occipital condyle.

In the following description (Osborn, 1931.846, pp. 17–24) references to the figures in the present Memoir have been substituted for the original figure numbers.

"SUBSPECIFIC CHARACTERS.—Displayed in the measurements, ridge-plate formulæ, and height of the ridge-plates, enumerated below; also illustrated in the type figures 1101, 1102, and 1103. Progressive evolution indicated as follows:

Pal. ant. typicus;[1] $M3\ \frac{16+}{17}$. M^3, length 254 mm., height of tallest ridge-plate 174 mm.; M_3, length 315 mm., height of tallest ridge-plate 126 mm.

Pal. ant. germanicus; $M\ 3\ \frac{17+}{18+}$. M^3, length 295 mm., height of tallest ridge-plate 190 mm.; M_3, length 425 mm., height of tallest ridge-plate 120 mm.

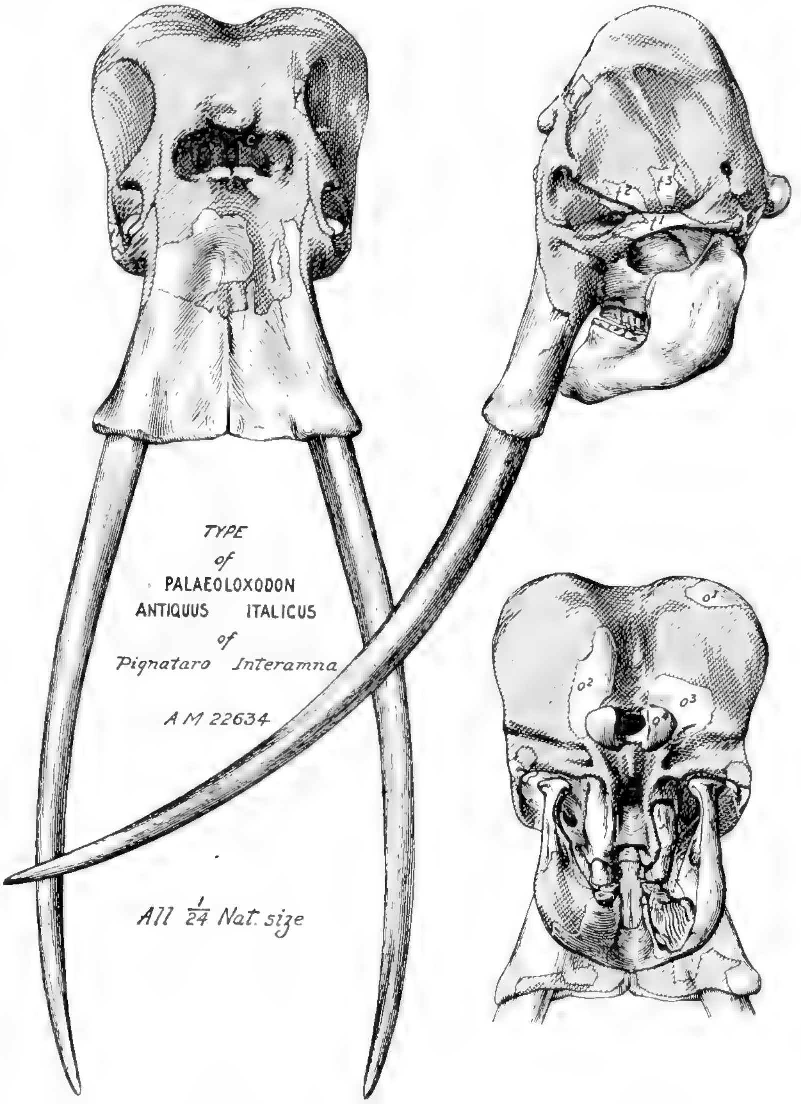
Pal. ant. italicus (type); $M\ 3\ \frac{20}{18+}$. M^3, length 295 mm., height of tallest ridge-plate 190 mm.; M_3, length 306 mm., height of tallest ridge-plate 128 mm."

"INCISIVE TUSKS.—The incisive tusks of the type are not fully grown [see Figs. 1100, 1099, 1106, 1107, 1108]. Total estimated length 3030–3070 mm., that is, 800e mm. within the alveolus plus 2230–2270 mm. beyond the alveolar border. The longest tusk recorded by Pohlig in the University of Rome collection measures 3900 mm., or 12 ft. 9½ in., in comparison with 10 ft., length of the present specimen. This indicates that a full-grown adult male of *Pal. ant. italicus* attained gigantic size."

"LOWER JAWS [FIGS. 1103, 1106].—The type inferior mandible is entirely complete, as represented in figure [1103], requiring little or no restoration. As compared with the more or less complete mandibles figured by Falconer, from the Lower Pleistocene of England, it closely resembles in profile aspect the typical '*Elephas antiquus*' jaw but is very much larger and more massive; it differs widely in every aspect from the mandibles belonging to any species of *Archidiskodon*, *Parelephas*, or *Mammonteus*; the rostrum is abruptly truncated but less abbreviate than in '*Elephas primigenius*,' which is more of the extreme bathycephalic type."

"SKULL.—The extremely broad rostrum, characteristic of all stages of the '*Elephas antiquus*' phylum, measuring 857 mm. or 2 ft. 9¾ in., is exactly the same width as that of the '*Elephas platyrhynchus*' of Graells, which measures 860e mm. or about 2 ft. 10 in. transversely; this animal is from the Pleistocene, at San Isidro, near Madrid, Spain."

"Most novel and surprising is the dome-like, highly arched occipito-parietofrontal contour [Figs. 1099, 1100, 1106, 1107, 1108] which superficially resembles that of the Indian elephant more



HESPEROLOXODON ANTIQUUS ITALICUS, TYPE

One twenty-fourth natural size. See figure 1105, one-sixteenth natural size

Fig. 1106. Type cranium of *Palæoloxodon antiquus italicus* (Amer. Mus. 22634) as reconstructed and mounted in the American Museum during 1929 and 1930. One twenty-fourth natural size. Restored parts (oblique lines); parts preserved (shading), namely, occipital condyles, portions of premaxillaries and maxillaries, and complete mandible. After Osborn, 1931.846, p. 7, fig. 6.

The measurements, as seen from the front, with but two exceptions accord with those given by De Lorenzo. The few original fragments seen in frontal aspect lie at the back of the narial chamber (*c*); along the border of the left temporal fossa (*t*), and along the temporal arch (t^1); in lateral aspect of the left side, as shown in the fragments in the left temporal fossa (t^2, t^3) just above the fragment of the right temporal arch (t^1), transferred to the left side for purposes of restoration. In posterior aspect, the occipital parts preserved are portion of the superior border (o^1), and parts of the posterior occipital plate (o^2, o^3) and the very broad condyles (o^4).

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[1] [On page 17 of American Museum Novitates, No. 460, Osborn presents the descriptions of three subspecies of *Palæoloxodon antiquus*, designated as *P. antiquus typicus*, *P. antiquus germanicus*, and *P. antiquus italicus*. According to current rules the name *typicus*, designating the type of the species *antiquus*, must be regarded as a still-born synonym of *antiquus*, since the name of the typical subspecies should be the same as the name of the species. Consequently the three subspecies would be:

Palæoloxodon antiquus antiquus (Falconer) *Palæoloxodon antiquus germanicus* (Stefănescu) *Palæoloxodon antiquus italicus* Osborn

On page 21 of this same publication, Osborn proposes the new genus *Hesperoloxodon*, with *Palæoloxodon antiquus italicus* as the generic type. But a genus is based upon a species, so that the type of *Hesperoloxodon* should be *antiquus* and all of its subspecies. In other words, a species cannot be split between two or more genera on the basis of its subspecies. (E. H. COLBERT.)

Nevertheless the author's plain intention was to recognize the distinction of a "new loxodont phylum of the west" (as opposed to the Indian *namadicus*); as a "type" of the "phylum" or "genus" (terms often used interchangeably by him) he designated *Palæoloxodon antiquus italicus*. Since this was his intention the subspecies *italicus* should have been raised to the rank of a species to serve as a type of the genus *Hesperoloxodon*. (W. K. GREGORY.)]

closely than that of either *Loxodonta africana* or *Palæoloxodon namadicus*. This lofty profile and corresponding bathycephaly are represented correctly in figures [1106 and 1107 of the present Memoir], because they accord . . . [Fig. 1098] with the measurements and photographs taken by De Lorenzo and Saverio Tiseo before this cranium was damaged. Moreover, beside the well preserved and extraordinarily broad occipital condyles (280 mm.), there are portions of the occiput ([Fig. 1106], o^1, o^2, o^3, o^4) which prove that the occiput is forwardly inclined. The chief comparative measurements between this restored cranium and the cranium of the adult African bull elephant (*Loxodonta africana peeli*—see Fig. 1107) are as [above].”

COMPARISON WITH AFRICAN ELEPHANT

	Loxodonta africana peeli		[Percentages plus (+) and minus (—)]	*Hesperoloxodon antiquus italicus*	
(1) From front of orbit to back of occipital condyle	746 mm.		+10%	=820c mm.	
(2) From summit of parieto-occipital crest to attritional surface of M³ (bathycephaly)	800		+24%	=990c	
(3) Occipital condyles, transverse	248		+13%	=280	
(4) Temporal arches, transverse width across	797		— 6%	=750c	
(5) Premaxillary rostrum, maximum width across	665		+29%	=857	
(6) Mandibular condyle, height above angle of jaw	489		— 2%	=478	
(7) Mandibular length, condyle to apex of rostrum	749		+ 7%	=800	
(8) Incisive tusks:	L	R		L	R
total length of	1960c	2010c		3030c	3070c
free length beyond rostrum	1905	1960		2230	2270
maximum diameter at exit from rostrum	156	160		145	139
total circumference of	460	467		433	432

Pohlig (letter May 5, 1929) gave a very high estimate of the length of the incisive tusks of ‘*Elephas antiquus*’ of Germany, namely, an average length of 5000 mm., or 16 ft. 4⅞ in., as compared with the incisive tusks of a Siberian ‘*Elephas primigenius*’ in the St. Petersburg Museum (4300 mm., or 14 ft. 1¼ in.). He adds: “The average incisor length of a Siberian Mammoth at Petersburg, measured and figured by me (1891, p. 321, Pl. B, fig. 3) is 4 m. 30,—so that the average length of the *Elephas antiquus* incisor (*op. cit.*, p. 51) must have been more than 5 meters.”

COMPARISON WITH LOXODONTA AFRICANA PEELI.—“In (4) width across temporal arches, *L. africana* [*peeli*] exceeds *Pal. ant. italicus* by six per cent. In percentages the cranium of *Pal. ant. italicus* in all other measurements is from seven to twenty-nine per cent. larger than that of *L. africana*, as follows:

(1) Orbit to occipital condyles	10%
(2) Cranial apex to grinding surface of M³	24%
(3) Transverse occipital condyles	13%
(5) Width across premaxillary rostrum	29%
(7) Mandibular length	7%”

“On the average of the five principal measurements, the cranium of *Pal. ant. italicus* is about fifteen per cent. larger than that of *L. africana*. If this fifteen per cent. increase obtains throughout the entire skeleton, the skeletal height of *Pal. ant. italicus* should be about 3673 mm. or 12 ft., as compared with the height *in the flesh* of a large adult bull of *L. africana*, namely, 3450 mm. or 11 ft. 4 in., or with the skeletal height of the *Palæoloxodon antiquus* (*andrewsi*?) [=*Hesperoloxodon antiquus*] of Upnor, from the top of the scapula to the ground, namely, 3700 mm. or 12 ft. 1⅝ in.; thus it appears from the cranial proportions only that the skeleton of *Pal. ant. italicus* was about fifteen per cent. taller at the shoulder than that of the African elephant and closely similar in height to that of the Upnor elephant.”

COMPARISON WITH PALÆOLOXODON NAMADICUS.—“Examined closely, the above measurements prove that the cranium of *Pal. ant. italicus* is profoundly different from that of ‘*E. namadicus*’ (the genotypic species [1] of *Palæoloxodon*) as well as from that of

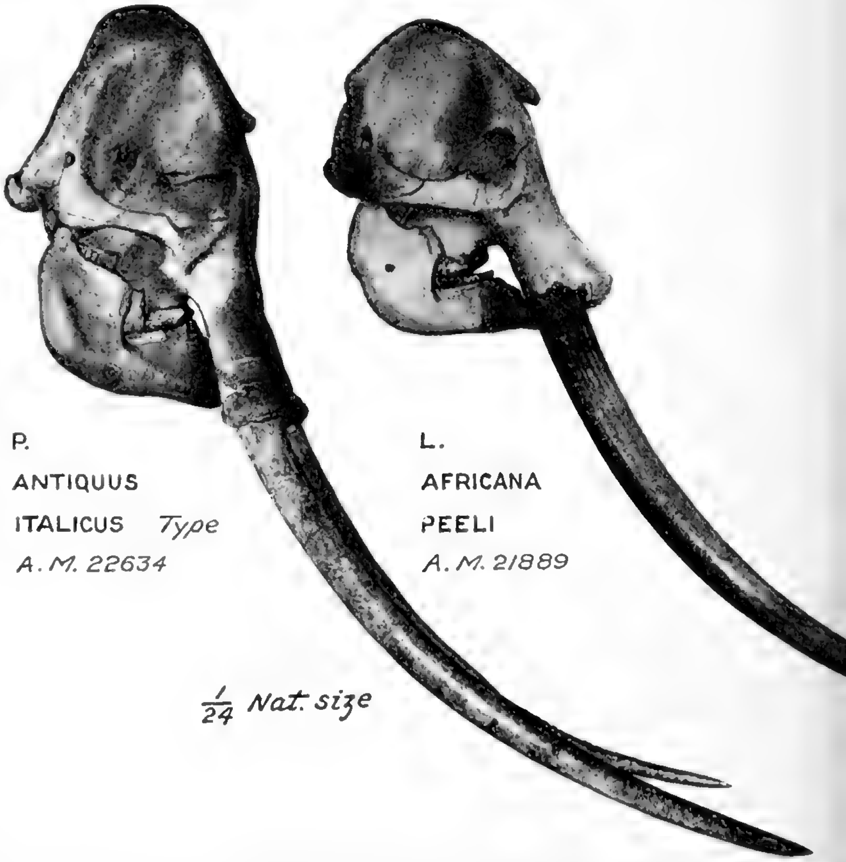

Fig. 1107. CRANIA OF HESPEROLOXODON AND LOXODONTA IN LATERAL VIEW

After Osborn, 1931.846, p. 18, fig. 13, one twenty-fourth scale. Compare figures 1106 and 1108, also measurements above.

(Left) Cranium and tusks of type of *Palæoloxodon* [*Hesperoloxodon*] *antiquus italicus* (Amer. Mus. 22634), right lateral aspect.

(Right) Cranium and tusks of *Loxodonta africana peeli* (Amer. Mus. 21889), adult male, from Mt. Kenya district. Same as in figure 1059.

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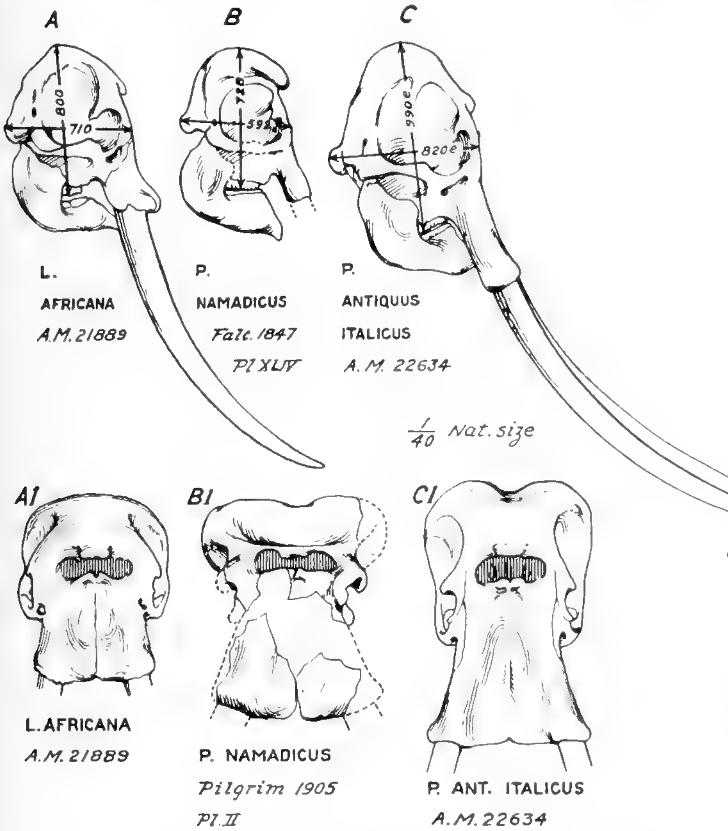
[1] “Described by Matsumoto (1924) under the subspecific name *Palæoloxodon namadicus naumanni*” [genotype *Elephas namadicus naumanni* Makiyama, 1924. See, however, footnote on p. 1247 above regarding genotypic usage.—Editor.]

Loxodonta africana, which is a relatively primitive cranium. Coördinated with its very tall grinding teeth, the cranium of the Italian specimen is much more bathycephalic (depth 990e mm. as compared with 800 mm. in *L. africana*); it is correspondingly less brachycephalic (750e mm. as compared with 797 mm.); this is in accord with the cranial proportions which are much nearer those of the Indian elephant than of the African elephant. This bathycephaly is, however, a parallelism rather than a point of affinity, because the very broad rostrum of *Pal. ant. italicus* presents an extreme difference from the very narrow rostrum of *Elephas indicus.* Comparison with the cranium of '*Elephas namadicus*' shows a strong resemblance in the breadth of the premaxillary rostrum but an extreme difference in the summit of the cranium, which in '*E. namadicus*' is relatively low and reinforced by the overhanging parieto-frontal crest."



COMPARATIVE BATHYCEPHALY OF THE LOXODONTINÆ

Fig. 1108. Frontal and lateral views of three adult males, one-fortieth natural size. After Osborn, 1931.846, p. 20, fig. 14.

A, A1, *Loxodonta africana.* Bathycephaly, 800: 710 mm. Male.

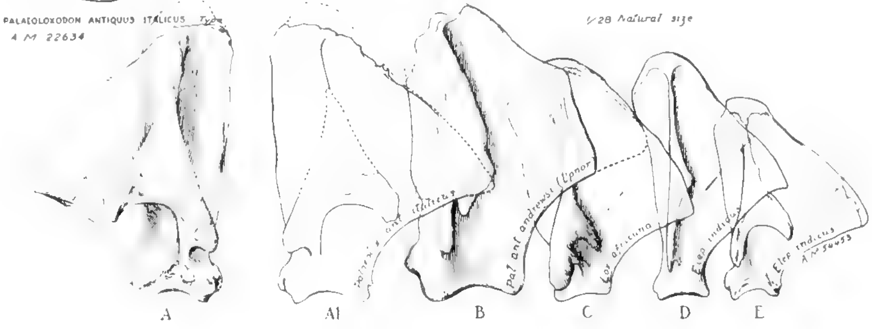
B, *Palæoloxodon namadicus.* Bathycephaly, 728: 592 mm. Female.

B1, *Palæoloxodon namadicus.* Male cranium of the Godávari Alluvium. After Pilgrim, 1905.

C, C1. *Palæoloxodon* [*Hesperoloxodon*] *antiquus italicus* type. Bathycephaly, 990e.: 820e mm.

Observe that *Pal.* [*Hesperoloxodon*] *antiquus italicus* is much more bathycephalic (990e: 820e mm.) than *Loxodonta africana* (800: 710 mm.), which is approximately the same as *Pal. namadicus* (728: 592 mm.). The *female* cranium (B) is much smaller than the large male cranium of the Godávari Alluvium (B1); compare the more accurate diagrammatic figure (Fig. 1110) of the same cranium.

"This points to *Pal. ant. italicus* as a member of a phylum quite distinct from that of the Siwalik '*E. namadicus,*' a phylum which if supported by other cranial and skeletal differences might well constitute a new genus to which the name HESPEROLOXODON, or 'loxodont of the west,' might be applied. This name is provisionally proposed, as I would not like to be forestalled a second time, as in the case of *Palæoloxodon,* a generic name assigned to '*E. namadicus naumanni*' by Matsumoto but a few weeks prior to my description of *Sivalikia.*



COMPARISON OF SCAPULÆ

One twenty-eighth natural size

Fig. 1109. Right scapula (A, A1 in reversed outline) of the type of *Pal.* [=*Hesperoloxodon*] *ant. italicus* (Amer. Mus. 22634) drawn to the same scale as the corresponding scapula of (B) *Pal. ant.* (*andrewsi?*),[1] of (C) *Lox. africana,* and of (D) *Elephas indicus,* juvenile (both after Andrews and Cooper, 1928, fig. 2), also of (E) *Elephas indicus,* adult (Amer. Mus. 54453), Vernay's middle-aged male, of which the entire forelimb is shown in figure 1194 of the present Memoir.

"SCAPULA.—The right scapula (1109A, A1) was found near the type and may be considered as belonging to the same individual (Amer. Mus. 22634); it greatly exceeds in size that of the African and Indian elephants of the same age [Fig. 1109C, D, E]. On the other hand, it is slightly exceeded in size by the left scapula [Fig. 1109B] preserved in the Upnor skeleton. The measurements of the scapulæ of *Pal. ant. italicus* and *Pal. ant.* (*andrewsi?*)[1] are taken with the restored border indicated in dotted lines:

SCAPULA	*Lox. africana oxyotis* (Jumbo) [Amer. Mus. 3283]	*Pal. ant. italicus* Pignataro [Amer. Mus. 22634]	*Pal. ant.* (*andrewsi?*)[1] Upnor [Brit. Mus.]
Height, superior border (restored) to center of glenoid border	925 mm.	+15% =1065 mm.	+10% =1170 mm.
Width, median, across pre- and post-scapular borders	594	+29% = 770	+12% = 868e
Anteroposterior diameter of neck of scapula	240	+28% = 307	+ 6% = 324
Anteroposterior diameter of glenoid border	187	+35% = 253	+15% = 290"

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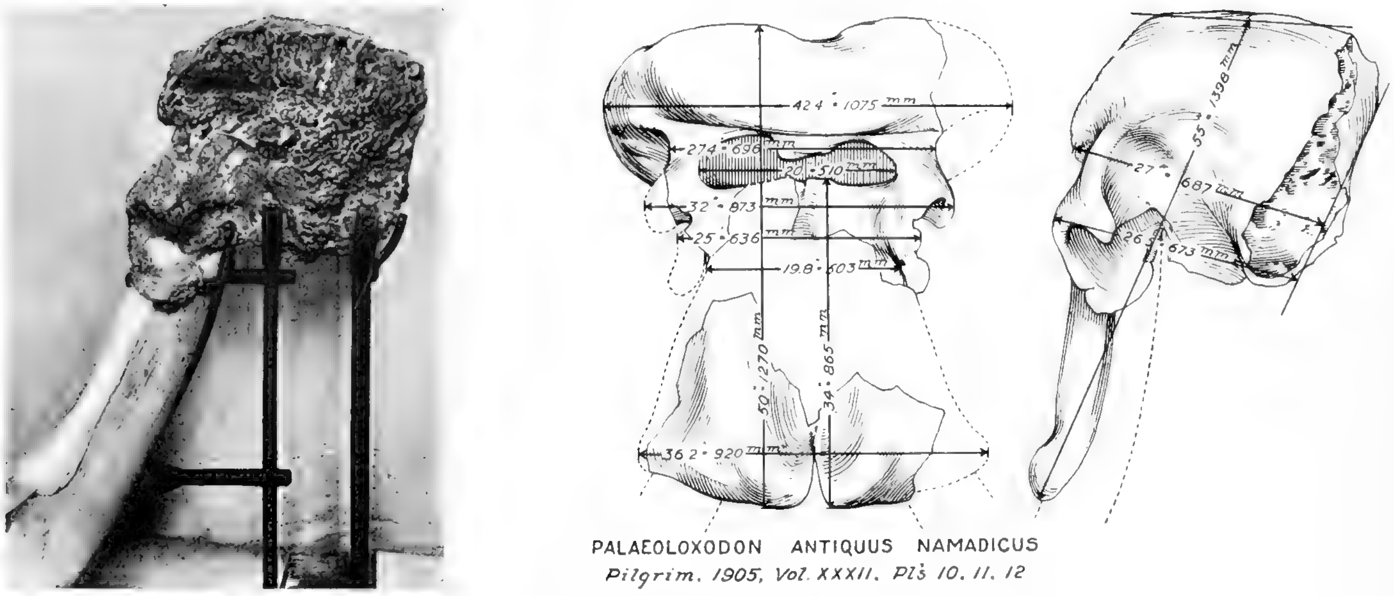
[1] [Equals *Hesperoloxodon antiquus*—see footnote on p. 1222 above.—Editor.]



Large Male Cranium of Palæoloxodon namadicus of the Godávari Alluvium
One-twentieth natural size

Fig. 1110. *Palæoloxodon namadicus*, large male cranium discovered in the Godávari Alluvium, at Nandúr Madmóshwar, India (cf. Pilgrim, 1905, Pls. 10, 11, 12). Measurements after Pilgrim and Osborn.

	P. namadicus	*H. ant. italicus*
Fronto-vertical length	1270 mm.	1400 mm.
Transverse premaxillary rostrum	920	857
Occiput, transverse width across	1075	875

This comparison shows that *Palæoloxodon namadicus* exceeds in breadth, while *Hesperoloxodon antiquus italicus* exceeds in depth.

"Estimates of Skeletal and Flesh Height.—It is important to compare the estimates of the shoulder height derivable from the scapula as well as from the cranium; they are found to agree exactly, as shown below. Neither the Upnor nor the Italian specimen is full-grown, yet combined they afford a priceless means of estimating the height of the full-grown '*Elephas antiquus*.' "

"In each of the four above dimensions the scapula of *Pal. ant. italicus* is from fifteen to thirty-five per cent. larger than that of *Lox. africana oxyotis* ('Jumbo,' Amer. Mus. Dept. Mam. 3283); the actual skeletal height of "Jumbo" is 10 ft. 5¾ in. or 3194 mm.; consequently if we add fifteen per cent. (the difference in scapular height) to the skeletal height of "Jumbo" we obtain 3673 mm. or 12 ft. ⅝ in. as the estimated skeletal height of the *Pal. ant. italicus* type; this agrees with the height estimated from the proportions of the cranium, namely, about 3673 mm. or 12 ft. ⅝ in."

"In height the scapula of *Pal. ant. italicus* is about ten per cent. less than that of *Pal. ant.* (*andrewsi?*)[1] of Upnor, the skeletal height of which is 3700 mm. or 12 ft. 1⅝ in."

Pal. ant. italicus:
  Total skeletal height *estimated* from proportions of cranium 3673 mm. = 12 ft. ⅝ in. ca.
  Total skeletal height *estimated* from proportions of scapula 3673 mm. = 12 ft. ⅝ in. ca.
Pal. ant. (*andrewsi?*)[1]:
  Total skeletal height *estimated* from proportions of entire fore limb 3700 mm. = 12 ft. 1⅝ in."

"To this estimated skeletal height should be added about six and one-third per cent. to obtain the height in the flesh, giving us an estimated height at the shoulder of 3905 mm. or 12 ft. 9¾ in."

"*Pal. ant. italicus* of Pignataro Interamna, adult:
  Estimated height in the flesh 3905 mm. = 12 ft. 9¾ in.
Pal. ant. (*andrewsi?*)[1] of Upnor, young adult:
  Estimated height in the flesh 3934 mm. = 12 ft. 10⅞ in.
Lox. africana, adult:
  Height in the flesh 3450 mm. = 11 ft. 3⅞ in."

"The Pignataro Interamna specimen is several years older than the Upnor specimen, as indicated by the fact that the posterior ridge-plates of the second molar and the anterior ridge-plates of the third molar [Fig. 1101] are in use, while in the Upnor specimen the ridge-plates of the second molar only are in use. Comparison with the growth of the large African elephant "Khartum" in the New York Zoological Park shows that in captive conditions at the age of twenty-seven years the animal grows three-quarters of an inch a year. By such an estimate the Pignataro Interamna adult is about five years older than the Upnor young adult; had it continued to increase in height, the fully adult bulls would measure about 13 ft. 6 in. in height, or two feet above the shoulder height of a large fully adult African bull elephant."

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[1] [Equals *Hesperoloxodon antiquus*—see footnote on p. 1222 above.—Editor.]

FEMORAL LENGTHS AFTER POHLIG

The *humerus* bears a more constant ratio to the height of an elephant than the *femur*, because the relative height of the fore and hind quarters differs in each phylum. Yet the *femoral* lengths where obtainable are very important as a key to *pelvic heights*. Consequently the following notes as to femoral lengths recently communicated by letter from Dr. Hans Pohlig, the leading historian of the fossil proboscideans of western Europe (whose portrait beside the femur of Rome appears in figure 1111 of the present Memoir) are of interest.

Pohlig, 1929–1931.—(Letter, "Bonn, 5.III, 29"): "The . . . *antiquus* femur (from Rome) is now at Lumbres, P. Calais (Dr. Pontier) [see Fig. 1111]. As my own height is 1 m. 70, the femur will be about 1 m. 50, but it is not quite entire and not quite adult; that of the large Taubach skeleton (the huge grinders of which are figured in my Mon., plate VI, fig. 2*a*, 1*b*, and the premaxillaries (average breadth 1 meter! ibid. fig. 3), is 1 m. 60 at least. . . . The largest [*Archidiskodon*] *meridionalis* femur at Florence is 1 m. 38. The [*Parelephas*] *trogontherii* femur at Budapest 1 m. 43, according to my Stegodon Osteologie."

The length measurements of femora thus kindly recorded by Doctor Pohlig for comparison with those recorded by others are as follows:

Hesperoloxodon antiquus italicus ref., femur from Rome now at Lumbres, Pas de Calais (Dr. Pontier), partly restored	1500c mm.	4 ft. 11 in.
Hesperoloxodon antiquus germanicus ref., femur of large Taubach skeleton (cf. huge molars, Pohlig, 1889, Pl. VI, figs. 2*a*, 1*b*)	1600c mm.	5 ft. 3 in.
Archidiskodon meridionalis ref., Florence Museum	1380 mm.	4 ft. 6¼ in.
Parelephas trongontherii ref., femur, Budapest	1430 mm.	4 ft. 8¾ in.

COMPARATIVE BRAIN CHARACTERS OF LOXODONTA AND HESPEROLOXODON

Although the entire upper portion of the type cranium of *Hesperoloxodon antiquus italicus* was practically destroyed, the solid walls of the brain case fortunately were preserved, revealing for the first time the brain characters of a member of the '*Elephas antiquus*' phylum. For immediate comparison intracranial casts were taken from the relatively young crania of the African and Indian elephants in the American Museum, affording the following brain cube comparison, as displayed in figure 1112:

	Brain and Volume cubic centimeters		Weight grams
C, *Elephas indicus* (Amer. Mus. 54261), young adult male	6686	—20%	= 5349
B, *Loxodonta africana* (Amer. Mus. 51939), young adult male	6651	—20%	= 5321
A, *Hesperoloxodon antiquus italicus* (Amer. Mus. 22634), adult male not full grown	6807	—20%	= 5446

Approximate Estimates.—Comparing the figures given by Weber (1896, p. 115) and by Gregory and Colbert (letters, May 26, 1931), the actual brain weight is about twenty per cent. less than the cubic centimeter volume of the intracranial cast (which includes the space occupied by the dura mater and the intracranial fluids). Consequently by deducting twenty per cent. from the above intracranial casts shown in figure 1112, we obtain a means of estimating the actual brain weight of *Hesperoloxodon antiquus italicus*, in comparison with the brain weights of *Elephas indicus* and *Loxodonta africana*, as in table below (p. 1252).

It will be observed that the large male *Elephas indicus* ratio (1:560) is selected for the male *Hesperoloxodon antiquus italicus*, in which the estimated brain weight of gr. 5446 and estimated body weight of gr. 3,049,760 exceed the corresponding weights of the large male Indian elephant. If we select the *Loxodonta africana* ratio (1:375), the body weight of *H. ant. italicus* falls to gr. 2,042,250, probably very much under the actual weight of an animal 12 ft. in height at the shoulder. These roughly approximate estimates of body weight are given in comparison with the maximum actual body weights in pounds and grams below.

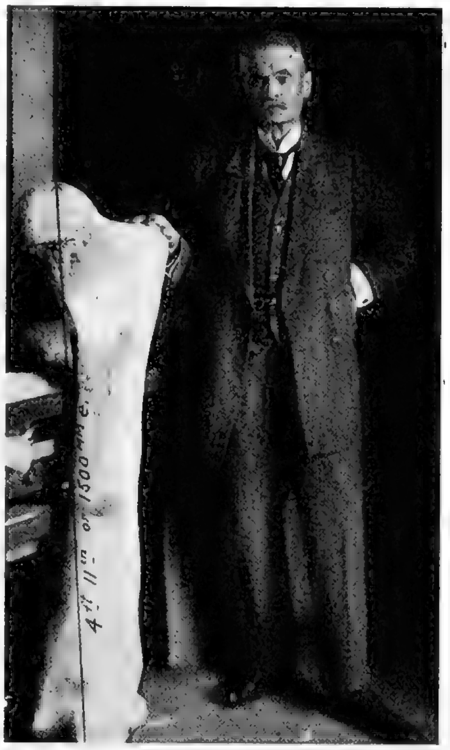


Fig. 1111. Left femur, largely restored, referable to *Hesperoloxodon antiquus italicus*. After photograph bearing the following inscription: "H. Pohlig mit dem Femur des Elefas antiquus von Rom. September 1918." This femur is estimated at 4 ft. 11 in. or 1500 mm.

From these actual figures of the ratio between body weight and shoulder height we may allow *an average of sixty-five pounds for one inch in height*; with such allowance we deduce the following:

Hesperoloxodon antiquus italicus, age 50 yrs. height 12 ft., estimated body weight 9360 lbs. or 4,250,000 grs.

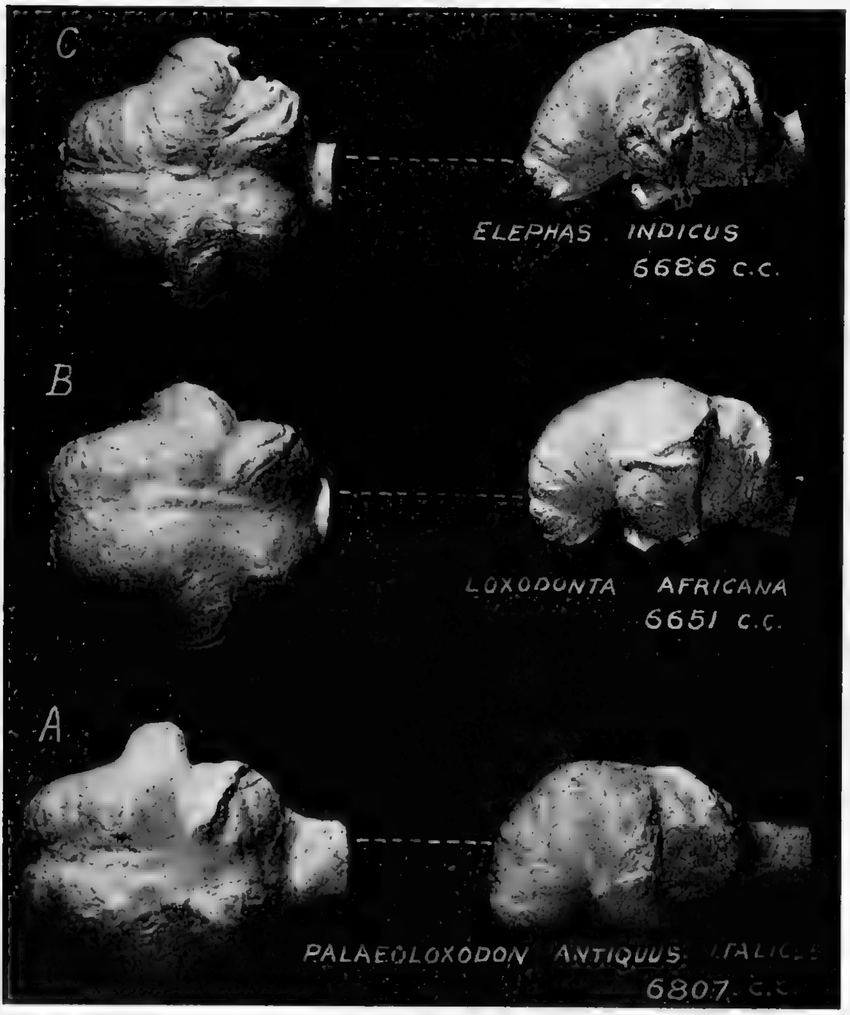
Max Weber (1896)	Brain weight (in grams)	Weber's ratio of brain weight to body weight	Body weight estimated in grams	Body weight estimated from brain weight in pounds
Elephas indicus, large male	5430	1: 560	3,048,000	6705
Elephas indicus female (20 yrs. old)	4660	1: 439	2,047,000	4503
Loxodonta africana, female	4370	1: 375	1,642,000	3612
Amer. Mus. specimens				
C, *Elephas indicus*, male, not fully adult	5349	1: 560	2,995,440	6590
B, *Loxodonta africana*, male, about half grown	5321	1: 375	1,995,375	4390
A, *Hesperoloxodon ant. italicus*, male, three-fourths adult	5446	1: 560 (Indian ratio)	3,049,760	6709

ACTUAL BODY WEIGHTS (NEW YORK ZOOLOGICAL PARK)

	Age	Height	Estimated Weight	
Loxodonta africana oxyotis (male)	28 yrs.	10 ft. 8½ in.	8,500 lbs.	3,863,636 gr.
Elephas indicus (female)	35	8 ft. 6 in.	6,200	2,818,182
Loxodonta africana pumilio (female)	13	6 ft.	2,450	1,113,636
Elephas indicus (male)	4	4 ft. 5 in.	1,025	465,909

Elephas indicus average weight from measurements of eight individuals:

Average age: 30 yrs. Average height: 7 ft. 9⁹⁄₁₆ in. Average body weight 6074 lbs. or 2,750,000 grs.



INTRACRANIAL CASTS OF PALÆOLOXODON [=HESPEROLOXODON], LOXODONTA, AND ELEPHAS

Fig. 1112.—Intracranial brain cast of the Pignataro Interamna type specimen (Amer. Mus. 22634) compared with casts of the African elephant and the Indian elephant, as exhibited in the American Museum. After Osborn, 1931.846, p. 22, fig. 16.

	Brain Cube c.c.
C, *Elephas indicus* (Amer. Mus. 54261)	6686
B, *Loxodonta africana* (Amer. Mus. Dept. Mam. 51939)	6651
A, *Palæoloxodon [Hesperoloxodon] antiquus italicus* (Amer. Mus. 22634)	6807

SUMMARY OF THE PIGNATARO INTERAMNA ELEPHANT, PALÆOLOXODON [HESPEROLOXODON] ANTIQUUS ITALICUS, NOVEMBER, 1931

Taken altogether, the Pignataro Interamna straight-tusked elephant, genotypic species[1] of *Hesperoloxodon*, marks a great step forward in our knowledge of the '*Elephas antiquus*' phylum of Falconer, 1847, 1857. (1) The lofty cranial dome resembling that of the *Elephas indicus* of India is in close agreement with the "Eléphant tracé en rouge" in the cavern of Pindal, also with the anterior dorsal hump of the Spanish and Algerian elephants (Fig. 1047). The entire cranial and dorsal hump silhouette (Fig. 1092) is quite different from that of the African elephant (Fig. 1093). (2) The cranial profile of *Hesperoloxodon italicus* is also entirely different from that of *Palæoloxodon namadicus* (Fig. 1070) and of *P. melitensis*[2] (Fig. 1121), both of which are characterized by a very prominent transverse frontal ridge for the attachment of the gigantic proboscis. (3) In both cranial and dental characters *H. italicus* differs profoundly from the African elephant, which is extremely conservative in its structure, in fact, much more conservative than any of the known fossil Pleistocene elephants of Eurasia. (4) *H. italicus* affords additional and positive evidence that the dwarfed elephants of the Mediterranean Islands (*Palæoloxodon falconeri*, *P. melitensis*, and *P. mnaidriensis*) were not derived from the '*Elephas antiquus*' phylum of Falconer, as hitherto universally believed, but sprang from some undiscovered phylum of elephants of African origin, which gave rise on the one hand to the dwarfed elephants of the Mediterranean Islands and on the other to the gigantic *P. namadicus* phylum of India and the Far East extending to Japan.

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[1] [See footnote on page 1247 above.—Editor.]

[2] [In Fig. 1121 referred to *Palæoloxodon mnaidriensis*.—Editor.]

HESPEROLOXODON ANTIQUUS GERMANICUS OF STEINHEIM

Many years ago (Feb. 26, 1901) Dr. Eberhard Fraas presented to the American Museum from his Steinheim collection a finely preserved superior molar, r.M^3 (Amer. Mus. 10655—Fig. 1115) which agrees approximately in its ridge formula ($M\ 3\frac{19}{}$) with progressive molars ($M\ 3\ \frac{18\frac{1}{2}}{18+}$) from the Taubach-Weimar region of Thuringia, described by Pohlig (1888–1891), as set forth in pages 1233–1235 of the present Memoir, and by Soergel (1912, Tab. I, VII, VIII).

During the years 1926 and 1928 the region of Steinheim on the river Murr yielded to the Stuttgart Museum a number of invaluable remains of "Der Waldelefant" or 'forest elephant,' a preliminary account of which has been given by Dr. Fritz Berckhemer, Konservator, Württemberg Naturaliensammlung, Stuttgart. Following his two articles of 1929 and 1930, Doctor Berckhemer kindly furnished (April, 1931) excellent photographs (Fig. 1114), with complete measurements, for inclusion in the present Memoir in comparison with *Hesperoloxodon antiquus italicus* (Fig. 1105).

Geologic Age.—Doctor Berckhemer describes (1929, p. 188) the related geologic levels and fauna as of *2d Interglacial* age. The present author regards them rather as of *3d Interglacial* age.

"[I. 1926] In Steinheim wurde zuerst die Kiesgrube von Sigrist aufgesucht, die 1926 einen ersten Schädel von *Elephas antiquus* geliefert hat, und in der vor zwei Jahren ein prächtiger Riesenhirsch . . . zutage kam. Im SO-Teil der Grube sind die Schotter zurzeit in einer Mächtigkeit von rund 10 m freigelegt; der anstehende Untergrund soll nach Aussage des Besitzers noch 3 m tiefer leigen. Über dem Schotter folgt hier eine Decke von rund 4 m Löss und Lösslehm. Der *antiquus*-Schädel [1926] lag in diesem Teil der Grube 8 m tief unter der Grenze Schotter/Lösslehm. Kurz vor der Tagung war noch ein Stirnschädel vom Wisent gemeldet worden, dessen Bergung in Gegenwart der Gesellschaft vorgenommen wurde. Das eindrucksvolle Stück fand sich im tieferen Teil der über dem *antiquus*-Lager folgenden Mammutschotter. Auf der gegenüberliegenden Seite der Strasse befindet sich die neue Grube von Bauer, die durch den Fund des *Buffelus murrensis* Berckh. . . . bekannt geworden ist."

"[II. 1928] Sie lieferte im vergangenen Jahr einen zweiten Schädel von *Elephas antiquus,* der soweit erhalten war, dass er zur vollen Gestalt ergänzt werden konnte. Er ermöglichte zusammen mit einem im Juni d.J. im selben Lager gefundenen *antiquus*-Stosszahn (einen Rest der bei der Bergung entstandenen Höhlung konnten die Teilnehmer in der Schotterwand noch bemerken) erstmals eine Rekonstruktion des *Elephas antiquus* durch den Stuttgarter Oberpräparator Böck."

In his article of 1930 (pp. 332, 333) Doctor Berckhemer adds the fauna:

"*e*" In this layer were discovered remains of (1) *Rhinoceros merckii,* (2) of the Murr water-buffalo (*Buffelus murrensis*), (3) a nearly perfect skull of the diluvial urus or aurochs (*Bos primigenius*), (4) very numerous remains of the stag (*Cervus elaphus*) and of the royal stag (*Megaceros*). Obviously during this period of the deposition of the lower white sands "*e*", the surrounding country was richly forested as the home of the forest elephant, '*Elephas antiquus,*' of the urus and of *Megaceros*; the layer "*e*" containing the cranium and tusks of *Elephas antiquus* of Steinheim accordingly belongs toward the close of the *2d Interglacial* period [*3d* (Osborn)]; in the same layer was found (5) the remains of *Leo* sp., of *Ursus* sp., and of *Meles taxus* (the badger).

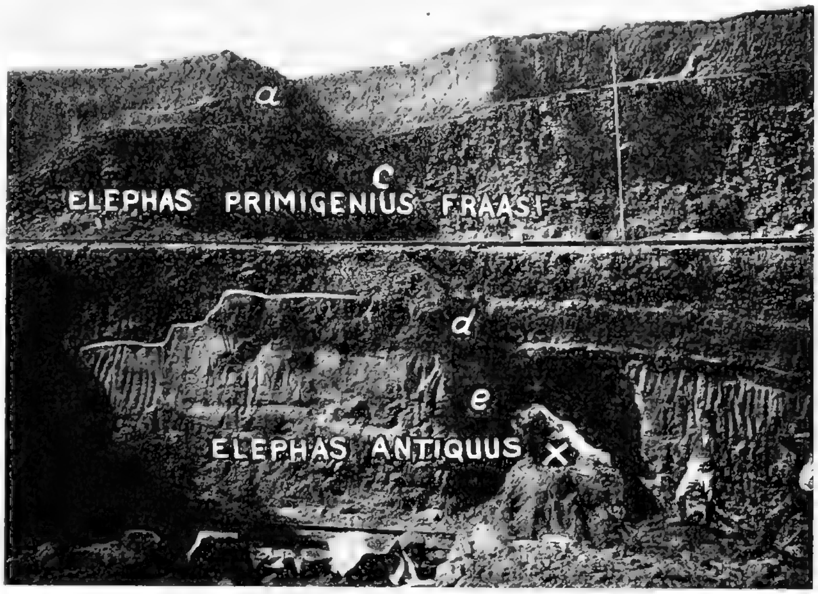


Fig. 1113. W. Bauer Quarry, Steinheim a. d. Murr, showing the Site of the 1928 Discovery

After original photograph kindly furnished by Dr. Berckhemer (cf. Berckhemer 1930, pp. 331, 332)

a. "Zu oberst haben wir noch Lösslehm und Löss."

c. "Es folgen nach oben rötlichbraune Schotter (c), die links im Bild auch an die Stelle der hier durch eine abtragende wasserströmung zuvor entfernten Lettenbank treten (Abtragungszone durch weisse Linie bezeichnet)." [*Elephas primigenius fraasi.*]

d. "Daruber liegt eine feinsandige Lettenbank von graugrüner bis dunkelbrauner Farbe."

e. [The layer consists of clear white sand of variable fineness, which toward the bottom is mingled with more or less gravel and sand.]

x. *Elephas antiquus* [*Hesperoloxodon antiquus germanicus*] cranium of 1928.

"*d*" The fine-sanded loam bank is a still water formation in which are found remains of *Bos, Megaceros,* and the bear (*Ursus arctos*).

"*c*" The reddish brown gravels and sands mark a decided change of climate, the *Elephas primigenius fraasi* replacing the 'forest elephant'; other remains, including the wisent (*Bison priscus*) and the wild horse (*Equus* sp.) which is quite frequent, indicate a drier and colder climate of the Glacial Period, with restricted forests.

Osborn: The *Elephas antiquus* horizon of Steinheim yields a fauna distinctive of the *3d Interglacial* stage, consequently these Steinheim remains may be provisionally referred to *Hesperoloxodon antiquus germanicus.*

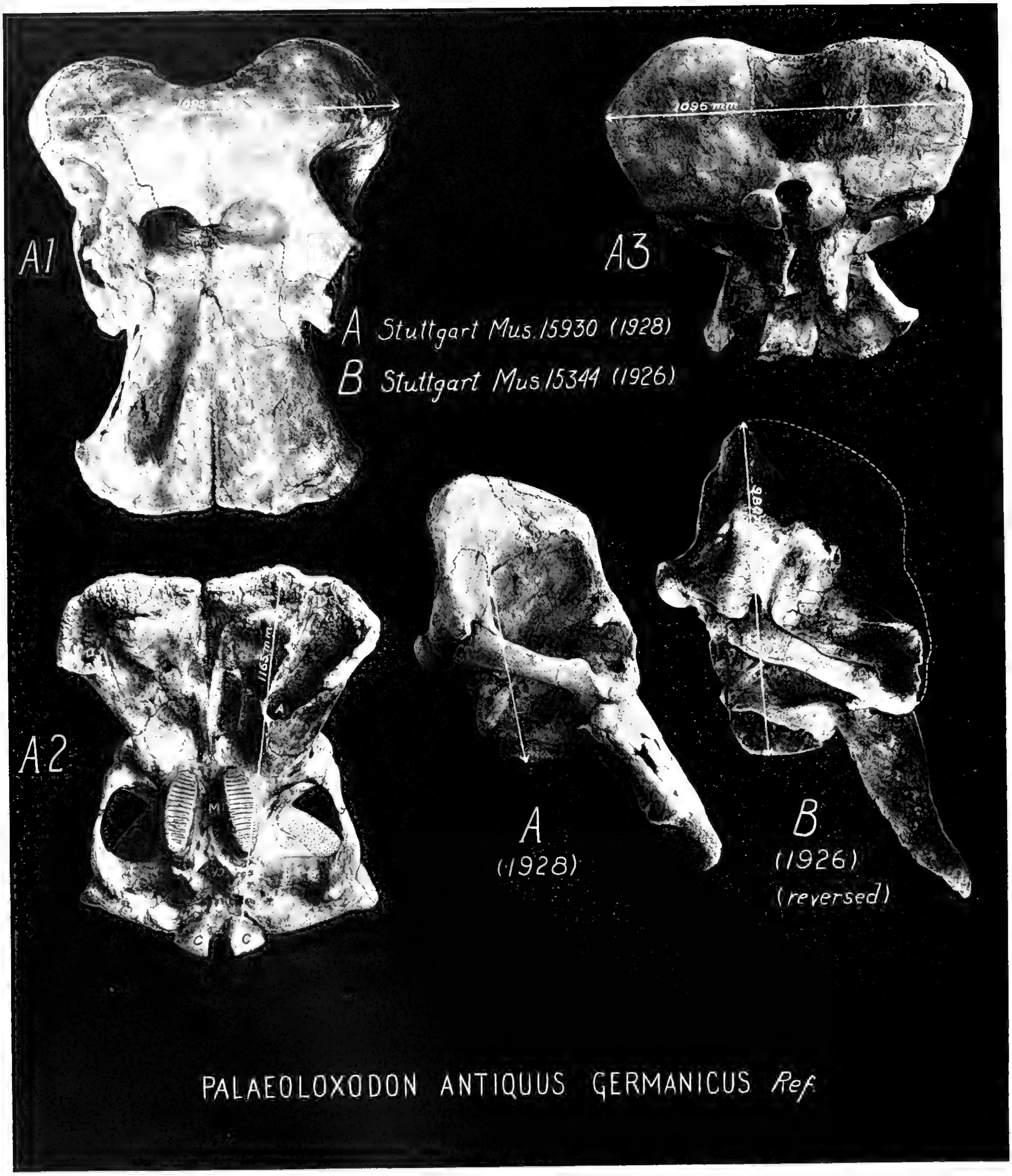
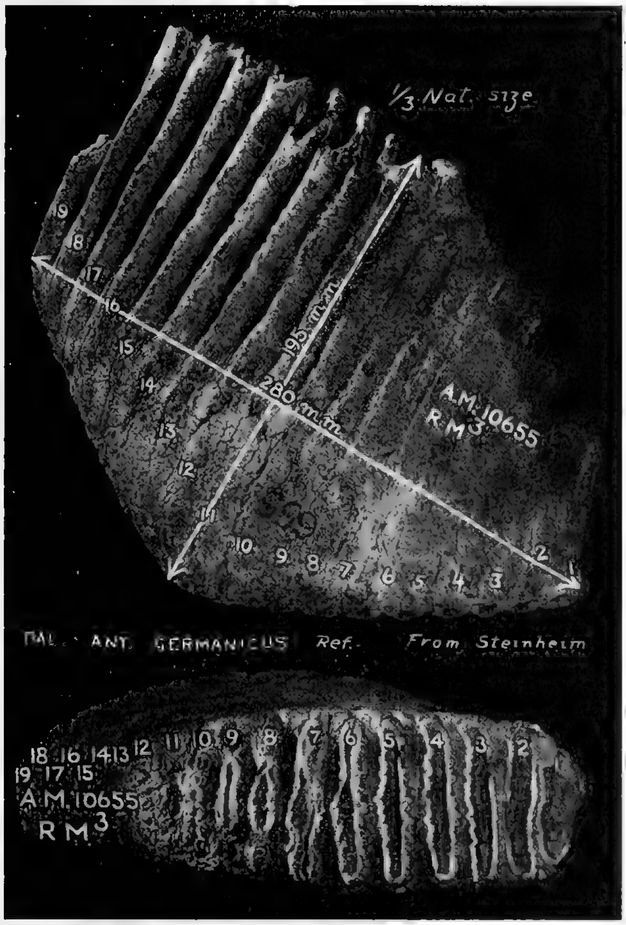


Fig. 1114. Hesperoloxodon antiquus germanicus ref. of Steinheim on the Murr, in the Stuttgart Museum

After photographs and indicated measurements (March 16, 1931) by Dr. F. Berckhemer. Reduced to a uniform scale of one-sixteenth natural size

A, Right lateral view of cranium of 1928 (Stutt. Mus. 15930).
A3, Posterior or parieto-occipital view of cranium.
A1, Superior view of cranium
A2, Palatal view of cranium, with third superior grinding teeth.
B, Cranium of 1926 (Stutt. Mus. 15344, reversed for comparison).

Observe the relatively broad, low occiput, exceeding in breadth that of *Hesperoloxodon antiquus italicus* (Fig. 1105), correspondingly broad in the palate. The adult cranium (B) is about equal in depth (bathycephaly) to that of *H. ant. italicus*. See comparative measurements (p. 1255). Observe also 16+ ridge-plates exposed out of a probable total of 19 ridge-plates (cf. Fig. 1115).



Referred Molar of Hesperoloxodon antiquus germanicus

Fig. 1115. Third superior molar of the right side, r.M^3 (Amer. Mus. 10655) found at Steinheim a. d. Murr and presented to the American Museum by Dr. Eberhard Fraas, February 26, 1901.

Observe 19 ridge-plates, 11 anterior worn; length 280 mm., height of 11th ridge-plate 195 mm. Compare figure 1088B, Weimar molar, length 295 mm., height 190 mm.; also figure 1114 A2, Steinheim specimen.

STEINHEIM SKULLS OF 1928 (FIG. 1114A) AND OF 1926 (FIG. 1114B)

Doctor Berckhemer's descriptions refer to an exceptionally perfect cranium (Fig. 1114, A) of 1928 (Stutt. Mus. 15930) and to a less perfect cranium (Fig. 1114, B) of 1926 (Stutt. Mus. 15344). These priceless new materials, with associated faunal remains, apparently enable us to establish the cranial characters of *Hesperoloxodon antiquus germanicus* as quite distinct from those of *H. ant. italicus* above described.

In Cranium A of 1928 (Stutt. Mus. 15930) sixteen ridge-plates are *exposed* on the worn surface of the left superior molar, l.M^3; the right molar, r.M^3, may show 15–16 ridge-plates as compared with the perfect superior molar (Fig. 1115) from Steinheim exhibiting 19 ridge-plates as compared with M 3 $\frac{18\frac{1}{2}}{18+}$ in the Taubach-Weimar horizons described by Pohlig (1888–1891) and Soergel (1912) mentioned above. The diameters of the crowns of M 3 are:

	A. Stutt. Mus. 15930	Amer. Mus. 10655
R. M^3 Length of 16 exposed ridge-plates	245 mm.	
Breadth	88	
Length of 11 exposed ridge-plates		168 mm.
Maximum height of 11th ridge-plate		195
L. M^3 Length of 16 exposed ridge-plates (total ?+17)	245	
Breadth	89	

In the Stuttgart Museum l.M^3 (No. 15344) exhibits a total of 19 ridge-plates; an r.M^3 (Stutt. Mus. 16515), length 300 mm., exhibits +18+ ridge-plates (total 20 ridge-plates).

In the right maxillary alveolus of A (Stutt. Mus. 15930) are found the remains of a tusk (Berckhemer, 1930, Abb. 5) which had been broken off during the lifetime of the animal, consequently the right alveolus had been diminished by the formation of new bony parts and the right premaxillary had correspondingly diminished in breadth as compared with the normal width of the left premaxillary (Fig. 1114, A2). The remaining left superior incisive tusk was not preserved with the skull. [The isolated right tusk, 3500 mm. in length, does not belong to this skull; Doctor Berckhemer, however, does not hesitate to ascribe it to the same species.]

Total width of premaxillaries as seen from above	850 mm.
Width of diminished right premaxillary	400
Width of full-grown left premaxillary	450

The cranial and dental characters of this remarkably well-preserved individual are beautifully shown in the accompanying photographs (Fig. 1114, A1–3). The principal measurements, in addition to those given above, are the following:

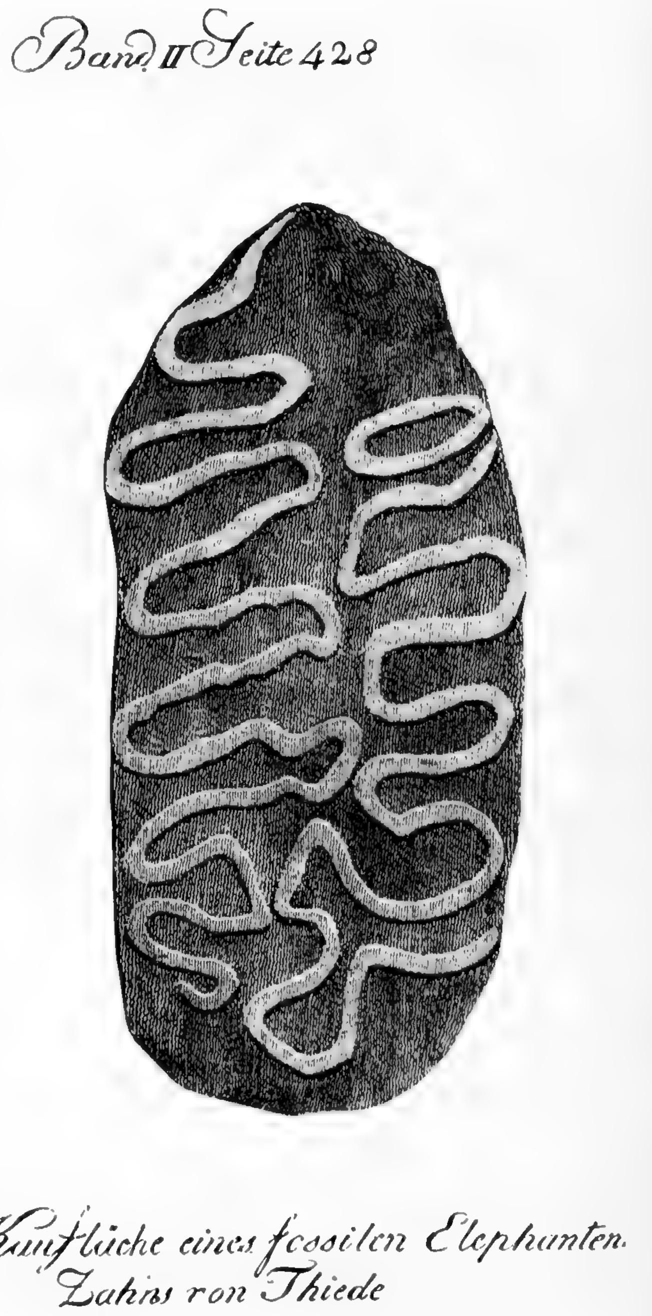
	Hesperoloxodon antiquus germanicus A: Cranium of 1928 (Stutt. Mus. 15930)	*Hesperoloxodon antiquus germanicus* B: Cranium of 1926 (Stutt. Mus. 15344)	*Hesperoloxodon antiquus italicus* (Amer. Mus. 22634)
Summit of occiput to tip of right premaxillary	1375 mm.		1400 mm.
Transverse across widest portion of occiput	1095		875e
Mid-length of cranium, occipital condyles to tip of premaxillary junction	1150		1130
Breadth across zygomatic arches	880	865 mm.	750e
Summit of parieto-occipital crest to attritional surface of r.M^3 (bathycephaly)	860	980+	990e
Summit of parieto-occipital crest (partly restored) to attritional surface of l.M^3	885		
Width of occipital condyles	295	307	280
Width of anterior nares	400		385e
Width across narrowest portion of maxillaries	545	480	530
Width across broadest portion of premaxillaries	850	890e	857
Occipital condyle to front border of orbit (left)	775	850	
Occipital condyle to front border of orbit (right)	765		820e

The B Cranium of 1926 (Stutt. Mus. 15344), from the above measurements, appears to belong to a somewhat older individual than the A Cranium of 1928 (Stutt. Mus. 15930). More of the dental ridge-plates in M^3 are exposed; the bathycephaly or depth (from the summit of the occiput to triturating surface of M^3) is 980+ mm. as compared with 860 mm. in the A Cranium of 1928; the horizontal measurement from the occipital condyle to the front border of the orbit in the B Cranium of 1926 is 850 mm. as compared with 775 mm. in the A Cranium of 1928; the occipital condyles as well as the orbit are more prominent and pediculated; the premaxillaries are more elongated. In brief, the B Cranium of 1926 (Stutt. Mus. 15344) belongs to a fully mature and adult, but not aged, bull of *Hesperoloxodon antiquus germanicus*.

HESPEROLOXODON ANTIQUUS GERMANICUS FROM THURINGIA

Elephas antiquitatis Krüger, 1823 [= Hesperoloxodon antiquus germanicus].—(Krüger, 1823, p. 832): "Eleph. antiquitatis. Europäischer Elephant. An einigen Orten in Europa werden einzelne Spuren von einer Elephantenart angetroffen, welche weniger dem asiatischen, und mehr dem afrikanischen Elephanten sich nähert. Sind auch die bei Thiede*) und bei Teschen am Boberfluss im Jahre 1795 entdeckten Zähne**) ächte Mammuthszähne mit abgenutzter Kaufläche gewesen, und gehören sie nicht einer davon abweichenden Art an, so zeigen sich doch bisweilen andere, welche den Zähnen des afrikanischen Elephanten sehr ähnlich sind. Selbst Cuvier, der nur eine Art, die asiatischen Mammuths, annimmt, muss doch zugestehen, dass sich bei Eichstedt ein dem afrikanischen Elephantenzahn ähnlicher gefunden habe***). So sind wahrscheinlich mehrere Ueberreste in den Sammlungen vorhanden, nur hat man sie bis jetzt übersehen, und aus Vorliebe für den nordischen Elephanten auf Abweichungen nicht geachtet."

Osborn, 1931: It is apparent from the above description, and figure from Breislak reproduced herewith, that Krüger had in mind the 'ancient' or 'straight-tusked' elephant as distinct in tusk structure from the modern Asiatic elephant and resembling rather the African elephant, since the first locality mentioned (Thiede) is in the Thuringian region, northern Germany. The tooth which we may select as Krüger's type (after Breislak, Bd. II, s. 428) is not improbably of the same *3d Interglacial* geologic age as Pohlig's and Stefănescu's '*Elephas germanicus*' of the Taubach-Weimar horizon. It is therefore for German palæontologists to determine whether the specific name '*Elephas antiquitatis*,' 1823, has priority over '*Elephas germanicus*' Pohlig—Stefănescu.



Hesperoloxodon antiquus germanicus Ref.

Fig. 1116. Type molar of *Elephas antiquitatis* Krüger, 1823, referred by the present author to *Hesperoloxodon antiquus germanicus*. After Breislak, 1820, p. 428.

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*Abgebildet in Breislak's Lehrb. d. Geologie. 2ter Bd. S 428.

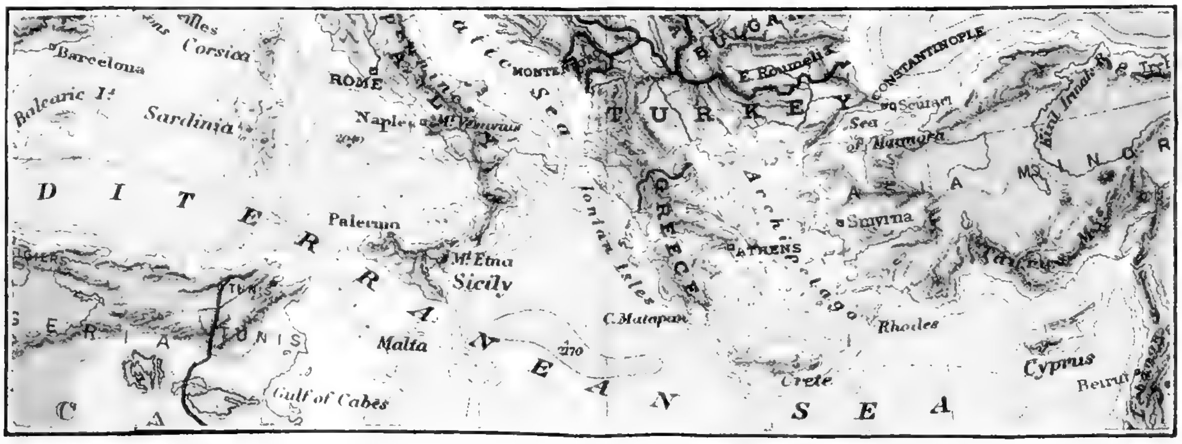
**Arch. d. Urw. III., 2. S 396.

***J'ai vu une molaire donnée comme d'Aichstedt, dans la collection d. M. Ebel à Brêmen; quoique d'apparence bien fossile, elle étoit remarquable par sa ressemblance avec les molaires d'Afrique. Rech. s. 1. Oss. foss. Th. I. S. 127.

IV. EXTINCT DWARFED SPECIES OF THE MEDITERRANEAN ISLANDS

(Continued from pp. 1182, 1183 of the present chapter, modified and extended; see also observations of Raymond Vaufrey, 1929, below, pp. 1268 to 1272.)

Of the greatest interest are the full-sized and dwarfed species of elephants found in the cavern deposits of the different islands of the Mediterranean, successively described by Busk (1867), Falconer (1862, 1868), Leith Adams (1870, 1874), Forsyth Major (1883), and Bate (1903 and 1907). To the latter author we are especially indebted for the most recent discoveries and descriptions of these insular proboscidean species and subspecies. Falconer and the older authorities related these dwarfed species to the '*Elephas antiquus*' of the European continent, but subsequent discovery has shown that they are more probably derived from certain of the extinct ancestral African species described below as *Palæoloxodon* (synonym *Pilgrimia*).[1]



BATHYMETRIC MAP OF THE MEDITERRANEAN ISLANDS

Fig. 1117. Dwarfed Mediterranean species of elephants are found east to west on the islands of Cyprus, Crete, Malta, Sicily, and Sardinia. The white areas are within the 100 fathom line (600 feet); the maximum depression of the sea or elevation of the land (in certain limited areas) was to the 216 fathom line (about 1300 feet) or 400 m. Reproduced by permission of Longmans, Green and Company, publishers, from map edited by Chisholm and Leete.

From a recent hydrographic chart (No. 4300 U. S. Navy, January, 1930), it is shown that the submerged land connections are now at the following depths: (1) Cyprus to Turkish mainland (N.E. to Gulf of Alexandria near Adana, Turkey), shallowest depth 320 fathoms, 1920 feet; (2) Crete to Turkish mainland (N.E. via island of Rhodes), shallowest depth 250 fathoms, 1500 feet; (3) Malta to Sicily, shallowest depth 74 fathoms, 444 feet; (4) Sicily to Italy across strait of Messina, 109 fathoms, 657 feet; (5) Tunisia to Sicily, shallowest depth, 168 fathoms, 1008 feet; (6) Sardinia to Corsica, 46 fathoms, 276 feet; Corsica (northern end) to Italy, 140 fathoms, 840 feet.

Before discussing these questions of affinity, and the conclusions reached by Pohlig (1888, 1893), we may follow the chronological order of systematic description.

1862	Malta, Zebbug Cave.	Type molar tooth of *Elephas* (*Loxodon*) *Melitensis* Falconer, described in 1862.
1867	Malta, Zebbug Cave.	Type skeleton of *Elephas falconeri* Busk, 1867.
1870	Malta, rock-fissure, Mnaidra Gap.	Type molar of *Elephas mnaidræ* Adams, 1870.
1883	Sardinia, sands of Morimentu.	*Elephas Lamarmorae* Major, 1883. Carpal and tarsal bones.
1903	Cyprus, Kerynia Hills.	*Elephas cypriotes* Bate, 1903. Cotype molars.
1907	Crete, cave near Cape Maleka.	*Elephas creticus* Bate, 1907. Nine imperfect molars, portion of an incisor, and dorsal half of a vertebra.
1912	Sicily, Carini.	*Elephas antiquus* var. *insularis* Soergel (name only).

Falconer was the first to describe before the British Association, October 6, 1862 (see "The Parthenon" for October 18, 1862, p. 780), one of the pygmy elephants of Malta found in the Zebbug Cave, namely, *Elephas*

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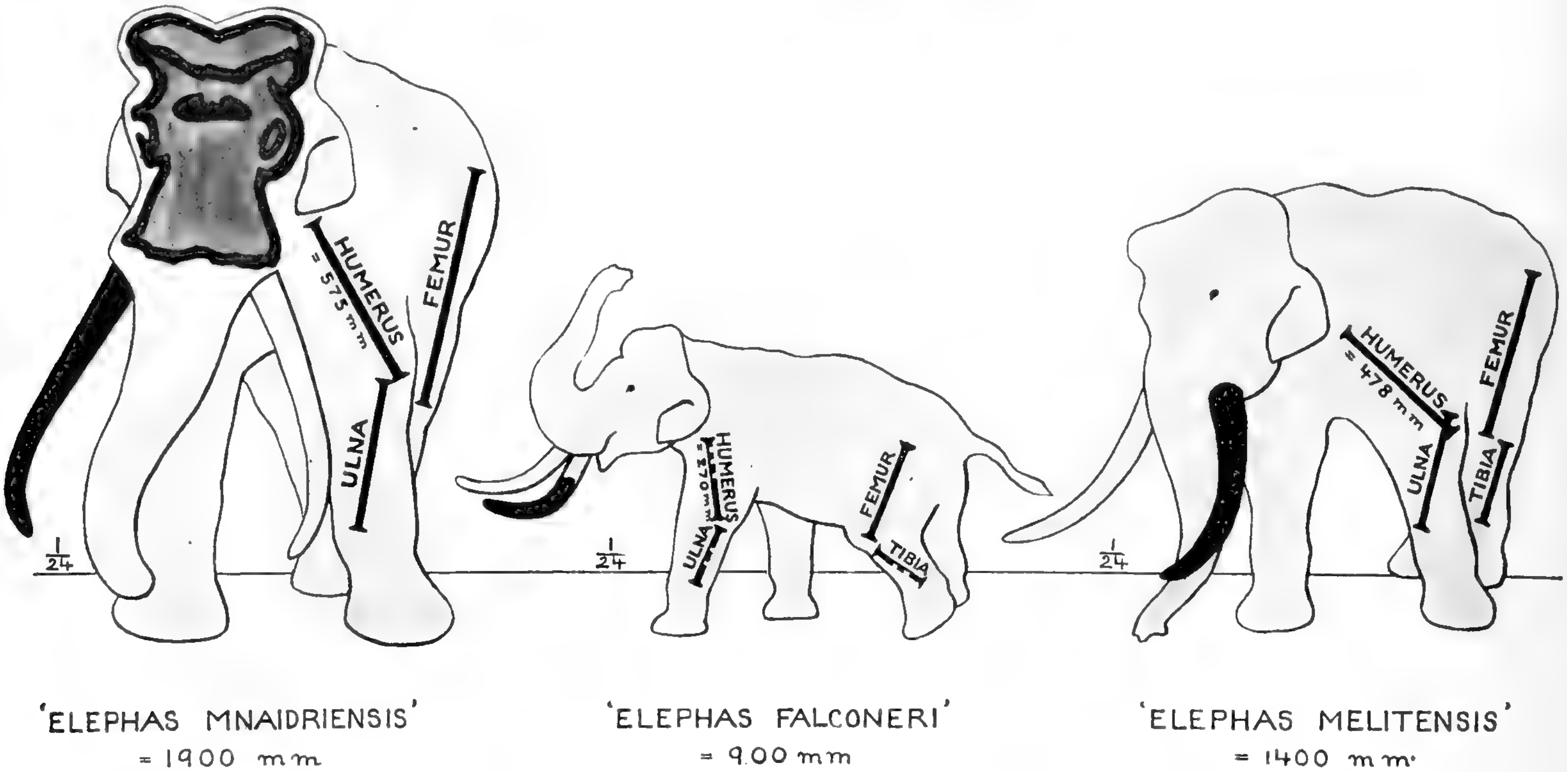
[1] [In a footnote on page 1 of Professor Osborn's Novitates article on the "Primitive *Archidiskodon* and *Palaeoloxodon* of South Africa" (Osborn, 1934.925) appears the following statement: "*Pilgrimia* Osborn (December 20, 1924) is antedated by *Palæoloxodon* Matsumoto (September 20, 1924)." Hence *Pilgrimia* becomes a synonym of *Palæoloxodon*.—Editor.]

Melitensis, which is supplemented by more detailed description in the "Palæontological Memoirs" of 1868 (Falconer, 1868, Vol. II, pp. 292-308). According to Leith Adams (1870, p. 223), *Elephas falconeri*, although found in the same cave, represents a more diminutive animal than the *Elephas melitensis* of Falconer.



Dwarfed Elephants [Palæoloxodon (syn. Pilgrimia)] of the Mediterranean Islands

One twenty-ninth natural size. Compare Figure 1119

Fig. 1118. Diagrammatic representation of the manner in which the three restorations of figure 1119 were calculated. As a rule the humerus affords the most reliable estimate of the height of the shoulders. Comparison of the relative heights of these animals may best be made with the Upnor elephant (*Hesperoloxodon antiquus*).

	Length of Humerus	Estimated Shoulder Height
H. antiquus of Upnor	1290 mm. = 4 ft. 2¾ in.	3700 mm. = 12 ft. 1⅝ in.
P. mnaidriensis of Malta	573 mm. = 1 ft. 10½ in.	1900 mm. = 6 ft. 2¾ in.
P. melitensis of Malta	478 mm. = 1 ft. 6¾ in.	1400 mm. = 4 ft. 7⅛ in.
P. falconeri of Malta	270 mm. = 10⅝ in.	900 mm. = 2 ft. 11⅜ in.

Broadly speaking, *Palæoloxodon mnaidriensis* is one-half the height of *Hesperoloxodon antiquus* of Upnor, *P. melitensis* is about two-fifths the height of *H. antiquus*, while *P. falconeri* is only about one-fourth the height of the Upnor animal. As fully explained in the text, these dwarfed elephants appear to be related to *P. namadicus* and to be descended from North African ancestral stages of *Palæoloxodon*.

The cranium (Fig. 1121)[1] and jaw (Fig. 1124) of *Palæoloxodon melitensis*, with broadly overhanging fronto-parietal crest, more closely resemble the *P. namadicus* of India than the *Hesperoloxodon antiquus* of western Europe.

Origin.—Comparison of the *type* grinding teeth of the dwarfed Mediterranean species with the type grinding teeth of the extinct African species described below reveals a striking general resemblance in the *narrow* proportions and in the rudiment or absence of the 'loxodont sinus,' characters which appear to relate these teeth to the phylum *Palæoloxodon* of Africa rather than to the typical *Loxodonta africana*. In Europe some of the *narrow-toothed* varieties of *Hesperoloxodon antiquus* may be related to the dwarfed insular elephants.[2] The characteristic body height and progressive ridge formulæ of these species were estimated by the authors as follows:

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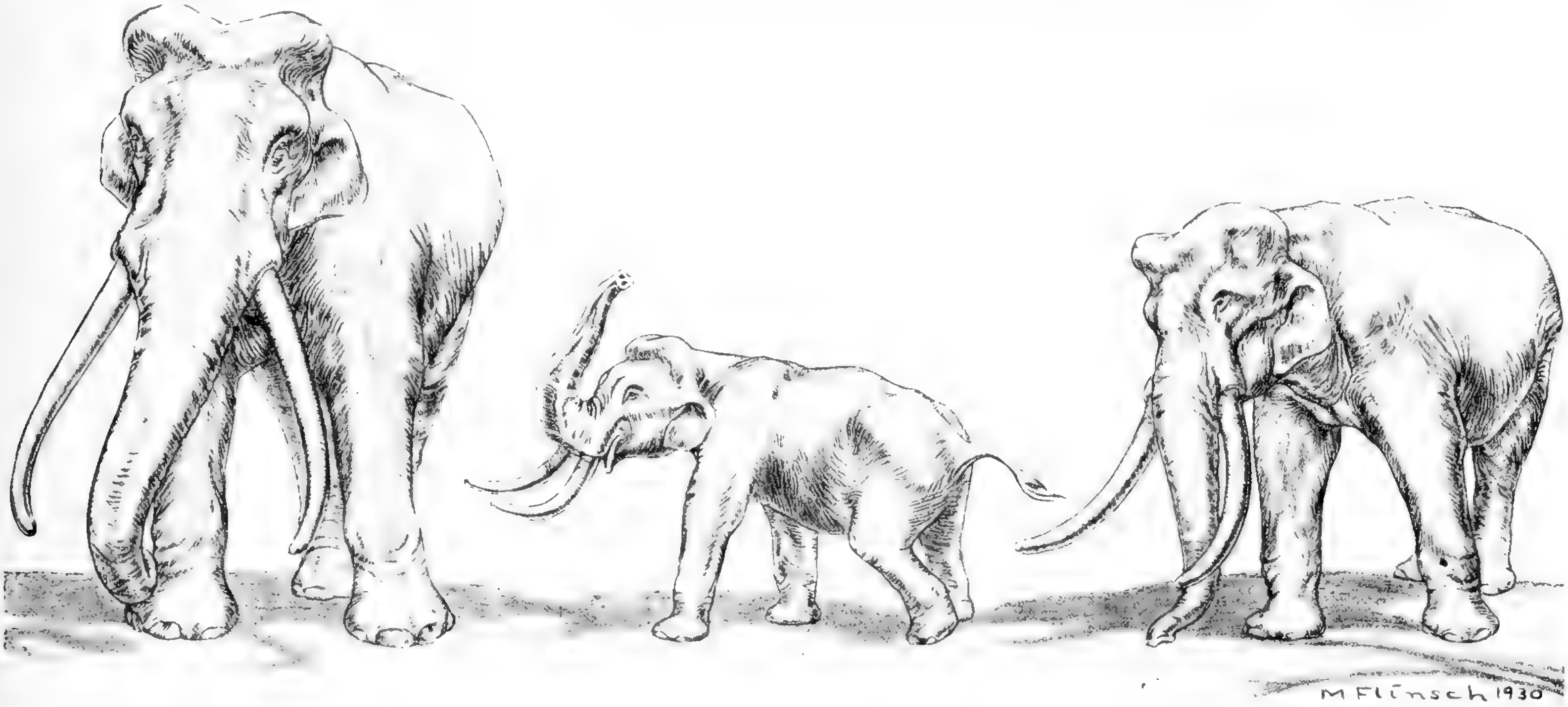
[1] [Referred by Professor Osborn to *Palæoloxodon mnaidriensis*.—Editor.]

[2] [See the opinion expressed by Professor Osborn on page 1252 above regarding the origin of the dwarfed elephants of the Mediterranean Islands.—Edtior.]

		Height	Ridge Formula
Malta	*Elephas melitensis* Falc., 1862, 1868	Height of Indian Tapir, i.e., 5 feet (1525 mm.)	M 3 $\frac{12}{12}$
	Elephas falconeri Busk, 1867	2 ft. 6 in. (760 mm.) to 3 feet (915 mm.)	M 3 —
	Elephas mnaidræ Adams, 1870	6 to 7 feet (1830 mm. to 2135 mm.)	M 3 $\frac{13}{13\frac{1}{2}}$
Sardinia	*Elephas Lamarmoræ* Major, 1883	2 to 3 feet (610 mm. to 915 mm.)	M 3 —
Cyprus	*Elephas cypriotes* Bate, 1903	?2 to 3 feet (610 mm. to 915 mm.)	M 3 $\frac{11-12}{11-12}$
Crete	*Elephas creticus* Bate, 1907	Slightly larger than *E. cypriotes*, max. 5 feet (1525 mm.)	M 3 $\frac{}{11+}$



DWARFED ELEPHANTS, PALÆOLOXODON (SYN. PILGRIMIA), OF THE MEDITERRANEAN ISLANDS

One twenty-fourth natural size. Compare Figure 1118

Fig. 1119. In descending scale of size from '*Elephas mnaidriensis*' (left), to '*E. melitensis*' (right), to the diminutive '*E. falconeri*' (center), the relative heights are very carefully estimated from the respective length of the limb bones (indicated in solid black in Fig. 1118). Drawn under the direction of the author by Margret Flinsch, 1930.

The larger stage (*E. mnaidriensis*) is that of which the complete cranium is known [=the *E.* (*antiquus*) *Melitæ* of Pohlig, 1893], probably resembling that of '*E. namadicus*'; the same form of cranium is attributed to *E. melitensis* and *E. falconeri*. The tusks are drawn from the recent comparative figures of Vaufrey. This restoration is entirely different from that of Adams (Fig. 1127), which is based solely on the theory that these dwarfed elephants were related to *Loxodonta africana*.

YOUNG AFRICAN PYGMY[1] ELEPHANT PASSING BENEATH ADULT INDIAN FEMALE ELEPHANT

Fig. 1120. The existing pygmy elephant *Elephas africanus pumilio* Noack, 1906, from the French Congo, attaining a height of 2 ft. 6 in. at the age of two and a half years and corresponding at this age in size with the most diminutive fossil species *Palæoloxodon falconeri*, *P. lamarmoræ*, and *P. cypriotes*. Photograph (1922) by Mr. Elwin R. Sanborn through the courtesy of the New York Zoological Park. The intimate companionship and friendship of these two elephants has been described (1928) in William T. Hornaday's volume "Wild Animal Interviews."

At the age of four and a half years the same animal attained a height of 4 ft. 4½ in., corresponding more nearly with *Palæoloxodon melitensis* and *P. creticus*. The full-grown *Loxodonta africana pumilio* (Amer. Mus. Dept. Mam. 35591) attains a height of 6 ft. 8 in., equaling that of the larger fossil Mediterranean species.

[1] [See editorial note on p. 1196 above.]

In comparison, the dwarfed or small forest[1] elephant of the Congo, *Loxodonta africana pumilio* (Fig. 1120), measured 2 ft. 6 in. in height (=760 mm.) at the age of two and a half years; consequently at this age it agreed with *Palæoloxodon falconeri*. The same animal at the age of four and a half years measured 4 ft. 4½ inches in height at the shoulders, and therefore attained the approximate height (=5 ft. or 1525 mm.) of *P. melitensis* or of *P. creticus*.

Ridge Formulæ.—In the following *type* and subsequent descriptions the ridge formulæ of the species are very carefully cited from the earlier and later publications by the authors who have successively treated the dentition of these interesting animals, namely, Falconer, Leith Adams, Pohlig, Busk, and Bate. These *type ridge formulæ* constitute an important part of the type descriptions; they differ widely from the *collective ridge formulæ* cited from Raymond Vaufrey (1929) below; compare, for example, the ridge formula of '*E. mnaidriensis*' ($\mathrm{M}\ 3^{12-13}_{12-13}$),

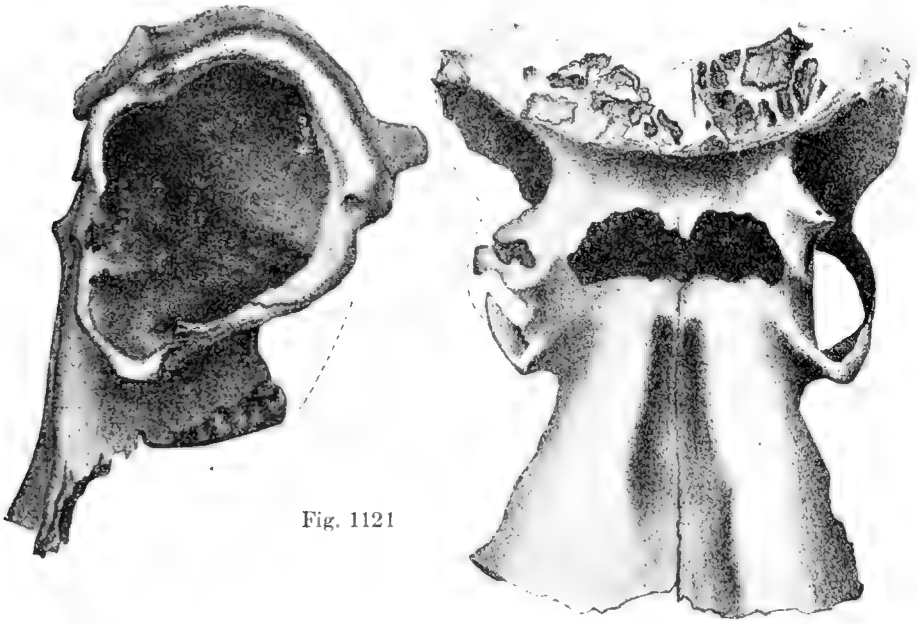
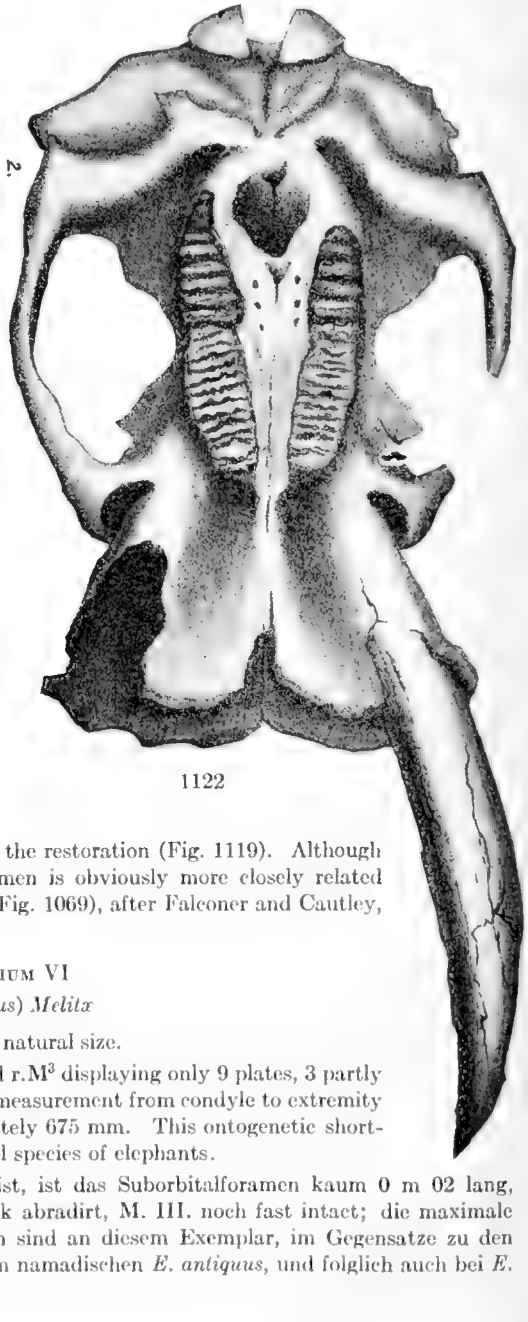


Fig. 1121



1122

Referred Palæoloxodon mnaidriensis. Palermo Collection, Cranium I

One-eighth natural size. After Pohlig, 1893, who referred it to *Elephas* (*antiquus*) *Melitæ*[2]

Fig. 1121. Fully adult cranium of "*Elephas* (*antiquus*) *Melitæ*" Falc., from the Interglacial layers of the Grotta di Pontale, Carini, Sicily, the most complete cranium in the collection of the Palermo Museum, exhibiting the characteristic prominent transverse frontal crest, comparable to that of '*Elephas* [=*Palæoloxodon*] *namadicus*' of India. After Pohlig, 1893, Taf. I, figs. 1, 1*a*, reduced to one-twelfth natural size.

For the proportion of this insular form to the full-grown *Palæoloxodon namadicus*, see figure 1069, also the restoration (Fig. 1119). Although these dwarf insular species of Malta usually have been referred to '*Elephas antiquus*,' the present specimen is obviously more closely related to *P. namadicus*, and, while adult, belongs to an individual inferior in size to the juvenile *P. namadicus* (Fig. 1069), after Falconer and Cautley, 1847, Pl. XXIV.A, fig. 4*a*.

Referred Palæoloxodon mnaidriensis. Palermo Collection, Cranium VI

One-eighth natural size. After Pohlig, 1893, who referred it to *Elephas* (*antiquus*) *Melitæ*

Fig. 1122. Palate of juvenile cranium (Palermo Coll. VI), after Pohlig, 1893, Taf. II, fig. 2, one-eighth natural size.

This juvenile cranium (Palermo Coll. VI), retaining the 8+ ridge-plated r.M^2, also the partly erupted r.M^3 displaying only 9 plates, 3 partly worn, is in a larger but younger stage than the adult cranium (Palermo Coll. I—Fig. 1121 herewith). The measurement from condyle to extremity of maxillaries is approximately 744 mm., while in the adult cranium the same measurement is approximately 675 mm. This ontogenetic shortening and deepening of the cranium as it grows older conforms with what we observe in the crania of all species of elephants.

(Pohlig, *op. cit.*, p. 90) "An Cranium VI, das, in basaler Ansicht, auf Tafel II, in Fig. 2, abgebildet ist, ist das Suborbitalforamen kaum 0 m 02 lang, obwohl der Schädel, der grösste sicilische, mehr als 0 m 7 maximaler Länge misst . . . . Die M. II. sind stark abradirt, M. III. noch fast intact; die maximale Breite der Schnauze, welche extrem divergente Lateralränder hat, beträgt ca. 0 m 48. . . . die Condylen sind an diesem Exemplar, im Gegensatze zu den kleineren Cranien, nach Form, Stellung und relativer Grösse sehr ähnlich wie bei dem typischen und dem namadischen *E. antiquus*, und folglich auch bei *E. africanus*."

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[1] [See editorial note on p. 1196 above.]

[2] Referred to '*Elephas mnaidriensis*' by Leith Adams and Raymond Vaufrey.

given by Leith Adams, 1874, p. 112, with that (M 3 $\substack{\times 14 \times \\ ? \times 17}$) of Vaufrey (1929, pp. 124, 128). It appears that Vaufrey (pp. 113–132, figs. 28–37) has intermingled the ridge formulæ of the grinding teeth of more than one species or mutation.

Pohlig on the Monospecific 'Elephas (antiquus) Melitæ' of Sicily

Pohlig (1893, pp. 75–108) described and figured fully the referred '*Elephas* (*antiquus*) *Melitæ*' Falc. from the famous elephant grotto of Carini, Sicily, where were found in great numbers the skeletal parts of this dwarfed species with numerous remains of the degenerate stag *Cervus* (*elaphus*) *Siciliæ* and less abundant remains of both *Bos* and *Bison*, *Bos* (*taurus*) *primigenii* and *Bison priscus*; also traces of *Hyæna spelæa* and of partly worked flint implements. Pohlig (*op. cit.*, p. 100) maintains that the cranial structure of the six best preserved skulls from Carini closely unites these insular pony-elephants with the European *E. antiquus*. The extraordinary transverse frontal crest (Fig. 1121) observed in the adult Carini specimens Pohlig regards as the compelling ground for the *specific union* of the three forms "*E. Namadi*, *E. Melitæ* und *E. antiquus typus*." Pohlig adheres (p. 101) to the conclusions reached in his earlier (1891) monograph on *E. antiquus* of the specific identity of *E. namadicus* and *E. antiquus*.

From these remains his geological inferences are as follows (*op. cit.*, p. 82):

> 2. Landverbindung zwischen Sicilien und Italien einerseits, Afrika andererseits [error], und Einwanderung der grossen Säugethiere, gegen das Ende der ersten diluvialen Glacialperiode.
>
> 3. Erneutes säculares Steigen des Meeresspiegels zu Beginn der diluvialen Interglacialzeit, erneute Isolation Siciliens, Ausbildung von diminutiven Formen grosser Säugethierarten, Anhäufung von Skelettheilen solcher auch in der Grotta di Pontale, einem Zufluchtsort namentlich für Elephanten, Edelhirsche und Rinder.

Pohlig's palæontological observations are (*op. cit.*, p. 83):

> In meiner angeführten Monographie des *Elephas antiquus* habe ich zuerst nachgewiesen, dass die Angaben de Anca's und Gemmellaro's von *Elephas armeniacus* und *E. africanus* aus Sicilien, ebenso die Artbezeichnungen *E. Falconeri* von Busk [Footnote: 'Transactions of the zoolog. soc. London 1868, VI., p. 5, No. 10.'] und *E. mnaidriensis* von L. Adams [Footnote: '*Ibid.* vol. IX, p. 1. 1877.'] aus Malta auf Irrthum beruhen, und dass der '*Elephas melitensis*' von Falconer nichts anderes ist, als eine insulare Diminutivrasse des Urelephanten, *Elephas antiquus*, für welche ich daher die Bezeichnung *E.* (*antiquus*) *Melitæ* Falc. vorschlug. Zugleich erbrachte ich die ersten Nachweise der Thatsache, dass die gleiche Zwergelephantenrasse, wenn auch nicht bis zu gleich extremer Grössenreduction, wie auf dem kleinen Malta, auch auf Sicilien und in anderen Mittelmeergegenden gelebt hat.

From this Carini grotto Pohlig describes and figures the most completely preserved crania in the Palermo Museum (*op. cit.*, pp. 84-98) concluding as follows (p. 98):

> Die Vereinigung der drei Speciesnamen *Elephas melitensis* Falc., *E. Falconeri* Busk und *E. mnaidriensis* L. Adams, die lediglich auf den Dimensions verhältnissen des Malteser Materiales beruhten, unter der Rassenbezeichnung *E. antiquus Melitæ* Falc. wurde in meiner Elephantenmonographie vorzugsweise begründet auf die wichtigste bis dahin bekannte Eigenthümlichkeit jener Diminutivformen, deren Dentition,—wobei der überraschende Nachweis in der Gestaltung der frühesten, in gleicher Weise sonst bisher von keiner Species bekannten Milchdentition der Malteser Elephanten, auch für den typischen Taubacher *E. antiquus*, ausschlaggebend sein musste.

According to my observations, Pohlig continues (*op. cit.*, p. 99), neither in North Africa nor in lower Italy (in the west) does any fossil species occur excepting '*E. antiquus*,' while in the Mediterranean islands not a single trace has been found of a specimen of the normal continental size. In Sicily occur only the larger types of dwarfed *E. antiquus* from one-half to two-thirds the size of the normal continental forms, corresponding in dimensions with the larger *E. mnaidriensis* Leith Adams of Malta. This larger subspecies obviously lived in Malta at a time when it was united with Sicily by a land bridge. There followed more severe living conditions on the smaller rocky islands which brought about further degeneration and reduction in size. According to the dimensions of the numerous limb bones from the Grotta di Pontale of Carini, in comparison with those of the typical *E. antiquus* the Sicilian *Elephas* (*antiquus*) *Melitæ* in its full growth or adult condition was about the size of a middle-aged Indian elephant; whereas on the continent the intermediate stages between the full-sized *E. antiquus* and the smaller forms of the known *E. antiquus* remains from the islands are without exception diminutive and all the specimens from the very rich material of Carini belong to the diminutive race. On the other hand, the single Sicilian molar found elsewhere corresponds with a small example of the true *E. antiquus*.

Osborn (1928) entirely dissents from Pohlig's opinion as to the specific union of *Elephas antiquus* Falc., 1847, with the earlier described species *E. namadicus* Falc., 1846. It would appear that Pilgrim (1905) was influenced by Pohlig in the same erroneous confusion of these two very distinct species of western Europe and the Siwaliks.

Osborn, 1930: The cranium of *E.* [*Palæoloxodon*] *mnaidriensis* (Fig. 1121) closely resembles that of *E.* [*Palæoloxodon*] *namadicus* of the Nerbudda, India, in the transverse crest; it differs widely from the cranium of *Palæoloxodon* [*Hesperoloxodon*] *antiquus italicus* (Fig. 1106).

SYSTEMATIC DESCRIPTION OF MEDITERRANEAN ISLAND SPECIES

Compare the specific revision by Vaufrey (1929)

Palæoloxodon melitensis Falconer, 1862

Figures 1041, 1068, 1069, 1118, 1119, 1123, 1124, 1127, 1131, 1133, Pl. xxiii

Pleistocene, Zebbug Cave, island of Malta. From the lower cave deposits or levels.

Elephas melitensis Falconer, 1862, "The Parthenon," October, 1862, p. 780; also "Palæontological Memoirs," 1868, Vol. II, pp. 292, 299, 307, 308. Type.—Third upper molar of the left side, l.M^3 (Brit. Mus. 44312). Horizon and Locality.—Pleistocene, Zebbug Cave, island of Malta. Type Figure.—*Op. cit.*, 1868, Vol. II, Pl. xi, figs. 1, 1*a*.

Type of Palæoloxodon melitensis

Fig. 1123. *Elephas Melitensis* Falconer, 1862, 1868, type molar tooth (Brit. Mus. 44312), one-half natural size. After Falconer, 1868, Vol. II, Pl. xi, figs. 1, 1*a*: "Views in plan and profile of last upper true molar, left side. Described at page 292." Lydekker (1886, p. 154) catalogues this tooth (Brit. Mus. 44312) as follows: "The third left upper true molar; from Zebbug Cave. Described and figured in 'Falconer's Palæontological Memoirs,' vol. ii. p. 292, pl. xi. figs. 1, 1*a*; and noticed by Busk, *op. cit.* [1867.1], p. 296, and by Leith-Adams, *op. cit.* [1874.1], x. p. 28. *Leith-Adams Collection. Purchased*, 1873."

Original Description.—This elephant was found in the Zebbug Cave, and is the first described of the "pigmy" elephants of Malta. Falconer ("Parthenon," Oct. 18, 1862, p. 780—see reprint in "Palæontological Memoirs," Vol. II, p. 308) states: "The pigmy Elephant was an animal of remarkably small proportions; an adult individual could not have exceeded the Indian Tapir in height and bulk, a creature not much larger than a full-grown Hog. Contrasted with the bones and teeth of an adult African Elephant the difference in size of these portions of its frame exhibited were most striking. . . . But though so small, the skeleton agreed in every particular with the one of greatest bulk. A series of harmonies ran through the two skeletons, one bone answering to another truly, and without ordinal or generic difference. The author could refer it unhesitatingly to his subgenus *Loxodon*, in the African group of Elephants."

Supplementary Description.—Falconer described the teeth of this species at the British Association, October 6, 1862 (an abstract of which appeared in "The Parthenon," as stated above) and in 1868, Vol. II, pp. 292, 299, he designated the type as follows: "One of the most characteristic of these [fossils] is an upper molar of the left side. . . . As this specimen is about to be returned to Malta, at Captain Spratt's request, it is necessary to make an accurate description of it, to accompany the figures drawn by Mr. Dinkel. (Pl. xi. figs. 1 and 1*a*.)" He also states on pages 283, 284, that Captain Spratt had "lately discovered in Malta numerous remains of a surprisingly small fossil Elephant, of the sub-genus

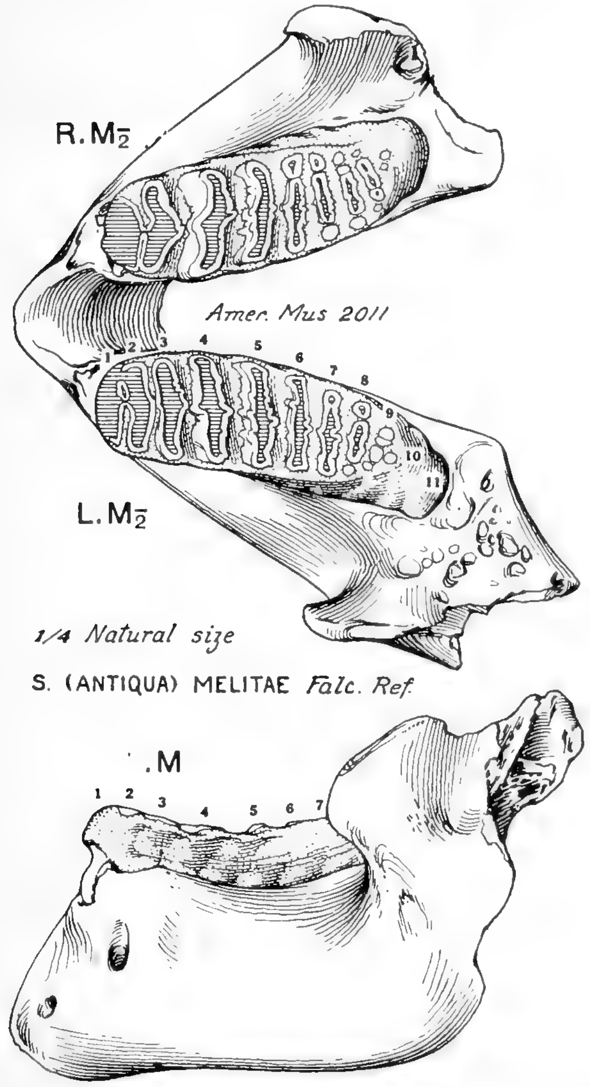
Loxodon, which I have named *E. Melitensis*," and on the "Description of Plate XI" he refers to this species as "*Elephas* (*Loxodon*) *Melitensis*."

Falconer (*op. cit.*, 1868, p. 298) gives the ridge formula of *E. melitensis* as follows:

$$[\mathrm{Dp}\ 2]\ \tfrac{3}{3}\ [\mathrm{Dp}\ 3]\ \tfrac{5}{5}\ [\mathrm{Dp}\ 4]\ \tfrac{8}{8}\ [\mathrm{M}\ 1]\ \tfrac{8}{8}\ [\mathrm{M}\ 2]\ \tfrac{9}{9}\ [\mathrm{M}\ 3]\ \tfrac{12}{12}.$$

Bate (cf. 1904, p. 357) observes that the ridge formula of *E. cypriotes* is slightly lower than that which Leith Adams, later than Falconer and after examining a further large amount of material, gives for *E. melitensis*:

$$\mathrm{Dp}\ 2\ \tfrac{3}{3}\ \mathrm{Dp}\ 3\ \tfrac{5}{5}\ \mathrm{Dp}\ 4\ \tfrac{8-9}{8-9}\ \mathrm{M}\ 1\ \tfrac{8-9}{8-9}\ \mathrm{M}\ 2\ \tfrac{10}{10}\ \mathrm{M}\ 3\ \tfrac{12}{12}.$$



REFERRED MANDIBLE OF PALÆOLOXODON MELITENSIS, FROM THE GROTTA DI PONTALE, SICILY

One-fourth natural size

Fig. 1124. Juvenile jaw containing right and left second inferior molars, r.M_2, l.M_2 (Amer. Mus. 2011), acquired by the Museum in exchange with the Padua University, Italy. Observe the sharply truncated vertical rostrum and the broad forwardly pitched coronoid process. The grinders exhibit nine complete elevated ridge-plates and two posterior half ridge-plates, or a total of eleven ridge-plates, namely, M 2 $\frac{}{9-\frac{1}{2}-\frac{1}{2}}$.

RÉSUMÉ BY DEPÉRET AND MAYET, 1923, PAGE 175

Nous résumons dans le tableau ci-dessous les données numériques qui caractérisent les *espèces* ou *mutations* du rameau de l'*E. melitensis :*

	Nombre de lames aux Mııı	Dimensions des Mııı en millimetres		
		Longueur totale	Largeur maxima	Hauteur au milieu
	—	—	—	—
E. cypriotes . . .	$\frac{11-12}{11-12}$	$\frac{94-95}{114-125}$	$\frac{25-30,5}{26-29}$	67–71
E. melitensis . . .	$\frac{8-9}{12}$	$\frac{105}{135-151}$	$\frac{33}{35}$	$\frac{84}{50}$
E. iolensis	$\frac{11}{12}$	$\frac{150}{140}$	$\frac{50}{36}$	$\frac{72}{70}$
E. mnaidrensis . .	$\frac{12-13}{12-13}$	$\frac{177}{190}$	$\frac{}{50}$	$\frac{}{70}$
E. atlanticus . . .	$\frac{12}{12}$	$\frac{324}{324-325}$	$\frac{78}{70-72}$	$\frac{}{140}$
E. priscus Falconer.	$\frac{}{10+2}$	$\frac{}{237}$	$\frac{}{72}$	$\frac{}{84}$

Palæoloxodon falconeri Busk, 1867

Figures 1068, 1118, 1119, 1127, 1131, Pl. XXIII

Pleistocene, Zebbug Cave, island of Malta. From the higher cave deposits or levels.

According to Leith Adams, this "lesser pigmy elephant" is the most diminutive insular proboscidean discovered, in which the average height could not have exceeded 2 ft. 6 in. to 3 ft. It is of more recent age than *E. melitensis.*

Elephas falconeri Busk, 1867. "Description of the Remains of three extinct Species of Elephant, collected by Capt. Spratt, C.B., R.N., in the Ossiferous Cavern of Zebbug, in the Island of Malta," etc., Trans. Zool. Soc. London, VI, Pt. V, p. 251. TYPE.—Fragments of skeleton. HORIZON AND LOCALITY.—Pleistocene, Zebbug Cave, island of Malta. TYPE FIGURE.—*Op. cit.*, Pls. XLIX, L, LI. It is not practicable to reproduce these type fragments.

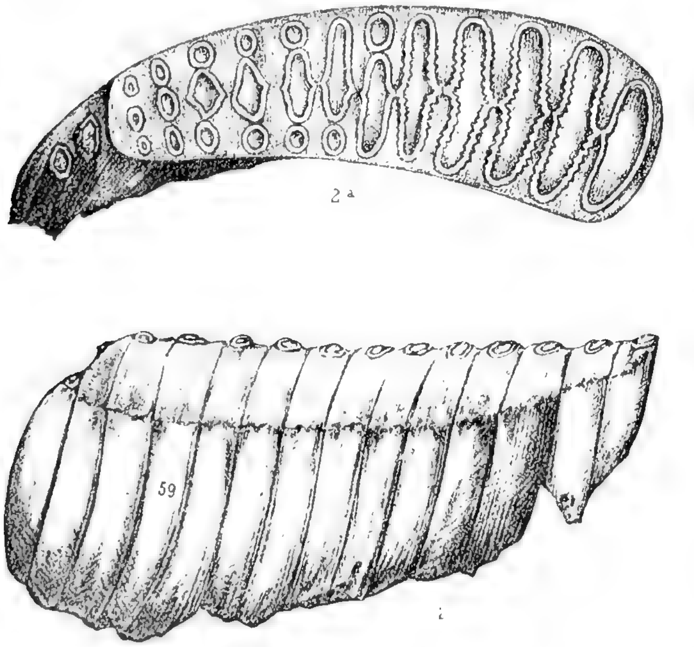
TYPE DESCRIPTION.—Busk's designation of the name and the type is as follows (*op. cit.*, p. 251): "With regard to the points of difference between it [femur of *melitensis*] and that of *E. falconeri*, I will reserve what I have to say until I come to that bone. . . . Of the remains referred to this second diminutive species, the following have been selected for the purpose of conveying some notion of the characteristics of the mature animal." The author cites portions of the skeleton, namely, atlas, several vertebræ, second rib, scapula, right humerus, left humerus, knee, phalanx, pelvis, femur, astragalus, left metatarsal. He then proceeds (*op. cit.*, pp. 251–283) to give a detailed comparison of the skeleton referred to *E. melitensis* with portions of the type skeleton of *E. falconeri*. This is followed by a very elaborate series of comparative measurements with *E. indicus, E. africanus, E. melitensis,* and *E. falconeri.*

Of this animal, Adams (1870, p. 223) remarks: "The Lesser Pigmy Elephant. *Elephas falconeri*, Busk. As before remarked, the presence of this species in the exuviæ of the Zebbug cave was determined by Mr. Busk after Dr. Falconer's death, and seemingly more or less from fragments of bones, which on comparison with similar portions of the skeleton of *Elephas melitensis* and a footbone (astragalus) discovered by me in Mnaidra gap, there appeared such differences both in size and configuration as to warrant the assumption that they represented a still more diminutive proboscidian, the average height of which at the withers could not have exceeded two feet six to three feet."

Osborn, 1930: As Busk's type (1867) is a diminutive skeleton without teeth, it remained for Bate (1903, 1904) to give the ridge formula of '*Elephas cypriotes*' cited below, without reference to the ridge formula of '*E. falconeri*.' So far as we can find, Vaufrey was the first to suggest that '*E. cypriotes*' is synonymous with '*E. falconeri*' and to give (1929, pp. 98, 99) the high collective ridge formula of *E. falconeri—E. cypriotes* as follows:

$$\mathrm{M}\ 2\ \frac{10\text{-}12}{11+}\ \mathrm{M}\ 3\ \frac{13\text{-}14}{14}.$$

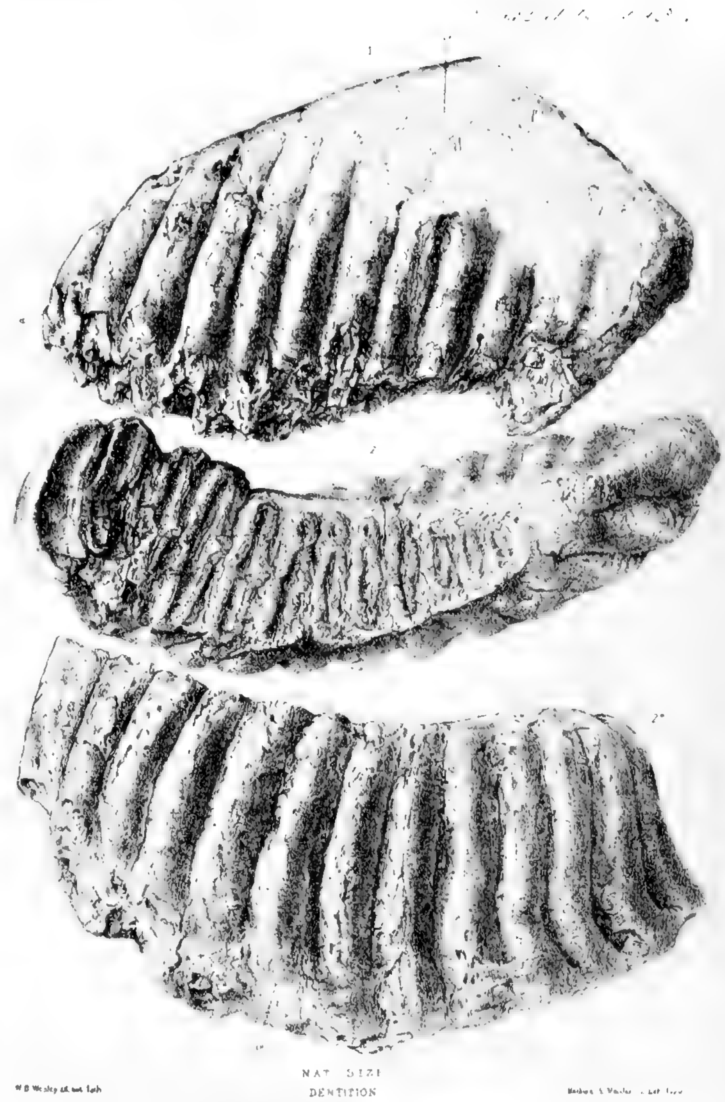
This is a higher ridge-plate formula than that ($\mathrm{M}\ 3\ \frac{12}{12}$) finally assigned to *E. cypriotes* by Bate, it equals that ($\mathrm{M}\ 3\ \frac{13\frac{1}{2}}{13\frac{1}{2}}$) of *E. mnaidriensis*, *fide* Adams. This discrepancy partly depends upon the reckoning of the half crests or talons omitted above.



Type of Palæoloxodon mnaidriensis

Fig. 1125. Type of *Elephas mnaidræ* Adams, 1870, Pl. II, figs. 2, 2a [=*Elephas mnaidriensis* Adams, 1874, p. 116], one-half natural size.

Adams (1874, p. 33) describes the same tooth and gives a much more accurate figure (Fig. 1126) of the type (Pl. VII, figs. 2, 2a). Lydekker (1886, p. 142) designated this molar (Brit. Mus. 44304) as follows: "The third right lower true molar, about one-third worn; from Mnaidra gap. Described and figured, *op. cit.* p. 33, pl. vii, figs. 2, 2a. The crown is remarkable for its excessive lateral curvature." See also figure 1126.



Type and Paratype Molars of Palæoloxodon mnaidriensis

Reproduced herewith one-half natural size

Fig. 1126. *Elephas mnaidriensis* Adams, from Mnaidra Gap, Malta. After Leith Adams, 1874, Pl. VII, figs. 1, 2 and 2a. Original figures (natural size) reproduced herewith one-half natural size.

(Upper figure, 1) Side view of a 14 ridge-plated third superior molar [paratype] of the right side, r.M^3, described by Leith Adams (*op. cit.*, p. 33) as follows:

"2. Two beautiful and highly suggestive examples of what must be considered last true molars, are represented by the entire specimens Nos. 64 & 59 (Pl. VII. figs. 1 & 2 & 2a). The former, an upper tooth, shows fourteen ridges, including the pygmy digitated posterior talon *a*, in a space of 7 inches [178 mm.]. Attached in front, although not shown in the figure, are two plates of the penultimate molar. As the crown is just being invaded, of course its pattern is not developed; the machærides are therefore well crimped, and the plates and enamel thick." Brit. Mus. 44306.

(Lower figures, 2, 2a) Crown and internal views of a right third inferior molar, r.M$_3$. This is the *type* molar; the same tooth as that shown in Adams' original figure (Fig. 1125 of the present Memoir). This beautifully preserved molar is described by Adams (*op. cit.*, 1874, p. 33) as follows:

The next, No. 59 (figs. 2 & 2a), is a much arcuated lower molar; the last ridge, although rounded and finger-like, rises like the others from the common base to the same level as the penultimate. There is a slight flattening on its base internally, but no trace of what could be called a pressure-mark. The crown is broad in front, tapering steadily posteriorly. The anterior talon is large and semilunar; and the anterior fang seems to support it and the succeeding plate only. Here we have fourteen ridges in 6.5 inches [166 mm.]." Brit. Mus. 44304.

Palæoloxodon mnaidriensis Adams, 1870

Figures 1068, 1118, 1119, 1121, 1122, 1125–1127, 1131, 1132, Pl. XXIII

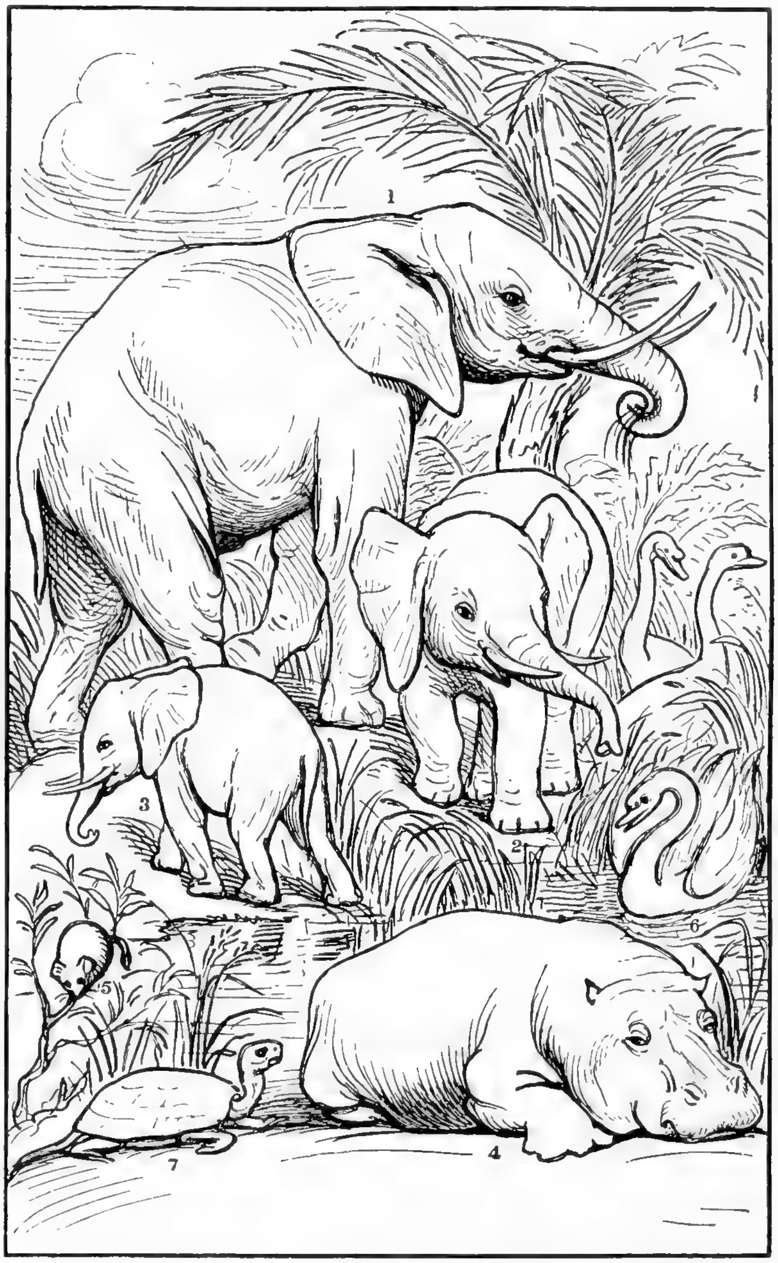
Pleistocene, Mnaidra Gap, island of Malta.

This is the third species to be described from the island of Malta. Adams (1870, p. 223) calls it the "Large Elephant of Malta," estimating its stature as six to seven feet, as compared with the *Elephas melitensis* of intermediate stature, and the *Elephas falconeri* of extremely dwarfed stature, namely, two to three feet.

Elephas mnaidræ Adams, 1870. "Notes of a Naturalist in the Nile Valley and Malta," etc., 1870, p. 223. TYPE.—A last lower molar of the right side, r.M_3 (Brit. Mus. 44304). PARATYPE.—A third superior molar of the right side, r.M^3 (Brit. Mus. 44306). HORIZON AND LOCALITY.—Pleistocene, Mnaidra Gap, island of Malta. TYPE FIGURE.—*Op. cit.*, Pl. II, figs. 2, 2*a*; also 1874, Pl. VII, figs. 2, 2*a*. Paratype, *op. cit.*, 1874, Pl. VII, fig. 1.

TYPE DESCRIPTION.—Adams (1870, p. 223) distinguishes this as "The Large Elephant of Malta," estimating its average stature (*op. cit.*, p. 228) as six feet ten inches to seven feet as compared with the average height of *E. falconeri* of two feet six inches to three feet (*op. cit.*, p. 223). As *E. falconeri* is distinguished by its extremely dwarfed stature, *E. mnaidræ* is distinguished by its relatively large stature, and *E. melitensis* by its intermediate stature. Adams (*op. cit.*, p. 228) concludes: "Thus, to all present appearances, we have represented by the remains hitherto collected in the Maltese islands no less than three distinct species of elephants of about the proportions indicated, and represented in the spirited and well-executed drawing, page 161 [Fig. 1127 of the present Memoir], for which I am indebted to the able pencil of Mrs. Blackburn, whose admirable representations of animals have obtained for her a high position as a delineator of natural objects." Subsequently Adams (1874, p. 116) added: "I believe that the bones of the Maltese fossil elephants are divisible into three varieties and two well-marked species, viz. a large and a small Elephant, the latter showing two forms represented by the *Elephas melitensis* of Falconer and Busk, which may have seldom attained a height of 5 feet, and a diminutive or pygmy form named by Mr. Busk *Elephas falconeri*, the smallest bones of which indicate an elephant about 3 feet in height. But there are intermediate-sized bones which easily bridge over the differences between the latter and the *Elephas melitensis*; nevertheless Mr. Busk has pointed out characters appertaining to the two, and is of opinion that they are distinct species. . . . I have named the largest Elephant *Elephas mnaidriensis,* in consideration of the circumstance that the gap, or rock-rent, from which I obtained the most perfect specimens of its bony structure is situated close to the ruins of the Mnaidra temple, a prehistoric and megalithic structure bearing evidences of the earliest human occupation of the Island of Malta." Leith Adams in this second contribution (1874, p. 116) changed the original name *mnaidræ* to *mnaidriensis*, the latter being the form cited by Lydekker (1886, p. 138), and gave an excellent new figure of the type molar (Pl. VII, figs. 2, 2*a*), also the following ridge formula (p. 112 and Pl. VII):

$$\mathrm{Dp}\,2\,\tfrac{3}{3}\ \mathrm{Dp}\,3\,\tfrac{6}{6}\ \mathrm{Dp}\,4\,\tfrac{8-9}{8-9}\ \mathrm{M}\,1\,\tfrac{8-9}{8-9}\ \mathrm{M}\,2\,\tfrac{10}{10}\ \mathrm{M}\,3\,\tfrac{12-13-[14]}{12-13-[14]}.$$



DENIZENS OF ANCIENT MALTA.—1. Large fossil Elephant (*Elephas mnaidræ*), p. 223. 2. Pigmy Maltese Elephant (*Elephas melitensis*), p. 216. 3. Smallest Dwarf Elephant (*Elephas falconeri*), p. 223. 4. Fossil Hippopotamus (*H. pentlandi*), p. 212. 5. Great Dormouse (*Myoxus melitensis*), p. 234. 6. Great extinct Swan (*Cygnus falconeri*), p. 237. 7. Large extinct fresh-water Turtle, p. 237.

ADAMS' RESTORATION AS DWARFED AFRICAN ELEPHANTS

Fig. 1127. Reproduced directly from Adams' figure in his book "Notes of a Naturalist in the Nile Valley and Malta," 1870, opposite page 161. In this very picturesque drawing we observe that Adams has restored the external ears of these three species in direct imitation of the very large ears of *Loxodonta africana*, whereas it is probable that these dwarfed elephants had the smaller ears which we have shown in figures 1047 and 1074 to be doubtless characteristic of *Hesperoloxodon antiquus* and all its descendants. It should be remembered, however, that the external ears of *Palæoloxodon namadicus*, to which the type of *P. melitensis* is more nearly related, are still unknown.

Compare the new restoration (Fig. 1119), under the direction of the present author, based on the obvious affinity of these dwarfed elephants to *Palæoloxodon namadicus* of India rather than to *Hesperoloxodon antiquus* of western Europe, also with small ears.

Palæoloxodon lamarmorae Forsyth Major, 1883

Sardinia, Quaternary sands of Morimentu near Gonnesa.

Elephas Lamarmorae Major, 1883. "Die Tyrrhenis," etc., Kosmos, 1883, VII Jahrg., Bd. XIII, p. 6. TYPE.—The author in describing this species designates as the *types* "die Extremitäten-Knochen eines kleinen, aber vollständig ausgewachsenen Elephanten zum Vorschein." HORIZON AND LOCALITY.—(*Op. cit.*, p. 6): "Aus quatern. Sanden von Morimentu b. Gonnesa (Sardinien)." TYPE FIGURE.—No figures published.

TYPE DESCRIPTION.—The animal is said to agree in size with *E. mnaidræ* [*E. mnaidriensis*] from Malta, but differs pretty sharply in the carpal and tarsal bones which constitute the type. The author's full description (Major, 1883, p. 7) is as follows: "Im vergangenen Jahre kamen in dem von LAMARMORA beschriebenen quaternären 'Grès' von Morimentu bei Gonnesa (Sardinien) die Extremitäten-Knochen eines kleinen, aber vollständig ausgewachsenen Elephanten zum Vorschein. Die von Malta bekannten Zwerg-elephanten, mit deren grösstem, *E. mnaidriensis*, der sardische in den Dimensionen ziemlich gut übereinstimmt, luden in erster Linie zur Vergleichung ein; es stellte sich aber heraus, dass die Carpal- und Tarsalknochen ziemlich bedeutend abweichen."

SUMMARY.—Agrees in size with *E. mnaidriensis* but differs pretty sharply in the carpal and tarsal bones which constitute the type.

Palæoloxodon cypriotes Bate, 1903

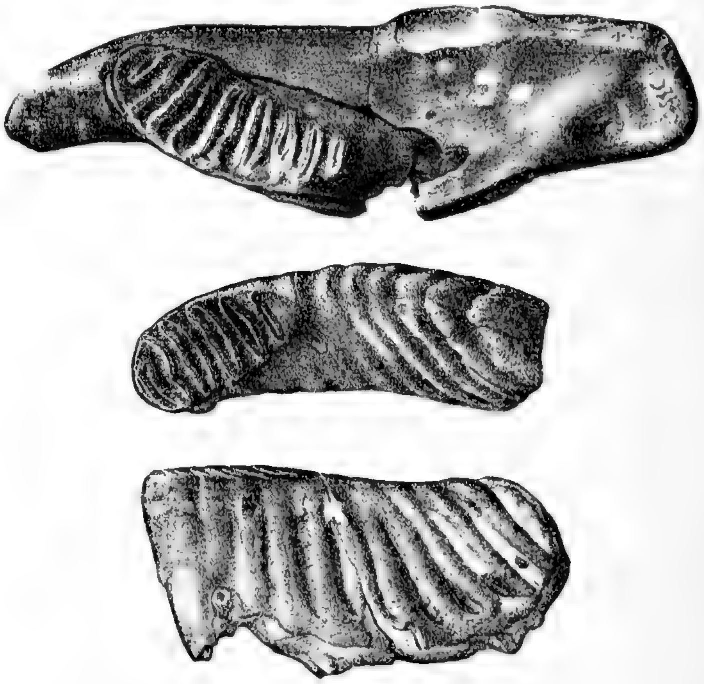
Figure 1128

Pleistocene, Kerynia Hills, island of Cyprus.

Elephas cypriotes Bate, 1903. "Preliminary Note on the Discovery of a Pigmy Elephant in the Pleistocene of Cyprus." Proc. Roy. Soc., London, 1903, Vol. 71, No. 475, pp. 498–500; also "Further Note on the Remains of Elephas Cypriotes from a Cave-Deposit in Cyprus." Phil. Trans. Roy. Soc. London, 1904, Vol. 197 (B), pp. 347–360. COTYPES.—The following have been selected by the present author from the many cotypes: a second true molar of the right side (Brit. Mus. M.8588), also a last lower true molar (Brit. Mus. M.8591). HORIZON AND LOCALITY.—Pleistocene, a single cave deposit situated on the southern side of the Kerynia Range, island of Cyprus. COTYPE FIGURES.—*Op. cit.*, 1904, Pls. XXI, XXII.

BATE (1903, P. 500).—In the original description the author observes: "Taking into consideration the several characters in which the teeth of the Cyprus elephant differ from those of all the hitherto described dwarf species (putting on one side *E. lamarmorae* . . . from the Pleistocene of Sardinia, the teeth of which are unknown to science) as well as the distinct habitat of the animal, I have come to the conclusion that it is specifically distinct from these other small forms, though possibly they were derived from a common ancestor, and I, therefore, propose to name it *Elephas cypriotes.*"

BATE (1904, P. 357): In a supplementary description the author states: "Undoubtedly there is a strong resemblance between the teeth of *E. cypriotes* and those of the Maltese and Sicilian forms, more especially *E. melitensis*, but this likeness is very apt to be over-estimated owing to the respective dwarf proportions of these island races. The Maltese pigmy species have been considered to be most closely allied to *E. antiquus* and *E. africanus*. . . . On the other hand it seems more probable that *E. cypriotes*, which so far as available material is concerned shows no close affinity to the African species, is rather connected with *E. antiquus* and *E. meridionalis*, agreeing with this last in the lowness of its ridge formula, . . . though differing in wanting the persistence of the strongly marked digitation of the plates which is usually found in the molars of that elephant.



COTYPES OF PALÆOLOXODON CYPRIOTES

Fig. 1128. *Elephas cypriotes* Bate, 1903, Kerynia Hills, island of Cyprus. Selection from the many cotype molars fully figured by Bate (1904, Pls. XXI, XXII).

(Upper) Pl. XXI, fig. 3, "Crown view of second true molar in right mandibular ramus. B.M., M.8588, p. 355." Reduced to one-half natural size.

(Lower) Pl. XXII, fig. 6, "Crown view of last lower true molar. B.M., M.8591, p. 355"; fig. 6a, "Side view of ditto." Both reduced to one-half natural size.

In this connection it is interesting to note that from the characters of the carpal and tarsal bones (the only remains known) of *E. lamarmorae*, the dwarf elephant of Sardinia, Dr. C. I. Forsyth Major considers it to have been most closely allied to *E. meridionalis*. . . . Since writing the first notice of *E. cypriotes* I have come to the conclusion that the average number of plates in the true molars is somewhat less than was at first supposed, therefore the corrected ridge-formula, exclusive of talons, would stand as follows:

$$[\textit{E. cypriotes}]\text{: } [\mathrm{Dp}\ 2]\ \div,\ [\mathrm{Dp}\ 3]\ \tfrac{5}{5},\ [\mathrm{Dp}\ 4]\ \tfrac{7-8}{7-8},\ [\mathrm{M}\ 1]\ \tfrac{7-8}{7-8},\ [\mathrm{M}\ 2]\ \tfrac{8-9}{8-9},\ [\mathrm{M}\ 3]\ \tfrac{11-12}{11-12}.$$

This is slightly lower than that of *E. melitensis* which Dr.

Leith Adams, later than Dr. Falconer and after examining a further large amount of material, gives as:

$$[\textit{E. melitensis}]:\ [\mathrm{Dp}\ 2]\ \tfrac{3}{3},\ [\mathrm{Dp}\ 3]\ \tfrac{5}{5},\ [\mathrm{Dp}\ 4]\ \tfrac{8-9}{8-9},\ [\mathrm{M}\ 1]\ \tfrac{8-9}{8-9},$$
$$[\mathrm{M}\ 2]\ \tfrac{10}{10},\ [\mathrm{M}\ 3]\ \tfrac{12}{12}.$$

The marked lateral compression of the tusks of *E. cypriotes* (Plate 22, fig. 9), which is a constant character in all the specimens so far obtained, would in itself be almost sufficient to distinguish this from the other pigmy elephants of the Mediterranean region. . . . Presupposing that the dwarf elephants of the Mediterranean region were all derived from a common ancestor, the simpler construction of the molars of *E. cypriotes* might be explained on the assumption that this species was isolated and subsequently differentiated from the parent stock, prior to a similar fate overtaking the Maltese and Sicilian races. This is borne out by the fact that *E. cypriotes* lived contemporaneously with *H.* [*Hippopotamus*] *minutus*, a more generalized and primitive form . . . than either *H. pentlandi* or *H. melitensis*, the associates of the pigmy elephants of Malta and Sicily. The geological evidence, as distinguished from the palæo-zoological, also supports this theory, for it appears probable that Cyprus became an island at an early period."

Palæoloxodon creticus Bate, 1907

Figure 1129

Pleistocene, cave deposit near Cape Maleka, island of Crete.

Elephas creticus Bate, 1907. "On Elephant Remains from Crete, with Description of *Elephas creticus*, sp. n." Proc. Zool. Soc., London, 1907, pp. 238–250. COTYPES.—Nine imperfect cotype molars. Two are figured in the present Memoir (Fig. 1129), namely, r.M_3 (Brit .Mus. M.9381) and an M_2 (Brit. Mus. M.9378). HORIZON AND LOCALITY.—Near Cape Maleka, island of Crete. FIGURES.—*Op. cit.*, Pls. XII, figs. 1–3, and XIII, figs. 1 and 2.

BATE (1907, P. 239).—The author described the type as follows: "The remains of the smallest of the Cretan Elephants were all obtained from a much damaged and weathered cave-deposit in the limestone cliffs near Cape Maleka in the west of the island, which has already been described [Footnote: 'Geol. Mag. n.s. dec. v. vol. ii. (1905) p. 195.'], and where only some teeth and limb-bones of small rodents were found besides those under discussion. These latter include nine imperfect molars and a few fragments, among which are a portion of an incisor and the dorsal half of a vertebra. As this small race differs from those of other Mediterranean islands, and its minute proportions being seemingly the result of specialisation due to isolation in Crete, it is suggested that it may be known by the above specific name denoting its island habitat."

Of the nine molars two belong to the upper series, namely, M^1 consisting of seven or seven and a half plates, length 54 mm., height about 32 mm. A referred M^2 includes eight plus plates. Of the cotype lower molars, one regarded as M_2 includes nine plates; other lower second molars include eight to nine plates. M_3 includes eleven plus plates.

(*Op. cit.*, p. 243): "From this brief account of the remains procured of *E. creticus*, it will be seen that this pigmy Elephant must have been of slightly larger proportions than *E. cypriotes* and approached in size more closely to *E. melitensis*; that is to say, it would have attained as a maximum a height of five feet. . . All the molars obtained differ from those of the two last-named dwarf species in being much lower in the crown; this is perhaps the most noticeable feature of the series. At the same time the teeth are wide, the cement-areas broad, and the enamel simple, though at times broken up into a number of rings. So far as can be ascertained from the scanty amount of material the ridge-formula must have been low."

$$\textit{E. creticus}:\ [\mathrm{M}\ 1\ \tfrac{7\frac{1}{2}}{\ }\ \mathrm{M}\ 2\ \tfrac{8+}{9}\ \mathrm{M}\ 3\ \tfrac{\ }{11+}].$$

COTYPES OF PALÆOLOXODON CRETICUS

Fig. 1129. *Elephas creticus* Bate, 1907, Pls. XII, fig. 3, XIII, fig. 1. Nine imperfect cotype molars from a cave deposit near Cape Maleka, Crete. Both molars two-thirds natural size.

(Left) Pl. XII, fig. 3: "Crown view of right lower third molar of *E. creticus*. ([Brit. Mus.] M.9381.)" +13 ridge-crests.

(Right) Pl. XIII, fig. 1: Crown view of second lower molar of *E. creticus*, Brit. Mus. M.9378. +7 ridge-crests.

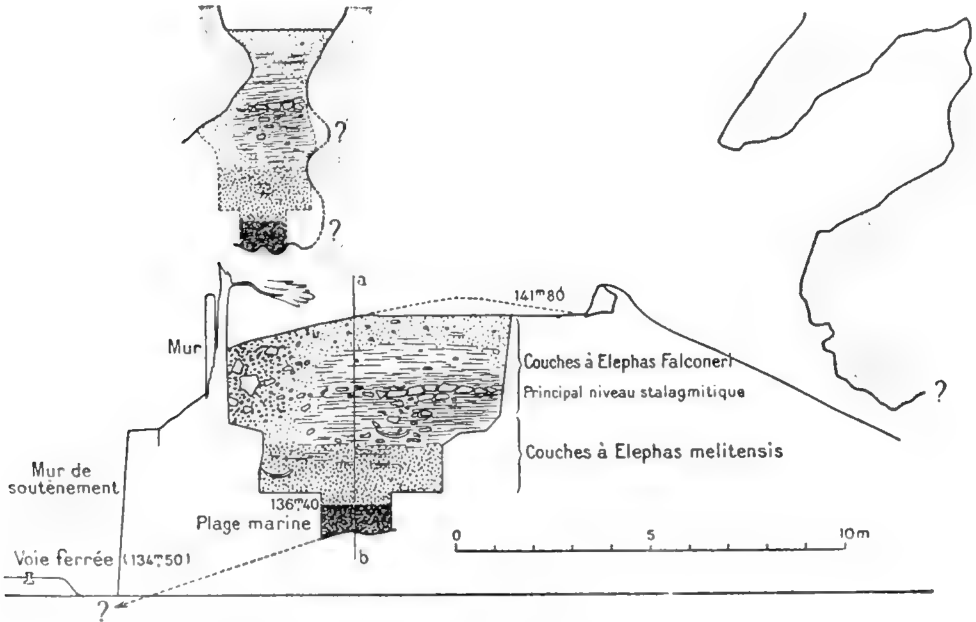
V. LES ÉLÉPHANTS NAINS DES ILES MÉDITERRANÉENNES ET LA QUESTION DES ISTHMES PLÉISTOCENÈS (VAUFREY, 1929)

> *Enfin, par plusieurs beaux spécimens de Palerme, nous connaissons le crâne de la plus grande, Elephas mnaidriensis, crâne qui présente tous les caractères propres à l'Elephas namadicus, c'est-à-dire à l'Éléphant antique, notamment le bourrelet suprafrontal si spécial. Il n'y a donc pas de doute que les formes naines des îles appartiennent toutes trois au phylum de l'Elephas antiquus et doivent être considérées comme des races de cette espèce"* (Vaufrey, 1929, p. 209).

The valuable Memoir of Dr. Raymond Vaufrey, "Les Éléphants Nains des Iles Méditerranéennes" (October, 1929), reached the Osborn Library in December, 1929. The present abstract of the observations and conclusions of the author should be compared with the previous history and abstracts of the extensive literature cited more or less fully above. The author, under the guidance of Dr. Marcellin Boule, had the advantage of visiting the various caves and rock-fissures in Sicily and Malta, in which these fossils occur, and of examining and comparing all the collections. Among the many geologic observations of value are those in the Grotto of Luparello near Palermo (Fig. 1130) which show that the lower geologic level of '*Elephas melitensis*' is much more ancient than the higher level containing '*Elephas falconeri*,' from which Vaufrey rightly infers that the extremely dwarfed '*E. falconeri*' is geologically more recent than the middle-sized '*E. melitensis*.'

Vaufrey throughout regards the species '*Elephas namadicus*' and '*E. antiquus*' as *synonymous*. On the contrary, it is shown above in the present Memoir, that '*E. namadicus*' Falc. (1846) antedates and is widely different specifically, if not generically, from '*E. antiquus*' Falc. (1847) of western Europe.

We need only abstract those portions of this Memoir which bear directly on the following questions: (1) The time of insulation or separation of these islands from the mainland; (2) the respective evidence of the relationship of the dwarfed elephants to (a) the typical '*Elephas antiquus*' of western Europe, or to (b) the '*Elephas namadicus*' of India, or to (c) the northwardly migrating elephants of Africa; (3) the time of entry of these dwarfed elephants into the Mediterranean Islands; (4) the geographic region from which they entered the islands.



PALÆOLOXODON FALCONERI MORE RECENT THAN P. MELITENSIS

Fig. 1130. Section of Grotto of Luparello, Palermo, Sicily, showing below the "Couches à Elephas melitensis" at the bottom of the cavern and separated above by a broad stalagmitic layer from the "Couches à Elephas Falconeri." After Vaufrey, 1929, fig. 7, p. 51. The underlying marine phase ("Plage marine"), 136^m, 40, is shown in the darkly tinted horizon at the bottom of the cavern. This "Plage marine" may be geologically correlated with the Monastirian stage (Depéret, 1918–1921, named after Monastir, Tunis), *elevation* of the sea level, or insular depression.

GEOLOGIC AND GEOGRAPHIC OBSERVATIONS

The *elevations* and *depressions of* the Mediterranean sea level and the consequent connections of its present islands with the surrounding mainland of Africa and Eurasia are fully treated in the *Introduction* (pp. 1–45), discussed throughout the descriptions of the islands and in the formal text (pp. 45–202), and summarized in the *Conclusions Générales* (pp. 203–216).

1^{a-b}. GEOGRAPHIC AND FAUNAL RELATIONS OF THE ISLANDS.—Vaufrey (p. 2) adopts Boule's (1906–1919) theory that in closing Miocene and early Pliocene time (Pontian) the western basin of the Mediterranean was by elevation reduced to large lakes between which, over great isthmuses, freely migrated the *Hipparion* fauna of Léberon, Eppelsheim, Pikermi, Samos, Maragha, etc. After this early Miocene-Pliocene Pontian stage of elevation there followed a great depression of the land, several hundred meters below the present level, or a rise of the seashore lines, which completely isolated Europe from the African continent as well as from parts of Asia. In closing Pliocene time [Villafranchian[1] stage of northern Italy, containing *Archidiskodon meridionalis, Hesperoloxodon ausonius, Parelephas trogontherioides*] there is evidence of renewed African connections and migrations, but *certainly no evidence of a Tunisian-Sicilian* land bridge (p. 203), for from the latest hydrographic charts (1916) the Mediterranean Sea, while 400 m. below its present level, was too high to form an isthmus for intermigrations between Africa and Europe by way of Tunis and Sicily. Moreover, the absence of a Tunisian-Sicilian land bridge, or, in fact, of any land connection between Sicily and north Africa during late Pliocene and Pleistocene times, is proved by the contrast (Pomel, 1895, Boule, 1899) between the Pleistocene fauna of north Africa, of Algeria, and of Tunis and that of the Mediterranean Islands, summarized by Vaufrey (pp. 204–206) as follows: (a) The Pleistocene fauna of north Africa is totally different from that of Europe or of the Mediterranean Islands; (b) the late Pleistocene entry of European forms into north Africa was not via a Mediterranean land bridge between Sicily and Tunis (p. 207) but by way of land connections along the eastern Mediterranean shore of Syria and the Suez; (c) whereas we find certain European and other Holarctic forms in the late Pleistocene of north Africa, we do not find a single African form in the Mediterranean Islands, more especially in the island of Sicily; (d) the fossil remains formerly attributed to the African elephant (*E. africanus*) belong rather to aberrant specimens of '*Elephas mnaidriensis*'; (e) thus rejecting (p. 208) all previous suggestions of north African relationship, Vaufrey summarizes his conclusions as to the geologic age, characters, and relationships of the dwarfed elephants as below.

SICILY	MALTA	SARDINIA	CYPRUS	CRETE
E. antiquus var. *insularis*				
E. mnaidriensis ref. (crania; etc.)	*E. mnaidriensis* type			*E. mnaidriensis* ref.
E. melitensis ref.	*E. melitensis* type	= *E. lamarmorae* type		= *E. creticus* type
E. falconeri ref.	*E. falconeri* type		= *E. cypriotes* type	

[THREE DWARFED SPECIES OR RACES ONLY]

"Cette démonstration, toutefois, ne pouvait se faire qu'en reprenant sur de nouvelles bases la question des Éléphants nains; elle n'eût donc pas été possible si le hasard ne m'avait fait découvrir à Luparello de nouveaux documents. Il ressort de cette étude que les Éléphants nains appartiennent à trois formes de tailles différentes: *Elephas mnaidriensis* (hauteur au garrot: environ 1^{m}, 90), *E. melitensis* (hauteur au garrot: 1^{m}, 40) et *E. Falconeri* (hauteur au garrot: environ 0^{m}, 90), caractérisées par la présence à la mandibule d'une première molaire [Dp_2] à racine unique, particularité qui n'existe que chez l'Éléphant antique, à l'exclusion dé toutes les autres espèces d'Éléphants. Par ce caractère comme par la morphologie des molaires, ainsi que par leur présence dans les mêmes gisements, ces trois formes apparaissent comme étroitement apparentées: elles présentent toutes trois les mêmes variations de la morphologie dentaire, déjà relevées par les auteurs dans les molaires d'*Elephas antiquus*. Enfin, par plusieurs beaux spécimens de Palerme, nous connaissons le crâne de la plus grande, *Elephas mnaidriensis*, crâne qui présente tous les caractères propres à l'*Elephas namadicus*, c'est-à-dire à l'Éléphant antique, notamment le bourrelet suprafrontal si spécial. Il n'y a donc pas de doute que les formes naines des îles appartiennent toutes trois au phylum de l'*Elephas antiquus* et doivent être considérées comme des races de cette espèce."

SYNONYMY (OP. CIT., P. 143).—"Les notions ainsi acquises nous ont permis, en même temps, de vérifier l'identité des espèces nouvelles créées en Sardaigne par Forsyth Major, en Crète et à Chypre par Bate. Il devient évident que le squelette de La Marimenta se compare exactement par la taille au squelette de Luparello et se rapporte donc à l'*Elephas melitensis*, que l'*Elephas creticus* par la morphologie et les dimensions des molaires s'assimile parfaitement aussi à cette même race, enfin que les diagnoses dentaires de l'*Elephas cypriotes* et de l'*E. Falconeri* sont si analogues qu'il n'y a aucune raison de les désigner sous deux noms différents. Il convient donc de parler d'*Elephas melitensis* de Sardaigne et de Crète et non d'*E. Lamarmoræ* et d'*E. creticus*, d'*Elephas Falconeri* de Chypre et non d'*E. cypriotes*. Exception faite, sans doute, pour quelques individus de taille normale, auxquels est dû l'introduction du phylum, les Éléphants ne sont donc représentés dans les îles que par trois races de taille décroissante: *E. mnaidriensis*, *E. melitensis* et *E. Falconeri*. D'une part, la morphologie dentaire, notamment en ce qui concerne les caractères des figures d'abrasion, nous interdit de considérer les races naines comme appartenant à plus d'une espèce; d'autre part, les caractères craniens d'*Elephas mnaidriensis*, ainsi que la présence dans les trois races d'une première molaire inférieure à racine unique, désignent cette espèce comme étant indubitablement *Elephas antiquus*.

INSULATION (OP. CIT., p. 181).—"De même qu'en Sicile, la faune à Éléphants nains nous apparaît donc, d'une manière générale, comme contemporaine du dernier Interglaciaire, et son extinction comme s'étant produite pendant la dernière période glaciaire au moment de la formation des couches qui la renferment. L'absence de toute trace de l'Homme dans ces couches confirme ce que nous ont appris déjà les grottes siciliennes; Sicile et Malte nous apparaissent une fois de plus comme des finisterres."

1_c. As to geologic age, Vaufrey concludes as follows (p. 209): "Rappelons enfin que les couches à Éléphants nains de Sicile et de Malte datent vraisemblablement de l'époque wurmienne, époque à laquelle l'Eléphant antique avait, sauf en Italie méridionale (*Romanelli*), disparu d'Europe occidentale et que, dans le gisement de Luparello, la plus petite des trois races (*Elephas Falconeri*) était superposée à celle de taille intermédiaire (*E. melitensis*)."

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[1] [See footnote 1 on page 1049 above regarding the possible Lower Pleistocene age of the Villafranchian.—Editor.]

2. Relationships.—The traditional opinion, seemingly shared by Vaufrey, is that the dwarfed elephants of the Mediterranean Islands should be regarded as the stranded descendants of the well-known early and late Pleistocene European species '*Elephas antiquus*,' which roamed over the Mediterranean lands before they were broken up into islands. Vaufrey does not distinguish between '*E. namadicus*' Falc., 1846, of India, and the typical '*E. antiquus*' Falc., 1847, of western Europe; his comparisons and measurements are chiefly with those of the late Pleistocene [*3d Interglacial*] stages of Weimar and Taubach (see Fig. 1088 of the present Memoir), which he designates as '*Elephas antiquus* normal,' selecting mean measurements between the larger and the smaller dimensions given by Pohlig (cf. Vaufrey, *op. cit.*, p. 138—see Tables below).

Comparative Measurements (cf. Vaufrey, 1929, p. 138)

Measurements in Millimeters	I. [Dp 2]	II. [Dp 3]	III. [Dp 4]	IV. [M 1]	V. [M 2]	VI. [M 3]
E. Falconeri	1, 10	$\frac{3,60}{3,20}$	$\frac{5,45}{5,60}$	$\frac{6,80}{7,25}$	$\frac{9,00}{11,50}$	$\frac{?}{14,30?}$
E. melitensis	1, 30	$\frac{?}{5,10}$	$\frac{7,10}{7}$	$\frac{8,75}{10,85}$	$\frac{12,70}{14,60}$	$\frac{14,50}{15,25}$
E. mnaidriensis	1, 60	$\frac{6,95}{7,40}$	$\frac{11,65}{11,50}$	$\frac{16,65}{17,60}$	$\frac{17,25}{21,10}$	$\frac{23,00}{29,00}$
E. antiquus normal	1, 82	$\frac{6,90}{6,60}$	$\frac{11,60}{11,25}$	$\frac{15,60}{16,45}$	$\frac{21,70}{23,50}$	$\frac{30,50}{37,70}$

Comparative Ridge Formulæ (cf. Vaufrey, 1929, pp. 91–128)

E. Falconeri	$\frac{\quad}{3-3\times}$	$\frac{\times 4\times-\times 5\times}{\times 5\times-7\times}$	$\frac{\times 6\times-\times 8\times}{8-9}$	$\frac{9}{10-\times 10\times}$	$\frac{\times 10\times-\times 12\times}{\times 11\times-?}$	$\frac{13-14}{\times 14}$
E. melitensis	$\frac{?}{?}$	$\frac{?}{6\times-7\times}$	$\frac{8\times-\times 8\times}{8}$	$\frac{9\times-10\times}{10-11\times}$	$\frac{12\times}{13\ ?}$	$\frac{\times 12\times}{13-14}$
E. mnaidriensis	$\frac{\quad}{3-3\times}$	$\frac{\times 5\times-7\times}{\times 6\times}$	$\frac{9\times}{\times 9\times}$	$\frac{11\times}{12\times}$	$\frac{11\times-13\times}{\times 12\times-13\times}$	$\frac{16(\times 14\times)}{?-\times 17}$

CHARACTERS OF THE SPECIES, AFTER VAUFREY

In all the species the 'première molaire' (Dp_2) is said to have a *single root*, a unique character of '*E. antiquus*' (p. 58).

Elephas antiquus Falconeri Busk (p. 91), represented by the rich dental series from Luparello, is regarded as identical with '*Elephas cypriotes*' Bate of Cyprus. Distinguished by small tusks of sharp upward curvature, with a maximum diameter of 0,045 m. The teeth from Luparello are said to agree with the types of '*E. falconeri*' from Malta and of '*E. cypriotes*' from Cyprus. The superior and inferior molar series (pp. 91–101), examined in great detail, give the following conclusions (p. 100): (1) Laminar frequence 4½ to 6 in 10 cm.; (2) marked reduction from '*E. antiquus*' in the laminar ridge formula, accompanied by a relative thickening of the laminæ: '*E. falconeri*,' max. M 3 $\frac{14}{15}$ ['*E. antiquus*' *typicus* M 3 $\frac{16\frac{1}{2}-17}{16\frac{1}{2}-17}$]; (3) incisive tusks with regular upward curvature [in contrast to the relatively straight tusks of '*E. antiquus*']; (4) posterior grinders long and narrow, and elevated as in '*E. antiquus*,' with similar median sinus or expansion; (5) molars of two types, with thick (*émail épais*) and with thin (*émail mince*) enamel respectively (Pls. III and IV); skeleton (p. 102), parts of vertebral column, humerus, ulna, radius, femur, tibia, carpus, and tarsus.

Elephas antiquus melitensis Falc. (pp. 103–112), of intermediate size, from lower or more ancient (Luparello) cavern deposits than '*E. falconeri*,' less completely known. (1) Incisive tusks relatively less robust and upcurved than those of '*E. falconeri*,' known only in Luparello. (2) Grinding teeth (lower Luparello level) similar to those of the type found in the grotto of Mnaidra, Malta; laminar frequence 4 to 5½ to 6½ in 10 cm. (Luparello and Malta). (3) Ridge-plates in third inferior molar (p. 108) 13–14, laminar frequence 3¼ (type pachyganal) to 6 (type endioganal). General specific characters (p. 110): Except for a difference in dimensions, (a) the general characters are similar to those of the typical '*Elephas antiquus*,' with more feeble development of the enamel foldings correlated with reduction in the size of the molars; (b) as in '*E. falconeri*,' there are two divergent tendencies in the grinding teeth, one of the fine enamel type (*émail mince*) with compression of the laminæ, the other of the thick enamel type (*émail épais*) with spreading of the laminæ, corresponding respectively with the broad and short molars and the long and narrow molars described by Leith Adams. (5) Skeleton: Portions of mandibles, vertebræ, femur, ulna, radius, attributable to '*Elephas melitensis*'; discovered also in Cyprus by Bate, in the cavern of Mnaidra by Adams, and in La Marimenta, Sardinia—the latter described by Forsyth Major as '*Elephas lamarmoræ*,' which Vaufrey regards as specifically identical with '*Elephas melitensis*.'

Elephas antiquus mnaidriensis Leith Adams (pp. 113–139). Remains of this larger race not discovered in the cavern of Luparello, but an ulna found in the cavern of San Teodoro; richly represented by molars in the Museum of Palermo from other localities in Sicily and from Malta, including especially from the cavern of Puntali, Sicily, several crania and the greater part of the bones of the limbs, to which Pohlig (1893) devoted his short Memoir; also a complete series of grinders of '*Elephas mnaidriensis*' (Pl. VI) from Sicily and Malta, mostly of the pachyganal (*émail épais*) character. (1) The molars (p. 114) of '*E. mnaidriensis*' almost reach the lower limits of size of the typical '*Elephas antiquus*' from which they are separated only by the constant absence of large individuals; nevertheless the bones from Puntali and the ulna from San Teodoro are invariably of inferior size to those of '*E. antiquus*' of the continent. (2) Tusks (Fig. 27, p. 115—Fig. 1131 of the present Memoir) longer and more slender, approaching those of '*E. antiquus*' of Tilloux (Fig. 1131,4) [which in turn resemble those of the Pignataro Interamna specimen (Fig. 1096)]; the length of the tusks is closely concordant with the length of the ulnæ (p. 113, figs. 26) as restored in figure 1134 of the present Memoir. (3) The grinders (pp. 116–132) include a nearly complete series (Dp 2–M 3) in which M 3 $\frac{\frac{1}{2}-14-\frac{1}{2}}{\frac{1}{2}-17}$ exibits a laminar frequence of 4¼ to 7½ in 10 cm.; the ridge-plates when worn show more or less median expansion [or 'loxodont sinus'] at the base (Figs. 28, 30) but none approaches the lozenge-shaped *Loxodonta africana* type; the enamel also varies in thickness from the *émail mince* with relatively close compression (Fig. 32, 4, 6) to the *émail épais* with wide compression (Fig. 37,5—Fig. 1132 of present Memoir). (4) The summary of dental characters (p. 131) is as follows: (a) A certain number of '*E. mnaidriensis*' molars from the Sicilian horizons approaches the classic structure of the continental '*E. antiquus*,' namely, "couronne élancée et étroite, lames d'épaisseur modérée, émail plissé, souvent avec une expansion losangique médiane modérée"; (b) from this central type, however, arose variations, some of which accent the median sinus, broaden the ridge-plates, thicken the enamel, while others narrow the ridge-plates, diminish the median sinus, and thin the enamel. The latter reach an extreme degree of thinness and plate compression which remind us of the '*Elephas armeniacus*' Falc. [=*Parelephas armeniacus* of the present Memoir]. In brief, there exist in the cavern of Puntali all intermediates between these extreme types, but none approaches the loxodont type of '*Elephas africanus*' or of the '*Elephas priscus*' of Falconer.

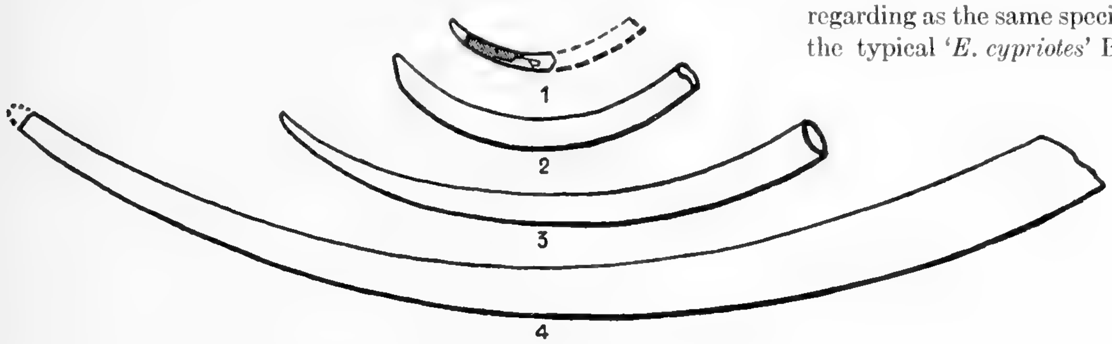

Fig. 27. — Schémas montrant les grandeurs relatives des défenses des races naines insulaires et de l'Éléphant antique normal.

1, *Elephas antiquus Falconeri* de Luparello ; 2. *E. a. melitensis* de Luparello ; 3. *E. a. mnaidriensis* des Puntali ; 4. *E. antiquus* de Tilloux (d'après M. Boule). — 1/20 de la grandeur naturelle.

Fig. 1131. Relative size, thickness, and curvature of the incisive tusks in the three dwarfed subspecies of the Mediterranean Islands, one-twentieth natural size. After Vaufrey, 1929, fig. 27, p. 115. The '*Elephas antiquus*' of Tilloux (4) is found with some individuals of this species.

OSBORN (1930) SUBSTITUTES A THEORY OF AFRICAN DESCENT BY WAY OF EASTERLY RATHER THAN NORTHERLY LAND CONNECTIONS

While recognizing the valuable and important observations of this Memoir, we are unable to accept many of Vaufrey's conclusions, for the following reasons: (1) The cranium of the dwarfed elephants cannot be derived from that of the typical '*Elephas antiquus*' of western Europe, from which it differs very widely; (2) all the known Upper Pliocene and Pleistocene stages of '*E. antiquus*' described in detail in the present Memoir, namely, '*ausonius*,' '*antiquus*' (typicus), '*germanicus*,' and '*italicus*,' are too highly specialized in their ridge formulæ and other characters to give rise to these dwarfed Mediterranean species, which are primitive in ridge formulæ, and related to *Palæoloxodon namadicus* in cranial structure; (3) the traditional opinion of '*E. antiquus*' origin *is not sustained* by our present knowledge of the highly diverse characters of the African, west European, and south Asiatic members of the Loxodontinæ; (4) the dwarfed elephants date from the closing stage of Glacial time, namely, IV GLACIAL = Würm of the Alpine region, a considerable period *after the disappearance*, during Interglacial Epoch 3 or Riss-Würm interval of the Alps, of the north German *Hesperoloxodon antiquus germanicus*, and *probably after the disappearance* of the southerly *H. antiquus italicus*; (5) the ridge formulæ which Vaufrey assigns to '*E. falconeri*' and to '*E. melitensis*' are *collective*; these 'collective ridge formulæ' may belong to one or more specific stages, whereas in a certain stage of evolution the ridge formula is constant; thus Vaufrey may not be right in regarding as the same species the typical '*E. falconeri*' of Malta and the typical '*E. cypriotes*' Bate of Cyprus, which has a lower ridge formula; again Vaufrey's ridge formula of '*E. melitensis*' differs widely from that which Leith Adams finally assigned to the same species; the ridge formula which Vaufrey assigns to '*E. mnaidriensis*' namely, $\frac{\times 14 \times}{?\text{-}\times 17}$, is much below that of the Upper Pleistocene species of Taubach and Weimar (Fig. 1088), i.e., *germanicus*, M 3 $\frac{17\text{-}19}{18+}$, *italicus*, M 3 $\frac{20}{18+}$; it is also below that of the Lower Pleistocene '*E. antiquus*' typical of the Forest Bed, M 3 $\frac{16\frac{1}{2}\text{-}17}{16\frac{1}{2}\text{-}17}$; (6) these facts seem to render highly improbable the descent of the dwarfed elephants from the large and specialized west European '*E. antiquus*,' or from the lower Upper Pliocene or the progressive Pleistocene stages, and render more probable the descent of these dwarfed elephants from east African forms, such as the '*Elephas antiquus recki*' Dietrich, 1916, M 3 $\frac{}{15\text{-}16\frac{1}{2}}$, or the Algerian '*E. jolensis*' Pomel, 1895, M 3 $_{13}$, or the Algerian '*E. atlanticus*' Pomel, 1879, M 3 $\frac{12}{12\text{-}14}$.

Finally, it appears probable that at least two separate lines of phyletic descent are represented in these dwarfed elephants of

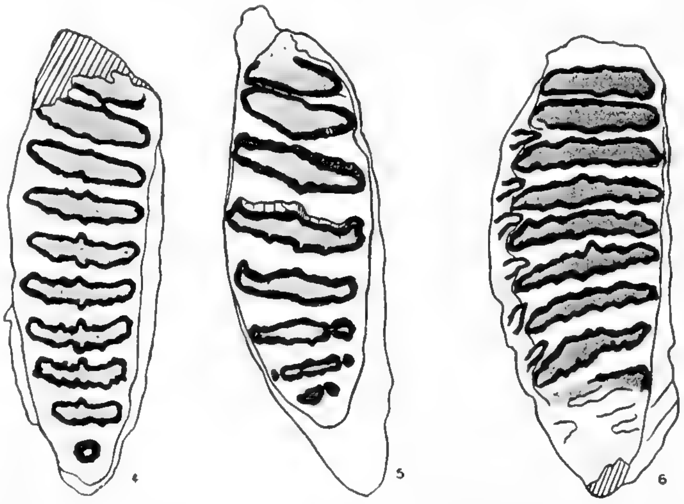

Fig. 1132. Two types of molars (A) and (B) figured by Vaufrey, 1929, fig. 37, Nos. 4, 5, 6, as belonging to '*Elephas mnaidriensis*':

(A) Nos. 4 and 6, from Shantiün and Puntali respectively, of the 'type endioganal' (*émail mince*); (B) No. 5, from Puntali, of the 'type pachyganal' (*émail épais*). In Osborn's opinion the 'type endioganal' (*émail mince*) belongs to a different species from the 'type pachyganal' (*émail épais*). One-sixth natural size.

the Mediterranean Islands, as illustrated by Vaufrey (p. 109, fig. 23), namely: (A) with coarse enamel and ridge-plates widely separated, that is, with a low laminar frequence of 3¼ in 10 cm., corresponding with Vaufrey's 'type pachyganal' (*émail épais*), e.g., figure 23,1, and (B) with fine enamel and close laminar frequence, corresponding with Vaufrey's 'type endioganal' (*émail mince*), e.g., figure 23,6. This distinction of (A) and (B) is in accordance with the failure of all earlier authors clearly to distinguish the phylum *Parelephas* and the phylum *Archidiskodon* from the phylum *Loxodonta*, which in the present Memoir are shown to be absolutely distinct from each other even at the close of Pliocene time. Thus we cannot support the author's union (pp. 109, 110) of these (A) and (B) types in the single species '*E. melitensis*,' in which (p. 110) he is erroneously supported by Leith Adams (1874, p. 35) as follows: "Comme chez l'Éléphant antique, il y a deux tendances divergentes, l'une vers la réalisation d'un type à émail mince avec resserrement des lames, l'autre vers celle d'un type à émail épais avec écartement des lames, aboutissant dans le premier cas à des molaires larges et courtes (variété A de Leith Adams), dans le second à des molaires longues et étroites (variété B de Leith Adams)."

Fig. 1133. Molars referred by Vaufrey to *Elephas* [=*Palæoloxodon*] *melitensis* from Luparello, Sicily, (No. 1), and Benghisa, Malta, (No.6), showing respectively widely separated ridge-plates, i.e., low laminar frequence, with coarse enamel ('type pachyganal') and close laminar frequence, with fine enamel ('type endioganal'). After Vaufrey, 1929, fig. 23, Nos. 1 and 6, one-half natural size. See also Fig. 1132 of the present Memoir.

Osborn's Conclusions (1930).—(1) Whereas the progessive known west European stages neither of *Hesperoloxodon antiquus* nor of the Indian *Palæoloxodon namadicus* appear to be ancestral to the dwarfed Mediterranean species, we seem to find on the continent of Africa a number of *more primitive* stages of *Palæoloxodon*, with more primitive ridge formulæ and long narrow grinding teeth, which further knowledge may prove to be ancestral to the dwarfed Mediterranean types. This will depend on the discovery of a cranium ancestral to that of '*Elephas melitensis*,' which, in turn, resembles that of '*E. namadicus*' of India.

(2) The true '*mnaidriensis*,' '*melitensis*,' and '*falconeri*' seem to constitute a single phylum of regressive degeneration or dwarfing of the 'endioganal' or *émail mince* type. But intermingled with the most ancient and larger '*mnaidriensis*' stage in certain of the caverns seem to be members of other phyla of the 'pachyganal,' or *émail épais* type.

Fig. 26. — Figure montrant les grandeurs relatives des cubitus des trois races naines d'*Elephas antiquus*.

De gauche à droite : *E. a. mnaidriensis*, *E. a. melitensis* (cubitus gauches), *E. a. Falconeri* (cubitus droit, avec un fragment du radius). — 1/6 de la grandeur naturelle.

Fig. 1134. Ulnæ of the three species. After Vaufrey, 1929, fig. 26, p. 113.

VI. ANCESTRAL STAGES OF PALÆOLOXODON IN AFRICA

Whereas most previous writers, including Vaufrey (1929), derive the Mediterranean dwarfed insular species from *Elephas antiquus* of western Europe, we would be inclined to regard them as dwarfed insular derivatives of those extinct African species of *Palæoloxodon*, with which the genus *Pilgrimia* is synonymous. On a large scale *'Elephas zulu'* Scott[1] resembles the types of *Elephas antiquus Recki* Dietrich, 1916, of *Elephas jolensis* Pomel, 1895, and of *Elephas atlanticus* Pomel, 1879, also of the dwarfed species of Malta, *Elephas melitensis* Falconer, 1862, 1868, *'Elephas falconeri'* Busk, 1867, and *Elephas mnaidriensis* Adams, 1870. From the subjoined table of ridge formulæ it appears that the dwarfed Mediterranean species differ from the west European species of *'Elephas antiquus'* [=*Hesperoloxodon antiquus*] but are closely similar to the African species of *Palæoloxodon.*

Firstly.—Since the first studies for this Memoir were begun (1900) evidence has rapidly accumulated not only to demonstrate that the Order Proboscidea originated in Africa, as recited in previous chapters of the present Memoir, but to render it probable that most of the separate genera and subfamilies also originated in Africa instead of Asia as formerly supposed.

This apparently is true of the *Archidiskodon* phylum and now begins to be apparent in the *Palæoloxodon* phylum, because Africa and the Mediterranean Islands reveal stages of *Palæoloxodon* more primitive in molar ridge formulæ at least than any hitherto found in Eurasia, as displayed in the following comparative table compiled from previous records and *type* formulæ:

Middle to Upper Pleistocene of India	*Elephas* [*Palæoloxodon*] *namadicus* Falc. and Caut., 1846, 1847	M 2 $\frac{}{?15}$	M 3 $\frac{15}{16}$
Lower Pleistocene of England	*Elephas* [*Hesperoloxodon*] *antiquus* Falc. and Caut., 1847, 1857	M 2 $\frac{12}{12}$	M 3 $\frac{16\frac{1}{2}-17}{16\frac{1}{2}-17}$
Malta	*Elephas* [*Palæoloxodon*] *mnaidriensis* Adams, 1870	M 2 $\frac{10}{10}$	M 3 $\frac{12-13-14}{12-13-14}$
	Elephas [*Palæoloxodon*] *melitensis* Falconer, 1862	M 2 $\frac{9-10}{9-10}$	M 3 $\frac{12}{12}$
	Elephas [*Palæoloxodon*] *falconeri* Busk, 1867 [ridge formula after Vaufrey, 1929]	M 2 $\frac{10-12}{11}$	M 3 $\frac{13-14}{14}$
East Africa	*Elephas* [*Palæoloxodon*] *recki* Dietrich, 1916	M 2 $\frac{}{11}$	M 3 $15-16\frac{1}{2}$
Algeria	*Elephas* [*Palæoloxodon*] *jolensis* Pomel, 1895	M 2 —	M 3 13
	Elephas [*Palæoloxodon*] *atlanticus* Pomel, 1879	M 2 $\frac{10}{10-12}$	M 3 $\frac{12}{12-14}$
Zululand	*Elephas* (*Loxodon*) [*Loxodonta*] *zulu* Scott, 1907	M 2 —	M 3 $\frac{}{12-13}$
East Central Africa	*Elephas* [*Loxodonta*] *zulu* ref. from Kaiso Bone Beds	M 2 —	M 3 $\frac{}{13}$
Recent	*Loxodonta africana*	M 2 $\frac{8}{8-9}$	M 3 $\frac{10}{11-12}$

Secondly.—The above ridge formulæ demonstrate that the recent *Loxodonta africana* is *more primitive* in dental ridge structure than any of the known Upper Pliocene or the Pleistocene species of *Palæoloxodon*; consequently *L. africana* cannot be descended from any known typical species of *Palæoloxodon* but may have sprung from a more primitive ancestral form still to be discovered.[2]

Thirdly.—It is a striking fact that the broad conspicuous 'loxodont sinus' of the recent *Loxodonta africana* is rudimentary or absent in all [see footnotes below, also pp. 1286-1288, this chapter] the extinct species of elephants thus far described from Africa or Eurasia. This absence or rudimentary condition of the 'loxodont sinus' removes certain extinct Pliocene and Pleistocene species from close relationship to the typical recent *Loxodonta africana* and relates them rather to the dwarfed species of the Mediterranean Islands which we also have grouped under the name *Palæoloxodon* (syn. *Pilgrimia*), as distinguished from the typical *Palæoloxodon namadicus* and *Hesperoloxodon antiquus*.

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[1] [*Elephas zulu* Scott referred to *Loxodonta* by Professor Osborn (see Osborn, 1934.925, p. 2).—Editor.]

[2] [See *Loxodonta prima* Dart, 1929, and *L. africana* var. *obliqua* Dart, 1929, below, this chapter, pp. 1287, 1288.—Editor.]

SYSTEMATIC DESCRIPTION OF AFRICAN SPECIES

Palæoloxodon atlanticus Pomel, 1879

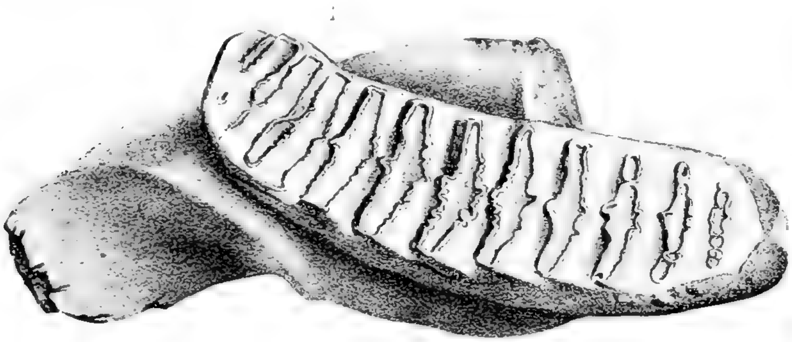
Figures 1047, 1135, 1136

Pleistocene. North Africa, Ternifine near Mascara, Algeria.

Specific Characters (Osborn, 1928).—The cotype second inferior molar (Fig. 1135), length 240 mm., breadth 60 mm., broadly resembles Falconer's type of *Elephas antiquus* (Fig. 1075) except that the median 'loxodont sinus' is more widely expanded, resembling the conditions shown in Falconer's aged referred '*Elephas priscus*,' (Fig. 1076); the ridge formula, $M\ 2\ \frac{10}{10}$, agrees with his identification of the cotype molar (Fig. 1135) as a "Pénultième (5^e) molaire inférieure"; counting the two 'talons' as ridges, it agrees with the ridge formula at present known of *Hesperoloxodon antiquus* (*typicus*), namely, $M\ 2\ \frac{12}{12}\ M\ 3\ \frac{16\frac{1}{2}-17}{16\frac{1}{2}-17}$. The following is Pomel's main ridge formula, omitting talons (1895, p. 51), of:

E. atlanticus: $Dp\ 2\ \frac{3}{?}\ Dp\ 3\ \frac{6}{?}\ Dp\ 4\ \frac{8}{?}\ M\ 1\ \frac{9}{9}\ M\ 2\ \frac{10}{10}\ M\ 3\ \frac{12}{12}$.

History.—Pomel first named this species in 1879 but did not figure it until 1895.



Cotype R.M_2 of Palæoloxodon atlanticus. One-third Natural Size

Fig. 1135. *Elephas atlanticus* Pomel, 1879. One of the cotypes of Pomel, 1895, Pl. viii, fig. 1: "Pénultième (5^e) molaire inférieure, vue par la couronne, ½, et montrant le canal symphysaire, très obtus; Ternifine;" identified as a right inferior molar, r.M_2. (*Op. cit.*, p. 44): "J'ai fait figurer, Pl. viii, fig. 1 et 2, une magnifique molaire très bien conservée, en partie encore contenue dans son os mandibulaire; elle a 240^{mm} de longueur avec une largeur de 60^{mm} au milieu; elle compte dix lames avec deux talons."

Observe: (1) That the central evaginations of the 'loxodont sinus' resemble those of the *Hesperoloxodon antiquus*, figured as '*Elephas priscus*' by Falconer in 1868 and reproduced in our figure 1076; (2) that the ridge formula is ½–10–½ or 12, instead of 10 as given in Pomel's description of 1895, p. 51; (3) that the measurements are, length 240 mm., breadth 60 mm.

Elephas atlanticus Pomel, 1879. "Ossements d'Éléphants et d'Hippopotames découverts dans une station préhistorique de la plaine d'Eghis (province d'Oran)." Bull soc. géol. France, Vol. VII, Ser. 3, 1879, p. 51. Cotype.—Second inferior molar, r.M_2. Musée d'Oran, Algeria. Horizon and Locality.—Ternifine, Mascara, Algeria. Cotype Figure.—Pomel, 1895, Pl. viii, figs. 1, 2.

Pomel figured this specimen as above in 1895, but he named it in 1879 (1879, p. 51): "Je me crois dès lors autorisé à donner à cette forme particulière, actuellement disparue de la région atlantique, mais seulement depuis une époque très-rapprochée des temps historiques, le nom d'*Elephas atlanticus*, rappelant le nom de la race d'hommes primitifs placés par la mythologie dans le massif du Nord de l'Afrique." He designated the locality in 1895 (*op. cit.*, p. 42): "J'ai désigné sous ce nom, dans diverses publications, une espèce très particulière d'éléphant découverte dans des stations de la pierre éclatée à Ternifine, près de Mascara, retrouvée près du village de la Sénia, par M. Féningre, dans des fouilles pour fondations et, plus récemment, dans la caverne aux hippopotames de Pointe-Pescade." In the same publication (*op. cit.*, p. 51) he defines the animal: "L'*elephas atlanticus* était armé de défenses robustes."

Osborn, 1930: Pomel's detailed description (1895, pp. 42–51, Pls. vi–x) indicates a ridge formula (including 'les talons') for this species of:

$M\ 2\ \frac{}{\frac{1}{2}-10-\frac{1}{2}=12}$ (length 240 mm., breadth 60 mm.). See page 44 of Pomel, also figure 1135 of the present Memoir.

$M\ 3\ \frac{\frac{1}{2}-12-\frac{1}{2}=14}{\frac{1}{2}-12-\frac{1}{2}=14}$ (length $\frac{324}{324}$ mm., breadth $\frac{84}{72}$ mm., height of middle plate $\frac{}{60}$ mm.). See pages 43 and 47 of Pomel, also figure 1136 of the present Memoir.

Thus *Palæoloxodon atlanticus*, while having a relatively low ridge-plate formula, namely, $M\ 2\ \frac{}{\frac{1}{2}-10-\frac{1}{2}}\ M\ 3\ \frac{\frac{1}{2}-12-\frac{1}{2}}{\frac{1}{2}-12-\frac{1}{2}}$, is a very large elephant, equaling in size the typical *Hesperoloxodon antiquus* of the Forest Bed (Fig. 1088), namely, $M\ 3\ \frac{16\frac{1}{2}}{17}$, length of inferior molar 315 mm., height of middle ridge-plate 126 mm.

Counting the large anterior and posterior talons (Pl. viii), the ridge-plate count of the cotype is $M\ 2\ \frac{}{12}$, of the referred superior molar from Ternifine $M\ 3\ \frac{14}{}$. Consequently the ridge-plate count may be actually higher than that given by Pomel.

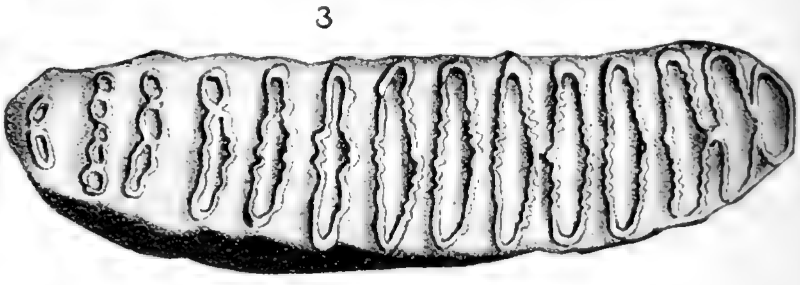


Fig. 1136. Referred third superior molar of the left side, l.M^3, of *Elephas atlanticus* Pomel. After Pomel, 1895, Pl. viii, fig. 3: "Dernière molaire supérieure, vue par la couronne; Ternifine; ⅓. Musée d'Oran."

This very large superior molar (*op. cit.*, 1895, p. 47), length 324 mm., breadth 84 mm., exhibits a ridge formula of $M\ 3\ \frac{14}{}$; the anterior and posterior ridge-plates rise to the surface of the crown and are described by Pomel as "*talons*."

Palæoloxodon jolensis Pomel, 1895

Figure 1137

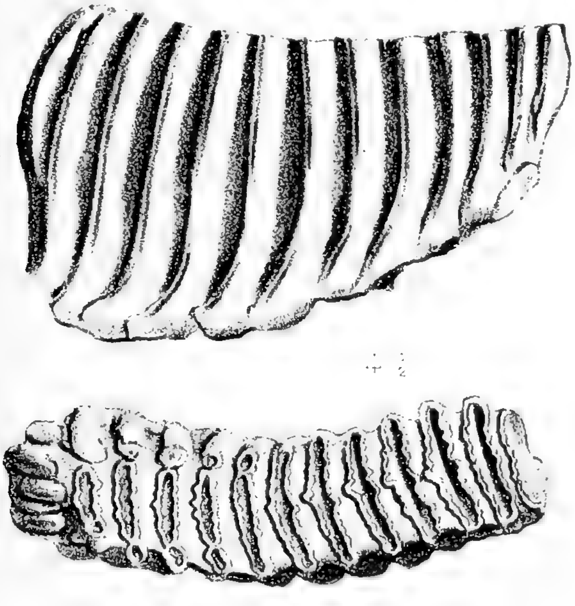
Pleistocene. Algerian seacoast, North Africa.

This is the second North African species described by Pomel, in the same year (1895) in which he published his type figure of *Elephas* [=*Palæoloxodon*] *atlanticus*.

Osborn, 1924: Pomel's type figure of M_3 of the left side exhibits the ridge formula $M\ 3\ \frac{}{13}$, a formula inferior to that of *Hesperoloxodon antiquus*, but exceeding that of *Palæoloxodon* *atlanticus*, laminar frequency 14 ridge-plates in 30 cm.; it may be an ascending progression above *P. atlanticus*.

Elephas jolensis Pomel, 1895. "Paléontologie Monographies. Les Éléphants Quaternaires." Carte Géol. de l'Algérie, 1895, p. 32. Type.—Third left inferior molar, l.M$_3$. École des Sciences, Algiers. Horizon and Locality.—(*Op. cit.*, explanation of Pl. v, fig. 3): " . . . trouvée à la ferme Beauséjour, dans l'ancienne plage émergée," Algeria, North Africa. Type Figure.—*Op. cit.*, Pl. v, figs. 3 and 4.

Type Description.—(*Op. cit.*, p. 32): "La pièce la plus importante pour la caractéristique de cette forme est représentée Pl. v, fig. 3 et 4. Elle a été trouvée à la ferme de Beauséjour, en aval du Krober-Roumia, dans la plage marine soulevée et a été donnée à l'Ecole des Sciences par M. Maupas, conservateur de la Bibliothèque nationale d'Alger. Elle est remarquable par sa longueur, par son étroitesse et par son incurvation. Elle compte treize lames dont la dernière, très étalée, peut à la rigueur passer pour un talon ambigu. . . . Cette dent est assez particulière par sa forme en long ruban, dont la partie postérieure est comme flanquée par une double rangée de disques de détrition séparés de la partie moyenne; ceux du côté extérieur se dédoublant plus habituellement que les intérieurs. Cette disposition est assez semblable à celle qu'offre la dernière molaire inférieure de l'*elephas antiquus*; mais dans celui-ci la dent est beaucoup plus grande; elle présente quatorze lames pour 30^{cm}de longueur (ou même quinze lames pour une longueur de 27^{cm}) au lieu de treize lames pour 14^{cm}."



Type Left Third Inferior Molar of Palæoloxodon jolensis

Fig. 1137. Type l.M$_3$ of *Elephas jolensis* Pomel, 1895, Pl. v, figs. 3 and 4, one-half natural size: 3. "Dernière molaire inférieure, vue de profil, ½, trouvée à la ferme Beauséjour, dans l'ancienne plage émergée." 4. "La même dent, vue par la couronne."

(Pomel, 1895, p. 38): "Le fossile algérien qui a treize lames à son arrière-molaire inférieure, a cette dent longue de 140^{mm} avec une largeur de couronne de 36 et une hauteur, à la septième lame, de 70^{mm}."

Osborn, 1928: This narrow thirteen ridge-plated left third inferior molar, l.M$_3$, clearly distinguishes this species from Pomel's '*Elephas atlanticus*.' It is of very small size and very primitive, as shown by the comparative measurements given by Pomel (cf. 1895, p. 38):

	Length l.M$_3$	Breadth M$_3$	Ridge-plates	Height Max.
Antiquus [*Elephas antiquus* (*typicus*)]	300	73	16	123
Mnaidriensis	170	50	13	70
Jolensis [Type]	140	36	13	70

Thus *Palæoloxodon jolensis* of Algeria is inferior in size to *P. mnaidriensis* of Malta; it is closely similar in size and in the number of ridge-plates to the *P. melitensis* of Malta.

Palæoloxodon recki Dietrich, 1916

Figure 1138

Oldoway-Tuffe, Serengetisteppe, northern Tanganyika Territory. [Pleistocene.]

Specific Characters.—The relatively broad eleven to twelve ridge-plated second inferior molar suggests comparison with *Loxodonta zulu* Scott, except that the ridge-plates appear to be more closely compressed and the dentinal exposures between the ridge-plates more narrow. This molar [lectotype], length 216 mm., breadth 62 mm. (Dietrich, 1916, p. 15), is relatively broader than Pomel's cotype of '*Elephas atlanticus*' (Fig. 1135).

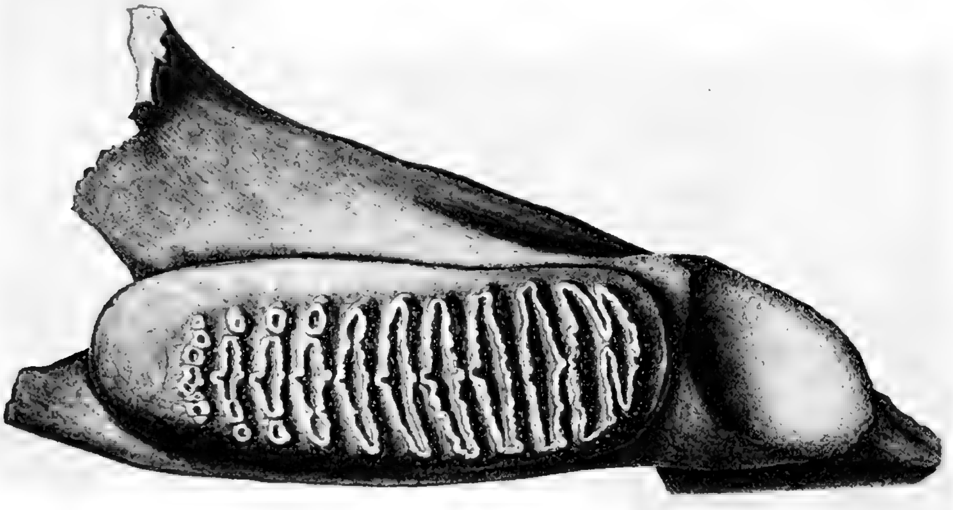
Mus. No. XVII 1384, l.M$_2$ with 12 ridge-plates, length 216 mm., breadth 62 mm., height 120–130 mm. (cf. Taf. i, fig. 2).

Mus. No. XIII 711, l.M$_3$, with ½–16–½ ridge-plates, length 330 mm., breadth 85 mm., height 150 mm. (cf. Taf. i, fig. 3, and explanation of Taf. i, also see Tab. i, p. 15).

Elephas antiquus Recki Dietrich, 1916. "Elephas antiquus Recki n.f. aus dem Diluvium Deutsch-Ostafrikas. . . . " Arch. Biontol., Bd. IV, Heft I, p. 22. Original in the Geologisch-Paläontologisches Institut der Universität, Berlin, XVII 1384. Lectotype.—Second inferior molar of the left side, l.M$_2$. Horizon and Locality.—Oldoway-Tuffe, Serengetisteppe, northern Tanganyika Territory. Lectotype Figure.—*Op. cit.*, Taf. i, fig. 2; cotypes, Taf. i–viii (in part).

Type Description.—The lectotype, M$_2$, is described by the author (*op. cit.*, p. 22) as follows: "Wir können aus den vorliegenden Funden eine neue Lokalrasse oder geographische Abart des *E. antiquus* ableiten, die ich Herrn Dr. H. Reck zu Ehren *Elephas antiquus Recki* benennen möchte; sie verhält sich in den Unterkieferzähnen folgendermassen: Die Kaufläche der M$_2$ ist wie bei *E. antiquus* typus schmal und bandförmig, die der M$_3$ dagegen entschieden breiter als bei jenem und von ovalem Umriss oder mit geraden von vorn nach hinten zusammenlaufenden Rändern. . . . Die Zahl der Lamellen der hintersten Backenzähne ist trotz der Verlängerung dieser Zähne geringer geblieben als bei den geologisch jüngsten Formen des *E. antiquus* . . . Da die Zähne keine Mittel- oder Übergangsstellung einnehmen, d. h. keine neue Mutation, sondern eine neue Variante des Antiquustyps vorliegt, so möchte ich die neue Bezeichnung *E. antiquus Recki* nicht als Namen für eine bestimmte Entwicklungsstufe im Antiquusstamm, sondern im zoologischen Sinn als Bezeichnung einer neuen geographischen Rasse . . . verstanden wissen."

Dietrich adds (*op. cit.*, p. 75): "Nach den vorhandenen Langknochen dürfen wir für die Oldowayer Elefantenrasse Riesenmasse annehmen, so die Höhe im Widerrist mit 4m, die in der Kruppe nicht weniger, sondern eher mehr, denn die Rückenlinie des *E. antiquus* senkt sich nicht wie beim Mammut von der Schulter nach hinten ab, sondern steigt wie beim afrikanischen Elefanten in der Kruppe wieder an. Der Riesenwuchs des *E. antiquus Recki* bestätigt die Tatsache, dass *E. antiquus* neben (nicht hinter) *E. meridionalis* zu den grössten Elefanten, ja zu den grössten Landsäugern überhaupt, zu rechnen ist."



Lectotype of Palæoloxodon recki

Fig. 1138. Lectotype l.M_2 of *Elephas antiquus Recki* Dietrich, 1916, Taf. I, fig. 2, one-third natural size. Geologisch-Paläontologisches Institut der Universität Berlin, XVII 1384. From the Oldoway-Tuffe, Serengetisteppe, northern Tanganyika Territory.

Reck (1914, pp. 306 and 307) makes the following observations: "Über die Merkmale der Unterkiefermolaren (M_2 und M_3) macht Dr. Dietrich zur vorläufigen Charakterisierung der neuen Elefanten folgende Angaben:

1. Lamelle plattig mit gebogenen seitlichen Umrissen.
2. Schmale Seitenpfeiler, breiter Mittelpfeiler der Lamelle, ausgesprochener Mamillenbau.
3. Mässig dicker, mässig gekräuselter Schmelz.
4. Weite Distanzierung der Lamellen durch breite Zementintervalle; doch ist die Tälerweite ein schwankendes Merkmal.
5. Verhältnismässig geringe Lamellenzahl (14 bis 16 bei M_3 11 bei M_2).
6. Breite Zahnkronen der letzten Molaren (M_3)."

". . . Die Unterschiede zum *Elefas Zulu* Scott endlich liegen hauptsächlich in den Punkten 1, 3 und 4 der Charakteristik des Oldowayelefanten. Einige der Zähne, nämlich die vorletzten Molaren erinnern stark an *E. antiquus* Falc. aus dem europäischen Diluvium; doch entfernt die Gesamtheit aller Merkmale, besonders der M_3 den Elefanten von Oldoway vom Urelefanten, während die Stosszähne beide Elefanten wiederum einander nähern (s. unten)."

Dietrich's ridge formula of *Elephas antiquus recki* is as follows:

$$\mathrm{M}\,2\,\frac{}{12}\;\mathrm{M}\,3\,\frac{\phantom{15-16\frac{1}{2}}}{15-16\frac{1}{2}}$$

Over-Estimated Heights (Dietrich, 1916, p. 76, 1924, p. 24).—Dietrich concludes (1916, p. 76): "Als wichtigstes Ergebnis hebe ich hervor, dass die grössten Höhen aller fossilen Elefanten um 4 m herum liegen, dass es keine 5 m hohen Elefanten gegeben hat, dass nicht einmal Dinotherium diese Höhe erreicht hat und dass schliesslich die stärksten Elefanten der Gegenwart hinter denen der Vergangenheit an Mass und Gewicht zurückstehen."

According to Dietrich's measurements and estimates of height, the '*Elephas antiquus recki*' is something over 4 m., namely, 4030 mm., in skeletal height, or 13 ft. 2⅝ in., exceeding the tallest living African elephant by 2 ft., or 610 mm. This estimated height of '*E. antiquus recki*' is inferior to that of the '*E. antiquus germanicus*' of Taubach, in which the humerus is about 1300 mm. in length. According to this estimate both these animals exceed the height of the tallest of the known imperial mammoths, namely, *Archidiskodon maibeni* (3826 mm. or 12 ft. 6⅝ in.), as shown in the comparative shoulder heights of living and extinct elephants (Chap. XVI, fig. 912). Dietrich's shoulder height of the '*E. antiquus germanicus*' of Taubach, estimated from the humeral length (1300 mm.), is still greater, namely, 4000+ mm. He assigns the same height (4000+mm.), estimated from the humeral length of 1300 mm., to the '*Elephas antiquus*' (*typicus*) of the Lower Pleistocene (Mauer) of western Europe.

The length of the humerus, namely, 1290 mm., of *Hesperoloxodon antiquus* of Upnor, as described above, agrees very closely with Dietrich's estimates and measurements, giving an estimated shoulder height of 3700 mm. or 12 ft. 1⅝ in.; this accords well with the fact that the Upnor skeleton is not full grown, because the second inferior and superior molars, M 2, are still in full use.

By the practical agreement of the Dietrich humeral measurements with those of Forster Cooper (1928), we may reach a nearly correct estimate of the maximum height of *'Elephas antiquus germanicus'* of Taubach, namely:

Humeral length	1300 mm.
Skeletal height at shoulder	3729
Height in the flesh at shoulder	3965

In brief, in comparison with the estimates of *Archidiskodon (imperator) maibeni*, as given in the legend of figure 912, and taking advantage of Dietrich's excellent table of comparative measurements (1916, p. 76), we may estimate the shoulder height of the skeleton (in millimeters) of the following species as below.

COMPARATIVE SKELETAL MEASUREMENTS AND HEIGHTS WITH THOSE OF 'ELEPHAS ANTIQUUS RECKI'
(DIETRICH, 1916; OSBORN, 1930)

The length of the humerus affords one standard means of estimating the skeletal height at the shoulder. In *Archidiskodon maibeni* the humerus is relatively shorter and the estimated shoulder height is made from the entire forelimb.

Millimeters	Length M_3	Length of humerus	Length of Mtc. III	Length of femur	Length of tibia	Estimated skeletal height at shoulder
E. antiquus recki Serengetisteppe, Tanganyika Territory	330	1235	240	1500[1]	900	3600 (H.F.O.)
E. antiquus germanicus, Taubach	330–350	1300 ca.	250	1500	900	3729 (H.F.O.)
E. antiquus (*typicus*), western Europe	243–310	1300		1400+	840	
Hesperoloxodon antiquus of Upnor		1290	246	?1520e	1020	3700
Parelephas jeffersonii, Indiana	298e	1090		1250		3200
Archidiskodon maibeni, Nebraska	244	1251				3826

VII. PALÆOLOXODON AND LOXODONTA OF SOUTH AFRICA

[The following section on *Palæoloxodon* and *Loxodonta* of South Africa has been compiled in accordance with Professor Osborn's expressed views in his article in Novitates, No. 741, "Primitive *Archidiskodon* and *Palaeoloxodon* of South Africa" (Osborn, 1934.925), that is, the type descriptions of the various species have been extracted in whole or in part from the original publications, under the generic reference of the present author, and reproductions have been made of the type figures.

The *Elephas* [*Loxodon*] *zulu* Scott, 1907, at first regarded by Professor Osborn as referable to the genus *Palæoloxodon*, was finally referred in his article of 1934 to *Loxodonta* (Osborn, 1934.925, p. 2). Consequently the description, originally placed under *Palæoloxodon* above, has been removed to page 1286 of the present section, as in the case of *Archidiskodon transvaalensis* and *A. sheppardi* Dart, 1927, now regarded as Palæoloxodonts rather than Archidiskodonts (see pp. 1284 and 1285 below).—Editor].

TYPICAL PALÆOLOXODON.—(Osborn, 1934.925, p. 14): "The type molars of the eight species referred to *Palaeoloxodon* . . . [below] are readily distinguished from *Archidiskodon* by the following five characters: (1) Dentine areas equal or exceed cement areas by relatively close compression of the ridge plates. (2) Absence of pre- and post-sinus central foldings, faint median expansion of the loxodont sinus. (3) Enamel relatively thin and more or less strongly and finely crimped. (4) Height of ridge plates increasing: *P. kuhni* = 100 mm., *P. wilmani* = 128 mm., *P. archidiskodontoides* = 145 mm., *P. sheppardi* = 188 mm., *P. transvaalensis* = 231 mm., *P. hanekomi* = 259 mm. (5) Number of ridge plates. It seems probable that Dart's type of *A. sheppardi*, displaying 1–13 ridge plates, is an LM^2, in which case *A. sheppardi* becomes a synonym of *A. transvaalensis* Dart with 1–14 ridge plates."

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[1] [See Dietrich, 1924, p. 24, where a length of 147 cm. is given as the greatest length.—Editor.]

Palæoloxodon(?) **andrewsi** Dart, 1929[1]

Figure 1139

Gong-Gong, Vaal River, South Africa. Middle terrace, 60-80 feet. Lower? Pleistocene.[2]

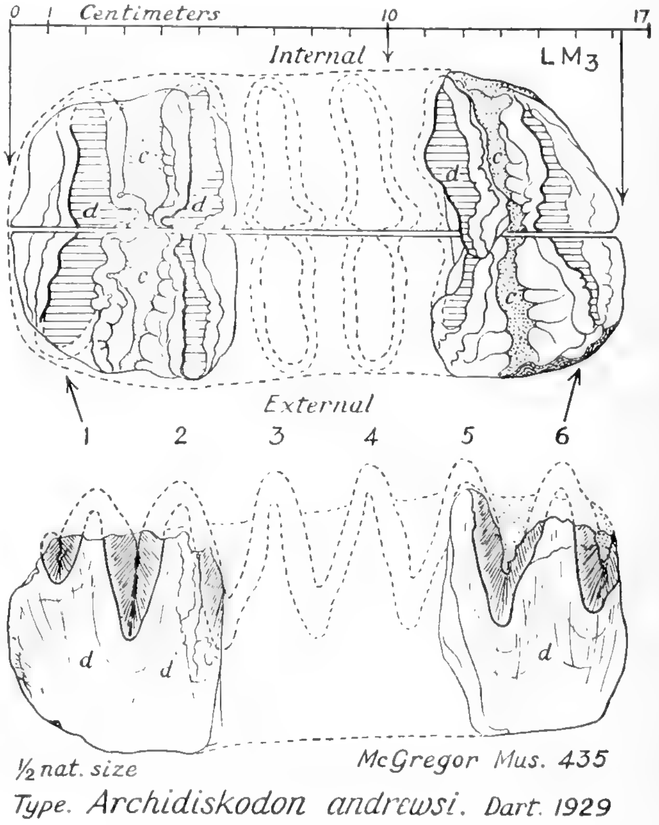
(Osborn, 1934.925, p. 14): "A primitive or ancestral member of the *Palaeoloxodon* group may be this problematic *A. andrewsi* Dart (Fig. 5 [=Fig. 1139 of the present Memoir]), a type which on sectioning and very careful reëxamination by the present author, proves to be distinct both from *A. planifrons* (Fig. 4 [=Fig. 876 of the present Memoir]) and *A. subplanifrons* (Fig. 1 [=Fig. 875 of the present Memoir]). The fragmentary type, f.LM$_3$, displays the following characters: Ridge plate height =48 mm. est., estimated number of ridge-plates=6. Feeble pre-sinus fold; very prominent post-sinus fold. Valleys V-shaped. Estimated length=164 mm. Estimated breadth=83 mm., estimated index=50. Enamel thick, crimped. It has been extremely difficult to restore this terribly shattered type specimen and deduce its outstanding characters . . . from the enamel folds which certainly belong at the front and back of the third inferior grinding tooth."

Archidiskodon andrewsi Dart, 1929. "Mammoths and Other Fossil Elephants of the Vaal and Limpopo Watersheds," So. African Journ. Sci., Vol. XXVI, pp. 711–713. TYPE.—McGregor Mus. 435, found by Mr. Luke Rademan and presented to the Museum by Mr. H. Rees. Cast Amer. Mus. 26968. [Regarded by Professor Osborn as a left third inferior molar, l.M$_3$.] HORIZON AND LOCALITY.—"Gong-Gong, Vaal River 'Deep diggings at a depth of 80 feet,' probably Middle Terrace. . . . ?Pliocene." Lower? Pleistocene.[2] TYPE FIGURE.—*Op. cit.*, 1929, fig. 14, p. 711 [=Fig. 1139 of the present Memoir].

TYPE DESCRIPTION.—(Dart, *op. cit.*, 1929, p. 712): "The fragments together embrace a length of 110 mm., the greatest width is approximately 80 mm. and the greatest height 60 mm. They include one fragment with two and a half plates and another with one and a half plates and a talon. The enamel is very thick (4–5 mm.). The plates are 17–22 mm. wide and display anterior and posterior buttresses as well developed as in *A.* [*Archidiskodon*] *loxodontoides*. Here the width of the plates is in the region of 25 mm. and by virtue of the abutment of adjoining buttresses upon one another the interlamellar cementum on either side of the tooth is separated into two parts as in *A. loxodontoides*."

"The enamel is markedly folded despite its thickness as in *A. loxodontoides*, but in coarse fashion. The distance between mid-points of adjacent ridge plates measured laterally is 1¼ in. The reduction (7–11 mm.) of interlamellar cementum on the medial side of the tooth and its almost complete absence on the lateral side in one fragment and its total absence in the other fragment together with the rapid contraction of the lamellar thickness (1 in. at base, ½ in. at grinding surface) are witness to the Stegodontine characteristics of the molar—a feature to which attention has been frequently drawn in dealing with all these primitive mammoths. Further, despite the worn aspect of these fragments, I do not think that the true height was very greatly in excess of what the fragments portray."

"In form, measurements and general appearance, the tooth approximates more closely to *A. loxodontoides* than to any of the types hitherto discussed, but the coarser folding of its enamel, its reduced height, its lack and almost total absence of interlamellar cementum demonstrate the virtual certainty that we have here a still more primitive form not very far removed from the Stegodonts and apparently ancestrally related to *A. vanalpheni* and *A. loxodontoides*."



TYPE OF ?PALÆOLOXODON ANDREWSI

Fig. 1139. Restored type of "*Archidiskodon*" *andrewsi* Dart, 1929, McGregor Museum 435, Kimberley, South Africa; cast Amer. Mus. 26968. Crown view restored with estimated 6½ ridge-plates. Observe subequal cement and dentinal areas; pre- and post-sinus folds and two anterior ridges in contact; sharply V-shaped valleys between enamel ridges which penetrate about half the crown, thus differing widely from the enamel ridge-plates of *A. subplanifrons*. This is provisionally referred to *Palæoloxodon*. One-half natural size. After Osborn, 1934.925, fig. 5, p. 13.

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[1] [It will be noted that the present species has been questionably referred by Professor Osborn to *Palæoloxodon* (see Chap. XVI, pp. 984, 985 above, where it is provisionally listed under both the *Metarchidiskodon griqua* and *Palæoloxodon transvaalensis* groups).—Editor.]

[2] Cf. Table VIII, p. 984, of the present volume.

Palæoloxodon hanekomi Dart, 1929

Figure 1140

Delpoort's Hope, Vaal River, South Africa. Level unknown—Pleistocene.

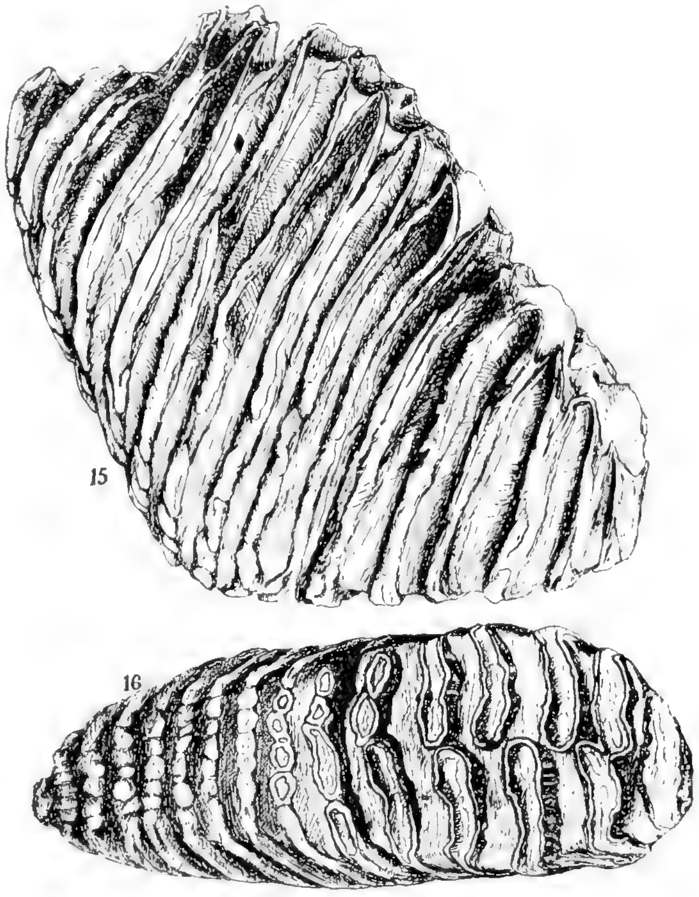
Archidiskodon hanekomi Dart, 1929. "Mammoths and Other Fossil Elephants of the Vaal and Limpopo Watersheds," So. African Journ. Sci., Vol. XXVI, pp. 713–715. Type.—McGregor Mus. 2930. "?Third right upper molar." Horizon and Locality.—"The old river bed of the Vaal River at a depth of 20 feet at Delpoort's Hope [South Africa]. ?Upper Pleistocene." Type Figure.—*Op. cit.*, figs. 15 and 16, p. 713 [=Fig. 1140 of the present Memoir].

Type Description.—(Dart. *op. cit.*, 1929, pp. 714, 715): "This tooth was found by Major C. J. Hanekom on 23 October, 1927. It differs entirely in form from any hitherto discovered in South Africa being considerably shorter (200 mm.) than it is high (259 mm.). All specimens previously found have a length in excess of their height except in one case (*A.* [*Palæoloxodon*] *transvaalensis*) in which both measurements are virtually identical. The great height of this tooth (10¼ inches) equals that of the most gigantic form of Archidiskodont known, namely, *A. imperator* Leidy of America. The greatest breadth (102 mm.) is virtually identical with that of *A.* [*P.*] *sheppardi* (100 mm.), but is not so great as that of *A.* [*P.*] *transvaalensis* (110 mm.). The number of plates also visible is 17 (Fig. 15 [=Fig. 1140 of the present Memoir]), that is, approximately identical with that of *A.* [*P.*] *transvaalensis* but in excess of *A.* [*P.*] *sheppardi*, where the number of lamellae is thirteen."

"In virtue of the hypsodonty of the specimen (Fig. 2 [=Fig. 1140 of the present Memoir]), there are only eight and a half plates in wear (Cf. figures of *Mammonteus prigimius* [*primigenius*] *compressus*, Osborn 1924). The irregularity of plate number in the worn area due to the curious nature of the enamel pattern—which forms an especially distinctive attribute of this particular species—is unparalleled in any South African mammoth type and recalls in some respects the irregularities of plate arrangements seen in *Mammonteus* (*Elephas*) *primigenius* (Cf. Zittel's 'Textbook of Palaeontology,' Vol. 3, Fig. 349, 1925)."

"The individual lamellae are as broad (11–15 mm.) as those of *A.* [*P.*] *sheppardi*, but do not reach so great a breadth as those of *A.* [*P.*] *transvaalensis* and the interlamellar cementum, unlike that in both those forms, is about as broad (10–12 mm.) as the lamellae. The lamellar walls are virtually parallel with one another, but only in the two anterior lamellae do they run entirely across the tooth and then only in a zig-zag fashion, demonstrating that each lamellar plate is virtually bifid to about 3 inches from its root base. These characters, coupled with the positive though not excessive fore and aft compression of the seventeen ridge plates and vertical elevation of the tooth or hypsodonty, show that we have in South Africa a further phase of mammoth evolution beyond what has heretofore been recorded for this country."

"The discovery of this exceedingly progressive form, whose hypsodont analogies are to be sought in America, renders it also probable that further discoveries of a convergent evolutionary nature between American and African forms will yet be made. . . .



Type of Palæoloxodon hanekomi

Fig. 1140. Type ?third right superior molar of *Archidiskodon hanekomi* Dart, 1929, from Delpoort's Hope, South Africa. McGregor Mus. 2930. After Dart, 1929, figs. 15 and 16, p. 713, side and crown views respectively. One-third natural size.

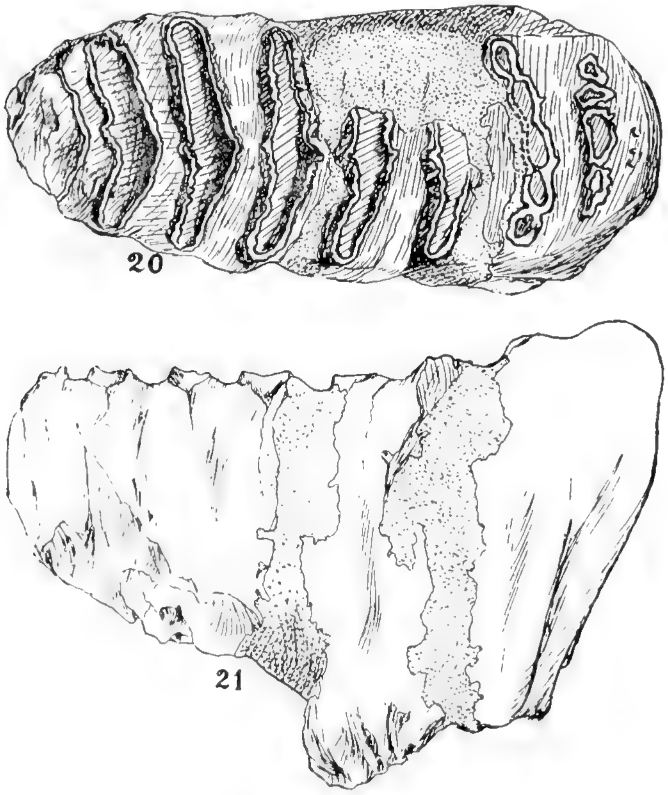
Actually, being discovered at a depth of twenty feet in the river bed gravels at Delpoort's Hope, it would seem that it belonged to an older geological horizon than *A.* [*P.*] *transvaalensis* and *A.* [*P.*] *sheppardi*, which were found at a depth of 4 to 5 feet in the river bed gravels higher up the river at Bloemhof. Mr. Lowe's discovery that these river bed gravels at Bloemhof present two different gravel strata of very variable depth, separated from one another by two different phases of stone implement culture, point to the necessity for similar investigations at Delpoort's Hope and the possibility, despite the depth at which it was found, that *A.* [*P.*] *hanekomi* belongs to a still more recent phase of the Pleistocene than does *A.* [*P.*] *transvaalensis*."

Palæoloxodon yorki Dart, 1929

Figure 1141

Near Christiana, South Africa, Vaal River. Middle(?) Pleistocene.

Pilgrimia yorki Dart, 1929. "Mammoths and Other Fossil Elephants of the Vaal and Limpopo Watersheds," So. African Journ. Sci., Vol. XXVI, pp. 719, 720. Type.—McGregor Mus. 4074, cast Amer. Mus. 22727. "Right lower (?third) molar." Found by Mr. Alf. York during diamond digging operations in 1927. Horizon and Locality.—"Lowest stratum of the river bed gravels on the farm Vanasswegenshoek, O. F. S., below Christiana, [South Africa], at a depth of within 6 feet. . . . ?Pleistocene." Type Figure.—*Op. cit.*, figs. 20 and 21, p. 719 [Fig. 1141 of the present Memoir].



Type of Palæoloxodon yorki

Fig. 1141. Type of *Pilgrimia yorki* Dart, 1929, from near Christiana, South Africa. "Right lower (?third) molar" (McGregor Mus. 4074; cast Amer. Mus. 22727). After Dart, 1929, figs. 20 and 21, p. 719, crown and side views, one-half natural size.

Type Description.—(Dart, *op. cit.*, 1929, pp. 719, 720): "This elephant tooth (Figs. 20, 21 [=Fig. 1141 of the present Memoir]), like the other remains found, is stony in nature and completely fossilised. It is a relatively diminutive tooth being 180 mm. long, 79 mm. broad, 115 mm. high, possessing 9 plates, all of which are in wear. There is no trace on the posterior plate or talon of a depression arising from the pressure of a tooth advancing behind it, as Falconer has pointed out (*Palaeont. Memoirs*, Vol. II, p. 294) is characteristic of a milk tooth. Hence the tooth must have been an adult one. . . . It approaches in number of ridge plates, enamel pattern, and tooth form to *E. priscus* Falconer and to *E. trogontherii* Pohl. There is exhibited a very slight tendency especially in the anterior crescents to throw out an anterior and posterior buttress, and hence to provide a vestigial loxodont sinus. The width of each lamella varies from the almost parallel regions where it is 12 mm., to 20 mm. in the region of the slight buttresses, but the lamellae are well separated by cementum across the whole grinding surface; the whole tooth is well encased in the abundant cementum."

"The numerical seriation of this grinder of the lower jaw is a matter of question. It may be a second molar, but in any case it indicates by its reduced width, its symmetrical anteriorly-concave crescents, its slight tendency to single fore and aft buttresses, its more delicate enamel (2-3 mm. thick), and finer crimping a distinctive type, so far as South Africa is concerned, whose relationships are with the most primitive Pilgrimia [=*Palæoloxodon*]. It is comparable in simplicity, but not in size, with *E. falconeri* Busk. . . . Of known fossil forms outside Africa, it seems to approximate most closely to *Elephas* (*Loxodon*) *priscus* Falconer, not only in its dimensions and regularly crescentic plates with sinuous outline as viewed laterally, but also in the actual number of plates and the tendency to buttressing. Indeed, the appearances are such that *A.* [*Palæoloxodon*] *yorki* might well be ancestrally related to the *E.* (*Loxodon*) *priscus* of Falconer, as in *A.* [*P.*] *yorki* the processes leading to the production of such forms as *E. priscus* and *E. trogontherii* seem to be incipient."

"*A.* [*P.*] *yorki* is the simplest of the Pilgrimia [*Palæoloxodon*] type yet recovered in Southern Africa."

Palæoloxodon wilmani Dart, 1929

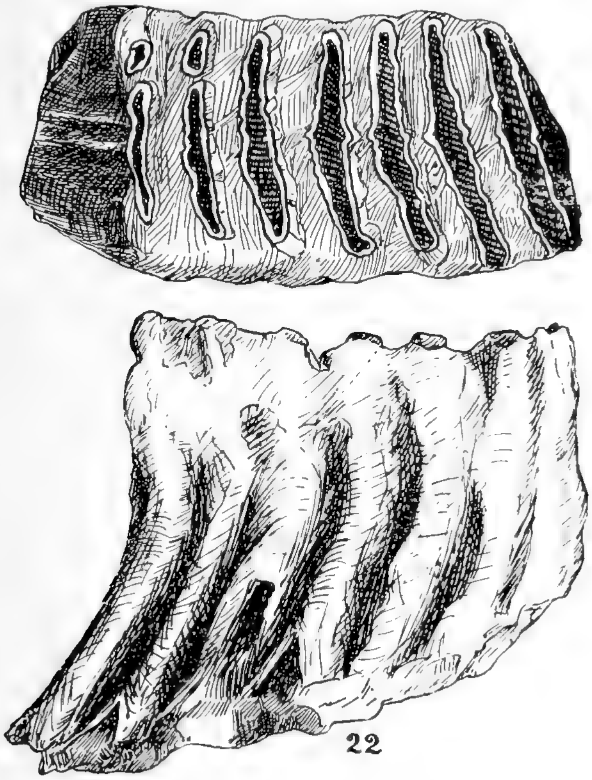
Figure 1142

Below Christiana, Vaal River, South Africa. Middle(?) Pleistocene.

Pilgrimia wilmani Dart, 1929. "Mammoths and Other Fossil Elephants of the Vaal and Limpopo Watersheds," So. African Journ. Sci., Vol. XXVI, pp. 720–722. Type.—McGregor Mus. 4075, cast Amer. Mus. 22726. "Left lower (?third) molar." Horizon and Locality.—"Lowest stratum of river bed gravels between the farms Vanasswegenshoek and Bloemheuvel, Transvaal, below Christiana at a depth of within 6 feet. . . ?Middle Pleistocene." Type Figure.—*Op. cit.*, fig. 22, p. 721 [Fig. 1142 of the present Memoir].

Type Description.—(Dart, *op. cit.*, 1929, pp. 721, 722): "This tooth fragment attains only the very narrow width of 70 mm. or 2¾ in., but the height of the largest plate is 128 mm. It is, therefore, both narrower and higher than *Pilgrimia* [*Palæoloxodon*] *yorki*. Unfortunately the tooth is incomplete, the length of the fragment being 115 mm. and including seven plates only. There must have been in the original tooth at least one and probably two more plates posteriorly and another one, or two, more plates anteriorly. The ridge plate number was . . . ±11 and apparently in excess of *P. yorki* (see Fig. 22 [Fig. 1142 of the present Memoir]). But the most striking dissimilarity between the two teeth lies in the character of the enamel plates which in this tooth are narrower (6 mm. in narrowest parts to 11 mm. in the slightly wider central parts), and are not so widely separated by the interlamellar cementum. Further, they run almost directly transversely across the grinding surface, displaying little if any tendency to crescentic outline on this aspect of the tooth. The lamallae are distinctly narrower laterally than medially (that is, the reverse of what is found in the modern African elephant and in *Loxodonta antiqua zulu*) where they are somewhat bulged, terminating in an anteriorly curved expanded portion almost as wide (9 mm.) as the widest central portion of the lamella."

"The same tendency towards a median buttress as was found in *P. yorki* is also encountered here, but to still less extent. The enamel also is more delicate (1½–2 mm. thick) and is more finely crimped than in *P. yorki*. In sharp contrast also with *P. yorki*, the tooth is not ensheathed in cementum but the ridge plates stand out to a depth of ¼ to ½ inch, except for the upper 1 to 1½ inches of the lateral aspect, nor are the ridge plates much less obvious on the medial aspect of the tooth."



TYPE OF PALÆOLOXODON WILMANI

Fig. 1142. Type of *Pilgrimia wilmani* Dart, 1929, from below Christiana, Transvaal, South Africa. "Left lower (?third) molar" (McGregor Mus. 4075; cast Amer. Mus. 22726). After Dart, 1929, fig. 22, p. 721, one-half natural size.

"There can be no question that this is another species of Pilgrimia [=*Palæoloxodon*], which I shall denominate *Pilgrimia wilmani*, in honour of Miss Wilman, Director of the McGregor Memorial Museum at Kimberley, who has been personally responsible for retrieving so many scientific treasures from the Vaal valley and permanently safeguarding them in that institution."

Palæoloxodon kuhni Dart, 1929

Figure 1143

Pniel Estate, South Africa. ?River bed gravels. Middle(?) Pleistocene.

Pilgrimia kuhni Dart, 1929. "Mammoths and Other Fossil Elephants of the Vaal and Limpopo Watersheds," So. African Journ. Sci., Vol. XXVI, pp. 723, 724. TYPE.—McGregor Mus. 4144, cast Amer. Mus. 22725. "?Lower left molar." HORIZON AND LOCALITY.—[P. 723] "Pniel Estate. ?River bed gravels. . . ?Pleistocene." [P. 724] "The site of discovery at Pniel must be fairly comparable with that at Vanasswegenshoek, and this indicates the necessity for stratigraphical study in the Pniel region in order to establish the correlation which is likely between these two widely separated sites along the Vaal valley. This is the more necessary in view of suggestions, which have been put forward from time to time, that the gravels of the river bed and of the terraces higher upstream are of a different age from the same gravel lower down stream. In the solution of this question the identification of elephant teeth types with particular gravels promises to be of premier importance." TYPE FIGURE.—*Op. cit.*, fig. 24, p. 725 [Fig. 1143 of the present Memoir].

TYPE OF PALÆOLOXODON KUHNI

Fig. 1143. Type of *Pilgrimia kuhni* Dart, 1929, Pniel Estate, South Africa. "?Lower left molar" (McGregor Mus. 4144; cast Amer. Mus. 22725). After Dart, 1929, fig. 24, p. 725, one-third natural size.

TYPE DESCRIPTION.—(Dart, *op. cit.*, 1929, pp. 723, 724): "The fragment consists of four plates and the greater portion of the anterior talon. Its dimensions (greatest length 96 mm., greatest width 75 mm. and greatest height 100 mm.) indicate to some extent its relationships. Its width and height are fairly closely comparable with those of certain specimens of *E. antiquus Recki* and in its general morphology it forms the closest approach to that form which I have hitherto seen in this country. In that form, however, the plates, as seen from the grinding aspect, are usually definitely crescentic, the horns of the crescents facing forwards. In this specimen they run transversely across the tooth. The anterior talon is vestigial, the most anterior true plate is continuous across the grinding surface, the second has a smaller left and a larger right island, while the third and the fourth have a central large island and internal and external smaller islets. These features indicate that the total length of the tooth could not have been great and the total number of plates in the tooth is unlikely to have exceeded seven or eight (see Fig. 24 [Fig. 1143 of the present Memoir])."

"The numerical seriation of the tooth is very doubtful. The enamel is very thin (2 mm.) and is, on the whole, very finely crimped."

Palæoloxodon archidiskodontoides Haughton, 1932

Figure 1144

Sydney-on-Vaal Breakwater, bed of the Vaal River, South Africa. Level unknown—Pleistocene.

Pilgrimia archidiskodontoides Haughton, 1932. "On Some South African Fossil Proboscidea," Trans. Roy. Soc. So. Africa, Vol. XXI, pp. 4–8. Cotypes.—". . . a fragmentary skull with two worn molars that can be fitted into their sockets, a humerus which lacks the proximal end, the glenoid portion of a scapula, and the fairly complete left side of a pelvis." McGregor Museum, Kimberley, South Africa. Horizon and Locality.—"Sydney-on-Vaal Breakwater in the bed of the Vaal River, 10½ feet 'below the maiden ground.'" Type Figure.—*Op. cit.*, Pls. i–iii [=Fig. 1144 of the present Memoir].

Type Description.—(Haughton, *op. cit.*, 1932, pp. 4–8): "In June 1930, Miss Wilman, the Curator of the McGregor Museum at Kimberley, forwarded to the writer for examination a collection of fragmentary mammalian remains which had been found by Mr. J. du Preez, jun., at the Sydney-on-Vaal Breakwater in the bed of the Vaal River, 10½ feet 'below the maiden ground.' In February 1931, thanks to the mediation of Major H. P. Tuckey, Miss Wilman received a further consignment, from the same locality, of material which was in the possession of Mr. J. J. de Jong. Among the heterogeneous collection of bones which made up these two consignments, the writer discovered some Elephantid remains—a fragmentary skull with two worn molars that can be fitted into their sockets, a humerus which lacks the proximal end, the glenoid portion of a scapula, and the fairly complete left side of a pelvis. These are the bones that are briefly described and figured here."

"*Teeth.*—Both the left and right upper molars are preserved, both showing very worn grinding surfaces. From the fact that the socket into which the right tooth fits is bounded posteriorly by a wall of bone with a thickened and somewhat rugose ventral surface, and further that posterior to this wall is another, unfilled, socket, it is concluded that the teeth are the second permanent molars."

"The left molar has nine plates and a posterior talon preserved. The three anterior plates are worn down to the roots, so that the enamel of each has coalesced with that of the succeeding plate. The degree of wearing is greater on the inner than on the outer side of the tooth. As preserved, the length of the tooth is 148 mm.; the greatest breadth was probably 94 mm.; the maximum thickness of the plates (4th and 5th) is 16 mm.; the height of the posterior plate is about 145 mm. The length of the posterior six plates is 107 mm.; and six and a half plates occur in a length of 100 mm."

"There is no evidence of any tendency to the formation of a median loxodont buttress."

Type of Palæoloxodon archidiskodontoides

Fig. 1144. Type of *Pilgrimia archidiskodontoides* Haughton, 1932, from Sydney-on-Vaal Breakwater, bed of Vaal River, South Africa. McGregor Museum, Kimberley, South Africa. After Haughton, 1932, Pl. i, fig. 1, and Pl. ii, figs. 1 and 2.

Pl. i, fig. 1. ?Second superior molar. About one-half natural size.

Pl. ii. Part of right humerus, anterior and posterior views.

"The enamel is of medium thickness (2.5–3 mm.), and is by no means strongly crimped."

"In the right molar the posterior talon is missing. Five plates occupy 80 mm., and there is very little interlamellar cement. The plates have their anterior and posterior faces roughly parallel, there being no marked antero-posterior thickening of the plate towards the root. Laterally there is a distance of 15 mm. from mid-point to mid-point of succeeding enamel ridge plates."

"Although they are wider than any of the three species described by Dart, these teeth seem—on account of their high lamellar frequency—to fall within the limits of the genus *Pilgrimia* [=*Palæoloxodon*]. . . . In *Pilgrimia* the frequency is 5–6 in *P. yorki* and 6.5 in *P. wilmani*; and the length-lamellae ratio is 18.2 in the former and 16 in the latter. In the form under discussion the figures are 6.5 and 15.4–15.6 respectively. The greater width of the two teeth described here tends to remove them from *Pilgrimia* as hitherto known in South Africa. Width, however, is a somewhat varying quantity within a species, as is evidenced by a study of a large number of molars of *Loxodonta africana* where the width varied from 60 mm. to 84 mm., and is dependent on the position and seriation of the tooth. Teeth from the lower jaw are always narrower than teeth from the upper jaw; and the upper molars of *Pilgrimia yorki* will certainly be found to be broader than 79 mm., which is the measurement given by the type lower molar. A breadth of 94 mm. is obviously not an impossibility for a *Pilgrimia* upper tooth."

"That the form differs from any of the teeth of *Pilgrimia* hitherto described from South Africa is evident. In its breadth and in the tapering form of its plates it recalls certain forms of *Archidiskodon* such as *A. yorki*; and I propose, therefore, for the sake of convenience, to designate it by the new name *Pilgrimia archidiskodontoides*."

"*Skull.*—A portion of the maxillae, into which the two molars fit, is preserved. It shows that the palate was narrow and vaulted, and that the molars diverged posteriorly. In front the width between the molars is about 50 mm., and at the back it was about 90 mm. The vault of the palate is 60 mm. above the grinding surface of the teeth. The alveoli of the tooth in use and the succeeding molar are separated by a wall of spongy bone, which is thicker ventrally than dorsally. In front of the molar, the palatal surface of the maxilla is strongly hollowed—a feature that is not seen in the skulls of *Loxodonta africana* that have been examined."

"*Humerus.*—Part of a right humerus is preserved, the bone lacking the proximal end. Its chief features can easily be discerned from the illustrations given. The bone is much more robust than that of *Loxodonta africana*. The shaft is thicker, and the deltoid crest much stronger and more prominent. The supinator crest is, proportionately, of about the same length; but, as in *P. antiqua recki*, its border is straight and has not the curved form with upper protuberance that is seen in *L. africana*."

"In actual size the bone is smaller than that of *P. antiqua recki* and that of *P. antiqua andrewsi*.[1] Its chief measurements are:—

	mm.	II.	III.	IV.
Maximum width, distal end	265+	350	350	227
Width, trochlear articular surface	230	285	306	. . .
Height of top of supinator crest above distal end	267	410?	450	275
Minimum thickness of shaft	125	145	167	80

Comparative measurements of other forms are given in parallel columns.

II—*P. antiqua recki* from Oldoway, East Africa.
III—*P. antiqua andrewsi* [=*Hesperoloxodon antiquus*] from Upnor, England.
IV—*Loxodonta africana* from Addo."

"Although the head of the bone is not preserved, it can be seen that the inner border is more strongly bowed than in *L. africana*, and it is concluded that the caput humeri was larger or stood away further from the main axis of the bone than in the modern form."

"*Pelvis.*—The left side of the pelvis is almost entire, lacking most of the ischium, the symphyseal region, and the upper iliac crest."

"In shape, the ilium differs considerably from that of *P. antiqua recki* as figured by Dietrich. The pre-acetabular portion of the iliac plate is considerably longer; at the narrowest part of the shaft the outer face of the bone is practically flat, and above this the outer face is far less concave than in the East African form. From the ilium of *L. africana* this bone differs very considerably."

"The pubis has a much stouter shaft than in either *P. antiqua recki* or *L. africana*. In view of the broken nature of the borders of the specimen it is not possible to give many measurements; but the following show some of the differences between this specimen and that of a male *L. africana* from Addo.

	P. archidiskodontoides		*L. africana*
		mm.	mm.
Greatest length of iliac blade	(As preserved)	680	646
Distance from supra-acetabular ridge to spina anterior		386	230
Thickness of ilium at spina anterior		145	85
Height of acetabulum		214	150
Width of acetabulum		200	144"

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[1] [Equals *Hesperoloxodon antiquus* (see footnote, p. 1222, above.)—Editor.]

Palæoloxodon transvaalensis Dart, 1927

Figure 1145

From near Bloemhof, lowest terrace, Vaal River, South Africa. Pleistocene.

Archidiskodon transvaalensis Dart, 1927. "Mammoths and Man in the Transvaal." Nature (Supplement), December 10, 1927, No. 3032, pp. 41–48. TYPE.—Right third superior molar, r.M^3, length 246 mm., breadth 110 mm., posterior height 247 mm. TYPE FIGURE.—*Op. cit.*, p. 47, fig. 6 (right), and p. 48, fig. 7 (left).

⅓ Nat. Size

DART'S TYPE OF PALÆOLOXODON TRANSVAALENSIS[1]

Fig. 1145. *Archidiskodon transvaalensis* Dart. Type right third superior molar, r.M^3, of the lowest Vaal River terrace gravels, near Bloemhof, South Africa. Pleistocene. Modified after Dart's photographs (cf. Dart, 1927, figs. 6, right, and 7, left), one-third natural size. Cast Amer. Mus. 27769.

This molar displays from 1–14 ridge-plates, the maximum height of the eleventh plate being 247 mm.

⅓ Nat. Size

DART'S TYPE OF PALÆOLOXODON SHEPPARDI[1]

Fig. 1146. *Archidiskodon sheppardi* Dart. Type left third superior molar, l.M^3, of the lowest Vaal River terrace gravels, near Bloemhof, South Africa. Pleistocene. Modified after Dart's photographs (cf. Dart, 1927, figs. 6, left, and 7, right), one-third natural size.

This molar displays from 1–13 ridge-plates, as numbered, the height of the eleventh ridge-plate as preserved being 202 mm.

TYPE DESCRIPTION.—(Dart, *op. cit.*, p. 47): ". . . the larger tooth was greater in every dimension. Although the anterior plates are missing, its present length equals that of the other tooth. It is 10 mm. broader and it is 50 mm. higher in its posterior portion. Apart from these points, the whole atmosphere of each tooth is different from that of the other. *From the lateral aspect,* despite its great height, the larger tooth has a massive squarish appearance, markedly different from the triangular form of this aspect in the smaller tooth. The individual plates are obscured in the larger tooth by a dense covering of cement over approximately the entire lower half (115 mm.) of this surface, and almost filling up the interlamellar clefts in the upper half, which are thus rendered broad and shallow. . . . *From the grinding aspect,* the larger tooth has a more bulging ovoid appearance than the narrower and more ellipsoidal appearance of the smaller tooth, as follows also from their respective length and width measurements. Despite the fact that the total lengths of the two specimens are virtually identical, there are three (and perhaps more) additional lamellæ in the larger than in the smaller tooth."

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[1] [Original specimens, formerly in the Ethnology Museum, University of the Witwatersrand, destroyed by fire.—Editor.]

Palæoloxodon sheppardi Dart, 1927

Figure 1146

Near Bloemhof, lowest Vaal River terrace, South Africa. Pleistocene.

Archidiskodon Sheppardi Dart, 1927. "Mammoths and Man in the Transvaal." Nature (Supplement), December 10, 1927, No. 3032, pp. 41–48. TYPE.—Left third superior molar, l.M^3, length 246 mm., breadth 100 mm., posterior height 202 mm. TYPE FIGURE.—*Op. cit.*, p. 47, fig. 6 (left), and p. 48, fig. 7 (right).

TYPE DESCRIPTION.—(Dart, *op. cit.*, pp. 47 and 48): "In the smaller tooth the lamellæ are covered with cement over approximately the lower third (60 mm.) only of this surface, and above this point the interlamellar clefts are extremely deep (5–10 mm.) and narrow in appearance. The same features are repeated on the medial aspects of the teeth. . . . the individual lamellæ are appreciably wider in the larger than in the smaller tooth, so that the interlamellar cement is more abundant in this tooth than in the former. There are also differences in form between the lamellæ of both teeth, in that the narrower lamellæ are more recurved posteriorly at each end of the lamellæ, and the laminæ of each lamella possess a narrower or finer enamel and are more nearly parallel in the smaller than in the larger tooth. . . . In the smaller tooth the pattern presented by the digitations as they come into wear is considerably different, there being only *three* plates showing transition stages from separate digitations to full plates. The most posterior of the three shows three small islets, the second shows four somewhat larger islets, and the third one very large medial islet and one small lateral islet. The remainder of the lamellæ form complete single islands across the grinding surface of the tooth. . . . Sufficient differential characteristics between the teeth have been discussed to indicate that it is highly improbable that they belonged to the same species. Even if we looked upon the smaller tooth as being a second molar from a female, it is scarcely likely that there would be so great a gap between the two. In view, therefore, of the Sheppard brothers' interest in securing the teeth and forwarding them for examination, I will denote the type indicated by this smaller upper and presumably third molar as *Archidiskodon Sheppardi*, sp. nov."

Dart concludes (p. 48): "It is evident, therefore, that the southern mammoths were represented in southern Africa by at least two distinct species of the genus [*Archidiskodon*], and that the line of their southerly migration is shown by the recovery of portion of a tooth of a nearly related species from the depth of 60–80 feet below the Nile at Khartum. . . . It has been shown that the lowest or *mammoth* [*Archidiskodon*] gravels of the Vaal bed are replete with evidences of the lower palæolithic type of culture. They are therefore presumably pre-Bushman in orientation. The only pre-Bushman type known from extreme southern Africa so far is Boskop man. Containing, as they do, extinct forms of mammalian life, there is presumptive evidence furnished that these gravels will yet supply this, and perhaps other hitherto unidentified forms of human-kind, and show them to have been responsible for that culture.

The recognition of extinct forms of mammalian life in the gravels of the river bed further enhances the age of the 60–80 ft. or *mastodon* terrace, and the evidences of palæolithic culture secured from this level and described by Hodkinson. The expectation of human remains there of great importance phylogenetically cannot be exaggerated, since this *mastodon* bed must reach back to a rather early phase of the Pleistocene.

The 200–300 ft. terrace and any fossil mammalian remains or evidences of human culture at that level, which would appear to approximate if not actually to be situate entirely within the Pliocene, must be of premier anthropological importance."

NOTES ON ARCHIDISKODON [=PALÆOLOXODON] TRANSVAALENSIS DART, 1927, AND ARCHIDISKODON [=PALÆOLOXODON] SHEPPARDI DART, 1927

Referring to the site of discovery of two molars from the third or youngest terrace, or river bed gravel, Vaal River, near Bloemhof, South Africa (see above, p. 944, also Fig. 823), Dart continues (*op. cit.*, 1927, p. 43): "The animal remains forwarded from Bloemhof consisted of two right [right and left] upper molars. . . . [p. 45] The present teeth have nothing in common with either *Loxodonta griqua* Haughton or with *Elephas* (*Loxodonta*) *Zulu* Scott. They represent an entirely different category altogether. . . [p. 46] They may, therefore, be included with those of *E. meridionalis*, *E. planifrons*, and *E. imperator* amongst the southern mammoths in the generic phylum Archidiskodon of the subfamily Mammontinæ. . . . [p. 45] They are respectively right and left upper molars, and both are presumably third molars. Their measurements are as follows:

	Right. [*P. transvaalensis*]	*Left.* [*P. sheppardi*]
Third upper molar length	246 mm.	246 mm.
" " " breadth	110 "	100 "
" " " height of posterior portion	247 "	202 "

The larger *right* superior molar (type of *Archidiskodon* [*Palæoloxodon*] *transvaalensis*) was found in a separate pit from the smaller *left* superior molar (type of *A.* [*P.*] *sheppardi*); they certainly belong to different individuals. There are thirteen ridge-plates in the *left* molar (*sheppardi*) and from sixteen to eighteen in the *right* molar (*transvaalensis*): "The lamellæ [i.e., ridge-plates] are not compressed but are *broad* (17–19 mm. in the central portions, 13–15 mm. near the margin, and 15–17 mm. at the medial margin in the larger tooth, *i.e.* right molar; 12–14 mm. in the central portion and 10–11 mm. near the inner and the outer margins of the smaller tooth, *i.e.* left molar). The lamellæ are considerably broader than the interlamellar discs of cementum; the cementum is nevertheless abundant in quantity—although not so abundant relatively as in *E. planifrons* and *E. meridionalis* types." The enamel is definitely crimped. There is no tendency, as seen in *E.* [=*Loxodonta*] *zulu* and *Loxodonta* [=*Metarchidiskodon*] *griqua*, to throw out a median posterior buttress or 'loxodont sinus.'

The author rightly continues [p. 46] that these grinders belong to a genus not previously described from South Africa.[1]

It remains to be determined whether the *left* (smaller tooth) represents a different species from the *right* (larger tooth); they present marked divergencies from one another in details, as shown in the accompanying type photographs (Figs. 1145 and 1146).

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[1] [Referred by Professor Osborn (Osborn, 1934.925, p. 2) to *Palæoloxodon*.—Editor.]

Loxodonta zulu Scott, 1907

Figures 1147, 1148

Zululand, South Africa, associated with the following extinct species: The *Hippopotamus ponderosus*, *Bubalus andersoni*, and *Opsiceros simplicidens* of Scott. Pleistocene.

Specific Characters.—This very large twelve or thirteen ridge-plated molar, identified by Scott as an l.M_3, is relatively broad, length 265 mm., breadth 85 mm., height of posterior portion 81 mm.; it has therefore the relatively broad dimensions of referred superior molars of *Elephas antiquus*, but the concave side of the ridge-plates (pointed forward) proves that this is a third left inferior molar, as identified by Scott. Consequently the ridge formula is apparently:

$$\mathrm{M}\,3_{12\text{-}13}$$

In describing this Upper Pliocene or Pleistocene species,[1] Scott observed that the type tooth does not resemble that of *Loxodonta africana*, because it lacks the characteristic *sinus loxodonte*. On a large scale it resembles the types of *Elephas antiquus Recki* Dietrich, 1916, of East Africa, and *Elephas atlanticus* Pomel, 1879, of Algeria, also the small *Elephas jolensis* Pomel, 1895, of Algeria, as well as the dwarfed species of Malta, *Elephas melitensis* Falc., 1862, 1868, and *Elephas mnaidræ* Adams, 1870.

Elephas (*Loxodon*) *zulu* Scott, 1907. "A Collection of Fossil Mammals from the Coast of Zululand." Third Rept. Geol. Surv. Natal and Zululand, 1907, pp. 259–262. Type.—Third right and left inferior molars, r.M_3, l.M_3. Horizon and Locality.—Zululand, southeast coast of Africa. Type Figure.—*Op. cit.*, Pl. xvii, fig. 6, Pl. xviii, fig. 1.

Type Description.—(*Op. cit.*, p. 261): "Indeed this tooth might almost be described as intermediate in character between Pohlig's two groups, the *Archidiscodonta* and the *Loxodonta*. The third lower molar is very large, almost equalling in size that of the most gigantic modern African elephants, and in shape is elongate and rather narrow, though broader relatively than in *E. africanus*, so much so as to verge upon the laticoronate type. It will be observed from the table of measurements that while the breadth of crown equals the maximum recorded, even of the upper molars, for any individual of the existing African or Indian species, the length is considerably less than in these exceptionally gigantic individuals. . . . It is plain, however, that the number of ridges, not including the talons, cannot have been less than 12, and may have been 13. . . . More significant than the number of the ridges is their shape, and one is immediately struck by the fact that in the fossil the pattern is decidedly less loxodont than in the recent African species; the median expansion of each lamina is less, and hence the successive ridges are more widely separated, while in the less abraded ridges the loxodont pattern is not displayed at all, the two enamel walls of each lamina being quite parallel. The enamel is very thick (pachyganal) and very strongly crimped. The lateral terminations of the laminæ are either rounded or trifoliate, and each ridge has a feebly curved or crescentic shape, with the horns directed forward. The three posterior ridges have only the points of the digitations exposed, and of these there are four to each ridge, and those of successive plates are arranged in longitudinal rows in a manner suggestive of *E. meridionalis*."

In several respects these teeth of *E. zulu* resemble the curious molars of *E. antiquus*, which were originally described by Falconer as *E. priscus*. . . .

Measurements.

Third lower molar, length	.265
" " " width	.085
" " " height of posterior portion	.081"

Scott regards this species as closely related to *Hesperoloxodon antiquus* and as possibly ancestral to *Loxodonta africana*. He concludes (*op. cit.*, p. 262): "Should *E. zulu* eventually prove to be the actual ancestor of *E. africanus*, it would tend to give the latter a less isolated position, connecting it with Asiatic and European species. At all events, it is extremely interesting and important to find in South Africa an elephant with so many points of resemblance to species characteristic of the northern hemisphere."

Reck (Sitzungsb. Ges. Naturf. Freunde zu Berlin, 1914, p. 307) remarks: "[1] Die Unterschiede zum *Elefas Zulu* Scott endlich liegen hauptsächlich in den Punkten 1, 3 und 4 der Charakteristik des Oldowayelefanten. [2] Einige der Zähne, nämlich die vorletzten Molaren erinnern stark an *E. antiquus* Falc. aus dem europäischen Diluvium; doch entfernt die Gesamtheit aller Merkmale, besonders der M_3 den Elefanten von Oldoway vom Urelefanten, während die Stosszähne beide Elefanten wiederum einander nähern (s. unten). [3] *E. Zulu* ist der nur aus zwei zusammengehörigen M_3 Molaren bekannte ganz vereinzelt dastehende Fund eines dem neuen Elefanten noch am nächsten stehenden Tieres der *Elefas hysudricus*-Reihe. Trotzdem er primitiver und auch älter (Altdiluvial?) ist

Type Left Third Inferior Molar of Loxodonta zulu

Fig. 1147. One of the two third inferior molars (left and right) constituting the type of *Elephas* (*Loxodon*) *zulu* Scott, 1907, Pl. xviii, fig. 1: "Left 3rd lower molar, crown-view; . . . Same tooth as Pl. xvii., fig. 6." Less than one-half natural size. Length 265 mm., breadth 85 mm.

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[1] [Professor Osborn first thought this species to be referable to *Palæoloxodon*, but in his article of 1934 on the "Primitive *Archidiskodon* and *Palaeoloxodon* of South Africa" (Osborn, 1934.925, p. 2) he definitely referred *Elephas* (*Loxodon*) *zulu* to *Loxodonta*.—Editor.]

als der Oldowayelefant, ist er doch schon zu viellamellig, um als direkte Ahnenform des Oldowayelefanten gelten zu können. Freilich ist das Material zu sicheren Schlüssen zu dürftig."

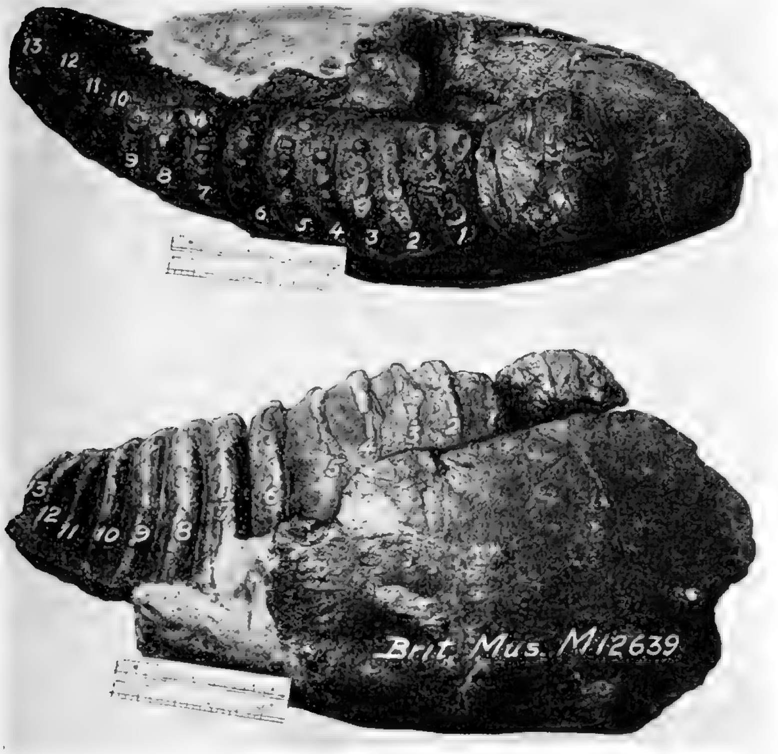


Fig. 1148. Referred *Loxodonta zulu* (Brit. Mus. 12639). A thirteen ridge-plated third left inferior molar, l.M$_3$, from the Kaiso Bone-beds, near Lake Albert, Africa. After photograph kindly furnished the present author by Dr. A. Tindell Hopwood (cf. Hopwood, 1926, Pl. III, fig. 1). One-fourth natural size. Length 272 mm., breadth 65 mm.

Loxodonta prima Dart, 1929

Figure 1149

Pilandsberg, Transvaal, bank of Rhenoster spruit tributary of the Limpopo River, South Africa. ?Recent.

Loxodonta prima Dart, 1929. "Mammoths and Other Fossil Elephants of the Vaal and Limpopo Watersheds," So. African Journ. Sci., Vol. XXVI, pp. 724–726. TYPE.—McGregor Mus. 4077, cast Amer. Mus. 26987. "Left lower third molar [l.M$_3$], fragment of right third molar, separated plates of upper molars." Discovered by John Mostert. HORIZON AND LOCALITY.—Bank of Rhenoster spruit tributary of the Limpopo River, at a depth of 4 feet on the farm Nooitgedacht, Pilandsberg, Transvaal. ?Recent. TYPE FIGURE.—*Op. cit.*, figs. 25 and 26, p. 725 [Fig. 1149 of the present Memoir].

TYPE DESCRIPTION.—(Dart, *op. cit.*, 1929, pp. 725, 726): "The outstanding character of this tooth (Figs. 25, 26 [Fig. 1149 of the present Memoir]) is its comparability with the living African species. It provides the first indubitable fossil evidence of a very close approximation to the distinctive lozenge-shaped lamellae of the living Loxodont grinding tooth. The absence of such a fossil type up to the present time according to Osborn 'is a striking circumstance.' The length of the reconstructed tooth is 254 mm., breadth 74 mm., and height 142 mm. opposite the 7th plate, there being only 9 plates (6 plates in 6 inches), corresponding closely with *L. africana* and all in wear."

"There can be no doubt that in this narrow-crowned, loxodont-simulating, few-plated, mountain-inhabiting specimen here depicted, we have a long-sought ancestral type from which the modern African elephant tooth might reasonably be derived by a progressive widening-out of the loxodont sinus, for which reason I have named it *Loxodonta prima*. This fossil is of importance not only in demonstrating an advancing, though still simple Loxodont tooth pattern in the Transvaal, but also in revealing Africa, and possibly South Africa as the evolutionary home of the true Loxodonta. Its habitat in the elevated and relatively waterless Pilandsberg suggests the possible reasons for Loxodont persistence, namely, their becoming inured to more arid conditions and more active movement, as compared with their more ponderous Archidiskodont relatives."

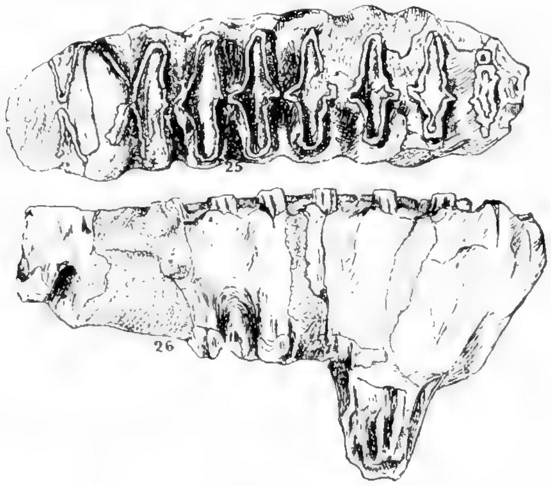


Fig. 1149. Type left third inferior molar, l.M$_3$, of *Loxodonta prima* Dart, 1929, figs. 25 and 26, p. 725, crown and side views respectively. McGregor Mus. 4077; cast Amer. Mus. 26987. One-third natural size. Found near Pilandsberg, Transvaal, South Africa.

Loxodonta africana var. **obliqua** Dart, 1929

Figure 1150

Valley of Steelpoort River tributary of Oliphants River, Northeast Transvaal, South Africa. ?Recent.

Loxodonta africana var. *obliqua* Dart, 1929. "Mammoths and Other Fossil Elephants of the Vaal and Limpopo Watersheds," So. African Journ. Sci., Vol. XXVI, pp. 726–728. TYPE.—McGregor Mus. 4078, cast Amer. Mus. 26988. "Right lower third molar [r.M$_3$]." HORIZON AND LOCALITY.—"Valley of Steelpoort River tributary of Oliphants River, N.-E. Transvaal, on the farm Kranzkloof, at a depth of 17 feet. . . . ?Recent." TYPE FIGURE.—*Op. cit.*, figs. 27 and 28, p. 726 [Fig. 1150 of the present Memoir].

TYPE DESCRIPTION.—(Dart, *op. cit.*, 1929, pp. 727, 728): "This molar, forwarded to me in February, 1928, by Mr. C. Howard, was brittle superficially but nevertheless in an excellent state of preservation. It is a well worn tooth 256 mm. long, 76 mm. broad, and 137 mm. in height, possessing eleven complete and one rudimentary posterior ridge plates, 12 in all. Its measurements correspond very closely with those of *Loxodonta prima* just described, and also with those of the living form. But its correspondence with the living African elephant is demonstrated not only by its measurements but also by the number of enamel plates and the definite Loxodont character of the enamel surfaces in wear. Indeed, its resemblances are so close as to render its separation from the existing species a matter of question."

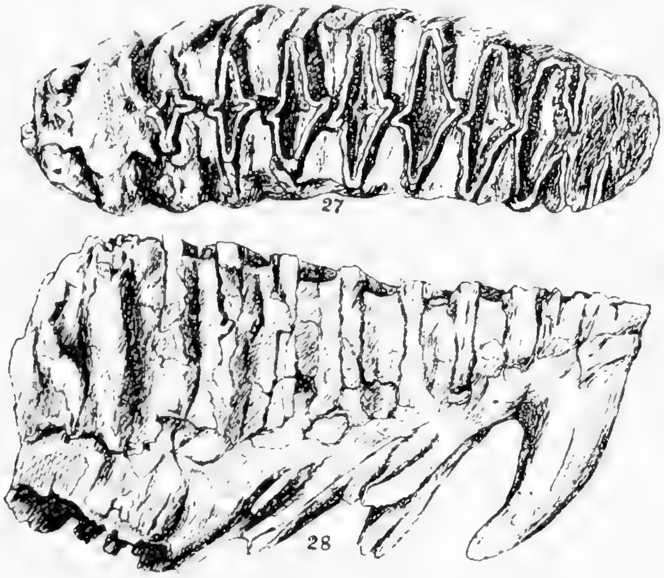
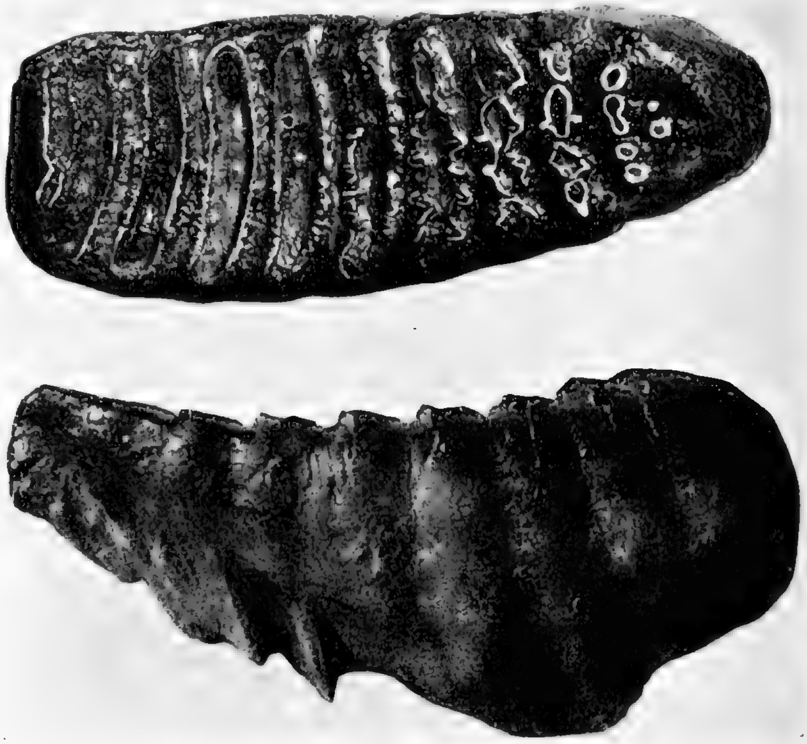


Fig. 1150. *Loxodonta africana* var. *obliqua* Dart, 1929. Type third right inferior molar, r.M_3, from the valley of the Steelpoort River, northeast Transvaal, South Africa. McGregor Mus. 4078; cast Amer. Mus. 26988. After Dart, 1929, figs. 27 and 28, p. 726, crown and side views. One-third natural size.

"Certain features which perhaps are characteristics of variety rank, may, however, be referred to. It may be noted that in no case do the median buttresses impinge directly on one another but rather overlap uniformly to such an extent that the anterior buttresses impinge anteriorly on the posterior aspect of the medial portion of the ridge plate immediately in front of it, while the posterior buttresses impinge posteriorly on the anterior aspect of the lateral portion of the ridge plate immediately behind it. In this way the ridge plate rhombs are not regular but markedly skew or oblique in outline and appearance (Figs. 27, 28 [Fig. 1150 of the present Memoir]). I should not have regarded this feature as being of special significance, seeing that a similar degree of obliquity due to overlapping of the rhombs is depicted in standard illustrations of the inferior molars of African elephants (e.g. Owen's 'Odontography,' 1840-1845, Pl. 148, Zittel's 'Textbook of Palaeontology,' 1925, Fig. 348), if it were not for the fact that in other illustrations (e.g. Falconer's 'Palaeontological Memoirs,' Vol. II, Plate 6, Fig. 1) of the same species, there is no evidence of such overlapping of the rhombs. In addition, there is present in this variety the full number of plates for the living species, together with a vestigial plate remnant posteriorly."

"The salient enamel (3–4 mm. thick) is crimped, but so slightly that the general appearance is one of lack of crimping. The lateral terminations of the rhombs are not flattened but are on the contrary pointed while the medial terminations tend to be more rounded and flattened in contrast with the classical description (Falconer, 1868, 'Palaeontological Memoirs') of the living species."



Type of Loxodonta subantiqua

Fig. 1151. Type of *Pilgrimia subantiqua* Haughton, 1932, from Delport's Hope, South Africa, "possibly a right lower molar, probably the second." McGregor Mus. 4286. After Haughton, 1932, Pl. IV, figs. 1 and 2, crown and side views. About two-fifths natural size.

"Whether these characteristics will prove in the long run adequate for the purpose of species differentiation it is difficult to assess. . . . In any case, I have regarded the features presented as sufficiently distinctive to look upon it as a variety and to draw attention to these details in recording the presence of a fossil form extremely closely related to the living African elephant at great depth in the valley of the Steelpoort river in the Transvaal."

Loxodonta subantiqua Haughton, 1932

Figure 1151

Delport's Hope, near Vaal River, Africa. Level unknown—Pleistocene.

Pilgrimia subantiqua Haughton, 1932. "On Some South African Fossil Proboscidea," Trans. Roy. Soc. So. Africa, Vol. XXI, pp. 8–10. Type.—McGregor Mus. 4286, presented by Mr. G. Barrell. "The tooth is possibly a right lower molar, probably the second." Horizon and Locality.—Delport's Hope, half a mile from the Vaal River, South Africa. Found at a depth of 40 feet in the 'higher terrace.' Pleistocene. TYPE FIGURE.—*Op. cit.*, Pl. IV, figs. 1 and 2 [Fig. 1151 of the present Memoir].

TYPE DESCRIPTION.—(Haughton, *op. cit.*, 1932, pp. 8-9): "The tooth is possibly a right lower molar, probably the second, and its grinding surface is strongly concave in an antero-posterior direction. Eleven plates are preserved, of which the first has been worn down to the roots, and the last is just coming into wear. There was probably a posterior talon. The plates are fully covered with cementum both on their medial and lateral sides. The greatest length of the tooth as preserved, including the posterior cementum, is 245 mm. Measured in a straight line, the ten and a half plates visible on the grinding surface occupy 206 mm., giving a length-lamellae quotient of 19.5. The lamellar frequency varies from 4.75 in the front part of the tooth to 5.75 in the back part, so that the individual lamellae increase in thickness towards the root. They also taper in width upwards. The maximum thickness of a plate (4th) is 19 mm., and the minimum thickness of interlamellar cementum is 4 mm. The greatest width (including cementum) is 92.5 mm., and the maximum width of a plate at the grinding surface 79 mm. The enamel is not thick and is coarsely crimped."

"The tooth is low. The greatest height of any plate preserved, above the roots, is about 75 mm., and it is doubtful if the maximum height of any of the posterior plates exceeded 85-90 mm."

VIII. LOXODONTINES OF JAPAN AND JAVA

(Continued from Chap. XIV, pp. 901 to 909, and from p. 1185 of the present chapter)

In this concluding historical and systematic section of the Loxodontinæ we may review the original as well as one of the most recent treatments of the far eastern loxodonts of Japan and of Java, at a time when these countries constituted the eastern portion of the Asiatic continent and successively attracted the mastodonts, the stegodonts, and the true elephants chiefly of the genus *Palæoloxodon*.

HISTORY.—During the years since Dubois described (1908) his '*Elephas hysudrindicus*' from the Kendeng formation of Java (now believed to be of Middle Pleistocene age), great changes in nomenclature have been made which are thoroughly set forth in the following systematic revision of eight species and subspecies[1] originally named and more or less fully described by Dubois, Makiyama, and Matsumoto, the total list to our present knowledge being as follows:

ORIGINAL REFERENCE	REFERENCE IN PRESENT MEMOIR	PROBABLE GEOLOGIC AGE	RIDGE FORMULA
JAVA			
Elephas hysudrindicus Dubois, 1908	= *Palæoloxodon hysudrindicus*	Middle(?) Pleistocene	M 3 $\frac{19}{19\frac{1}{2}}$
JAPAN			
Elephas namadicus naumanni Makiyama, 1924	= *Palæoloxodon namadicus naumanni*	Middle Pleistocene (?)	M 3 $\frac{19}{17}$
Elephas namadicus namadi Makiyama, 1924	= *Palæoloxodon namadicus namadi*	Middle Pleistocene (?)	M 3 $\frac{14+}{}$
Euelephas protomammonteus Matsumoto, 1924	= *Palæoloxodon protomammonteus*	Upper Pliocene (?)	M 3 $\frac{}{16\frac{1}{2}-17}$
Loxodonta (Palæoloxodon) tokunagai Matsumoto, 1924	= *Palæoloxodon tokunagai*	Upper Pliocene (?)	M 3 $\frac{}{\frac{1}{2}-13-\frac{1}{2}}$
Parelephas protomammonteus proximus Matsumoto, 1926	= *Palæoloxodon protomammonteus proximus*	Upper Pliocene (?)	M 3 $\frac{}{9+}$
Loxodonta (*Palæoloxodon*) *namadica* (*Yabei*) Matsumoto, 1929	= *Palæoloxodon namadicus yabei*	Middle Pleistocene	M 3 $\frac{}{\frac{1}{2}-17-\frac{1}{2}(?)}$
Lox. (*Pal.*) *Tokunagai junior*, mut. Matsumoto, 1929	= *Palæoloxodon tokunagai* mut. *junior*	Upper Pliocene(?) or Lower Pleistocene	M 2 $\frac{}{+11\frac{1}{2}}$

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[1] [To these should possibly be added the following species described since this text was written and not examined by Professor Osborn: *Parelephas* [?*Palæoloxodon*] *protomammonteus matsumotoi* Saheki, 1931, from Mishima, Province of Kazusa, *Palæoloxodon yokohamanus* Tokunaga, 1934, from Yokohama, and *Palæoloxodon aomoriensis* Tokunaga, 1936, from Tenjinbayashi, Aomori Prefecture.—Editor.]

Whereas Dubois and Makiyama gave merely a preliminary description of the three species named by them (*E. hysudrindicus, E. naumanni, E. namadi*), Matsumoto named five species and contributed a succession of short articles and memoirs, fully listed in the Bibliography of the present Memoir; also in aid of the publication of the present Memoir, he sent the author in 1924 a letter giving his views at that time (June 24, 1924). His more mature views are expressed in his two memoirs entitled, "On *Loxodonta* (*Palæoloxodon*) *namadica* (Falconer and Cautley) in Japan," with six plates (Matsumoto, 1929.1,) and "On *Loxodonta* (*Palæoloxodon*) *tokunagai* Matsumoto, with Remarks on the Descent of Loxodontine Elephants," with one plate (Matsumoto, 1929.2).

SUMMARY OF MATSUMOTO'S FINAL OBSERVATIONS AND THEORIES OF 1924 AND 1929

The present author differs widely from Matsumoto's opinions and theories as to phylogeny, geographic distribution, and nomenclature; palæontologists are nevertheless deeply indebted to him for his great labors in setting forth the characteristics, geographic distribution, and geologic succession of the Japanese loxodonts. The following gives a summary of Matsumoto's observations and theories.

Matsumoto, 1924. We owe to Doctor Matsumoto (letter, June 24, 1924) his geologic section (Fig. 790) of the fossil bearing formations of Japan and a series of valuable notes on the Japanese forms referable to *Loxodonta* [=*Palæoloxodon*] *namadica*. It appears that all varieties of *L. namadica* from Japan were distinguished by *smaller and narrower grinding teeth* than those of the typical *L. namadica* of the Nerbudda Valley. This relatively *small* and relatively *narrow* molar proportion is characteristic of all the insular species of the genus *Loxodonta* [=*Palæoloxodon*]; it is also a *primitive* character of all loxodontines.

According to the 1924 observations of Matsumoto: (1) The parent forms of *Loxodonta* [=*Palæoloxodon*] migrated into Japan *early* in Pleistocene time, namely, in the Calabrian-Villafranchian age, in which occurs an older type almost similar to *Loxodonta* [=*Hesperoloxodon*] *ausonia* in its evolutionary stage; this is perhaps of Upper Pliocene Calabrian or Villafranchian age; (2) in the succeeding Cromerian-Sicilian stage there occurs an ascending mutation, the *Loxodonta namadica* var. *naumanni* of Makiyama [since made the "subgenotype" of *Palæoloxodon* by Matsumoto], almost similar to the type of *L.* [=*Hesperoloxodon*] *antiqua* which occurs in the Cromer Forest Bed; (3) a still more modern type, approaching more nearly the typical *L.* [=*P.*] *namadica* of India, occurs in the terrace gravels corresponding perhaps with the Monastirian or Tyrrhenian stage of Depéret. In descending geologic order these species appear to Matsumoto (letter, June 24, 1924) as follows:

III. *Loxodonta namadica* ?mut. = a final mutation of the younger terrace gravels of ?Monastirian-Tyrrhenian age. Narrow toothed, like the species *naumanni*, but thin ridged and thin enameled; loxodonty absent or very slight in the upper grinders, and slight loxodonty in the lower grinders; laminar frequency 7–8.

II. *Loxodonta antiqua* var. *naumanni* Makiyama = an older type, mutation of the Tokyo beds of ?Cromerian-Sicilian age. Almost similar to the species of the Cromer Forest Bed *Loxodonta antiqua*, as well as to the *L. hysudrindica* of Java, in its evolutionary molar stage; laminar frequency 6–6.5.

I. Older type, almost similar to *Loxodonta ausonia* of the Villafranchian = mutation of Minato, its geographical locality. Almost similar to *L. ausonia* in its evolutionary stage; crown low, M_3 about 120 mm.; laminar frequency 6–6.5; perhaps of Calabrian-Villafranchian age.

According to the observations of Matsumoto, the narrow-toothed Japanese elephants differ from the typical broad-toothed *Loxodonta* [=*Palæoloxodon*] *namadica* types of India and resemble the typical narrow-toothed *L.* [*Hesperoloxodon*] *ausonia* types of southern Europe, the Mediterranean Islands, and North Africa.

Matsumoto, 1929.—The following passages are taken from Matsumoto's Memoirs of 1929 (1929.1, 1929.2), entitled:

On *Loxodonta* (*Palæoloxodon*) *namadica* (Falconer and Cautley) in Japan. Sci. Rept. Tôhoku Imp. Univ., Second Series (Geology), Vol. XIII, No. 1, (1929.1).

On *Loxodonta* (*Palæoloxodon*) *tokunagai* Matsumoto, with Remarks on the Descent of Loxodontine Elephants. Sci. Rept. Tôhoku Imp. Univ., Second Series (Geology), Vol. XIII, No. 1, (1929.2).

(Matsumoto, 1929.1, p. 1): "Assistant Professor Makiyama of the Kyôto Imperial University has really laid the cornerstone of further progress in the study of *Elephas namadicus* Falconer & Cautley in Japan, of which two subspecies have been distinguished by him. Subsequently, his *E. namadicus Naumanni* was selected by the present writer to be the subgenotype of *Palæoloxodon*, which is referred to *Loxodonta*. The writer has now come to distinguish three races of the species in question in Japan. One of them, corresponding to the subspecies *Naumanni* Makiyama, represents the Lower Pleistocene mutation of the species, while the other two appear to be characteristic of the Middle Pleistocene. Thus, the racial subdivision of the present species may play a part, the writer hopes, in the geological correlation of the Japanese Pleistocene."

(Matsumoto, 1929.2, pp. 7, 10): "An interesting archetypal Loxodontine elephant of Japan, named *Loxodonta* (*Palæoloxodon*) *Tokunagai* by the writer, as well as the subgenus *Palæoloxodon* created by him, has not yet been fully described in a European tongue. The writer here wishes to furnish a description of the elephant with a few remarks concerning the descent of Loxodonts. On this occasion, the writer has the pleasure to express his hearty thanks to the authorities of both the Imperial Museum of Uëno and the Geological Institute of the Kyôto Imperial University, by whom he was permitted to study the specimens described in the present report."

"Rise of Palæoloxodon"

"As specially noticed by Lydekker [Footnote: 'Lydekker, Brit. Mus. Cat. Foss. Mamm., Pt. IV., 1886, pp. 102, 103 & 106, text-fig. 25.'], a small form of very archetypal elephant is recorded from India under the name of *Elephas planifrons*. This form appears to be deviant from *Archidiscodon* in being narrow-toothed, though it appears to be closely related to the same in having the loxodont sinus of an obtuse type in the grinders. Again, by the first mentioned characteristic, it appears to be close to and by the second to be deviant from *Palæoloxodon*. Phylogenically, it is, in all probability, ancestral to *Palæoloxodon*, and hence to the *Loxodontine* elephants as a whole. Thus, the affinity of this form appears to be stronger to the side of *Palæoloxodon* than to the side of *Archidiscodon*. A generic and a specific name have already been proposed to receive it [Footnote: 'Matsumoto, on *Leith-Adamsia Siwalikiensis*, Jap. Journ. Geol. & Geogr., Vol. V., No. 4, 1926-1927.']. *Palæoloxodon*, of which the most archetypal known form appears to be represented by *Lox.* (*Pal.*) *Tokunagai*, might have arisen from such an earlier form as represented by the aforementioned species through the partial perfection of the loxodonty of the grinders. No doubt, the Loxodonts as a whole were originally a narrow-toothed type, with a low ridge-formula. The acquisition of loxodonty might mechanically be correlated with the combined facts of their being narrow-toothed and long retaining a low ridge-formula. *Palæoloxodon* appears to have originated in the region extending from India to Japan, and then to have been distributed over practically the entire southern Palæarctic."

[*Leith-Adamsia siwalikiensis* Mats. is a synonym of *Archidiskodon planifrons* Falc. and Caut. (see Chap. XVI, p. 959, of the present Memoir).]

"Palæoloxodon and Loxodonta, s.s."

"The writer has never seen a molar of *Palæoloxodon*, which is more like those of *Loxodonta*, s.s., than the type-specimen of *Lox.* (*Pal.*) *Tokunagai*, in being very narrow-crowned and in the very markedly lozenge-shaped disks of the well-worn ridges. If we suppose that the cheek-teeth of just this type had acquired hypsodonty of a very high degree, without increasing their width and the number of ridges, then we may obtain cheek-teeth of a type just characteristic of *Loxodonta*, s.s. The modern Loxodonts might have originated in such a way, probably in Africa."

"Specific Groups in Palæoloxodon"

"The most archetypal group in *Palæoloxodon* corresponds evidently to that represented by the phyla of *Lox.* (*Pal.*) *prisca* in Europe and of *Lox.* (*Pal.*) *Tokunagai* in Japan, showing the distinctive characteristics already stated. The question arises whether the group of pygmy Loxodonts of the Mediterranean islands and coasts, typified by *Lox.* (*Pal.*) *melitensis* (Falconer), is a close ally of the group just mentioned. The answer must be negative. Though the cheek-teeth of the group in question have a low ridge-formula, the disks of their ridges, as well as their general shape, appear to display an unmistakable similarity with those of the later phases of the phylum of *Lox.* (*Pal.*) *antiqua.* The low ridge-formula in this group may [be] due to degeneration as a result of having been dwarfed. Phylogenically, this group by itself is far from being a natural one. It can be considered natural only when it is taken as a group subordinate to the phylum of *Lox.* (*Pal.*) *antiqua.* By far the greatest part of *Palæoloxodon* is occupied by the group represented by the phyla of *Lox.* (*Pal.*) *namadica* in Southern to Eastern Asia and of *Lox.* (*Pal.*) *antiqua* in Europe. As indicated by the evolutionary tendencies observed in the mutations of the phylum of *Lox.* (*Pal.*) *namadica* in Japan, *Lox.* (*Pal.*) *Tokunagai* is probably ancestral to this phylum. Again, it appears probable, that the phylum of *Lox.* (*Pal*). *antiqua*, might also have had an almost similar form for its ancestor. It does not appear probable, however, that *Lox.* (*Pal.*) *prisca* was actually ancestral to that phylum, as a younger aspect appears to be present in the molars of this species in having the opposite loxodont sinus of two neighbouring ridges well-spaced."

OSBORN'S SUMMARY (1930) OF THE OBSERVATIONS OF MAKIYAMA (1924)[1] AND OF MATSUMOTO (1924–1929)

From these descriptions and plates we conclude: (1) That *Palæoloxodon* is the only genus of true elephants that penetrated Japan; (2) that the primitive species *P. tokunagai* may have entered as early as Upper Pliocene time, and (3) that in ascending geologic levels there occur more progressive species, either indigenous or migrants from the *P. namadicus* stock of India. (4) In the present historic, geologic, and systematic revision, therefore, we shall present in each case Matsumoto's opinions of 1924, and, in conclusion, give his opinions of 1929 under each species.

Osborn, 1930: Osborn does not accept any of the phylogenetic or geographic theories expressed by Matsumoto above; he regards *Palæoloxodon* as an entirely independent phylum originally derived from Africa and subsequently migrating through India to the Far East. He condenses from the invaluable observations of Makiyama and of Matsumoto the following synopsis of their observations upon the *ascending geologic successions and specific characteristics* of the Japanese loxodonts:

Palæoloxodon tokunagai Matsumoto, 1924, possibly of Upper Pliocene age, is regarded as the most archetypal group of *Palæoloxodon* in Japan, probably as ancestral to *Palæoloxodon namadicus* of southern and eastern Asia and to *P.* [*Hesperoloxodon*] *antiquus* of Europe (1929.2, pp. 10, 11). Estimated ridge formula of M 3 $_{½-1\ 3-½}$. Ridge frequency 5 in 100 mm. Length 295e mm., breadth 80 mm.; relatively low crowned. (No figure.)

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[1] [For the results of Makiyama's recent studies, see his article "Japonic Proboscidea," Mem. Coll. Sci. Kyoto Imp. Univ., Ser. B, Vol. XIV, No. 1, Art. 1, May, 1938.—Editor.]

Palæoloxodon tokunagai mut. *junior* Matsumoto, 1929, a mutation of *Loxodonta* (*Palæoloxodon*) *tokunagai*. Very primitive; either of Upper Pliocene or Lower Pleistocene age. Similar to *Loxodonta* (*Palæoloxodon*) *prisca* of Falconer. Differs from *P. tokunagai* which has molars of larger size, with slightly higher ridge formula and slightly more perfect lozenge-shaped discs of the ridges. Low crowned. Enamel thick. (Matsumoto, 1929.2, p. 10, also Pl. VII, fig. 1, type r.M_2, our Fig. 1157.)

Palæoloxodon protomammonteus Matsumoto, 1924, 1926, regarded as of Upper Pliocene (?), Basal Calabrian age (Fig. 1154). Lower molars small and narrow crowned. Estimated ridge-plate formula ($M\ 3\ \frac{}{\frac{1}{2}-17-\frac{1}{2}}$) similar to that of the Lower Pleistocene *Hesperoloxodon antiquus*.

Palæoloxodon protomammonteus proximus Matsumoto, 1926. Upper Pliocene(?). Lower Calabrian age. Molars rather large and moderately wide. Type fragment, l.M_3, with 9+ ridge-plates. Ridge frequency 5 in 100 mm. (Fig. 1155.)

Palæoloxodon namadicus naumanni Makiyama, 1924, characteristic of the Lower Pleistocene, very widely distributed. A narrow-toothed variety. Ridge frequency 5–6 in 100 mm. in M_3, 6 in 100 mm. in M^3. Relatively broad crowned. Ridge formula of $M\ 3\ \frac{\frac{1}{2}-17-\frac{1}{2}}{17}$ [$\frac{19}{17}$, Fig. 1152]. Length M^3 303 mm., breadth 76 mm., max. height 216 mm.; length M_3 270 mm., breadth 72 mm.

Palæoloxodon namadicus yabei Matsumoto, 1929, characteristic of the Middle Pleistocene, very abundant. Estimated ridge formula of $M\ 3\ _{\times 17 \times}$; length 255 mm., width 74 mm.; ridge frequency 6.5–7 in 100 mm. (Fig. 1156.)

Palæoloxodon namadicus namadi Makiyama, 1924, probably of Middle Pleistocene age. The largest and most numerous group of the Japanese loxodonts, representing a broad-toothed variety. Ridge frequency 5 in 100 mm. in M_3. The type upper molar, r.M^3 (Fig. 1153), exhibits +12+ ridge-plates indicating a larger total, as observed by Makiyama (1924, p. 263): "There is a loss of several posterior ridges, leaving fourteen in a space of 211 mm. The crown is very broad being 77 mm. in front, 90 mm. at the middle and 65 mm. posteriorly, measured on the second, fifth and fourteenth ridges respectively."

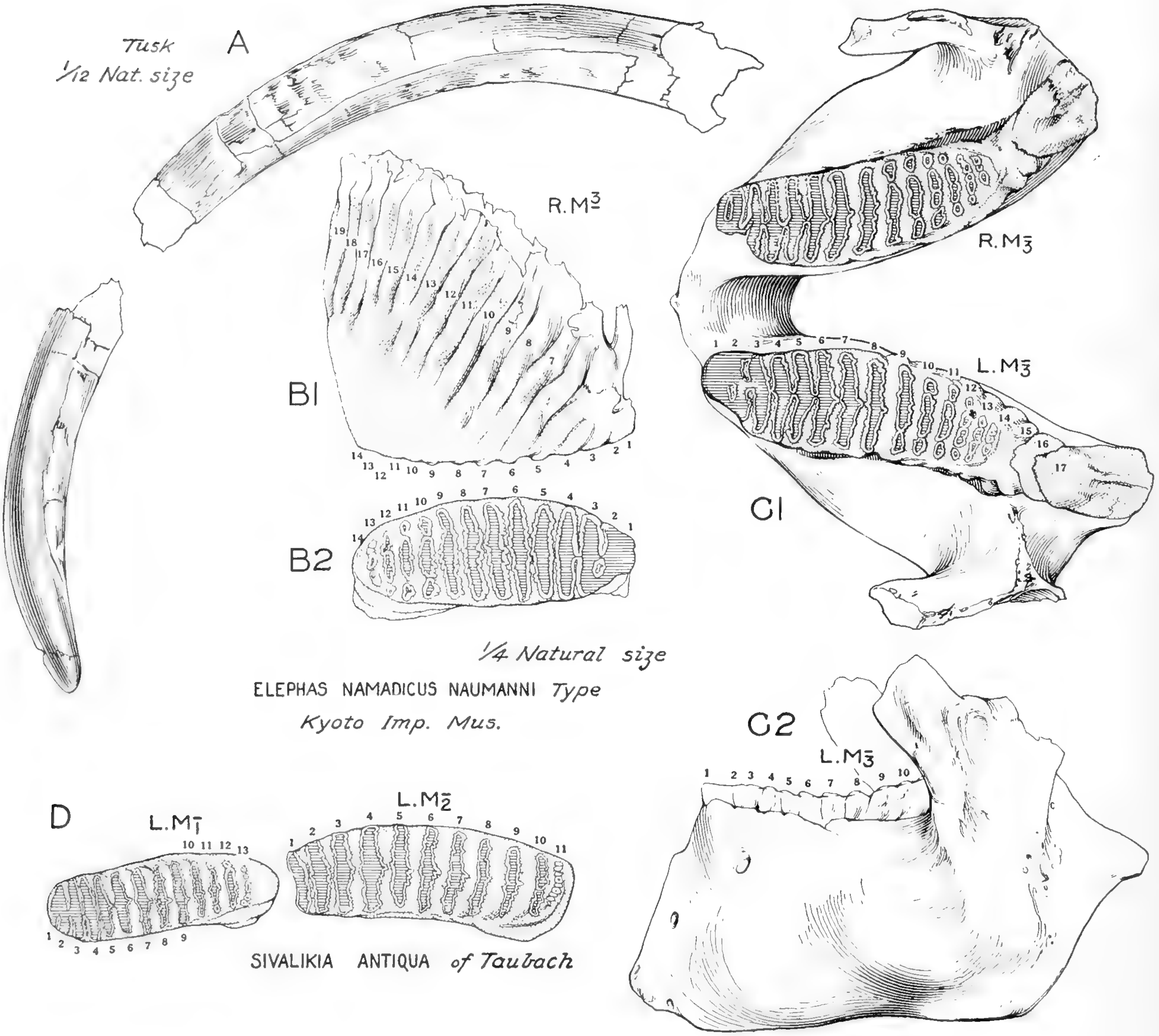
According to the above summary, the genus *Palæoloxodon* from Japan probably appeared in Upper Pliocene time as a narrow-toothed, coarse-enameled species, and ascended from Lower into Middle Pleistocene time, terminating in the species *Palæoloxodon namadicus yabei*, characteristic of the Middle Pleistocene and so closely resembling *P. namadicus* that it was first described by Matsumoto as *Palæoloxodon namadicus typicus*. This ascending order of phylogenetic succession, with broadening molar crowns and ridge-plates multiplying from $M\ 3\ \frac{}{\frac{1}{2}-13-\frac{1}{2}}$ estimated (*tokunagai*) to $M\ 3\ \frac{19}{17}$ estimated (*naumanni*) differs widely from that shown in figure 790, which represents Matsumoto's earlier observations of the year 1924.

The Japanese species of Palæoloxodon may all be derived from the same Upper Pliocene African stock, with narrow and low ridge formula, progressive in breadth and in ridge formula as follows:

(Upper Pliocene) $M\ 3\ \frac{}{13}$ to (Lower Pleistocene) $M\ 3\ \frac{}{15}$ to (Middle Pleistocene) $M\ 3\ \frac{19}{17}$.

TWO JAPANESE SUBSPECIES DESCRIBED BY MAKIYAMA (1924)

Makiyama in a paper entitled "Notes on a Fossil Elephant from Sahamma, Tôtômi" (1924.2, pp. 261, 262, 264) expresses the opinion that there are at least two varieties of Japanese fossil elephants, namely, the narrow toothed (e.g., *Palæoloxodon naumanni*) and the broad toothed (e.g., *P. namadi*), which hitherto have been called



Genotypic Species (A–C) of Palæoloxodon Matsumoto; (D) Hesperoloxodon antiquus germanicus of Taubach

All figures one-fourth natural size, same scale as figure 1073 excepting tusk (A) one-twelfth natural size

Fig. 1152. Diagrammatic outline sketch of the *type* of *Elephas namadicus naumanni* Makiyama, 1924 [= *Palæoloxodon namadicus naumanni*], see Pls. xii, xiii, xiv, xv, and xvi, fig. 1, in comparison with *Elephas antiquus* [*Hesperoloxodon antiquus germanicus*], after Pohlig, 1888, Pl. iii, fig. 7, Pl. iv, fig. 3. All figures one-fourth natural size, with the exception of the incisive tusk which is one-twelfth natural size.

A, Incisive tusk, length 1930 mm. (Pl. xii).

B1, Third right superior molar, exhibiting 14 worn and 5 unworn ridge-plates, total 19. Side view. (Pl. xiii, fig. 1. Length 303 mm., breadth 76 mm., max. height 216 mm.)

B2, Crown view of same superior molar (Pl. xiii, fig. 2).

C1, Type inferior mandible, with M 3 *in situ* exhibiting 14 worn and 3 unworn ridge-plates, total 17. Superior view. Length of right ramus 405 mm., of left ramus 413 mm.; length of l.M_3, 270 mm.; max. breadth of same 72 mm. at fifth ridge (Pl. xv).

C2, Same mandible, left lateral view (Pl. xvi, fig. 1).

D, *Elephas* [= *Hesperoloxodon*] *antiquus* [*germanicus*] from Taubach, after Pohlig, 1888, Pl. iii, fig. 7, left M_1, crown view, and Pl. iv, fig. 3, left M_2, crown view. Compare figure 1075, type second left inferior molar, l.M_2, exhibiting 12–13 ridge-plates, of '*Elephas antiquus*' Falc.

Observe that the type of '*Elephas namadicus naumanni*' Makiyama is decidedly inferior in size to the *Palæoloxodon namadicus* of the Nerbudda, figure 1073, but that the grinders exceed in relative breadth those of *Hesperoloxodon antiquus germanicus* of Taubach (D, l.M_1, l.M_2), as figured by Pohlig.

Elephas namadicus by many authors. Osborn, on the contrary, interprets the 'narrow toothed' as more primitive and geologically ancient, the 'broad toothed' as more progressive and geologically younger; *progressive broadening of the grinding teeth and multiplying of the ridge-plates distinguish each line of ascent.*

Narrow toothed.—(*Op. cit.*, pp. 263, 264: "The second variety, to which the elephant of Sahamma belongs [i.e., *Palæoloxodon namadicus naumanni*], is diagnosed by its narrower [76–79 mm.] bandy crown and lozenge-shaped discs. . . . I give here, a new subspecific name *Elephas namadicus Naumanni* to the second variety, for which type the lower teeth from Sahamma should be chosen. . . . The second variety is apparently referable to *E. antiquus* in many respects. Therefore, it is not unreasonable that Brauns [Footnote: 'Ueber Japanische Diluviale Säugetierer, Zeitsch. Deut. Geol. Ges., 1883, pp. 35–42.'] had supposed the possibility of direct migration of *E. antiquus* from Europe to Japan through Central Asia in the early Pleistocene age. He also pointed out some differences between his *E. antiquus* in Japan and the types of *E. namadicus* in India."

Broad toothed.—(*Op. cit.*, pp. 263, 264): "The first variety [*Palæoloxodon namadicus namadi*] is diagnosed by the broad [90 mm.] elliptical crown and less-crowded bandy discs. . . . The first variety referred to as typical *E. namadicus* should be called more strictly *Elephas namadicus namadi*."[1]

While Matsumoto (1929.1, p. 1) gives the original reference of these two subspecies as "Chikyû—The Globe, Vol. I, 1924, p. 381, Pl. viii," this publication is not available to the present author and he is therefore citing from Makiyama's supplementary descriptions in English (Makiyama, 1924.2) mentioned above.

Palæoloxodon namadicus naumanni Makiyama, 1924[1]

Figures 1152, 1189

From Sahamma, Tôtômi Province, Japan. Recorded from the Lower Pleistocene by both Makiyama and Matsumoto. Probably Middle Pleistocene. Genotypic species of *Palæoloxodon* Matsumoto, September 20, 1924.

This subspecific name was applied by Professor Makiyama of the Kyôto Imperial University to an excellent medium-toothed type (Fig. 1152) rivaling in the dimensions of the teeth the '*Elephas antiquus*' of Weimar (Fig. 1088B, M^3), in which the referred formula is M 3 $\frac{17+}{19}$, the enamel thick and strongly crimped, the dentinal discs expanding mesially and coming into contact with extreme wear; the superior tusks strongly curved, the frontocranial structure unknown—on the whole, resembling the large Upper Pleistocene '*E. antiquus* [*germanicus*]' of Weimar—distinguished both from the broad-toothed variety (maximum breadth 90 mm.) and from the extremely narrow-crowned variety.

Elephas namadicus Naumanni Makiyama, 1924. "Notes on a Fossil Elephant from Sahamma, Tôtômi." Mem. College Sci. Kyôto Imp. Univ., Ser. B, Vol. I, No. 2, June 30, 1924, pp. 255–264. Type.—Cranium broken to pieces, leaving complete mandible with third inferior molars, also third superior molars, and inferior incisor. (*Op. cit.*, p. 264): "I give here, a new subspecific name *Elephas namadicus Naumanni* to the second variety, for which type the lower teeth from Sahamma should be chosen." Horizon and Locality.—Excavated at Sahamma, about 12 kilometers northeast of Hamamatsu, Tôtômi Province, Japan, in 1921. Type Figure.—Makiyama, *op. cit.*, Pls. xii (incisor), xiii (third right superior molar), xiv (third left superior molar), xv (mandible), xvi, fig. 1 (left lateral aspect of same mandible).

Specific Characters (cf. Makiyama, pp. 260–264).—Superior incisor 1930 mm. in length, strongly upcurved (Pl. xii). Third left superior molar (Pl. xiv), length 286 mm., breadth 79 mm. at fourth ridge-plate, maximum ridge-plate height 217 mm., ½–16–½ ridge-plates in 286 mm.; third right superior molar (Pl. xiii), length 303 mm., breadth 76 mm., maximum ridge-plate height 216 mm., total ridge-plates 19, laminar frequency 17 in 303 mm., worn anterior plates exhibiting six lens-shaped discs with pronounced plications. Mandible (Pls. xv, xvi, fig. 1) with both third inferior molars *in situ*; symphyseal rostrum abrupt, subvertical; l.M_3, length 270 mm., breadth 72 mm., laminar frequency 17 ridge-plates in a space of 270 mm.; 14 anterior ridge-plates well worn "showing a lozenge-shaped complete figure of enamel with minute but well-defined central angulations in touch with each other as obtained in *E. africanus*, and regularly crimped, comparatively thick enamel layers."

Comparisons.—In dimensions the upper right last molar, r.M^3, is very like that of *Elephas antiquus* [*germanicus*] from Weimar cited by Soergel (1913, Taf. viii). It also resembles the thick-plated variety of *E. antiquus* (cf. Leith Adams, 1877, Pt. I, p. 31). An M^2 described but not figured, length 204 mm., breadth 72 mm., height 140 mm., differs in dimensions from those of *E. antiquus*, corresponding more nearly to those of *E. meridionalis*

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[1] [Original description in Japanese: "Chikyû—The Globe," Vol. I, 1924, p. 381, Pl. viii (*fide* Matsumoto, 1929.1, p. 1). See also Chapter XXI of the present Memoir, p. 1408, under "1924 *Elephas namadicus naumanni*," and p. 1413, under "1929 *Elephas* (*Palæoloxodon*) *namadicus setoensis*," for Doctor Makiyama's recent (1938) conclusions.—Editor.]

(Soergel, 1913, Taf, VI); the discs are feebly rhombic and never touch at the central part. The mandible (Pl. XVI, fig. 1) in many respects resembles that of *E. antiquus*.

Final Diagnosis (Matsumoto, 1929.1, p. 2).—"The race now under consideration can be diagnosed as follows: Cheek-teeth moderate in size, narrow-crowned. Well worn surface of the last upper molar shaped like an elongated ellipsoid, and that of the last lower molar band-like, with the outer border almost linear or concave. Frequency of ridges low, numbering about 6 or less in a length of 100 mm. in the last upper molar and 5-6 or less in the lower. Mammillæ of the summits of ridges stout and rather few, remaining proximally widely spaced to some extent. Disks of much or moderately worn ridges lozenge-shaped, without any marked differentiation of mesial portion and lateral arms. Even the lateral portions of disks are rather thick antero-posteriorly, the opposite loxodont sinus of the two neighbouring disks in the much or moderately worn portion of crown being in contact with or very closely set to each other. Layer of enamel rather thick; its plication being rather coarse, irregular and rather strong. . . . Age: The present race appears, in all likelihood, to be characteristic of the Lower Pleistocene, ranging in occurrence very probably from its base, as at Ôkine, up to its very close, as at Tabata."

Palæoloxodon namadicus namadi Makiyama, 1924[1]

Figures 1153, 1189

Dredged off the island of Shôdo, Sanuki Province, Japan. Probably Middle Pleistocene (*fide* Matsumoto, 1929.1, p. 4).

Elephas namadicus namadi Makiyama, 1924. "Notes on a Fossil Elephant from Sahamma, Tôtômi." Mem. College Sci., Kyôto Imp. Univ., Ser. B, Vol. I, No. 2, June 30, 1924, p. 264. Type.—Last upper molar, right side, r.M^3. Horizon and Locality.—Dredged off the island of Shôdo, Sanuki Province, Japan. Probably of Middle Pleistocene age (*fide* Matsumoto, 1929.1, p. 4). Type Figure.—*Op. cit.*, Pl. XVI, fig. 2.

Type Description.—(*Op. cit.*, 1924.2, pp. 263, 264): "An excellent example of the first variety is furnished by the last upper true molar. . . . There is a loss of several posterior ridges, leaving fourteen in a space of 211 mm. This crown is very broad being 77 mm. in front, 90 mm. at the middle and 65 mm. posteriorly, measured on the second, fifth and fourteenth ridges respectively. The grinding surface displays a characteristic oval outline and well-spaced bandy discs with minute median angulations. The enamel layer is less well-crimped and thinner than that of the Sahamma form. . . . The first variety referred to as typical *E. namadicus*, should be called more strictly *Elephas namadicus namadi*."

Type Molar of Palæoloxodon namadicus namadi

Fig. 1153. Type r.M^3 of *Elephas namadicus namadi* Makiyama, 1924, exhibiting 12 worn ridge-plates, one anterior ridge-plate missing, posterior ridge-plates not shown in photograph. Breadth 90 mm. After Makiyama, 1924.2, Pl. XVI, fig. 2. One-half natural size.

Final Diagnosis (Matsumoto, 1929.1, p. 3).—"The present race is the largest group of the Japanese Loxodonts and represents the broad-toothed variety of the present species in Japan. . . . This race can be diagnosed as follows. Cheek-teeth large and rather broad. Well worn surface of the last lower molar shaped like an elongated ellipsoid. Frequency of ridges low, numbering about 5 or less in a length of 100 mm. in the last lower molar. Mammillæ of the summits of ridges stout and few. Disks of only the very strongly worn ridges lozenge-shaped as a whole; those of the moderately worn ridges consisting of a lozenge-shaped mesial portion and of nearly parallel-sided lateral arms. Interspaces between lateral arms of successive disks broad antero-posteriorly. Opposite loxodont sinus of the two neighbouring disks of moderately worn ridges widely separated from each other. Layer of enamel rather thick; its plication being coarse, irregular and feebly displayed."

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[1] [Original description in Japanese: "Chikyû—The Globe," Vol. I, 1924, p. 381, Pl. VIII (*fide* Matsumoto, 1929.1, p. 1). See also Chapter XXI of the present Memoir, p. 1408, under "1924 *Elephas namadicus naumanni*," and p. 1413 under "1929 *Elephas* (*Palæoloxodon*) *namadicus setoensis*," for Doctor Makiyama's recent (1938) conclusions.—Editor.]

FIVE JAPANESE LOXODONTINES DESCRIBED BY MATSUMOTO (1924–1929)

(Continued from Chap. XIV, pp. 906-908 of the present Memoir)

During the period 1924–1929, Matsumoto described two species and three subspecies of the true elephants of Japan under the following names: *Euelephas protomammonteus*, 1924, *Loxodonta* (*Palæoloxodon*) *tokunagai*, 1924, *Parelephas protomammonteus proximus*, 1926, *Loxodonta* (*Palæoloxodon*) *namadicus yabei*, 1929, and *Loxodonta* (*Palæoloxodon*) *tokunagai junior*, mut., 1929. Matsumoto's Memoir of 1924, "Preliminary Note on Fossil Elephants in Japan" (September 20), which contains the original descriptions of his subgenus *Palæoloxodon*, and of his species *Euelephas protomammonteus* and *Loxodonta* (*Palæoloxodon*) *tokunagai*, was published in the Japanese language; consequently the present author in the systematic description of the species and subspecies has cited freely from Matsumoto's later Memoirs of 1926 and 1929 (which appeared in the English language) as given below.

Osborn, 1929: Since the names *Euelephas* (*Parelephas*) *protomammonteus* (1924, 1926) and *Parelephas protomammonteus proximus* (1926) were assigned by Matsumoto under the impression that the genus *Parelephas* Osborn was represented in Japan, and since they were not included in the author's subsequent memoirs of 1929, our conclusion is that both these specimens belong to *Palæoloxodon*. See also *Elephas indicus Buski* Mats., 1927 [=*Palæoloxodon buski*] below, p. 1333.

Palæoloxodon protomammonteus Matsumoto, 1924, 1926[1]

Figure 1154

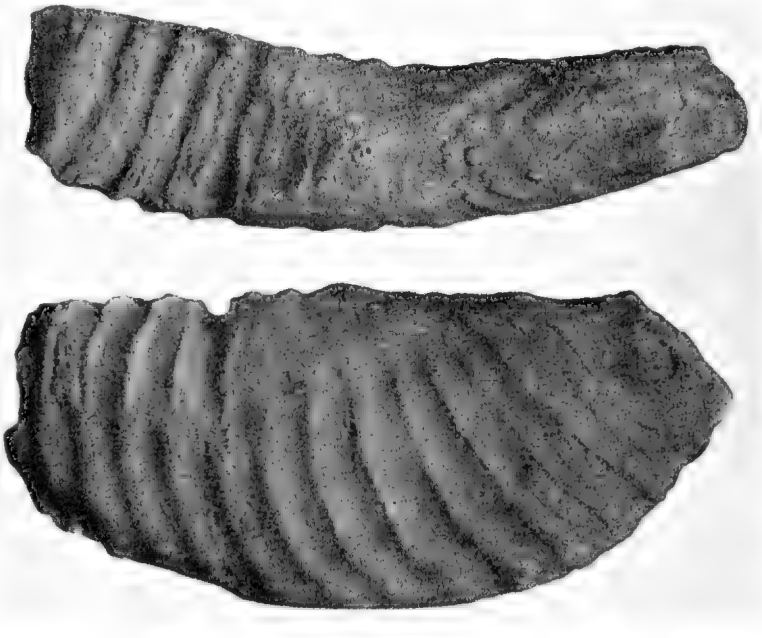
Nagahama, Town of Minato, Kimitsu District, Province of Kazusa, Japan. Upper Pliocene (?), Lower Pleistocene.

Euelephas protomammonteus Matsumoto, 1924. "Preliminary Note on Fossil Elephants in Japan." Journ. Geol. Soc., Tokyo, 1924, Vol. XXXI, p. 262 (in Japanese language). *Parelephas protomammonteus* (Matsumoto) *typicus* Matsumoto, 1926. "On the Archetypal Mammoths from the Province of Kazusa." Sci. Rept. Tôhoku Imp. Univ., (2), Geology, Vol. X, No. 2, pp. 43–50. TYPE.—A third inferior molar of the left side, l.M_3, belonging to Mr. Natsume of the Town of Minato. HORIZON AND LOCALITY.—Probably from the very base of the Narita series. Nagahama, Town of Minato, Kimitsu District, Province of Kazusa, Japan. TYPE FIGURE.—Matsumoto, 1926.2, Pl. XVIII, figs. 1, 2. PARATYPE.—A third inferior molar of the right side, r.M_3. From the same locality as the type; figured on Pl. XIX, figs. 1–3.

In view of the fact that the original type description was published in the Japanese language, we may cite from Matsumoto's Memoir of 1926, p. 50 (published in the English language):

"Stage I. *Parel. protomammonteus* (*typicus*). Basal Calabrian. Molars small and especially narrow-crowned. Inner and outer sides of ridges not very convex. Bases of ridges prominent, and valleys acutely pointed proximally. Basal cingula, and sometimes also accessory columns, well developed."

Osborn, 1928: Matsumoto's type figure and description appear to establish beyond question a strong resemblance to *Palæoloxodon* [*Hesperoloxodon*] *antiquus* typical form of the Lower Pleistocene of England; the ridge-plate formula is practically the same, i.e., M 3 $\frac{}{16\frac{1}{2}\text{-}17}$. Matsumoto observes (*op. cit.*, p. 44): "This molar is decidedly of a narrow-crowned type, much resembling in general



TYPE OF PALÆOLOXODON PROTOMAMMONTEUS

Fig. 1154. Type figure of *Euelephas* (*Parelephas*) *protomammonteus* (*typicus*), a third inferior molar of the left side, l.M_3, crown and internal aspects, one-third natural size. From Nagahama, Town of Minato, Kimitsu District, Province of Kazusa, Japan. After Matsumoto, 1926.2, Pl. XVIII, figs. 1 and 2, one-half natural size. Observe +16½ ridge-plates.

(Matsumoto, *op. cit.*, p. 44): "The holotype, M_3, lacking its most anterior part, consists of sixteen ridges and a posterior talon. Its original ridge formula might probably be about ×17×. Its length, as preserved, is 275 mm.; and its original length might probably be some 300 mm. The maximal width is 75 mm. at the seventh ridge, as estimated above, and the height of the crown is 134 mm. at the eleventh ridge, as estimated above, which had just commenced to wear. The frequency of ridges in a length of 100 mm. is 5½–6 at the sides and about 7 at the grinding surface."

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[1] [See Chapter XXI of the present Memoir, p. 1408, note under "1924 *Elephas namadicus naumanni* Makiyama."—Editor.]

shape the corresponding ones of the phyla of *Loxodonta* (*Palæoloxodon*) *namadica* and *antiqua*, in contrast to *Parel. trogontherii* and higher mammoths. Consequently, the sides of the ridges in fore and aft views are only weakly convex, instead of being so strongly so as in the two last-mentioned species, and are not so strongly convergent toward the base as in the same. The ridges, except the very posterior ones, are curved forward in lateral views, quite as those of the lower molars of *Parel. trogontherii*."

Osborn agrees in the close resemblance of *Palæoloxodon protomammonteus* to *Hesperoloxodon antiquus*, but does not agree that it is related to the *Parelephas trogontherii* phylum.

Palæoloxodon tokunagai Matsumoto, 1929

Soyama, Gokayama, Hira-mura, Higashi-Tonami District, Province of Etchû, Japan. Recorded as of Upper Pliocene or Lower Pleistocene age.

Loxodonta (*Palæoloxodon*) *tokunagai* Matsumoto, 1924. "Preliminary Note on Fossil Elephants in Japan." Journ. Geol. Soc., Tokyo, Vol. XXXI, September 20, 1924, p. 267 (Japanese language). Supplementary Description (1929.2): "On *Loxodonta* (*Palæoloxodon*) *tokunagai* Matsumoto, with Remarks on the Descent of Loxodontine Elephants." Sci. Rept. Tôhoku Imp. Univ., (2), Geology, Vol. XIII, No. 1, pp. 7–10 (English language). TYPE.—A third inferior molar of the right side, r.M_3. Originally belonging to the Imperial Museum of Uëno, numbered 2208—now in the Museum of Education at Ochanomizu, Tokyo. HORIZON AND LOCALITY.—Soyama, Gokayama, Hira-mura, Higashi-Tonami District, Province of Etchû, Japan. Of Upper Pliocene or Lower Pleistocene age. TYPE FIGURE.—The present author has been unable to locate a type figure.

TYPE DESCRIPTION.—(Cited from Matsumoto's Memoir of 1929.2, p. 8): "Description of the type-specimen: This last molar consists, as preserved, of eleven ridges and the single-columned posterior talon. Judging from the general shape of the molar, two more ridges in all likelihood, might have originally been present anterior to the most anterior ridge as preserved. Thus, the ridge-formula appears to be nearly ×13×. Its length as preserved measures 258 mm.; its original length can be estimated as about 295 mm. Its full maximal width is 80 mm. at the ninth ridge as preserved, which is quite abnormal in having a superfluous column standing out on its inner side. Not including this superfluous column, however, the true maximal width of the molar measures 74 mm. at the sixth to eighth ridges as preserved."

"The frequency of ridges in a length of 100 mm. is about 5 on both the inner and outer sides, as well as at the grinding surface. From an inner or outer view, the ridges are seen gradually narrowed distally, though the proximal ends of the valleys, with the exception of the most posterior ones, are of a rather obtuse type. The curvature of the ridges varies from very to rather slight for a lower molar."

"The smallness of the transverse width of the more anterior ridges is quite remarkable; and the disks of the well worn ridges are very markedly lozenge-shaped,—to such a degree that they remind us of those in *Loxodonta*, s.s. The tips of the anterior loxodont sinus of one ridge and the posterior loxodont sinus of the one immediately preceding in the well worn portion of the molar are in close contact with each other. . . . The layer of enamel is very thick, measuring 2.5-3 mm. across; and its plication is very coarse and indistinct. There is a distinct, linear, transverse streak, or even fissure, in each area of cement between two disks at the grinding surface."

Palæoloxodon protomammonteus proximus
Matsumoto, 1926

Figure 1155

Lower part of the Narita Series. Isone, Kokubo, Ônuki-mura, Kimitsu District, Province of Kazusa, Japan. Upper Pliocene (?).

Referring to Matsumoto's definition of *Euelephas* (*Parelephas*) *protomammonteus* (*typicus*), that species is regarded as basal Calabrian, whereas the following species belongs on a higher level, namely, lower Calabrian (Matsumoto, 1926.2, p. 50):

"Stage II. *Parel. protomammonteus proximus.* Lower Calabrian."

"Molars rather large and moderately wide. Inner and outer sides of ridges not very convex. Bases of ridges more or less prominent, and valleys acutely pointed proximally. Basal cingula apparently not well developed."

Parelephas protomammonteus proximus, mut. nov. Matsumoto, 1926. "On the Archetypal Mammoths from the Province of Kazusa." Sci. Rept. Tôhoku Imp. Univ., (2), Geology, Vol. X, No. 2, pp. 48–50. TYPE.—Fragment of a third inferior molar of the left side, l.M_3, belonging to Mr. Katô of Kokubo. HORIZON AND LOCALITY.—"This specimen appears to have been derived, very probably, from a certain lower part of the Narita Series." Isone, Kokubo, Ônuki-mura, Kimitsu District, Province of Kazusa, Japan. TYPE FIGURE.—Matsumoto, *op. cit.*, 1926, Pl. XXIV, figs. 1, 2.

TYPE DESCRIPTION.—In addition to Matsumoto's type figure and type description quoted below in the legend, Matsumoto compares this stage with his *Euelephas* (*Parelephas*) *protomammonteus* as follows: The type molar of *Parelephas protomam-*

TYPE OF PALÆOLOXODON PROTOMAMMONTEUS PROXIMUS

Fig. 1155. Type figure of *Parelephas protomammonteus proximus*, mut. nov. Matsumoto, 1926.2, Pl. XXIV, fig. 1, one-half natural size, from Isone, Kokubo, Ônuki-mura, Kimitsu District, province of Kazusa, Japan. Fragment of a left inferior molar, l.M_3, crown view.

(Matsumoto, 1926.2, p. 48): "This specimen, representing the anterior part of M_3, consists of nine ridges and measures 168 mm. in length as preserved. Its maximal width is 88 mm. at the seventh ridge as preserved, and its height is 128 mm. at the last ridge as preserved, which is slightly worn. The frequency of ridges in 100 mm. is 5."

monteus proximus is distinguished from the type molar of *Parelephas protomammonteus* by its greater width and by the slightly less prominent bases of its ridges; as a whole *P. proximus* is a mutation intermediate between *P. protomammonteus* and *P. trogontherii*. This phylogenetic opinion is expressed by Matsumoto on page 50 (*op. cit.*, 1926.2) as follows:

Stage III. *Parel. trogontherii.* Calabrian to Tyrrhenian.

Stage II. *Parel. protomammonteus proximus.* Lower Calabrian.

Stage I. *Parel. protomammonteus* (*typicus*). Basal Calabrian.

Osborn, 1930.–In the above description Matsumoto expresses the opinion, not shared by Osborn, that these specimens are referable to the *Parelephas trogontherii* phylum. Osborn regards them rather as loxodonts referable to the *Palæoloxodon* phylum and quite distinct from any of the phyla of the Mammontinæ. Both in the ridge formulæ, and in the proportions and the structure of the ridge-plates these types appear to agree quite closely with *Hesperoloxodon antiquus* and *Palæoloxodon namadicus* and to be very distinct from the *Parelephas trogontherii* phylum.

Palæoloxodon namadicus yabei Matsumoto 1929[1]

Figure 1156

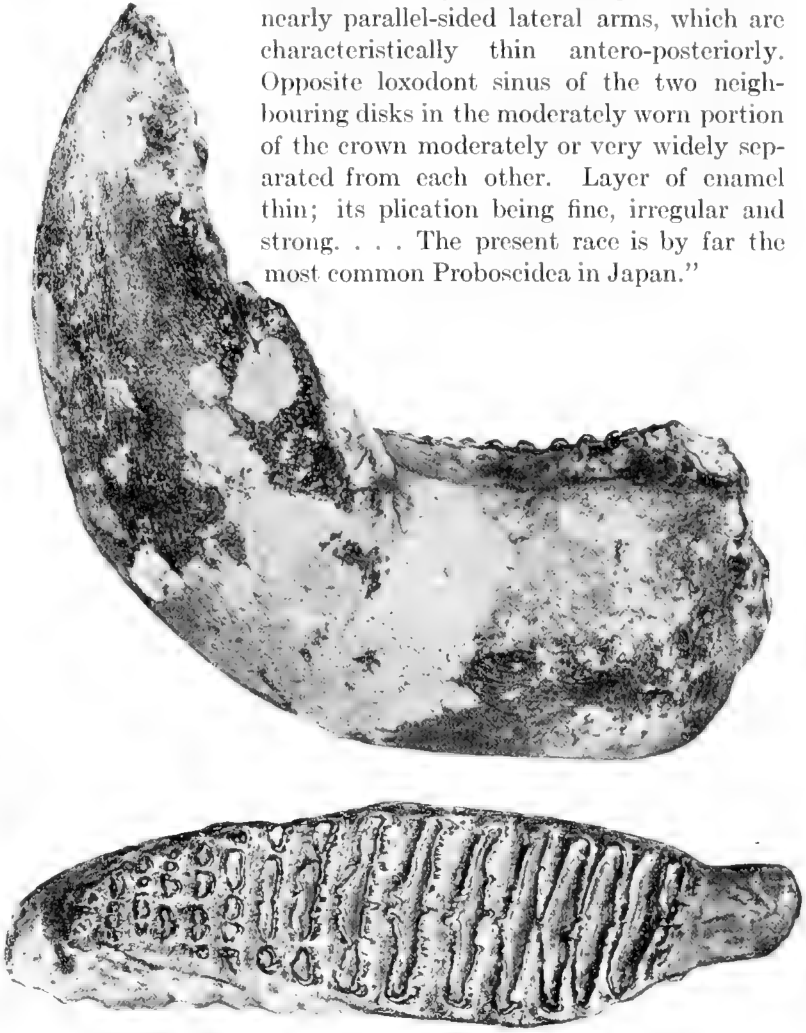
Inland Sea, Japan. Recorded as of Middle Pleistocene age.

Loxodonta (*Palæoloxodon*) *namadica* (*Yabei*) Matsumoto, 1929. "On *Loxodonta* (*Palæoloxodon*) *namadica* (Falconer and Cautley) in Japan." Sci. Rept. Tôhoku Imp. Univ., (2), Geology, Vol. XIII, No. 1, pp. 4 and 5. Type.—"Right ramus of mandible, bearing last molar in situ; belonging to the Second High School." Horizon and Locality.—Inland Sea. "The present race appears to be characteristic of the Middle Pleistocene." Type Figure.—*Op. cit.*, 1929.1, Pl. iii, fig. 2, and Pl. iv.

Type Description.—(*Op. cit.*, 1929.1, p. 4): "The molar of the type-specimen is nearly complete, save that the most anterior portion of the crown, corresponding to the most anterior root, is broken away. The lost portion mentioned very probably consisted of the anterior talon and first two ridges. Since this molar, as preserved, contains fifteen complete ridges and the posterior talon, it is almost probable, that its original ridge-formula corresponds to ×17×. Its total length, including the broken portion, above the margin of the jaw, is about 255 mm. Its maximal width is 74 mm. at the eighth ridge. Its frequency of ridges in 100 mm. counts 6.5–7."

Referred Specimen.—"Penultimate upper molar of right side; belonging to our Institute of Geology and Palæontology." The locality of the referred specimen is Sorachi, Uryû District, Province of Ishikari, Hokkaidô.

Matsumoto (op. cit., 1929, p. 5): "This race can be diagnosed as follows. Cheek-teeth moderate in size, narrow-crowned. Well worn surface of the last lower molar shaped like an elongated ellipsoid. Frequency of ridges rather high, that of the last lower molar of the type-specimen counting 6.5–7 in a length of 100 mm. Mammillæ of the summits of ridges slender, tending to be numerous and closely set; the clefts between the mammillæ extending proximally to a considerable height. Disks of the much worn ridges lozenge-shaped; those of the moderately worn ridges consisting of an expanded mesial portion and of nearly parallel-sided lateral arms, which are characteristically thin antero-posteriorly. Opposite loxodont sinus of the two neighbouring disks in the moderately worn portion of the crown moderately or very widely separated from each other. Layer of enamel thin; its plication being fine, irregular and strong. . . . The present race is by far the most common Proboscidea in Japan."



Type of Palæoloxodon namadicus yabei

Fig. 1156. Type right ramus of mandible, containing r.M_3 *in situ*, of *Loxodonta* (*Palæoloxodon*) *namadica* (*Yabei*) Matsumoto, 1929. Ridge-plates of r.M_3 $\overline{\tfrac{1}{2}\text{-}1\ 7\text{-}\tfrac{1}{2}}$, length 255 mm., breadth 74 mm., ridge frequency 6.5–7 in 100 mm. After Matsumoto, 1929.1, Pl. iii, fig. 2, and Pl. iv. Jaw one-fourth natural size; molar two-fifths natural size.

Palæoloxodon (Archidiskodon?) tokunagai mut. **junior** Matsumoto, 1929

Figure 1157

Japan, precise locality unknown. Probably upper part of the Upper Pliocene or Lower Pleistocene.

The thick enamel, the widely spread ridge-plates, and the alleged 'Upper Pliocene' or 'Lower Pleistocene'(?) age suggest a possible reference to *Archidiskodon* (cf. pp. 957–959, *A. plani-*

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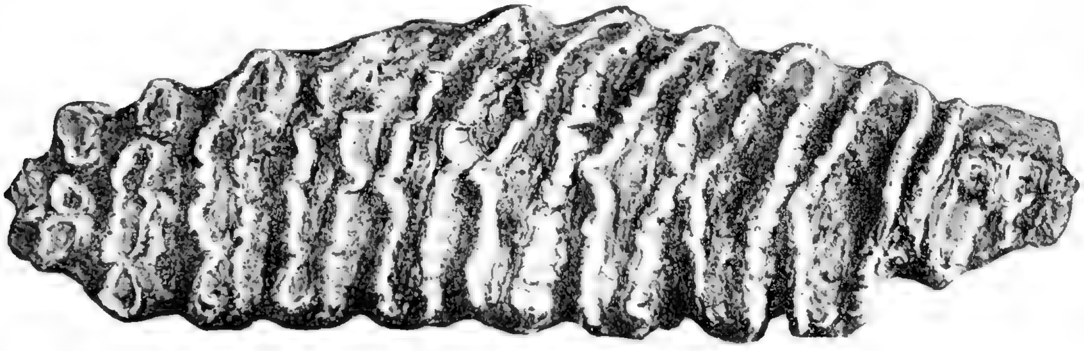
[1] [See Chapter XXI of the present Memoir, p. 1408, note under "1924 *Elephas namadicus naumanni* Makiyama."—Editor.]

frons of the Siwaliks). The side view of the type (Matsumoto, 1929.2, Pl. VII, fig. 2) displays a relatively low-crowned, widely ridge-plated molar.

Lox. (*Pal.*) *Tokunagai junior*, mut. nov. Matsumoto, 1929. "On *Loxodonta* (*Palæoloxodon*) *tokunagai* Matsumoto, with Remarks on the Descent of Loxodontine Elephants." Sci. Rept. Tôhoku Imp. Univ., (2), Geology, Vol. XIII, No. 1, p. 10. TYPE.—Second inferior molar of the right side, r.M_2, belonging to the Geological Institute of the Kyôto Imperial University. HORIZON AND LOCALITY.—Japan, precise locality unknown. ". . . judging from the less but still archetypal feature, and from a comparison of the specimen to the Lower Pleistocene mutation—*Naumanni* Makiyama—of *Lox.* (*Pal.*) *namadica* in Japan, as well as from the degree of fossilisation, the. . . specimen can probably be referred to either an upper part of the Upper Pliocene or to the Lower Pleistocene." TYPE FIGURE.—*Op. cit.*, 1929.2, Pl. VII, figs. 1, 2.

TYPE DESCRIPTION.—(*Op. cit.*, 1929.2, p. 10): In a comparison of the type of the present mutation, namely, *Loxodonta* (*Palæoloxodon*) *tokunagai junior*, with the type of *Loxodonta* (*Palæoloxodon*) *tokunagai*, Matsumoto notes the following differences which can be observed between them: (1) The more anterior portion of the crown of the mutation *junior* is not so narrow as that of *tokunagai*, on the whole, it appears to be less narrow crowned; (2) the disks of ridges are less lozenge shaped; (3) the opposite loxodont sinus of the two neighbouring disks of the well worn ridges are closely set in the *junior* mutation, whereas they are in contact with each other in *tokunagai*; (4) the plication of enamel is stronger, and (5) the layer of enamel appears to be thinner in the *junior* mutation than in *tokunagai*, though this difference in the absolute thickness should be underestimated in the present case. "The writer proposes, in passing, to refer the mutation represented by the . . . specimen to *Lox.* (*Pal.*) *Tokunagai junior*, mut. nov."



PRIMITIVE TYPE MOLAR OF PALÆOLOXODON (ARCHIDISKODON?) TOKUNAGAI MUT. JUNIOR

Fig. 1157. Second inferior molar of the right side, r.M_2, of *Loxodonta* (*Palæoloxodon*) *Tokunagai junior* mut. Matsumoto, 1929. Original in the Geological Institute of the Kyôto Imperial University. Upper Pliocene or Lower Pleistocene(?). After Matsumoto, 1929.2, Pl. VII, fig. 1. Two-thirds natural size. This molar exhibits +11½ ridge-plates. Length as preserved 223 mm., estimated length about 240 mm., breadth 73 mm. at fifth ridge as preserved.

JAPANESE SPECIES DESCRIBED BY SAHEKI AND TOKUNAGA (1931, 1934)

Parelephas protomammonteus matsumotoi

Saheki, 1931[1]

Figure 1158

From Mishima, Kimitsu District, Chiba Prefecture, Province of Kazusa, Japan.

[The description and figure of this subspecies were not studied by Professor Osborn. Inasmuch, however, as he referred *Parelephas protomammonteus* and *P. protomammonteus proximus* of Matsumoto to the genus *Palæoloxodon*, the present subspecies has been inserted in this section under the generic designation of the original author, namely, *Parelephas*.—Editor.]

TYPE OF PARELEPHAS PROTOMAMMONTEUS MATSUMOTOI

Fig. 1158. Portion of left mandibular ramus, with M_3 *in situ*, of *Parelephas protomammonteus matsumotoi* Saheki, 1931, Pl. XV, fig. 1, one-fourth natural size. From Mishima, Province of Kazusa, Japan.

Parelephas protomammonteus (Matsumoto) *matsumotoi* n. var. Saheki, 1931. "On Parelephas protomammonteus (Matsumoto) Recently Found in the Province of Kazusa." Japanese Journ. Geol. and Geog., Vol. VIII, No. 3, pp. 125–129, Pl. XV, 1 text fig. TYPE.—". . . fragment of a left mandibular ramus, including symphysis, and bearing M_3, *in situ*." HORIZON AND LOCALITY.—From Mishima, Kimitsu District, Chiba Prefecture, Province of Kazusa, Japan. (*Op. cit.*, pp. 128, 129): "Lower Calabrian in age. The conglomerate of the region undoubtedly belongs to the base of the Sanuki bed of Dr. H. Matsumoto, [Footnote: 'The name "Sanuki bed" here used is different from what Mr. F. Ueda calls by the same name, but may correspond to his "Umegase bed." '] which is considered to be the basal horizon of the Narita series; to the Upper Miura series of Dr. H. Yabe and

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[1] [See Chapter XXI of the present Memoir, p. 1416, note under "1931 *Parelephas protomammonteus* (Matsumoto) *matsumotoi* Saheki."—Editor.]

Mr. S. Nomura; to the Sasage bed of Mr. J. Makiyama; to the Higashi-Higasa bed of Mr. Y. Otsuka, and to the Umegase bed of Mr. F. Ueda. As to the age of the bed, the first proposes that it is Calabrian and correlates it to the Naganuma bed of the Miura Peninsula, while the last says it is Lower Pliocene and compares it to the Koshiba bed of Lower Pliocene in Miura. But according to Dr. O. Abel, the Elephas group first appeared in Middle Pliocene, while nearly all the other paleontologists state that it first appeared in later Pliocene. According to Dr. H. Matsumoto, 'any well-established true Elephant is as yet unknown throughout the world before the earlier boundary of Calabrian.' Moreover, *Stegodon orientalis Owen* (*typicus*) which is found associated with *Parelephas protomammonteus* (Matsumoto) *typicus* Matsumoto in this case, . . . has never been found to be older than Upper Pliocene. [Footnote: 'Mr. J. Makiyama stated that *Stegodon orientalis* in our country, is Pleistocene, (Proceedings of the Third Pan-Pacific Science Congress).']"

"In view of the foregoing, I am convinced that the bed is Calabrian in age, and is to be correlated to the Naganuma bed of the Miura Peninsula, . . . as Dr. H. Matsumoto does. As to its stratigraphical position, however, I am inclined to favour Mr. F. Ueda's views, separating it from the so-called Sanuki bed of Narita series as another unit of geologic formation [Footnote: 'This concerns the problem of the boundary between Pliocene and Pleistocene. The conspicuous unconformity between Shimosuyeyoshi bed, i.e. the lower part of Narita series in the Miura Peninsula site and the Naganuma bed has been observed recently by Mr. Y. Ôtsuka, as well as by Mr. J. Makiyama.']—the Umegase bed as it may be called." TYPE FIGURE.—*Op. cit.*, Pl. XV, figs. 1 and 3 [Fig. 1158 of the present Memoir].

TYPE DESCRIPTION.—(Saheki, *op. cit.*, 1931, pp. 125–129): "Since 1928, the conglomerate bed exposed at the river cliff of the Koito, has been worked for grit in the construction of prefectural roads newly opened in the village of Mishima, Kimitsu district, Chiba Prefecture. In the course of the work in December, 1928, the left half of a mandibular ramus, bearing a cheek tooth and some pieces of bone of a certain mammal, was found in the conglomerate bed at Higashi-Higasa of the village."

"The mandibular ramus of the specimen measures as follows (in mm.):

"Mandibular angle seems to be conspicuously smaller than *P. protomammonteus* (Matsumoto) *typicus* Matsumoto."

"Length from anterior end of symphysis to posterior end of M_3	455
Length of symphysis	75-a
Width of ramus just anterior to base of ascending bar	160
Depth of symphysis	75"

"The symphysis is very short-spouted. The ridges of diastemata are rather concavely arched, instead of being linear as in those of *P. protomammonteus* (Matsumoto) *typicus* Matsumoto, and sloping down obliquely from the anterior ends of the alveolar margins to that of the symphysis more gently than those of *P. protomammonteus* (Matsumoto) *typicus* Matsumoto. The anterior end of the alveolar margin lies at a distance anterior to the posterior end of the symphysis."

"Three anterior mental foramina are present, though Matsumoto's specimen is reported to have four—all along the ridge of the diastemata—the middle one being the largest."

"The M_3 of this mandibular ramus measures 287 mm. in length as preserved, lacking only some lower part of the posterior talon, consisting of eighteen ridges and a posterior talon. Its maximal width is 76 mm. at the seventh ridge, and its height is ca. 130 mm. at the twelfth ridge, which just shows signs of wearing. The frequency of ridges in 100 mm. is 6 on the inner side, 7 on the outer side, and less than 6 at the grinding surface."

"The worn surface of the molar is oval and more highly concaved than that of *P. protomammonteus* (Matsumoto) *typicus* Matsumoto, as also the mid-ridges which are concaved considerably to the anterior. The layer of enamel of the rather slightly worn ridges on the grinding surface is irregularly wavy; that of the more worn ridges is irregularly and coarsely plicated; while that of the still more worn ridges is gently waving and their enamel layer shows regular, fine, and weak plication."

"The layer of enamel is 1.8—2 mm. thick."

Palæoloxodon yokohamanus Tokunaga, 1934[1]

Figure 1159

From Yokohama, Japan. Lower(?) Pleistocene.

[The following text has been prepared from a translation kindly furnished by Mr. Ushinosuke Narahara of the American Museum. The original description by Doctor Tokunaga was not seen by Professor Osborn.—Editor.]

Palæoloxodon yokohamanus Tokunaga, 1934, pp. 363–371, "Fossil Elephant Teeth found at Yokohama and Kakio, Kanagawa Prefecture," Journ. Geog., Vol. XLVI, No. 546, July, 1934 (in Japanese). TYPE.—A second right superior molar, r.M^2. HORIZON AND LOCALITY.—Found at the mouth of the Tsurumigawa in 1931, Yokohama, Japan. Lower Pleistocene. TYPE FIGURE.—*Op. cit.*, Pl. VIII, figs. 1 and 2.

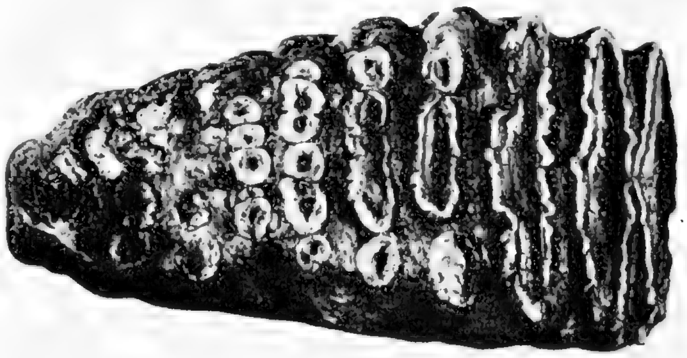

Fig. 1159. Type second right superior molar, r.M^2, of *Palæoloxodon yokohamanus* Tokunaga, 1934, Pl. VIII, fig. 1. Length of molar as preserved 178 mm. From Yokohama, Japan.

The author states that the molar is of a dark brown color and very shiny. It has ten preserved ridge-plates, two probably lacking, making a total of 12. Length of molar as preserved 178 mm., greatest breadth 76 mm., maximum height 177 mm., 5, 6 ridge-plates in 100 mm. Regarded by the author as of Lower Pleistocene age.

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[1] [See Chapter XXI of the present Memoir, p. 1408, note under "1924 *Elephas namadicus naumanni* Makiyama."—Editor.]

JAVANESE SPECIES DESCRIBED BY DUBOIS

Palæoloxodon hysudrindicus Dubois, 1908

Figure 1160

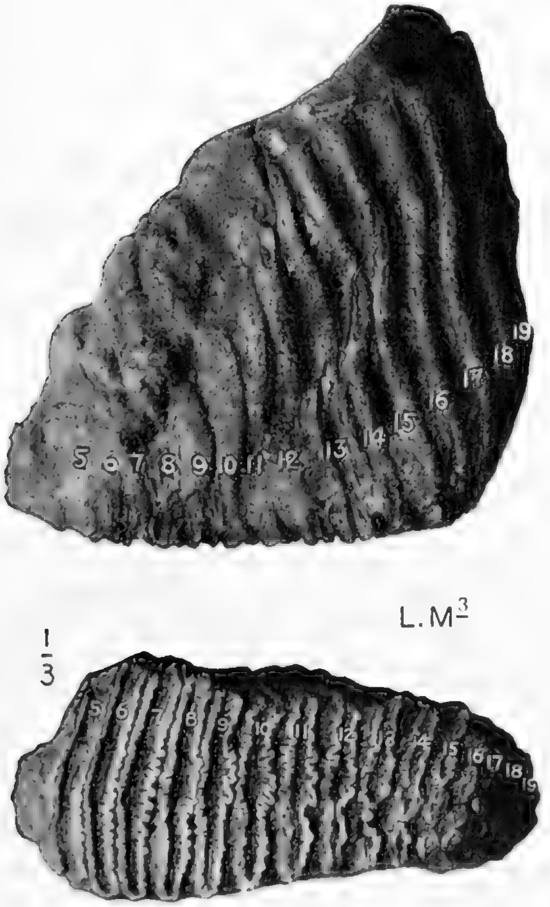
Contemporary of the Trinil Ape Man, *Pithecanthropus*, Middle(?)Pleistocene.

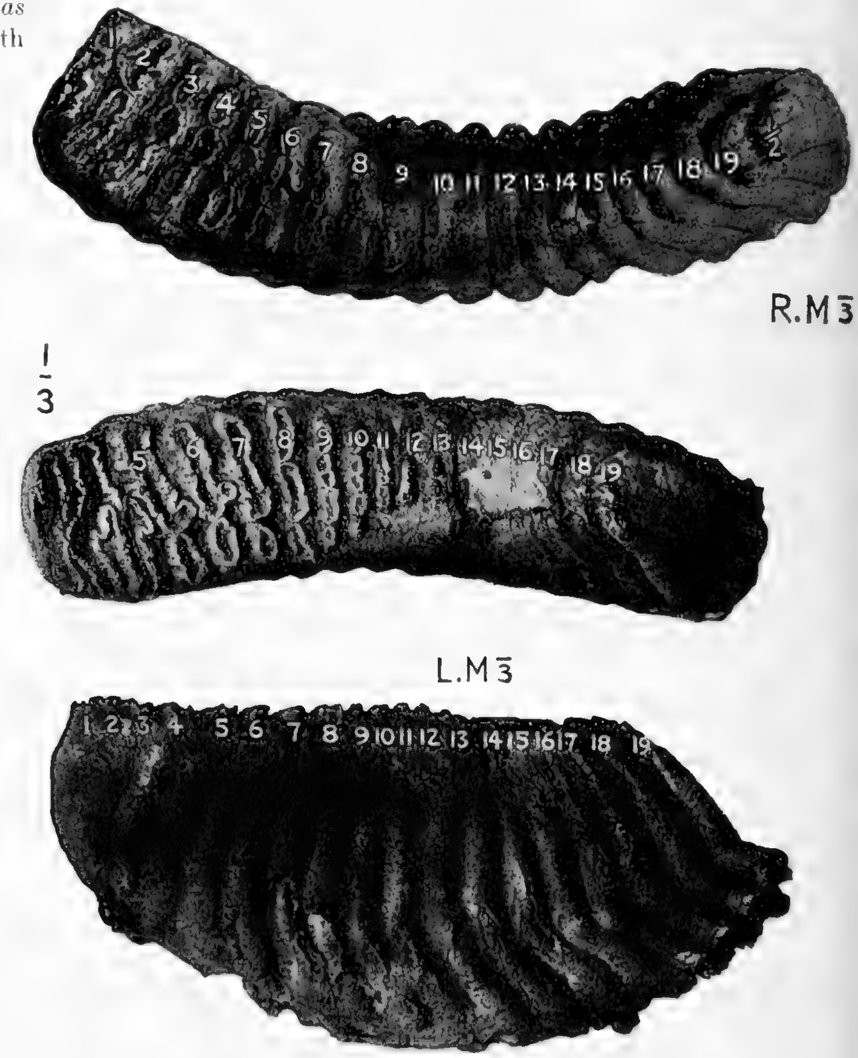
Kendeng-Schichten, Pithecanthropus zone, Lower (or Middle?) Pleistocene of Java. This zone, originally determined as Upper Pliocene, has recently (Dietrich) been regarded as Middle Pleistocene, because it also contains the very progressive species *Stegodon airâwana*.

The cotypes below (Fig. 1160), reproduced from original photographs kindly sent to the present author by Doctor Dubois, are of great interest as positively demonstrating that *'Elephas hysudrindicus'* is a very progressive species of *Palæoloxodon* with a high ridge-plate formula:

P. hysudrindicus $M\ 3\ \frac{19}{19\frac{1}{2}}$.

The long and narrow right and left third inferior molars (B 122 E3 and B 122 E 2C, Dubois Coll., Leiden) are beautifully preserved and, coming from the same individual, firmly establish the dimensions, the number of the ridge-plates, and the low crown of this progressive mid-Pleistocene species; rM_3 measures 324 mm., lM_3, 297 mm., as reproduced one-third natural size. The ridge-plate formula ($M\ 3\ \frac{19}{19\frac{1}{2}}$) surpasses that of *Palæoloxodon namadicus naumanni* ($M\ 3\ \frac{19}{17}$), the genotypic species of *Palæoloxodon* Matsumoto.





Cotypes of Palæoloxodon hysudrindicus. Contemporary with Pithecanthropus

Compare type of *Hesperoloxodon antiquus ausonius* (Fig. 1087).

Fig. 1160. *Elephas hysudrindicus* Dubois, 1908, after photographs of the original cotypes kindly furnished by Dr. Eugen Dubois for this Memoir. Uniformly reduced to one-third natural size.

$L.M^3$, a third left superior molar (B 85 Dubois Coll., Leiden) from the Kendeng deposits, Java, of an aged individual with ridge-plates 5–16 more or less worn, ridge-plates 1–4 completely worn away, ridge-plates 17–19+ still unworn. Length 209 mm., reduced to 70 mm. or one-third natural size. External and crown views.

$R.M_3$, a third right inferior molar (B 122 E3 Dubois Coll., Leiden) from the Kendeng deposits, Java, of a middle-aged individual with ridge-plates 1–8 more or less fully worn, ridge-plates 9–19½ completely unworn. This grinder measures 324 mm. in length; it is reduced to 108 mm. or one-third natural size. Crown views.

$L.M_3$, a third inferior grinder (B 122 E 2C Dubois Coll., Leiden) from the Kendeng deposits, Java, of a more aged individual with ridge-plates 3–11 fully or partly worn and ridge-plates 1–3 worn away or imperfect, ridge-plates 12–19 unworn. This grinder measures 297 mm. in length; it is reduced to 99 mm. or one-third natural size. Crown and lateral aspects.

The cotype superior molar (B85 Dubois Coll.) of *Palæoloxodon hysudrindicus* (Fig. 1160) exhibits, especially on ridge-plates 5 to 12, enamel foldings or plications more numerous and deeper than those of the type of *P. namadicus namadi* (Fig. 1153); these plications resemble those of the '*Elephas namadicus*' (Fig. 1189) described by Lydekker, 1886:2, as "from the Pleistocene between Kanagawa and Tokio (Yedo), Japan"; it was this crimping or plication and the absence of the 'loxodont sinus' which led Dubois to relate these grinders to *Elephas indicus*.

Dubois (1908) named this species as among his "Kendeng-fossilien"; Stremme (1911) remarked that Dubois had no *Elephas* remains from Trinil in his large collection. Dubois (1908) distinguished *Elephas hysudrindicus* as standing near *Elephas hysudricus*, but still more close to the living *Elephas indicus*; consequently he named it *Elephas hysudrindicus*. Stremme (1911, p. 144), however, remarked on its closer relationship to *Elephas* [=*Hesperoloxodon*] *antiquus*: "In bezug auf die Zahl der Joche steht dieser dem *E. antiquus* näher als dem rezenten *E. indicus*."

Elephas hysudrindicus Dubois, 1908. "Das Geologische Alter der Kendeng-Oder Trinil-Fauna." Tijdschr. Nederl. Aardr. Genoots. Amsterdam, Tweedie Serie, Deel XXV B, No. 6, p. 1257. Cotypes.—Molar teeth with lamellæ not exceeding 19½; skull subsequently found (see description below), but type specimen not clearly designated or figured. Horizon and Locality.—Kendeng-Schichten, Java, Middle? Pleistocene. Cotype Figures.—Not published by the author (see Fig. 1160 of the present Memoir).

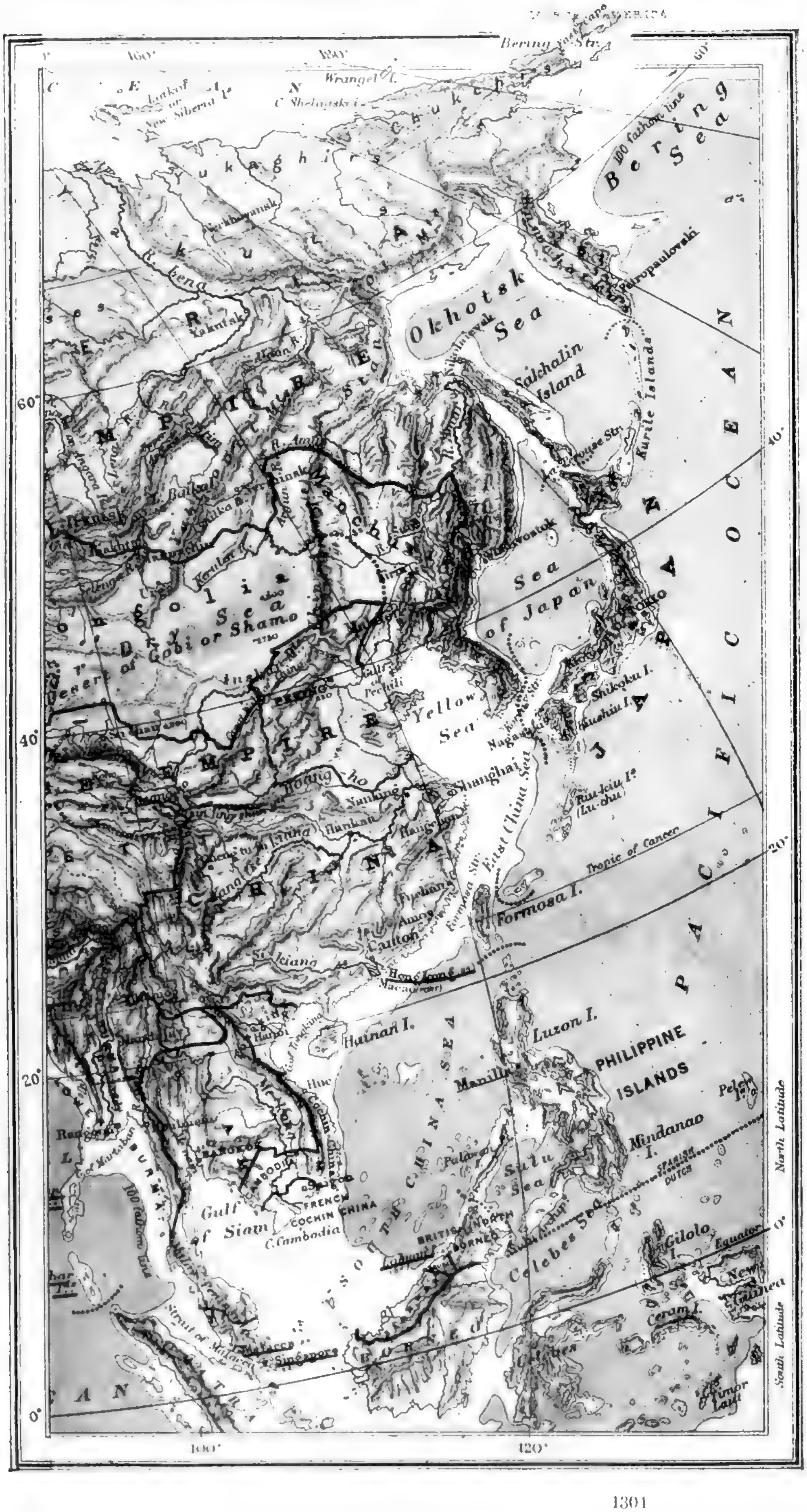
Original Description.—(Dubois, 1908, p. 1257): "Auch von *Elephas* liegt unter meinen Kendengfossilien nur *eine einzige* Art vor, worüber mich genaue Durchsicht der vielen gesammelten Molaren und besonders auch Bekanntwerden mit der Schädelform belehrt hat. Es ist diese eine dem *Elephas hysudricus* sehr nahe stehende, jedoch noch mehr als letzterer sich dem jetzt lebenden *Elephas indicus* annäherende Art, die ich deshalb als *Elephas hysudrindicus* n. sp. bezeichnen will. Hatte man die Art aus den Siwalik-Schichten bereits als die vermutliche Stammform des lebenden asiatischen Elephanten erkannt, durch die neue Art von Java wird diese verwandtschaftliche Beziehung noch klarer. Die grosse Ähnlichkeit der Molaren hatte mich anfänglich sogar dazu verführt die Anwesenheit des *E. indicus* unter der Kendeng-Fauna anzunehmen, obgleich die Lamellen-Zahl der fossilen javanischen Molaren nicht über 19 geht, also viel geringer ist als bei *E. indicus*; der (später bekannt gewordene) Schädel nähert sich aber bedeutend mehr der Siwalik- als der lebenden Art, namentlich durch sein Profil, durch die grössere laterale Entwickelung der parietofrontalen Höcker, und durch die geraden Alveolen für die Stosszähne, doch ist die Breite zwischen den Schlafengruben bereits grösser geworden; hierin nähert sich die javanische ausgestorbene beträchtlich der lebenden indischen Art, als deren unmittelbaren Stammvater wir die erstere wohl unzweifelhaft anzusehen haben."

(Stremme, 1911, p. 144): "Ein wichtiges Leitfossil wäre eventuell *Elephas*, dessen Zahnbruchstück Janensch dem *Elephas antiquus* am nächsten stellt. Das Stück stammt nicht von Trinil; auch Dubois hat keine *Elephas*-Reste von Trinil in seiner grossen Sammlung. Dubois selbst ist nicht geneigt, an Altersunterschiede der Fundstellen bei diesem eigenartigen Fehlen zu denken, sondern er hält die Lebensweise der Elefanten in bezug auf die Verteilung ihrer Reste für massgebend. Dubois hat nach seinem grösseren Material des Elefanten diesen als *Elephas hysudrindicus* n. sp. bezeichnet und stellt ihn namentlich nach dem Vergleiche der Schädel nahe an *Elephas hysudricus* aus den Siwalik-Schichten vom Pendschab und den subhimalajischen Bergen und aus dem Altpleistocän des Narbadatales."

Stremme also observes (*op. cit.*, p. 143): "Der Elephantenzahn zeigt nach Janensch mehr loxodonten Charakter als *Elephas indicus* und erinnert mehr an *Elephas antiquus*. (Der Vertreter des *E. antiquus* in Indien, nach Leith Adams *Elephas namadicus* Falc. aus dem Altpleistocän des Narbadatales, wird aber ausdrücklich von Janensch als verschieden bezeichnet.)" Janensch ("Die Proboscidier-Schädel der Trinil-Expeditions-Sammlung," 1911, p. 194) does not comment directly on the characters of the species *E. hysudrindicus* Dubois beyond the observation quoted from Stremme above.

Osborn, 1930: This progressive stage of *Palæoloxodon*, like that of *Stegodon airâwana*, is of great anthropological interest as establishing the Middle Pleistocene age of *Pithecanthropus erectus*, first pointed out by Dietrich.

IX. SUMMARY OF GEOGRAPHIC DISTRIBUTION ALONG THE EASTERN COAST OF ASIA



Altogether, the monographic researches of Matsumoto and Makiyama supplement those of Falconer, of Owen, and of Osborn and prove that primitive species of the genus *Palæoloxodon* spread eastward across all of southern Asia during Upper Pliocene time until their march was arrested by the ancient Pliocene shore lines of Japan and of the East Indies, including Burma, Java, and Sumatra. It is in the Kendeng stratum of Java, now regarded as of Middle Pleistocene age (as fully treated above, Chap. XIV, the Stegodontinæ, especially p. 887) that we find another advanced stage of *Palæoloxodon,* to which Dubois applied the name '*Elephas hysudrindicus.*'

The bathymetric maps of Chisholm and Leete (Fig. 1161) and of Yabe (Fig. 1162) are extremely interesting and important in displaying three features, namely:

(1) The ancient coast of northern and southern Asia and of the East Indies during late Pliocene and early to mid-Pleistocene times; (2) the successive northerly *range* over the Bering Strait region of *Archidiskodon,* (?)*Parelephas,* and *Mammonteus* to North America; (3) the southerly and southeasterly *range* of *Stegolophodon, Stegodon,* and *Palæoloxodon,* and finally of *Elephas.*

Fig. 1161. Japan as part of the Asiatic continent in Plio-Pleistocene time, showing in white the broad true continental border on the 100-fathom or 600-foot line. Reproduced by permission after Longmans' New School Atlas. This shows clearly the migration lines through Sumatra, Borneo, the Philippine Islands, Japan, and Kamchatka. Compare with the more recent figure after Yabe (Fig. 1162).

The three outstanding facts are:

The geologically oldest or Lower Pliocene[1] range of the Stegodonts[2] covers an area from the type locality of *Stegolophodon latidens* on the Irrawaddy River, Burma, 1300 miles southeast, to the northern Bruni district of Borneo, namely, Brit. Mus. M.2498, described by Lydekker (1886.2, pp. 75, 76, Fig. 19) as '*Mastodon latidens*' but which the present author made the type of *Stegolophodon lydekkeri* in Vol. I, p. 700, of the present Memoir.

Of Upper Pliocene and Lower Pleistocene age is the transcontinental range of descendants of North African species of *Palæoloxodon*, such as *Palæoloxodon jolensis* and *P. atlanticus* of Pomel, and *P. recki* of Dietrich, to Japan; this must have occurred in late Pliocene or early Pleistocene time, because the more primitive Japanese stage described by Matsumoto, namely, *P. tokunagai* (M 3 $_{\frac{1}{2}-1\overline{3-\frac{1}{2}}}$), corresponds closely in ridge formula with the more primitive North African species and those of the Mediterranean Islands.

Finally there is the *Palæoloxodon namadicus* stage (M 3 $\frac{15}{16}$) of the Middle to Upper Pleistocene of India, which corresponds closely with the *P. namadicus naumanni* of Makiyama, although the latter has a higher ridge formula, namely, M 3 $\frac{19}{17}$.

Of the true Stegodonts, the *Stegodon elephantoides* of the Irrawaddy River (M 3 $_{9\frac{1}{2}-\overline{10}}$), including *Stegodon cliftii* of Falconer (l.M 1 with $_{6\frac{1}{4}}$ ridge-crests), may be ancestral to the *Stegodon insignis birmanicus* of Burma (M 3 $_{\overline{12\frac{1}{2}}}$) and to the *S. orientalis grangeri* (M 3 $_{\overline{13+}}$) of the Yangtze River, China.

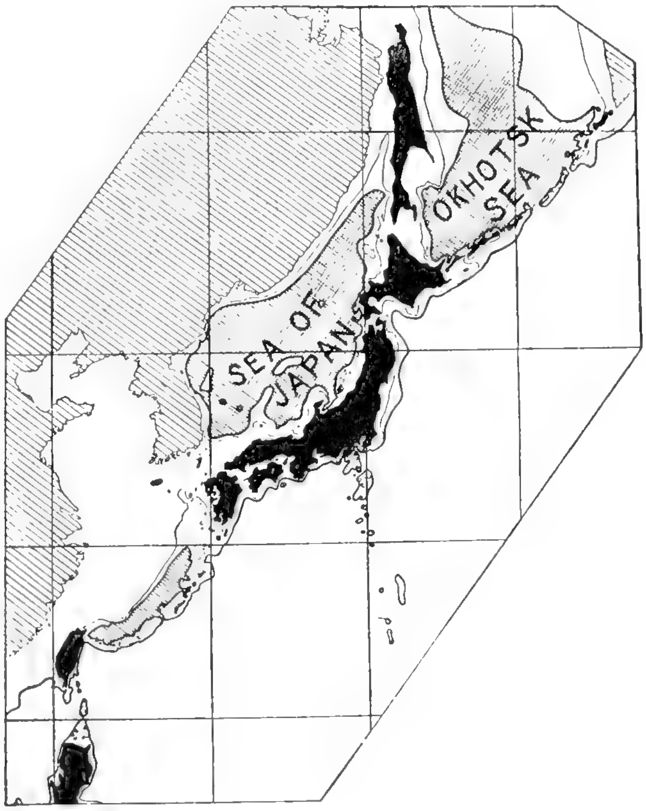


Fig. 1162. Japan as part of the Asiatic continent in Plio-Pleistocene time and two landlocked internal basins. After Yabe, 1929, map, p. 169, who describes the latest land connection of the Japanese Islands with the Asiatic continent as follows (p. 168):

"The sea floor now encircling the Japanese Islands to the depth of some 720 m., in the average, was once a land surface and the land submerged below the sea level in a time geologically not much remote from the present. Prior to this great submergence of land, the Japanese Islands were some 720 m. [2375 ft.] more elevated than they are at present and directly connected with the Asiatic continent, as the annexed map shows. The 720 m. line, which marks the true continental border of eastern Asia more properly than the 160 m. line, follows closely the present Pacific coasts of Taiwan, the Riukiu Group, Kyûshû, Shikoku, Honshû Hokkaidô, the Chishima Group and Kamchatka. The entire region lying inside this line is regarded once to have been a dry land, with the exception of two extensive basins—one occupying the greater part of the Japan Sea and the other [the] southernmost part of the Okhotsk Sea—, and a narrow, linear one lying along the inner border of the island arc of the Riukiu Group. All these basins, now more than 700 m. deep, are thought by the writer as having existed there as entirely or almost land-locked basins during the continental stage of the Japanese Islands; . . . It was at the time of the maximal extension of land in the continental stage of the Japanese Islands that the land took the outline stated above. . . . In other words, the continental stage of the Japanese Islands continued from the time of land emergence to the 90 m. line to the time of land submergence to the same line."

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[1] [Probably Lower Pleistocene—see note on page 824 above.—Editor.]

[2] [See footnote on page 837 above.—Editor.]

Fig. 1163. Referred Elephas indicus. Male and female Elephants photographed in Ceylon by Plate Ltd. of Kandy.

CHAPTER XX

THE SUBFAMILY ELEPHANTINÆ (SUPERFAMILY ELEPHANTOIDEA), OF EASTERN ASIA, INCLUDING THE RECENT ELEPHAS AND RELATED LOWER PLEISTOCENE SPECIES

Classical references to elephas. Establishment by Linnæus of the genus and species elephas indicus (1735–1758). Characters of the subfamily Elephantinæ and included species and subspecies or geographic varieties, by Corse, de Blainville, Falconer, Temminck, Matsumoto, and others (1799–1927). Fossil lower pleistocene and upper pliocene species described by Falconer and by Osborn (1845–1930).

I. Historical Introduction and Nomenclature (850? B.C.-1936).
  1. Falconer (1868) on the specific unity and vertebral formulæ of the Asiatic elephants.
  2. Corse, de Blainville, and Falconer on characters of the geographic varieties.
  3. Living specific or subspecific forms, continental and insular.
  4. Fossil forms more or less closely related to *Elephas indicus*.
  5. Names of species and subspecies of the subfamily Elephantinæ in order of description.

II. Characters of the Subfamily Elephantinæ and Included Genera and Species.
  Genus *Elephas*.
  1. Systematic description of species of *Elephas*.
      Elephas indicus Linnæus.
      Elephas indicus ceylanicus de Blainville.
      Elephas indicus bengalensis de Blainville.
      Elephas indicus sumatranus Temminck.
      Elephas indicus hirsutus Lydekker.
      Elephas indicus Buski Matsumoto [=?*Palæoloxodon buski*].
  2. Distinctions and measurements of the Indian elephant.

III. Characters of the Upper Pliocene and Lower Pleistocene Species Hypselephas hysudricus and Platelephas platycephalus.
  1. Falconer's original descriptions of *Elephas* [*Hypselephas*] *hysudricus*.
  2. Observations of Osborn on the fourteen specimens collected by Barnum Brown (1922) referred to *Hypselephas hysudricus*.
  3. Cranial characters and affinities of *Hypselephas hysudricus*.
      Juvenile crania with dentition.
  4. Genus *Platelephas*.
      Platelephas platycephalus.

Appendix.

It is a striking circumstance that we have not as yet discovered the direct ancestry of either of the typical living elephants, namely, the *Elephas indicus* of India or the *Loxodonta africana* of Africa. Both of these typical living species, around which center historical as well as zoological references from the time of Homer (850? B.C.) to the present time, are still lacking the phylogenetic background of their history. All attempts both by zoologists and palæontologists to trace back either *Elephas indicus* or *Loxodonta africana* to previously living or fossil forms[1] are shown in the present Memoir to be problematical, because neither in the cranium, the teeth, nor the skeleton do any of the known fossil elephants meet all the phylogenetic conditions. Even the *Platelephas platycephalus* of the Upper Pliocene and the *Hypselephas hysudricus* of the Lower Pleistocene of India, very fully described below in the present chapter, fail to meet all the conditions ancestral to the true *E. indicus*. The conclusion is inevitable, that in some as yet unexplored region of Asia the direct ancestors of *E. indicus* were slowly evolving, while in some unexplored area, probably west of central Africa, the very conservative ancestors of *L. africana* were also slowly evolving. In brief, we now know the phylogeny of most of the other subfamilies of the Elephantidæ better than we know the phylogeny of the Elephantinæ, typified by the genus *Elephas*.

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[1] [According to Pomel (1895) the true *Loxodonta africana* occurs in comparatively recent deposits of North Africa, and Dart (1929) refers to the discovery in the Pilandsberg (Transvaal) of a primitive form of *L. africana* (cf. *Loxodonta prima* Dart, 1929, Chap. XIX above, p. 1287). –Editor.]

The early historical references or allusions to this most majestic of all living quadrupeds of the Asiatic continent are full of fascination and interest.[1] The uses of these animals in industry, in transportation, in art, and in war would fill volumes. But here, as a fitting conclusion to the previous nineteen chapters of the history of the Proboscidea, we must confine ourselves rigidly to the slow emergence and clarification of zoological nomenclature and anatomical analysis from the time of the Greeks onward to the present time.

As in the Loxodontinæ (Chap. XIX) and in the Mammontinæ (Chap. XVIII), the strict application of the Rules of the International Commission on Zoological Nomenclature (Congress of Berlin, 1901, and of Monaco, 1913) to types and descriptions of the early part of the nineteenth century is beset with insuperable difficulties, as exemplified in the classic case of whether the Indian elephant should be called '*Elephas indicus*' or '*Elephas maximus*.' The grounds for the adoption of '*Elephas maximus*' are herewith shown to be either precarious or absolutely untenable.

I. HISTORICAL INTRODUCTION AND NOMENCLATURE (850? B.C.-1936)

The very ancient name 'elephant' has risen in rank, becoming the type of the subfamily Elephantinæ, family Elephantidæ, superfamily Elephantoidea.

History of Nomenclature.—*Elephas* is a Greek name of uncertain origin, subsequently Latinized. It is treated by Liddell and Scott (1883) and by James A. H. Murray (1891) as follows:

> (Liddell and Scott, 1883, p. 454): **ἐλέφας, αντος, ὁ** *the elephant,* first mentioned by Hdt. as a native of Africa, 3.114., 4.191; whereas Arist. H. A. 2.I, 45 treats only of *Elephas Indicus,* cf. 9.I, 30, etc., though the African is mentioned by him in Cael. 2.14,19:—not generally known in Greece till the time of Alexander, Paus. 1.12,4. **II.** known to Hom. only as the name for *the elephant's tusk, ivory,* II. 5. 582, and so Hes. and Pind.; for ivory was brought by Phoenician traffic to Greece long before the animal was known to Greek travellers; Hdt. calls the tusks more accurately **ἐλέφαντος ὔδοντες**, 3. 971:—Hom. brings false dreams through an ivory gate, v. sub **ἐλεφαίρομαι**, . . . (Pott and others refer to the Hebr. *Eleph* (*ox*), and compare *bos Lucas,* the old Lat. name of the elephant, Lucret. 5. 1301; as Paus. (9.21, 2) calls a rhinoceros **ταῦρος Αἰθιοπικός**. On the other hand the Hebr. name for the animal, *ibâh,* recalls the Skt. *ibhas,* which is identical with the latter part of **ἐλ-έφας**, and the first part of the Lat. *eb-ur,* whence *iv-oire,* etc.)
>
> (Murray, 1891, III, Pt. 2, p.84): Elephant . . . Gr. ἐλέφας (gen. ἐλέφαντος). The refashioning of the word after Lat. seems to have taken place earlier in Eng. than in Fr., the Fr. forms with *el-* being cited only from 15th c. . . . Of the ultimate etymology nothing is really known. As the Gr. word is found (though only in sense 'ivory') in Homer and Hesiod, it seems unlikely that it can be, as some have supposed, of Indian origin. The resemblance in sound to Heb. . . . *eleph* 'ox' has given rise to a suggestion of derivation from some Phœnician or Punic compound of that word; others have conjectured that the word may be African.

Elephas was named as a genus by Ray (1693, p. 131 [=p. 123 of authors]), and was included in the "Systema Naturæ" of Linnæus in 1735 in the same division of quadrupeds with the rhinoceros (see below facsimile of portion of page 10 of the First Edition of the "Systema Naturæ" of Linnæus, 1735). The genus *Elephas* Linn. dates from 1735, the species *indicus* dates from 1754, the species *maximus* dates from 1758, as shown in the three facsimile Linnæan definitions from (1) the "Systema Naturæ," First Edition, 1735, p. 10; (2) Memoir of the Museum Adolphi Friderici Regis, Holmiæ [Stockholm], 1754, p. 11, and finally in the Tenth Edition of the "Systema Naturæ," 1758, p. 33.

Dr. C. Davies Sherborn of the British Museum, the greatest living authority on generic and specific names, believes that it is impossible to determine which elephant, African or Asiatic, Linnæus had in mind in proposing the term *maximus,* a name without standing in Sherborn's opinion:

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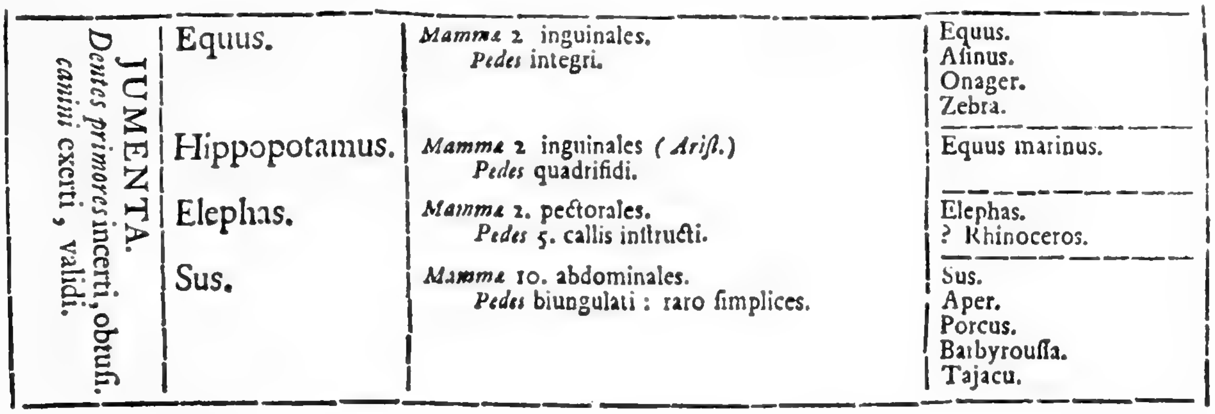
[1] Kunz, George F., 1916. Ivory and the Elephant in Art, in Archæology and in Science.

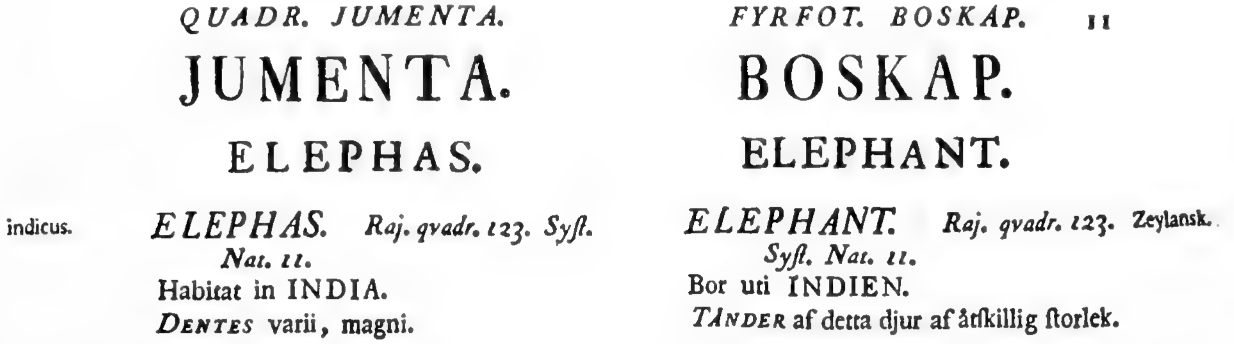
> (Sherborn, 1929, letter of July 14) "In reply to your enquiry about *Elephas maximus*, Linnæus. Linnæus' type seems to have been Ray, Quadr. 131. Blainville, Eléphants (p. 47) in his 'Ostéographie,' says Ray saw a young elephant in Florence. Now Ray gave no locality for his specimen but described it in much detail. In the Mus. Adolf. Frid. in 1754 Linnæus says 'Indien' both in his Latin and his Swedish version and why or on what authority he puts the word Zeylansk in opposition to 'indicus' passes my understanding. So far as I know there is no authority for Zeylansk and in the S. N., ed. XII, 48, Linnæus clearly spatchcocks the whole lot into one species both for Asia and Africa and considers that there is only one Elephant. And as that beast has been more or less of a domesticated animal since before Alexander the Great, I don't think Linnæus was far wrong in such a guess. In such a case it appears to me that you have no option but to say 'INDETERMINATE' and proceed to the next person who divided the subject, e.g. Blumenbach in 1797 for 'africanus' and Cuvier in 1798 for 'indicus.' Unless one can definitely say what beast Linnæus saw when he gave the name 'maximus,' which apparently is now a thing impossible to decide, it appears to me that 'maximus' has no standing and must be swept aside." [See Lönnberg (letter of 1929) quoted below, also footnote on page 1323].

In 1754 the specific name *indicus* appears and in our present language this was the original genotypic species of *Elephas*; it was universally used as such by all writers on the elephant family until 1901. Unfortunately, and for some reason unknown to us, in the Tenth Edition of the "Systema Naturæ" Linnæus substituted the name *Elephas maximus* Linn. for that of *E. indicus* Linn., which, with all other names in the Tenth Edition, was officially adopted by the Fifth International Congress of Zoology held at Berlin in 1901 (see Verhandlungen des V. Internationalen Zoologen-Congresses zu Berlin, 12.–16. August, 1901, published 1902, p. 967).



JUMENTA. *Dentes primores* incerti, obtusi. *canini* exserti, validi.	Equus.	*Mammæ* 2 inguinales. *Pedes* integri.	Equus. Aſinus. Onager. Zebra.
	Hippopotamus.	*Mammæ* 2 inguinales (*Ariſt.*) *Pedes* quadrifidi.	Equus marinus.
	Elephas.	*Mammæ* 2. pectorales. *Pedes* 5. callis inſtructi.	Elephas. ? Rhinoceros.
	Sus.	*Mammæ* 10. abdominales. *Pedes* biungulati: raro ſimplices.	Sus. Aper. Porcus. Babyrouſſa. Tajacu.

Fig. 1164. Facsimile of portion of page 10, in same size, of the First Edition of Linnæus' "Systema Naturæ," 1735, in which appears his first definition of the genus *Elephas*, bracketed with ?*Rhinoceros*.



QUADR. JUMENTA.

JUMENTA.

ELEPHAS.

indicus. *ELEPHAS.* *Raj. qvadr.* 123. *Syſt. Nat.* 11.
Habitat in INDIA.
DENTES varii, magni.

FYRFOT. BOSKAP. 11

BOSKAP.

ELEPHANT.

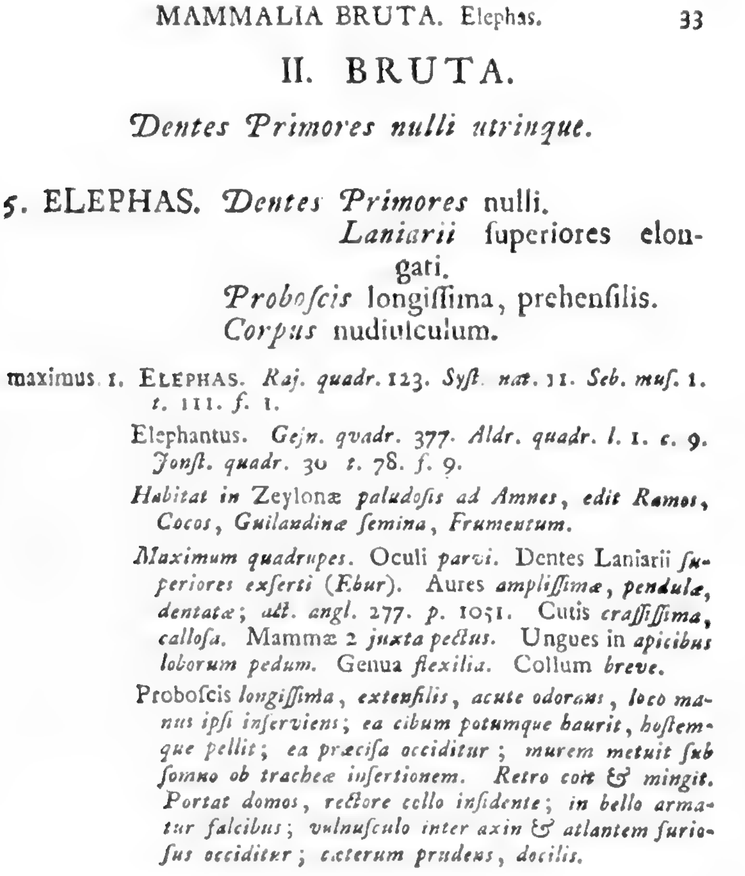
ELEPHANT. *Raj. qvadr.* 123. Zeylansk. *Syſt. Nat.* 11.
Bor uti INDIEN.
TÄNDER af detta djur af åtſkillig ſtorlek.

Fig. 1165. Facsimile of portion of page 11, reduced in size, of Linnæus' Memoir of the Museum Adolphi Friderici Regis, Stockholm, 1754, in which first appears the species *Elephas indicus*, habitat India.

In the present Memoir, to avoid confusion with the entire literature prior to 1901, the earlier specific name *Elephas indicus* Linn. is used throughout as a 'Linnæan collective species' embracing several geographic subspecies. We have seen repeatedly in the present Memoir that the rules of the Congress of 1901 are impracticable when one attempts to apply them to early stages of palæontological nomenclature. We must remember that Linnæus believed that the number of created species was limited; in his mind the Indian and African elephants were of the same species. This is indicated in the following letter from Professor Einar Lönnberg (July 31, 1929):

> LINNÆUS' TYPE OF ELEPHAS INDICUS (LÖNNBERG, LETTER, JULY 31, 1929).—"In reply to your letter concerning the type of Linnæus' *Elephas indicus* in Museum Adolphi Friderici Regis, 1754, I may say that it is not a skeleton nor a stuffed animal but a fœtus, which still is kept in this Museum. The King had bought it together with several other natural history specimens from Holland, where it once was kept in 'Museum Sebae.' It is of an African Elephant, probably from West Africa.
>
> The reason why Linnæus speaks of India and Ceylon is probably that he quotes Rajus in the first rank. I have not looked up what Rajus says, but you can easily find that yourself after the quotation: 'Raj. quadr. 123.
>
> In Systema Naturæ, ed. X., Rajus is also quoted in the first rank and Seba only in the third rank. But Seba's specimen is the same as that of Museum Adolphi Friderici Regis, 1754. Seba has figured his specimen in his 'Thesaurus,' Vol. I, tab. CXI, fig. 1, and he says that it is 'Een ongeboren Olifant uit Africa.'
>
> From the above is evident, that the name *Elephas maximus* L. 1758 refers as well to the Indian (Rajus quoted first) as the African (Seba quoted as third) Elephant."

GENUS (LINNÆUS, 1735, 1754, 1758).—The genus *Elephas* Linnæus dates from 1735 ("Systema Naturæ," First Edition, p. 10) without mention of a genotypic species. In 1754 (Memoir, Mus. Adolphi Friderici Reg., Stockholm, p. 11) reappears the generic name *Elephas* with the species *indicus*, habitat India (Zeylansk), indicating that Linnæus based the species on the Ceylon variety of elephant. In 1758 ("Systema Naturæ," Tenth Edition, p. 33) again appears the generic name *Elephas*, habitat India (Zeylonæ), with the new specific name *Elephas maximus*. This edition (known as the Editio Decima, Reformata) was reprinted in 1901 and adopted as the standard by the Fifth International Congress of Zoology of 1901, held at Berlin.



MAMMALIA BRUTA. Elephas. 33

II. BRUTA.

Dentes Primores nulli utrinque.

5. ELEPHAS. *Dentes Primores* nulli.
Laniarii ſuperiores elongati.
Proboſcis longiſſima, prehenſilis.
Corpus nudiulculum.

maximus. 1. ELEPHAS. *Raj. quadr.* 123. *Syſt. nat.* 11. *Seb. muſ.* 1. *t.* 111. *f.* 1.

Elephantus. *Geſn. qvadr.* 377. *Aldr. quadr. l.* 1. *c.* 9. *Jonſt. quadr.* 30 *t.* 78. *f.* 9.

Habitat in Zeylonæ *paludoſis ad Amnes, edit Ramos, Cocos, Guilandinæ ſemina, Frumentum.*

Maximum quadrupes. Oculi *parvi.* Dentes Laniarii *ſuperiores exſerti* (*Ebur*). Aures *ampliſſimæ, pendulæ, dentatæ; act. angl.* 277. *p.* 1051. Cutis *craſſiſſima, calloſa.* Mammæ 2 *juxta pectus.* Ungues in *apicibus loborum pedum.* Genua *flexilia.* Collum *breve.*

Proboſcis *longiſſima, extenſilis, acute odorans, loco manus ipſi inſerviens; ea cibum potumque haurit, hoſtemque pellit; ea præciſa occiditur; murem metuit ſub ſomno ob tracheæ inſertionem. Retro coit & mingit. Portat domos, rectore collo inſidente; in bello armatur falcibus; vulnuſculo inter axin & atlantem furioſus occiditur; cæterum prudens, docilis.*

Fig. 1166. Facsimile of page 33, in same size, of Linnæus' original Tenth Edition of the "Systema Naturæ," 1758, in which *Elephas maximus* is substituted for *Elephas indicus*, and the genus *Elephas* and species *maximus* are defined. Habitat in Zeylonæ.

In 1795 the name *Elephantus* was used by Geoffroy and Cuvier, and in 1801 was cited by Cuvier and Lacépède as *Elephantus indicus*, as Cuvier continued to ignore the terminology of the "Systema Naturæ" of Linnæus.

GENOTYPIC SPECIES.—The species *indicus* of Linnæus, which we select as genotypic, is important, because of the recent substitution by the Congress of 1901 of *Elephas maximus* Linnæus (1758) for the original name *Elephas indicus* Linnæus (1754). Why did Linnæus abandon the appropriate name *Elephas indicus* and substitute the inappropriate name *Elephas maximus*? Is not the explanation found in his belief that the Indian and the African elephant were of the same species?

First.—There is little doubt[1] that the genotypic species *Elephas indicus* Linn., 1754 (= *Elephas maximus* Linn., 1758) was a domesticated elephant from the island of Ceylon in which occurs the native or indigenous small, typical Ceylonese variety named by de Blainville (1845) *Elephas indicus ceylanicus*. This subspecies of Ceylon is clearly distinguished by its small, slender tusks pointing obliquely downwards, by its narrow, elevated head, with narrow narial openings, by its gentle

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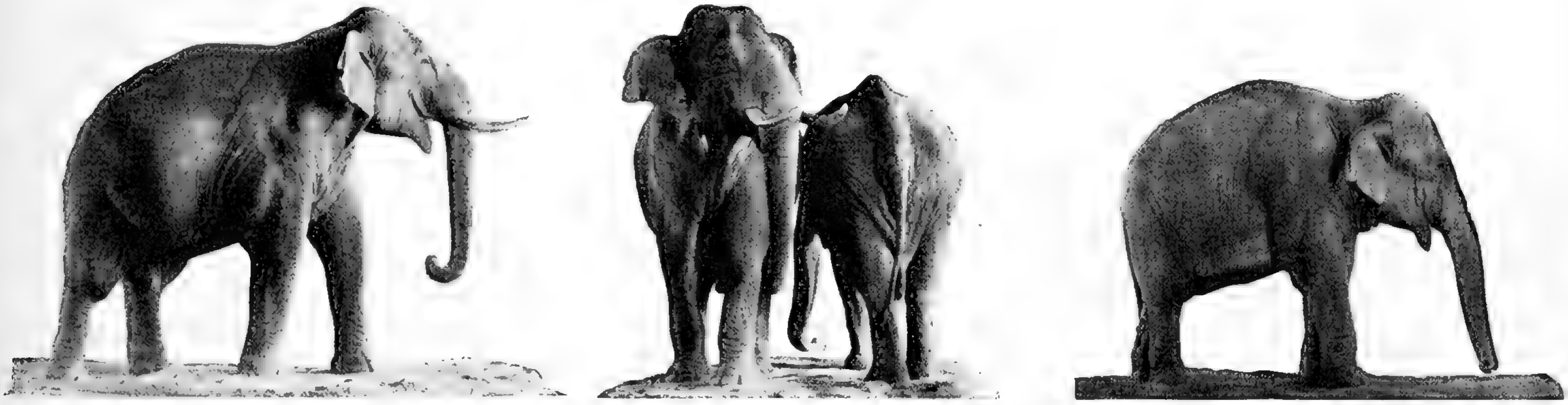
[1] In 1758, as shown in the accompanying facsimile of page 33 of the Tenth Edition of the "Systema Naturæ," Linnæus follows Ray, as of first rank: "maximus. 1. ELEPHAS. *Raj. quadr.* . . . . . Habitat in Zeylonæ."

disposition facilitating domestication, and by its typical 20 dorsal vertebræ—characters which would now entitle it to distinct subspecific rank from the large, broad-headed, and otherwise different elephant of Bengal (see comparative figures 1171 and 1170). The subspecies *ceylanicus*, moreover (Osborn, 1930), resembles the small, slender-tusked *Elephas indicus* var. Mukna of Falconer and Cautley (1847).

Second.—The characters of the Ceylonese genotypic species *Elephas indicus* (= *E. maximus* Linn.) are, however, confused by the fact that the larger Bengal elephant was imported into Ceylon, and it may have been one of these larger Bengalese types of India imported into Ceylon which Linnæus had in mind in applying his second specific name *Elephas maximus.* On this point Lydekker observed (1916, p. 82):

> The name *Elephas maximus* is typified by a Ceylon elephant, and at first sight it would seem that Ceylon should be taken as the typical locality of the species. But there are two races of elephants in that island; one—probably indigenous—in which the tusks of the males are insignificant, and the other—almost certainly introduced—in which they are large. Now it seems almost certain that the big-tusked race formed the type of Linne's species; and if so, Ceylon will not be the typical locality. Unfortunately, it is uncertain whether the tusker-race was imported from the Indian mainland . . . or from Lower Burma. . . . Under these circumstances the writer [Lydekker] has considered it advisable to take southern India (say Mysore) as the type locality, and to regard the small tusked Ceylon form as a second race.

Third.—From the above historic résumé it appears technically that Linnæus named as the genotypic species the Ceylonese variety *Elephas indicus ceylanicus*; that Linnæus' type specimen, however, was according to Lönnberg (see letter, July 31, 1929, on p. 1310) the fœtus of an African elephant (*Loxodonta africana*); that in the substitution of *Elephas maximus* for *Elephas indicus* he had both the African and the Indian elephant in mind, apparently in the belief that they constituted a single created species. For these reasons it is preferable to retain the name *Elephas indicus.*



Indian Elephant Group

Fig. 1167. The specimens in this group are from the hills in the Province of Mysore, India, about 35 miles south of the city of Mysore. They were shot in the spring of 1923, by Mr. Arthur S. Vernay, who presented them to the American Museum of Natural History. While they are not record specimens (see Fig. 1194, where one of the tallest elephants is given an estimated height of 10 ft. 6 in.), they are very fine examples and form an imposing central group in the Vernay-Faunthorpe Hall.

The male (Amer. Mus. 54453) is at the left; the female (Amer. Mus. 54452) at the right.

Estimated Measurements
(See caption to Fig. 1194)

	Male			Female
Skeletal height at shoulder	2558 mm. or	8 ft.	4¾ in.	
Height in the flesh	2720	8	11	2490 mm. or 8 ft. 2 in.
Scapula	676	2	2⅝	
Humerus	879	2	10⅝	
Ulna	673	2	2½	

1. FALCONER (1868) ON THE SPECIFIC UNITY AND VERTEBRAL FORMULÆ OF THE ASIATIC ELEPHANTS

(Continued from pp. 930, 931 of the present Memoir)

As to specific unity, Falconer ("Palæontological Memoirs," Vol. II, pp. 267–270), after prolonged residence in Ceylon and India and very careful study, erroneously concluded that there were no constant specific differences either in the vertebral formulæ or in the structure of the cranium between the Bengal, or continental Indian elephant, and the insular elephant of Ceylon, as appears in the following summary of his observations and his conclusion *that there is but a single species of Asiatic elephant*:

Sumatran Elephant:	20 dorsals and 20 pairs of ribs (Schlegel)—constant.
Ceylon Elephant: Brought to Paris in 1795	20 dorsals and 20 pairs of ribs (Peter Camper, Cuvier, de Blainville). 4 lumbars; total dorso-lumbars 24.
Indian Elephant [Bengal?]: Schlegel states that "all the Indian [Bengalese] elephants which he had examined had, without exception, only 19 dorsal vertebræ and 19 pairs of ribs."	19 dorsals and 19 pairs of ribs (Schlegel); by no means certain that the number is constantly limited to 19. [See 20 dorsals cited below, 'Duvaucel' and 'Choonee.']
Bengal Elephant: Duvaucel male skeleton in Paris Museum [see de Blainville, 1839–1864, Pl. III—Fig. 1170 of the present Memoir].	20 dorsals. Schlegel meets this exceptional case by the hypothesis that the live animal may have been imported from Ceylon into Bengal.
Bengal Elephant: "Choonee." Imported from Bengal in 1810, on board E. I. C. ship "Astell" by Capt. Hay. College of Surgeons.	20 dorsals and 20 pairs of ribs.

"This case, coupled with the Duvaucel skeleton in the 'Jardin des Plantes,' seems to establish, without searching for others, that the Continental Elephant of Northern India varies in the number of its dorsal vertebræ from 19 to 20, as the African varies from 20 to 21." Footnote: "The ingenious view advanced by Prof. Schlegel regarding the inverse relation between the number of *laminæ* in the molars and the number of dorsal vertebræ in the different species (*supra*, p. 263), does not appear to be tenable against the evidence adduced above, of the numerical variability in the living species."

Bengal Elephant: Brit. Mus. Killed in jungles on banks of Ganges, at no great distance from Meerut, in May, 1833 Ceylon Elephant: College Surgeons 2656.	These two skulls agree in general form and proportions. In the Ceylon and Indian elephants the crania are "so closely similar, that, in a museum, without a record, the mere form will not instruct the observer whence the specimen came—whether continental or insular." [Falconer's statement is not supported by de Blainville's plate showing the Ceylon and Bengal crania in profile, as reproduced in our Fig. 1170.]

"The hypothesis entertained by Professor Schlegel, upon the statement of Diard, that Ceylon Elephants are frequently imported into Bengal is, I am satisfied, untenable. . . . On a review, therefore, of the whole case, the evidence in every aspect appears to fail in showing that the Elephant of Ceylon and Sumatra is of a species distinct from the Continental Indian form. . . . The result of this range of observation, combined with long osteological study, has been to establish the conviction in my mind that there is but a single species of Asiatic Elephant at present known, modified, doubtless, according to his more northern or southern habitat, but not to an extent exceeding that of a slight geographical variety."

In Falconer's opinion the cases above cited establish the fact that *Elephas indicus*, including the continental and insular varieties, varies in the number of dorsal vertebræ from 19 to 20, in contrast to the African elephant which varies from 20 to 21.

Osborn, 1929: From the above detailed observations of Falconer, together with those cited from Falconer on pp. 930, 931 of Chapter XV of the present Memoir, it appears probable that: (1) In the insular Ceylon elephant, *Elephas indicus ceylanicus* de Blain., there is a constant number of 20 dorsal vertebræ and 20 pairs of ribs together with certain constant differences in the cranium, tusks, etc., clearly establishing the subspecies; (2) in the continental form the vertebral formula is not constant, 19 dorsals and 19 pairs of ribs are recorded in certain skeletons of Bengal, while 20 dorsals and 20 pairs of ribs are recorded in other cases. (3) This would indicate that on the continent there are two hereditary blood strains, one characterized by 19 dorsals, the other by 20, possibly arising from the race indigenous to Bengal mingled with the race indigenous to Ceylon. (4) It would be interesting to ascertain whether there is a correlation between these two vertebral strains and the two cranial strains respectively known as 'Mukna' and 'Dauntela.' (5) The case may be parallel with that seen in the Equidæ, namely: (a) Pure Arab strain of horses (*Equus caballus africanus*), in which there are 23 dorso-lumbar vertebræ, (b) the pure northern strain (*Equus caballus nordicus*), in which there are 24 dorso-lumbar vertebræ; there are 5 lumbar vertebræ in the Arab strain and 6 in the Nordic strain, the rib-bearing dorsals being 18 in each subspecies.

2. CORSE, DE BLAINVILLE, AND FALCONER ON CHARACTERS OF THE GEOGRAPHIC VARIETIES

(Continued more in detail on pages 1325–1333 of the present chapter)

It appears that the subspecific forms of *Elephas indicus* are less numerous and somewhat less diverse than those of *Loxodonta africana* described above in Chapter XIX. The obvious explanation is that there is far less physiographic variation in the range of the Indian as compared with the African elephant.

The geographic varieties or subspecies of the Indian elephant which have been successively named are:

In 1841: *Elephas indicus Isodactylus* Hodgson, of Nepal, Tarai, N. India.
Elephas indicus Heterodactylus Hodgson, of Nepal, Tarai, N. India.

While Hodgson did not name the above subspecies until 1841, he observed as early as 1832 the differences in the Indian elephant inhabiting the Ceylon and Bengal regions:

> (Hodgson, 1832, pp. 344, 345): "The elephant and rhinoceros abound in the forest and hills of the lower region of Nepal, where they breed, and have their fixed abode; and whence, in the season of the rains, they constantly issue into the cultivated parts of the Taráï to feed upon the rice crops. Both these genera are entirely unknown to the central and northern regions. The elephant is that so well known as the Indian variety, and as such is contra-distinguished from the African variety. But it may be questioned, if there be not two distinct varieties or species in India alone, viz. the Ceylonese, and that of the saul forest [Bengal]. The former differs materially from the latter by having a smaller lighter head, which is carried more elevated, and by higher forequarters. It is also said to be larger, and of a more generous and bold temper. The difference of size, however, is certainly a mistake. I cannot speak to the point of temper."

In 1845: *Elephas indicus ceylanicus* de Blainville, the elephant of the island of Ceylon.
Elephas indicus bengalensis de Blainville, the elephant of Bengal, continental.

De Blainville figures in Pl. III [Fig. 1170 of the present Memoir] of his "Ostéographie" of 1839–1864 the two subspecies from Ceylon and Bengal respectively, describing them briefly in the legend as follows:

E. Indicus Ceylanicus, à grandes défenses. De profil, avec la mandibule en place; sexe inconnu.
E. Indicus Bengalensis, à grandes défenses. De profil, avec la mandibule en place. D'un individu mâle dont le squelette, préparé par M. Duvaucel, a été envoyé par lui au Muséum.

Geographic distinctions between the two continental races or varieties in India, known as the 'Dauntela' and 'Mukna' (as fully cited below) had been observed and very clearly stated by Corse as early as 1799 and accepted and amplified by Geoffroy St. Hilaire and Frédéric Cuvier in 1825 (also cited below). Falconer states (1868, Vol. II, p. 257):

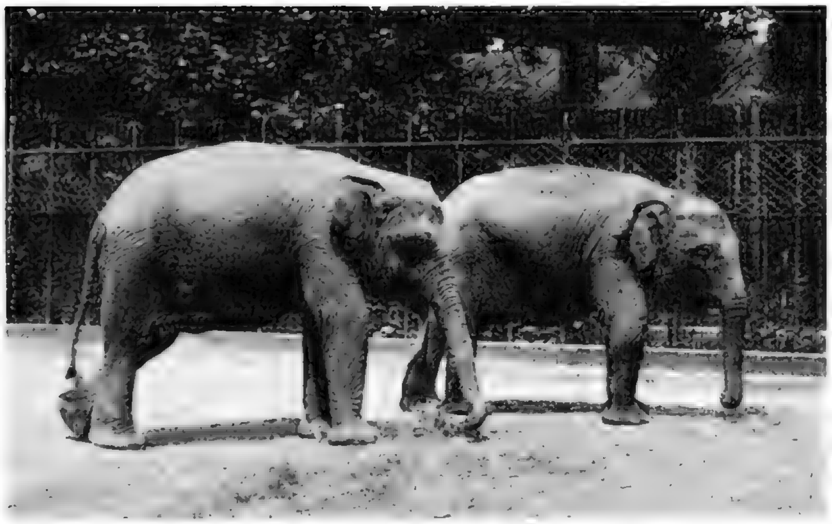
> But even in the Sàl forests of North Western India, at the extreme northern limit of the species at the present day, the difference of slender-built and squat-built Elephants is well known, being expressed by Corse, for the Bengal variety, under the designation of '*mirghi*,' or Cervine [*merghee*, slender built, of Corse] for the former, and '*Koomarea*' [*koomareah*, deep bodied, squat built, of Corse] for the latter, or when the characters are combined '*Sunkareah*.'

Falconer and Cautley accordingly gave geographic varietal names to these two very distinct continental forms of the Indian elephant, known among the natives as 'Dauntela' and 'Mukna,' and published in his plates the following designations of these varieties:

In 1847: *Elephas indicus* (Dauntela var.), the Dauntela variety [=deep bodied, *koomareah* of Corse].
Elephas indicus (Mukna var.), the Mukna variety [=slender built, *merghee* of Corse].

Temminck designated the Sumatran elephant under the following specific name and held that by its vertebral and other characters it was thoroughly entitled to specific distinction from the Indian elephant, a point disputed by Falconer in 1868:

In 1847: *Elephas sumatranus*, the elephant of Sumatra.



ELEPHAS INDICUS SUMATRANUS, THE SUMATRAN SUBSPECIES

Fig. 1168. Pair of young elephants from Sumatra (*Elephas sumatranus*) captive (1921) in the Zoological Park of Washington. Photograph kindly presented by Secretary Charles D. Walcott.

(Broili, letter, August 12, 1929): In the State Zoological Museum of Munich there is an adult mounted specimen of *Elephas sumatranus* Temminck, the skeleton of which is not mounted but the skull is on exhibition. Head Preparator Kusthardt of the zoological collection writes (August 10, 1929) that the adult mounted specimen came from Sumatra in 1907; that the young mounted specimen (six months of age) exhibits dark brown hair and red woolly hair.

Fig. 1169. The Sumatran elephant, apparently a female, living in the Amsterdam Zoological Gardens, August, 1913. After a photograph kindly presented by Mr. Graham Renshaw, inscribed "*Elephas indicus sumatrensis*, Amsterdam Zoological Gardens, August, 1913."

(Letter of transmittal, November 21, 1923): "The Sumatran elephant was remarkable for the tessellation of the hide; as you see it was not a large animal . . . Buttikofer in the Guide to the Rotterdam Zoo figured another Sumatran elephant."

3. LIVING SPECIFIC OR SUBSPECIFIC FORMS, CONTINENTAL AND INSULAR

(Continued more in detail on pages 1323 to 1333 of the present chapter).

Falconer (1863, p. 81), in addition to his analysis of the vertebral characters, discusses very fully the unity or plurality of species among the existing Asiatic elephants, namely, types from Ceylon, Nepal, Bengal, and Sumatra, and decides in favor of the unity of the species *Elephas indicus*. He points out (1868, Vol. II, p. 258) the geographic variations which distinguish not only the Ceylonese and the Bengalese elephants, but the effects of climate and breeding in different regions, namely, Assam, Silhet, Chittagong, Tipperah, or Cuttack. He concludes that the specific distinctions of Temminck and Schlegel founded upon external characters, as in the case of *Elephas sumatranus*, completely fail. He also believes that *E. sumatranus* is barely distinguished by the characters of the ridge laminæ. He points out (p. 260) that while the typical ridge formula of *E. indicus* is:

$$\mathrm{Dp}\ 2\tfrac{4}{4}\quad \mathrm{Dp}\ 3\tfrac{8}{8}\quad \mathrm{Dp}\ 4\tfrac{12}{12}\quad \mathrm{M}\ 1\tfrac{12}{12}\quad \mathrm{M}\ 2\tfrac{16}{16}\quad \mathrm{M}\ 3\tfrac{20\text{-}24}{20\text{-}24}$$

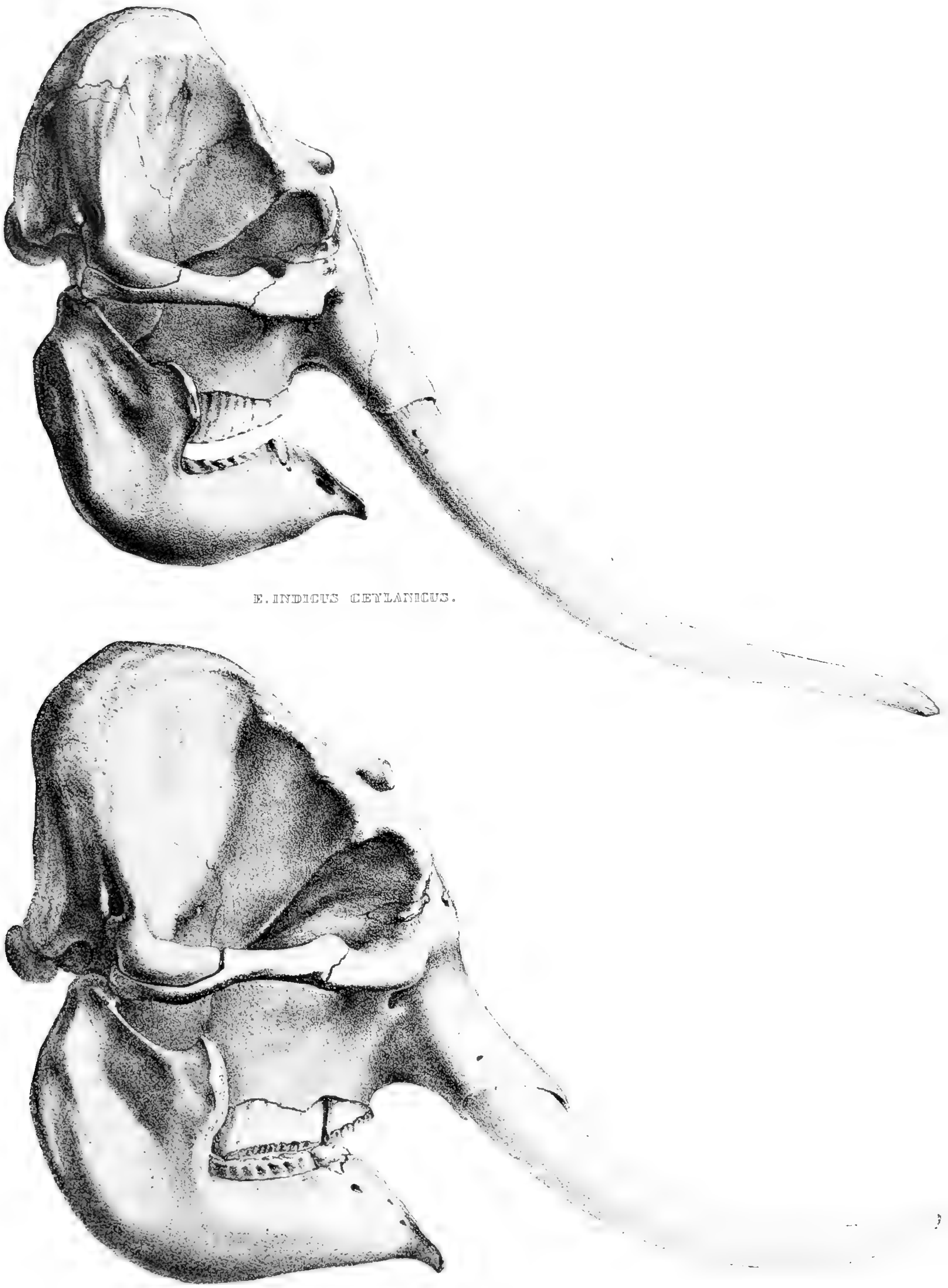
the last true molar, M_3, never shows less than 20 ridge-plates, commonly about 22 ridge-plates, but sometimes in the lower jaw attaining as many as 27 ridge-plates. He remarks (p. 269) "the evidence in every aspect appears to fail in showing that the Elephant of Ceylon [*E. indicus ceylanicus*] and of Sumatra [*E. sumatranus*] is of a species distinct from the Continental Indian form [*E. indicus*]. Again (p. 270) he observes: "The result of this range of observation, combined with long osteological study, has been to establish the conviction in my mind that there is but a single species of Asiatic Elephant at present known, modified, doubtless, according to his more northern or southern habitat, but not to an extent exceeding that of a slight geographical variety." He admits that the Ceylon elephants are occasionally imported into Bengal but does not admit, as claimed by Schlegel, that this is an explanation of the variation in the vertebral and rib formulæ of the Indian elephants. Falconer (1863), while inclined to accept Darwin's theory of the evolution of species, does not recognize the very great importance of geographic isolation and of insulation in causing real geographic variation and subspecific and varietal evolution both in external and internal characters. He is inclined to maintain the Linnæan idea of species and to oppose the more modern idea of geographic subspecies and geologic ascending mutations.

Osborn believes that the wide variations in cranial and vertebral characters as well as in dental and dermal characters and in the shape of the external ear support the subdivision of *Elephas indicus* into at least four out of the large number (12) of geographic varieties or subspecific forms successively named, as follows:

COLLECTIVE SPECIES *ELEPHAS INDICUS* LINNÆUS, 1754

Synonyms:
- *Elephas maximus* Linnæus, 1758; *Elephas asiaticus* Blumenbach, 1797; *Elephantus indicus* (Cuvier), 1801.

Varieties and subspecies:
- *Elephas indicus Isodactylus* Hodgson, 1841 (named, without definition). Nepal, Tarai, N. India.
- *Elephas indicus Heterodactylus* Hodgson, 1841 (named, without definition). Nepal, Tarai, N. India.
- *Elephas indicus ceylanicus* de Blainville, 1845 (figure and plate description), the Ceylonese variety.
- *Elephas indicus bengalensis* de Blainville, 1845 (figure and plate description), the Bengalese variety.
- *Elephas indicus* var. Dauntela Falc. and Caut., 1847 (figure and plate description, without subspecific name). Compare *Elephas indicus bengalensis* de Blainville.
- *Elephas indicus* var. Mukna Falc. and Caut., 1847 (figure and plate description, without subspecific name). Compare *Elephas indicus ceylanicus* de Blainville.
- *Elephas sumatranus* Temminck, 1847. The Sumatran variety.
- *Elephas maximus zeylanicus* (Lydekker), 1907, 1916. Identical with *Elephas indicus ceylanicus* de Blainville, 1845.
- *Elephas maximus maximus* (Lydekker), 1916. Compare *Elephas indicus bengalensis* de Blainville, 1845.
- *Elephas maximus sumatranus* (Lydekker), 1900, 1916. Identical with *Elephas indicus sumatranus* Temminck.
- *Elephas maximus hirsutus* Lydekker, 1914, 1916 (= *Elephas indicus hirsutus*). Malay variety.
- *Elephas indicus Buski* Matsumoto, 1927 (= ?*Palæoloxodon buski*).



De Blainville's Types of Male Elephas indicus ceylanicus and E. indicus bengalensis

Fig. 1170. The narrower-skulled, slender-tusked Ceylon [cf. Mukna var.] and the broader-skulled, large-tusked Bengal [cf. Dauntela var.] races of the Indian elephant. After de Blainville, 1839-1864 [1845], Pl. III, one-eighth natural size.

Subspecies *Elephas indicus ceylanicus*. Summit of cranium more pointed (hypsicephalic); orbits relatively closer to condyles (cyrtocephalic). Premaxillary sockets longer; mandible shallower and more slender. The original of this cranium is not in the Muséum National d'Histoire Naturelle, Paris; Doctor Anthony reports (letter, July 16, 1930) that he does not know where this fine cranium is preserved; it is not the same as the female cranium in the Paris Museum shown in figure 1172 of the present Memoir.

Subspecies *Elephas indicus bengalensis*. Occipitofrontal crest more rounded, less elevated; condyles to orbits relatively less cyrtocephalic. Premaxillaries shorter, tusks broader; inframaxillaries more powerful. Mus. d'Hist. Nat. A.8016.

The discovery and naming of these geographic varieties and subspecies are recited above and continued more in detail on pages 1327 to 1334 of the present Memoir.

Since all the above varietal and subspecific names were given prior to the adoption of the modern system of nomenclature, we await monographic research and comparison of the living varieties and subspecies of *Elephas;* meanwhile those that seem best entitled to consideration at present are the following:

1845 *Elephas indicus ceylanicus* de Blainville
  Syn.: *Elephas maximus zeylanicus* Lydekker, 1916
  Compare *Elephas indicus* var. Mukna[1] Falc. and Caut., 1847
1845 *Elephas indicus bengalensis* de Blainville
  Syn.: *Elephas maximus maximus* Lydekker, 1916
  Compare *Elephas indicus* var. Dauntela[1] Falc. and Caut., 1847
1847 *Elephas* [*indicus*] *sumatranus* Temminck
  Syn.: *Elephas maximus sumatranus* Lydekker, 1916
1916 *Elephas maximus hirsutus* Lydekker [= *E. indicus hirsutus*][2]

XXIII. A. E. INDICUS.(DAUNTELA var)

XXIII B E. INDICUS (MUKNA var)

Fig. 1171. The broader, large-tusked Dauntela and narrower, small-tusked Mukna varieties of *Elephas indicus.* After Falconer and Cautley, 1846 [1847], Pl. XLII, figs. XXIII.A (Dauntela) and XXIII.B (Mukna), one-sixteenth natural size. Falconer's distinctions between the Dauntela and Mukna varieties are still more clearly shown in figure 1204 below.

Dauntela var. Cranium relatively broader (brachycephalic), and less elevated. Premaxillaries shorter, with deep median excavation, highly characteristic of the Elephantinæ. Compare *Hypselephas hysudricus.*

Mukna var. Cranium relatively narrower in proportion to its height; occiput more elevated, anterior nares narrower. Premaxillaries more elongate; tusks less divergent.

Fig. 1172. Elephas indicus bengalensis Type and E. indicus ceylanicus Referred. Paris Museum

After special photographs kindly taken under the direction of Dr. R. Anthony

(Left) Full facial view of the cranium of *Elephas indicus bengalensis* (Mus. d'Hist. Nat. A.8016) described by Dr. R. Anthony (Paris, letter, July 16, 1930) as follows: Cranium of a male Bengal elephant, same as that figured in profile by de Blainville in his "Ostéographie," 1839–1864, Pl. III [Fig. 1170 of the present Memoir]. Found along the Ganges River by Duvaucel in 1824. In this cranium the left intermaxillary is broken away and missing. The measurement h to h' is 925 mm. or 3 ft. $\frac{3}{8}$ in. Reproduced one-sixteenth natural size.

(Right) Full facial view of the cranium of *Elephas indicus ceylanicus* (Mus. d'Hist. Nat. A.8014). Of this specimen Doctor Anthony writes (Paris, July 16, 1930): A female born in Ceylon, brought from Holland, lived in the Jardin des Plantes 1797–1816; dissected by Cuvier and Rousseau; figured by de Blainville in his "Ostéographie," 1839–1864, Pls. I and II. Total facial height of cranium h to h^1 975 mm. or 3 ft. $2\frac{3}{8}$ in. Reproduced one-sixteenth natural size.

The resemblance of *Elephas indicus ceylanicus* de Blain. to the *E. indicus* var. Mukna Falc. and Caut. is afforded by the drawings of the cranium (side view) by de Blainville and Falconer and Cautley figured fully below. A fine front view of the cranium of *bengalensis* is compared with the front aspect of the cranium of *ceylanicus* (Fig. 1172), as described by Doctor Anthony in the legend above.

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[1] [Referring to the use of the terms "mukna" and "dauntelah," Mr. Dunbar Brander commented (November, 1930) that he did not like a classification which used these two native terms, since a tuskless elephant (mukna) was apt to appear in any region and the term had no diagnostic value for any character other than tusklessness.—Editor.]

[2] [See footnote under description of *hirsutus* on page 1332 below.—Editor.]

The resemblance of the *Elephas indicus bengalensis* de Blain. to the *E. indicus* var. Dauntela Falc. and Caut. is also supported by a comparison of the crania and figures (lateral view). Further comparison should be made of the front views of the crania in these two subspecies and varieties.

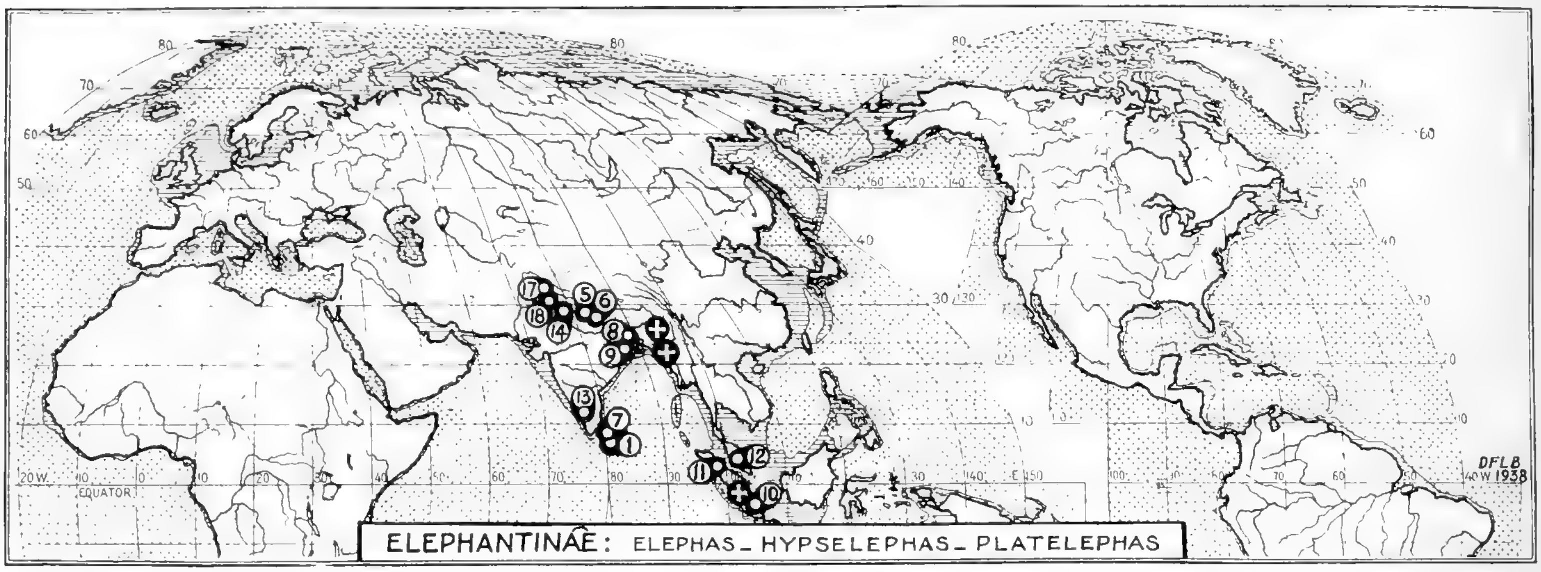

Fig. 1173. Geographic distribution of the principal species and subspecies (living and extinct) of *Elephas*, also of *Hypselephas* and *Platelephas*, according to the numbers given in the list on the opposite page. The white dots within the black areas represent the approximate localities where the types were discovered; these dots each carry a number in a circle, representing the chronologic sequence of type description. The + locates some of the principal referred specimens.

4. FOSSIL FORMS MORE OR LESS CLOSELY RELATED TO ELEPHAS INDICUS

It is remarkable that no fossil Pliocene ancestors of the recent Indian elephant have as yet been discovered. While the cotypes of *Elephas hysudricus*, attributed by Pilgrim to the Boulder Conglomerate zone, are in part recorded as found near Moginand, Simla Hills (Fig. 1196), *none* of the specimens personally collected by Barnum Brown in 1922 was actually found in the Boulder Conglomerate zone; they all appear as if washed or eroded out of this zone with more or less adherent gravel or concretionary material; they were found in hollows or ravines cut into the underlying Pinjor horizon.

1846 [1845]. *Elephas hysudricus* Falconer and Cautley, of the Lower Pleistocene, found 'below the conglomerates' of India, shows few resemblances in the cranium to the *E. indicus* (Dauntela var.) of Falconer and Cautley, and no very marked resemblances in the grinding teeth; this species appears to be unique.

1908. *Elephas hysudrindicus.* Dubois described this species as theoretically intermediate between *Elephas hysudricus* and *E. indicus*, but Stremme rightly regards this animal as more nearly related to '*E. namadicus.*' Osborn treats this animal (Chap XIX) as belonging to *Palæoloxodon*, namely, *Palæoloxodon hysudrindicus.*

1927. *Elephas indicus Buski.* Matsumoto, having become convinced of the occurrence in Japan of the true Asiatic elephant in the fossil state (first suggested by Busk in 1868), described a first superior molar from the Ninohe District as the type of this subspecies. Osborn regards this tooth as referable to *Palæoloxodon.*

1929. *Elephas platycephalus.* Osborn in the present Memoir redescribes this species from the Upper Pliocene or Lower Pleistocene of India, recorded by Barnum Brown as from 'below the conglomerates,' a level higher than that in which *Archidiskodon planifrons* occurs and lower than that in which *E.* (*Hypselephas*) occurs. As shown in figure 1174, this is a very ancient and primitive animal. It is now made the genotype of *Platelephas*.

1929. *Elephas platycephalus angustidens.* Based upon a single second superior molar, r.M^2, originally mistaken by Osborn for a third inferior molar, which now proves to belong to *Elephas* [=*Hypselephas*] *hysudricus*.

5. NAMES OF SPECIES AND SUBSPECIES OF THE SUBFAMILY ELEPHANTINÆ IN ORDER OF DESCRIPTION

See Figure 1173

A summary of the names applied to the above living and fossil forms actually or apparently related to *Elephas* is as follows:

LIVING SPECIES

Collective Species			Original Name	Specific Reference in Present Memoir	Type Habitat
Species	1.	1754	*Elephas indicus* Linnæus	*Elephas indicus*	Ceylon, India
	1.	1758	*Elephas maximus* Linnæus	*Elephas indicus*	Ceylon, India
	2.	1797	*Elephas asiaticus* Blumenbach	*Elephas indicus*	(?)
	3.	1801	*Elephantus indicus* (Cuvier)	*Elephas indicus*	
	4.	1811	*Elephas gigas* Perry	*Elephas indicus*	
Subspecies	5.	1841	*Elephas indicus Isodactylus* Hodgson	Indeterminate	Nepal, India
	6.	1841	*Elephas indicus Heterodactylus* Hodgson	Indeterminate	Nepal, India
	7.	1845	*Elephas indicus ceylanicus* de Blainville	*Elephas indicus ceylanicus*	Ceylon, India
	8.	1845	*Elephas indicus bengalensis* de Blainville	*Elephas indicus bengalensis*	Bengal, India
	8.	1847	*Elephas indicus* (Dauntela var.) Falconer and Cautley	*Elephas indicus* var. Dauntela	Bengal, India
	9.	1847	*Elephas indicus* (Mukna var.)	*Elephas indicus* var. Mukna	Bengal, India
Species	10.	1847	*Elephas sumatranus* Temminck	*Elephas indicus sumatranus*	Sumatra, Palembang District
Subspecies	11.	1900, 1916	*Elephas maximus sumatranus* (Lydekker)	*Elephas indicus sumatranus*	Sumatra, Deli [Labuan Deli?]
	7.	1907	*Elephas maximus zeylanicus* (Lydekker)	*Elephas indicus ceylanicus*	Ceylon, India
	12.	1914, 1916	*Elephas maximus hirsutus* Lydekker	*Elephas indicus hirsutus*[1]	Malay Peninsula, Negri Sembilan
	13.	1916	*Elephas maximus maximus* (Lydekker)	*Elephas indicus bengalensis*	Mysore,[2] India

EXTINCT SPECIES

Collective Species			Original Name	Specific Reference in Present Memoir	Type Habitat
Species	14.	1845, 1846	*Elephas hysudricus* Falconer and Cautley	*Hypselephas hysudricus*	Upper Siwaliks, India
	15.	1915	*Elephas hysudricus hysudricus* Soergel	[Not determined by the present author]	
	16.	1915	*Elephas hysudricus primitivus* Soergel	[Not determined by the present author]	
		[1927	*Elephas indicus Buski* Matsumoto	?*Palæoloxodon buski* see this chapter, p. 1333]	
	17.	1929	*Elephas platycephalus* Osborn	*Platelephas platycephalus*	Siswan, India
	18.	1929	*Elephas platycephalus angustidens* Osborn	*Hypselephas hysudricus*	Chandigarh, India

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[1] [See footnote on page 1332 below, where reasons are given for regarding this subspecies as of doubtful validity.—Editor.]

[2] [Lydekker states on page 82 of his "Catalogue of the Ungulate Mammals in the British Museum (Natural History)," 1916, that he has chosen Mysore as the typical locality of Linnæus' "*Elephas maximus.*" Professor Osborn has chosen Ceylon, for the reasons stated above.—Editor.]

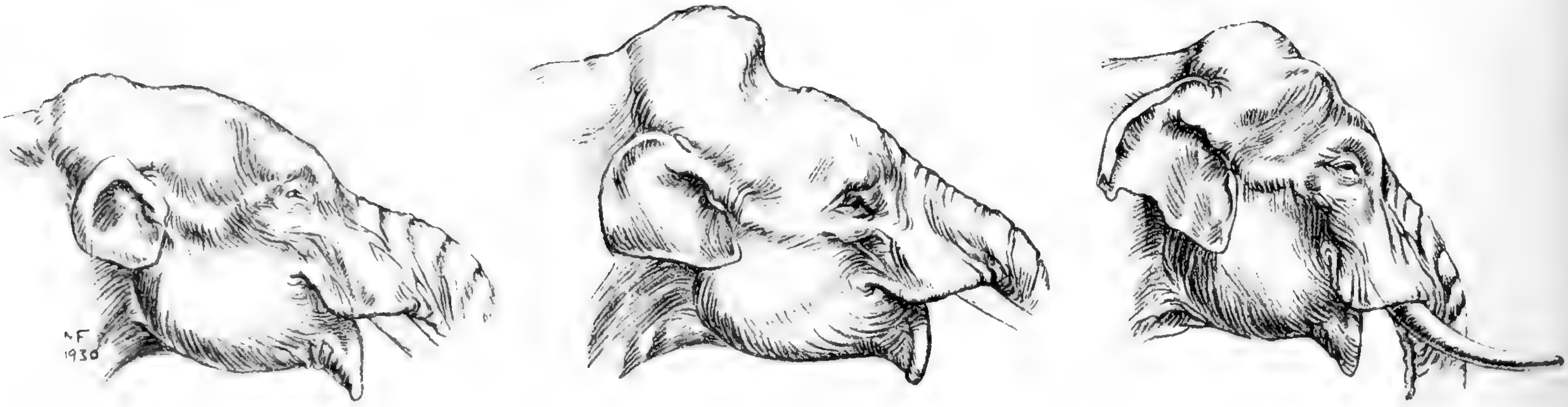

FIG. 1174. RESTORATIONS OF PLATELEPHAS PLATYCEPHALUS, HYPSELEPHAS HYSUDRICUS, AND ELEPHAS INDICUS. APRIL, 1930.
All three heads reduced to a uniform one twenty-fourth scale

(Left) *Platelephas platycephalus* drawn directly on the cranium, slightly crushed downwards; ears of supposed primitive size, occipitofrontal line drawn directly on top of cranium. Observe the eye in normal position.

(Center) *Hypselephas hysudricus* profile drawn directly on Falconer's outline of the cranium (Fig. 1204). Observe the extremely low position of the eye, corresponding with the occipital concavity, namely, quite close to the premaxillary socket. The ear is given a slender elephantine outline, as in *E. indicus*. The small tusks correspond with the relatively small alveoli in this specimen.

(Right) *Elephas indicus*, a middle-aged female. Observe the relatively high position of the eye midway between the lip and the summit of the cranium; also the lack of the occipitofrontal crest and the presence of the prominent occipitofrontal convexity and muscular ridge for the supratemporals.

II. CHARACTERS OF THE SUBFAMILY ELEPHANTINÆ AND INCLUDED GENERA AND SPECIES

SUPERFAMILY: ELEPHANTOIDEA Osborn, 1921
FAMILY: ELEPHANTIDÆ Gray, 1821

SUBFAMILY: **ELEPHANTINÆ** Osborn, 1910

Original reference: "The Age of Mammals in Europe, Asia and North America," Osborn (1910.346, p. 558); also Osborn, 1918.468, p. 135.

Compare: Elephantina Bonaparte, 1838; Elephantini Winge, 1906.

SUBFAMILY CHARACTERS.—(1) Skull brachycephalic, progressive from platycephalic (*Elephas* [*Platelephas*] *platycephalus*) to hypsicephalic (*E. indicus*). (2) Jaws, including rostrum, progressively abbreviating and deepening, completely brevirostral in recent time (*E. indicus*). (3) Premaxillaries and tusk alveoli relatively narrow, in contrast to the broad rostrum of the Loxodontinæ. (4) Upper tusks upturned, out-turned, finally inturned, attaining moderate length, as compared with *Loxodonta*. (5) Grinding teeth progressively hypsodont. Ridge-plates increasingly compressed and enamel finely folded (*E. indicus*). (6) Ridge-plate formula of third molar multiplying from M 3 $^{16\frac{1}{2}}$ (*platycephalus*), to $\frac{18+}{17\text{-}18\text{-}19}$ (*hysudricus*), to $\frac{24}{24\text{-}27}$ (*indicus*). (7) Inferior ridge-plates exceeding superior ridge-plates in number (*E. indicus*), in contrast to the Mammontinæ (*Parelephas*, M 3 $\frac{25\text{-}30}{24\text{-}26}$). (8) Including the progressive *E. indicus*, readily distinguished by its cranial axes and contours from all the known members of the Loxodontinæ (Chap. XIX), and Mammontinæ (Chaps. XVI-XVIII). (9) Provisionally including three extinct specific if not generic phyla, represented by *E.* [*Platelephas*] *platycephalus*, *E.* [*Hypselephas*] *hysudricus*, and *E. indicus*, not constituting a single ascending phylum but probably polyphyletic.

DOUBTFUL RELATIONSHIPS. The above definition of the subfamily Elephantinæ is continued from Chapter II, pp. 11–13 and 16, also from Chapter XV, pp. 913, 915, and 918. It is provisional and heterogeneous, because *Elephas hysudricus* Falc. and Caut. and *E. platycephalus* Osborn are at present known by cranial characters only and appear to represent generic or subgeneric phyla distinct from the true *Elephas*. There are three separate lines of cranial adaptation in the fossil and living species embraced within the subfamily Elephantinæ. This is in contrast to the cranial uniformity which prevails in the Mammontinæ and the clearly defined phylogenetic succession observable in the three included genera (*Archidiskodon*, *Parelephas*, *Mammonteus*). These three generic or subgeneric lines may be compared and distinguished phyletically as follows:

Phylum I	Phylum II	Phylum III
PLATELEPHAS Osborn	HYPSELEPHAS Osborn	ELEPHAS Linnæus
Typified by *Elephas platycephalus*. Upper Pliocene or Lower Pleistocene.	Typified by *Elephas hysudricus* and *E. platycephalus angustidens*. Lower Pleistocene.	Typified by *Elephas indicus*. Extreme Upper Pleistocene and Recent.
Cranium relatively elongate, dolichocephalic, and platycephalic, occipital condyles somewhat above level of grinding surface of molars.	Cranium elevated or hypsicephalic, condyles well raised above grinding surface of molars, occiput elevated with broadly transverse frontal crest, frontals deeply concave.	Cranium bathycephalic, cyrtocepahlic, hypsicephalic, occipitofrontal dome more or less rounded, not acute, with expanding diploë, frontals gently concave.
Premaxillaries greatly elongated in front of molars, somewhat divergent; tusks unknown.	Premaxillaries relatively narrow or laterally compressed, not deeply extended below front of molars; tusks relatively straight, incurved, somewhat divergent at base; rostrum of lower jaw elongate, prominent, ramus shallow.	Premaxillaries relatively narrow, subvertical, borders relatively close to front of molars; tusks relatively straight, incurved, used in feeding and uprooting habits, unlike the adult *Mammonteus*. Jaw with extremely abbreviated rostrum.
Orbits large, elevated, near frontal profile.	Orbits large, depressed, near maxillary rostrum.	Orbits large, elevated.
Grinding teeth relatively low, ridge-plates directly transverse, as in *Elephas*, no rudiment of 'loxodont sinus.' Ridge-plate formula:	Grinding teeth with ridge-plates convexo-concave, reversed above and below, trace of a median 'loxodont sinus,' of less height but otherwise as in *Elephas*. Ridge-plate formula:	Grinding teeth with finely plicated enamel, not rising to the extreme hypsodonty of *Parelephas*, *Archidiskodon*, or *Mammonteus*. Ridge-plates multiplying:
$\mathrm{M}\,3\ ^{16\frac{1}{2}}$	$\mathrm{M}\,3\ \frac{18+}{17-18-19}$	$\mathrm{M}\,3\ \frac{24}{24-27}$
Habits unknown, probably like those of *Elephas indicus*.	Habits unknown, but from the tusks and grinding teeth probably similar to those of *Elephas indicus*.	Known habits chiefly browsing, crushing of coarse leafage and herbage, secondarily grazing.
Very primitive in cranial structure and in the limited number of ridge-plates.	Progressive in cranial structure and in the somewhat larger number of ridge-plates, although the molar crowns are still low.	Highly progressive and distinctive in cranial structure, with maximum number of plicated ridge-plates.

I. As the Pleistocene is now recognized as extending over approximately a million years of geologic time, *Platelephas platycephalus* was nearly contemporary with *Archidiskodon planifrons* and with *Hesperoloxodon antiquus* of far western Europe and was separated by an enormous interval of geologic time from the recent *Elephas indicus*, but despite its very primitive cranial structure it would be rash to disbar it entirely from the ancestry of the modern *E. indicus*.

II. Similarly *Hypselephas hysudricus* of the Lower Pleistocene is perhaps a million years older than *Elephas indicus* but its cranium does not appear to be evolving in the direction of that of *E. indicus*.

III. Therefore the recent species *Elephas indicus* of southeastern Asia is left without a known ancestral form, just as its living contemporary *Loxodonta africana* is left without a known ancestral form.[1] In both cases this ancestral time gap will probably be filled by discoveries in northerly unexplored regions of Eurasia and of Africa respectively.

In view, therefore, of the uncertainty regarding the ancestral relationships of *Platelephas platycephalus* and of *Hypselephas hysudricus* to *Elephas indicus*, we may at present define the genus *Elephas* from the characters preserved in the genotypic species *E. indicus* and in its geographic varieties and subspecies, as follows.

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[1] [See *Loxodonta prima* Dart, 1929, also *L. africana* var. *obliqua* Dart, 1929, Chapter XIX, pp. 1287, 1288 of the present Memoir.—Editor.]

A HERD OF WILD BENGAL ELEPHANTS (ELEPHAS INDICUS BENGALENSIS)

Fig. 1175. A herd of wild elephants in a bamboo jungle of Mysore. Photograph by Mr. Wiehle of Bangalore, originally published in *The Illustrated London News* of January 8, 1910, and reproduced by courtesy of Mr. Bruce S. Ingram, Editor. The title of this remarkable photograph is "Quietly dreaming in the jungle." The giant bull to the left of the center illustrates the extreme prominence of the occipitofrontal convexities.

SUPERFAMILY: ELEPHANTOIDEA Osborn, 1921

FAMILY: ELEPHANTIDÆ Gray, 1821

SUBFAMILY: ELEPHANTINÆ Osborn, 1910

GENUS: **ELEPHAS** Linnæus, 1735-1758

Pleistocene and Recent of Siam and India: Ceylon, Bengal, Burma, and Sumatra.
Syn.: *Euelephas* Falconer (in part), 1857; *Elephantus* Cuvier and E. Geoffroy, 1795; *Polydiskodon* Pohlig (in part), 1888.
Genotypic species: *Elephas indicus* of Ceylon.
Geographic varieties and subspecies: *Elephas indicus ceylanicus, Elephas indicus bengalensis, Elephas indicus sumatranus, Elephas indicus hirsutus.*

GENERIC CHARACTERS.—(Linnæus, 1758, p. 33): "*Maximum quadrupes.* Oculi *parvi.* Dentes Laniarii *superiores exserti* (*Ebur*). Aures *amplissimæ, pendulæ, dentatæ*; *act. angl.* 277. *p.* 1051. Cutis *crassissima, callosa.* Mammæ 2 *juxta pectus.* Ungues in *apicibus loborum pedum.* Genua *flexilia.* Collum *breve.*

Proboscis *longissima, extensilis, acute odorans, loco manus ipsi inserviens*; *ea cibum potumque haurit, hostemque pellit*; *ea præcisa occiditur*; *murem metuit sub somno ob tracheæ insertionem. Retro coit & mingit. Portat domos, rectore collo insidente*; *in bello armatur falcibus*; *vulnusculo inter axin & atlantem furiosus occiditur*; *cæterum prudens, docilis.*

(Osborn, 1924): Genotypic species *Elephas indicus* (=*maximus*). Cranium widely distinct in form from that of *Loxodonta africana*, of *Archidiskodon*, of *Parelephas*, of *Mammonteus*, namely, relatively acrocephalic, hypsicephalic, moderately bathycephalic. Frontals gently concave, occiput decidedly convex (male), fronto-occipital crest uniformly convex, moderately elevated (female), i.e., acrocephalic. Molars of intermediate breadth, absence of 'loxodont sinus' in *Elephas indicus*, faintly indicated in *Hypselephas hysudricus*; moderately compressed enamel ridges of intermediate thickness, extremely crimped or sinuous in *E. indicus*; more ridge-plates in inferior than in superior molars; ridge-plate formula of *E. indicus*, M 3 $\frac{24}{24-27}$, of *H. hysudricus* (?) ref., M 3 $\frac{18+}{17-18-19}$. Dorsal or rib-bearing vertebræ 19–20. Digits of manus with five horny sheaths or nails; digits of pes with either four or five horny sheaths or nails. Digital formula: Manus 5, pes 4–5.

As shown in the cranial and dental sections of the present Memoir, the genus *Elephas* may be clearly defined as readily distinguishable both in cranial and dental characters not only from *Loxodonta* but from *Archidiskodon*, *Parelephas*, and *Mammonteus*.

Ridge-Plate Comparison with Parelephas.—It is a striking fact that Falconer's ridge formula (*Elephas indicus*), namely, M 3 $\frac{24}{24-27}$, assigns a higher number of ridge-plates to the last *inferior* molar than to the last *superior* molar; this reverses the condition observed in *Parelephas progressus* in which the ridge formula is M 3$\frac{25-30}{24-26}$. If this difference proves to be constant, it affords additional means of distinguishing species of *Parelephas* from species of *Elephas*, as follows: In *Parelephas* there are more ridge-plates in the *superior* molars than in the *inferior*, whereas in *Elephas indicus* there are more ridge-plates in the *inferior* molars than in the *superior*.

1. SYSTEMATIC DESCRIPTION OF SPECIES OF ELEPHAS

ELEPHAS INDICUS Linnæus, 1735–1754, Collective Species[1]

Figures 794, 796–800, 802–814, 816, 893, 912, 992, 995, 1042–1044, 1081, 1082, 1084, 1109, 1112, 1120, 1163, 1174, 1176–1178, 1190–1194, 1234, 1243, 1244

Syn: *Elephas maximus* Linn., 1758; *Elephas asiaticus* Blumenbach, 1797; *Elephantus indicus* Cuvier, 1801 (in Cuvier and Lacépède); *Elephas gigas* Perry, 1811; *E.* (*Euelephas*) *indicus* Falconer, 1857.

The history, nomenclature, and general characters of this collective species are fully set forth in the present chapter, pages 1308 to 1321 above.

It is shown that Linnæus (1754, p. 11—see facsimile, p. 1309 above) in naming *Elephas indicus*, while depending upon Ray, Seba, and others, was very indefinite as to the *type locality*, mentioning both the continent of Asia and the island of Ceylon. When he changed the specific name to '*maximus*' (1758, p. 33) he may have had in mind the African elephant, of which he had a fœtal specimen, but he subsequently states "Habitat in Zeylonae." Consequently we are inclined to the technical opinion that Linnæus' *type*, both of his 1754 description of *Elephas indicus* and of his 1758 description of *Elephas maximus*, was the Ceylon animal subsequently named by de Blainville (1845) *Elephas indicus ceylanicus*. If this historic interpretation is correct, *E. indicus ceylanicus* is not only the type of the collective species *Elephas indicus*, but it is genotypic of the genus *Elephas* itself.

The main descriptions, figures, measurements, and characterizations by all other authors have been of the better known continental variety, to which de Blainville (1845) applied the subspecific name *Elephas indicus bengalensis*. It becomes necessary, therefore, to review the observations and history of opinion on the specific forms of the collective species '*Elephas indicus*.'

[Elephas gigas Perry, 1811 (=synonym of E. indicus, fide Colbert).—This species is described (p. Ii) and figured (plate opposite that page) in George Perry's article of 1811 in the "Arcana," a portion of which description is cited herewith: "*Natural Order*—Mammalia. *Species*—Elephas gigas. *Generic Character*—No fore-teeth in either jaw; the tusks of the upper are elongated and projecting, none in the lower; the proboscis or trunk very long and prehensile; the body armed with a very thick skin, covered with a few scattered hairs."

"The Elephant may justly be considered as the largest and strongest animal at present known, and is plentifully found in a wild state in the extensive regions of Africa and Asia."

"There is also found a second and different species, which is said to reside in the kingdom of Thibet, and being much smaller and of an opposite form, is to be considered as a separate animal from the above, under the title or Name of the Elephas socotrus [indeterminable from the description]." Neither species determined by the present author.—Editor.]

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[1] Ray, in his description of *Elephas* (1693, pp. 131, 132), speaks of the elephant of Sumatra in reference to its weight, and to the skeleton in Florence in reference to the number of ribs, characters of the tusks, etc.

Seba (1734, p. 175, Pl. CXI) gives a very full description of the Foetus Elephantis Africani ineditus, which Lönnberg refers to as the type. In this early stage of zoology no one dreamed of selecting any particular specimen and designating it as the *type*.

FALCONER DESCRIBES THE CONTINENTAL BREEDS OF BENGAL AND ASSAM

The characters of these continental breeds of Indian elephant were more profoundly and thoroughly studied by Falconer than by any previous or subsequent writer. Falconer's discussion of the vertebral formulæ as well as of the varietal and subspecific characters is fully given above in the present chapter; he was not inclined to admit the constancy of the subspecific characters claimed by Schlegel, Temminck, and other observers. Consequently the following citations from Falconer refer to *Elephas indicus* as a 'Linnæan collective species.'

FALCONER (1868), DENTAL CHARACTERS.—In comparison with the grinding teeth of *Elephas* [*Hypselephas*] *hysudricus* (Figs. 1197, 1198, of this Memoir), Falconer's description of the superior grinding teeth of *Elephas indicus* is as follows (Falconer, 1868, I, p. 78): "The existing Asiatic elephant, *E. Indicus*, furnishes the next modification represented in this plate. Fig. 2, Pl. v. (or fig. 2*a*, Pl. I., F.A.S.), shows a section of the penultimate upper molar of this species. The gradual attenuation of the plates, successively exhibited from *E. insignis* to *E. Hysudricus*, is here carried to excess, eighteen of these divisions being comprised within the space occupied by about nine in the equivalent tooth of the African species. They are produced vertically in the same proportion, the height of the middle plate being about three-fourths of the entire length of the tooth; they, in fact, represent parallel perpendicular lamellæ, of nearly uniform thickness from the base to the apex, interstratified with layers of cement of nearly the same thickness. The layer of enamel is attenuated into a thin transversely undulated brittle plate, the surface of which is deeply wrinkled with striæ, for the firm cohesion of the cement. The general character of the section is a pectinated arrangement of the lobes like the teeth of a comb, which contrasts strongly with the chevron-formed ridges of *E. insignis*, and the cuneiform plates of *E. planifrons*. The mass of ivory at the base of the tooth is much thinner than in the corresponding molar of *E. Hysudricus*, bearing but a very slender proportion to the height of the tooth; and numerous small and distinct fangs are given off from its inferior edge. This tooth had been some time in use, the anterior part of the crown being worn off as far as the ninth plate. The plane of the truncated portion is very oblique, being inclined nearly at a right angle to the coronal surface of the unworn portion. This specimen is 8.2 inches in length."

RIDGE FORMULA OF ELEPHAS INDICUS (FALCONER, 1868).—Falconer appears to have finally based the ridge formula of M_3 on an Indian elephant from Assam (Falconer, 1846, p. 43 [1845, fig. 2*b*], with 27 ridge-plates); it is probable, therefore, that Falconer's observations on the grinding teeth refer chiefly to the northern race, *Elephas indicus bengalensis* (cf. Falconer, "Palæontological Memoirs," Vol. I, p. 422, Pl. I): *Elephas indicus.* Plate I, fig. 2*b*, Indian elephant from Assam. M_3 with 27 ridges, length of crown about 15 in. The final formula of Falconer (1868) is consistent with that of Falconer (1863), namely: *E. indicus* of Assam, $\mathrm{M}\,3\,\frac{}{27}$. Thus Falconer corrected his earliest ridge formula (1857, p. 315) of *Elephas indicus* and substituted (1863, p. 65) the following collective ridge formula of *E.* (*Euelephas*) *indicus*:

$$\mathrm{Dp}\,2\,\tfrac{4}{4}\ \mathrm{Dp}\,3\,\tfrac{8}{8}\ \mathrm{Dp}\,4\,\tfrac{12}{12}\ \mathrm{M}\,1\,\tfrac{12}{12}\ \mathrm{M}\,2\,\tfrac{16}{16}\ \mathrm{M}\,3\,\tfrac{24}{24\text{-}27}$$

Falconer considers and repeatedly states that the ridge formula of *Elephas* [*Mammonteus*] *primigenius* is closely similar to that of his subgeneric group *E.* (*Eueleph.*) *indicus* (cf. the ridge-plate formulæ of the ascending mutations of *M. primigenius* above (p. 1138), namely, $\mathrm{M}\,3\,\frac{20}{20}$ to $\mathrm{M}\,3\,\frac{27}{(?)27}$).

Fig. 1176. (Falconer, 1868, Vol. I, p. 422): "*Elephas indicus.* Vertical section of unusually large specimen of last lower molar of an Indian Elephant from Assam, in India House [London] collection. The entire length of the crown is about fifteen inches, and it includes as many as twenty-seven ridges, of which the anterior thirteen are more or less abraded. The first five or six ridges incline a little forwards, while the posterior ridges incline so much in an opposite direction, that the hindermost are nearly horizontal, producing the flabelliform character that so readily distinguishes in most instances the last from the penultimate lower molar. The same disposition and proportions of the dental substances are observed as in the upper grinder." After Falconer and Cautley, 1846 [1845], Pl. I, fig. 2*b*. One-fourth natural size.

INFERIOR MOLAR, M_3, ASSAM BREED.—(Falconer, 1846, p. 43): "Fig. 2*b* represents the section of a very fine specimen of the last inferior molar of the existing Indian Elephant of Assam, from the collection at the India House. It is an unusually large specimen, showing as many as twenty-seven plates, the anterior twelve of which have been in use. Precisely the same disposition of the dental substances is observed in this case as in the upper grinder, and they are developed in the same relative proportions. The vertical height of the plates is still greater than in the corresponding lower molar of *E. hysudricus.* The upper surface is concave, and the under very convex. The anterior plates are nearly vertical, while the posterior gradually slope backwards till they become almost horizontal in the hindmost portion, with a corresponding gradual diminution in their height. This is a mechanical arrangement arising from the contracted diameter of the posterior part of the dental canal, in which the back part of the tooth is developed, close under the condyle, the plates being disposed so as to occupy the least vertical space. The basal mass of ivory between the plates and the fangs is reduced to a small quantity. This tooth measures 15¼ inches long in a straight line."

RIDGE FORMULÆ OF ASSAM, CEYLON, AND SUMATRAN FORMS

Falconer "Palæontological Memoirs," 1868, Vol. II, pp. 256, 260.

Since the posterior ridge-plates of M^3, M_3 develop very late in life, the ridge-plate formula is difficult to determine. Schlegel, Temminck, and other authorities contend that the very high ridge-plate formula of the Assam breed, $M\,3\,\frac{24}{24-27}$, is not obtained in the insular breeds of Ceylon and Sumatra, to which they assign not only a lesser ridge-plate formula but a greater thickness of the enamel ridge-plates, as quoted by Falconer (1868, II, pp. 256, 260):

"(B.) *Molar teeth.*—Ribbons (discs of wear) in form like those of the Indian species, *i.e.* the enamel-plates highly crimped, parallel, and free from the rhomb-shaped expansion of the African Elephant; but the ribbons wider (in the direction of the long axis), and *consequently less numerous than in the Indian species*; the difference being in the ratio of 3 or 4:1 in the Sumatran, and 4 or 6:1 in the Continental Indian form (Schlegel in Temminck). Ribbons of enamel nearly [or] quite as wide as in the African Elephant. (C. L. Buonaparte.)"

(Schlegel in Falconer, *op. cit.*, p. 260): " 'The laminæ of the teeth afford another distinction which however is less apparent to the eye than that taken from the number of vertebræ. These laminæ, or bands, in *E. Sumatranus*, are wider (or if one may so say, broader in the direction of the long axis of the teeth) than in *E. Indicus.*' "

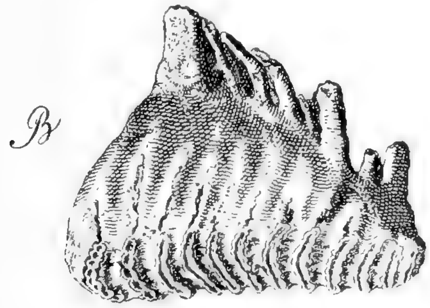


Fig. 1177. Type r.M¹ of *Elephas asiaticus* Blumenbach, 1797 (Blumenbach 1797.2, No. 19): "B. vom *Asiatischen* Elephanten, . . . Nur bilden jene beym *Elephas asiaticus* geschlängelte an beiden Enden paarweis zusammenlaufende Linien; hingegen beym *africanus* rautenförmige Leisten. Diese Zähne der beiderlei Elephanten sind nach Originalen im hiesigen academischen Museum gezeichnet." Inverted to show natural position of molar.

Blumenbach's type figure is apparently a first superior molar of the right side, r.M¹, outer side convex, inner side plane or slightly concave, exhibiting twelve ridge-plates, as in Falconer's typical ridge-plate formula of *Elephas indicus*.

Falconer, after the examination of a very large quantity of materials in India and Europe, concludes that the ridge formula runs thus (*op. cit.*, p. 260):

$$\underset{\text{Milk molars.}}{\frac{4,\ 8,\ 12}{4,\ 8,\ 12}} \quad : \quad \underset{\text{True molars.}}{\frac{12,\ 16,\ 20\text{-}24}{12,\ 16,\ 20\text{-}24\ [\text{-}27]}}$$

This he regards as typical, stating (cf. p. 261) that neither Schlegel nor any of the other advocates of distinct specific ridge formulæ have proved that either the Ceylon or the Sumatran species shows a lesser number than $M\,2\,\frac{16}{16}$. He concludes: "These instances prove, so far as they go, that the ridge-formula is the same in the Ceylon and Sumatran form as in the Indian." He also contests the alleged differences in the width of the enamel bands and shape of the discs, stating as regards *Elephas sumatranus* that the supposed width of the enamel bands is due to the obliquity of the section (cf. p. 262).

Falconer's entire discussion (*op. cit.*, pp. 256–270) of the unity or plurality of species confirms his conviction that there is but a single species of Asiatic elephant, modified only to the extent of a slight geographical variety.

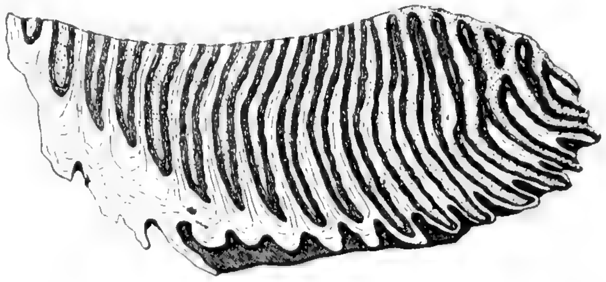


FIG. 238. — Coupe d'une dernière molaire inférieure d'*Elephas indicus*, au 1/4 de grandeur.

Fig. 1178. Section of a partly worn third inferior molar of *Elephas indicus*. After Gaudry, 1878, p. 179, fig. 238, one-fourth natural size.

Observe that six or more anterior ridge-plates have been worn off, the total number being twenty-four or more.

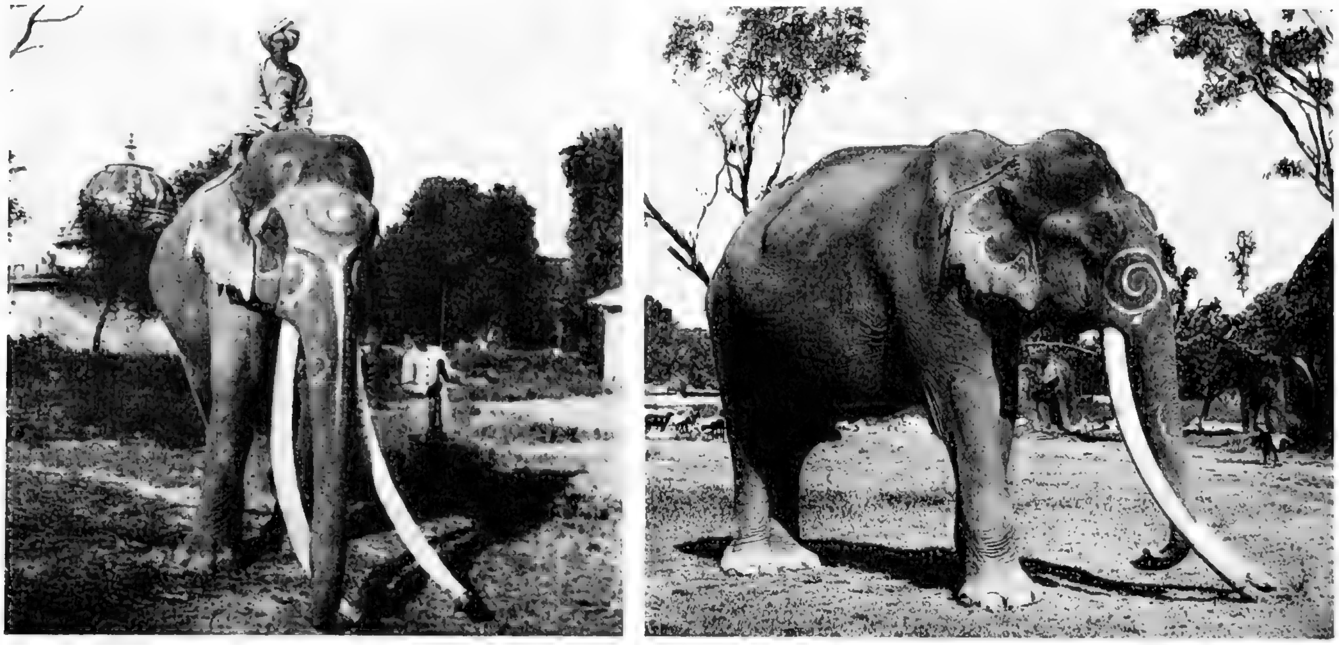
DISTINCTIONS BETWEEN THE VARIETIES OF THE INDIAN ELEPHANT, CORSE (1799), GEOFFROY SAINT-HILAIRE AND FRÉDÉRIC CUVIER (1825), TEMMINCK (1847), DE BLAINVILLE (1839-1864), AND FALCONER (1867, 1868)

(Continued from p. 1313 of the present chapter)

It is not clear from the following descriptions by Corse (1799) and by Geoffroy and Cuvier (1825) in what part of India these two varieties occur; probably they refer to the continental varieties of Bengal.

The derivation of the words mooknah, dauntelah, and pullung daunt, as given by Corse, is as follows: "Probably from *mookh*, the mouth or face . . . *Dauntelah* signifies toothy; having large or fine teeth. . . *Pullung* signifies a bed or cot, and *daunt*, teeth; and, from the tusks projecting so regularly, and being a little curved and elevated at the extremities, the natives suppose a man might lie on them at his ease, as on a bed [i.e., Pullung]."

(Corse, 1799, p. 208): "After premising these general observations, I may here observe, that elephants have two tusks, in the upper jaw only; but those in some of the females are so small as not to appear beyond the lip, whilst in others they are almost as large as in one variety of the male, named *mooknah*. . . . The largest tusks, from which the best ivory is supplied, are taken from that species of male named *dauntelah*, . . . in consequence of his large tusks, and whose countenance, from this circumstance, is the most opposite, in appearance, to that of the *mooknah*; which, as I have just observed, is hardly to be distinguished, by his head,



Elephas indicus bengalensis

Fig. 1179. A famous individual known as the 'giant tusker of Udiapur.' His tusks grew to such a length that he was unable to lie down and they were shortened at the extremities and encased in metal. After photograph by F. D. Fayrer, originally published in *Asia Magazine*, Vol. 29, June, 1929. Reproduced by courtesy of "Mondiale" through *Asia Magazine*. Scale approximately one-fiftieth natural size.

from a female elephant. Though there is a material difference in the appearance of a *mooknah* and a *dauntelah*, as well as in the value of the tusks, yet, if they are of the same cast, (*zat*), size, and disposition, and perfect, that is, free from any defect or blemish, there is scarcely any difference in their price. . . . There must be five nails on each of his fore feet, and four on each of the hind ones, making eighteen in all; his head well set on, and carried rather high. The arch or curve of his back rising gradually from the shoulder to the middle, and thence descending to the insertion of the tail; and all his joints firm and strong. There are several other points, of less consequence, which are taken notice of by the natives as well as Europeans. The *dauntelah* is generally more daring, and less manageable, than the *mooknah*; for this reason, until the temper and disposition of the two species are ascertained, Europeans will prefer the *mooknah*; but the natives, who are fond of show, generally take their chance, and prefer the *dauntelah*; which, when known to be of a mild and gentle disposition, will always be preferred, both by Europeans and natives. The varieties between the *mooknah* and *dauntelah* are considerable, and for these there are appropriate names, according as the form of the tusks varies from the projecting horizontal, but rather elevated, curve of the *pullung daunt* . . . of the perfect *dauntelah*, to the nearly straight tusks of the *mooknah*, which point directly downwards."

(Geoffroy Saint-Hilaire and F. Cuvier, 1825, p. 7, Éléphant d'Asie): "Nous avons déjà vu que les femelles des Indes n'ont jamais que de très-courtes défenses: il y a des mâles qui n'en ont pas de plus longues, sans qu'on en sache la raison. On les appelle *Mookna*. Ceux qui les ont longues se nomment *Dauntelah*, du mot *daunt* qui est le même que notre mot *dent*. Cette différence n'en apporte pas dans le prix. Lorsqu'on ne connaît pas le caractère d'un Éléphant, les Européens aiment mieux l'acheter sans grandes défenses, parce qu'il aura moins de moyens de nuire s'il se trouve méchant: mais les Indiens préfèrent assez les individus à longues défenses, pour s'exposer à tous les risques. Lorsque le bon naturel de l'animal est connu, les deux nations l'aiment mieux avec de grandes défenses. Il y a une infinité de variétés parmi les *Dauntelahs*, par rapport à la direction et à la courbure de leurs défenses. Les plus estimés sont ceux ou elles approchent le plus de la direction horizontale. Les princes indiens ont aussi un respect superstitieux pour les *Dauntelahs* qui n'ont qu'une défense, comme cela arrive quelquefois."

Osborn, 1930: From the facts and comparisons cited in the early part of the present chapter and given more in detail above, it appears probable that the continental Indian varieties, as observed by Corse, Falconer, Geoffroy, and others, represent the descendants of two wild indigenous races or subspecies, including the larger, more vigorous northern form (var. Dauntela) and the smaller, more slender southern form (var. Mukna), which, freely interbreeding, according to Corse, have given rise to a large number of intermediate forms. It also appears probable, as suggested by Schlegel, that the smaller, more slender continental form is related to the *Elephas indicus ceylanicus* of de Blainville, while the larger, more vigorous form is related to the *E. indicus bengalensis* of de Blainville. On further research it is possible that these two subspecies may be clearly defined not only by the cranial characters described below, but by the vertebral formulæ enumerated above (p. 1312), as well as by the number of ridge-plates in the grinding teeth. It seems premature, however, to attempt subspecific definition at present.

DE BLAINVILLE (1839-1864) SEPARATES THE BENGAL AND CEYLON BREEDS

From the measurements and characters assigned by Corse, Geoffroy and F. Cuvier, de Blainville, and Falconer, may be deduced the following:

Elephas indicus ceylanicus de Blainville, 1845
Figures 1170–1172, 1180, 1204, 1226

Island of Ceylon and mainland of India.
Compare *Elephas indicus* var. Mukna Falc. and Caut., 1847

VAR. MUKNA FALC. (CF. E. INDICUS CEYLANICUS DE BLAIN.)

See Falconer, "Palæontological Memoirs," 1868, I, p. 477, and 1845, Pls. I-III of de Blainville's "Ostéographie," 1839–1864.

Small slender tusks, nearly straight and pointing obliquely downwards.

Head smaller, hard to be distinguished from female elephant; premaxillary rostrum narrow, more elongate.

Cranial dome more pointed, less brachycephalic, more hypsicephalic (see Figs. 1180, 1204).

Narial openings narrower and smaller (see Fig. 1171).

Five nails on each of the fore feet and four on each of the hind feet.

Of gentle disposition; more manageable.

Elephas indicus bengalensis de Blainville, 1845
Figures 801, 936, 963, 1013, 1170–1172, 1175, 1179, 1180, 1204

Chiefly Bengal, Assam.
Compare *Elephas indicus* var. Dauntela Falc. and Caut., 1847.

VAR. DAUNTELA FALC. (CF. E. INDICUS BENGALENSIS DE BLAIN.)

See Falconer, "Palæontological Memoirs," 1868, I, p. 477, and 1845, Pls. I-III of de Blainville's "Ostéographie," 1839-1864.

Large and fine tusks, projecting horizontal, but rather elevated, curve of the perfect Dauntela, known as the "Pullung daunt."

Head larger, premaxillary rostrum broader, less elongate.

Cranial dome more rounded, more brachycephalic; frontals more convex (see Fig. 1204).

Narial openings broader (see Fig. 1171).

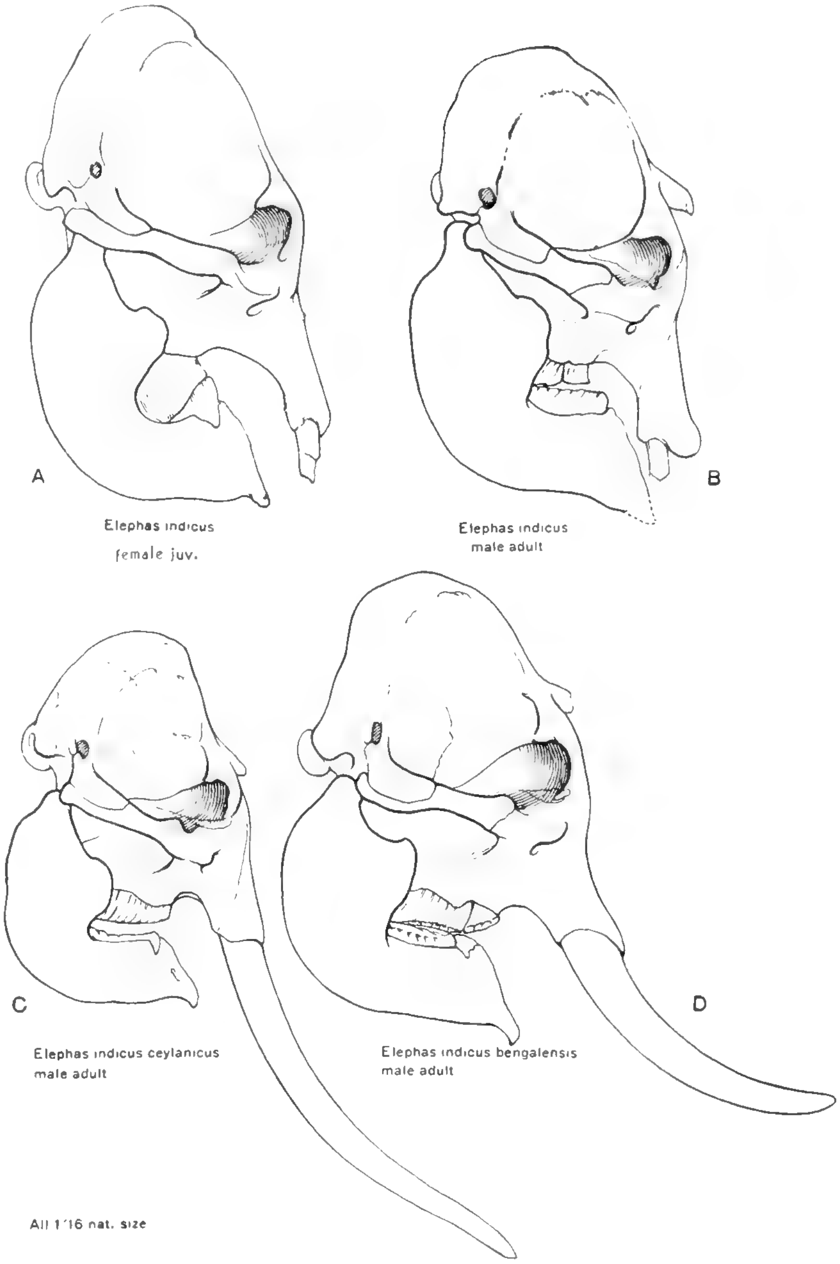
Five nails on each of the fore feet and four on each of the hind feet.

Of more daring disposition; less manageable.

CONTINENTAL AND INSULAR SUBSPECIES (DE BLAINVILLE, 1839–1864).—Preceding Falconer's distinction between the *Elephas indicus* (Mukna var.) and the *E. indicus* (Dauntela var.) were de Blainville's observations and his superb plates of 1845. When we compare these plates and the subspecific descriptions of de Blainville with the descriptions of Corse, Geoffroy Saint-Hilaire and F. Cuvier, and Falconer, we are struck by an obvious *cranial* resemblance, either due to affinity or to analogy, namely:

Elephas indicus ceylanicus de Blainville, 1845, resembles *Elephas indicus* (= Mukna var.) Falc. and Caut., 1847.

Elephas indicus bengalensis de Blainville, 1845, resembles *Elephas indicus* (= Dauntela var.) Falc. and Caut., 1847.



COMPARISON OF ELEPHAS INDICUS CEYLANICUS (A, FEMALE, JUVENILE; C, MALE) WITH ADULT MALES (B, D) OF E. INDICUS BENGALENSIS

Fig. 1180. Male, female, and geographic characters in the skull of *Elephas indicus*. All figures copied, with identifications, from de Blainville's "Ostéographie," 1839–1864, reduced to one-sixteenth natural size. Compare frontal aspect of crania (Fig. 1172).

A, Female of *Elephas indicus* (?) *ceylanicus*, with tusks in place. The frontal curvature and extreme hypsicephaly remind us strongly of the profile of the juvenile *Hypselephas hysudricus* (Fig. 1213).

B, Male of *Elephas indicus* (?)*bengalensis*, with adult tusks in place.

C, Adult male skull of *Elephas indicus ceylanicus*, the geographic type of Ceylon.

D, Adult male skull of *Elephas indicus bengalensis*, the geographic type of the Bengal district.

Observe the marked resemblance of the extremely hypsicephalic and cyrtocephalic cranium (A) to that of the juvenile *Hypselephas hysudricus* cranium (Figs. 1213, 1214), as well as to that of the *Elephas indicus* displayed in figure 797.

De Blainville's Priority.—According to de Blainville's figures of the Ceylon and Bengal crania, which represent individuals of approximately the same age, de Blainville (1845) separated these two crania subspecifically as types of two subspecies, namely: *Elephas indicus ceylanicus* and *Elephas indicus bengalensis*; this subspecific separation is fully justified by the more or less hypsicephalic characters of the skull, and differences in the jaws and tusks; all these characters are widely different in these two geographic subspecies. As indicated above, these subspecific characters appear to be the same as those which separate *Elephas indicus* (Dauntela var.) from *Elephas indicus* (Mukna var.) of Falconer. From this comparison, it would appear that Falconer's two varietal names ('Mukna' and 'Dauntela') proposed in 1847 may prove to be synonymous with the two subspecific names of de Blainville proposed in 1845.

Ontogenetic and Sexual Characters.—De Blainville's observations (1839–1864) on the sexual characters of *Elephas indicus* are clearly displayed in figure 1180, copied from his plates. We observe in figure 1180A a female apparently of *Elephas indicus ceylanicus*, with extremely hypsicephalic head; in figure 1180C we observe an adult male of the same subspecies, *E. indicus ceylanicus*. In figure 1180B we observe an adult male, apparently of *Elephas indicus bengalensis*, with its rounded superior occipito-frontal dome; in figure 1180D we observe another adult male of *E. indicus bengalensis*, with the same rounded dome but with more massive cranial proportions.

The crania of these subspecies, both male and female, are distinguished: (1) By numerous differences in the profile both of the cranium and of the jaws; (2) by the abbreviation of the jaw (C), the oldest individual figured; (3) by the uniformly convex fronto-occipital profile (B and D), growth stages of *E. indicus bengalensis*; (4) by the more pointed and hypsicephalic fronto-occipital profile (A and C), growth stages of *E. indicus ceylanicus*.

Falconer's Two Varieties.—It remained for Falconer also to name and distinguish these two continental varieties, signifying that he considered them of permanent varietal or subspecific value, as follows (footnote, Falconer, 1867, p. 57, and 1868, I, p. 477):

"Comparison between *Mukna* and *Dauntela* varieties of *Elephas Indicus.*

	Mukna (big head). Inches	Dauntela. Inches
Extreme length of cranium	40.5	41.5
Width between zygomatics	29.5	29.75
Ditto post-orbitary processes	22.5	24.0
Length from niche of occiput to tips of nasals	22.0	21.0
Greatest width of occiput	31.0	30.5
Width of nasal opening	14.0	15.0
Depth of ditto	5.75	5.75
Width of tusk-sheaths	14.25	17.5
Narrow width of brow	13.5	13.25
Depth of orbit	6.5	6.5
Height from condyles to occiput	22.25	22.0
Across condyles	8.75	8.5
From condyles to tip of tusk-sheath	33.0	35.25
From ditto to anterior margin of molar alveolus	22.5	22.25
From anterior margin occipital hole to posterior border palate	12.0	11.5
Length of palate	8.0	9.5
Depth of head from condyles to frontal surface at middle, opposite nasal opening	23.5	23.5
Height from diastemal surface to bulge of occiput	30.75	31.25
Length of condyloid surface	6.5	6.25
From ear-hole to top of occiput	19.0	19.0
Length of anterior tooth, upper jaw	8.37	dropped out
Width ditto ditto	3.5	
Number of plates, about ten		
Length of anterior tooth, lower jaw	9.	dropped out
Width ditto ditto	3.37	

Falconer also stated in this same footnote that "The plates of teeth in the *Mukna* variety slope greatly backwards and are excessively and finely crimped; those of *Dauntela* are much less crimped."

Osborn, 1930: We observe that Falconer omits the most distinctive *bathycephalic* measurement, namely, (*a*) from the summit of the occiput to the occlusal surface of the superior grinders, as compared with (*b*) occipital condyles to the orbital level of the frontals. These two measurements are shown in figures 805 and 806 and give us what may be called the bathycephalic index of the skull.

Summary of Osborn, 1930: (1) Prior to Falconer's description (1847, 1867), de Blainville in 1845 separated the insular Ceylon animal as a subspecies, *Elephas indicus ceylanicus*, from the mainland Bengal animal, subspecies *Elephas indicus bengalensis*. (2) Falconer (1847) distinguished the two varieties 'Dauntela' and 'Mukna.' (3) Lydekker observes (Ency. Brit. 11th Ed., p. 259) that the insular "Ceylon animal, which is generally tuskless, may be the typical *E. maximus* [of Linnæus], in which case the Indian race will be *E. maximus indicus*." (4) It appears probable that the Ceylon animal (*E. indicus ceylanicus*) with slender tusks was introduced into India by breeders, giving rise by crossing to the two varieties or hybrids designated by Falconer as Dauntela var. and as Mukna var.[1] This theory was suggested by Schlegel, but Falconer (1868), as quoted above, did not admit that the insular Ceylon breed ever exerted any considerable influence on the northern Bengalese breeds, nor did he admit the specific distinction of the Ceylonese or Sumatran elephants. (5) As shown by Osborn in a close comparison of the crania, Falconer's Mukna var. has a cranium closely similar to that of de Blainville's *E. indicus ceylanicus*, while Falconer's Dauntela var. has a cranium more similar to de Blainville's *E. indicus bengalensis*. (6) Another explanation is that the island of Ceylon did not separate from the mainland until recent geologic time and that the *E. indicus ceylanicus* ranged through continental southern India.

This problem of the continental and insular races and subspecies, however, requires further investigation from the original materials.

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[1] [See footnote 1 on page 1317 above.—Editor.]

Elephas indicus sumatranus Temminck, 1847

Figures 1168, 1169, 1181–1185

District of Palembang, Island of Sumatra.

The profound cranial differences which divide the Ceylon and Bengal elephants from each other as well as from the Sumatran elephant in all probability will be found to differentiate the Sumatran and other still undiscovered extinct types. By comparison with the evolution of other Pleistocene ungulates it appears probable that a very long period of time separated these continental and insular subspecies and species from each other, a period of time equivalent perhaps to nearly half of Pleistocene time or 500,000 years, during which through isolation and segregation the subspecific and specific characters were thoroughly founded. Here again monographic research is essential before we can reach a final conclusion.

It is interesting to note that this Sumatran species, which we may now regard as a subspecies, was partly distinguished by the Dutch naturalist Temminck as early as 1847. He pointed out that *Elephas sumatranus* has one more dorsal vertebra, i.e., 20, than *E. indicus*, i.e., 19; that the free portion of the intermaxillaries is shorter, the nasal cavities are shorter, the space between the orbits is narrower, the posterior portion of the cranium is broader than in *E. indicus*, the grinders have the narrower proportions of *Loxodonta africana*, the ridge-plate formula is intermediate between that of *L. africana* and that of *E. indicus*, and that portions of the *E. sumatranus* grinders and ridge-plate formula are intermediate to those of *L. africana*, while the shape of the plates is like that of the plates of *E. indicus*.

Elephas sumatranus Temminck 1847. "Coup-d'Œil Général sur les Possessions Néerlandaises dans L'Inde Archipélagique," II, 1847, p. 91. DESCRIPTION.—Temminck distinguishes *Elephas sumatranus* from the African and Indian species as follows:

	Elephas sumatranus	*Elephas indicus*	*Loxodonta africana*
Characters distinguishing E. *sumatranus* from *E. indicus* and *Loxodonta africana* (cf. Temminck, 1847, pp. 91, 92):	Enamel ridges thick crenulated, lamellæ broad, less numerous; ratio 3 or 4 lamellæ to 1 of width of grinder; 6 lamellæ in 12 centimeters	Enamel ridges thin, crenulated, lamellæ narrow; ratio 4 or 6 to 1 of width of grinder; 6 to 8 lamellæ in 12 centimeters	Enamel bands lozenge shaped, broad as in *E. sumatranus*; ratio 3 or 4 lamellæ to 1 of width; 6 lamellæ in 12 centimeters
Vertebral formula:			
Cervicals	7	7	7
Dorsals	20	19	21
Lumbars	3	3	3
Sacrals	4	5	4
Caudals	34[1]	34	26
True ribs	6	6	6
Floating ribs	14	13	15

Subsequent research and comparison, especially by Falconer, both as regards the vertebral and the ridge-plate formulæ, appear to demonstrate that the two characters of supposed specific value, namely, the number of dorsal vertebræ and the ridge-plate formula, may not be constant or valid. Consequently we are inclined to the opinion that *Elephas sumatranus* is a case of geographic isolation or insulation with characters of not more than subspecific value.

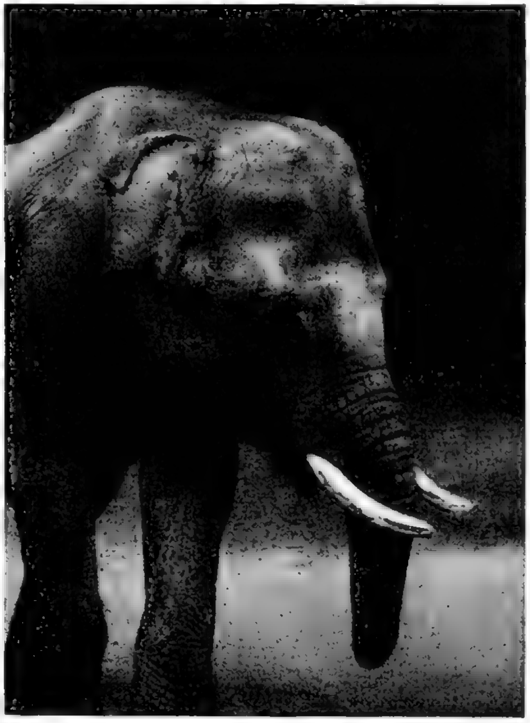

Fig. 1181. *Elephas indicus sumatranus* from Deli [Labuan Deli?], Sumatra. Oblique front view of head, showing small and peculiarly formed ears and small tusks of a young male. Photographed in the Rotterdam Zoological Gardens. After Lydekker, 1916, Vol. V, fig. 24, p. 83, through the courtesy of the British Museum (Natural History), August 10, 1929.

Director E. D. van Oort of the Leiden Museum (letter from Dr. Max Weber, August 15, 1929) informs us that the "Catalogue ostéologique des Mammifères," published by Jentink, in 1887,

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[1] [See Sclater's translation of Schlegel's paper on "The Sumatran Elephant," Nat. Hist. Rev., 1862, p. 75, where it is stated that the number of caudal vertebræ in both *E. sumatranus* and *E. indicus* is usually thirty-three, but in very young examples sometimes only thirty.—Editor.]

Fig. 1182. *Elephas sumatranus* Temminck, cotype male and female crania from Palembang, Sumatra, in the Leiden Museum. Compare Jentink, Cat. Ostéol. des Mamm., Mus. d'Hist. Nat., Tome IX, 1887, p. 169. Reçu en 1845 de M. J. C. Baud (cf. Temminck, Coup d'œil poss. Néerl. Inde arch., Tome II, 1847, p. 91). After photographs kindly furnished by Director E. D. van Oort.

A, Male cranium. Cat. *a*. Height of occipital crest to tip of premaxillaries 973 mm.

B, Female cranium. Cat. *b*. Height of occipital crest to tip of premaxillaries 832 mm.

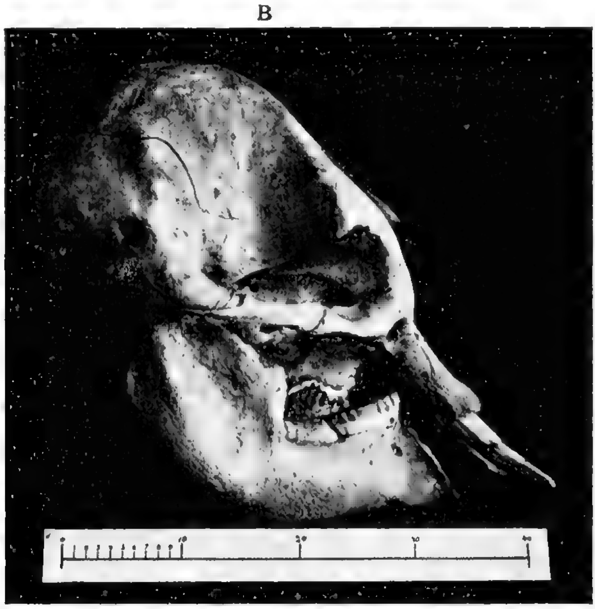
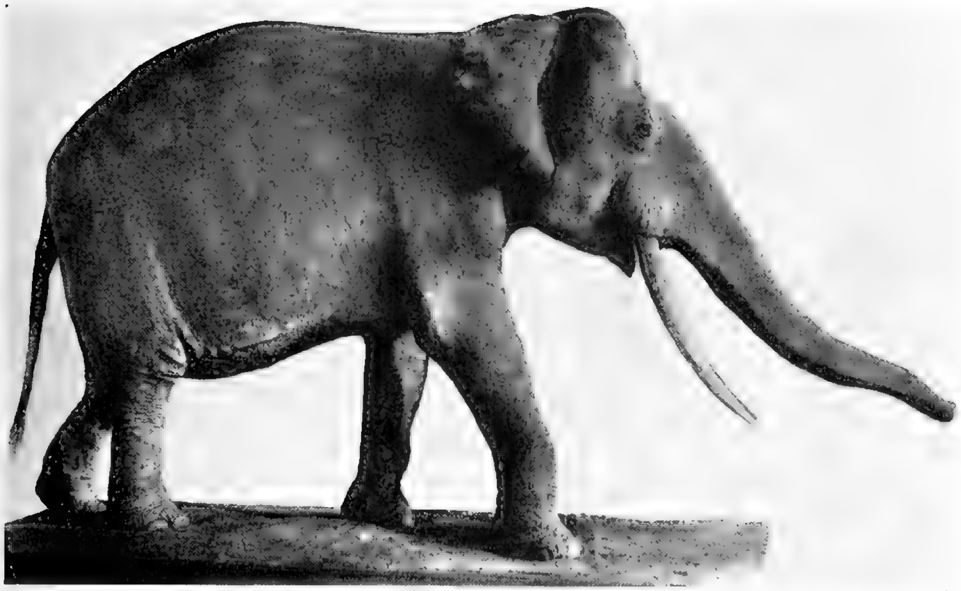


Fig. 1183. *Elephas sumatranus* crania from Sumatra in the Munich Museum. After photographs kindly furnished by Dr. Hermann Dürck and Herr Gustav Küsthardt, November 13, 1930.

A, Adult cranium from Batang Serangan, Unterlangkat, east coast of Sumatra, belonging to the mounted specimen represented in figure 1184. Observe the depressed and prominent position of the lower border of the orbits, as compared with *Elephas indicus bengalensis* (Fig. 1170), approaching rather *E. indicus ceylanicus* (Fig. 1170), and widely contrasting with the Loxodontinae (Fig. 1108A-C); also the slender tusks, although a male, and extreme bathycephaly (750 mm. x 550 mm.).

B, Infantile cranium from Sumatra (exact locality unknown to the present author), belonging to the mounted specimen represented in figure 1185. Compare the position of the external ear with that in the cranial profile of the adult *E. sumatranus* skull (Fig. 1184).



Sumatran Elephant in the Munich Museum

After photographs and measurements by Dr. Hermann Dürck and Herr Gustav Küsthardt (November 13, 1930)

Fig. 1184. This specimen was measured immediately after it was shot at Batang Serangan, Unterlangkat, east coast of Sumatra. Cranium, right lateral view of same individual as that shown in figure 1183A.

Total length, tip of tusk to tip of tail	790 cm.	= 23 ft.	3⅛ in.
Height of shoulder above forelimb	294	= 9	7¾
Height above hind quarters	290	= 9	6¼
Length of ear to point	70	= 2	3½
Breadth of ear	89	= 2	11
Total length of tusk	130	= 4	3¼

Observe slender tusks, although a male, and extreme bathycephaly (750 mm. x 550 mm.).

enumerates not less than three skeletons of *E. sumatranus* and several skulls, also one from Borneo. The elephants of Borneo are restricted to the northeasterly part of the island; they are not indigenous but are feral, having been sent originally as a present to one of the Rajahs. The elephant of Sumatra (van Heurn, 1929), long an economic factor in the life of the island, has recently been trained for military purposes.

Cotypes.—Four skeletons of the wild Sumatran elephant procured in August, 1845, from the district of Palembang, Sumatra, and forwarded to the Royal Museum at Leiden (see Schlegel, Verslagen en Mededeelingen der Koninklijke Akademie van Wetenschappen, Afd. Natuur., XII, 1861, p. 101; translation by Sclater, Nat. Hist. Rev., London, 1862, p. 72); characters described by Schlegel and communicated to Temminck, who published his species in 1847 ("Coup d'œil,"Vol. II, p. 91) under the name *Elephas sumatranus*, as cited below.

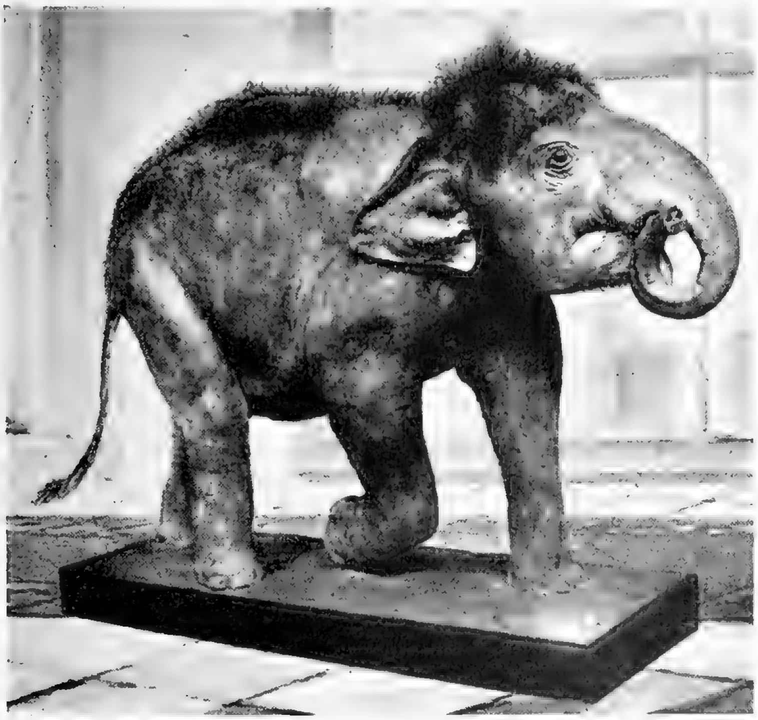
Original Description (Temminck, 1847, Vol. II, p. 91).—The cotype skeletons of *Elephas sumatranus* are in the Leiden Museum. We may cite from the original description, as follows: (*Op. cit.*, footnote 1, Chap. III) "Elephas Sumatranus *nob.* ressemble par la forme générale du crâne à l'eléphant du continent de l'Asie; mais la partie libre des intermaxillaires est beaucoup plus courte et plus étroite; les cavités nasales sont beaucoup moins larges; l'espace entre les orbites des yeux est plus étroit; la partie postérieure du crâne au contraire est plus large que dans l'espèce du continent."

"Les mâchelière se rapprochent, par la forme de leur couronne, plutôt de l'espèce asiatique que de celle qui est propre à l'afrique; c'est-à-dire que leur couronne offre la forme de rubans ondoyés et non pas en losange: mais ces rubans sont de la largeur de ceux qu'on voit à la couronne des dents de l'Eléphant d'Afrique; ils sont conséquemment moins nombreux que dans celui du continent de l'Asie. Les dimensions de ces rubans, dans la direction d'avant en arrière, comparées à celles prises dans la direction transversale et laterale, sont en raison de 3 ou 4 à 1; tandis que dans l'Eléphant du continent elles sont comme 4 ou 6 à 1. La longueur totale de six de ces rubans, dans l'espèce nouvelle de Sumatra, ainsi que dans celle d'Afrique, est d'environ 12 centimètres, tandis que cette longueur n'est que de 8 à 10 cent. dans l'espèce du continent de l'Asie."

"Les autres formes ostéologiques sont à peu près les mêmes dans les trois espèces; mais il y a différence dans le nombre des os dont le squelette se compose, ainsi que le tableau comparatif ci-joint l'éprouve."

Materials.—Lydekker (1916, p. 83) treats the animal as *Elephas maximus sumatranus* and figures a male elephant of this subspecies from Deli, Sumatra, formerly living in the Rotterdam Zoological Gardens (see Fig. 1181 of the present Memoir).

Graham Renshaw (letter, July 27, 1925) writes: "In the Munich Museum there is said to be a male of *Elephas indicus sumatranus* stuffed, from Lower Landak, East Sumatra. The skull



Infantile Sumatran Elephant in the Munich Museum

Fig. 1185. Observe the triangular form of the ear, the hairy covering at the top of the head and of the back, and the infantile profile of the cranium (Fig. 1183B), in contrast to the type of *Elephas maximus hirsutus* (Fig. 1187), in which the hair covers the entire body. After photograph and measurements by Dr. Hermann Dürck and Herr Gustav Küsthardt.

of the extraordinary elephant with tusks sweeping round in a huge curve, mammoth fashion, was in the Indian Pavilion at the Wembley Exhibition, where I saw it. You will remember it was shot by Theobald and figured some years ago in the Bulletin of the New York Zoological Society."

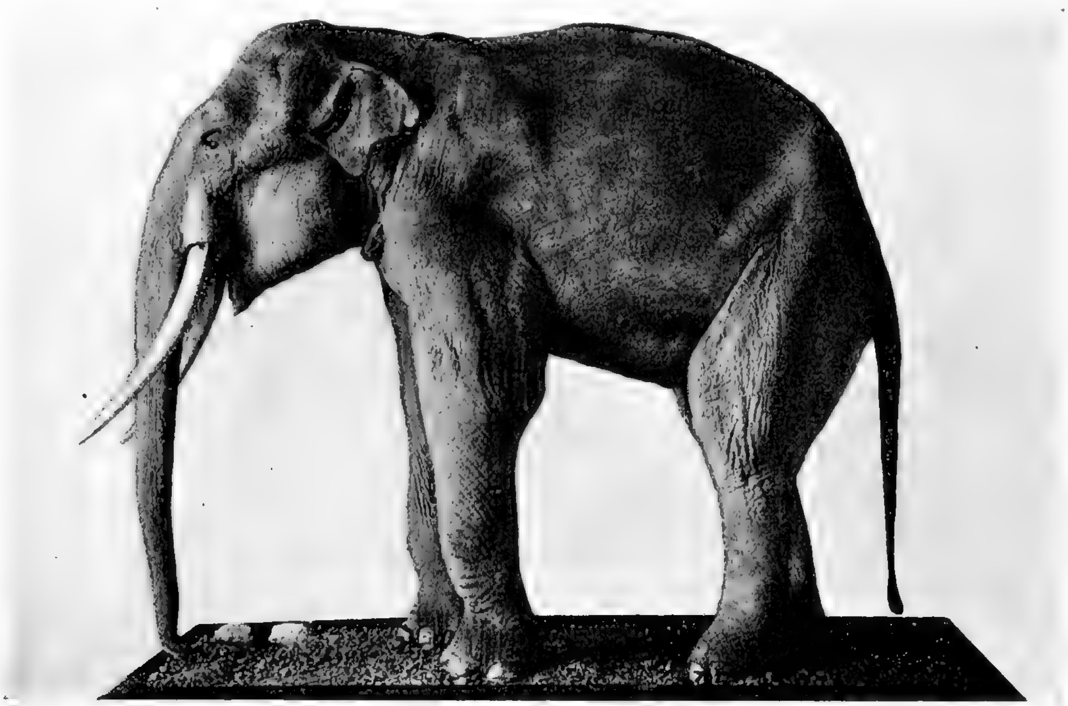


Fig. 1186. Burmese elephant mounted by the taxidermist Mr. H. Brazener of Manchester, England. After photograph by Mr. G. Cameron, presented for the purposes of the present Memoir by Mr. Graham Renshaw (see letter of March 30, 1924). While comparatively a small animal, superficially it does not present any clear differences from the northern *Elephas indicus bengalensis*. One-thirtieth natural size.

Elephas indicus hirsutus Lydekker, 1914[1]

Figure 1187

From the Kuala Pila District, Negri Sembilan Province, Malay Peninsula.

Elephas maximus hirsutus Lydekker, 1914. Abstract Proc. Zool. Soc. London, Vol. I, No. 130, March 17, 1914, p. 20. Paper read March 17, 1914, under the title, "The Malay Race of the Indian Elephant, *Elephas maximus hirsutus*," Proc. Zool. Soc. London, Vol. I, Art. 18, pp. 285–288. TYPE.—Young female Negri Sembilan Elephant, formerly living in the Gardens of the Zoological Society of London. British Museum (14.2.16.1). LOCALITY.—Kuala Pila district of the Negri Sembilan province, Malay Peninsula. TYPE FIGURE.—Lydekker, 1914.2, p. 285, text fig. 1 (taken when alive in the Society's Gardens); 1916, p. 84, fig. 25, as mounted in the British Museum.

TYPE DESCRIPTION.—(Lydekker, 1914.1, p. 20): "*Elephas maximus hirsutus*, subsp. n., characterized by the square, instead of triangular, form of the ear, the early date at which its upper margin is bent over, and the presence in the young condition—at least, in some cases—of a thick coat of black and in part bristly hair."

(Lydekker, 1914.2, pp. 285–288): "Thanks to the Trustees of the estate of the late Mr. Rowland Ward, the Natural History Branch of the British Museum has received the mounted skin of the young Malay Elephant which died in the Society's Gardens during the latter part of last year. While yet alive, the extraordinary hairiness of this animal attracted the attention of naturalists; and this feature, coupled with a peculiarity in the form of the ears, seems so well marked and so distinctive as to justify the recognition of the Malay Elephant as a distinct local race of the Asiatic species . . . this Elephant came from the Kuala Pila district of the Negri Sembilan province of the Malay Peninsula, and is believed to have been about three years old at the time of its death. As shown in the accompanying photograph from life (text fig. 1), it has a somewhat stunted appearance—suggestive, at first sight, of its belonging to a small raĉe,—the height of the specimen, as mounted, being about 3 feet 8 inches. This stunted appearance may, however, be merely due to the effects of early captivity, for Mr. T. R. Hubback, in his book on Elephant and Seladang Hunting

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[1] [The differentiating characters ascribed to this subspecies are the excessive quantity of hair and the peculiarity of the ears; but as these characters are not known to persist in any adult specimens, it is considered a subspecies of doubtful validity. (Note prepared by Dr. Barnum Brown, September 19, 1938).—Editor.]

[In 1932, Professor Osborn stated in a letter to the editor that the Curator of the Raffles Museum regarded Lydekker's hairy type of the Sumatran Elephant (*E. hirsutus*) as pathological. Professor Osborn added, however, that this subspecies was very small and its ears peculiar.—Editor.]

in the Federated Malay States, . . . records that the Elephants of the Negri Sembilan are of ordinary size, although of late years most of the big bulls have been killed off. He also mentions that practically all the bulls are tuskers, and very generally have one tusk much smaller than the other. . . . The tail is considerably longer than in the Indian calf, but since, according to Sanderson, there is considerable variation in this respect among Indian Elephants—which may or may not eventually prove to be of racial value,—I do not for the present propose to take any account of this feature. The great difference in the contour of the ear, coupled with the excessive development (at least in some instances) of black and in part bristly hair in the juvenile condition, seems sufficient to justify the separation of the Elephant of the Malay Peninsula as a distinct race, under the name of *Elephas maximus hirsutus*."

TYPE OF ELEPHAS INDICUS HIRSUTUS

Fig. 1187. Type of *Elephas maximus hirsutus*, from Negri Sembilan, Malay Peninsula, formerly in the Gardens of the Zoological Society, Regent's Park, London. After Lydekker, 1916, Vol. V, p. 84, fig. 25, reproduced through the courtesy of the British Museum (Natural History), August 10, 1929.

Elephas indicus Buski Matsumoto, 1927[1]

[=?**Palæoloxodon buski**]

Figure 1188

Type: Ninohe District, Province of Mutsu, Japan. Post-Pleistocene to Recent.

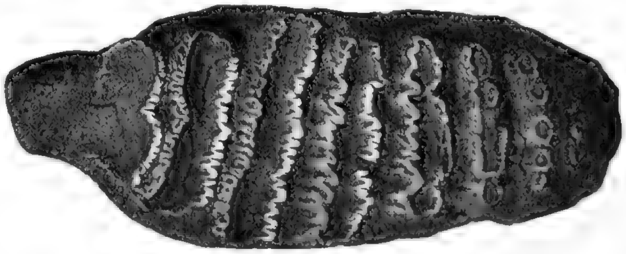
Referred localities (Matsumoto, 1927, p. 58): "Over forty miles from the sea-shore between Kanagawa and Tôkyô (Leith Adams); Yedobashi, Tôkyô (Naumann); Province of Mino (Tokunaga); Sapporo, Province of Ishikari, Hokkaidô (Tokunaga); . . . Prefecture of Wakayama."

Matsumoto (1927, p. 57) remarks that the "occurrence of the Asiatic elephant in a fossil state in Japan was stated for the first time by Leith Adams and communicated by Busk [Footnote: 'Leith Adams: Has the Asiatic Elephant Been Found in a Fossil State? *Quart. Journ. Geol. Soc.*, London, Vol. XXIV, 1868, pp. 496–498, text-fig.;—Busk, Additional Remarks, *id.*, pp. 498, 499.']. According to Busk, a certain fossil elephant from Japan is referred to *Elephas indicus*, representing, however, a form with teeth somewhat larger than the average of the existing one. Quite recently the writer has come to be fully convinced about this first record, which appears to have been overlooked so long, and proposes here to call the Japanese form in question to the credit of Busk, as follows. *Elephas indicus* Linné *Buski*, subsp. nov."

This interesting specimen, as described by Matsumoto, is as follows:

Elephas indicus Linné *Buski* Matsumoto, 1927. "On a New Fossil Race of the Asiatic Elephant in Japan." Sci. Rept. Tôhoku Imp. Univ., Second Series (Geology), Vol. X, No. 3, pp. 57, 58. TYPE.—"Antepenultimate upper molar of left side [l.M^1]." Inst. Geol. and Palæont. 7266. HORIZON AND LOCALITY.—(*Op. cit.*, p. 58): "Judging from the exceedingly feeble fossilization of the remains, as far as examined by the writer, the present form may probably belong to a very late geological age, such as the Post-Monastirian. The occurrence of the present form may indicate a warmer climate, that being well in accord with certain geological evidence already known." From Ninohe District, Province of Mutsu, Japan. TYPE FIGURE.—*Op. cit.*, 1927, Pl. XXVII, figs. 2 and 3.

TYPE DESCRIPTION.—(Matsumoto, 1927, p. 57): "The type-specimen consists of eleven ridges besides the anterior and posterior talons, and measures 155 mm. in length, 60 mm. in the greatest width at the third ridge, and 154 mm. in the greatest height of crown at the seventh ridge, which was just ready to commence to wear. The middle part of the crown is peculiarly narrowed, being narrower than both anterior and posterior parts. In a palatal view, the crown is more or less bent inwards. Its frequency of ridges in a length of 100 mm. is about 8 on both the sides and about 7 on the grinding surface. The ridges are only very weakly flexuous; their inner and outer sides in a fore-and-aft view are not very markedly convex, being almost parallel at the greater middle part of the height of the ridges. The anterior and the posterior side of the moderately to strongly worn ridges at the grinding surface are nearly parallel, without any loxodont sinus. The plication of enamel of those ridges is almost uniform from end to end, and is very fine, regular, and strong, as a very distinctive characteristic of the present species. The figure of enamel seen in the rather



ELEPHAS INDICUS BUSKI MATSUMOTO, 1927 [=?PALÆOLOXODON BUSKI]

Fig. 1188. Type figure of *Elephas indicus buski* Matsumoto, 1927, Pl. XXVII, fig. 3, one-half natural size, from Ninohe District, Province of Mutsu, Japan. Original in Institute of Geology and Palæontology, Tôhoku Imperial University (No. 7266). A first superior molar of the left side, l.M^1, crown view.

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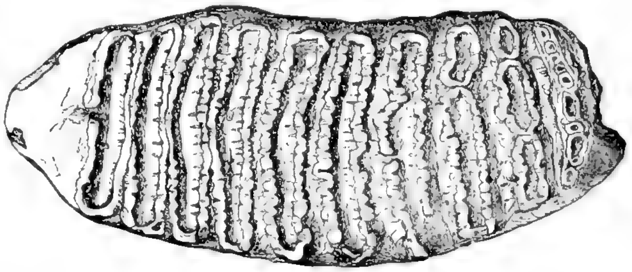
[1] Osborn, 1930: At first disposed to place this type near *Elephas indicus*, comparison with figure 1177, an M^1 of *E. indicus* (=*asiaticus*) proves that such reference is doubtful. It appears rather to belong near *Palæoloxodon namadicus naumanni*, *P. namadicus namadi*, or *P. hysudrindicus*.

slightly worn ridges is mesially laminar and laterally annular. The worn surface of the sixth ridge, which is very slightly worn, consists of five mammillæ arranged in a transverse row. The layer of enamel is considerably thin, measuring about 1–1.5 mm. in thickness on the anterior and the posterior side of the ridges."

Leith Adams and Busk (1868).—(1) In 1868, as mentioned above, page 1062, Leith Adams (1868, p. 497) described and figured a "Fossil Tooth of *Elephas Indicus* from Japan," discovered forty miles inland between Kanagawa and Jeddo. He rightly interpreted this tooth (Fig. 1189 of present Memoir) as an r.M², describing it as follows: "This penultimate true molar, right side, upper jaw, although partaking of the characters of *E. Armeniacus*, Falc., differs from the latter in its thick plaits, their less approximation, the festooning being carried round the loops of the disks of wear, and the total absence of any mesial expansion." (2) Busk (*op. cit.*, p. 498), after comparing the tooth with *E.* [*Parelephas*] *Armeniacus* Falc. and *E.* [*P.*] *columbi* Falc., and finally with a corresponding fossil tooth [in his opinion an l.M¹ of *E. indicus*], concludes as follows: "But these differences [referring to his comparison with *E. indicus*] do not appear to be of much importance, and there seems to be every reason to believe that the Japanese fossil tooth belonged to a form of *E. indicus*, with teeth somewhat larger than the average of the existing one." (3) The teeth described and figured by Adams and Busk (1868) and by Matsumoto (1927) are not dissimilar in respect to thickness and the interspacing of the enamel ridge-plates, but in the type of *Elephas indicus buski* the enamel foldings or plications are much closer and more compact and consequently more numerous. The ridge-plates in the Adams-Busk grinder (Fig. 1189) also in the type of *E. indicus buski* (Fig. 1188) are much more widely interspaced than in Dubois' type superior molar (Fig. 1160) of *Palæoloxodon hysudrindicus.*

Osborn, 1930: From the above comparisons Osborn is inclined to agree with Lydekker that the above grinding teeth, namely, the type of *Elephas indicus buski* (Fig. 1188) and *E. namadicus* ref. Lydekker (Fig. 1189), belong either to *E.* [*Palæoloxodon*] *namadicus naumanni, E.* [*P.*] *namadicus namadi,* or to some even more progressive species of *Palæoloxodon,* e.g., *E.* [*P.*] *hysudrindicus.*



Second Right Superior Molar referred to Palæoloxodon

Fig. 1189. A second right superior molar, r.M², probably from the Middle Pleistocene of Japan, between Kanagawa and Tokio (Yedo). After Lydekker, 1886.2, p. 168, fig. 29, about one-half natural size. Original in the Museum at St. John, New Brunswick, Canada.

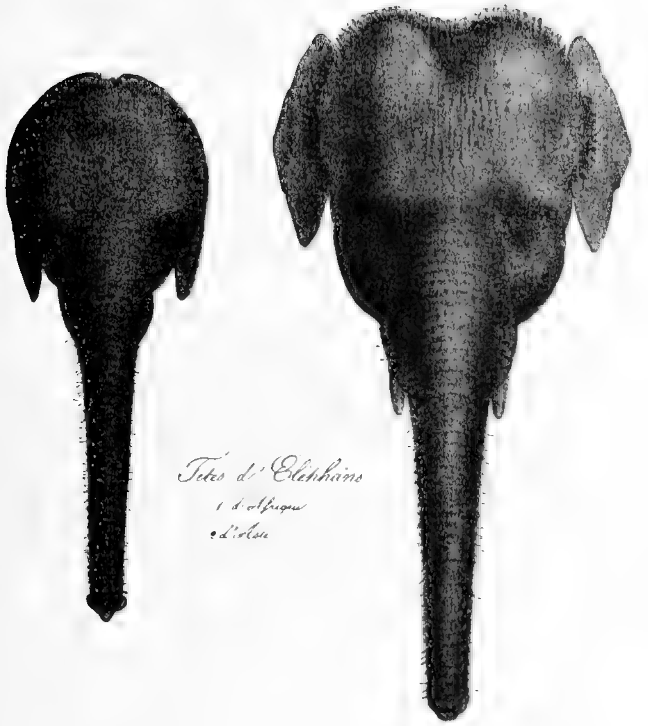
This molar, first figured by Leith Adams and Busk (1868, p. 497), and interpreted as a "Fossil Tooth of *Elephas Indicus* from Japan," was compared by the same authors (*op. cit.*, p. 498) with the *E.* [*Parelephas*] *armeniacus* Falc. of Armenia and of China. Length 187 mm., width 76 mm., height 111 mm. The present author regards it as referable either to *Palæoloxodon namadicus naumanni, P. namadicus namadi,* or *P. hysudrindicus.* Observe crimping or plication of the enamel and absence of 'loxodont sinus,' resemblance to *Elephas indicus* grinders. Observe similar plication or crimping in the type (Fig. 1160) of *P. hysudrindicus.*

2. DISTINCTIONS AND MEASUREMENTS OF THE INDIAN ELEPHANT

Comparison has been made in Chapter XV between the Indian and the African elephants as regards dental, cranial, and vertebral structure and prevailing feeding habits. As to dental structure, the very earliest observers remarked the profound differences between the crown view of the molars of the African and of the Asiatic elephants, finally figured and described (1846) by Richard Owen (Fig. 1191). It is not possible that the African elephant, with its coarse-plated, relatively low-crowned grinders, can attain the same age as the Indian elephant, with its very high and long-lived grinding teeth.

Detailed observations by Falconer (fully discussed in Chap. XV) on the food of the Indian and African elephants indicate that the straight tusks of the African elephant, as in all other Loxodontines, are used as crowbars in uprooting trees as well as in combat. It does not appear that the shorter and more slender tusks of the Indian elephant are used to so great a degree for such purposes; they are invariably more slender and more strongly upcurved, and those of the old Indian bulls may attain great length (Fig. 1179). Doubtless for a very long period of time the Asiatic elephant was hunted for its ivory, even before it was domesticated, both in India and Ceylon. The ivory tusks, both of the Indian and Ceylonese varieties, are capable of carrying very heavy logs, held in place across the tusks by the trunk.

In longitudinal section (Fig. 1192) it appears that the low-browed African cranium, in perfect harmony with its low-crowned grinders, is in very wide contrast to the high-browed Indian cranium, with its very high grinding teeth. On the principle explained in Chapter XV, the Indian cranium (Fig. 800) is far more *bathycephalic* than



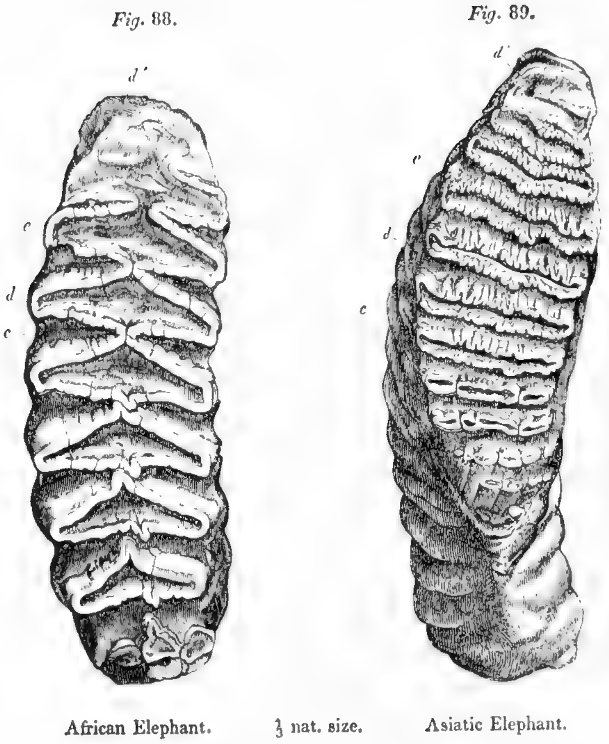


Fig. 1190. Superior view of the head of a young African elephant (left) and of an adult Indian elephant (right). After Geoffroy Saint-Hilaire and Fréderic Cuvier, 1825, Livr. LI, LII, one twenty-fourth natural size.

The superior view of the head of the adult *Elephas indicus* should be compared with the superior view of the heads of the adult male (*Loxodonta africana albertensis*) and female (*Loxodonta africana peeli*), as mounted in the American Museum collection and photographed from above in figure 1063 of this Memoir. The very marked differences between the male or female *Loxodonta* and the male or female *Elephas* are indicated in this comparison. *Loxodonta* is distinguished by the rounder occiput, lacking the pronounced air sinuses of *E. indicus*, also by the greater elongation of the antorbital or facial region of the cranium. The differences between the cranium of *Loxodonta* and of *Elephas* are quite as pronounced as the differences between the grinding teeth displayed in figure 1191.

Fig. 1191. Crown view of the third inferior molar of the right side of: Fig. 88, *Loxodonta africana*; Fig. 89, *Elephas indicus*, one-third natural size. After Owen, "A History of British Fossil Mammals and Birds," 1846, pp. 230–232: "Thus in the African Elephant, (fig. 88), in which the lozenge-shaped plates are always much fewer and thicker than the flattened ones in the Asiatic species, the variation which can be detected in any number of the grinders of the same size is very slight. . . . In the molars of the Asiatic Elephant, (fig. 89), which, besides the difference in the shape of the plates, have always thinner and more numerous plates than those of the African species, a greater amount of variation in both these characters obtains; . . . and the like caution is still more requisite in the comparison of the molars of the Mammoth (*Elephas primigenius*), which, having normally more numerous and thinner plates than in the existing Asiatic Elephant, present a much greater range of variety."

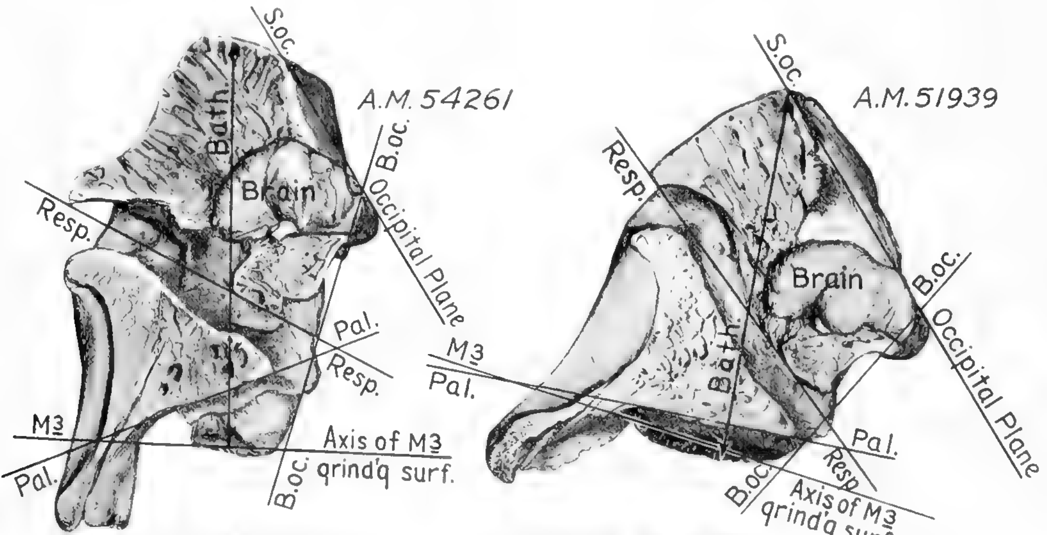


Fig. 1192. Contrasts of (right) the low-browed African cranium (Amer. Mus. Dept. Mam. 51939) with (left) the high-browed Indian cranium (Amer. Mus. Dept. Mam. 54261). Compare figures 805, 806, 800, 1061, and 1053. The brain, deeply embedded below the cranial air cells, is seen to be slightly larger in the Indian elephant (6686 ccm.) then in the African elephant (6651 ccm.). Compare figure 1112.

Bath., the vertical bathycephalic diameter from summit of occiput to crown of grinding teeth.

S.oc.—S. oc., the supraoccipital axis (=occipital plane).

B. oc.—B. oc., the basioccipital axis (=basioccipital plane).

Resp.—Resp., the respiratory axis from the anterior to the posterior nares (=respiratory plane).

Pal.—Pal., palatal axis of the roof of the mouth.

M^3—M^3, grinding surface of the superior molar teeth.

the African cranium (Fig. 1061), yet the African elephant, as shown in the measurements (legend to Fig. 1053) of the growing "Khartum" (*Loxodonta africana oxyotis*) attains its greater height very rapidly, namely, from a height of 4 ft. 1¼ in. in October, 1906, to a height of 10 ft. 8¾ in. in January, 1930, or an average annual growth of 3¼ in. in twenty-four years. The extreme shoulder height of the African elephant, in the flesh, is estimated at 11 ft. 6½ in. (see footnote 2 on page 1022, caption to Fig. 912), whereas, as shown in the observations below, there are only two records (neither of which is absolutely reliable) of the attainment by the Indian elephant of a greater height than 10 ft. 6 in., the average being about 9 feet.

SHOULDER HEIGHTS OF THE INDIAN ELEPHANT

Throughout this Memoir the estimates of shoulder heights are based on the fully extended forelimb, with certain allowance for the cartilages between the bones, for the foot pads, and for the great muscles of the neck.

UNGULIGRADISM. RADIOGRAPH OF RIGHT FOOT OF YOUNG INDIAN ELEPHANT

Fig. 1193. This beautiful radiograph of the pes of a young elephant taken from the inner side of the foot exhibits clearly the complete inner or first digit, including *Ph. II, Ph. I, Mts. I, Cu., Nav., Astrag., Cal., Ep.,* and *Tibia.* The remaining four digits are faintly seen in outline. The pes is shown to be *unguligrade,* i.e., to rest upon the ungues surrounding the tips of the terminal phalanges, in this case *Ph. II;* it proves that *Elephas* is in no sense plantigrade. It also exhibits the cartilaginous interspaces, which add considerably to the height of the skeleton. The scale is approximately two-fifths natural size. Reproduced through the courtesy of Dr. G. M. Vevers of the London Zoological Society.

As compared either with the African or with the great extinct elephants of Pleistocene time, the Indian elephant is generally inferior in stature; it exceeds *Mammonteus primigenius* in height by a foot to eighteen inches; the somewhat doubtful 'record' of the Indian shoulder height, as shown in figure 1194, namely, 10 feet 6 inches, agrees with the highest figure given by Corse below, while the average large Indian elephant rarely exceeds 9 feet.

The observations of Corse (1799, p. 35) chiefly relate to the heights of domesticated elephants and are very interesting to cite in this connection:

> (Cf. Corse, 1799, p. 35): "elephants attain their full size between eighteen and twenty-four years of age. . . . In India, the height of females is, in general, from seven to eight feet; and that of males, from eight to ten feet, measured at the shoulder." One elephant, on good authority, exceeding ten feet, was a male, measuring as follows:

From the top of the shoulder, perpendicular height	10 ft.	6 in.
From the top of the head, when set up,	12 "	2 "
From the front of the face to the insertion of the tail	15 "	11 "

> Of 150 Bengal elephants only a few males attained 9 feet 6 inches, not one of them attained 10 feet. The Ceylon elephants are neither higher nor superior in any respect to those of Bengal.

Contrary to prevailing opinion, the elephant is in no sense plantigrade; as shown in the radiograph reproduced herewith (Fig. 1193) the foot is *unguligrade*; the phalanges are subvertical in position, the terminal phalanges are greatly reduced in size and are encased in horny sheaths which protect the front part of the foot from injury, while a posterior elastic pad is pressed down in a walking or running gait.

In the accompanying figure (Fig. 1194) are given the estimated shoulder heights of three elephants in the American

Museum collection, ranging from 8 ft. 4¾ inches to 8 feet 8¾ inches, as compared with that of a very large male measuring 10 feet 6 inches in the flesh,[1] according to Rowland Ward's "Records of Big Game" and a measurement taken from Dollman-Bather, 1927. This 10 feet 6 inches maximum agrees with the single exceptionally large specimen reported by Corse.

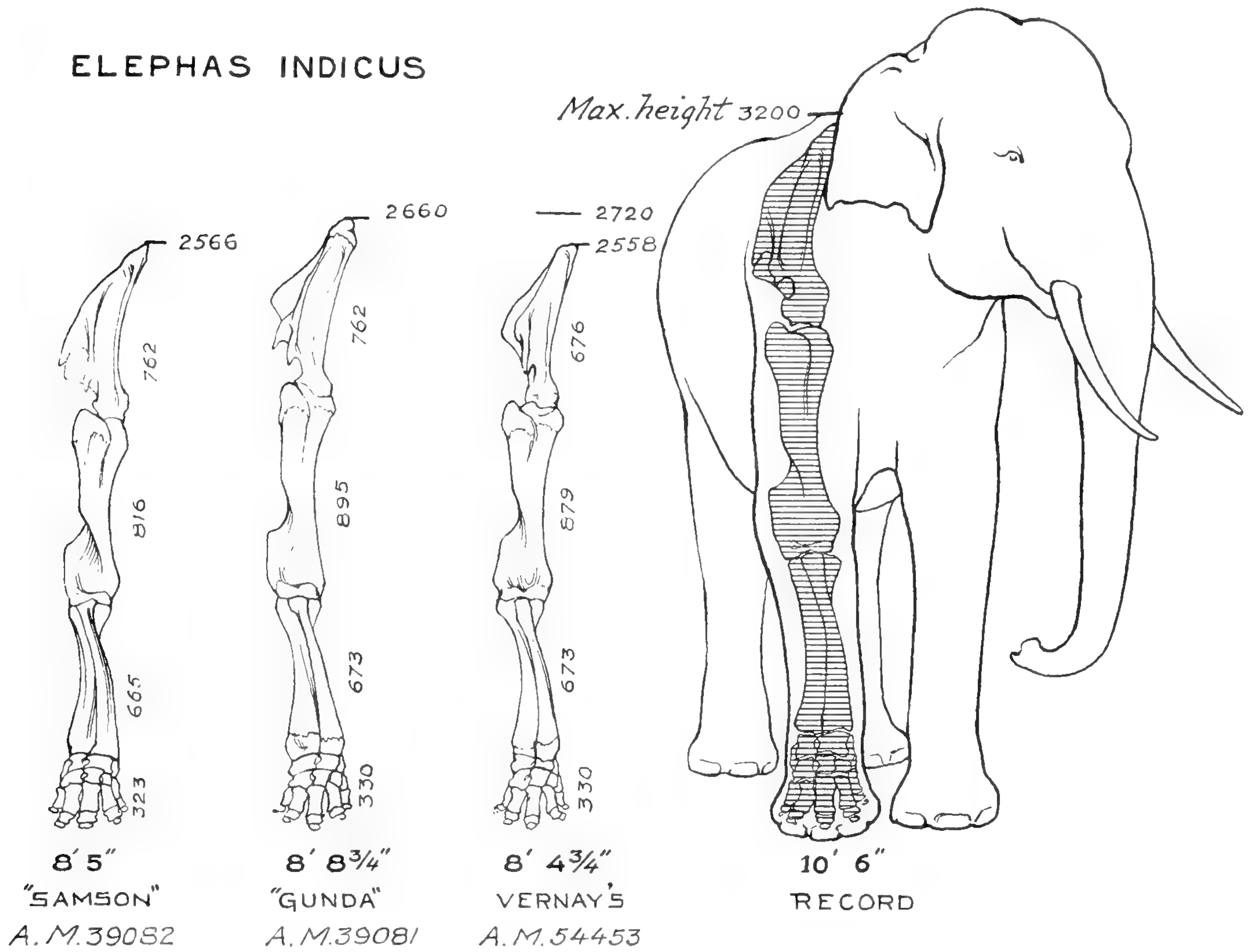


Fig. 1194. Estimated Shoulder Heights of the Indian Elephant, Skeletal and Flesh

[Professor Osborn's method, used in the present Memoir, of estimating the height in the flesh is to add six and a third per cent. to the skeletal height.—Editor.]

		Skeleton	Flesh
Small male, "Samson" (Amer. Mus. 39082), skeletal height to summit of scapula	2566 mm.	8 ft. 5 in.	
Larger male, "Gunda" (Amer. Mus. 39081), about twenty-one years, total extended limb segments, skeletal height	2660 mm.	8 ft. 8¾ in.	
Male wild elephant, Vernay Coll. (Amer. Mus. 54453), skeletal height	2558 mm.	8 ft. 4¾ in.	
height in flesh	2720 mm.		8 ft. 11 in.
Very large male, alleged record (Ward, also Dollman-Bather, in Bather, 1927, p. 104) in the flesh (skeleton not measured)	3200 mm.		10 ft. 6 in.[1]

According to Rowland Ward ("Records of Big Game," 1922, p. 468), the record shoulder height of the large male wild Indian elephant is 10 feet 6 inches. [A subsequent record (Ward, edition of 1928, p. 451) gives a height of 10 ft. 8 in.—Editor.]

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[1] This "record" is not thoroughly authentic, as shown below in citations from Corse and others; it is very difficult to measure a prostrate elephant accurately. The record of the large Haslemere specimen exceeds this, the living height at the withers being recorded as 11 ft. 1 in. The following is cited from The Haslemere Museum Gazette, Vol. I, No. 1, May, 1906, p. 13: "It is that of a very large Ceylon elephant, shot by Mr. W. H. Varian, at Chalampi Madua, in the North Coast Province of Ceylon, in 1882 . . . . The following measurements of this animal, taken immediately after death, . . . Height at arch of back, 11 feet 9 inches; height at withers, 11 feet 1 inch; length from the tip of the tail to the tip of the trunk, 26 feet; girth of the body at thickest part, 22 feet 4 inches; weight about 8 tons." The measurements of the large Haslemere cranium agree closely with those of the two crania given by Falconer (1868, Vol. I, p. 477).

European Stages.	Sind and Mekran Coast.		Baluchistan.		Punjab and N.W. Frontier.		Simla Hills.		Eastern Himalayas.	Assam.		Burma.	
	Marine.	Terrestrial.	Marine.	Terrestrial.	Marine.	Terrestrial.	Marine.	Terrestrial.	Terrestrial.	Marine.	Terrestrial.	Marine.	Terrestrial.
Uppermost Pliocene(?) and Lower Pleistocene	..	U. Manchhar, conglomerates (the lower limit of this series is uncertain)	..	**Conglomerates (the lower limit of these is uncertain)**	Upper Siwaliks	**Boulder conglomerate stage**	Upper Siwaliks	Conglomerates, *Stegodon ganesa*, *Buffelus palaeindicus*, *Elephas hysudricus*	Sandstones and conglomerates (the lower limit of these is uncertain)	..	Dihing beds, conglomerates (the lower limit of these is uncertain)	..	..
Middle to Upper Pliocene	..	..	..	..		**Pinjor stage, *Elephas planifrons*, *Equus sivalensis*, *Bos*.**		Pinjar sandstones, only recognized in the Siwalik Hills, *Elephas planifrons*, *Equus*, *Camelus antiquus*	..	..	..	..	
Lower to Middle Pliocene	Gwadar stage of Mekran coast	..	..	..		**Tatrot stage, *Amphibos*, *Leptobos*, *Sivatherium***		**Not definitely recognized**	..	..	..	..	Higher beds of the Irawaddy series
Pontian	Talar stage of Mekran coast	L. Manchhar (upper beds), clays and sandstones	..	**Middle Siwaliks of the Bugti Hills (the lower limit of this is uncertain), clays and sandstone**	Middle Siwaliks	**Dhok Pathan stage, *Stegodon latidens* *Sus titan*, *Hipparion*, *Helladotherium*, large antelopes**	Middle Siwaliks	**Dhok Pathan stage, sandstones and clays with *Tetrabelodon corrugatus* and *Stegodon latidens***	..	..	..	**Akauktaung series of S. Burma, sandstones with *Ostrea virleti*, lower limit doubtful, but may extend downward to the Pyalo stage**	**Basal beds of the Irawaddy series at Yenangyoung**
Sarmatian	Marine beds definitely referable to this period have not been recognized	L. Manchhar (upper beds)	Kojak shales, shales and sandstones, "Flysch" facies corresponding to the calcareous facies of Sind and Eastern Baluchistan	..		**Nagri stage, *Hemimeryx*, *Hyotherium indicum*, *Giraffokeryx*, *Stegodon cautleyi***		Nagri stage, clays and sandstones, *Stegodon cautleyi*	..	..	..	..	..
Tortonian		L. Manchhar (middle beds)		..	Lower Siwaliks	**Chinji stage, *Hyotherium chinjiense*, small antelopes**	Lower Siwaliks	**Nahan series, mostly sandstones, with *Hyotherium* (?) *chinjiense***	..	..	..	..	..
Helvetian		L. Manchhar (basal beds). *Tetrabelodon angustidens* sandstones and conglomerates	Kojak shales	Lower Siwalik (basal beds), with *Tetrabelodon angustidens*		**Kamlial stage Kasauli (Upper Murree) stage**		**Kasauli stage, lacustrine sandstones with plant remains, *Tetrabelodon angustidens***	..	Uppermost sandstones of the Garo hills (Dalu and Bagmara)	Uppermost sandstones of the Garo hills (Karaibari), *Choeromeryx silistrensis*	..	..
Burdigalian	Upper Gaj, limestones, with *Ostrea latimarginata*	Bhagathoro beds, coarse sandstones	A thin representative of the Gaj in some places underlying the fluviatile Bugti beds	**Bugti beds, coarse sandstones, *Anthracotherium bugtiense*, *Cadurcotherium***	..	**Murree (purple sandstone), dies away towards the Salt Range, Fatehjano beds *Anthracotherium bugtiense***	..	Dagshai series, purple sandstones and shales	..	**Sandstones of the Garo, Khasia, and Jaintia hills, 10,000 feet (lower limit of these is uncertain)**	**Tipam sandstones of Upper Assam and the Naga hills (fossil wood), occasional shell beds (the upper and lower limits of this series are uncertain)**	Pyalo stage, sandstones, S. Burma, with *Ostrea latimarginata*	Variegated clays and sand at top of Yenangyoung sequence, with large *Batissa*. Lower beds contain *Dorcatherium birmanicum*
Aquitanian	**Lower Gaj, limestones, with *Lepidocyclina marginata***	..	**Kojak shales**	..	..	..	..	..	..	..	..	**Kama clay of S. Burma**	**"Freshwater Pegus" with *Cadurcotherium***

'ELEPHAS PLANIFRONS' AND 'ELEPHAS HYSUDRICUS' LIFE ZONES. AFTER PILGRIM

Fig. 1195. This plate (Pilgrim, 1926, pp. 932, 933) differs from the synthetic plate of Pilgrim, 1910-1927, and Osborn-Colbert, 1935 (Fig. 413, Vol. I) in separating the marine and terrestrial stages of Sind, Baluchistan, Punjab, Northwest Frontier, Simla Hills, eastern Himalayas, Assam, and Burma. Of these the richest and most clearly successive Plio-Pleistocene formations are the 'terrestrial' of the Simla Hills. Pilgrim (*op. cit.*, p. 914) describes the zone containing *Elephas hysudricus* as follows:

> *Boulder Conglomerate zone—Upper Pliocene* (?) *and Lower Pleistocene.* This deposit completes the history of the Tertiaries of the Punjab Gulf and the great westward flowing Siwalik river. . . . The Boulder Conglomerate is widely spread in this region, and overlaps many of the older fluviatile deposits . . . it seems probable that little if any of the Boulder Conglomerate zone which lies 5,000 feet higher than the Moginand beds, can be placed in the Pliocene.

Of these the 'Simla Hills' best exposes the 'Boulder Conglomerate' in the Upper Pliocene(?) and Lower Pleistocene.

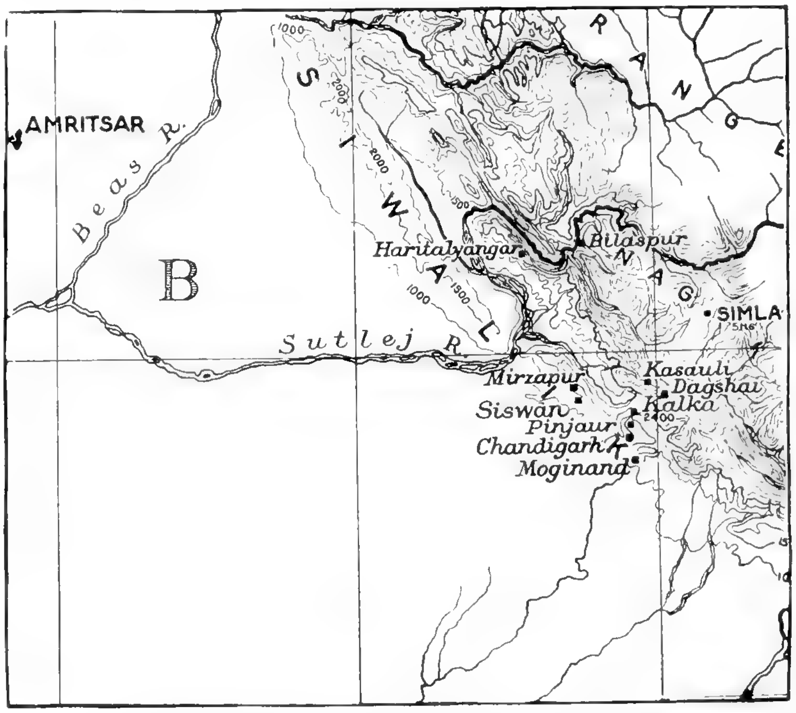
III. CHARACTERS OF THE UPPER PLIOCENE AND LOWER PLEISTOCENE SPECIES HYPSELEPHAS HYSUDRICUS AND PLATELEPHAS PLATYCEPHALUS

First it is important to note the great geologic antiquity and wide separation in time of the two fossil species, now to be described, from the living *Elephas indicus* and its geographic subspecies.

This great geologic time interval between *E. indicus, Hypselephas hysudricus*, and *Platelephas platycephalus* practically spans the whole Pleistocene period or Glacial Age, now estimated at about 1,000,000 years, in contrast to the relatively brief period of 400,000 years which may have been in the mind of Falconer from the estimates of Pleistocene time by his contemporary Charles Lyell.

Among the fossil types of the Siwaliks and contemporary geologic horizons of India, as displayed in the geologic table of Pilgrim-Brown-Osborn-Colbert (1910–1927–1935—Fig. 413), also the more detailed correlation table of Pilgrim (1926 Fig. 1195), it appears that *Hypselephas hysudricus* was extremely abundant in the Lower Pleistocene fluviatile deposits of the Simla Hills (Fig. 1196) below or eroded from what is known as the "Boulder Conglomerates."

Hypselephas hysudricus occurs as a companion of the giant stegodont species *Stegodon insignis-ganesa*, also of the bovine *Buffelus palæindicus*. Its remains are very numerous and in the present Memoir references are given to 29 specimens very carefully described and in many cases beautifully figured by Falconer both in the "Fauna Antiqua Sivalensis" and in the "Palæontological Memoirs" of 1868, also to 14 specimens collected by Barnum Brown in 1922 and referred by Osborn to *Hypselephas hysudricus*, in addition to a specimen also collected by him from the "base of conglomerates," described herewith as *Platelephas platycephalus*. In brief, the collections of Falconer and of Brown include upwards of 43 type and other specimens referable to *H. hysudricus*, so that the cranium and dentition of this species are very well known, in fact, better known than of many of the living subspecies of elephants.



Upper Siwalik Exposures of the Simla Foothills, India
Compare Folding Map (Pl. xxv), also figure 1195 opposite and localities listed on p. 1347 below

Fig. 1196. In the very thick Plio-Pleistocene horizons of this region occur the formations which have yielded in the Falconer and Barnum Brown collections not less than 66 specimens of *Archidiskodon planifrons*, in addition to numerous specimens referred to *Stegodon insignis-ganesa* from the overlying variegated beds at the base of the Boulder Conglomerate formation. The Falconer and Brown collections include also remains of *Hypselephas hysudricus*, in addition to the new forms *Stegodon pinjorensis, Platelephas platycephalus*, etc. This region therefore is the richest known in remains of the Plio-Pleistocene proboscideans of India.

Eleven specimens of the typical *Hypselephas hysudricus* are recorded by Barnum Brown as from 'below conglomerates' or 'top of variegated beds,' apparently deposited by erosion from the "Boulder Conglomerates" and three from the "Upper Siwaliks." Brown's localities are near Chandigarh, Siswan, and Kalka, as shown in the present figure.

Osborn's analysis proves that *Elephas hysudricus* represents a distinct generic phylum which may be named *Hypselephas*;[1] in this phylum for the present are placed two species:

Elephas hysudricus Falconer and Cautley, 1845, 1846 = *Hypselephas hysudricus*.

Elephas platycephalus angustidens Osborn, 1929 = *Hypselephas hysudricus*.

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[1] [See Osborn, 1934.926, p. 285, and Vol. I, p. 12, of the present Memoir.—Editor.]

Wholly distinct is the very primitive, flat-headed *Platelephas platycephalus* Osb. Before defining and characterizing these new forms, the classic '*Elephas hysudricus*' of Falconer may be fully described, preceded by the generic characters of *Hypselephas*, as follows.

Superfamily: ELEPHANTOIDEA Osborn, 1921
Family: ELEPHANTIDÆ Gray, 1821
Subfamily: Elephantinæ Osborn, 1910

Genus: **HYPSELEPHAS** Osborn, 1936

Original reference: Osborn, 1934.926, p. 285 (*nomen nudum*), and Vol. I of the present Memoir (1936), p. 12.

Genotypic species: *Elephas hysudricus* Falconer and Cautley, 1845, 1846, and *Elephas platycephalus angustidens* Osborn, 1929.

Generic Characters.—Primitive elephants of India, progressive in cranial structure; cranium elevated (hypsicephalic); occiput elevated with broadly transverse frontal crest, frontals deeply concave. Premaxillaries relatively narrow or laterally compressed; tusks relatively straight, incurved, somewhat divergent at base; rostrum of lower jaw elongate, prominent, ramus shallow. Orbits large, depressed, near maxillary rostrum. Molar crowns low; ridge-plates convexo-concave, reversed above and below, rudimentary 'loxodont sinus.' Ridge-plate formula: M 3 $\frac{18+}{17\text{-}18\text{-}19}$.

1. FALCONER'S ORIGINAL DESCRIPTIONS OF ELEPHAS [HYPSELEPHAS] HYSUDRICUS

Hypselephas hysudricus Falconer and Cautley, 1845, 1846
Figures 794, 1174, 1197–1206, 1209–1215, 1218

Lower Pleistocene, apparently deposited by erosion from the Boulder Conglomerate zone, India. In the same zone occur *Stegodon ganesa*, *Dicerorhinus platyrhinus*, the horse of India (*Equus sivalensis*), and the camel of India (*Camelus sivalensis*). Localities: Near Siswan, Chandigarh, Charnian, Kalka, as recorded by Brown.

E. [*Elephas*] *Hysudricus* Falconer and Cautley, 1845, 1846. "Fauna Antiqua Sivalensis," 1845, and 1846, p. 41. Type.—Second superior molar, M^2. Paratype.—Portion of third inferior molar, M_3. Horizon and Locality.—Siwalik Hills, India, Lower Pleistocene. Type and Paratype Figures.—*Op. cit.*, Pl. I, figs. 3*a*, 3*b* [Fig. 1197 of the present Memoir].

Relationships.—This specific phase was abundant in the Lower Pleistocene of India, for in the present Memoir comparative measurements are given of 29 specimens described by Falconer and of 14 specimens collected by Dr. Barnum Brown in 1922, in all 43 specimens.

By Falconer *Elephas hysudricus* was believed to be related to *Elephas indicus*. By Leith Adams it was considered ancestral to both *Elephas* and *Loxodonta*. By Pohlig it is considered ancestral to *Elephas* [= *Palæoloxodon*] *namadicus*. By Osborn it is regarded, on the whole, as more closely related to *Elephas indicus* although by no means ancestral. The cranium is widely distinct from that of *Palæoloxodon namadicus* or of *Loxodonta africana*; the grinding teeth are relatively shorter than those of *P. namadicus*, they resemble rather certain of the grinding teeth referred in this Memoir to species of *Palæoloxodon* of East India and of Japan. The extreme hypsicephalic and compressed juvenile cranium of *Elephas hysudricus* as figured by Falconer and Cautley (Fig. 1213) also by Osborn in the present Memoir (Fig. 1214) closely resembles the juvenile cranium of *Elephas indicus* as figured by de Blainville (Fig. 1180A). These tall, highly compressed crania differ widely from the low, flattened juvenile crania of *Loxodonta*. Observe the rudimentary loxodont sinus on the grinders (Figs. 1198, 1199, 1203).

Type Description.—(Falconer and Cautley, *op. cit.*, 1846, p. 41): "Fig. 3*a*, of this plate [Pl. I] shows a section of the penultimate upper molar [Fig. 1197, 3*a*] of an undescribed Indian fossil species named *E. Hysudricus* in this work. The tooth is in the middle stage of wear, eleven of the thirteen plates of which it is composed, having been in use, and the two anterior ridges being worn out. The same vertical disposition of ivory, enamel, and cement, is presented as in the African Elephant, but the plates are thinner and a greater number of them is included in the same length, nine or ten plates in the latter being developed in the space occupied by thirteen or fourteen plates in the equivalent teeth of *E. Hysudricus*. The plates are also more vertical, the interspaces occupied by the cement are wider in general than the ivory plates which represent very attenuated wedges. The layer of enamel is proportionally thicker than in the African Elephant, approaching, in this respect, the teeth of *E. planifrons*, fig. 5. The vertical height of the tooth is comparatively less in this specimen than in the African species, the difference being compensated by a greater development of the basal mass of ivory. This specimen measures 7.7 inches in length. A portion of the last molar of the lower jaw of this species is shown in vertical section in fig. 3*b*, comprising about fifteen plates [Fig. 1197, 3*b*]. The entire tooth, which is seen in figs. 12 and 12*a* of pl. 7, *in situ* in the jaw [Fig. 1198 of present Memoir], is more elongated, and includes a greater number of divisions than is usual in the last inferior grinder of *E. Hysudricus*."

Lydekker (1886, p. 117) erroneously selects the adult cranium as the type, in the following sentence: Brit. Mus. "M.3109. The cranium of an adult, with the crowns of the molars broken off. Figured by Falconer and Cautley in the 'Fauna Antiqua Sivalensis,' pls. IV., and V. figs. 1, 2. This and the following specimens are the types of the species. *Purchased*, 1838."

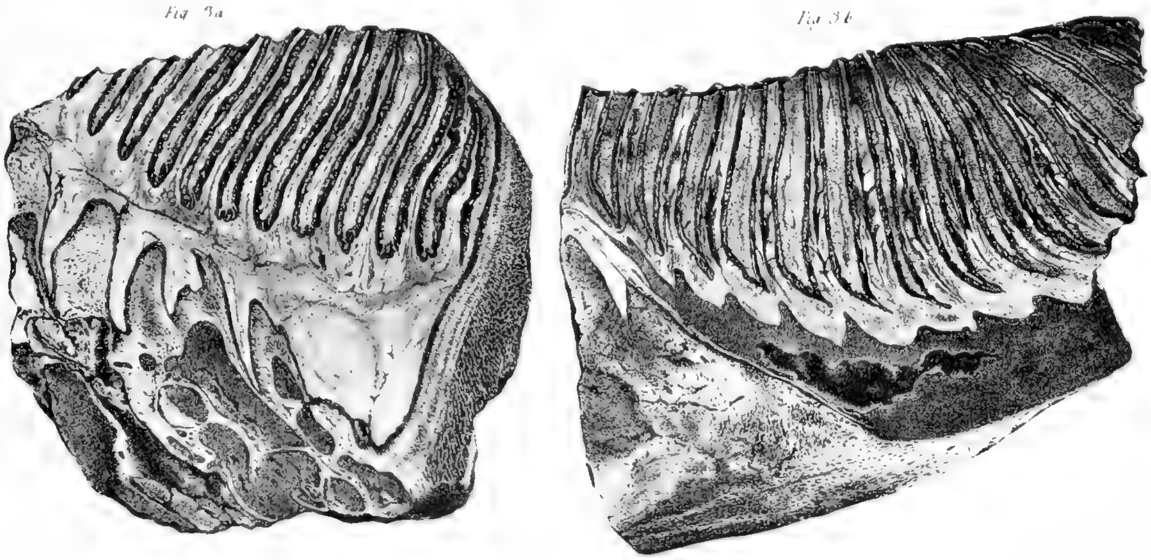
This adult cranium (Brit. Mus. M.3109—Fig. 1205 of the present Memoir) contains only the badly fractured crowns of M^3, M_3, consequently it cannot be the type, although Lydekker's confusion may have arisen from Falconer's description of Plate I, fig. 3*a* (1868, I, p. 422), to which is added "(Reproduced in Pl. V, fig. 1.)."

FALCONER'S RIDGE FORMULA.—In addition to his clearly recognizable type, Falconer examined twenty-nine specimens (from the ?Boulder Conglomerate zone) which he referred to the same species. These specimens are admirably figured in his great Atlas of the "Fauna Antiqua Sivalensis" (1845–1847); from this Atlas and from Falconer's text in the "Palæontological Memoirs" of 1868, Vol. I, pp. 421–440, may be derived the following notes:

Plate I. [TYPE].—Fig. 3*a*, M^2 (section), 11 ridge-plates in use, 2 anterior being worn out; fig. 3*b* [PARATYPE, Osborn] M_3 (section), about 15 ridge-plates. Plate IV. Front view of skull:

Length of cranium from occipital protuberances to left incisive	45. in.	1140 mm.
Extreme width of head (restored on left side)	38.5	980
Length of alveolus of M^3	10.5	266
Width of alveolus of M^3	4.75	121

Plate V, figs. 1, 2, 3, 4. Different views of same skull as above. Plate VI, figs. 1, 2, perfect small skull, Dp^3 with 5 ridge-plates, Dp^4 with +7+ ridge-plates; fig. 3, under surface of young skull, Dp^3 with 5 ridge-plates, Dp^4 with +8+ ridge-plates. [Footnote:



HYPSELEPHAS HYSUDRICUS. FIG. 3A, FALCONER'S TYPE, L.M^2; FIG. 3B, OSBORN'S PARATYPE, R. M_3, SECTION
SEE ALSO FIGURE 1201 OF SECTIONS OF REFERRED THIRD SUPERIOR AND INFERIOR MOLARS

Fig. 1197. Type and paratype of *Elephas Hysudricus* Falconer and Cautley, 1846 [1845], Pl. I, figs. 3*a*, 3*b*, from the Siwalik Hills, Lower Pleistocene, possibly Boulder Conglomerate zone, India. One-third natural size. Fig. 3*a*, Brit. Mus. M. 3127. Fig. 3*b*, Brit. Mus. M.3146.

TYPE. (Falconer, *op. cit.*, 1846, p. 41): 3*a*.—". . . section of the penultimate upper molar [M^2] . . . in the middle stage of wear, eleven of the thirteen plates of which it is composed, having been in use, and the two anterior ridges being worn out."

(Falconer, 1868, I, p. 422): 3*a*.—"*Elephas Hysudricus*, from the Sewalik Hills. Vertical section of penultimate upper molar, left side. The tooth is in the middle stage of wear, eleven of the thirteen plates of which it is composed having been in use, and the two anterior ridges being worn out. The same vertical disposition of ivory, enamel, and cement is presented as in the African Elephant, but the plates are thinner and more vertical; the layer of enamel is proportionally thicker; and the interspaces occupied by the cement are wider in general than the ivory plates.—B.M. (Reproduced in Plate V, fig. 1). Length, 7.7 in. [= 180 mm.]. Length of 10 plates, 5.75 in. [= 147 mm.] ."

PARATYPE.—(Falconer, *op. cit.*, 1846, p. 41): 3*b*.—" . . . portion of the last molar of the lower jaw [M_3], . . . comprising about fifteen plates [posterior plates broken off]."

(Falconer, 1868, I, p. 422): 3*b*.—"*Elephas Hysudricus*. Vertical section of portion of last molar of lower jaw, comprising about fifteen plates. The same general character, in the disposition and relative proportion of the ivory, enamel, and cement are exhibited as in the upper molar, bearing in mind that the latter is a younger and consequently smaller tooth. The layer of enamel, however, is thinner than in the upper molar. The ivory segments curve back near their base, and the apices of the posterior plates lean towards the front of the tooth, a disposition still more marked in the existing Indian Elephant. The dark shade below the ivory indicates a core of sandstone, occupying the place of the unossified part of the pulp nucleus, and of the undeveloped fangs.—B.M."

(Lydekker, 1886, p. 121): Brit. Mus. M.3146. "Fragment of the right ramus of the mandible, containing the third true molar, which has been longitudinally and vertically bisected, and shows eighteen ridges. Figured by Falconer and Cautley, *op. cit.*, pl. i, fig. 3*b*, and pl. VII. figs. 12, 12*a*. The enamel is very thin and much plicated."

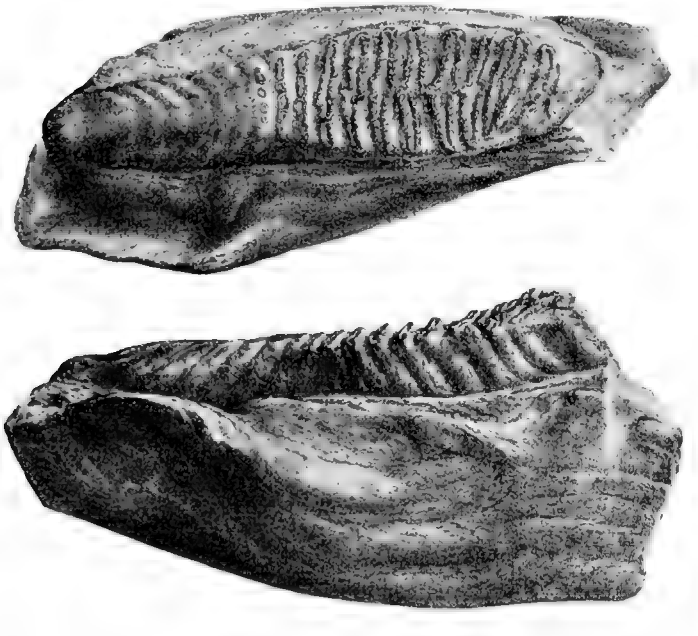
Small head, Dp^3 with 5+ ridge-plates, Dp^4 with +7+ ridge-plates; another imperfect head of young animal, Dp^3 with 5+ ridge-plates, Dp^4 with +8+ ridge-plates. Fragment of large cranium; l.Dp^4 with +7+ ridge-plates; M^1 with +8+ ridge-plates.] Plate vii, fig. 1, fragment of upper jaw, Dp^3 and Dp^4; figs. 2, 2*a*, r.M^1 with 12 ridge-plates (see vertical section); figs. 3, 3*a*, M^2 with 13 ridge-plates (see vertical section); fig. 5, l.Dp_3 with 7 or 8 ridge-plates; fig. 6, ?l.Dp_3 with 9 ridge-plates; figs. 7, 7*a*, l.Dp_3 with 7 or 8 ridge-plates; fig. 8, l.Dp_4 with 9 ridge-plates; fig. 9, Dp_4 with 9 ridge-plates; figs. 10, 10*a*, M_1 with 12 ridge-plates; figs. 11, 11*a*, ?M_2 with 12 ridge-plates; figs. 12, 12*a*, M_3 with 17–18 ridge-plates, enamel thin, plicated. Plate viii, fig. 1, cranium with M^{1-2} and tusks; M^1 with 5 remaining ridge-plates and a heel, M^2 with 10–11 ridge-plates; fig. 3, lower jaw; fig. 4, entire lower jaw, M_1 with +9+ ridge-plates, M_2 (in germ) with 9 exposed; fig. 5, extremely aged right jaw, M_3 with 5 remaining ridge-plates only. Plate xii, fig. 13*a*, r.M_3 with 10+ ridge-plates, one or two plates gone—an enormous tooth. Plate xii.b, fig. 4, M^1 with 8 ridge-plates (remarkable in having so few ridge-plates), M^2 (in germ) showing 11 ridge-plates. Plate xii.c, figs. 6, 6*a*, l.M_1 with +10+ ridge-plates (believed to have come from Nerbudda).

Falconer's (1868) Ridge Formula of Hypselephas hysudricus.—From the foregoing descriptions of twenty-nine type and referred specimens of *Elephas hysudricus* examined by Falconer may be deduced the following ridge formula, in which the minimum figures represent young or partly developed teeth, while the maximum figures represent the specific and mutational stage attained by this species at the beginning of Pleistocene time:

$$\mathrm{Dp}\ 3\,\frac{5-5\frac{1}{2}}{7-9}\ \mathrm{Dp}\ 4\,\frac{+7-8+}{9}\ \mathrm{M}\ 1\,\frac{10-12}{9+-12}\ \mathrm{M}\ 2\,\frac{13}{9+-12}\ \mathrm{M}\ 3\,\frac{}{17-18}$$

Affinities of Hypselephas hysudricus.—Falconer in his type description (1846, p. 41) of the molar teeth of *Elephas hysudricus* (Fig. 1197) intimates that these teeth are to be regarded as more primitive than those of *E. indicus*, that is, with fewer and shorter ridge-plates. In his comparison of the last superior molars of *E. indicus* with those of *E. hysudricus*, as quoted in full below, he again intimates that the grinding teeth of *E. indicus* may be derived from those of *E. hysudricus*. It was not his wont to discuss phylogeny.

Leith Adams.—The next author to discuss the relationships of *E.* [*Hypselephas*] *hysudricus* was Leith Adams in his "Monograph on the British Fossil Elephants," 1877–1881, p. 244. Leith Adams, as quoted by Lydekker (1886, p. 98) erroneously suggests that *Elephas hysudricus* gave rise to two branches, one comprising



Hypselephas hysudricus, Paratype Crown of Third Right Inferior Molar

Compare section (Fig. 1197, right)

Fig. 1198. Eighteen ridged third inferior molar of the right side, r.M_3 (cf. *Elephas hysudricus*). After Falconer and Cautley, 1846 [1845], Pl. vii, figs. 12 and 12*a*, described in 1867 (Falconer, 1867, p. 8, and 1868, Vol. I, p. 428) as follows: "Fragment of lower jaw, with last molar, entire, *in situ*. The tooth is more elongated, and includes a greater number of divisions (17 or 18) than is usual in the last inferior grinder of *E. Hysudricus*. The specimen is now cut into sections.—B. M." (Lydekker, 1886, p. 121): Brit. Mus. "M.3146. Fragment of the right ramus of the mandible, containing the third true molar, which has been longitudinally and vertically bisected, and shows eighteen ridges. . . . The enamel is very thin and much plicated." Reproduced two-ninths natural size.

Compare l.M_3 (Amer. Mus. 19869*a* Fig. 1199) also l.M_3 (Amer. Mus. 19867—Fig. 1203).

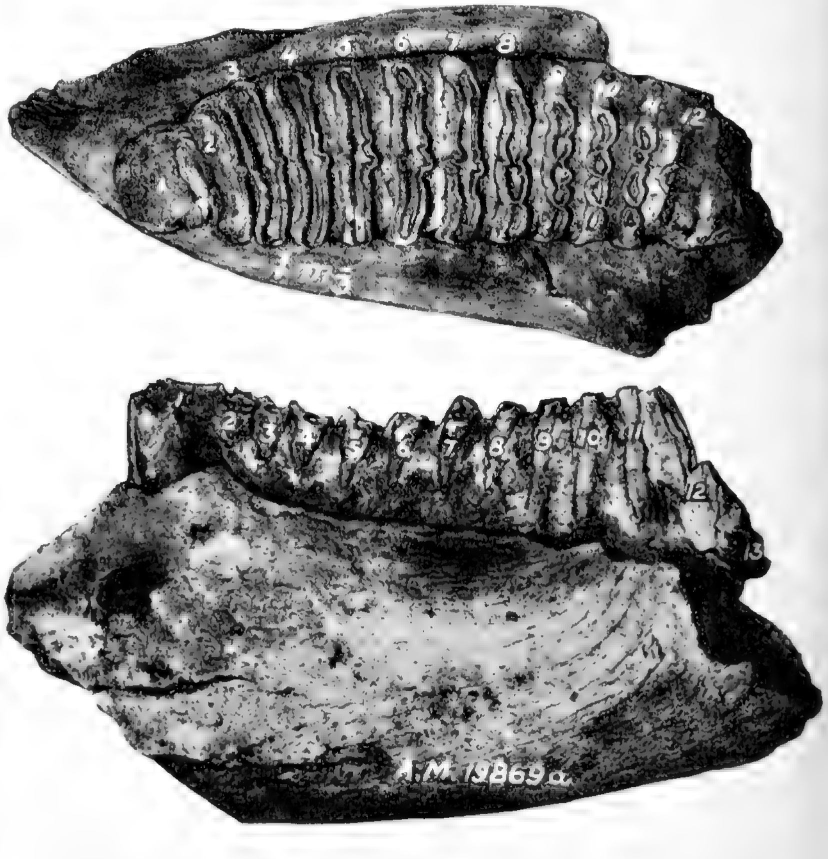


Fig. 1199. Referred third left inferior molar, l.M_3, with 13+ ridge-plates (typical 17–18), of *Hypselephas hysudricus* (Amer. Mus. 19869a). Collected by Barnum Brown in 1922 below Boulder Conglomerates, 'Upper Siwaliks,' near Siswan, India. One-third natural size. See section of same molar (Fig. 1201).

Observe that the 12 ridge-plates exposed agree very closely in character, with slightly expanded 'loxodont sinus,' with those of Falconer's paratype (Brit. Mus. M.3146) as shown in figure 1198 opposite.

?Elephas primigenius and *E. indicus*, the other comprising *Elephas namadicus, E. antiquus*, and *E. africanus*; this suggestion of Leith Adams that *E. hysudricus* gave rise on the one hand to the Indian elephant and to the mammoth, and on the other hand to the African elephant and its relatives *E. namadicus* and *E. antiquus*, arose from the very confused ideas and theories of phylogeny at the time when Leith Adams wrote his valuable monograph.

Falconer's comparative measurements (1868, Vol. I, pp. 435, 436) of the ridge-plates of M_3 in *Elephas hysudricus, E. namadicus, E. indicus* [*bengalensis*], and *E. primigenius* are extremely valuable for reference as well as an index of progressive evolution.

The comparison below (p. 1344) indicates that as the ridge-plates *increase in height and in number* they *decrease in the thickness of the enamel and in the width of the intervening spaces.*

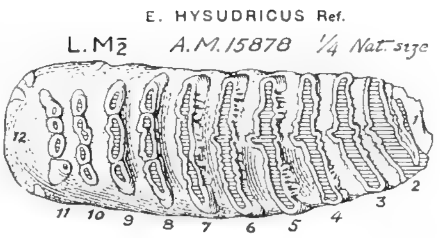


Fig. 1200. Second left inferior molar, l.M_2, of *Elephas* [*Hypselephas*] *hysudricus* ref. (Amer. Mus. 15878), acquired through exchange with the British Museum in 1911. One-fourth natural size. Observe 11 to 12 ridge-plates as in Falconer's figure (1846 [1845], Pl. VII, figs. 11, 11*a*), described in the "Palæontological Memoirs," Vol. I, p. 428, and noted in the table of measurements herewith.

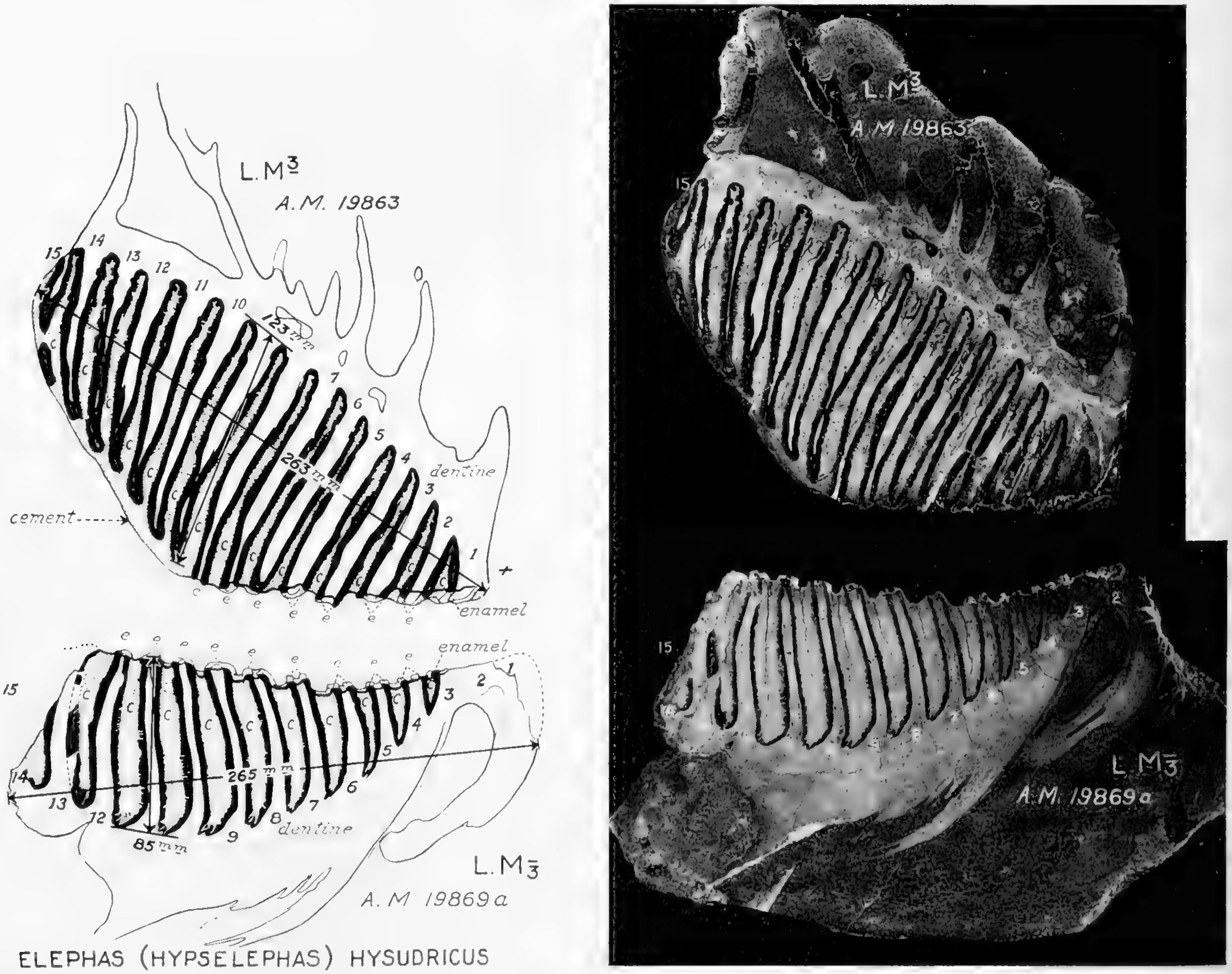
Specific Characters.—(Osborn, 1929) Infantile cranium and jaws extremely hypsicephalic, forehead plane (Figs. 1213, 1214). Adult cranium with very broad rugose fronto-occipital expansion,

TABLE XVI. Twenty-nine Specimens, Type and Referred by Falconer (1868, I, pp. 421-440), of Elephas hysudricus Figures, Page References, Measurements, and Indices

Superior	Plate	Figure	Molar	Length in. mm.	Breadth in. mm.	Index	Height in. mm.	Ridge-plates
Third Molars	XII	Footnote, p. 434. Unfig.	M^3	11. = 280	3.4 = 87	31	8th 5.4 = 138	
Second Molars	VIII	1	l.M^2	8. = 204	3. = 76	37		10-11
	I [Type]	3*a*	l.M^2	7.7e = 197e				13 [Fig. **1197**]
	VII	3, 3*a*	M^2					13
First Molars		2, 2*a*	M^1					12
	VI	Footnote, p. 427. Unfig.	M^1	6. = 153	2.6 = 66	43		½-8-½ = 10
	VIII	1	M^1	4.1 = 104	2.7 = 69	66		+5½
	XII.B	4	M^1					8
Fourth Deciduous	VI	3	Dp^4	4.3 = 111	2. = 51	46		½-8-½ = 10
		Footnote, p. 427. Unfig.	Dp^4	4.1 = 104	2. = 51	49		½-7-½ = 9
		Footnote, p. 427. Unfig.	Dp^4	4.6 = 116	2.3 = 60	52	6th 2.6 = 66	½-8-½ = 10
		2	Dp^4	4.3 = 111	2.1 = 53	48		½-7-½ = 9
		Footnote, p. 427. Unfig.	l.Dp^4	3.8 = 98	2.6 = 66	67		½-7-½ = 9
Third Deciduous		Footnote, p. 427. Unfig.	Dp^3	2.3 = 60	1.7 = 43	72		5½
		Footnote, p. 427. Unfig.	Dp^3	2.5 = 64	1.6 = 41	64		5½
		3	Dp^3	2.2 = 56	1.6 = 41	73		5e
		1	Dp^3	2.1 = 53	1.6 = 41	77		5
Inferior								
Third Molars	I [Paratype]	3*b*	M_3					15e [Fig. **1197**]
	XII	13*a*	r.M_3	11.3 = 289	4.4 = 113	39		10+
	VII	12, 12*a*	M_3					17-18 [Fig. **1198**]
Second Molars		11, 11*a*	?M_2					12
First Molars	VIII	4	r.M_1?	5.4 = 138	2.3 = 60	43		½-9-½ = 11
	VII	10, 10*a*	M_1					12
	XII.C	6, 6*a*	l.M_1	8. = 204	2.6 = 66	32	8th 4.2 = 107	+10+
Fourth Deciduous	VII	8	l.Dp_4	5.5 = 140	2.2 = 56	40		9
		9	Dp_4					9
Third Deciduous		6	l.Dp_3?	3.4 = 87	1.8 = 47	54		9
		7, 7*a*	l.Dp_3	3.1 = 79	1.5 = 39	49		7-8
		5	l.Dp_3					7-8

forehead concave (Fig. 1205). Anterior nares broadly depressed (Fig. 1205). Premaxillaries and tusk insertions narrow, nearly parallel (Figs. 1213, 1205) as in *Elephas*. Inferior mandible shallow, primitive, with very prominent rostrum (Figs. 1214, 1205). Orbits very low and prominent, unworn ridge-plates (Fig. 1203) low, primitive, composed of 4–8 conelets, totally unlike the ridge-

Measurements in Inches and Millimeters	*Elephas hysudricus*	*Elephas namadicus*	*Elephas indicus* (Assam)	*Elephas primigenius*
Height of 10th ridge-plate	4. 8=123	7.5=191	7.4=188	6.2=158
Average thickness of enamel ridge-plates	0.15= 40	0.2= 2	0.1= 1	
Length of eleven anterior ridge-plates measured near base	7. 7=197	8.1=206	5.7=146	4.5=115
Total maximum number of ridge-plates in M_3 [Osborn]	18–19	17–19	27	27



Third Superior and Inferior Molars of Elephas (Hypselephas) hysudricus in Section

One-third natural size

Fig. 1201. These beautiful sections, in comparison with those of M^3, M_3 of *Elephas indicus*, display the extraordinary evolution of the ridge-plates, especially of M^3, during Pleistocene time. The third inferior molar section, l.M_3 (Amer. Mus. 19869a) is the same molar as that shown in figure 1199; the third superior molar section, l.M^3 (Amer. Mus. 19863) is the same molar as that shown in figure 1203. All from the American Museum (Barnum Brown) Collection.

plates of *Elephas indicus*. Ridge-plate formula (Osborn, 1930):

$$\text{Dp } 3\,\frac{}{6\tfrac{1}{2}}\ \text{Dp } 4\,\frac{8+}{10}\ \text{M } 1\,\frac{11}{11+}\ \text{M } 2\,\frac{\tfrac{1}{2}-12-\tfrac{1}{2}}{\tfrac{1}{2}-12-\tfrac{1}{2}}\ \text{M } 3\,\frac{18+}{19}$$

Total number of ridge-plates, including Dp 2, in successive use: $\frac{\text{Superior } 58+}{\text{Inferior } 61+}$. As compared with the total, including Dp 2, *Elephas indicus* ridge-plates (Falconer, 1863, p. 65): $\frac{\text{Superior } 76}{\text{Inferior } 79}$.

Cranial Comparison with Elephas indicus.—The phyletic relationship of *Elephas hysudricus* to *Elephas indicus* is somewhat uncertain; *E. hysudricus* differs in its narrow molar teeth and in the presence of a faintly indicated 'loxodont sinus,' characters which are also observed in certain Japanese and East Indian specimens now referred in this Memoir to the genus *Palæoloxodon*, subfamily Loxodontinæ. The cranial profile of *E. hysudricus*, on the contrary (see comparative figure 1204), approaches that of *Elephas indicus* var. *Dauntela*, which, in turn, agrees with the extreme *E. indicus bengalensis* or continental variety of Indian elephant. The true relationship of *E. hysudricus* to the existing species and subspecies of *E. indicus* can only be determined by fundamental sections of the basicranial axes. Meanwhile *Elephas hysudricus* is provisionally placed in the same subfamily (Elephantinæ) with *Elephas indicus*.

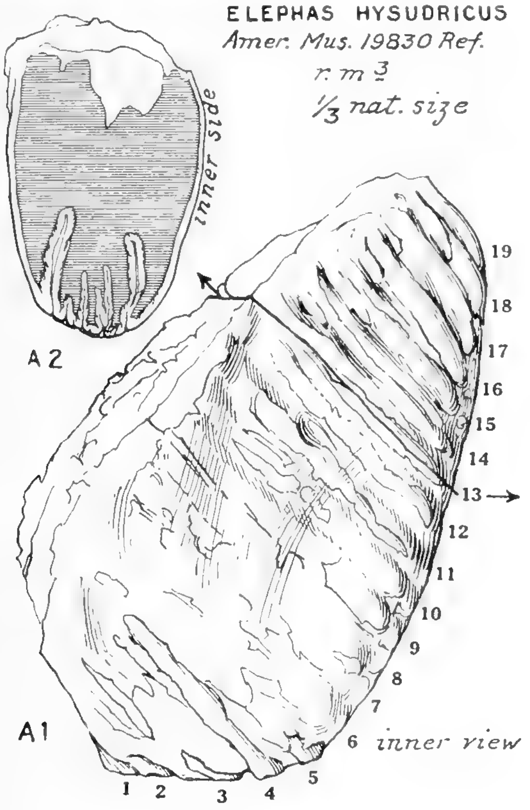


Fig. 1202. This specimen was found by Barnum Brown in 1922 at the top of the variegated clay beds, 'below conglomerates,' nine miles west of Kalka, India.

A1, Referred third right superior molar of *Hypselephas hysudricus* (Amer. Mus. 19830), exhibiting 19 ridge-plates, of which the anterior ridge-plates 1 to 5 only are worn, as shown in A3. Length 271 mm., breadth 84 mm.

A2, Transverse section of ridge-plate 13, as indicated by the arrows.

A3, Photograph of occlusal surface showing more or less fully worn anterior ridge-plates (1–5).

2. OBSERVATIONS OF OSBORN ON THE FOURTEEN SPECIMENS COLLECTED BY BARNUM BROWN (1922) REFERRED TO HYPSELEPHAS HYSUDRICUS

The following tables, giving detailed measurements of the specimens in the American Museum (Barnum Brown) collection, (namely, length, breadth, index, number of ridge-plates, and frequency of ridge-plates in 10 cm.), supplemented by lateral and crown views of seven specimens shown in figure 1203, afford for the first time a complete knowledge of the superior and inferior grinding teeth of *Elephas* [*Hypselephas*] *hysudricus* Falc. The ridge-plate formula, based on the above fourteen specimens in the American Museum, is somewhat higher than that deduced from Falconer's *twenty-nine* specimens, as follows:

$$\text{Falconer (1868): Dp } 3\,\frac{5-5\tfrac{1}{2}}{7-9}\ \text{Dp } 4\,\frac{+7-8+}{9}\ \text{M } 1\,\frac{10-12}{9+-12}\ \text{M } 2\,\frac{13}{9+-12}\ \text{M } 3\,\frac{}{17-18}$$

$$\text{Osborn (1930): Dp } 3\,\frac{}{6\tfrac{1}{2}}\ \text{Dp } 4\,\frac{8+}{10}\ \text{M } 1\,\frac{11}{11+}\ \text{M } 2\,\frac{\tfrac{1}{2}-12-\tfrac{1}{2}}{\tfrac{1}{2}-12-\tfrac{1}{2}}\ \text{M } 3\,\frac{18+}{19}.$$

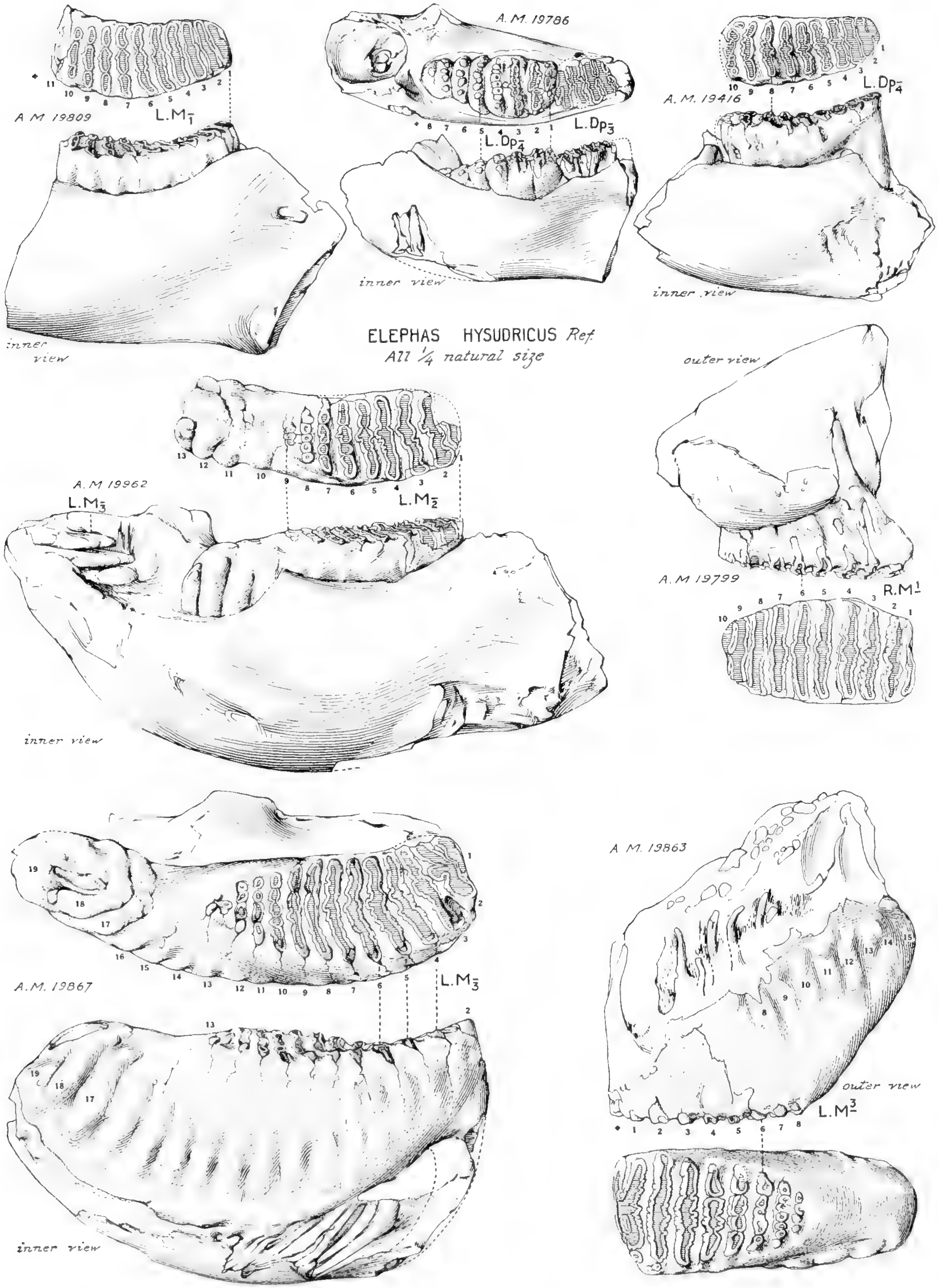


Fig. 1203. Detailed caption will be found on opposite page. See also figure 1201 for section of third superior molar (Amer. Mus. 19863).

Since the American Museum (Barnum Brown) collection is very precisely recorded as to geologic level and locality (Fig. 1196, Pl. xxv), that is, not *in situ* but found redeposited "below conglomerates" or "base of conglomerates," near Siswan, Chandigarh, Charnian, and Kalka, and since the detailed measurements and indices taken by Osborn demonstrate the close agreement with the *Elephas hysudricus* of Falconer, it is important to record this collection in the same detail as the American Museum (Barnum Brown) collection of *Archidiskodon planifrons* (p. 955) from the Pinjor horizon of the same region.

HYPSELEPHAS HYSUDRICUS REF. AND PLATELEPHAS PLATYCEPHALUS TYPE, COLLECTED BY BARNUM BROWN (1922) BELOW BOULDER CONGLOMERATES, NOT IN SITU

Elephas [Hypselephas] hysudricus Falconer

LEVEL BELOW BOULDER CONGLOMERATES	LOCALITY	AMER. MUS. NUMBER	MATERIALS	FIGURE
'Top of variegated beds, below conglomerates'	3 miles west of Chandigarh	Amer. Mus. 19866	Juvenile cranium, with Dp^1, l.M^1 *in situ*	1213, 1214 1211
			Lower jaw, with Dp_4, M_1 of both sides *in situ*	1214
'Top of variegated beds, below conglomerates"	3 miles northwest of Chandigarh	Amer. Mus. 19786	Jaw, with l.Dp_3, l.Dp_4, *in situ*	1203
'Below conglomerates'	2½ miles south of Charnian	Amer. Mus. 19809	Jaw, with l.M_1 *in situ*	1203
'Below conglomerates'	2 miles south of Charnian	Amer. Mus. 19799	Right M^1	1203
'Upper Siwaliks'	Near Siswan	Amer. Mus. 19962	Fragment of jaw, with l.M_2 *in situ*	1203
'Below conglomerates'	3 miles north of Siswan	Amer. Mus. 19783	Fragment of jaw with M_1 *in situ*, M_2 with 9 anterior ridge-plates exposed (not figured in present Memoir)	
'Below conglomerates'	3 miles north of Siswan	Amer. Mus. 19867	Left M_3	1203
'Upper Siwaliks'	Near Siswan	Amer. Mus. 19863	Left M^3	1203
'Upper Siwaliks'	Near Siswan	Amer. Mus. 19869a	Left M_3	1199, 1201
'Top of variegated beds, below conglomerates'	9 miles west of Kalka	Amer. Mus. 19830	Right M^3	1202
'Below conglomerates'	2½ miles south of Charnian	Amer. Mus. 19809A	Fragment of jaw, with l.M_1 *in situ*	1206
'Below conglomerates'	3 miles west of Chandigarh	Amer. Mus. 19956	Jaw, young, with l.Dp_3	
'Upper clays, below conglomerates'	2½ miles northeast of Charnian	Amer. Mus. 19416	Left Dp_4	1203
'Below conglomerates'	3 miles west of Chandigarh	Amer. Mus. 19915	Right M^2	1215
Platelephas platycephalus Osborn, Type				
'Upper Siwaliks' 'Base of conglomerates'	Siswan, bed of Amilee Creek	Amer. Mus. 19818	Skull	1217–1219, 1207

INFERIOR AND SUPERIOR GRINDERS OF HYPSELEPHAS HYSUDRICUS REF., AMERICAN MUSEUM (BROWN COLLECTION, 1922)

Compare with Type and Paratype (Figs. 1197, 1198). Uniform one-fourth scale

Fig. 1203. This figure clearly displays crown and lateral views of seven out of the fourteen inferior and superior grinding teeth collected by Barnum Brown in 1922 in the Upper Siwaliks of India, as follows:

L.Dp_3, l.Dp_4, crown and lateral (Amer Mus. 19786), 3 miles northwest of Chandigarh	5+, 8+
L.Dp_4, crown and lateral (Amer. Mus. 19416), 2½ miles northeast of Charnian	10
L.M_1, crown and lateral (Amer. Mus. 19809), 2½ miles south of Charnian	11+
R.M^1, crown and lateral (Amer. Mus. 19799), 2 miles south of Charnian	10+
L.M_2, crown and lateral (Amer. Mus. 19962), near Siswan	13
L.M_3, crown and lateral (Amer. Mus. 19867), 3 miles north of Siswan	19
L.M^3, crown and lateral (Amer. Mus. 19863), near Siswan. Two to three anterior ridge-plates worn off	+15 = 18+

TABLE XVII. FOURTEEN SPECIMENS COLLECTED (1922) BY BARNUM BROWN (EXCLUSIVE OF AMER. MUS. 15878) AND REFERRED BY OSBORN TO HYPSELEPHAS HYSUDRICUS, ALSO TYPE OF PLATELEPHAS PLATYCEPHALUS, LOWER PLEISTOCENE

Figure in Present Memoir	Amer. Mus. No.	Molar	Length mm.	Breadth mm.	Index	Height mm.	Ridge-plates	Ridge-plates in 10 cm.
1202	19830	r.M^3	271	84	31	6th = 137	19	6½
1203	19863	l.M^3	268	98	36	8th = 128	15	5½–6
1215	19915[1]	r.M^2	270	80	30	3d = 99	½—12—½ = 14	5
1213, 1214	19866	l.M^1	180	57	32	7th = 103	11	6
1203	19799	r.M^1	152+	79	52	3d = 56+	10	6
1213, 1214	19866	l.Dp^4	104	55	53	7th = 40	8½	8½
1203	19867	l.M_3	365	101	28	12th = 145	½—17—½ = 19	6
1199, 1201	19869a	l.M_3	270e	78	29	10th = 91	13+	5
1203	19962	l.M_2	224	69	31	8th = 90e	12½ = 13	6
	19783	r.M_2	128+	76e	59e	8th = 105e	9+	
[1200	15878[2]	l.M_2	230	85	37	11th = 91	11½ = 12	5]
1203	19809	l.M_1	139+	64	46	11th = 70e	11+	7
1206	19809A	l.M_1	144	71	49	7th = 72	½—7+ = 8	5½
	19783	r.M_1	130	73	56	6th = 60	+6½	5½
1203	19786	l.Dp_4	133e	46	36	3d = 38	8+	8
1203	19416	l.Dp_4	130	54	41	8th = 42e	10	8
1214	19866	r.Dp_4	112	55	49	7th = 40e	9	8½
1214		l.Dp_4 (worn)						
1203	19786	l.Dp_3	58	36	62		5+	
	19956	l.Dp_3	74	41		2d = 48	6⅓	
			Platelephas platycephalus Type					
1207, 1219	19818	M^3 fractured		87			16½	

The slight difference in the Falconer (1868) and Osborn (1930) ridge-plate formulæ apparently does not indicate a progressive ascending mutation; it would seem that the forty-three specimens (Falconer 29, Osborn 14) represent a similar stage of evolution.

MAXIMUM MEASUREMENTS OF FORTY-THREE SPECIMENS FROM THE FALCONER (LEFT) AND THE BROWN (RIGHT) COLLECTIONS

	Max. Length	Max. Breadth	Index	Max. Height	Max. Ridge-plates
Third superior molar:	280–271	87–98	31	138–137	18+
Third inferior molar:	289–365	113–101	29–39	145	19

To supplement Falconer's excellent figures of *Elephas hysudricus*, seven out of the fourteen members of the dental series represented in the Barnum Brown collection of 1922, namely, Dp 3, Dp 4, M 1, M 2, M 3, are figured in great detail in figure 1203, both in crown and lateral views.

3. CRANIAL CHARACTERS AND AFFINITIES OF HYPSELEPHAS HYSUDRICUS

ADULT CRANIA.—Superficially the cranium of *Elephas* [*Hypselephas*] *hysudricus*, as observed below (Fig. 1204), is wholly *distinct* from that of any species of *Loxodonta* and the frontal profile broadly resembles that of *E. indicus* (Dauntela var.); but the cranium as a whole is far less bathycephalic. The deep concavity of the forehead is exaggerated by the overhanging fronto-occipital crest, doubtless for the attachment of the great muscles of

---

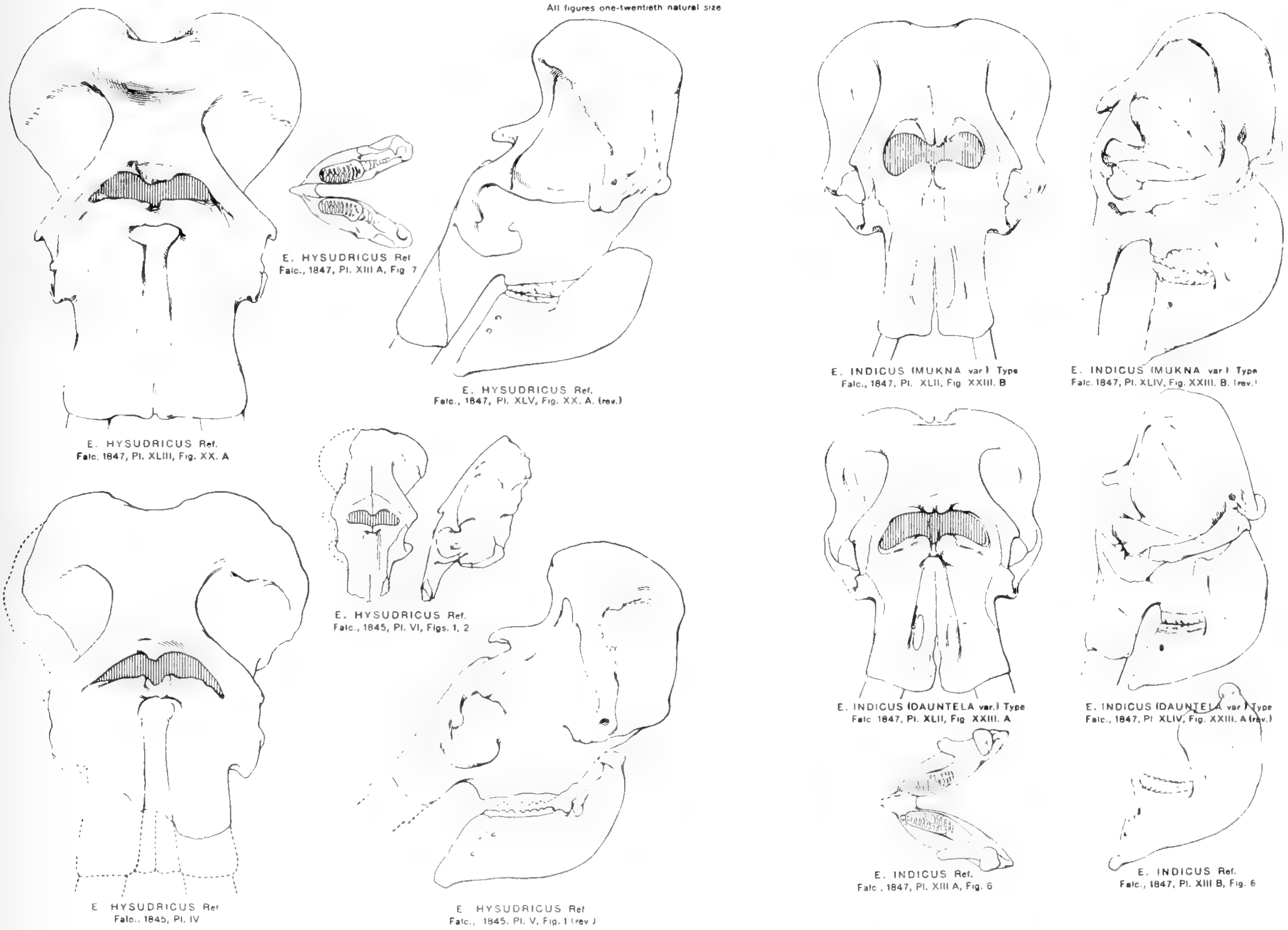
[1] This r.M^2 (Amer. Mus. 19915) Osborn erroneously made the type of *Elephas platycephalus angustidens* (Osborn, 1929.797, pp. 22,23) identifying it as an l.M_3. It now proves to be an r.M^2 of *Elephas* [*Hypselephas*] *hysudricus*.

[2] Acquired through exchange with the British Museum, 1911.

the head, neck, and proboscis. We observe in *E. indicus* (Dauntela var.) somewhat similar profile and front views (Fig. 1204) correlated with the very powerful muscular attachments and greatly enlarged tusks. Differing from either *Loxodonta* or *Elephas* are the lowered orbits of *Hypselephas*.

With the exception of this distinctively low position of the orbits the front view of the cranium of *Hypselephas hysudricus* is observed (Fig. 1204) to bear a closer resemblance to that of the broad-narial variety *Elephas indicus*

SKULLS OF ASIATIC ELEPHANTS (AFTER FALCONER)
All figures one-twentieth natural size



COMPARISON OF TWO CRANIA OF HYPSELEPHAS HYSUDRICUS WITH MUKNA AND DAUNTELA VARIETIES OF ELEPHAS INDICUS

The juvenile cranium '*E. hysudricus*' ref. (Falconer, 1845, Pl. VI, figs. 1 and 2) is regarded as belonging to *Hypselephas hysudricus*

Fig. 1204. Comparison of *Elephas* [*Hypselephas*] *hysudricus* (Lower Pleistocene of India) with *Elephas indicus* (Mukna var.) and *E. indicus* (Dauntela var.) living today in India. After Falconer and Cautley, 1846 [1845 and 1847]. One-twentieth natural size.

The two adult crania of *Elephas* [*Hypselephas*] *hysudricus* reproduced in the above figure from Falconer and Cautley, 1845, Pl. IV, Pl. V, Fig. 1, and 1847, Pl. XLIII, Fig. XX.A, are distinguished from the crania of *E. indicus* (Mukna var.) and *E. indicus* (Dauntela var.) not only by much less depth and greater breadth (bathycephaly), but by the *extremely depressed position of the orbits* which are placed barely above the roots of the grinding teeth, whereas in *E. indicus* the orbits are relatively elevated or directly opposite the occipital condyle and in *E. hysudricus* entirely *below* the level of the occipital condyle.

This deeply depressed position of the orbits is also observed in the juvenile cranium, figured to the same scale above as '*E. hysudricus*' ref., Falc., 1845, Pl. VI, Fig. 2, referred in this Memoir to *Hypselephas hysudricus*.

Observe that this marked lowering of the orbits also characterizes the juvenile cranium in the American Museum, Brown Collection (Amer. Mus. 19866) reproduced in figures 1213 and 1214, giving *Hypselephas hysudricus* not only an entirely different aspect, as shown in the restoration (Fig. 1174), but in our opinion precluding the possibility of the derivation of the cranium of either variety of *E. indicus* from the cranium of *E. hysudricus*.

bengalensis (Dauntela var.) than to the narrow-narial variety *Elephas indicus ceylanicus* (Mukna var.). Both in frontal and lateral aspect the two skulls referred to *E. hysudricus* by Falconer, and beautifully figured in his Atlas of the "Fauna Antiqua Sivalensis," bear a superficial resemblance to the frontal and lateral aspect of the cranium of *E. indicus* (Dauntela var.). This resemblance, however, is certainly a *convergence,* because the low, narrow grinding teeth of the type of *Hypselephas hysudricus* are wholly different in proportion from those of *E. indicus*. The molars exhibit some resemblance or analogy to the extinct *Palæoloxodon* of Africa in (1) their loxodont sinus, and (2) their long, narrow proportions.

The juvenile cranium (Figs. 1213, 1214) of '*Elephas hysudricus*' [=*Hypselephas hysudricus*] moreover bears a somewhat close resemblance to the juvenile cranium of *E. indicus* (Fig. 1180A) at the time when the fourth upper and lower milk molars, l.Dp_4, l.Dp^4, are in use; the extreme elevation or hypsicephaly of the skull at this stage seems to be an adaptation to the large, elongate, permanent grinders, $M^{1\text{-}2}$, $M_{1\text{-}2}$.

From cranial and juvenile characters alone we are thus inclined to regard *Hypselephas hysudricus* as an early offshoot in Lower Pleistocene times of the main stem which gave rise to *Elephas indicus* of recent times. It is interesting to note that the progression of the ridge formula in the case of these two species is similar to that which separates other Upper Pleistocene and recent types, namely:

Recent: *Elephas indicus*, M 3 $\frac{24}{24\text{-}27}$. Total number of ridge-plates (Dp 2–M 3): $\frac{76}{79}$.

Lower Pleistocene: *Hypselephas hysudricus*, M 3 $\frac{18+}{17\text{-}19}$. Total number of ridge-plates (Dp 2–M 3): $\frac{58+}{61+}$.

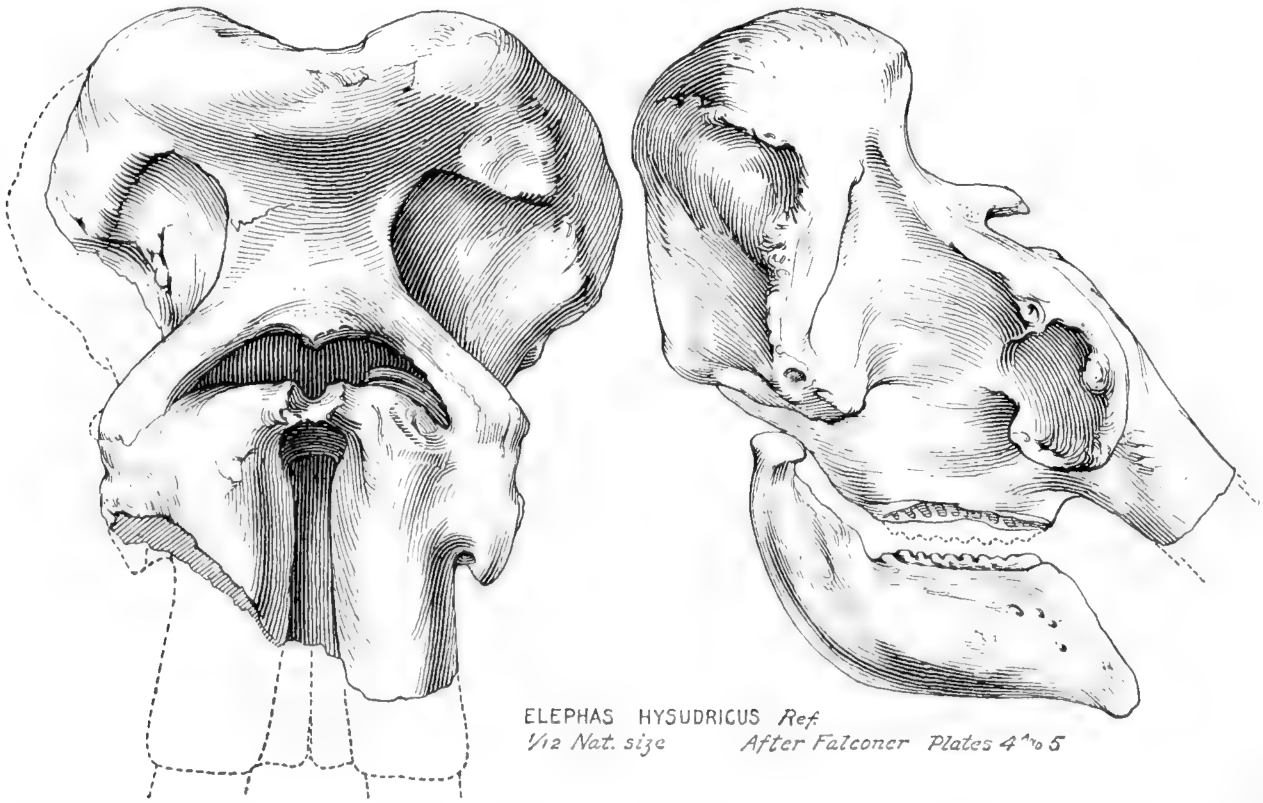


Fig. 1205. Referred adult male cranium of *Elephas* [*Hypselephas*] *hysudricus*, after Falconer and Cautley, 1846 [1845, Pl. IV, and Pl. V, fig. 1]. Brit. Mus. M.3109. Reproduced one-twelfth natural size.

Grinding Mechanism.—The relatively low-crowned grinding teeth in the upper and lower jaws, with maximum elevations of the ridge-plates of M^3 (138–137) and of M_3 (145) are correlated with the two very important and distinctive characters of the cranium and jaws, which are clearly displayed in figure 1205, reproduced from Falconer and Cautley, 1846 [1845, Pl. iv, and Pl. v, figs. 1 and 2], Brit. Mus. M.3109. The jaws seem to be relatively shallow and primitive with prominent rostrum. Since the crowns of the superior grinding teeth are relatively low, the very prominent orbits with their rugose borders are placed immediately above the roots. We observe that this cranium is of an adult male, with primitive lower jaw associated; premaxillaries contracted, as in *Elephas indicus*; inframaxillary rostrum very prominent; molar ridge-plates probably $\frac{18+}{17-19}$ (compare Figs. 1204 and 1213).

Falconer's description (1867, p. 6, and 1868, Vol. I, pp. 425 and 426) is as follows:

> Plate IV. *Elephas Hysudricus* (Falc. and Caut.), from the Sewalik hills. Front view of skull, one-fifth nat. size. This fine specimen was purchased from Conductor Dawe.—B. M.
>
> Length of the cranium from the protuberances of the occipital to the broken tip of left incisive, 45. in. Length from broken occipital condyles to anterior border of alveolus, 28. in. Vertical height of head, from broken condyles to the pyramidal bulge of sinciput, 26. in. Vertical height from surface of occipital to the tip of the nasals, 27.75. Extreme width of the head restored on left side, 38.5 in. Width at narrowest part of forehead between zygomatic fossæ, 10.5 in. Width of naso-maxillary fissure, 18.5 in. Depth from tip of nasals to anterior margin of naso-maxillary fissure, 3.5 in. Depth of rami of naso-maxillary fissure, 4. in. Width between middle of the orbits, mesial, 26. in. Greatest width of zygomatic fossa, 12. in. Depth from hollow of frontal to condyles, 20. in. Depth from posterior border alveolus to margin of naso-maxillary fissure, 21.5 in. Length of alveolus of last grinder, 10.5 in. Depth of hollow of frontal below mesial plane, 4.5 in. Extreme width of alveolus, 4.75 in. Width of incisive sheath in front of the alveolus, 18.5 in. Transverse diameter of the left tusk, 7.5 in. Antero-post. of the left tusk, 7.75 in. Depth below mesial plane of the occipital hollow, 8.5 in. Width of bottom of occipital hollow, 5.75 in. Depth of posterior bulge of the cranium from the occipital bone to surface of zygomatic fossa, 15.5 in. Least width at back part of cranium behind the alveoli, 8.5 in. Depth from posterior broken surface of condyle to the posterior border of the alveolus, 19. in. Depth of infra-orbital foramen, 2.5 in. Transverse diameter of foramen, 1.75 in. Length of infra-orbital canal, 6. in. Depth of the left orbit, 6.75 in. From anterior margin auditory foramen to anterior border of the orbit, 20. in. Vertical diameter auditory foramen, 1.5 in. Depth of the fossa between incisive sheaths at the top of it, 6.5 in. Width across fossa, 3. in. Depth of the naso-maxillary vault, 12. in. Depth of skull from posterior end of socket to the orbit, 22.5 in.

Fig. 1206. Anterior portion of left ramus of *Hypselephas hysudricus* (Amer. Mus. 19809A) containing alveolus of l.Dp_4, and crown of l.M_1 exhibiting 8 anterior ridge-plates of the typical 11–12. A young jaw with greatly elongated rostrum, from the Upper Siwaliks, near Charnian, below the 'conglomerates.'

The Amherst Cranium (Fig. 1210).—Supplementing the above description by Falconer of an adult male cranium, with large tusks, enormously expanded occipitofrontal crest, and relatively flat, backwardly sloping occiput, is a female cranium in the Amherst Museum represented in figure 1210, characterized

PALATAL ASPECTS OF PLATELEPHAS PLATYCEPHALUS, ARCHIDISKODON PLANIFRONS, AND E. (HYPSELEPHAS) HYSUDRICUS

ALL ONE-EIGHTH NATURAL SIZE BY A UNIFORM REDUCTION

Observe that there is an extremely wide contrast in the *axial planes* of *Platelephas platycephalus* (Fig. 1207), of *Archidiskodon planifrons* (Fig. 1208), and of *Hypselephas hysudricus* (Fig. 1209), as follows: (1) In *P. platycephalus* and in *A. planifrons* the *basi-occipital, palatal,* and *maxillo-premaxillary* planes are nearly on the same horizontal level. The *H. hysudricus* cranium, on the contrary, is greatly modernized, because the *basi-occipital, palatal,* and *maxillo-premaxillary* planes, which form three acute angles with each other, conform with the relative *bathycephaly*, or deepening, and *brachycephaly*, or broadening, of this cranium. In brief, *H. hysudricus* possesses a modernized cranium with a relatively primitive condition of the grinding teeth or molars.

Fig. 1207. Type cranium of *Platelephas platycephalus* (Amer. Mus. 19818), adult male, probably from the Upper Pliocene Pinjor horizon, Upper Siwaliks, India, not *in situ.* One-eighth natural size. The 16½ ridge-plated third superior molars are imperfectly shown in this retouched photograph. Compare figure 1219 A1, same cranium one-twelfth natural size, and figure 1218A, one-sixteenth natural size.

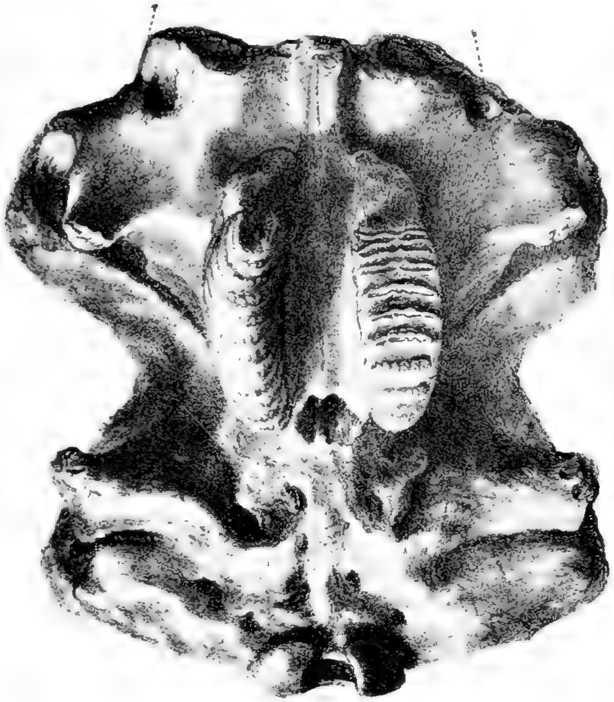


Fig. 1208. Referred adult cranium of *Archidiskodon planifrons*, a supposed female with small tusks (Brit. Mus. M. 3060). Observe the relative elongation of this Upper Pliocene basi-occipital and palatal region. After Falconer and Cautley, 1846 [1845, Pl. x, fig. 2]. One-eighth natural size.

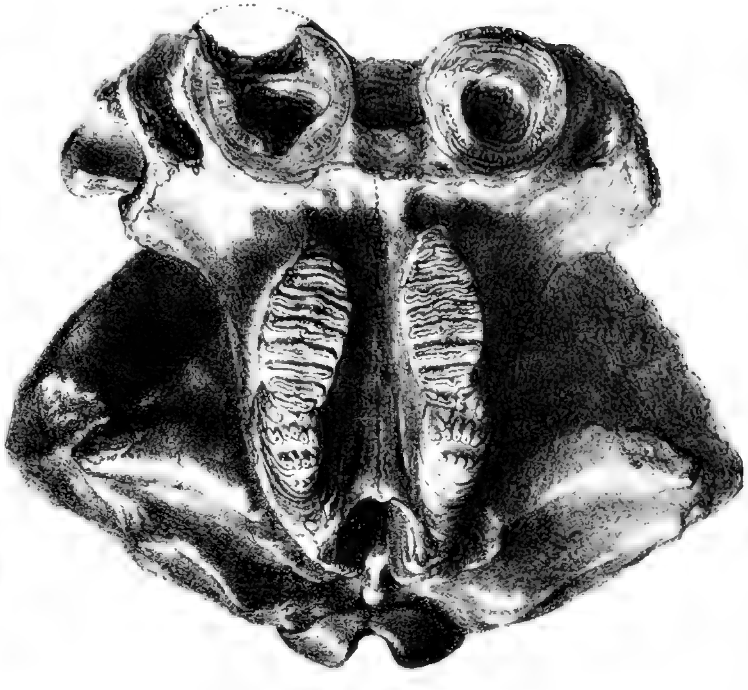
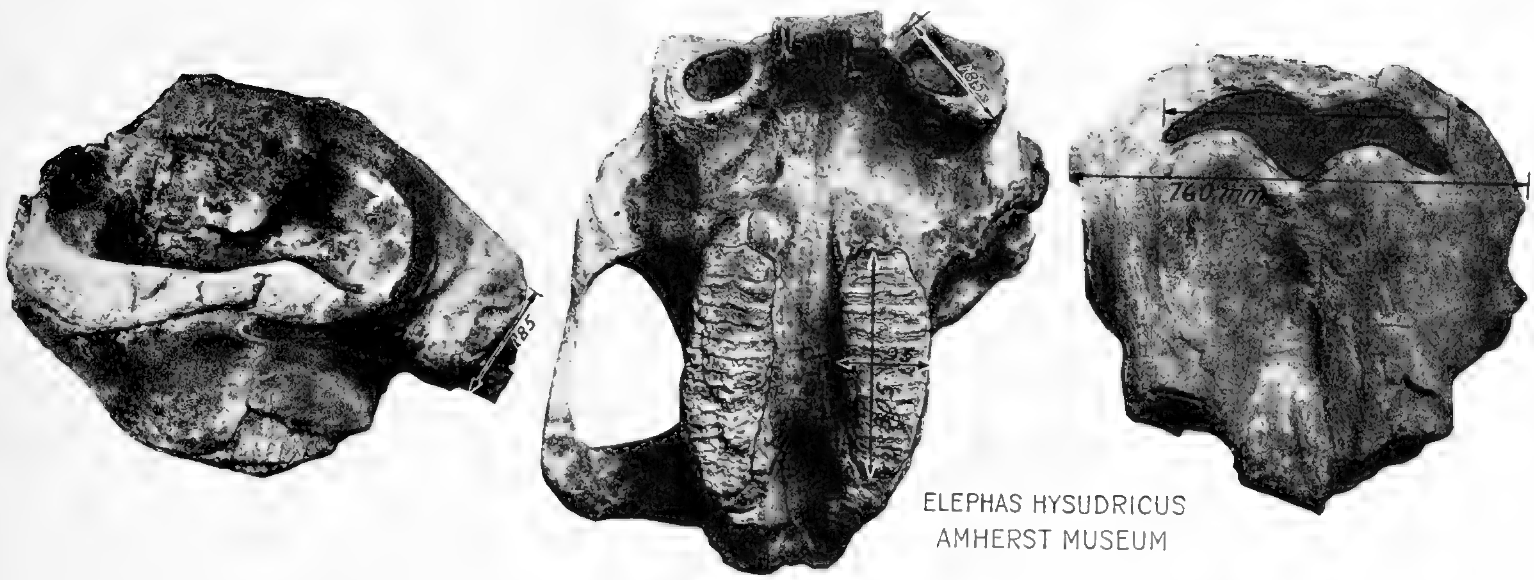


Fig. 1209. Palatal aspect of male cranium of *Hypselephas hysudricus* with large downwardly directed tusks; age indicated by second superior grinders, M^2, in place, third superior grinders, M^3, just coming into use (Brit. Mus. M. 3110). Observe extreme brachycephaly of occipital region and extreme fore-and-aft shortening of cranium by approximation of incisive tusks to condyles. After Falconer and Cautley, 1846 [1845, Pl. v, fig. 3 (rev.)]. One-eighth natural size.



HYPSELEPHAS HYSUDRICUS IN AMHERST MUSEUM, RIGHT LATERAL, PALATAL, AND FRONTAL ASPECTS
Compare with Falconer's cranium (Fig. 1205), also with palate of *Platelephas platycephalus* (Fig. 1219) below

Fig. 1210. Female cranium referred to *Hypselephas hysudricus* collected near Kullu, a district of the Punjab, lying north and northwest of Simla, by M. M. Carleton between 1854 and 1861 and presented by him to the Amherst Museum. The skull was originally covered with very coarse conglomerate, possibly indicating its horizon as the Pleistocene Boulder Conglomerate.

The third left superior grinder, l.M^3, length 305 mm., width 95 mm., displays 17+ ridge-plates, of which the anterior 6 are worn. It thus resembles an l.M^3 of *Hypselephas hysudricus* ref. (Amer. Mus. 19863—Fig. 1203 of the present Memoir) and establishes its specific position as *Hypselephas hysudricus* rather than *Archidiskodon planifrons*.

by relatively small tusks; the less rugose orbits, in a similarly depressed position, are seen to lie (Fig. 1210, left) directly upon the premaxillary sockets of the tusks instead of being raised above the tusk sockets, as in *E. indicus* (Mukna var.) and *E. indicus* (Dauntela var.). The agreement of the crania in the British Museum with the imperfect cranium in the Amherst Museum in this very exceptional position of the orbits tends further to demonstrate that *Hypselephas hysudricus* belongs in a totally distinct phylum or line of descent, which is not to be regarded as ancestral to the collective *Elephas indicus* type.

In palatal view the extreme *brachycephaly* of the *Hypselephas hysudricus* cranium is clearly displayed (Fig. 1209) in contrast to the more elongate and less widely expanded palate of *Archidiskodon planifrons* (Fig. 1208) and to the extremely primitive and elongate palate of *Platelephas platycephalus* (Fig. 1207). We observe that in *Hypselephas hysudricus* (Falc., 1845, Pl. v, fig. 3) the tusks are vertically crowded close to the second superior molars, that the space between the third molars and the occipital condyles is extremely short, that the posterior nares open close to the occipital condyles, that the occiput is enormously broadened.

In contrast the tusks of *Archidiskodon planifrons* (Fig. 1208) point obliquely forwards and downwards instead of directly downwards, there is a very wide space between the posterior grinding teeth with their widely set ridge-plates and the occipital condyles, the paroccipital palate is much narrower than in *Hypselephas hysudricus*. Finally, in *Platelephas platycephalus* (Fig. 1207) we observe a wholly distinct type of cranium, much more primitive than that of *A. planifrons* and far more primitive than that of *Hypselephas hysudricus*.

JUVENILE CRANIA WITH DENTITION

Figure 1204 above (p. 1349) illustrates the extreme contrast between the juvenile and adult crania of *Hypselephas hysudricus* as reproduced to a one-twentieth scale from Falconer and Cautley's beautiful lithographic drawings. Falconer's material (1868, Vol. I, p. 426) included a "Perfect small head from the Geol. Soc. Museum, with the second [Dp^3] and third [Dp^4] milk molars and first true molar in germ." This small head is reproduced herewith in figure 1212, also in figure 1213 (after Falconer and Cautley, Pl. vi, figs. 1, 2). Another figure (Falconer and Cautley, 1846 [1845, Pl. vi, fig. 3]) is that of the under surface of a young skull (see Falconer, 1868, Vol. I, p. 426): "Fig. 3.—*Elephas Hysudricus*, under surface of young skull. This specimen agrees in age and characters with that shown in figs. 1 and 2, except that the third [Dp^4] milk molar has 8 principal ridges, with a front and back heel, instead of 7 as in the other.—B.M. Length of second [Dp^3] milk molar, 2.2 in. Width of second [Dp^3] milk molar, 1.6 in. No. of plates about 5. Length of third [Dp^4] milk molar, 4.3 in. Width, 2. in. Interval between second [third] teeth, 1.2 in. Between third [fourth], 2.1 in."

In the American Museum collection is a slightly more mature juvenile cranium (Amer. Mus. 19866) shown in our figures 1211, 1213, and 1214, with the 8–9 ridge-plated l.Dp^4 in full use, and the l.M^1 just coming into use (Fig. 1214).

The American Museum also has another specimen, an isolated r.M^2 (Amer. Mus. 19915), which from its extreme narrowness was mistaken by Osborn (Osborn, 1929.797, pp. 22 and 23) for a third lower molar and erroneously made the type of *Elephas platycephalus angustidens;* further examination proves that this is a right second superior molar, r.M^2, of *Hypselephas hysudricus* Falconer and Cautley, with ½–12–½ ridge-plates (=14 ridge-plates), agreeing with the typical M^2 ridge-plate formula, as shown in our revised figure (Fig. 1215).

With these specimens we are now enabled to measure, describe, and portray completely the characters of the palate, jaws, and dentition, including M^1 M^2, of the juvenile *Hypselephas hysudricus.*

Molar Crown Characters.—The first striking peculiarity of the young American Museum skull (Fig. 1214) is: 1) The extreme length and narrow width of the molar crowns, the successive indices of Amer. Mus. 19866 being:

Amer. Mus. 19866	Length	Breadth	Index
8½ ridge-plated l.Dp^4	103	53	51
11 " " l.M^1	171	60e	35e
9 " " r.Dp$_4$	111	55	50
Amer. Mus. 19915			
14 ridge-plated r.M^2	267	80	30

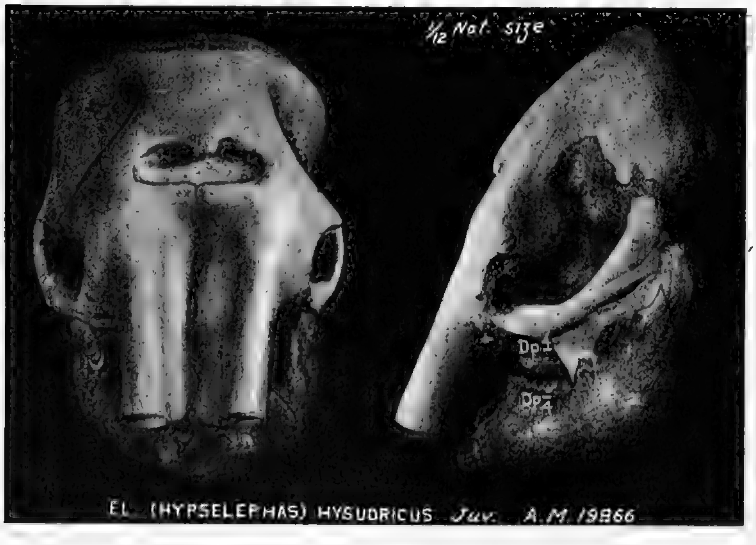
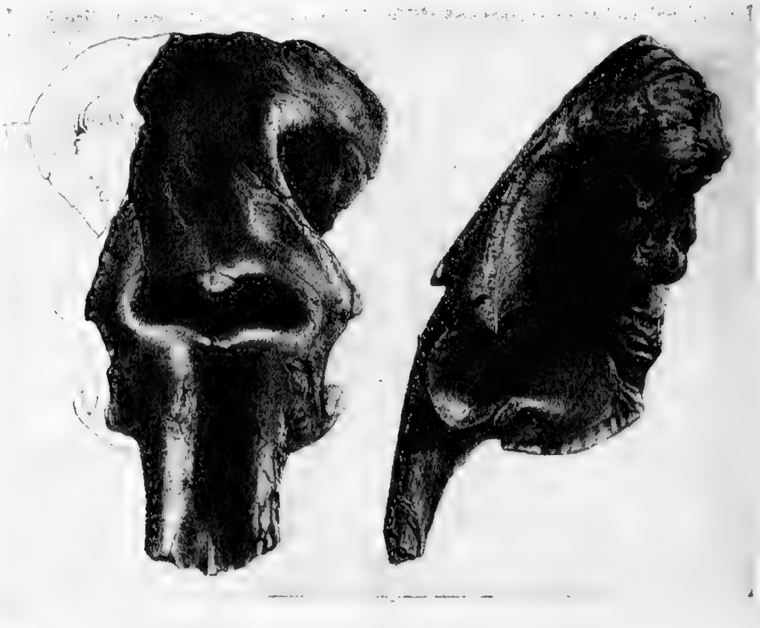


Fig. 1211. Photographic view of restored juvenile skull of *Hypselephas hysudricus* ref. (Amer. Mus. 19866), with Dp^4 and anterior portion of M^1 in use. Collected by Barnum Brown in 1922, 'top of variegated beds, below conglomerates,' three miles west of Chandigarh. One-twelfth natural size. See caption to figure 1213 for measurements. Same cranium and jaws shown in figure 1214.



Referred Cranium of Hypselephas hysudricus

Fig. 1212. "Perfect small head from the Geol. Soc. Museum [presented by the Council of the Geological Society to the British Museum—Brit. Mus. M.3114], with the second [Dp^3] and third [Dp^4] milk molars and first true molar in germ." After Falconer and Cautley, 1846 [1845, Pl. vi, figs. 1, 2], front and side views, about one-eighth natural size. Same cranium diagrammatically drawn in Fig. 1213.

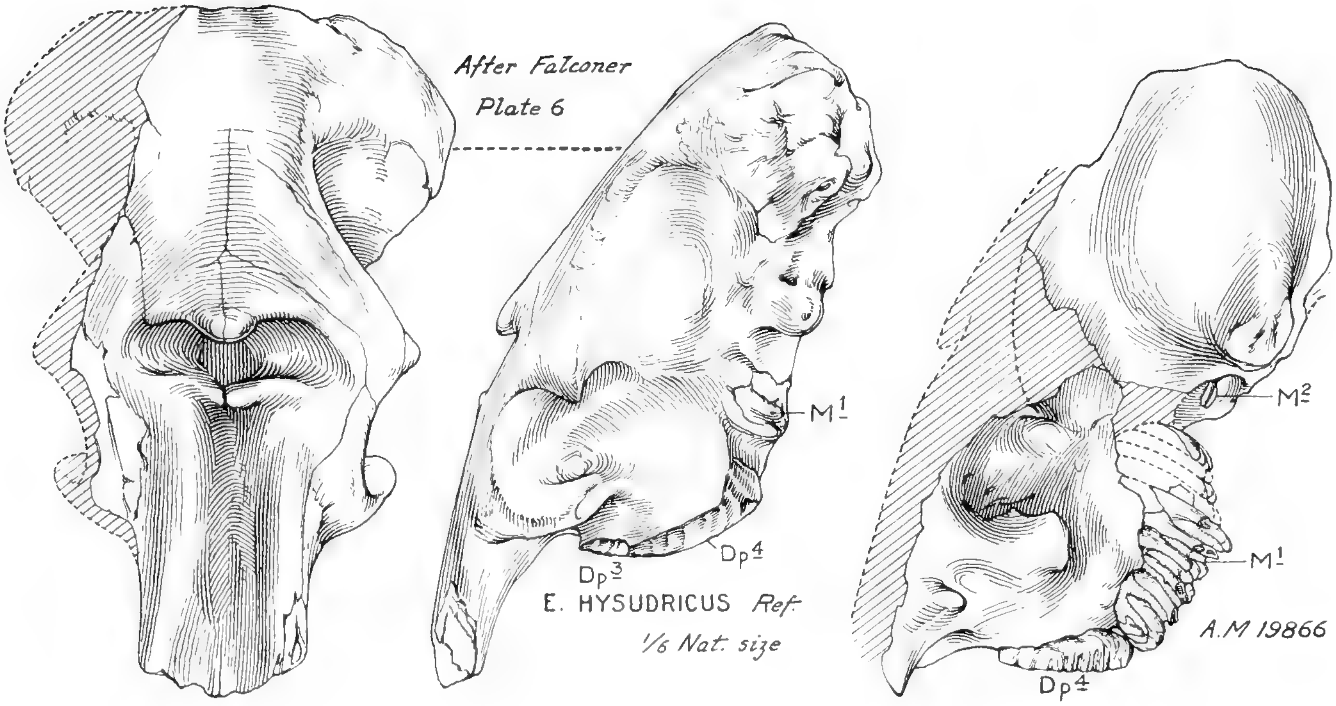


Fig. 1213. JUVENILE CRANIA OF HYPSELEPHAS HYSUDRICUS, BRITISH AND AMERICAN MUSEUMS

One-sixth natural size. Compare figures 1211, 1212, 1214

(Left and center) British Museum cranium, a younger stage with 4½ ridge-plated Dp^3 and ½-7-½ ridge-plated Dp^4 in use. Same cranium as figure 1212.

(Right) American Museum cranium (Amer. Mus. 19866), somewhat older, Dp^3 shed, the 8½–9 ridge-plated Dp^4 and the anterior portion of the 10-11 ridge-plated M^1 in use; M^2 in germ.

(Left) After Falconer and Cautley, 1846 [1845, Pl. vi, figs. 1, 2]. A referred juvenile cranium presented to the British Museum by the Council of the Geological Society (and now bearing the catalogue number, Brit. Mus. M.3114). This specimen is described by Falconer (1867, p. 6, and 1868, I, p. 426) as a "Perfect small head from the Geol. Soc. Museum, with the second [third] and third [fourth] milk molars, and first true molar in germ," namely, Dp^3 with 4½ ridges, Dp^4 with ½–7–½ ridges. Observe the extreme hypsicephaly and fore-and-aft compression, the plane forehead, the occiput without the superior expansion seen in the adult, and the extremely narrow premaxillary rostrum.

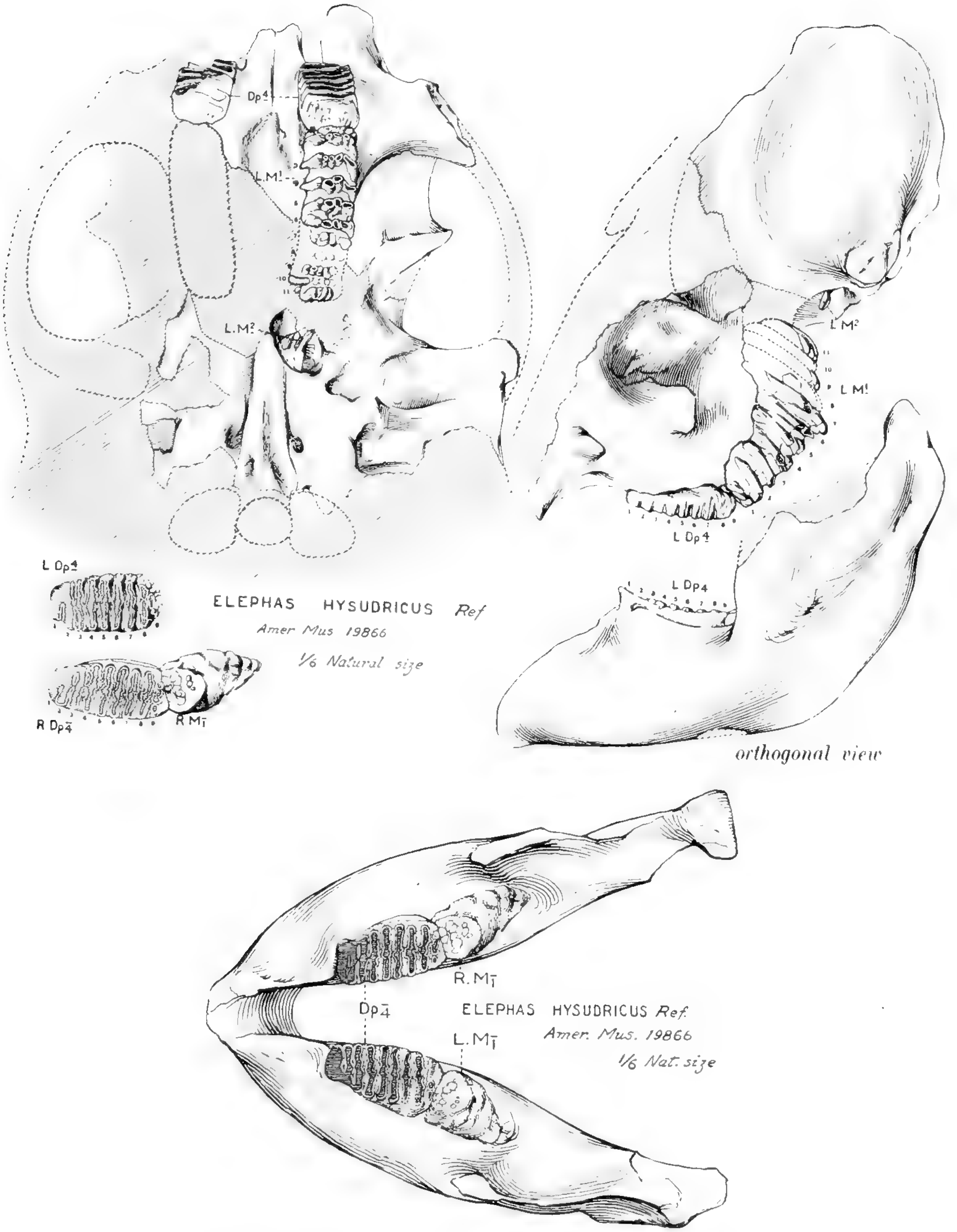
(Right) Reconstructed juvenile cranium (Amer. Mus. 19866), somewhat older, because the 8½–9 ridge-plated Dp^4 is still in complete use, the 10–11 ridge-plated l.M^1 is partly in use, the l.M^2 is in germ. Compare the Barnum Brown table of measurements (p. 1348), also figure 1214 of the same cranium on a one-sixth scale, and figure 1211 on a smaller one-twelfth scale.

Measurements (Falconer, 1868, Pl. VI, Figs. 1, 2, p. 426, and Amer. Mus. 19866)

	B. M.	A. M.
Extreme length		Restored
Occipital crest to broken incisor	594 mm.	
Occiput to tip of nasals	351	
Nasal opening		
Width	180	
Depth at sides	72	
Lower end to tip of incisives	242	
Tip of nasals to left orbit	162	
Width of brow	320	
At temporal contraction	153	
Width at contraction of incisive sheaths	144	257e
Width at tips of incisive sheaths	144	Restored
Orbits		
Extreme length	88	
From outer margin of orbit to occiput	427	

	B. M.	A. M.
Left incisive tusk		Missing
Vertical diameter	47 mm.	
Transverse diameter	39	
Second [third] milk molar, Dp^3		
Length	53	
Width behind	40	
Number of plates	4½	
Third [fourth] milk molar, Dp^4		
Length	110	104
Width in front	53	55
Number of ridges	½-7-½	8½-9
First true molar, M^1		
Length		171
Maximum width	In germ	60e
Number of ridge-plates		11

Observe the extreme hypsicephaly, bathycephaly, and cyrtocephaly of these two crania in the juvenile condition, very similar to that in the juvenile *Elephas indicus* female cranium (Fig. 1180A, after de Blainville), totally different from the juvenile *Loxodonta africana* crania illustrated in Chapter XIX.



JUVENILE CRANIUM AND JAWS OF REFERRED HYPSELEPHAS HYSUDRICUS

Fig. 1214. This important juvenile specimen (Amer. Mus. 19866) was collected by Barnum Brown in 1922 in the Upper Siwaliks of India, not *in situ* but in erosion material 'below the conglomerates,' 3 miles west of Chandigarh. Reproduced herewith one-sixth natural size.

(Upper left) Palatal view showing Dp^4 with 8½ to 9 ridge-plates in full use; the 11 ridge-plated $l.M^1$ is obliquely placed showing the slight wear of the apices of ridge-plates 1 to 6. Observe the extreme simplicity of the *five conelets* composing the ridge-plates of $l.M^1$—a very primitive condition. Compare figure 1203.

(Lower left) Detailed view of crown of $l.Dp^4$ with 8½ to 9 ridge-plates, $r.Dp_4$ with 9 ridge-plates, and $r.M_1$.

(Upper right) Left lateral view of cranium showing the germ of $l.M^2$; the partly restored $l.M^1$ *in situ* with 11 ridge-plates (to be compared with the crown view of same in upper left) exhibiting the very simple condition of 4 to 5 conelets; and the worn 8½-9 ridge-plated $l.Dp^4$.

(Lower right) Left lateral aspect of mandibular ramus with very prominent rostrum.

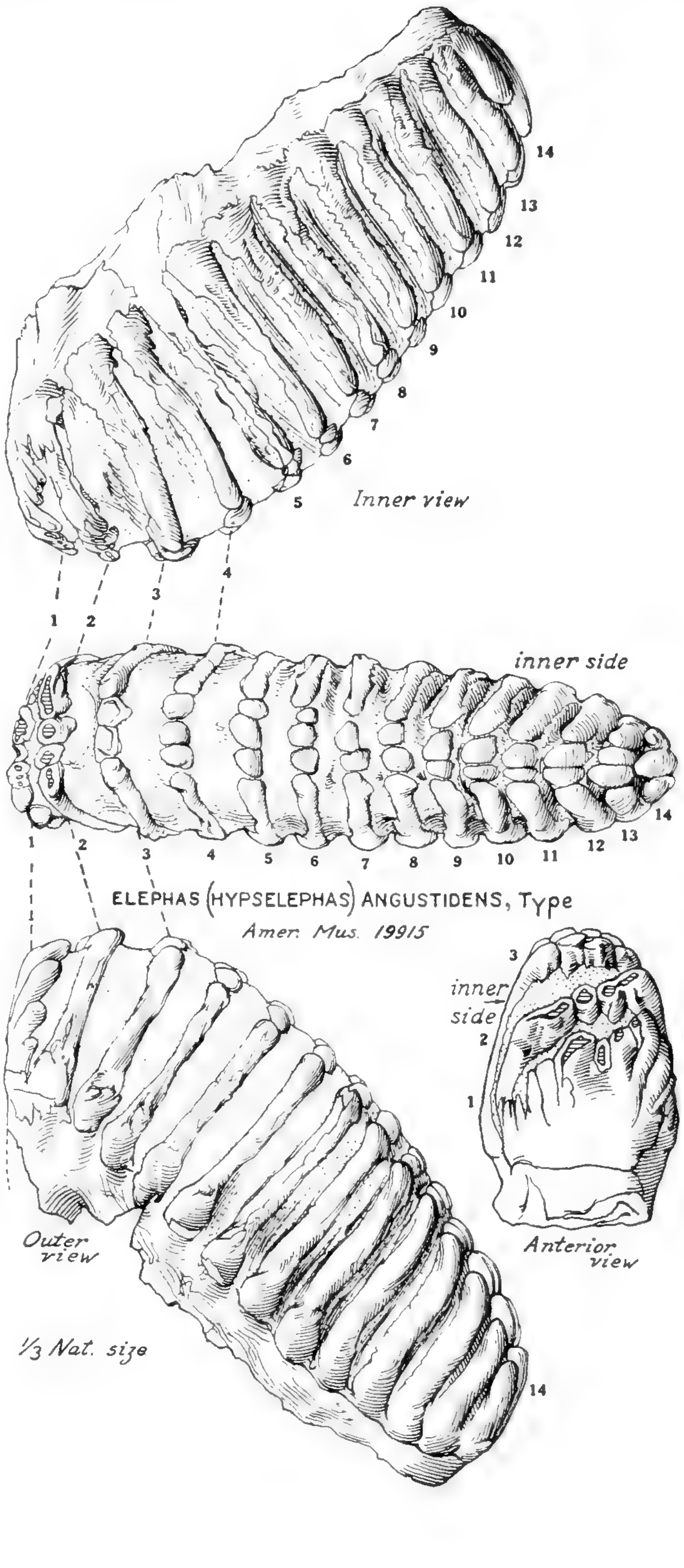
(Lower center) Coronal aspect of the same juvenile jaw (Amer. Mus. 19866); Dp_4 with 8½-9 ridge-plates, typical of *Hypselephas hysudricus*; $r.M_1$ with 3 worn ridge-plates. Observe the elongation of the rostrum.

2) A second distinction, as clearly displayed in l.M^1 (Fig. 1214), and in r.M^2 (Fig. 1215), is the compression and simplicity of the conelets on the summits of the crowns; in l.M^1 the three anterior ridge-plates bear 5 conelets each, the eight succeeding ridge-plates bear 4 conelets each; in r.M^2 the six anterior ridge-plates bear 5 conelets each, the succeeding seven to thirteen ridge-plates bear 4 conelets each.

3) A third distinctive character (Fig. 1215) is the wide separation by cement filled valleys of the seven anterior ridge-plates.

4) A fourth distinction is the relatively uniform height of the ridge-plates, the maximum at the 5th plate in r.M^2 (Fig. 1215) being 102 mm.

Elephas platycephalus angustidens (=Synonym of Hypselephas hysudricus).—The type of this subspecies was collected by Dr. Barnum Brown in 1922 three miles west of Chandigarh, Siwalik Hills, India, 'below conglomerates' (see Osborn,1929.797, p. 22, also fig. 22, p. 23). It was at first regarded by the present author (cf. p. 1354 above) as a third inferior molar of the left side, l.M$_3$, because of its extreme narrowness. On further study it proved to be a second superior molar of the right side, r.M^2, referable to *Hypselephas hysudricus* (Fig. 1215).



Hypselephas hysudricus

Fig. 1215. A second superior molar of the right side, r.M^2, with 14 ridge-plates, of which the three anterior (1–3) are partly worn. One-third natural size. This is the molar tooth originally selected by Osborn (Osborn, 1929.797, pp. 22, 23) as the type of *Elephas platycephalus angustidens*; erroneously interpreted as a third inferior molar; the simple ridge-plate structure corresponds exactly with that in the young cranium of *Hypselephas hysudricus* ref. (Amer. Mus. 19866—Figs. 1213, 1214).

SUPERFAMILY: ELEPHANTOIDEA Osborn, 1921

FAMILY: ELEPHANTIDÆ Gray, 1821

SUBFAMILY: ELEPHANTINÆ Osborn, 1910

GENUS: **PLATELEPHAS** Osborn, 1936

Original reference: Osborn, 1934.926, p. 285 (*nomen nudum*); Vol. I of present Memoir (1936), p. 12, and Pl. XI.

Genotypic species: *Elephas platycephalus* Osborn, 1929.797, p. 21.

GENERIC CHARACTERS.—Cranium relatively elongate, dolichocephalic, and platycephalic; occipital condyles not greatly elevated above level of grinding surface of molars; deeply indented supra-occipital border. Premaxillaries greatly elongated in front of molars, somewhat divergent; tusks unknown. Orbits large, elevated, near frontal profile. Grinding teeth imperfectly known, relatively low, ridge-plates directly transverse, as in *Elephas*, no rudiment of 'loxodont sinus.' Ridge-plate formula, as far as known, M 3 $\frac{16\frac{1}{2}}{}$. Habits unknown, probably like those of *Elephas indicus*. Very primitive in cranial structure and in the broad, depressed ridge-plates.

This unique cranial type representing a hitherto unknown and very primitive stage was found in a separate mass of consolidated gravel which had apparently been washed down from an original boulder conglomerate bed and into a shallow region bordering Amilee Creek, near Siswan, Simla Hills, India. While not found *in situ*, it is apparently of the same Lower Pleistocene age as the 'Boulder Conglomerate formation' above.

Fig. 1216. UPPER PLIOCENE AND LOWER PLEISTOCENE STRATA NEAR SISWAN, INDIA

After photographs by Barnum Brown

(Left) Cranium of *Platelephas platycephalus* as found on the banks of Amilee Creek, near Siswan, India, not *in situ*. 'Conglomerate' matrix was attached to the skull, indicating that it had been deposited above the 'variegated clays,' as shown to the right. With the exception of a single skull of *Boselaphus*, no fossils were found in the 'conglomerates.'

(Right) Alternating 'variegated clays' and 'conglomerates' typical of the region at Siswan, India, near which was found much of the material collected by Dr. Barnum Brown in 1922.

The upper levels, consisting of 'variegated clays' alternating with 'conglomerates,' are below the true Boulder Conglomerate zone.

In brief, the proportions of this cranium, as compared with those of the middle-aged *Elephas indicus*, may be described as dolichocephalic rather than brachycephalic, as platycephalic rather than hypsicephalic, as longirostral rather than brevirostral—all of which are primitive characters. The present phyletic reference is to the subfamily ELEPHANTINÆ.

Platelephas platycephalus Osborn, 1929

Figures 1174, 1207, 1216–1219

From near Siswan, bed of Amilee Creek, Simla Hills, India. Upper Pliocene or Lower Pleistocene.

Elephas platycephalus Osborn, 1929. "New Eurasiatic and American Proboscideans," Amer. Mus. Novitates, No. 393, Dec. 24, 1929, pp. 21 and 22. TYPE.—Cranium with M^3 of both sides partly exposed. Amer. Mus. 19818. Collected by Barnum Brown in 1922. HORIZON AND LOCALITY.—Upper Pliocene or Lower Pleistocene. Near Siswan, bed of Amilee Creek, Simla Hills, India. TYPE FIGURE.—Osborn, *op. cit.*, 1929.797, p. 22, fig. 21.

TYPE DESCRIPTION.—"SPECIFIC CHARACTERS.—Cranium of very primitive elephantine affinity, low, flattened; orbits widely separated from occiput; premaxillary rostrum somewhat broadened, resembling that of *Elephas*; posterior nares deeply indented; occipital condyles on relatively low plane, not greatly elevated above grinders; relatively long and narrow cranial proportions. Cranium widely different from the elevated *Elephas* [*Hypselephas*] *hysudricus* or the greatly elevated *Elephas indicus* crania. Ridge-plates of type molars fractured or absent. Estimated ridge-plate formula: M 3 $\frac{16\frac{1}{2}}{}$."

DISCOVERY.—This animal appears to belong to a primitive stage in the evolution of the Elephantinæ, although it cannot at present be regarded as ancestral either to *Hypselephas hysudricus* possibly of the Boulder Conglomerate formation, or to *Elephas indicus* of closing Pleistocene and Recent time.

Both the cranium and the grinding teeth are profoundly distinct from those of *Archidiskodon planifrons*, a species so very abundant in the lower levels of the Pinjor horizon; thus *Platelephas platycephalus* cannot be related to the genus *Archidiskodon*, as clearly shown in comparative views (Figs. 1207, 1208). The relatively narrow premaxillaries and closely appressed superior tusks forbid its relationship to *Palæoloxodon namadicus* of the much more recent Middle [to Upper] Pleistocene of India. Consequently it seems best to place it temporarily in the true Elephantinæ phylum.

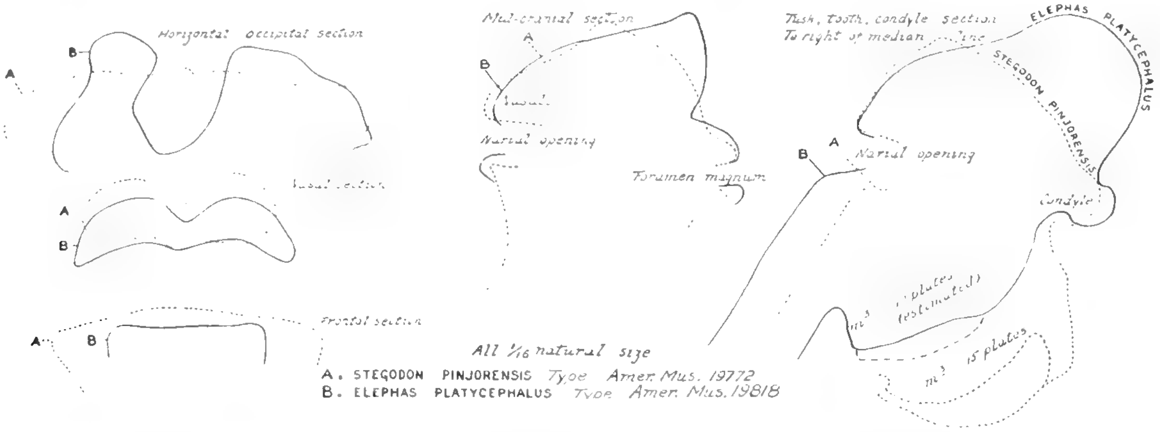
As shown especially in figures 1217 and 1218, the cranium is widely different from that of *Stegodon pinjorensis* or of *S. insignis-ganesa*. The specific name *platycephalus* refers to the highly characteristic and primitive lowering of the fronto-occipital profile and the placing of the occipital condyle only slightly above the horizontal level of the maxillary border of the superior grinders, as shown in figure 1219A. Whereas the juvenile and adult *Hypselephas hysudricus* crania (Figs. 1213, 1205, 1218) are markedly hypsicephalic, the adult cranium of *Platelephas platycephalus* is relatively platycephalic. The breadth-length index, as measured from the summit of the occipital crest to the extremity of the premaxillaries, compared with the greatest breadth across the orbits, is 60, indicating that this cranium is also relatively *dolichocephalic.*

The principal measurements of the type are as follows:

CRANIAL MEASUREMENTS OF PLATELEPHAS PLATYCEPHALUS TYPE

Length	
Occipital condyles to extremity of premaxillaries	1085
Postoccipital crest to extremity of premaxillaries	1140
Breadth across	
Supra-orbital processes	680
Occipitotemporal region (Fig. 1219 A3)	665
Orbitofrontal region	332
Extremity of premaxillaries	522e
Widest portion of zygomatic arches	800e
Height	
From level of supra-occipital prominence to maxillary borders of grinders	616
Occiput, condyles to occipital crest	425
Alveolar border of M^3 to top of frontals	555
Grinding surface of M^3 to midfrontal region	605e
Length	
Occipital condyles to posterior borders of third grinder, r.M^3	342
Facial length, front of M^3 to tips of premaxillaries	507
Alveolus of left superior grinder	
Length	220e
Width	90e
Alveolus and crown of right superior grinder	
Length of r.M^3 (preserved portion)	175
Width of r.M^3	87
Transverse diameter of incisive alveoli	120–135e

The first distinctive character is the height from the grinders to the midfrontal region, namely, 605e mm., as compared with 645 mm. in the cranium of *Elephas indicus*. The second distinction of importance is the primitive elongation of the cranium, the basicranial region measuring from the occipital condyles to the tip of the premaxillaries 1085 mm., as compared with the maximum occipital or temporal width of 665 mm. The third distinction is the marked separation of the orbits and the width across the supra-orbital region, 680 mm., as compared with the relatively closely placed orbits of *E. indicus*, 561 mm.



COMPARISON OF THE TYPES OF PLATELEPHAS PLATYCEPHALUS AND STEGODON PINJORENSIS

Fig. 1217. *Platelephas platycephalus* (—— - -) type cranium in vertical section (right) has a totally different fronto-paroccipital profile from *Stegodon pinjorensis* (.......), when the occipital condyles are placed at the same level.

The midcranial section (center) differs much less, because of the deep indentations in the fronto-occipital condyles, as shown in figure 1219 A2.

The horizontal occipital section (left) of *Stegodon pinjorensis* (.......) is shown to be much broader than that of *Platelephas platycephalus*; the nasal sections are about the same breadth; the *frontal* section of *S. pinjorensis* is much broader than that of *P. platycephalus*.

COMPARATIVE MEASUREMENTS OF CRANIA OF PLATELEPHAS PLATYCEPHALUS AND ELEPHAS INDICUS

	Elephas platycephalus (Amer. Mus. 19818)	*Elephas indicus* (Amer. Mus. Dept. Mam. 54261) Male
Width across temporals..........	665 mm.	710 mm.
Maximum width of occiput.......	680	755
Maximum width across occipital condyles................	216	214
Height of occiput from condyles to occipital crest............	425	440
Width across supra-orbital processes	680	561
Width across extremities of premaxillaries..................	522e	414
Width of narial opening (inside)...	435	323
Length, front of right molar to tip of premaxillaries...............	507	325
Length of premaxillaries to occipital condyles..................	1085	925
Height of cranium, grinders to mid-frontal region...............	605e	645
Width across midtemporal region..	332	334
Length of tusks (outer curve)......		2245
Transverse diameter of tusk at emergence, i.e., width of alveoli	120–135e	117

The premaxillaries are distinguished from those of *Palæoloxodon namadicus* by less expansion, the width being 522e mm., as compared with 857 mm. in the Pignataro skull of *Hesperoloxodon antiquus italicus*; they are, however, somewhat broader and relatively more expanded than the cranium of *Elephas indicus*, in which they measure transversely 414 mm. A fourth distinction is the elongation of the premaxillaries in front of the third upper

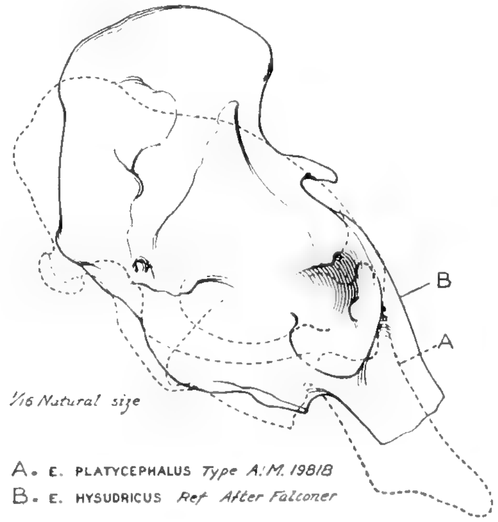


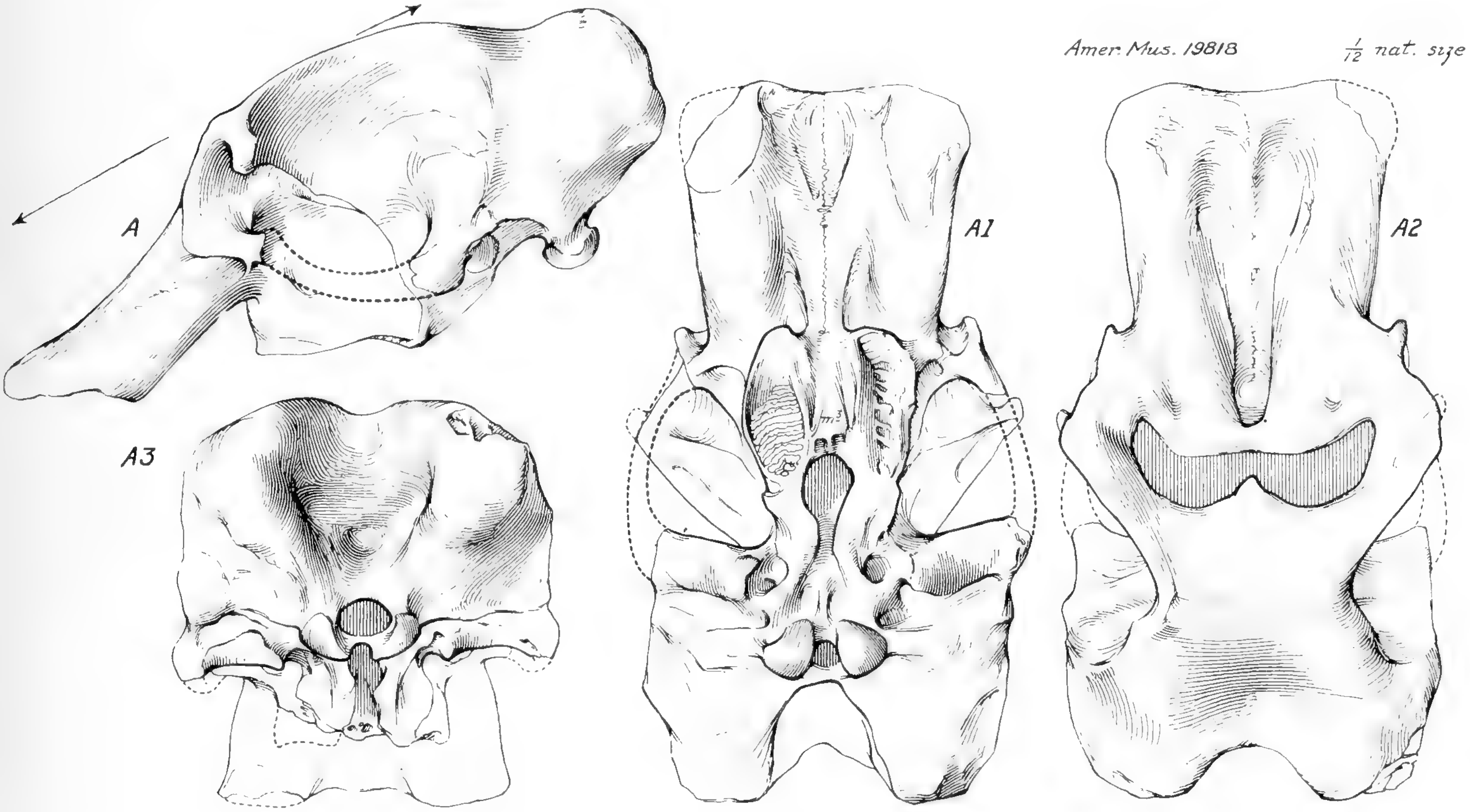
Fig. 1218. Right cranial profile of *Platelephas platycephalus* (......) and of *Hypselephas hysudricus* (——), one-sixteenth natural size.

This figure illustrates the primitive platycephaly of the *Platelephas platycephalus* type as compared with the relative hypsicephaly of the *Hypselephas hysudricus* type. Both crania may be regarded as adult and fully developed. Observe that *P. platycephalus* does not in the least resemble the juvenile profile of *H. hysudricus* (Fig. 1213); it is much more primitive (cf. Figs. 1207, 1209).

grinders, the distance being 507 mm., as compared with 325 mm. in *E. indicus*.

Special features are: (1) Very deep excavation of the superior border of the occiput, totally unlike that of either *Archidiskodon* or *Elephas*; (2) the relative breadth of the anterior nares, measuring transversely 435 mm.; (3) the very deep excavation just below the anterior nares of the space between the premaxillary sockets and the tusks; (4) and finally the great prominence of the orbital rims, indicating that the eyes were set very wide apart.

Platelephas platycephalus, therefore, is totally different in profile as well as in superior and palatal aspects from either *Archidiskodon planifrons* or *Elephas indicus*.



Type Cranium of Platelephas platycephalus

Fig. 1219. Four aspects of the type cranium of *Platelephas platycephalus* (Amer. Mus. 19818), discovered by Barnum Brown in 1922 above the Pinjor horizon of the Upper Siwaliks, 'below conglomerates.' One-twelfth natural size. Compare Osborn, 1929.797, p. 22, fig. 21.

A, Left lateral aspect, exhibiting orbits, auditory openings, and occipital condyles on practically the same level.

A1, Palatal view, exhibiting slightly broadened premaxillary rostrum, maxillary prominence containing fractured M^3 with 16½ ridge-plates, deeply indented posterior nares, and relatively low plane of occipital condyles.

A2, Superior aspect, exhibiting moderately broadened premaxillaries, flattened fronto-occipital plane with deeply indented supra-occipital border without rugosity, and relatively long and narrow cranial proportions.

A3, Posterior aspect, exhibiting moderately small, elevated occipital condyles when cranium is placed in exactly the same plane as (A). Compare with widely different cranial profile of *Hypselephas hysudricus* (Fig. 1205) and of *E. indicus ceylanicus* or *E. indicus bengalensis* (Fig. 1170), in which the occipital condyles are elevated above the level of the orbits.

APPENDIX TO CHAPTER XX

[In a recent Memoir (1936) by Père Teilhard de Chardin and Dr. C. C. Young, "On the Mammalian Remains from the Archaeological Site of Anyang," Pal. Sinica, (C), XII, Fasc. 1, pp. 1, 52, and 53) they have given their views regarding the existence in historical times of the wild Indian elephant in China, from which the following has been extracted. The reader is also referred to the map on page 1594 which gives the range of *Elephas indicus*, its varieties and subspecies, as far as known.—Editor.]

Close to the modern city of Changteho (N. Honan) are buried under the mud of the Chinese maritime plain the remains of Anyang, the latter city being the old capital of the Shang dynasty (Circa 1400 B.C.—1100 B.C.).

Remains of Elephant are not uncommon in Anyang (fragmentary young skulls and limb-bones). We only have at our disposal an incomplete lower molar of a young individual, probably a tooth number 3. Six lamellae are preserved, occupying a length of 68 mm. Thickness of one lamella 5 mm.; breadth 48 mm. The lamellae are widely separated and set rather obliquely.

As much as we can judge from this unsatisfactory specimen, we most probably are dealing here with an *Elephas indicus*, and not at all with *E. primigenius*, as supposed by Matsumoto (1916), basing on a centrum of vertebra and Hopwood (1934), using fragmentary molars. This reference of the Anyang Elephant to the Mammoth group was only possible when the deposits were still held as being of Pleistocene age.

The presence of *E. indicus* in Honan once more raises the question as to how far north this form was living in China, and as to how long it lasted there, in historical times. Of course, palæontologically, we have no evidence to suggest as yet that the species ever existed in China proper. Its closest ally, *E. namadicus*, has never been found in the post-Loessic deposits. And no *Elephas* (but only *Stegodon*) occur in the Szechuan Pleistocene fissures. But historically it has been stated in some Chinese texts which were recovered in Anyang that 'the king hunted and killed an Elephas(?)'. A critical discussion of those texts was given by Dr. Chang (1926). Dr. Chang concluded that there are no historical evidence proving the presence of wild Elephant and Rhinoceros in N. China since historical times. This view seems to be so far the most conservative and the best supported by facts.

We shall therefore admit here that the Anyang Elephant, just like the Tapir of the same locality, represents a southern type imported to the city as a tribute, possibly for hunting purposes. . . It has to be noted in this connection that these exotic animals were brought and kept alive. Both in the case of the Elephant and the Tapir, our fossils belong to young individuals represented not only by some ivory but also by perfectly useless bones.

CHAPTER XXI

NOMENCLATURE OF THE PROBOSCIDEA

HISTORY OF NOMENCLATURE OF THE MASTODON AND THE MAMMOTH. CHRONOLOGIC LISTS OF SUPERFAMILIES (1921–1935), FAMILIES (1821–1937), SUBFAMILIES (1838–1937), GENERA AND SPECIES (1735–1939).

1. History of nomenclature of the Mastodon and the Mammoth.
2. List of superfamilies.
3. List of families.
4. List of subfamilies.
5. Genera and species of the Proboscidea in the order named by the authors in the original descriptions.

Professor Osborn regarded nomenclature as "the *tool* rather than the *master* of palæontologic thought" and believed that "no technical principles should override the work of the early discoverers and naturalists." As repeatedly observed in the present Memoir (see especially Vol. I, Chap. I, pp. 5–13, also Vol. II, p. 1173), he thought it "impracticable in *palæontology* to apply all the principles of nomenclature established in *zoology* and botany, because the classification of the imperfectly known fossil forms is ever changing with our increasing knowledge of *origins, adaptive radiations, and phyletic successions.* Such mutability does not disturb the nomenclature of living animals and plants, in which priority of adequate description, figure, and definition is the chief concern of systematists."

Doctor Hopwood in his Memoir of 1935 on the "Fossil Proboscidea from China" (p. 11) states that he has "attempted to make of the Rules [International Rules of Zoological Nomenclature] a useful servant, rather than to allow them to become a blind, unreasoning, master." The extent of the difficulties encountered in Proboscidean palæontology may be judged from the accompanying nomenclature of the Mastodon and the Mammoth.

This chapter was not completed by the author, but has been compiled by the editor from materials left by Professor Osborn, under the conditions mentioned in the "Publication Note" on page viii of Volume I.

1. HISTORY OF NOMENCLATURE OF THE MASTODON AND THE MAMMOTH

1788 The genus *Mammonteus* Osborn (1924.633, p. 2; *Mammonteum* Camper, 1788, p. 251) is of doubtful validity; in fact, it is possible that Professor Osborn would have abandoned it in his final revision of the present Volume and adopted *Mammuthus* Burnett, 1830, as the reader may conclude from the following account of the nomenclature of the northern or woolly mammoth and of the true mastodon (*Mastodon americanus*), the descriptive literature of which is so involved that the history of one is inseparable from that of the other. Consequently the subject is treated chronologically, dating from 1788 to the present time.

THE AMERICAN MASTODON (MASTODON AMERICANUS)

1792 KERR.—In 1792, p. 116, Robert Kerr proposed the name *Elephas americanus* for tusks and grinders found at Big Bone Lick near the banks of the Ohio River, Boone County, Kentucky.

1797 BLUMENBACH.—(1) In 1797 Blumenbach in his "Abbildungen Naturhistorische Gegenstände," employed the term *Ohio-Incognitum,* which first occurs on the back of the title-page following other specific names, *i.e.,* "11. *Simia troglodytes* . . . 19. Backenzähne von fossilen *Ohio-Incognitum,* und von den beiderlei Gattungen des Elephantengeschlechts." The name again appears opposite figure 19*A*.

In a letter from C. W. Andrews to Professor Osborn (June 6, 1922) he quotes C. Davies Sherborn as follows: "The words *'Ohio incognitum'* are not used in a generic or specific sense; they mean simply 'the Ohio incognitum' as is easily seen by the second page of the description, and are quite invalid." (See Article 25 of the International Rules of Zoological Nomenclature.)

1799 (2) Subsequently (1799.1, p. 698) Blumenbach in his sixth edition of the "Handbuch der Naturgeschichte" assigned the name *Mammut ohioticum* to the same animal. In the French edition of the
1803 "Handbuch" (translated in 1803 by Soulange Artaud under the supervision of Blumenbach) *mammout Ohioticum* appears on page 408, also *Ohio-Incognitum* occurs under the figure 19*A*, first used in the 1797 "Abbildungen" of Blumenbach (see Vol. I of the present Memoir, caption to fig. 113, where it is stated by Professor Osborn that it is "technically a type figure").

Dr. Edwin H. Colbert in a note to the editor (1937) makes the point that as Kerr, the author of *Elephas* [=*Mastodon*] *americanus*, did not include a figure in his description, we cannot be sure that figure 113 just referred to is a figure of the type.

1806 Cuvier.—It was 1806 before Cuvier applied "Le Grand Mastodonte" (1806.2) and "Mastodonte de l'Ohio (1806.3) to the American Mastodon, which in 1817 (see below) he redescribed under the specific designation of *Mastodon giganteum*.

Fischer de Waldheim.—The following generic names were applied to the Mastodon by Fischer de Waldheim:

1808 *Harpagmotherium.*

1814 *Mastotherium.*

1816 Oken.—The final form *Mastodon* was published by Oken in 1816, p. 789, citing Cuvier's five classic species ("Lehrbuch der Naturgeschichte," Theil III, p. 789).

1817 Cuvier.—Although anticipated by Oken by one year (see above, 1816) in the use of the term *Mastodon* (see 1817, "Le Règne Animal," I, p. 233, for description of *Mastodon giganteum*), Cuvier has been regarded as the author of this genus, since he first used the French form *Mastodonte* in his description of 1806.

1868 Leidy.—Leidy (1868, p. 175) was the first to use the name *Mastodon americanus*, embracing the *Mastodon ohioticus* or *M. giganteum* of authors.

1869 Leidy in 1869 (p. 392) lists *Mamonteum* Camper among the synonyms of *Mastodon americanus*.

1902 Hay.—*Mammut* Blumenbach was revived by Hay (1902, p. 707) and adopted by many subsequent authors. In his last work (1930, p. 623) Hay names the new subfamily Mammutinæ to include the Mastodonts, although he places it under the Elephantidæ without recognition of the family Mastodontidæ.

1904–1905 Trouessart.—The term *Mammut* Blumenbach was regarded by Trouessart (p. 600) as a misnomer: "Le nom barbare de 'Mammut,' basé par Blumenbach sur une erreur grossière (l'identité du *Mastodonte de l'Ohio* avec l'*Elephas primigenius*), n'a aucun droit, malgré sa priorité, a être substitué à celui de 'Mastodon,' genre bien caractérisé par Cuvier."

1920 Allen (excerpts from letter of Dr. Joel A. Allen to Professor Osborn, dated November 16, 1920):

> In your letter (October 22, 1920) you ask whether I consider Blumenbach's name *Mammut* entitled to recognition. I certainly do, although with regret that such name was . . . ever proposed as a generic designation. Neither its barbarous form nor the fact of his misconception that it was the mammoth renders it invalid . . . . All modern codes or rules of nomenclature declare that such names are not to be rejected on the ground that they are nonclassical, and that incorrectly formed classical names are not subject to emendation.

1935 Hopwood.—Doctor Hopwood substitutes *Mastodon* for *Mammut*, as stated in his "Fossil Proboscidea from China," 1935, p. 42: "To retain Cuvier's generic name instead of Blumenbach's, is to follow convenience rather than rule. The generic term *Mammut* and the vernacular Mammoth are so much alike that one or other should be suppressed in the interests of clarity. It is very much easier to discourage the use of an unfamiliar name than a well-known popular one, so that, whilst acknowledging Blumenbach's prior claim, I have given the preference to Cuvier."

1936 Osborn's Conclusions in Volume I, pp. 6 and 7, of the Present Memoir.—For the reason that *Mammut* (signifying 'earth-burrower' and suggesting the mammoth) was employed to describe the Mastodon; that if a vernacular name were to be accepted *Ohio-Incognitum* had priority, and lastly that inasmuch as Cuvier's "Mastodonte" (*Mastodon*) had been used throughout the literature of the past century, Professor Osborn committed himself to the genus *Mastodon* in the following citation from his Memoir (Vol. I, p. 6): "Consequently to rob Cuvier of his clear conception of grinding tooth structure, which he termed *Mastodonte*, and to substitute the barbaric term *Mammut*, signifying 'earth-burrower,' would be gross injustice to the founder of vertebrate palæontology."

The Northern or Woolly Mammoth (Mammonteus primigenius)

1799 Blumenbach.—In the same article in which Blumenbach described *Mammut ohioticum*, namely, in the "Handbuch der Naturgeschichte," sixth edition (1799.1, p. 698), he also described *Elephas primigenius* (p. 697), stating that there are abundant remains in Germany, but he mistakenly gives as an example a skeletal specimen from Burg-Tonna (now in the Gotha Museum), which proves to belong to *Elephas* [= *Hesperoloxodon*] *antiquus* Falconer and not to the northern Mammoth.

1799 Cuvier.—In the autumn of the same year that Blumenbach described *Elephas primigenius* (1799), Cuvier assigned the name *Elephas mammonteus* to the mammoth; subsequently, however, he adopted Blumenbach's name *E. primigenius*.

The following is a list of the names assigned to the Mammoth (*Elephas primigenius*):

1830 *Mammuthus* Burnett, Quart. Journ. Sci. Lit. & Art, XXVIII, p. 352.

1837 *Dicyclotherium* E. Geoffroy St. Hilaire, Compt. Rend. Acad. Sci., Paris, pp. 119, 120, fig. 1.

1845 *Mammontheum* de Blainville, 1839–1864, "Ostéographie," p. 237.

1848 *Cheirolites* von Meyer, (in Bronn's "Handbuch einer Gesch. d. Natur.," III, Index Pal., p. 286).

1850 *Synodontherium* Costa, Palaeont. del Regno di Napoli, Pt. I, pp. 271–275, Tav. iii, figs. 1–4.

1888 *Polydiskodon* Pohlig, Nova Acta Leop. Carol. Deutsch Akad., LIII, pp. 138, 252.

With the removal by Professor Osborn of *Mammut* Blumenbach from the valid genera of the Proboscidea, and the adoption of *Mastodon* Cuvier, there arose the question of the correct genus to which *Elephas primigenius*, the northern Mammoth, should be referred. Professor Osborn chose Camper's name *Mammonteum*, 1788, which, like *Mammut*, had reference to a specimen of the American Mastodon and not to the Mammoth. The revival of *Mammonteum* (*Mammonteus*) by Professor Osborn occurs in his article "Parelephas in Relation to Phyla and Genera of the Family Elephantidæ" (Osborn, 1924.633, p. 2) as follows:

1924

> By many authors all the generic phyla of the mammoths are still referred to the genus *Elephas*. Such reference, from our present knowledge, is inconsistent with the fact that none of the mammoths contains the ancestral characters of *Elephas*. (1) We thus revive the ill-defined name *Mammonteus* Camper for the *Elephas primigenius* phylum, which Depéret and Mayet have traced back to the Upper Pliocene *Elephas primigenius astensis* of northern Italy and into the Lower Pleistocene *E. meridionalis cromerensis* of the Forest Bed of Cromer. Here this line terminates in the typical *E. primigenius* of western Europe and onward into the progressive new subspecies *Mammonteus primigenius compressus* of North America.

1934 Preparatory to the final revision of the present Volume of the Memoir, Professor Osborn, in 1934, called the attention of Dr. A. Tindell Hopwood to the *Mammuthus* of Burnett (1830) as having priority over *Dicyclotherium* Geoffroy (1837). Doctor Hopwood adopted the name *Mammuthus* in his Memoir on 1935 "The Fossil Proboscidea from China," 1935, p. 98, from which we cite:

> *Remarks.*—With the progress of research on the Proboscidea, it has become ever clearer that the Mammoth is distinct from the Indian Elephant, which typifies the genus *Elephas*. Professor Osborn has sought to give expression to this result by reviving an alleged genus of Peter Camper's and emending the name. If I do not adopt the same name, it is because Camper was not referring to the Mammoth, and because he was using the word 'Mamonteum' as a vernacular. In the section 'De ossibus Mamonteis' Camper (1788, p. 259) uses 'Mamonteum' in an adjectival sense throughout. Not only so, but he also makes it quite clear that he is referring to an animal from America, and Pallas contributes a foot-note on p. 261 in which he explains that whereas in Russia the term 'Mammontean bones' is commonly applied to the bones of Elephants found in superficial deposits, it has suited Camper to apply the name to bones found in America. With so much evidence as to Camper's meaning, it is not possible to argue that the phrases on p. 251 of the same work refer to the Mammoth as distinct from the Elephant.
>
> Several names have been applied to the Mammoth, but the first that is valid, in so far as it possesses a genotype, appears to be *Mammuthus* Burnett, 1830. Under 'Elephantidæ, Elephant-kind' he groups the following,—

Genera.	*Species.*	
Elephas.	Indicus.	Indian Elephant.
	Africanus.	African.
Mammuthus.	Borealis.	Fossil Mammoth.
	Meridionalis.	
Mastodon.	Giganteum.	Gigantic.
	Angustidens.	Lesser.

> From this table it is clear that he used the word Mammoth in the sense generally accepted today, and did not apply it to the American Mastodon after the manner of the majority of English and American authors at the beginning of the nineteenth century, (*cf.* Cuvier, Ossemens foss., Ed. 1, Vol. II, Art. Sur le grand mastodonte), and that his *Mammuthus borealis* is the equivalent of *Elephas primigenius* Blum.

Doctor Hopwood then described a molar from Mongolia (regd. M10941) and fragment of another from Honan (regd. M14102) which he refers to *Mammuthus primigenius* (Blumenbach).

The following excerpts from the correspondence between Doctor Hopwood and Professor Osborn are self explanatory:

> September 10, 1935. Professor Osborn wrote as follows: "Among the Elephantidæ I regret that you substituted *Mammuthus* Burnett for *Mammonteus* Camper . . . If we stood on technicalities, the specific name *Elephas primigenius* is based on a species indubitably belonging to *Hesperoloxodon antiquus* . . . Technical methods would compel us to alter the entire nomenclature of the fossil Proboscidea. As in religion the *spirit rather than the letter is important.*"

October 19, 1935. Doctor Hopwood replied to Professor Osborn: "With regard to the substitution of *Mammuthus* for *Mammonteus*, I should not have done this had it been possible to show that Camper was referring to a European fossil, but the evidence that the reference is to the American Mastodon is so strong that I had no other alternative. The case of *E. primigenius* and *H. antiquus* is hardly parallel; Blumenbach was naming a new species, and later authors have misinterpreted him. The error is theirs, not Blumenbach's."

October 25, 1935. Professor Osborn replied at once as follows: "Your point that Camper was referring to the American *Mastodon* when he used the name *Mammonteus* is a very strong one and I shall immediately refresh my memory on this point, although I fear it may be difficult to correct it now."

October 29, 1935. Five days later he added the following postscript to the foregoing letter. "I am looking up Camper's use of the name *Mammonteus*. At the time, it was believed that there was only one extinct elephant, the true Mammoth in the Old World and the Mastodon in the New. First allusions to the American Mastodon speak of it as the Mammoth. It is interesting to note that Kerr gave the name *Elephas americanus* in 1792, several years before Blumenbach gave the name *Elephas primigenius* in 1799. I already have the complete bibliography of names applied to the European Mammoth and shall give them in my Monograph. Perhaps the first properly defined generic name was *Dicyclotherium*. Palmer, 'Index Generum Animalium,' 1904, p. 397, gives Mammont as applied to *Mastodon americanus*, *Mammuthus* Burnett. Burnett simply gives the name and the species *Mammuthus borealis*, a species not listed in Sherborn's Index nor anywhere defined. I doubt if *Mammont*, *Mammuthus*, or *Mammut* can be adopted on any rules of nomenclature, since a genus must rest on a type species. At present I prefer the Latin name *Mammonteum* Camper, which rests, according to Camper's description, both on the specimens found in Siberia and in North America, but I shall keep an open mind and settle this question in Volume II."

Professor Osborn's death occurred November 6, 1935.

1937 CONCLUSIONS.—A recent note from Dr. Edwin H. Colbert to the editor reads as follows:

1830 *Mammuthus* Burnett Type designated as *Mammuthus borealis*, which is a synonym of *Elephas primigenius* Blumenbach. Therefore the designation becomes *Mammuthus primigenius* (Blumenbach). Hopwood's arguments (1935) are valid.

1937 Dr. William Berryman Scott in his recent (1937) revision of "A History of Land Mammals in the Western Hemisphere," adopts *Mammuthus* Burnett.

Owing to the fact that *Mammonteus* has appeared so frequently in the literature of the past decade and has been used throughout the entire text of the present Memoir, it has been decided to retain the name herein, with the explanatory notes above, despite the evidence in favor of its abolishment.—Editor.]

2. LIST OF SUPERFAMILIES

YEAR	NAME	AUTHOR	BIBLIOGRAPHIC REFERENCE	REFERENCE IN PRESENT MEMOIR
1921	MŒRITHERIOIDEA	Osborn,	Amer. Mus. Novitates, No. 1, p. 2. See also Volume I, p. 24, of the present Memoir. Includes the family Mœritheriidæ of Andrews, 1906.	MŒRITHERIOIDEA
1921	DINOTHERIOIDEA	Osborn,	*loc. cit.* Includes the family Curtognati [=Curtognathidæ, this Memoir] of Kaup, 1833.	DEINOTHERIOIDEA
1921	MASTODONTOIDEA	Osborn,	*loc. cit.* Includes the families Mastodontidæ of Girard, 1852, and the Bunomastodontidæ of Osborn, 1921.	MASTODONTOIDEA
1921	ELEPHANTOIDEA	Osborn,	*loc. cit.* Includes the family Elephantidæ Gray, 1821.	ELEPHANTOIDEA
1935	STEGODONTOIDEA	Osborn,	Proc. Nat. Acad. Sci., XXI, No. 6, p. 408, also fig. 2; Vol. I, pp. 22, 25, and Vol. II, p. 807, of the present Memoir. Includes the family Stegodontidæ Young-Hopwood, 1935.	STEGODONTOIDEA

3. LIST OF FAMILIES

Year	Name	Author	Bibliographic Reference	Reference in Present Memoir
1821	ELEPHANTIDÆ	Gray	London Medical Repository, XV, No. 88, p. 305.	ELEPHANTIDÆ
			1838, Bonaparte, Nuov. Ann. Sci. Nat. Bologna, Anno I, Tom. II, p. 112.	ELEPHANTIDÆ
			1850, Bonaparte, "Conspectus Systematis Mastozoologiæ. Mammalia."	ELEPHANTIDÆ
			1852, Girard, Proc. Amer. Assoc. Adv. Sci., for the year 1851, pp. 326, 328.	ELEPHANTIDÆ
			1891, Zittel, "Handbuch der Palaeontologie," p. 458.	ELEPHANTIDÆ (in part), also Mastodontidæ, Bunomastodontidæ, Serridentidæ, Humboldtidæ, Stegodontidæ
			1910, Osborn, "The Age of Mammals," p. 558.	ELEPHANTIDÆ (in part), also Curtognathidæ, Mastodontidæ, Bunomastodontidæ, Stegodontidæ
1821	MASTODONADÆ	Gray	London Medical Repository, XV, No. 88, p. 306.	MASTODONTIDÆ
1833	CURTOGNATI	Kaup	Neues Jahrb. Min., p. 516. Dinotheriidæ Bonaparte, 1850.	CURTOGNATHIDÆ
1842	ELEPHASIDEÆ	Lesson	"Nouveau Tableau du Règne Animal," p. 156. Embraces one *Mastodon*, "*Elephas arvernensis*" Croizet and Jobert.	ELEPHANTIDÆ
1845	DINOTHERIDÆ	Bonaparte	"Catalogo metodico dei Mammiferi Europei," p. 4 (*fide* Palmer, 1904, p. 738).	CURTOGNATHIDÆ
1850	DINOTHERIIDÆ	Bonaparte	"Conspectus Systematis Mastozoologiæ. Mammalia."	CURTOGNATHIDÆ
			1918, Osborn, Bull. Geol. Soc. Amer., XXIX, p. 134. In Vol. I, pp. 26, 82, 83, this Memoir, changed to Curtognathidæ, based on family Curtognati Kaup, 1833.	CURTOGNATHIDÆ
1852	MASTODONTIDÆ	Girard	Proc. Amer. Assoc. Adv. Sci., for the year 1851, pp. 326, 328.	MASTODONTIDÆ
			1918, Osborn, Bull. Geol. Soc. Amer., XXIX, p. 134 (in part).	MASTODONTIDÆ
1906	MŒRITHERIIDÆ	Andrews	"A Descriptive Catalogue of the Tertiary Vertebrata of the Fayûm, Egypt," p. 99.	MŒRITHERIIDÆ
1906	PALÆOMASTODONTIDÆ	Andrews	*Op. cit.*, p. 130. Regarded by the present author as invalid, because founded on the generic characters of *Phiomia* rather than *Palæomastodon*.	BUNOMASTODONTIDÆ
1921	BUNOMASTODONTIDÆ	Osborn	Amer. Mus. Novitates, No. 1, pp. 2, 4. Replaced the subfamily Bunomastodontinæ Osborn, 1918, pp. 134–136 (see Vol. I, p. 27, this Memoir). Bunomastodontidæ inadmissible, however, under the rules of zoological nomenclature (see Scott, 1937, p. 287). See also Trilophodontidæ Simpson, 1931, p. 1369, and Gomphotheriidæ Cabrera, 1929, below, this list.	BUNOMASTODONTIDÆ
1927	AMEBELODONTIDÆ	Barbour	Neb. State Mus., Bull. 13, I, p. 131. Subsequently changed by Barbour (1929.2, p. 139) to Amebelodontinæ.	BUNOMASTODONTIDÆ (subfam. AMEBELODONTINÆ)
1929	MAMMUTIDÆ	Cabrera	Rev. Mus. La Plata, XXXII, p. 74.	MASTODONTIDÆ
1929	GOMPHOTHERIIDÆ	Cabrera	*Ibid.*, p. 75.	BUNOMASTODONTIDÆ (in part), also Serridentidæ, Humboldtidæ

1931	TRILOPHODONTIDÆ Simpson	Bull. Amer. Mus. Nat. Hist., LIX, Art. V, p. 281. Substituted for inadmissible name Bunomastodontidæ. Adopted by Scott, 1937, pp. 267, 280, 287. [Doctor Simpson now prefers Gomphotheriidæ Cabrera, 1929 (see p. 1525 below).—Editor.]	BUNOMASTODONTIDÆ
1935	HUMBOLDTIDÆ Osborn	Proc. Nat. Acad. Sci., XXI, No. 6, fig. 2 (name only). 1936, Osborn, this Memoir, Vol. I, pp. 575, 722. Without a type genus. Stegomastodontidæ substituted by Scott, 1937 (see below, this list).	HUMBOLDTIDÆ
1935	SERRIDENTIDÆ Osborn	Proc. Nat. Acad. Sci., XXI, No. 6, fig. 2 (name only). 1936, Osborn, this Memoir, Vol. I, p. 729.	SERRIDENTIDÆ
1935	STEGODONTIDÆ Young	Pal. Sinica, Ser. C, IX, Fasc. 2, p. 5. 1935, Hopwood, Pal. Sinica, Ser. C, IX, Fasc. 3, p. 71. Included both *Stegolophodon* and *Stegodon*. Restricted in present Memoir to *Stegodon*.	STEGODONTIDÆ
1935	DIBUNODONTIDÆ Hopwood	Pal. Sinica, Ser. C, IX, Fasc. 3, pp. 11, 55. See especially Hay, 1925, Journ. Wash. Acad. Sci., XV, p. 382.	BUNOMASTODONTIDÆ (in part, *i. e.*, only the Brevirostrinæ of Osborn)
1937	STEGOMASTODONTIDÆ Scott	"A History of Land Mammals in the Western Hemisphere," pp. 267, 281, 294. Substituted for Humboldtidæ, which is without a type genus.	HUMBOLDTIDÆ

4. LIST OF SUBFAMILIES

YEAR	NAME	AUTHOR	BIBLIOGRAPHIC REFERENCE	REFERENCE IN PRESENT MEMOIR
1838	ELEPHANTINA	Bonaparte	Nuov. Ann. Sci. Nat. Bologna, Anno I, Tom. II, p. 112; 1850, "Conspectus Systematis Mastozoologiæ. Mammalia."	ELEPHANTINÆ
1841	DINOTHERINA	Bonaparte	Trans. Linn. Soc. London, XVIII, p. 253.	DEINOTHERIINÆ
1850	DINOTHERIINA	Bonaparte	"Conspectus Systematis Mastozoologiæ. Mammalia."	DEINOTHERIINÆ
1869	MASTODONTINA	Brandt	Mém. Acad. Imp. Sci. St. Pétersb., (VII), XIV, No. 1, p. 35.	MASTODONTINÆ
1906	MŒRITHERIINI	Winge	"Jordfundne og nulevende Hovdyr (Ungulata) fra Lagoa Santa, Minas Geraes, Brasilien," p. 172.	MŒRITHERIINÆ
1906	DINOTHERIINI	Winge	*Loc. cit.*	DEINOTHERIINÆ
1906	ELEPHANTINI	Winge	*Loc. cit.*	ELEPHANTINÆ
1910	DINOTHERIINÆ	Osborn	"The Age of Mammals," p. 558.	DEINOTHERIINÆ
1910	MASTODONTINÆ	Osborn	*Loc. cit.*	MASTODONTINÆ
1910	ELEPHANTINÆ	Osborn	*Loc. cit.;* 1918, Bull. Geol. Soc. Amer., XXIX, p. 135.	ELEPHANTINÆ
1918	BUNOMASTODONTINÆ	Osborn	Bull. Geol. Soc. Amer., XXIX, pp. 134–136.	Replaced by BUNOMASTODONTIDÆ (in part)
1918	STEGODONTINÆ	Osborn	*Ibid.*, pp. 135, 136.	STEGODONTINÆ
1918	LOXODONTINÆ	Osborn	*Ibid.*, pp. 135, 136.	LOXODONTINÆ

Year	Name	Author	Bibliographic Reference	Reference in Present Memoir
1918	Euelephantinæ	Osborn	*Ibid.*, p. 136. Invalid because the genus *Euelephas* is invalid (see Chap. XIX, p. 1177, of present Memoir).	Invalid
1918	Longirostrinæ	Osborn	*Ibid.*, p. 136. Without type genus. See Trilophodontinæ Scott, 1937, p. 1371 below, this list.	Longirostrinæ
1918	Rhynchorostrinæ	Osborn	*Ibid.*, p. 136. See Rhynchotheriinæ Cabrera, 1929, on this page below; Scott, 1937, pp. 267, 280, 292, also adopts the form Rhynchotheriinæ.	Rhynchorostrinæ
1918	Brevirostrinæ	Osborn	*Ibid.*, p. 136. See Pentalophodontinæ Scott, 1937, p. 1371 below, this list.	Brevirostrinæ
1921	Mammontinæ	Osborn	Amer. Mus. Novitates, No. 1, pp. 1, 14. Should *Mammonteus* prove to be invalid, this would leave the subfamily Mammontinæ without a type genus.	Mammontinæ
1921	Serridentinæ	Osborn	Bull. Geol. Soc. Amer., XXXII, p. 330.	Serridentinæ
1921	Notorostrinæ	Osborn	*Ibid.*, p. 330. Without type genus. See Cordillerioninæ Scott, 1937, p. 1371 below, this list.	Notorostrinæ
1923	Mœritheriinae	Winge-Osborn	Amer. Mus. Novitates, No. 99, p. 1.	Mœritheriinæ
1923	Zygolophodontinæ	Osborn	*Loc. cit.*	Zygolophodontinæ
1927	Archidiskodontinæ	Dietrich	Neues Jahrb. Min., I, Abth. B (Referate), p. 313.	[Mammontinæ (in part)]
1927	Parelephantinæ	Dietrich	*Loc. cit.*	[Mammontinæ (in part)]
1928	Platybelodontinæ	Borissiak	Ann. Soc. Paléont. Russie, VII, p. 119.	Platybelodontinæ
1929	Amebelodontinæ	Barbour	Neb. State Mus., Bull. 16, I, p. 139.	Amebelodontinæ
1929	Rhynchotheriinæ	Cabrera	Rev. Mus. La Plata, XXXII, p. 75.	Rhynchorostrinæ
1929	Gomphotheriinæ	Cabrera	*Loc. cit.*	Longirostrinæ (in part) Tetralophodontinæ Serridentinæ
1929	Cuvieroniinæ	Cabrera	*Ibid.*, p. 76.	Notorostrinæ (in part) Notiomastodontinæ
1929	Anancinæ	Cabrera	*Ibid.*, p. 76.	Notorostrinæ, Humboldtinæ, and Brevirostrinæ (in part)

Year	Name Author	Bibliographic Reference	Reference in Present Memoir
1930	Mammutinæ Hay	"Fossil Vertebrata of North America," II, p. 623. Name without definition but indicates the inclusion of the subfamilies of the Mastodontoidea of Osborn.	[Mastodontoidea of Osborn]
1932	Tetralophodontinæ van der Maarel	"Contribution to the Knowledge of the Fossil Mammalian Fauna of Java," p. 108.	Tetralophodontinæ
1934	Humboldtinæ Osborn	Proc. Amer. Phil. Soc., LXXIV, No. 4, p. 277, fig. 3, and p. 283, also Vol. I, p. 575, of present Memoir.	Humboldtinæ
1935	Gnathalodontinæ Barbour and Sternberg [emend. Osborn Gnathabelodontinæ]	Neb. State Mus., Bull. 42, I, p. 395.	Gnathabelodontinæ
1936	Palæomastodontinæ Osborn	This Memoir, Vol. I, p. 691.	Palæomastodontinæ
1936	Stegolophodontinæ Osborn	*Op. cit.*, p. 700.	Stegolophodontinæ
1936	Notiomastodontinæ Osborn	*Op. cit.*, p. 730.	Notiomastodontinæ
1937	Trilophodontinæ Scott	"A History of Land Mammals in the Western Hemisphere," pp. 267, 280. Substituted for Longirostrinæ which is without a type genus.	Longirostrinæ
1937	Cordillerioninæ Scott	*Loc. cit.* Substituted for Notorostrinæ which is without a type genus.	Notorostrinæ
1937	Pentalophodontinæ Scott	*Op. cit.*, pp. 267, 292. Founded on *Pentalophodon* Falconer, 1857, 1865. Compare Anancinæ Cabrera, 1929, above, this list.	Brevirostrinæ
1937	Stegomastodontinæ Scott	*Op. cit.*, pp. 267, 281. Replaces Humboldtinæ which is without a type genus.	Humboldtinæ

5. GENERA AND SPECIES OF THE PROBOSCIDEA IN THE ORDER NAMED BY THE AUTHORS IN THE ORIGINAL DESCRIPTIONS[1]

The following Tables present a revised chronologic list (1735–1939) of generic and specific names as originally and subsequently spelled by their authors, which rest upon the authority of the authors mentioned, or cited (e.g., *fide*) in cases where the original references were not available to the present author.

LIST OF GENERA

Year	Genus Author	Bibliographic Reference	Genotypic Species	Generic Reference in Present Memoir
1735–1758	*Elephas* Linnæus,	"Systema Naturæ," 1st to 9th editions.	*Elephas indicus* Linnæus	*Elephas*

[In the 10th edition of the "Systema Naturæ" (known as the Decima Reformata), 1758, p. 33, Linnæus substituted the name *Elephas maximus* Linn. for that of *E. indicus* Linn., which, with all other names in that edition, was officially adopted by the Fifth International Congress of Zoology, held in Berlin in 1901.—Editor.]

For first use of *Elephas*, see John Ray, 1693, p. 131 [p. 123 of authors].

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[1] [The author of the present Memoir refused to recognize privately printed publications (unless on sale, bearing the name of the publisher) as a source of systematic names; consequently such references have been omitted from the present list.—Editor.]

Year	**Genus**	**Author**	**Bibliographic Reference**	**Genotypic Species**	**Generic Reference in Present Memoir**
1788	*Mammonteum*	Camper,	Nova Acta Acad. Sci. Imp. Petropol., II, for the year 1784, p. 251; *Mammonteus* Osborn, 1924, Amer. Mus. Novitates, No. 152, p. 2. Camper's designation of *Mammonteum* is cited above. Hay (1902, p. 708) and J. A. Allen (letter, Nov. 23, 1920) do not regard it as valid. Allen writes: "the names of the fossil mammals he [Camper] discusses are vernacular names rendered into Latin. They have no nomenclatural significance." Osborn nevertheless adopts *Mammonteum* Camper, 1788, in preference to *Dicyclotherium* Geoffroy, 1837, as a distinct generic name assigned to *E. primigenius.* While Allen in the above letter objects to *Mammonteum* as a vernacular name rendered into Latin, in a letter (Nov. 15, 1920) on the subject of barbarous names as generic names, he nevertheless agrees with Palmer ("Index Generum Mammalium," 1904, pp. 45, 46) and says: "All modern codes of [or] rules of nomenclature declare that such names are not to be rejected on the ground that they are nonclassical, and that incorrectly formed classical names are not subject to emendation." See also Allen's note on the word "*Mammut.*"	[Refers to an animal from America (cf. Hopwood, 1935, p. 98).]	*Mammonteus*[1]
1795	*Elephantus*	Cuvier and Geoffroy,	Revue Encyclopédique (or Mag. Encyclopédique), II, (6), p. 189.	Genotype not given in 1795, but in 1801 (Cuvier and Lacépède) *indicus* is mentioned	*Elephas*
1797	*Ohio*	Blumenbach,	Abbild. naturhist. Gegens., Heft 2, No. 19, fig. A, and back of title-page. Not a valid generic description. See introduction to this chapter.	*Ohio-incognitum* Blumenbach	*Mastodon*
1799	*Mammut*	Blumenbach,	Handb. d. Natur., 6th edition, p. 698. A vernacular name preoccupied by *Ohio* for *E. primigenius.* Allen, however, writes (letter, Nov. 15, 1920): "In your letter you ask whether I consider Blumenbach's name *Mammut* entitled to recognition. I certainly do, although with regret that such name was not [*sic*] ever proposed as a generic designation. Neither its barbarous form nor the fact of his misconception that it was the mammoth renders it invalid." Murray, 1908, VI, Pt. 2, p. 98: "MAMMOTH. . . . Also 8 mammuth, mamant, maman, mamont, mammon, mammot (mammoht), 8–9 mammouth. [a. Russian, . . . Маммотъ, *mammot*, whence *mammotovoi kost*, mammoth's bones (Ludolf, Gram. Russ. 1696, p. 92); now Мамантъ, mamant. Hence also F. *mammouth*, . . . mamant, . . . mammont. The word is of obscure origin; the alleged Tartar word *mama* 'earth' (usually cited as the etymon) is not known to exist.]"	*Mammut ohioticum* Blumenbach	*Mastodon*
1805 [1806]	*Mastodonte*	G. Cuvier	Ann. Mus. d'Hist. Nat., VIII, pp. 270, 272, 293. Falconer and Cautley, 1846, letterpress, p. 18: "But in his second extended and elaborate memoir, published in 1805 [1806], which formed the groundwork of what he has written on the subject in the 'Ossemens Fossiles,' Cuvier separated the Elephants with mammillated molars from the ordinary forms with lamelliform molars, and united the former into a genus which he designated *Mastodon*, taking the North American species, under the name of *M. giganteum*, as the type [Footnote: 'Annales du Muséum d'Histoire Naturelle, tom. viii. "Sur le grand Mastodonte." ']." See also de Blainville (1834–69, p. 245); and Leidy (1869, p. 393): "The earliest date at which I have been able to find the name of *Mastodon* systematically expressed, is in the work here quoted [Cuvier, 1817, p. 233]. Previously, Cuvier appears only to have used the gallicized term of Mastodonte. Bronn, in the 3d edition of the Lethaea Geognostica, page 820, credits *Mastodon* to Cuvier as early as 1805, but does not give the reference." [See Oken, 1916, this chapter, p. 1364 above.]	*Le Grand Mastodonte* Cuvier	*Mastodon* By courtesy to Cuvier restricted to *M. americanus*
1808	*Harpagmotherium*	Fischer de Waldheim	Prog. d'Invit. Séance, Pub. Soc. Imp. Nat. Moscou, September, pp. 19, 20 (*fide* Palmer, 1904, p. 311). Compare Sherborn, "Index Animalium," who gives on page 1022 (Sect. 2, Pt. 5, 1924) *Harpagonotherium canadense*, and on page 2915 (Sect. 2, Pt. 12, 1927) *Harpagmotherium.*	*Harpagmotherium canadense* Fischer de Waldheim	*Mastodon*

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[1] [*Mammuthus* Burnett, 1830 (see below, this list) selected by Dr. A. Tindell Hopwood, 1935, p. 27. For complete historical account of the names *Mammonteus, Mammut, Mastodonte, Mastodon,* up to the year 1935, see pp. 1363–1367 above.—Editor.]

Year	Genus	Author	Bibliographic Reference	Genotypic Species	Generic Reference in Present Memoir
1814	*Mastotherium*	Fischer de Waldheim	"Zoognosia," III, p. 337.	Species cited: *M. megalodon* (Cuv.)	*Mastodon americanus*
				leptodon (Cuv.)	*Trilophodon angustidens*
				microdon (Cuv.)	*Turicius tapiroides*
				hyodon (Cuv.)	*Cordillerion andium*
				humboldtii (Cuv.)	*Cuvieronius humboldtii*
1816	*Mastodon*	Oken	Lehrbuch Natur., Theil III, Abth. 2, p. 789.		*Mastodon* Cuv.

First use of the term *Mastodon* for Cuvier's *Mastodonte*, citing Cuvier's five classic species.

Year	Genus	Author	Bibliographic Reference	Genotypic Species	Generic Reference in Present Memoir
1817	*Mastodon*	G. Cuvier	"Le Règne Animal," I, pp. 232, 233.	*Mastodon giganteum* Cuvier, *Mastodon angustidens* Cuvier	*Mastodon*
1817	*Mastodontum*	de Blainville	Nouv. Dict. Hist. Nat., IX, p. 276.		[*Mastodon* Cuv.]
1825–1827	*Loxodonte* [=*Loxodonta*, 1827, 1828]	F. Cuvier	"Hist. Nat. Mamm.," III, Livr. LI, LII, with 2 pp. text, 1827, 1828, Zool. Journ., London, III, p. 140 (unsigned review).	*Elephas africanus* Blumenbach	*Loxodonta*

Geoffroy Saint-Hilaire, Étienne, et Cuvier, Frédéric, 1824-1829 [1825], (Loxodonte), p. 2: "Je proposerai pour nom générique de cette espèce, le mot de *Loxodonte*, qui peut rappeler le caractère de ses dents, les losanges qu'on aperçoit sur leur coupe."

A review (unsigned) of this work appeared in the Zool. Journ., London, 1827, 1828, III, p. 140, noticing the "dismemberment of the genus *Elephas*, for the purpose of establishing a new one under the name of Loxodonta. . . . For the Elephant of Asia he [Cuvier] retains the original generic name *Elephas*. The surfaces of its molar teeth present fasciæ of enamel irregularly festooned; while in those of the African Elephant, the type of the new genus *Loxodonta*, the enamel is disposed in lozenges. In addition to this striking distinction derived from the dentary system, M. F. Cuvier also enumerates the other characters which have hitherto been regarded as specific. The smaller, more elongated, and less irregular head of the African animal when compared with the Asiatic; the rounded forehead of the former, strongly contrasted with the deep depression in the middle of that of the latter; the ear of the former also twice the extent, while the tail is only half the length, &c."

Year	Genus	Author	Bibliographic Reference	Genotypic Species	Generic Reference in Present Memoir
1829	*Deinotherium*	Kaup	Isis, [XXII], Heft IV, p. 401, Taf. I.	*Deinotherium giganteum* Kaup	*Deinotherium*
1830	*Mammuthus*	Burnett	Quart. Journ. Sci., London, July-December, 1829, p. 352.	*Mammuthus borealis* Burnett	*Mammonteus*

[See introduction to the present chapter, pp. 1366 and 1367.]

Year	Genus	Author	Bibliographic Reference	Genotypic Species	Generic Reference in Present Memoir
1830	*Tetracaulodon*	Godman	Trans. Amer. Phil. Soc., N. S., III, p. 484.	*Tetracaulodon mastodontoideum* Godman	*Mastodon*
1837	*Gomphotherium*	Burmeister	Handb. d. Natur., p. 795.	Not cited.	*Mastodon*

Burmeister, 1837, p. 795: "*Mastodon.* Wie *Elephas*, aber die Backzähne mit 2 Reihen kegelförmiger Höcker.—Von mehreren untergegangenen Arten findet man Knochen in Nordamerika, besonders am *Ohio*, daher *Ohiothier*. Stosszähne in beiden Kiefern besass die gleichfalls untergegangene Gatt. GOMPHOTHERIUM."

Osborn, 1922: The name *Gomphotherium* is invalid: (1) Because no genotypic species except the Ohio mastodon is mentioned; (2) because several different genera of mastodonts display the same character, namely, "Stosszähne in beiden Kiefern," e. g., *Tetracaulodon* Godman, a four-tusked true *Mastodon americanus*. Matthew (unpublished manuscript of 1918) states: "Apparently the author [Burmeister] had primarily in mind certain specimens of the American mastodon which retain the lower tusks; but for these the name *Tetracaulodon* Godman had been proposed in 1830." (3) Confusion as to mastodons with four tusks is demonstrated further by the fact that Kaup first used Godman's term in describing his Eppelsheim species, viz., *Tetracaulodon longirostre*. (4) It is consequently clear that we cannot be certain what animal Burmeister had in mind. (See note under *Gamphotherium* Gloger below.) Hay adopted the name in 1917 (see *Gomphotherium gratum* and *G. elegans*, p. 1405 below).

Year	Genus	Author	Bibliographic Reference	Genotypic Species	Generic Reference in Present Memoir
1837	*Dicyclotherium*	E. Geoffroy Saint-Hilaire	Compt. Rend. Acad. Sci., Paris, IV, No. 4, pp. 119, 120, fig. I.	*Elephas primigenius* Blumenbach	*Mammonteus*

This name assigned in reference to the fact that the genus was supposed to pass through two cycles of time. Assigned by Geoffroy in an important communication on the influence of climate on evolution.

<table>
<tr><th>Year</th><th>Genus Author</th><th>Bibliographic Reference</th><th>Genotypic Species</th><th>Generic Reference in Present Memoir</th></tr>
<tr><td>1840?</td><td><i>Missourium</i> Koch</td><td>"Fossil Remains," pp. 1, 2.</td><td><i>Missourium Kochii</i> Koch</td><td><i>Mastodon</i></td></tr>
<tr><td></td><td></td><td colspan="3">First described as Koch's Missourian in 1839 (American Journal of Science, XXXVII, pp. 191, 192). In 1841 Koch renamed it the Missouri Leviathan, or <i>Leviathan missourii</i>, and in 1843 he described it as the Missourium Theristocaulodon or <i>Leviathan missouriensis</i>.</td></tr>
<tr><td>1841</td><td><i>Cymatotherium</i> Kaup</td><td>"Akten der Urwelt," pp. 11–14, Tab. IV.</td><td><i>Cymatotherium antiquum</i> Kaup</td><td>SIRENIAN?</td></tr>
<tr><td></td><td></td><td colspan="3">[Professor Osborn did not regard this as a proboscidean molar. It was originally listed by Kaup as a Sirenian, but neither Dr. G. G. Simpson nor Dr. E. H. Colbert considers it as such; they think it possible that it may be an embryonic tooth of a proboscidean.—Editor.]</td></tr>
<tr><td>1841</td><td><i>Leviathan</i> Koch</td><td>"Description of the Missourium, or Missouri Leviathan," etc., London, p. 17.</td><td><i>Leviathan Missourii</i> (= <i>Leviathan missouriensis</i> = <i>Missourium theristocaulodon</i>)</td><td><i>Mastodon</i></td></tr>
<tr><td>1841</td><td><i>Gamphotherium</i> Gloger</td><td>"Gemeinnütziges Hand- u. Hilfsbuch Naturgesch.," I, pp. xxxii, 119. See also Oldfield Thomas, 1895, Ann. Mag. Nat. Hist., (6), XV, pp. 191, 192.</td><td><i>Mastodon angustidens</i> Cuvier</td><td><i>Trilophodon</i></td></tr>
<tr><td></td><td></td><td colspan="3">Gloger, 1841, p. 119: "Letztere theilte mit ihm noch ein anderes, welches man füglich Schnabel-Mammuth nennen kann, (<i>Gamphotherium angustidens</i>,) obwohl bei ihm die unteren Stosszähne selbst nicht bloss klein blieben, sondern auch nur in der Jugend vorhanden waren und dann bald für immer ausfielen."
<i>Gamphotherium</i> is regarded as a misspelling of <i>Gomphotherium</i> Burmeister, 1837, by most authors (Matthew, Hay, Allen); Oldfield Thomas, however, writes (letter, Oct. 20, 1920): "<i>Gamphotherium</i> Gloger has as its genotype, by monotypy, <i>G. angustidens</i>—no other species being referred to. There appears to be no reason to suppose the word has any special connection with <i>Gomphotherium</i>, either as misspelling or correction. . . it <i>may</i> have been a misprint for <i>Gomphotherium</i> of Burmeister, but there is no evidence for this, & the <i>a</i> occurs equally in Gloger's Systematic Index, in the body of the work, and in the alphabetical index at the end. . . The genotype of <i>Trilophodon</i> Falc. & Caut., 1846, is quite clearly <i>ohioticus</i>, no other species being mentioned in the paragraphs referring to it."
Hopwood, 1935, pp. 13, 14: "Burmeister's genus <i>Gomphotherium</i> was originally diagnosed thus, 'Stosszähne in beiden Kiefern besass die gleichfalls untergegangene Gatt. <i>Gomphotherium.</i>' (Burmeister, <i>loc. cit.</i>), but he mentioned no species as belonging to this genus. The late Dr. O. P. Hay (Hay, 1923, [1923.2] p. 109), regarded this as coming under Opinion 46 of the International Commission on Zoological Nomenclature and adopted it as a valid genus with genolectotype <i>M. angustidens</i> Cuvier (cf. Cope & Matthew, 1915, expl. to pl. cxx). Since the American Mastodon occasionally has mandibular tusks, it is clear that Burmeister's diagnosis does not distinguish <i>Gomphotherium</i> from <i>Mastodon</i> under which he expressly mentions 'Ohiothier', <i>i. e., Mastodon americanus</i>. On this we may regard <i>Gomphotherium</i> as invalid, because the diagnosis is inadequate. Not only is it invalid, but it also antedates <i>Gamphotherium</i> Gloger. Oldfield Thomas (1895, p. 189) regards this latter as a new generic name, and (<i>op. cit.</i>, p. 191) italicises it as a name which is not a simple synonym of an earlier name. The spelling, however, is quite clearly either an error of transcription, or a <i>lapsus calami</i>, or even a misprint, and the word should be written <i>Gomphotherium</i>, thus becoming a synonym of <i>Gomphotherium</i> Burmeister. The next name, <i>Trilophodon</i>, was originally proposed for the species <i>M. ohioticus</i> and <i>M. angustidens</i>. Of these the former is the genotype of <i>Mastodon</i>, hence the latter only remains in <i>Trilophodon</i> and may be regarded as the genotype of that genus. For these reasons <i>Trilophodon</i> is here adopted as a valid genus to include all the bunolophodont proboscideans grouped round <i>Mastodon angustidens</i>."</td></tr>
<tr><td>1846</td><td colspan="2"><i>Trilophodon</i> (Section name) Falconer and Cautley "Fauna Antiqua Sivalensis," letterpress, p. 54: "<i>Mastodon.</i> Sect. Trilophodon.—<i>M. Ohioticus.</i>—The next degree of deviation from the ordinary dental rule is presented by <i>Mastodon Ohioticus.</i>" In 1847 Falconer and Cautley (Pls. XLII–XLV) use the same term, e. g.,</td><td></td><td><i>Trilophodon</i>
Collective genus. By courtesy to Falconer restricted to <i>M. angustidens</i> (see <i>Trilophodon</i> Falc., 1857).</td></tr>
</table>

Year	Genus	Author	Bibliographic Reference	Genotypic Species	Generic Reference in Present Memoir
			Mastodon Sect. Trilophodon, to include the species: III. *Mastodon tapiroides*, IV. *M. ohioticus*, V. *M. angustidens*, VI. *M. andium*; the same species are listed by Falconer (1867, p. 56) as "I. Trilophodontes," with the addition of *Deinotherium giganteum* and *D. indicum*. This does not appear as a generic definition; see also *Tetralophodon* Falconer and Cautley below. Compare also Warren (1852, p. 139): "The Mastodons are separated into two groups; one called Trilophodon, and the other, not particularly named, which might be called Tetralophodon." Defined by Falconer as a subgenus of *Mastodon* (Falconer, 1857, pp. 313, 316, and Synop. Tab. opp. p. 319 with addition of four species and transfer of *andium* to *Tetralophodon*).		
1847	*Tetralophodon*	(Section name) Falconer and Cautley	*Op. cit.*, Pls. XLII-XLV, (as distinguished from Sect. Trilophodon) applied as a section of *Mastodon* to include the species: VII. *M. perimensis*, VIII. *M. sivalensis*, IX. *M. arvernensis*, X. *M. longirostris*, XI. *M. latidens*; these five species in the order named are again listed by Falconer (1867, p. 56) as: "II. Tetralophodontes," as distinguished from "I. Trilophodontes" and "III. Stegodontes." This designation of the Section *Tetralophodon* is not a generic definition; see also *Trilophodon* above. Defined by Falconer as a subgenus of *Mastodon* (Falconer, 1857, pp. 313, 316, and Synop. Tab. opp. p. 319 with addition of *andium*). See Vol. I, Chap. IX, p. 348, of the present Memoir.		*Tetralophodon* Collective genus. By courtesy to Falconer restricted to *M. longirostris* (see *Tetralophodon* Falc., 1857).
1847–1857	*Stegodon*	Falconer and Cautley	*Op. cit.*, Pl. XLII, figs. XII–XV. Also Falconer, 1857, Quart. Journ. Geol. Soc. London, XIII, pp. 314, 318, and Synop. Tab. opp. p. 319. Falconer, 1857, p. 314: "To this group we have assigned the subgeneric name of *Stegodon* [Footnote: 'From ότέγη *tectum*, and ὀδούς *dens*, having reference to the gable-end form of the section of the ridges.']. It is limited to extinct forms confined at present to the Indian Tertiaries. The Stegodons constitute the intermediate group of the Proboscidea from which the other species diverge through their dental characters, on the one side into the Mastodons, and on the other into the typical Elephants." *Stegodon* is admirably characterized by Falconer by four species belonging in the same phylum. It preoccupies *Emmenodon* Cope, 1889.	*Elephas cliftii* Falc. & Caut., *E. bombifrons* Falc. & Caut., *E. ganesa* (?) Falc. & Caut., *E. insignis* Falc. & Caut.	*Stegodon*
1847–1857	*Loxodon*	Falconer and Cautley	*Op. cit.*, [1847, Pls. XLII, XLIV] (name). Falconer, 1857, Quart. Journ. Geol. Soc. London, XIII, pp. 315, 318, Synop. Tab. opp. p. 319; 1865, *ibid.*, XXI, p. 263. *Loxodon* Falconer, 1847, 1857, preoccupied by *Loxodon* Müller and Henle, 1841, for a genus of sharks. Compare *Loxodonte* F. Cuvier, 1825, and *Loxodonta* (unsigned review of F. Cuvier, 1827, 1828—see above, this list).	*Elephas planifrons* Falconer & Cautley, *E. africanus* Blumenbach, *E. priscus*(?) Goldfuss	*Loxodonta*
1847	*Elasmodon*	Falconer and Cautley	*Op. cit.*, Pl. XLII. A subgeneric name based upon species now known to belong to five different genera (see p. 1177 of the present Memoir), namely, *Elephas* [*Hesperoloxodon*] *antiquus*, *E.* [*Hypselephas*] *hysudricus*, *E.* [*Archidiskodon*] *meridionalis*, *E.* [*Palæoloxodon*] *namadicus*, *E. indicus*, and *E.* [*Mammonteus*] *primigenius*. Name, moreover, preoccupied by *Elasmodus*, replaced by *Euelephas* Falconer, 1857, p. 315 (see *Euelephas*, p. 1376, below).		INVALID, PREOCCUPIED
1848	*Cheirolites*	von Meyer	(In Bronn's Handb. einer Gesch. d. Natur, III, Index Pal., p. 286). Compare Owen, 1846, p. 228: "A separate plate [of molar tooth], with its digital processes, offers a rude resemblance to a hand, and such specimens have been figured by the older collectors of petrifactions, under the name of 'Cheirolites,' as the fossilized hand of a monkey or a child."	*Elephas primigenius* Blumenbach	*Mammonteus*

Year	Genus	Author	Bibliographic Reference	Genotypic Species	Generic Reference in Present Memoir
1850	*Synodontherium*	Costa	Atti Accad. Pontaniana, V, Pt. I, pp. 271–275, Tav. III, figs. 1–4.	Tooth belonging to *Elephas primigenius* (*fide* Leidy, Marschall).	*Mammonteus*
1852	*Tetralophodon*	Warren	"The Mastodon Giganteus of North America," p. 139. Collective genus invalid because based upon specimens now known to belong to three different genera. Moreover, preoccupied by *Tetralophodon* Falconer and Cautley, 1846 [1847].	*Mastodon latidens* Clift, *M. arvernensis* Croizet & Jobert, *M. sivalensis* Cautley	INVALID, PREOCCUPIED
1855	*Anancus*	Aymard	(In Dorlhac, Ann. Soc. Agric. Puy, XIX, for 1854, p. 507). *Anancus* is the first valid generic name applied to a member of this phylum. A preceding invalid collective name is *Tetralophodon* Warren. Succeeding synonymous terms are *Tetralophodon* Falconer and Cautley (in part), *Pentalophodon* Falconer, *Bunolophodon* Vacek (in part), *Stegomastodon* Pohlig, *Rhabdobunus* Hay, *Dibunodon* Schlesinger. The name *Anancus* first appeared in a list in Dorlhac (1855, p. 507) which he says was borrowed from a verbal communication to the above Society by Aymard in 1855; later in 1859, p. 493, Lartet established its validity by making *Mastodon arvernensis* the type.	*Anancus macroplus* Aymard (= *M. arvernensis*)	*Anancus*
1857	*Trilophodon*	Falconer	Quart. Journ. Geol. Soc. London, XIII, p. 313; defined as a subgenus, p. 316 and Synop. Tab. opp. p. 319. [See above, this list, under *Gamphotherium*, 1841, for conclusions of Dr. Hopwood regarding validity of *Trilophodon*.]	*Mastodon angustidens* and other trilophodonts, as listed above under *Trilophodon*, 1846 (Section mame)	*Trilophodon* By courtesy to Falconer restricted to *M. angustidens*
1857	*Euelephas*	Falconer	Quart. Journ. Geol. Soc. London, XIII, pp. 315–318, Synop. Tab. opp. p. 319, subgenus of *Elephas*. Falconer, 1857, p. 315, footnote: Substitution of *Euelephas* for *Elasmodon*. Sclater in 1900, p. 317, erroneously specified *Elephas planifrons* as the genotype of *Euelephas*, because this species was not included in the original definition of *Elasmodon* (see Chap. XIX, p. 1177 above).	*Elephas Hysudricus* Falconer & Cautley, *antiquus* Falconer & Cautley, *meridionalis* Nesti, *Namadicus* Falconer & Cautley, *indicus* Linnæus, *primigenius* Blumenbach	INVALID SUBGENERIC NAME
1857	*Tetralophodon*	Falconer	Quart. Journ. Geol. Soc. London, XIII, pp. 313, 317, and Synop. Tab. opp. p. 319, defined as a subgenus of *Mastodon*, with the doubtful inclusion of *Andium* at this time.	*Mastodon longirostris* and other species, as listed above under *Tetralophodon*, 1846 [1847] (Section name).	*Tetralophodon* By courtesy to Falconer restricted to *M. longirostris*
1857–1865	*Pentalophodon*	Falconer	Quart. Journ. Geol. Soc. London, XIII, p. 314; 1865, *ibid.*, XXI, p. 262. As a subgenus of *Mastodon*, name without genotype in 1857, name with genotype (*M. sivalensis*) in 1865. Falconer, 1857, p. 314: "For reasons which will be explained in the sequel, it would seem that there has existed in nature another subgeneric group of *Mastodon*, of which only a single form is at present known, in which the crowns of the 'intermediate molars' are divided upon a quinary ridge-formula. This group in our arrangement would be characterized, in harmony with the others, as *Pentalophodon*." In Falconer's paper of 1857, *M. sivalensis* is repeatedly placed in the subgenus *Tetralophodon;* Falconer states on page 317 that: "*Mastodon Sivalensis*, although with five-ridged 'intermediate molars,' is provisionally included under *Tetralophodon*." (See also Synop. Tab. opp. p. 319.) Finally, in 1865, p. 262, Falconer adopts the name *Pentalophodon* with the genotypic species *M.* (*Tetralophodon*) *sivalensis*.	No species cited in 1857; *Mastodon sivalensis* referred to *Tetralophodon*, 1857; made the genotype, 1865.	*Pentalophodon* Collective genus. By courtesy to Falconer and Cautley restricted to *M. sivalensis*

Year	**Genus Author**	**Bibliographic Reference**	**Genotypic Species**	**Generic Reference in Present Memoir**
1867–1883	*Leptodon* Gunn	Geol. Mag., IV, p. 422 (name only); 1883. Geol. Mag., Dec. II, N. S., X, p. 458. Gunn, 1867, p. 422: "(*b*) the necessity for establishing a new species, called by Mr. Gunn *Leptodon*, from the fineness of the enamel." Gunn, 1883, p. 458: "submitted to a meeting of the Geological Society at Somerset House in 1867, under the names of *Leptodon minor* and *Leptodon giganteus*." Type: *E.* (*Leptodon*) *antiquus*; Forest bed stage, England. Generic name *Leptodon* preoccupied by Gaudry, 1860, for a genus of chalicotheres; by Sundevall, 1835, for a genus of birds.	*Leptodon minor*, *L. giganteus* Gunn	*Hesperoloxodon*
1868	*Antoletherium* Falconer	"Palæont. Mem." [editor: Murchison], I, p. 416, Pl. XXXIV, figs. 1, 2. Footnote on p. 416: "It does not appear from Dr. Falconer's notes that he had seen the specimen, which is here described from a drawing made by Col. Baker.—[Ed.]"		*Deinotherium*
1868	*Rhynchotherium* Falconer	(MS. 1856); "Palæont. Mem.," II, pp. 74, 75. See also Falconer, 1863, pp. 44, 56, 60, and Osborn, 1918.468, p. 136. Falconer, 1868, II, pp. 74, 75: "Extract of Letter from Dr. Falconer to M. Lartet, September 12, 1856. 'At Genoa [Geneva] I saw a cast of a large lower jaw of a Mastodon from Mexico, with an enormous *bec* abruptly deflected downwards and containing one very large lower incisor. The beak is much thicker than in *M.* (*Trilophodon*) *angustidens* and larger than in *M.* (*Tetralophodon*) *longirostris*. You know that every one (Laurillard, Gervais, &c.) has insisted on the absence of the lower incisors from both of the South American species. The outline of the jaw resembles very much the figure in Alcide D'Orbigny's Voyage, described by Laurillard as *M. Andium*. The specimen is unpublished material, and I was therefore only allowed to examine it very cursorily. The Genoese palæontologists had provisionally named it *Rhynchotherium*, from the enormous development of the beak, approaching Dinotherium.'" Search for this cast was unavailing for many years, but finally (1931) it was located at the Natural History Museum in Geneva, Switzerland (see Vol. I, p. 477). In the meantime Osborn (1921.515, p. 5) validated this genus: "The original genotype may be termed *Rhynchotherium tlascalæ*, new species, from the locality Tlascala." Compare figure 448.	Cast of lower jaw from Mexico, in Geneva Museum	*Rhynchotherium*
1877	*Cænobasileus* Cope	Proc. Amer. Phil. Soc., XVI, pp. 584, 585 (Pal. Bull. 24). Based on an artifact; name withdrawn by Cope in 1889 (Amer. Nat., XXIII, p. 207).	*C. tremontigerus* Cope (=*M. americanus*, *fide* Hay, 1902, p. 708).	NOT A PROBOSCIDEAN
1877	*Zygolophodon* Vacek	Abhand. geol. Reichsanst., VII, Heft IV, p. 45. Wien. A clear and admirable designation of the four species which together appeared to constitute a single distinct genus. Osborn, however, in 1926 (1926.706) removed the species *M. turicensis*, making it the type of a new genus *Turicius*; in the present Memoir he assigns *M. tapiroides* Cuvier to the genus *Turicius* (see Vol. I, pp. 203, 217) leaving *M. borsoni* and *M. pyrenaicus* as typical of *Zygolophodon* (see Vol. I, Chap. VII). Hopwood, 1935, p. 42: "Vacek (1877) used the genus *Mastodon* strictly in the Cuvierian sense, and sub-divided it into two groups, *Zygolophodon* and *Bunolophodon*, including in the former, *M. tapiroides* Cuv., *M. pyrenaicus* Lartet, 'Form von Baltavár', '*M. Turicensis* von Pikermi', *M. Borsoni* Hays, and *M. ohioticus*. Of these species Matthew (1918, p. 200) selected *M. tapiroides* as the genotype. Osborn (1926 [1926.706]) has taken *M. borsoni* as genotype, but under the rules of priority this selection is inadmissible. . . . The first mention of *M. tapiroides* is in Desmarest (1822, p. 386) who latinised Cuvier's vernacular, and took as his type the specimen figured by Cuvier. Hence, the genotype of *Zygolophodon* is *M. tapiroides* Desmarest, spec. indet., and thus *Zygolophodon* remains an indeterminate genus." See also this Memoir, Vol. I, p. 203, footnote.	*Mastodon borsoni* Hays, *M. turicensis* Schinz, *M. tapiroides* Cuvier, *M. pyrenaicus* Lartet	*Zygolophodon* By courtesy to Vacek restricted to *M. borsoni*
1877	*Bunolophodon* Vacek	*Loc. cit.*	*Mastodon atticus* Wagner, *M. longirostris* Kaup, *M. angustidens* Cuvier, *M. arvernensis* Croizet and Jobert, *M. pentelici* Gaudry	Collective genus. INVALID = *Anancus*, = *Trilophodon*, etc.

Year	Genus	Author	Bibliographic Reference	Genotypic Species	Generic Reference in Present Memoir
1882	*Notelephas*	Owen	Proc. Roy. Soc. London, XXXIII, p. 448; also Phil. Trans. Roy. Soc. London, 1883, CLXXIII, Pt. III, p. 777. See note under *Notelephas australis*, 1882 (p. 1397 below), from Jack and Etheridge, 1892, p. 683.	*Notelephas australis* Owen	DIPROTODON, a marsupial
1884	*Dibelodon*	Cope	Proc. Amer. Phil. Soc., XXII, pp. 2–8. Invalid because preoccupied by *Rhynchotherium* (see this Memoir, I, p. 525).	*Mastodon shepardi* Leidy	INVALID
1884	*Tetrabelodon*	Cope	*Ibid.*, pp. 4–5. Invalid because preoccupied by *Trilophodon* (see this Memoir, I, pp. 249, 525).	*Mastodon angustidens* Cuvier	INVALID
1885	*Archidiskodonten*	Pohlig	Zeitschr. deutsch. geol. Ges., XXXVII, p. 1027.	*Elephas planifrons* Falconer and Cautley	*Archidiskodon*
1888	*Archidiskodon*	Pohlig	Nova Acta Leop. Carol., LIII, pp. 138, 252. Pohlig, 1885, p. 1027: "8. Ich theile die Elephanten nach Kronenformen und Lamellenzahlen der Molaren ein in Archidiskodonten (*E. planifrons, E. meridionalis*), Loxodonten (*E. africanus, ?E. antiquus*) und Polydiskodonten (*E. primigenius, E. indicus*, etc.), die Stegodonten mit Clift wieder zu *Mastodon* zählend." An excellent generic distinction of two very closely related species (*E. planifrons, E. meridionalis*), to which may now be added *Elephas imperator*.	*Elephas meridionalis* Nesti, *E. planifrons* Falconer and Cautley	*Archidiskodon*
1885	*Loxodonten*	Pohlig	Zeitschr. deutsch. geol. Ges., XXXVII, p. 1027.	*Elephas africanus* Blumenbach, ?*E. antiquus* Falc. & Caut.	*Loxodonta*
1888	*Loxo-(disko)-donten* *Loxo(-disko-)don*	Pohlig	Nova Acta Leop. Carol., LIII, pp. 138, 252. Proposed as a group or sectional name, equivalent to the Loxodontinæ of Osborn. See note under *Archidiskodon*, 1885–1888, above, first paragraph.	*Elephas africanus* Blumenbach, *E. priscus* Goldfuss, *E. antiquus* Falc. & Caut.	
1885	*Polydiskodonten*	Pohlig	Zeitschr. deutsch. geol. Ges., XXXVII, p. 1027.	*Elephas primigenius* Blumenbach, *E. indicus* Linnæus	INVALID
1888	*Polydiskodon*	Pohlig	Nova Acta Leop. Carol., LIII, pp. 138, 252. Proposed in 1885 as a group or sectional name; in 1888 as a genus. See note under *Archidiskodon*, 1885–1888, above, first paragraph. Collective genus invalid, because based on species now known to belong to three different genera, *Mammonteus, Elephas*, and *Palæoloxodon*.	*Elephas primigenius* Blumenbach, *E. indicus* Linnæus, *E.* (?) *namadicus* Falc. & Caut.	
1885	*Stegodonten*	Pohlig	Zeitschr. deutsch. geol. Ges., XXXVII, p. 1027.	No species cited	
1888	*Stego(-lopho-)don*	Pohlig	Nova Acta Leop. Carol., LIII, p. 252. Proposed in 1885 as a group or sectional name. See note under *Archidiskodon*, 1885–1888, above, first paragraph.		
1889	*Emmenodon*	Cope	Amer. Nat., XXIII, p. 194. Invalid because based upon two species which are typical members of the genus *Stegodon*.	*Elephas cliftii* Falc. & Caut., *Mastodon elephantoides* Clift	INVALID

Year	Genus	Author	Bibliographic Reference	Genotypic Species	Generic Reference in Present Memoir
1901	*Palæomastodon*	Andrews	Zoologist (4), V, Aug. 15, pp. 318, 319 (name only); Tageblatt V Internat. Zoologen-Cong., Berlin, No. 6, Aug. 16, p. 4 (published vol. 1902, p. 528); Geol. Mag., Dec. IV, N. S., VIII, pp. 400–409.	*Palæomastodon beadnelli* Andrews	*Palæomastodon*
1901	*Mœritherium*	Andrews	Tageblatt V Internat. Zoologen-Cong., Berlin, No. 6, Aug. 16, p. 4 (name only); Geol. Mag., Dec. IV, N. S., VIII, pp. 400–409.	*Mœritherium lyonsi* Andrews	*Mœritherium*
1902	*Phiomia*	Andrews and Beadnell	"A Preliminary Note on Some New Mammals from Upper Eocene of Egypt," Surv. Dept., Pub. Works Ministry, pp. 1–9.	*Phiomia serridens* Andrews and Beadnell	*Phiomia*
1912	*Promastodon*	Pohlig	Bull. Soc. belge Géol., XXVI, Procès-verbaux, p. 192. Pohlig, 1912, p. 192: "...illustrée aussi par celui de Puerco (prototype de *Promastodon* Pohlig)." Founded on a supposed *missing link* in the American Paleocene Puerco; possibly Cope's *Polymastodon*, a multituberculate. This invalid description of *Promastodon* precedes (p. 192) the valid generic definition of *Stegomastodon* cf. *mirificum*, page 193, as cited below.	Puerco mammal	INVALID
1912	*Stegomastodon*	Pohlig	*Ibid.*, p. 193. Pohlig, 1912, p. 193: "...c'est prouvé, notamment, par une superbe dent de *Stegomastodon* cf. *mirificum* Leidy (prototype de *Stegomastodon* Pohlig)."	*Mastodon mirificus* Leidy	*Stegomastodon*
1912	*Hemimastodon*	Pilgrim	Mem. Geol. Surv. India (Pal. Indica), N. S., IV, Mem. 2, pp. 17–21. Type *Tetrabelodon crepusculi* Pilgrim, 1908 (p. 157) subsequently named *Hemimastodon*, 1912.	*Tetrabelodon crepusculi* Pilgrim	SUINA
1914	*Eubelodon*	Barbour	Univ. Neb. Studies, XIV, p. 194.	*Eubelodon morrilli* Barbour	*Eubelodon*
1914–1917	*Megabelodon*	Barbour	Neb. Geol. Surv., IV, Pt. 14, p. 217 (as a subgenus); 1917, *ibid.*, IV, Pt. 30, p. 512 (raised to higher rank). Barbour, 1914.2, p. 217: "For this new species, we wish to propose the name Tetrabelodon lulli, for Professor Lull. It is not unlikely that it is entitled to rank as a new subgenus at least, and it might not be amiss to propose the name Megabelodon." Barbour, 1917, p. 512: "In the case of Tetrabelodon lulli, the sub-generic title *Megabelodon* ... was proposed, but it seems entitled to higher rank [i. e., genus]."	*Tetrabelodon lulli* Barbour	*Megabelodon*
1914	*Rhabdobunus*	Hay	Iowa Geol. Surv. Ann. Rept. for 1912, XXIII, pp. 59, 373. Preoccupied by *Stegomastodon* Pohlig, 1912, above (cf. also Hay, 1930, Publ. Carnegie Inst. Wash., No. 390, p. 633).	*Mastodon mirificus* Leidy	*Stegomastodon*
1917	*Stegolophodon*	Schlesinger	Denk. Naturhist. Hofmus., I, p. 115 (as a subgenus). Schlesinger, 1917, p. 115, footnote: "Ich schlage für *M. latidens*, das sich durch seine kurze Symphyse von dem Subgenus *Bunolophodon*, durch seinen Molarenbau von *Dibunodon* entfernt, den Untergattungsnamen *Stegolophodon* vor. Der Name bringt einerseits die nahen Beziehungen zum Genus *Stegodon*, anderseits die Loslösung der Untergattung von *Bunolophodon* und ihre Sonderstellung gegenüber *Dibunodon* zum Ausdruck." See *Stego(-lopho-)don* Pohlig, 1888, above, this list.	*Mastodon latidens* Clift	*Stegolophodon*
1917	*Dibunodon*	Schlesinger	*Ibid.*, p. 124 (as a subgenus, with definition).	*Mastodon* (*Dibunodon*) *arvernense* Croiz. & Jobert	*Anancus*
1917	*Chœrolophodon*	Schlesinger	*Ibid.*, p. 181 (as a subgenus). Type: *Mastodon* (*Chœrolophodon*) *pentelici* Gaudry and Lartet. Schlesinger, 1917, p. 181: "Schädel niedrig, langgestreckt mit zwei aufwärts und auswärts geschwungenen schmelzbandlosen Stosszähnen. Unterkiefer mit mässig langer Symphyse ohne untere Inzisoren. Molaren choerodont (hochgradig suid)." See text and figures, Vol. I, Chap. VIII, this Memoir.	*Mastodon pentelicus* Gaudry and Lartet	*Trilophodon* (*Choerolophodon*)

Year	Genus	Author	Bibliographic Reference	Genotypic Species	Generic Reference in Present Memoir
1917	*Genomastodon*	Barbour	Neb. Geol. Surv., IV, Pt. 30, p. 512. Barbour, 1917, p. 512: "Longirostral mastodons seem to have reached their maximum in such forms as Tetrabelodon willistoni, lulli, osborni, and the like. For the present at least, the above may be grouped under a new and distinct genus, Genomastodon. . . . In the case of Tetrabelodon lulli, the sub-generic title Megabelodon . . . was proposed, but it seems entitled to higher rank [i. e., genus]." *Tetrabelodon lulli,* therefore, is preoccupied by *Megabelodon lulli;* by the process of elimination, *Genomastodon* applies to *T. willistoni* and *T. osborni* only.	*Tetrabelodon willistoni* Barbour, *T. lulli* Barbour, *T. osborni* Barbour	*Trilophodon* (*Genomastodon*)
1917	*Mastelephas*	Barbour	*Loc. cit.*	No definition and no genotypic species given.	NOMEN NUDUM
1922	*Miomastodon*	Osborn	Amer. Mus. Novitates, No. 49, p. 4.	*Mastodon merriami* Osborn	*Miomastodon*
1923	*Cuvieronius*	Osborn	Amer. Mus. Novitates, No. 99, p. 1. Cabrera (1929) erroneously refers *Mastodon humboldtii* to the genus *Stegomastodon* Pohlig, which, as shown above, is based on Leidy's '*Mastodon mirificus,*' wholly distinct from *M. humboldtii.*	*Mastodon humboldtii* Cuvier (in Desmarest)	*Cuvieronius*
1923	*Serridentinus*	Osborn	*Ibid.*, p. 2. Osborn, this Memoir, I, pp. 285, 286: "(December, 1932) On very close reëxamination of the cast (Amer. Mus. 1909) of Leidy's classic type (Figs. 232, 233) of '*Mastodon*' *obscurus*, also of the original type molar fragments of '*Serridentinus*' *simplicidens* Osborn, these two species prove to belong in the genus *Trilophodon* because of the presence of 'central conules' uniting as central trefoils with the median conules. . . . Osborn, 1933: Final study of the veritable type of *Mastodon obscurus* Leidy proves that it does not belong in the genus *Serridentinus* Osborn, but in the related though distinct genus *Trilophodon* Falconer. The phylogenetic position of *T. obscurus* appears to be distinct from the species *Mastodon* (=*Serridentinus*) *productus* of Cope and *M.* [=*Ocalientinus* (*Ser.*)] *floridanus* of Leidy."	*Mastodon productus* Cope, *M. serridens* Cope, *M. floridanus* Leidy, *M. obscurus* Leidy, *Serridentinus simplicidens* Osborn	*Serridentinus*
1923–1926	*Prostegodon*	Matsumoto	(In Osborn, Amer. Mus. Novitates, No. 99, p. 2). Subsequently proposed by Matsumoto (1924.3, pp. 324–327) as a subgenus of *Stegodon;* preoccupied by *Stegolophodon* Schlesinger, 1917, a genus also based upon the *Mastodon latidens* of Clift. This description appeared in the Japanese language. In 1926.1, p. 9, Matsumoto published his English text on this genus.	*Mastodon latidens* Clift	*Stegolophodon*
1924	*Harpagonotherium*	Fischer de Waldheim, 1808	(*Fide* Sherborn, 1924, Pt. V, p. 1022).		
1924	*Parastegodon*	Matsumoto	Journ. Geol. Soc. Tokyo, XXXI, pp. 256, 257, 262 (in Japanese); 1929, Sci. Rept. Tôhoku Imp. Univ., (2), Geology, XIII, No. 1, pp. 13–15 (in English). *Elephas* (*Parastegodon*) *auroræ*, well established on an excellent type, is, like *Stegodon mindanensis,* either a highly progressive member of the *Stegodon* phylum or a primitive member of the *Archidiskodon* phylum, a point which can only be determined positively by the discovery of the cranium of *Parastegodon auroræ.*	*Elephas auroræ* Mats., 1915, 1918	*Archidiskodon*? or a progressive *Stegodon*
1924	*Palæoloxodon*	Matsumoto	Journ. Geol. Soc. Tokyo, XXXI, pp. 255–272 (in Japanese); 1929, Sci. Rept. Tôhoku Imp. Univ., (2), Geology, XIII, No. 1, pp. 7, 10 (in English).	*Elephas namadicus naumanni* Makiyama	*Palæoloxodon*
1924	*Sivalikia*	Osborn	Amer. Mus. Novitates, No. 152, p. 2.	*Elephas namadicus* Falconer and Cautley	*Palæoloxodon*

Year	Genus Author	Bibliographic Reference	Genotypic Species	Generic Reference in Present Memoir
1924	*Pilgrimia* Osborn	*Loc. cit.*	*Elephas falconeri* Busk; other species cited, *E. melitensis* Falconer, *E. mnaidræ* Adams, *E. antiquus Recki* Dietrich	*Palæoloxodon*
1924	*Mammonteus* Osborn	*Loc. cit.* Compare *Mammonteum* Camper, 1788, above, this list.		*Mammonteus*
1924	*Parelephas* Osborn	*Ibid.*, p. 4.	*Elephas jeffersonii* Osborn	*Parelephas*
1924	*Morrillia* Osborn	*Ibid.*, No. 154, p. 1. Raised to rank of genus, this Memoir, I, pp. 690, 739.	*Tetralophodon barbouri* Osborn	*Morrillia*
1924	*Lydekkeria* Osborn	*Ibid.*, p. 2. See Volume I, p. 353, where it is stated that possibly *Lydekkeria* may become a synonym of *Tetralophodon*.	*Mastodon (Trilophodon) falconeri* Lydekker	*Tetralophodon (Lydekkeria)*
1926	*Pliomastodon* Osborn	*Ibid.*, No. 238, p. 1.	*Mastodon (Miomastodon) matthewi* Osborn	*Pliomastodon*
1926	*Turicius* Osborn	*Ibid.*, p. 3. Separated from *Zygolophodon* by Osborn.	*Mastodon turicense* Schinz	*Turicius*
1926	*Cordillerion* Osborn	*Ibid.*, p. 15. The generic name *Cordillerion* replaces the preoccupied name *Dibelodon*, as used by Cope and Lull, and *Mastodon humboldtii* Cuv. In 1923 Osborn proposed *Cuvieronius* to embrace *M. humboldtii*. Cabrera (1929, p. 90) erroneously holds that the genotype of *Cordillerion* (*Mastodon andium* Cuv.) belongs to the same genus as the genotype of *Cuvieronius* (*M. humboldtii* Cuv.), and hence are alike referable to *Stegomastodon* Pohlig based on *M. mirificus* Leidy. He accordingly substitutes *Notiomastodon* gen. nov., 1929, p. 90, for *Cordillerion* Osborn.	*Mastodonte des Cordilières* Cuvier = *Mastodon cordillerarum* Desmarest = *Mastodon andium* Cuvier	*Cordillerion*
1927	*Leith-Adamsia* Matsumoto	Japanese Journ. Geol. and Geog., V, No. 4, Art. XII.	*Leith-Adamsia siwalikiensis* Matsumoto	*Archidiskodon*
1927	*Amebelodon* Barbour	Neb. State Mus., Bull. 13, I, pp. 131–134.	*Amebelodon fricki* Barbour	*Amebelodon*
1928	*Platybelodon* Borissiak	Ann. Soc. Paléont., Russie, VII, for the year 1927, pp. 105–120.	*Platybelodon Danovi* Borissiak	*Platybelodon*
1929	*Synconolophus* Osborn	Amer. Mus. Novitates, No. 393, pp. 9, 10.	*Synconolophus dhokpathanensis* Osborn	*Synconolophus*
1929	*Notiomastodon* Cabrera	Rev. Mus. La Plata, XXXII, pp. 90, 91.	*Notiomastodon ornatus* Cabrera	*Notiomastodon*
1929	*Torynobelodon* Barbour	Neb. State Mus., Bull. 16, I, pp. 147–153.	*Torynobelodon loomisi* Barbour	*Torynobelodon*
1930	*Prodinotherium* Éhik	Geol. Hungarica (Palaeont. Ser.), Fasc. 6, pp. 3–21.	*Prodinotherium hungaricum* Éhik	*Deinotherium*
1931	*Teleobunomastodon* Revilliod	Mém. Soc. Paléont. Suisse, LI, pp. 20, 21.	*Mastodon bolivianus* Philippi	*Cordillerion*(?)
1931	*Hesperoloxodon* Osborn	Amer. Mus. Novitates, No. 460, p. 21.	*Palæoloxodon antiquus italicus* Osborn	*Hesperoloxodon*

Year	Genus Author	Bibliographic Reference	Genotypic Species	Generic Reference in Present Memoir
1933	*Blickotherium* Frick	Bull. Amer. Mus. Nat. Hist., LIX, Art. IX, pp. 505, 509, 515, 527–531.	*Blickotherium blicki* Frick	*Blickotherium*
1933	*Aybelodon* Frick	*Ibid.*, pp. 505, 527, 532.	*Aybelodon hondurensis* Frick	*Aybelodon*
1933	*Ocalientinus* Frick	*Ibid.*, pp. 505, 576, 579.	*Ocalientinus ojocaliensis* Frick	*Ocalientinus*
1933	*Trobelodon* Frick	*Ibid.*, pp. 505, 576, 580.	*Trobelodon taoensis* Frick	*Trobelodon*
1933	*Tatabelodon* Frick	*Ibid.*, pp. 505, 576, 581.	*Tatabelodon riograndensis* Frick	*Trilophodon* (*Tatabelodon*)
1933	*Paraplatybelodon* Frick	*Ibid.*, p. 592.		NOMEN NUDUM
1933	*Serbelodon* Frick	*Ibid.*, pp. 506, 592, 594.	*Serbelodon barbourensis* Frick	*Serbelodon*
1933	*Cryptomastodon* von Koenigswald	Wetenschappelijke Mededeelingen, Dienst Mijnbouw Nederl.-Indië, I Teil, No. 23, pp. 111, 112.	*Cryptomastodon martini* von Koenigswald	?SIRENIAN
1934	*Metarchidiskodon* Osborn	Amer. Mus. Novitates, No. 741, pp. 2, 12.	*Loxodonta griqua* Haughton	*Metarchidiskodon*
1934–1941	*Hypselephas* Osborn	Proc. Amer. Phil. Soc., LXXIV, p. 285 (name only); 1936, this Memoir, I, p. 12; 1941, *op. cit.*, II, p. 1340.	*Elephas hysudricus* Falconer and Cautley and *Elephas platycephalus angustidens* Osborn	*Hypselephas*
1934–1941	*Platelephas* Osborn	Proc. Amer. Phil. Soc., LXXIV, p. 285 (name only); 1936, this Memoir, I, p. 12, Pl. XI; 1941, *op. cit.*, II, p. 1358.	*Elephas platycephalus* Osborn	*Platelephas*
1935	*Gnathabelodon* Barbour and Sternberg	Neb. State Mus., Bull. 42, I, pp. 395, 396.	*Gnathabelodon thorpei* Barbour and Sternberg	*Gnathabelodon*

LIST OF SPECIES, SUBSPECIES, AND VARIETIES

Year	Name Author		Reference in Present Memoir
1754	*Elephas indicus* Linnæus	"Systema Naturæ," p. 11. Hab.: India, Ceylon. This name was first used by Linnæus in 1754, but in the 1758 edition of the "Systema Naturæ," p. 33, he used *Elephas maximus* for the Ceylon elephant.	*Elephas indicus* (pre-Linnæan)
1758	*Elephas maximus* Linnæus	"Systema Naturæ," edition 10, p. 33. Hab.: India, Ceylon. Sherborn (letter, July 14, 1929) is of the opinion that *maximus* should be "swept aside."	*Elephas indicus*
1775(?)	*Elefante Indiano* Giovanni Targioni Tozzetti		*Elephas* [*Archidiskodon*] *meridionalis* Nesti, 1825 (*fide* Weithofer, 1890, p. 133)
1792	*Elephas americanus* Kerr	"Animal Kingdom of Linnæus," I, p. 116. Type loc.: Big Bone Lick(?), Boone County, Kentucky, near Ohio River. Leidy, 1869, p. 392, footnote: "Cuvier, in the works quoted [Tabl. Elem. Hist. Nat. (an. 6) 1798, 149; Mem. Inst. Nat. Sci. (An VII [1799], 19, 21.], and De Blainville, in his Osteog. Gen. Elephants, 327, 245, attribute this name to Pennant. Falconer and Cautley, in the Fauna Antiq. Sival., 17, also observe, 'that Pennant first ventured in 1793 to designate the American fossil animal, in a systematic work, as a species of Elephant by the name of *E. americanus*.' I have been unable to find the name thus expressed in any of the works of Pennant, nearer than the words 'American Elephant,' which occur in the Synopsis of Quadrupeds of 1771 and in both editions of the History of Quadrupeds, that of 1781 and 1793."	*Mastodon americanus*

Year	Name	Author	Reference in Present Memoir
1796	*Elephas Mammoth*	Cuvier [and Geoffroy] Falconer, 1868, II, p. 158: 'Cuvier was undoubtedly the first to characterize the extinct species with exactness, in his joint memoir with Geoffroy, under the name of *Elephas Mammoth*, in the year 1796 [Footnote: 'Mém. de l'Institut, 1$^{\text{re}}$ Classe, tom. ii.']."	*Mammonteus primigenius*
1797	*Ohio-Incognitum*	Blumenbach Abbild. naturhist. Gengens., No. 19. Hab.: Ohio River, North America.	*Mastodon americanus*
1797	*Elephas asiaticus*	Blumenbach "Handb. d. Natur.," 5th edition, p. 124. Hab.: India. Type fig.: Blumenbach, Abbild. naturhist. Gegens., No. 19, fig. B.	*Elephas indicus*
1797	*Elephas africanus*	Blumenbach "Handb. d. Natur.," 5th edition, p. 125. Hab.: South Africa. Type fig.: Blumenbach, Abbild. naturhist. Gegens., No. 19, fig. C. Not in the edition of the "Handbuch der Naturgeschichte" of 1779 [First Edition] but in the Fifth Edition (1797); in "Abbild. Naturhist. Gegenstände," Heft 2, No. 19, fig. C, the name is already used... The arrangement of the lamellæ would indicate its Cape origin. It can only be a question of the Cape Colony and the Congo, perhaps of the French Congo. The confluence of the anterior lamellæ is peculiar. (Matschie, letter, 1921.) Sherborn (1902, Pt. I, p. 22) lists *E. africanus* as in the Fifth Edition of the "Handbuch" (1797.1, p. 125), but reference is not made to a figure in this edition. In 1923, Pt. II, p. 135, he cites *E. africanus* in Blumenbach, Man. Hist. Nat., I, 1803, p. 155.	*Loxodonta africana*
1798	*Elephas indicus*	Cuvier "Tabl. Elémen. Hist. Nat. Animaux," p. 148. Hab.: India. See Cuvier's figure, with description, 1799, Mém. Inst. Nat. Sci. et Arts. Sci., Mathém. et Phys., II, Fructidor, an VII [1799], p. 21, and Plates (ii, figs. 1, 2; iv, fig. 1; v, fig. 1; vi, fig. 2).	Name preoccupied by Linnæus, 1754
1798	*Elephas capensis*	Cuvier "Tabl. Elémen. Hist. Nat. Animaux," p. 149. Hab.: South Africa. Type fig.: Cuvier, 1799, Mém. Inst. Nat. Sci. et Arts. Sci., Mathém. et Phys., II, Fructidor, an VII [1799], Pl. iii and Pl. iv, fig. 2. *Elephas capensis* G. Cuvier, "Tableau Elémen.," 1798. Cuvier had at his disposal one skeleton from the Senegal and one skull from the Cape ["Cap de Bonne-Espérance," Cuvier, Mém. Inst. (de France) National des Sciences et Arts, sometimes called the Académie des Sciences, Vol. II, année 7 (1799?)]. (Matschie, letter, 1921.)	*Loxodonta africana capensis*
1799	*Elephas primigenius*	Blumenbach "Handb. d. Natur.," 6th edition, p. 697. Hab.: Siberia and northern Germany. No original type figure.	*Mammonteus primigenius*
1799	*Mammut ohioticum*	Blumenbach *Op. cit.*, p. 698. Hab.: Ohio River, North America.	*Mastodon americanus*
1799	*Elephas mammonteus*	Cuvier (1796 MS.), published August-September, 1799, Mém. Inst. Nat. Sci. et Arts. Sci., Mathém. et Phys., II, Fructidor, an VII [1799], p. 21, Pls. v, fig. 2, and vi, fig. 1. Falconer, 1868, II, p. 158: "In the same year [1796] he [Cuvier] read a memoir [MS.] at the first public meeting of the 'Institute,' but which was not published until 1806 [1799, p. 21], in which the diagnostic marks are very pointedly expressed under the designation of *Elephas Mammonteus*: ... [subsequently—1806, Ann. Mus. hist. nat., VIII, p. 264] he abandoned the name *E. Mammonteus* of his [MS.] memoir of 1796, and adopted the designation of *Elephas primigenius*, proposed by Blumenbach [Footnote: 'Voigt's Mag. 1803, Band v, p. 16.'], in 1803 which is that now generally accepted among palæontologists." See, however, Bibliography, Cuvier, 1799.1.	*Mammonteus primigenius*
1801	*Elephantus indicus*	Cuvier and Lacépède "La Ménagerie du Muséum National d'Histoire naturelle ou Les Animaux Vivants," An X. Hab.: India.	*Elephas indicus*
1803	*Elephas macrocephalus*	A. Camper Original text of 1802 not available. Atlas of 1803 gives the name *Elephas macrocephalus* under Fig. 18. Sherborn, 1922–1933, "Index Animalium" (1928, p. 3760) gives the following reference: "'*Elephas macrocephalus*,' Camper, Œuvres de P. Camper, II, 1803, 18, f. n. [*non usu* spec.]."	*Mastodon americanus*

Year	Name	Author	Reference in Present Memoir
1806	*Le Grand Mastodonte* Cuvier	Ann. Mus. hist. nat., VIII, pp. 270, 293 (Cuvier, 1806.2). Hab.: Ohio River, North America. Type fig.: Cuvier, *ibid.*, Pl. 49 [I], figs. 1–5. Cuvier, *ibid.*, pp. 270, 272: "Animal très-voisin de l'éléphant, mais à mâchelières hérissées de gros tubercules, dont on trouve les os en divers endroits des deux continens, et surtout près des bords de l'Ohio, dans l'Amérique Septentrionale, improprement nommé Mammouth par les Anglais et par les habitans des États-Unis. . . .Nous empruntons le nom de *mastodonte* de deux mots grecs qui signifient *dents mammelonnées,* et qui expriment par conséquent son principal caractère." Cf. *Mastodonte de l'Ohio* Cuvier, below, this list.	*Mastodon americanus*
1806	*Mastodonte de l'Ohio* Cuvier	*Ibid.*, p. 412 (Cuvier, 1806.3). Hab.: Ohio River, North America. Cf. *Le Grand Mastodonte* Cuvier, 1806, above, and *Mastodon giganteum* Cuvier, 1817, below, this list.	*Mastodon americanus*
1806	*Mastodonte à dents étroites* Cuvier	*Loc. cit.* Type loc.: Simorre, France. Type fig.: Cuvier, *ibid.*, Pl. 66 [I], fig. 4. Cf. *Mastodon angustidens* Cuvier, 1817, below, this list.	*Trilophodon angustidens*
1806	*Petit mastodonte* Cuvier	*Ibid.*, p. 413. Type loc.: Montabusard, France. Type fig.: Cuvier, *ibid.*, Pl. 68 [III], fig. 6.	*Turicius tapiroides*
		Loc. cit. Type loc.: Saxony, Germany. Type fig.: Cuvier, *ibid.*, Pl. 67 [II], fig. 11. Cuvier applied the term "Petit mastodonte" to two distinct types, from Montabusard and Saxony, to which he subsequently assigned the names *Mastodonte tapiroïde*, 1821, and *M. minutus*, 1824, respectively (see below, this list, and also *M. parvus*, 1834).	*Trilophodon angustidens minutus*
1806	*Mastodonte des Cordilières* Cuvier	*Loc. cit.* Type loc.: Near volcano of Imbaburra, Quito, Ecuador. Type fig.: Cuvier, *ibid.*, Pl. 67 [II], fig. 1. This is the single type which Cuvier subsequently (1824) called *Mastodon andium* (see below) and which Desmarest called *M. cordillerarum*. The first distinctive generic name applied to these animals was *Mastotherium* Fischer (1814). Subsequent names: *Dibelodon* Cope (1884.2), *Cordillerion* Osborn (1926). See List of Genera above.	*Cordillerion andium*
1806	*Mastodonte humboldien* Cuvier	*Loc. cit.* Type loc.: Near Concepcion, Chile. Type fig.: Cuvier, *ibid.*, Pl. 67 [II], fig. 5. Cf. *Mastodon humboldtii* Cuvier, in Desmarest, 1818–1824, below, this list.	*Cuvieronius humboldtii*
1807	*Elephas mammouth* Link	Beschr. Nat. Samml. Univ. Rostock (4) 1807, 3 (*fide* Sherborn, 1928, p. 3845).	*Mammonteus primigenius*
1808	*Elephas primævus* Blumenbach	(In Adams, translation from the French by Sir Joseph Banks, Phil. Mag. (Tilloch), XXIX, London, p. 152); cited by Tilesius, 1815, p. 452. Hab.: Lena River, Siberia. Cf. *Elephas brachyramphus* Brandt, 1832, below, this list.	*Mammonteus primigenius*
1808	*Elephas minimus* Nesti	Attributed by Falconer and Cautley, 1846, "Fauna Antiqua Sivalensis," letterpress, p. 13, to Nesti, but not found by the present author in the original reference. Name abandoned by Nesti.	
1808	*Harpagmotherium canadense* Fischer de Waldheim	Prog. d'Invit. Séance, Pub. Soc. Imp. Nat. Moscou, September, p. 19. Hab.: Ohio River, North America.	*Mastodon americanus*
1809	*Mastotherium ohioticum* (Blum.) Fischer de Waldheim	Mém. Soc. Imp. Nat. Moscou, II, p. 252.	[*Mastodon americanus*]
1811	*Elephas gigas* G. Perry	"Arcana," p. li and plate.	[*Elephas indicus*]
1811	*Elephas socotrus* G. Perry	*Op. cit.*, p. li.	[Indeterminate]
1814	*Mastotherium megalodon* Fischer de Waldheim	"Zoognosia," p. 340. Hab.: Ohio River, North America. Cf. *Le Grand Mastodonte* and *Mastodonte de l'Ohio* Cuvier, 1806, above, this list.	*Mastodon americanus*
1814	*Mastotherium leptodon* Fischer de Waldheim	*Loc. cit.* Type loc.: Simorre, France. Cf. *Mastodonte à dents étroites* Cuvier, 1806, above, this list.	*Trilophodon angustidens*

Year	**Name**	**Author**	**Reference in Present Memoir**
1814	*Mastotherium microdon*	Fischer de Waldheim *Loc. cit.* Type loc.: Montabusard, France. Cf. *Petit mastodonte*, à petites dents, Cuvier, 1806, above, also *Mastodon tapiroides* Cuvier, in Desmarest, 1822, below, this list.	*Turicius tapiroides*
1814	*Mastotherium hyodon*	Fischer de Waldheim *Op. cit.*, p. 341. Hab.: Cordilleras. Cf. *Le Mastodonte des Cordilières* Cuvier, 1806, above, this list.	*Cordillerion andium*
1814	*Mastotherium humboldtii*	Fischer de Waldheim *Loc. cit.* Cf. *Mastodonte humboldien* Cuvier, 1806, above, and *Mastodon humboldtii* Cuvier, in Desmarest, 1818 1824, below, this list.	*Cuvieronius humboldtii*
1814	*Mastodon Macrodon*	Rafinesque Specchio Sci., II, No. 12, p. 182. Hab.: North America.	*Mastodon americanus*
1814	*Mastodon rhomboides*	Rafinesque *Loc. cit.* Hab.: Cordilleras.	*Cordillerion andium*
1814	*Mastodon humboldianus*	Rafinesque *Loc. cit.* Hab.: South America.	*Cuvieronius humboldtii*
1814	*Mastodon Senodon*	Rafinesque *Loc. cit.* Hab.: France and Europe.	*Trilophodon angustidens*
1814	*Mastodon microdon*	Rafinesque *Loc. cit.* Hab.: Europe.	(?)*Turicius tapiroides*
1815	*Elephas primordialis*	Blumenbach (In Tilesius, Mém. Acad. Imp. Sci. St. Pétersb., (V), V, p. 470). Hab.: Germany and Siberia. See also *E. primordialis* Brayley, 1831, Phil. Mag., IX, pp. 411–418; Bronn's Neues Jahrb., 1833, p. 372, and the "Index palæontologicus" of von Meyer and Göppert, in Bronn's "Handbuch einer Geschichte der Natur," 1848, III, p. 455. Hab.: Eschscholtz Bay, Alaska.	*Mammonteus primigenius*
1817	*Mastodon giganteum*	Cuvier "Le Règne Animal," p. 233. Type loc.: Big Bone Lick, Boone County, Kentucky, North America. Cf. *Le Grand Mastodonte* Cuvier, 1806, *Mastodonte de l'Ohio* Cuvier, 1806, *Mastotherium megalodon* Fischer, 1814, above, also *Mastodon maximus* Cuvier, 1824, *Mastodon ohioticum*, 1832, and *Mastodon americanus* Leidy, 1868, below, this list.	*Mastodon americanus*
1817	*Mastodon angustidens*	Cuvier *Loc. cit.* Type loc.: Simorre, France. Type fig.: Cuvier, 1806, Ann. Mus. hist. nat., VIII, Pl. 66 [I], fig. 4. Not until the year 1817 did Cuvier substitute the name *Mastodon angustidens* for his "Mastodonte à dents étroites" of 1806. Cf. *Mastotherium leptodon* Fischer, 1814, above, this list.	*Trilophodon angustidens*
1818	*Mastodon minor*	Cuvier (In Desmarest, Nouv. Dict. d'Hist. Nat., XIX, p. 446). Cf. *Petit Mastodonte* Cuvier, 1806, above, and *Mastodon minutus* Cuvier, 1824, below, this list.	*Trilophodon angustidens minutus*
1818 1824	*Mastodon humboldtii*	Cuvier (In Desmarest, *ibid.*, p. 447); Cuvier, 1821–1824, "Ossemens Fossiles," V, Pt. 2, p. 527. Type loc.: Near Concepcion, Chile. Type description: Cuvier, 1806, Ann. Mus. hist. nat., VIII, p. 413. Type fig.: Cuvier, *ibid.*, Pl. 67 [II], fig. 5. Cf. *Mastodonte humboldien* Cuvier, 1806, also *Mastotherium humboldtii* Fischer, 1814, above, this list.	*Cuvieronius humboldtii*
1820	*Elephas jubatus*	Schlotheim "Die Petrefactenkunde," p. 4. Hab.: Germany.	*Mammonteus primigenius*
1821	*Mastodonte tapiroïde*	Cuvier "Ossemens Fossiles," I, p. 268. Type loc.: Calcaire de Montabusard, France. Cf. *Petit mastodonte* Cuvier, 1806, above, this list. Not until the year 1821 did Cuvier replace "Petit mastodonte" with the name *tapiroïde*, subsequently written *tapiroides* (Desmarest, 1822, p. 386; Cuvier, 1821-1824, V, Pt. 2, p. 527).	*Turicius tapiroides*
1821	*Elephas priscus*	Goldfuss Nova Acta Acad. Leop. Carol., X, Pt. II, Pl. XLIV. Type loc.: Near (?)Cologne, Germany. Falconer (1868, II, p. 94) retained the name *Elephas* (*Loxod.*) *priscus* [=*Hesperoloxodon antiquus* of present Memoir] for undoubted Pleistocene fossil teeth from Gray's Thurrock and elsewhere, although he states (p. 95) that the actual type of Goldfuss, 1821, "conveyed to my mind a corresponding impression that the molar was probably of modern origin." Subsequently Falconer (cf. Leith Adams, 1877–1881, pp. 1, 2) abandoned the name *Elephas priscus* Goldfuss, and it is now considered (*fide* Pohlig) as a synonym of *Loxodonta africana*.	*Loxodonta africana*

Year	Name	Author	Reference in Present Memoir
1822	*Mastodon cordillerarum*	Desmarest "Mammalogie," Seconde partie, p. 385. Cf. *Mastodonte des Cordilières* Cuvier, 1806, and *Mastotherium hyodon* Fischer, 1814, above, also *M. andium* Cuvier, 1824, below, this list.	*Cordillerion andium*
1822	*Mastodon minus*	Desmarest *Op. cit.*, p. 386. Cf. *Petit mastodonte* Cuvier, 1806, above, and *Mastodon minutus* Cuvier, 1824, below, this list.	*Trilophodon angustidens minutus*
1822	*Mastodon tapiroides*	Cuvier (In Desmarest, *loc. cit.*). Also Cuvier, 1821–1824, "Ossemens Fossiles," V, Pt. 2, p. 527. Type loc.: Montabusard, France. Type description: Cuvier, 1806, Ann. Mus. hist. nat., VIII, p. 411. Type fig.: Cuvier, *ibid.*, Pl. 68 [III], fig. 6. Cf. *Petit mastodonte* Cuvier, 1806, *Mastotherium microdon* Fischer, 1814, *Mastodonte tapiroïde* Cuvier, 1821, above, this list.	*Turicius tapiroides*
1823	*Elephas antiquitatis*	Krüger "Geschichte der Urwelt," p. 832. Type loc.: Thiede, Germany. Type fig.: Breislak, 1820, "Lehrbuch der Geologie," II, p. 428.	*Hesperoloxodon antiquus germanicus*
1824	*Mastodon maximus*	Cuvier "Ossemens Fossiles," V, Pt. 2, p. 527. Type loc.: Big Bone Lick, Boone County, Kentucky. Cf. *Mastodon giganteum* Cuvier, 1817, above, this list.	*Mastodon americanus*
1824	*Mastodon Andium*	Cuvier *Loc. cit.* Type loc.: Near Volcano of Imbaburra, Quito, Ecuador. Type description: Cuvier, 1806, Ann. Mus. hist. nat., VIII, pp. 411, 413. Type fig.: Cuvier, 1806, *ibid.*, Pl. 67 [II], fig. 1. Cf. *Mastodonte des Cordilières* Cuvier, 1806, above, this list. The name *Mastodon andium* is erroneously dated by Trouessart and others as 1806. We cannot find the name earlier than 1824. It is thus technically preoccupied by *Mastotherium hyodon* Fischer, 1814, and *Mastodon cordillerarum* Desmarest, 1822, but the name *Mastodon andium* Cuvier is adopted, following de Blainville and Falconer (see footnote on p. 122 of Vol. I of the present Memoir).	*Cordillerion andium*
1824	*Mastodon humboldtii*	Cuvier "Ossemens Fossiles," V, Pt. 2, p. 527. Cf. *Mastodon humboldtii* Cuvier, in Desmarest, 1818–1824, above, this list.	*Cuvieronius humboldtii*
1824	*Mastodon minutus*	Cuvier *Loc. cit.* Type loc.: Saxony. Type description: Cuvier, 1806, Ann. Mus. hist. nat., VIII, p. 411. Type fig.: Cuvier, *ibid.*, Pl. 67 [II], fig. 11. Cf. *Petit mastodonte* Cuvier, 1806, *M. minor* Cuvier, in Desmarest, 1818, above, and *M. parvus* Cuvier, in Hays, 1834, below, this list.	*Trilophodon angustidens minutus*
1824	*Mastodon turicense*	Schinz "Naturgesch. u. Abbild. d. Säugethiere," p. 278. Type loc.: Elgg, Canton Zurich, Switzerland. Type fig.: Schinz, 1833, Denk. schweiz. Ges. Naturw., I, Abth. 2, Taf. I, fig. 1, and p. 59.	*Turicius turicensis*
1825	*Elephas meridionalis*	Nesti Nuov. Giorn. Lett., XI, No. 24, p. 211. Type loc.: Val d'Arno supérieure, northern Italy. Type figs.: Nesti, *ibid.*, Tav. I, figs. 1, 2 (lectotype cranium C); Tav. I, fig. 3 (cotype cranium A).	*Archidiskodon meridionalis*
1828	*Mastodon arvernensis*	Croizet and Jobert "Ossemens Fossiles . . . Puy-de-Dome," p. 138. Type loc.: Perrier, Auvergne, France. Cotype figs.: Croizet and Jobert, *op. cit.*, Pl. I, figs. 1–4, Pl. II, fig. 7.	*Anancus arvernensis*
1828	*Mastodon latidens*	Clift Trans. Geol. Soc. London, (2), II, Pt. III, pp. 369–375. Type loc.: Near Yenangyaung, Irrawaddy River, Burma. Lectotype and cotype figs.: Clift, *ibid.*, Pl. XXXVII, fig. 1, and Pl. XXXVIII, fig. 1.	*Stegolophodon latidens*
1828	*Mastodon elephantoides*	Clift *Ibid.*, pp. 372, 373. Type loc.: Near Yenangyaung, Irrawaddy River, Burma. Lectotype fig.: Clift, *ibid.*, Pl. XXXVIII, fig. 2.	*Stegodon elephantoides*
1829	*Deinotherium giganteum*	Kaup Isis, [XXII], Heft IV, p. 401. Type loc.: Eppelsheim, Germany. Type fig.: Kaup, *ibid.*, Taf. I.	*Deinotherium giganteum*
1829	*Elephas mammonteus*	Fischer de Waldheim Nouv. Mém. Soc. Imp. Nat. Moscou, I, pp. 285, 286. Hab.: Russia. Cf. *Elephas mammonteus* Cuvier (MS. 1796, published 1799) above, this list.	*Mammonteus primigenius*

Year	**Name**	**Author**		**Reference in Present Memoir**
1829	*Elephas paniscus*	Fischer de Waldheim	*Ibid.*, pp. 285, 289. Hab.: Volga, Russia. Written also *panicus*.	*Mammonteus primigenius*
1829	*Elephas periboletes*	Fischer de Waldheim	*Ibid.*, pp. 285, 290. Type loc.: Podolia, Russia. Type fig.: Fischer, *ibid.*, Tab. xvii, fig. 1. Also written *proboletes*.	*Mammonteus primigenius*
1829	*Elephas pygmæus*	Fischer de Waldheim	*Ibid.*, pp. 285, 292. Type loc.: District of Calomna and of Zwenigorod, Russia. Type fig.: Fischer, *ibid.*, Tab. xvii, fig. 2.	*Mammonteus primigenius*
1829	*Elephas campylotes*	Fischer de Waldheim	*Ibid.*, pp. 285, 291. Type loc.: Borders of the Bug, Russia.	*Mammonteus primigenius*
1829	*Elephas Kamenskii*	Fischer de Waldheim	*Ibid.*, p. 276. Hab.: Siberia.	*Mammonteus primigenius*
1830	*Mammuthus borealis*	Burnett	Quart. Journ. Sci., London, p. 352.	[*Mammonteus*(?) *primigenius*]
1830	*T.* [*Tetracaulodon*] *Mastodontoideum*	Godman	Trans. Amer. Phil. Soc., N. S., III, pp. 478–485. Type loc.: Near Newburgh, Orange County, New York. Type figs.: Godman, *ibid.*, Pls. xvii, xviii.	*Mastodon americanus*
1831	*M.* [*Mastodon*] *intermedius*	Eichwald	"Zoologia Spec.," III, p. 361. Type loc.: Volhynia, Russia. Type: Maxilla (no figure found). Paratype: Jaw (supplementary description, 1835, Nova Acta Acad. Leop. Carol., XVII, p. 737, Pls. lviii, lix).	*Anancus intermedius*
1831	*Dinotherium maximum*	Kaup	"Fossil Saugeth. Rheinhessens." (*Fide* de Blainville, 1839–1864, "Ostéographie," p. 18, on Dinotherium; *fide* von Meyer, 1832, "Palæologica z. Geschichte der Erde," p. 78). Type loc.: Eppelsheim, Germany.	*Deinotherium giganteum*
1831	*Deinotherium Bavaricum*	von Meyer	Neues Jahrb. Min., p. 297. Type loc.: Gmünd, Bavaria. Supplementary description: von Meyer, 1832, Nova Acta Acad. Leop. Carol., XVI, Pt. II, p. 487, Tab. xxxiv, figs. 12–15, Tab. xxxvi.	*Deinotherium bavaricum*
1831–1833	*Elephas primordialis*	Brayley	Cf. *Elephas primordialis* Blumenbach, in Tilesius, 1815, above, this list. *Elephas primordialis* Brayley, 1831 (without name); in Bronn, 1833, who attributes the name to Brayley.	
1832	*Mammut Sibiricum*	von Meyer	"Palæologica z. Geschichte der Erde," p. 64. Von Meyer attributes this name to Schlotheim.	*Mammonteus primigenius*
1832	*Dinotherium maximum*	von Meyer	(Ex MS. Kaup), "Palæologica z. Geschichte der Erde," p. 78. Type loc.: Eppelsheim, Germany.	*Deinotherium giganteum*
1832	*Dinotherium Cuvieri*	Kaup	"Description d'Ossements Fossiles," Cahier I, pp. 2, 14. Hab.: Comminge, Carlat-le-Comte, Chevilly, France.	*Deinotherium cuvieri*
1832	*Tetracaulodon longirostre*	Kaup	Isis, [XXV], Heft VI, p. 628. Type loc.: Eppelsheim, Germany. Type fig.: Kaup, *ibid.*, Taf. xi, fig. A. At first thought to be referable to *Mastodon angustidens*. Kaup, however, substituted the name *Tetracaulodon longirostre*, which subsequently (1835, p. 65) he changed to *Mastodon longirostris* (see below, this list) by which name it has since been known. Its reference in the present Memoir is to *Tetralophodon longirostris*.	*Tetralophodon longirostris*
1832	*Mastodon ohioticum*		(In Bronn, Neues Jahrb. Min., p. 355. In Gervais, 1848–1852, Zool. Pal. Françaises, I, p. 187.)	*Mastodon americanus*
1832	*Elephas brachyramphus*	Brandt	Mém. Acad. Imp. Sci. St. Pétersb., (6), II, Math. et Phys., Bull. Sci., No. 2, p. xi. Type loc.: Mer glaciale, near mouth of Lena River, Siberia. Type: Adams skeleton in the Zoological Museum of the Academy of Sciences, Leningrad, U. S. S. R. Figured by Tilesius, 1815, Mém. Acad. Imp. Sci. St. Pétersb., (V), V, Tab. x. Described by Adams, 1808, Phil. Mag. (Tilloch), XXIX, and Tilesius, 1815. Cf. *Elephas primævus* Blumenbach, in Adams, 1808, above, this list.	*Mammonteus primigenius*
1832	*Elephas homotaphrus*	Brandt	*Ibid.*, p. xii (name only).	

Year	Name	Author	Reference in Present Memoir
1832	*Elephas giganteus*	Brandt *Loc. cit.* Type loc.: Indigirka River, Siberia. Type: Messerschmidt cranium. Figured by Breyne, 1741, Phil. Trans. Roy. Soc. London, XL, Pl. I, figs. I, II; and by Cuvier, 1806, "Ossemens Fossiles," Pl. 39, fig. 1, and Pl. 41, fig. 11.F.	*Mammonteus primigenius*
1832	*Elephas commutatus*	Brandt *Loc. cit.* Type loc.: "Bords du Volga." Type: "Crâne du Comte Mussin Puschkin." Figured by Cuvier, 1825, "Recherches Ossemens Fossiles," 3d edition, I, Pl. IX, fig. 7, and p. 179.	*Mammonteus primigenius*
1832	*Elephas stenotoechus*	Brandt *Ibid.*, p. xiii. No locality given. Type in Zoological Museum of the Academy of Sciences, Leningrad, U. S. S. R.	*Mammonteus primigenius*
1832	*Elephas platytaphrus*	Brandt *Ibid.*, p. xiv. No locality given. Type in Zoological Museum of the Academy of Sciences, Leningrad, U. S. S. R. Type fig.: Cuvier, 1825, "Recherches Ossemens Fossiles," 3d edition, I, Pl. IX, figs. 5, 6.	*Mammonteus primigenius*
1832	*Elephas affinis*	Brandt *Ibid.*, p. xiv. The history of this specimen (a skeleton in the Zoological Museum of the Academy of Sciences, Leningrad, U. S. S. R.) is given in Oken's Isis of 1832, XXV, Heft X, pp. 1111–1114, by a writer signing himself "Ein Naturforscher in St. Petersburg." He states that this skeleton together with other materials was originally discovered in a hole beneath an oven of a house in St. Petersburg which was built upon ground formerly a swamp and which was torn down in 1828. This anonymous reviewer refers to the author of the description as "Herr B" and expresses doubt as to the specimen being a fossil. See also Neues Jahrb. Min., 1833, p. 611.	
1833	*Dinotherium medium*	Kaup Neues Jahrb. Min. p. 419. Type loc.: Eppelsheim, Germany. Type fig.: Kaup, *ibid.*, Taf. VII, fig. 1, reproduced in Kaup, 1835, "Description d'Ossements Fossiles," Cahier IV, Add. Tab. I. Supplementary description: Kaup, 1833, Neues Jahrb. Min., p. 509.	*Deinotherium medium*
1834	*M.* [*Mastodon*] *parvus*	Cuvier (In Hays, Trans. Amer. Phil. Soc., N. S., IV, p. 333.) Cf. *Petit mastodonte* Cuvier, 1806, of Saxony, above, this list.	
1834	*M.* [*Mastodon*] *Borsoni*	Hays *Ibid.*, p. 334. Type loc.: Near Villanova d'Astica, Piedmont, Italy. Type fig.: Borson, 1823, Mem. Accad. Sci. Torino, XXVII, Tav. II (as *M. giganteum*).	*Zygolophodon borsoni*
1834	*M.* [*Mastodon*] *Cuvieri*	Hays *Ibid.*, pp. 322, 323, 334. Fragment of lower jaw in cabinet of the American Philosophical Society. Type fig.: Hays, *ibid.*, Pl. XXIV.	*Mastodon americanus*
1834	*M.* [*Mastodon*] *Jeffersoni*	Hays *Ibid.*, pp. 323, 334. Fragment of right lower jaw and portion of left ramus in cabinet of the American Philosophical Society. Type fig.: Hays, *ibid.*, Pl. XXV.	*Mastodon americanus*
1834	*T.* [*Tetracaulodon*] *Collinsii*	Hays *Ibid.*, pp. 326, 327, 334. Portion of right lower jaw in cabinet of the American Philosophical Society. Type fig.: Hays, *ibid.*, Pl. XXVIII.	*Mastodon americanus*
1834	*T.* [*Tetracaulodon*] *Godmani*	Hays *Ibid.*, pp. 327, 334. Fragment of right lower jaw in cabinet of the American Philosophical Society. Type fig.: Hays, *ibid.*, Pl. XXIX.	*Mastodon americanus*
1834–1843	*Mastodon Chapmani*	Hays *Ibid.*, explanation of Pl. XXII, figs. 3 and 4, p. 338 (without name); name used by Hays, 1843, Proc. Amer. Phil. Soc., II, p. 270. Type loc.: Unrecorded locality in the United States. Type lost or misplaced. Type fig.: Hays, 1834, Trans. Amer. Phil. Soc., N. S., IV, Pl. XXII, figs. 3 and 4.	*Stegomastodon chapmani*
1834	*Elephas macrorynchus*	Morren "Mém. Ossemens Fossiles Éléphans Belg.," p. 23. Type loc.: Tamise, Belgium. Type fig.: Morren, *op. cit.*, Pl. II, figs. 1–4.	*Mammonteus primigenius*
1834	*Mastodon dubius*	Kaup and Scholl "Verzeichniss der Gypsabgüsse von den ausgezeichnetsten urweltlichen Thierresten des Grossherzoglichen Museum zu Darmstadt," p. 22. Type loc.: Eppelsheim, Germany. *Mastodon dubius* is a synonym of *M. longirostris* (*fide* Kaup, 1835, p. 77).	*Tetralophodon longirostris*
1834	*Mastodon grandis*	Kaup and Scholl *Op. cit.*, p. 25. Type loc.: Eppelsheim, Germany. Type fig.: Kaup, 1835, "Description d'Ossements Fossiles," Pl. XVIII, fig. 9. *Mastodon grandis* is a synonym of *M. longirostris* (*fide* Kaup, 1835, p. 77).	*Tetralophodon longirostris*

Year	Name	Author	Reference in Present Memoir
1835	*Elephas odontotyrannus*	Eichwald Nova Acta Acad. Leop. Carol., XVII, p. 723. Type loc.: Banks of Nieman River, Dist. of Novogrodek, gouv. Vilna, Russia. Type fig.: Eichwald, *ibid.*, Pl. LXIII, figs. 1, 2.	*Mammonteus primigenius*
1835	*Mastodon podolicum*	Eichwald *Ibid.*, p. 736. Type loc.: Near Tultschin, Podolia, Russia. Type figs.: Eichwald, *ibid.*, Pls. LVI, LVII. See Vol. I, p. 85 (footnote) of the present Memoir.	*Deinotherium podolicum*
1835	*Dinotherium proavum*	Eichwald *Ibid.*, p. 741. Hab.: Podolia, Russia. Type fig.: Eichwald, *ibid.*, Pl. LX, figs. 1–5. First mentioned as *T.(Tapirus) proavus* by Eichwald in 1827 (Naturhistorische Skizze, p. 239—not available to the present author). Described as *Tapirus proavus* in "Zoologia Specialis," 1831, III, pp. 353, 360. See de Blainville, 1839–1864, "Du Dinotherium," pp. 12, 19.	*Deinotherium proavus*
1835	*Dinotherium uralense*	Eichwald *Ibid.*, p. 742. Hab.: Ural Mts. See Pallas, 1777, p. 213, Tab. IX, fig. 4; also de Blainville, 1839–1864, p. 19; and Lartet, 1859, p. 482.	*Deinotherium uralense*
1835	*Mastodon longirostris*	Kaup "Description d'Ossements Fossiles," Cahier IV, p. 65. Cf. *Tetracaulodon longirostre* Kaup, 1832, *Mastodon dubius* Kaup, 1834, and *Mastodon grandis* Kaup, 1834, above, this list.	*Tetralophodon longirostris*
1836	*Dinotherium secundarium*	Kaup (In Lartet, Bull. Soc. géol. France, (1), VII, p. 218.) Type loc.: Simorre, France. Cited also by de Blainville, 1839–1864, "Du Dinotherium," p. 19. Original description by Kaup not found by the present author.	*Deinotherium secundarium*(?)
1836	*M. tapiroides-minus*	Lartet *Loc. cit.* Type loc.: Simorre, France.	*Turicius tapiroides-minus*
1836	*M. angustidens minus*	Lartet *Loc. cit.* Type loc.: Simorre, France.	*Trilophodon angustidens minutus*
1836	*M.* [*Mastodon*] *Sivalensis*	Cautley Journ. Asiatic Soc. Bengal, V, p. 294. Type loc.: Doab Canal, vicinity of Nahun, India. Type fig.: Cautley, *ibid.*, Pl. XI, figs. 2, 3.	*Pentalophodon sivalensis*
1838	*E.* [*Elephas*] *jacksoni*	Mather "First Annual Rept. Geol. Survey Ohio," pp. 96, 97 (notice of discovery, without name); Amer. Journ. Sci., (1), XXXIV, p. 358 (description, without name); *ibid.*, pp. 362–364 (final description, with name). Type loc.: Salt Creek, Jackson County, Ohio. Type fig.: Mather, Amer. Journ. Sci., (1), XXXIV, p. 363, fig. A. Present location of type specimen unknown.	*Parelephas jacksoni*
1840(?)	*Missourium kochii*	Koch "Fossil Remains," p. 2. Type loc.: 22 miles south of St. Louis, Jefferson County, vicinity of Sulphur Springs, Missouri. The type skull was found in May, 1839, and first described (Amer. Journ. Sci., (1), XXXVII, pp. 191, 192) as Koch's Missourian; in a subsequent paper ("Fossil Remains," supposedly of date 1840, p. 2) Koch published a supplementary description, assigning the name *Missourium kochii*. See Horner, 1840, Proc. Amer. Phil. Soc., I, pp. 279–283, for remarks on the collection of Koch.	*Mastodon americanus*
1841	*Leviathan Missourii*	Koch "Description of the Missourium, or Missouri Leviathan," p. 13. Type loc.: Near the shores of the river La Pomme de Terre, a tributary of the Osage River, Benton County, Missouri. Skeleton excavated in March, 1840, and regarded by Koch as belonging to the same genus, namely, *Missourium*; he named it, however, Missouri Leviathan (1841, p. 13). Changed in 1843 to *Missourium Theristocaulodon* (see below, this list).	*Mastodon americanus*
1841	*T.* [*Tetracaulodon*] *Osagii*	Koch "Description of the Missourium, or Missouri Leviathan," another edition, p. 1. Hab.: Missouri.	*Mastodon americanus*
1841	*Tetracaulodon Tapyroides*	Koch *Loc. cit.* Hab.: Missouri.	*Mastodon americanus*
1841	*Elephas indicus Isodactylus*	Hodgson Journ. Asiatic Soc. Bengal, N. S., X, p. 907 (name without definition).	Indeterminate
1841	*Elephas indicus Heterodactylus*	Hodgson *Loc. cit.* (name without definition).	Indeterminate

Year	Name	Author		Reference in Present Memoir
1841	*Dinotherium Königii*	Kaup	"Akten der Urwelt," pp. 49, 50. Type loc.: Eppelsheim, Germany.	
1841	*Dinotherium minutum*	von Meyer	Neues Jahrb. Min., p. 459. Type loc.: Mösskirch, Germany.	
1842	*T.* [*Tetracaulodon*] *kochii*	Koch	Proc. Geol. Soc. London, III, p. 715. Hab.: Missouri. Koch, 1842, p. 715: "It does not require a close examination. . . to perceive that the animal to which these remains belonged was neither male, female, nor young Mastodon, or Missourium, the whole inner and outer conformation of the upper tusks showing that they were calculated to be used in harmony with the lower tusk in grubbing and rooting."	*Mastodon americanus*
1842	*Tetracaulodon Haysii*	Grant	*Ibid.*, III, Pt. II, p. 771. Cf. Koch, 1845, p. 29.	*Mastodon americanus*
1842	*Tetracaulodon Bucklandi*	Grant	*Loc. cit.* Cf. Koch, 1845, p. 29.	*Mastodon americanus*
1842	*Mastodon Brasiliensis*	Lund	(In Lesson, "Nouv. Tabl. Règne Animal," p. 157.) Type loc.: Valley of the Velhas River, Province of Minas Geraes, Brazil. *Mastodon Brasiliensis*, the specific name of which is attributed to Lund by Lesson, appears as "*Mastodon* sp." in Lund (1839, p. 133), compared with *M. andium* and *M. humboldtii* but not figured by Lund. See Lund, 1839, pp. 117, 129, 130, 133 ("12. *Mastodon* sp.").	*Cuvieronius brasiliensis*
1842	*E.* [*Elephas*] *americanus*	De Kay	"Natural History of New York," p. 101. Type loc.: Irondiquoit River, Monroe County, near Rochester, New York. Was in cabinet of the Lyceum of Natural History, New York, but was destroyed by fire. Type fig.: De Kay, *op. cit.*, Pl. XXXII, fig. 2.	*Mammonteus primigenius americanus*
1843	*Missourium Theristocaulodon*	Koch	"Description of the Missourium Theristocaulodon," pp. 9, 15, frontispiece. First named by Koch, 1841, *Leviathan Missourii*.	*Mastodon americanus*
1843	*Leviathan missouriensis*	Koch	*Op. cit.* (in title). Corrected form of *Leviathan Missourii* but changed to *Missourium Theristocaulodon* in 1843 (see preceding item).	*Mastodon americanus*
1843	*Dinotherium Australe*	Owen	Ann. Mag. Nat. Hist., XI, pp. 329–332, figs. 1, 2. Type loc.: Darling Downs, Australia. See Owen, 1843, *ibid.*, pp. 7–12, especially p. 9, figs. 2 and 3, for first description of femur and molar but without name. See also Owen, 1844, *ibid.*, XIV, p. 268 (*Dinotherium australe* = *Diprotodon australis*).	DIPROTODON
1844	*Mastodon australis*	Owen	*Ibid.*, XIV, p. 271, figs. 1 and 2 on p. 269. Type loc.: Specimen brought by native to Count Strzlecki in Australia, from cave further in the interior than the ossiferous caves of the Wellington valley. Probably a South American specimen accidentally misplaced with Australian specimens by this traveler (Count Strzlecki). See Falconer, 1857, table opposite p. 319, and 1868, II, pp. 271–276; also Jack and Etheridge, 1892, p. 683.	DIPROTODON
1845	*Mastodon arborense*	Koch	"Die Riesenthiere der Urwelt," p. 18. Apparently erroneously ascribed to von Meyer. See von Meyer and Göppert, 1848, p. 705: "[*Mastodon*] *Arborense* [nusquam Myr.] Koch Riesenthiere 18." Also p. 706: "*Mastodon Arborense* (Mey.) Koch [err. typ. ?pro] = Mastodon Arvernensis."	*Mastodon americanus*
1845	*Mastodon rugatum*	Koch	*Op. cit.*, p. 20. See also Giebel, 1847, p. 202.	*Mastodon americanus*
1845	*Dinotherium angustidens*	Koch	*Op. cit.*, p. 41. Type loc.: Compubay [Cambay(?), cf. pp. 85 and 90 of present Memoir], India. See von Meyer and Göppert, 1848, pp. 424, 425: "Dinotherium. . . angustidens Koch = Mastodon angustidens Cuv."	*Deinotherium* sp.(?)

Year	Name	Author	Reference in Present Memoir
1845	*Elephas kamensis*	de Blainville "Ostéographie," p. 202. De Blainville cites this species as *Elephas Kamenskii* or *kamensis* (see *Elephas Kamenskii* Fischer, 1829, above, this list).	*Mammonteus primigenius*
1845	*Elephas africanus priscus*	de Blainville *Op. cit.*, p. 205. European specimens considered by some palæontologists to be referable to *Loxodonta africana*, by others as of doubtful determination. Reviewed by Pomel, 1895.1, p. 20.	
1845	*Elephas ohioticus*	de Blainville *Op. cit.*, p. 261. Hab.: Ohio River.	*Mastodon americanus*
1845	*Dinotherium intermedium*	de Blainville *Op. cit.*, Atlas, Pl. iii. Hab.: France.	*Deinotherium intermedium*
1845	**E.* [*Elephas*] *primigenius sibiricus*	de Blainville *Op. cit.*, Atlas, Pl. iii. Hab.: Siberia. See also Depéret and Mayet, 1923, pp. 183 201.	*Mammonteus primigenius*
1845	**E.* [*Elephas*] *primigenius germanicus*	de Blainville *Op. cit.*, Atlas, Pl. iii. Hab.: Germany.	
1845	**E.* [*Elephas*] *indicus ceylanicus*	de Blainville *Op. cit.*, Atlas, Pl. iii. Hab.: India, Ceylon. Living form.	*Elephas indicus ceylanicus*
1845	**E.* [*Elephas*] *indicus bengalensis*	de Blainville *Op. cit.*, Atlas, Pl. iii. Hab.: India, chiefly Bengal and Assam. Living form. Compare Falconer and Cautley's figures (1846 [1847, Pl. xlii]) of *E. indicus* (Dauntela var.) and *E. indicus* (Mukna var.), also Falconer (1867, p. 57) in which he presents a detailed comparison of the measurements between the Mukna and Dauntela varieties of *Elephas indicus*. He adds (p. 58): "The plates of teeth in the *Mukna* variety slope greatly backwards and are excessively and finely crimped; those of *Dauntela* are much less crimped."	*Elephas indicus bengalensis*
1845	**E.* [*Elephas*] *primigenius meridionalis*	de Blainville *Op. cit.*, Atlas, Pl. iii.	
1845	*Dinotherium* [*gig.*] *majus*	de Blainville "Ostéographie, Du Dinotherium," p. 60. See Weinsheimer, 1883, p. 210.	*Deinotherium giganteum*
1845	*Dinotherium* [*gig.*] *medium*	de Blainville *Loc. cit.* See Weinsheimer, 1883, p. 210.	*Deinotherium giganteum*
1845	*Dinotherium* [*gig.*] *minus*	de Blainville *Loc. cit.* See Weinsheimer, 1883, p. 210.	*Deinotherium giganteum*
1845	*Dinotherium indicum*	Falconer Quart. Journ. Geol. Soc. London, I, p. 361. Type loc.: Perim Island, India. Type fig.: Falconer, *ibid.*, Pl. xiv, figs. 1, 1a. Falconer, 1845, pp. 370, 371: "The Dinotherium of Eppelsheim is known to range through a very wide difference of size, dependent on sexual or individual peculiarities, and several nominal species, chiefly founded upon this character, have been described by authors. But Dr. Kaup informs me, that he now admits but two species, *D. giganteum* and *D. Kœnigii*, as he regards all the rest, such as *D. Cuvieri*, *D. Bavaricum*, *D. proavum*, &c., to be merely dwarfed varieties, or females of *D. giganteum*. M. De Blainville has arrived at nearly the same conclusion in his Ostéographie. It would be unsafe, therefore, to found any opinion regarding the Indian fossil merely on a difference of size."	*Deinotherium indicum*
1845 1846	*Elephas Hysudricus*	Falconer and Cautley "Fauna Antiqua Sivalensis," Pl. i, fig. 3*a* (type), fig. 3*b* (paratype). Hab.: Siwalik Hills, India. Type description: Falconer and Cautley, 1846, "Fauna Antiqua Sivalensis," letterpress, p. 41.	*Hypselephas hysudricus*
1845 1846	*E.* [*Elephas*] *planifrons*	Falconer and Cautley *Op. cit.*, Pl. ii, fig. 5*a* (lectotype), fig. 5*b* (cotype). Hab.: Siwalik Hills, India. Type description: Falconer and Cautley, 1846, *op. cit.*, letterpress, p. 38.	*Archidiskodon planifrons*
1845 1846	*Elephas insignis*	Falconer and Cautley *Op. cit.*, Pl. ii, fig. 6*a* (lectotype), fig. 6*b* (cotype). Hab.: Siwalik Hills, India. Type description: Falconer and Cautley, 1846, *op. cit.*, letterpress, pp. 37, 38.	*Stegodon insignis-ganesa*

"*These perhaps may be regarded as geographic designations rather than as subspecies."

Year	Name	Author	Reference in Present Memoir
1845 1846	*Elephas ganesa*	Falconer and Cautley *Op. cit.*, Pl. iii, fig. 7*a*. Hab.: Siwalik Hills, India. Type description: Falconer and Cautley, 1846, *op. cit.*, letterpress, p. 45.	*Stegodon insignis-ganesa*
1846	*Elephas minimus*	Nesti (In Falconer and Cautley, 1846, *op. cit.*, letterpress, p. 13.) Falconer attributed *Elephas minimus* to Nesti, 1808, but the present author was unable to find this name in either of Nesti's articles of 1808 or 1825.	
1846	*Elephas Namadicus*	Falconer and Cautley *Op. cit.*, letterpress, p. 45. Hab.: Valley of the Nerbudda River, India. Type figs.: Falconer and Cautley, 1847, *op. cit.*, Pls. xii.a, and xii.b, figs. 1 and 3. Supplementary description: Falconer, 1867, "Description of the Plates in the Fauna Antiqua Sivalensis," p. 15.	*Palæoloxodon namadicus*
1846 1847 1857 1867 1868	*E.* [*Elephas*] *priscus*?	Falconer and Cautley *Op. cit.*, letterpress, p. 45 (name only); also Pl. xiv, figs. 7, 7*a*, 7*b*. E. [Elephas] (Loxod.) priscus (*Goldf.*) Falconer, 1857, Quart. Journ. Geol. Soc. London, XIII, pp. 345, 346, and table opp. page 319. Type loc.: Gray's Thurrock, England. Type description: Falconer, 1867, "Description of the Plates in the Fauna Antiqua Sivalensis," p. 21. Type fig.: Falconer and Cautley, 1847, *op. cit.*, Pl. xiv, figs. 7, 7*a*, 7*b*. Supplementary description: Falconer, 1868, "Palæontological Memoirs," II, p. 94, and Pl. vii, as *Elephas* (*Loxod.*) *priscus*. Name preoccupied by Goldfuss, 1821 (see above, this list).	*Hesperoloxodon antiquus*
1846	*E.* [*Elephas*] *bombifrons*	Falconer and Cautley *Op. cit.*, letterpress, p. 46. Hab.: Siwalik Hills, India. Lectotype fig.: Falconer and Cautley, 1847, *op. cit.*, Pl. xxvi; cotype figs.: Pls. xxvii, xxviii.	*Stegodon bombifrons*
1846	*E.* [*Elephas*] *cliftii*	Falconer and Cautley *Op. cit.*, letterpress, p. 47. Type loc.: Near Yenangyaung, Irrawaddy River, Burma. Type fig.: Clift, 1828, Trans. Geol. Soc. London, (2), II, Pt. III, Pl. xxxix, fig. 6, as *M. elephantoides*.	*Stegodon elephantoides* (=*cliftii*)
1846	*Mastodon brevirostre*	Gervais and de Serres Ann. Sci. Nat., (3), V, p. 268. Type loc.: Montpellier, Hérault, France. Cotype figs.: Gervais, 1859, "Zoologie et Paléontologie Françaises," Deuxième ed., Pl. i, fig. 3, Pl. iii, fig. 7 (same as in First Edition of 1848–1852). Until it is positively determined by further research that the "*M.*" *brevirostris* of Montpellier is identical with the "*M.*" *arvernensis* of Auvergne, it seems best to retain this form as a subspecies of *Mastodon* [*Anancus*] *arvernensis*.	*Anancus arvernensis brevirostris*
1846	*Elephas minimus*	Giebel Neues Jahrb. Min., p. 459. Type loc.: Seveckenberg near Quedlinburg, northern Germany. See Giebel in Isis, 1845, Heft VII, p. 483, Heft XII, p. 905, also in Fauna der Vorwelt, 1847, I, Abth. I, p. 211, for description but without name.	
1847 1857 1867	*Elephas antiquus*	Falconer and Cautley "Fauna Antiqua Sivalensis," Pl. xii.d. E. (Eueleph.) antiquus Falconer, 1857, Quart Journ. Geol. Soc., London, XIII, Synop. Tab. opp. p. 319. Hab.: Locality not recorded, but undoubtedly England. Type description: Falconer, 1867, "Description of the Plates in the Fauna Antiqua Sivalensis," p. 18. Type fig.: Falconer and Cautley, 1847, "Fauna Antiqua Sivalensis," Pl. xii.d, figs. 4, 4*a*. *Elephas antiquus* misnamed *E. meridionalis* on plate (see Falconer, 1867, p. 18, and 1868, I, p. 438, together with legend), but corrected by Falconer in copy of the "Fauna Antiqua Sivalensis" belonging to the British Museum. See also Falconer, 1868, II, pp. 176–188.	*Hesperoloxodon antiquus*
1847	*Mastodon perimensis*	Falconer and Cautley *Op. cit.*, Pl. xxxi, figs. 9, 9*a*. Type loc.: Perim Island, India. Type description: Falconer, 1867, "Description of the Plates in the Fauna Antiqua Sivalensis," p. 44. Type fig.: Falconer and Cautley, 1847, *op. cit.*, Pl. xxxi, figs. 9, 9*a*. Lydekker chose as type Brit. Mus. M.2882 (Pls. xxxviii and xxxix of the "Fauna Antiqua Sivalensis"), regarded as the paratype in the present Memoir.	*Anancus perimensis*
1847	*Elephas Indicus*	(Dauntela var.) Falconer and Cautley *Op. cit.*, Pl. xlii, fig. xxiii.a. Hab.: India. Type description: Falconer, 1867, *op. cit.*, p. 57; 1868, *op. cit.*, I, p. 477. Living form.	*Elephas indicus* var. Dauntela

Year	**Name**	**Author**	**Reference in Present Memoir**
1847	*Elephas Indicus* (Mukna var.)	Falconer and Cautley *Op. cit.*, Pl. XLII, fig. XXIII.B. Hab.: India. Type description: Falconer, 1867, *loc. cit.*, 1868, *loc. cit.* Living form.	*Elephas indicus* var. Mukna
1847	*Mastodon vellavus*	Aymard Bull. Soc. géol. France, (2), IV, p. 414. Type loc.: Velay, France. No record of figure. While the author stated on p. 193, Vol. I, of the present Memoir that he believed both *"M." vellavus* and *"M." Vialetii* to be referable to *"M."* [*Zygolophodon*] *borsoni*, he thought it best nevertheless to retain these as subspecific names (p.632). Compare also Falconer, 1868, II, p. 20.	*Zygolophodon borsoni vellavus*
1847	*Mastodon Vialetii*	Aymard *Ibid.*, p. 415. Type loc.: Vialette, France. No record of figure. See note above under *Mastodon vellavus* Aymard, 1847.	*Zygolophodon borsoni vialetii*
1847	*Elephas sumatranus*	Temminck "Coup d'Œil Général," II, p. 91. Type loc.: District of Palembang, Sumatra. Type skeletons in Leiden Museum. No record of original type figure (see figure 1182 of present Memoir). Living form.	*Elephas indicus sumatranus*
1848	*Mastodon Cuvieri*	Pomel Bull. Soc. géol. France, (2), V, p. 258. Hab.: Gers and l'Orléanais, France. Synonym of *Mastodon angustidens* Cuv. (*fide* Trouessart, 1897, p. 700).	*Trilophodon angustidens cuvieri*
1848	*Mastodon Buffonis*	Pomel *Loc. cit.* Type loc.: Auvergne, Perrier, France. Synonym of *Mastodon borsoni* Hays (*fide* Trouessart, 1897, p. 705).	*Zygolophodon borsoni buffonis*
1850	*Elephas affinis*	Eichwald "Palæont. Rossii," p. 179 (*fide* Sherborn, 1922, "Index Animalium," p. 124). See also Eichwald, 1853, "Lethaea Rossica," p. 350, Pl. XI, fig. 36. Type loc.: Vicinity of Taganrogh, Russia, near river Mjousse. Original in Mus. Inst. des Mines, Leningrad.	
1851	*Mastodon Simorrense*	Lartet "Notice sur La Colline de Sansan," p. 24. Type loc.: Simorre, France. Synonym of *Mastodon angustidens* Cuv. (*fide* Trouessart, 1897, p. 700).	*Trilophodon angustidens*
1851	*Mastodon Gaujaci*	Lartet *Op. cit.*, p. 27. Type loc.: Lombez, France. Synonym of *Mastodon angustidens* Cuv. (*fide* Trouessart, 1897, p. 700).	*Trilophodon angustidens gaujaci*
1852	*Mastodon humboldtius*	Warren "The Mastodon Giganteus of North America," p. 126. Hab.: South America. Warren states that Cuvier, de Blainville, and Owen regarded this species as referable to *angustidens*.	*Cuvieronius humboldtii*
1854	*Elephas Rupertianus*	Richardson "Zoology of Voyage of H.M.S. Herald," pp. 101, 102, 141. Type loc.: Swan River, basin of Lake Winnipeg, Canada.	*Mastodon americanus rupertianus*
1855	*Anancus macroplus*	Aymard (In Dorlhac, Ann. Soc. Agric. Puy, XIX, for 1854, p. 507). Type loc.: Mt. Coupet, near Puy, France. Synonym of *M. arvernensis* (*fide* Lartet, 1859, p. 493). Depéret, 1885, p. 159: "Le nom d'*Anancus macroplus* donné par M. Aymard aux molaires des sujets adultes du bassin du Puy, très distinctes des molaires de lait décrites par Croizet et Jobert, doit également disparaître devant le nom plus ancien d'*arvernensis*." See also Depéret, 1890, pp. 62, 66.	*Anancus arvernensis*
1856 1862 1867	*Mastodon pentelicus*	Gaudry and Lartet Compt. Rend. Acad. Sci., XLIII, p. 273 (name only). Type loc.: Pikermi, Greece. Type description: Lartet, 1859, Bull. Soc. géol. France, (2), XVI, p. 497; Gaudry, 1862, "Animaux Fossiles," p. 142. Type figs.: Gaudry, 1862–1867, *op. cit.*, Pl. XXII, figs. 1–3, also Pl. XXIII. The name *Choerolophodon* is provisionally retained as a subgenus of *Trilophodon* for the species *M. pentelicus*, although the type of the species *M. pentelicus* is close to *Tetralophodon longirostris*.	*Trilophodon* (*Choerolophodon*) *pentelicus*

Year	Name	Author	Reference in Present Memoir
1857	*E.* [*Elephas*] *giganteus*	Aymard (In Falconer, Quart. Journ. Geol. Soc. London, XIII, p. 321; and Falconer, 1868, "Palæontological Memoirs," II, p. 20, footnote.)	*Archidiskodon meridionalis*(?)
1857	*M.* (*Triloph.*) *Pandionis*	Falconer Quart. Journ. Geol. Soc. London, XIII, p. 317 and Synop. Tab. opp. p. 319. Type loc.: Deccan, India [error, probably Larkana District of Sind (*fide* Hopwood, letter, Feb. 10, 1932)]. Supplementary description: Falconer, 1868, "Palæontological Memoirs," I, p. 124. Type fig.: Falconer, 1868, *op. cit.*, Pl. xxxiv, figs. 6, 7.	*Trilophodon pandionis*
1857–1859	*M.* (*Triloph.*) *Pyrenaicus*	Lartet (Ex MS. Lartet, in Falconer, Quart. Journ. Geol. Soc. London, XIII, Synop. Tab. opp. p. 319.) *M.* [*Mastodon*] *pyrenaicus* Lartet, 1859, Bull. Soc. géol. France, (2), XVI, p. 513. Type loc.: Near Ile-en-Dodon, (Haute-Garonne), France. Type fig.: Lartet, 1859, *ibid.*, Pl. xv, fig. 4.	*Zygolophodon pyrenaicus*
1857	*E.* [*Elephas*] (*Eueleph.*) *Armeniacus*	Falconer *Ibid.*, Synop. Tab. opp. p. 319. Type loc.: Near Khanoos, Province of Erzerum, Armenia. Supplementary description: Falconer, 1863, Nat. Hist. Rev., III, pp. 74, 75. Type fig.: Falconer, 1863, *ibid.*, Pl. ii, fig. 2.	*Parelephas armeniacus*
1857	*E.* [*Elephas*] (*Loxod.*) *priscus* (*Goldf.*)	Falconer *Ibid.*, pp. 345, 346, Synop. Tab. opp. p. 319; 1868, "Palæontological Memoirs," II, p. 94, as *Elephas* (*Loxod.*) *priscus*. Type loc.: Gray's Thurrock, England. See above, *E.* [*Elephas*] *priscus*? Falconer and Cautley, 1846, 1847. Name preoccupied by Goldfuss, 1821 (see above, this list).	*Hesperoloxodon antiquus*
1857	*E.* [*Elephas*] (*Eueleph.*) *antiquus*	Falconer See under *Elephas antiquus* Falconer, 1847, above, this list.	
1857–1868	*E.* [*Elephas*] (*Eueleph.*) *Columbi*	Falconer Quart. Journ. Geol. Soc. London, XIII, Synop. Tab. opp. p. 319. Type loc.: Brunswick canal, near Darien, Georgia. Supplementary description: Falconer, 1863, Nat. Hist. Rev., III, pp. 43–52, 114. Type fig.: Falconer, 1863, *ibid.*, p. 114, Pl. i; 1868, "Palæontological Memoirs," II, Pl. x, fig. 1. Neotype loc.: Phosphate Beds near Charleston, S. C.	*Parelephas columbi*
1857	*Mastodon atticus*	Gaudry and Lartet (In Wagner, Abh. bayer. Akad. Wiss., VIII, Abth. I, Cl. II, p. 140.) Type loc.: Pikermi, Greece. Gaudry, 1862, p. 142: "C'est par une inadvertance de copie que Wagner a employé le nom d'*atticus*; car il nous attribue ce nom, et le seul que nous ayons proposé est celui de *pentelicus*."	*Turicius atticus*
1858	[*Mastodon*] *dissimilis*	Jourdan (MS. 1840) Ann. Soc. Imp. Agric. Lyon, (3), II, p. lxxxiv. Type loc.: Saône Basin, France.	*Anancus arvernensis dissimilis*
1858	*Mastodon mirificus*	Leidy Proc. Acad. Nat. Sci. Phila., X, pp. 10, 28. Type loc.: "Loup Fork of Platte River," Nebraska (Leidy, 1873, Rept. U. S. Geol. Surv. Terr., I, p. 330); possibly near Seneca, Thomas County, Nebraska (*fide* Hay, 1924, Publ. Carnegie Inst. Wash., No. 322A, p. 100); "Pawnee Loup Branch of Platte River, Middle Loup, probably Hooker Co." (*fide* Lugn and Schultz, 1934, Neb. State Mus., Bull. 41, I, p. 372). Type fig.: Leidy, 1869, Journ. Acad. Nat. Sci. Phila., (2), VII, Pl. xxv, figs. 1, 2. Cf. *Rhabdobunus mirificus* Hay, 1914, below, this list.	*Stegomastodon mirificus*
1858	*Elephas imperator*	Leidy *Ibid.*, pp. 10, 29. Type loc.: Loup Fork of Platte River, Nebraska (Leidy, 1869, Journ. Acad. Nat. Sci. Phila., (2), VII, p. 254; and Hay, 1914, Iowa Geol. Surv., Ann. Rept. for 1912, XXIII, pp. 421, 422), possibly Seneca, Thomas County, Nebraska (see Hay, 1924, Publ. Carnegie Inst. Wash., No. 322A, p. 100); "Pawnee Loup Branch of Platte River = Middle Loup, probably Hooker Co. [Nebraska]" (*fide* Lugn and Schultz, 1934, Neb. State Mus., Bull. 41, I, p. 373). Type fig.: Leidy, 1869, Journ. Acad. Nat. Sci. Phila., (2), VII, Pl. xxv, fig. 3. Osborn's neotype: 1922, Amer. Mus. Novitates, No. 41, p. 4, fig. 4, from Guadalajara, Mexico.	*Archidiskodon imperator*
1859–62	*Elephas texianus*	Owen Rept. Brit. Assoc. Adv. Sci., 28th meeting, p. lxxxvi (name); and Blake, 1861, Geologist, IV, p. 470 (name). Type loc.: San Felipe de Austin, Brazos River, Texas. Type description: Blake, 1862, Geologist, V, p. 58. Type fig.: Blake, 1862, *ibid.*, Pl. iv.	*Parelephas columbi*

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1861	*Dinotherium levius*	Jourdan	Compt. Rend. Acad. Sci., LIII, p. 1011. Type loc.: Grive Saint-Alban, Isère, France.	*Deinotherium levius*
1861	*Elephas intermedius*	Jourdan	*Ibid.*, p. 1013. Type loc.: Near Lyons, Rhone Valley, France. No figure recorded, but see Lortet and Chantre, 1872 [1876], Arch. Mus. hist. nat. Lyon, I, frontispiece, plate of referred skeleton (Fig. 944 of present Memoir), also referred molars in the Muséum de Ville, Lyons (Fig. 943 of present Memoir). Very similar to *Elephas trogontherii* Pohlig (*fide* Depéret letter, August 26, 1921).	*Parelephas intermedius*
1862–1868	*Elephas Melitensis*	Falconer	"The Parthenon," p. 780. See Falconer, 1868, "Palæont. Mem.," II, pp. 292, 299, 307, 308. Type loc.: Zebbug Cave, Malta. Type fig.: Falconer, 1868, *op. cit.*, Pl. XI, figs. 1, 1a.	*Palæoloxodon melitensis*
1867	*Elephas falconeri*	Busk	Trans. Zool. Soc. London, VI, Pt. V, p. 251. Type loc.: Zebbug Cave, Malta. Type fig.: Busk, *ibid.*, Pls. XLIX, L, LI (not figured in present Memoir). See Falconer, 1868, II, p. 292, footnote, where it is stated by the editor that this and other Maltese specimens had been identified by Falconer as early as July, 1860.	*Palæoloxodon falconeri*
1867	*Mastodon virgatidens*	von Meyer	Palæontogr., XVII, p. 61. Type loc.: Near Fulda, northeast of Frankfort, Germany. Type fig.: von Meyer, *ibid.*, Taf. IV, figs. 1–5.	*Turicius virgatidens*
1868	*Mastodon Andaranus*	Falconer	"Palæont. Mem.," I, p. 124, footnote. Type loc.: Deccan, India. See Vol. I, p. 267, of the present Memoir.	*Trilophodon pandionis*
1868	*Dinotherium Perimense*	Falconer	*Op. cit.*, I, p. 415 (name only). Type loc.: Perim Island, India.	*Deinotherium indicum*
1868	*Dinotherium Pentapotamicum*	Falconer	*Op. cit.*, II, p. 5. See *Dinotherium pentapotamiæ* Lydekker, 1876, below.	
1868	*Elephas minutus*	Nesti	(In Falconer, *op. cit.*, II, pp. 104, 105). See note under *Elephas minimus* Nesti, 1846, above, this list.	
1868	*Trilophodon Ohioticus*	Falconer	*Op. cit.*, II, pp. 176 (footnote), 204. Hab.: North America.	*Mastodon americanus*
1868	*Mastodon americanus*	Leidy	Proc. Acad. Nat. Sci. Phila., XX, p. 175. Hab.: North America. See Leidy, 1869, Journ. Acad. Nat. Sci. Phila., (2), VII, pp. 240, 395. Leidy first used the term *Mastodon americanus* in the 1868 article, as the equivalent of *M. ohioticus* and *M. giganteus* of authors.	*Mastodon americanus*
1869	*Mastodon obscurus*	Leidy	Journ. Acad. Nat. Sci. Phila., (2), VII, pp. 244, 396. Type loc.: Near Greensburgh (Greensboro), Caroline County, Maryland. Type fig.: Leidy, *ibid.*, Pl. XXVII, fig. 13. Merrill (1907, Bull. U. S. Nat. Mus., No. 53, p. 45) regarded a third superior molar, r.M^3, from Tarboro, North Carolina, as the type of *Mastodon obscurus*. The present author refers it to *Ocalientinus* (*Serridentinus*) *obliquidens* of this Memoir (see Vol. I, p. 286).	*Trilophodon obscurus*
1870	*Stegodon sinensis*	Owen	Quart. Journ. Geol. Soc. London, XXVI, Pt. I, p. 417. Type loc.: Alleged to be from marly beds vicinity of Shanghai, China. Type fig.: Owen, *ibid.*, Pl. XXVII, figs. 1–3.	*Stegodon sinensis*
1870	*Stegodon orientalis*	Owen	*Ibid.*, p. 421. Type loc.: (?)Cave near city of Chungkingfoo, Province of Szechuan, China. Type fig.: Owen, *ibid.*, Pl. XXVIII, figs. 1–4.	*Stegodon orientalis*
1870	*Elephas mnaidræ*	Adams	"Notes of a Naturalist in Nile Valley and Malta," p. 223. Type loc.: Mnaidra Gap, Malta. Type fig.: Adams, *op. cit.*, Pl. II, figs. 2, 2*a*. Supplementary description as *Elephas mnaidriensis*: Adams, 1874, Trans. Zool. Soc. London, IX, Pt. I, p. 116; with figures of the type, Pl. VII, figs. 2, 2*a*; of the paratype, Pl. VII, fig. 1.	*Palæoloxodon mnaidriensis*

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1870	*Elephas Cornaliae*	Aradas	Atti Accad. Gioenia sci. nat. Catania, (3), IV, p. 235. Type loc.: Catania, near the monastery of Santa Chiara, Sicily. Type figs.: Aradas, *ibid.*, figs. 1, 2.	*Loxodonta cornaliæ*
1871	*Mastodon shepardi*	Leidy	Proc. Acad. Nat. Sci. Phila., XXII, p. 98. Type loc.: Dry Creek, Stanislaus County, California. Type fig.: Leidy, 1873, Rept. U. S. Geol. Surv. Terr., I, Pl. XXI, figs. 3, 4.	*Rhynchotherium shepardi*
1872	*Elephas Indianapolis*	Foster	Proc. Amer. Assoc. Adv. Sci., August, 1872, p. 259 (name only). Same specimen from Indiana for which the name *Elephas Mississippiensis* was subsequently proposed. See next item.	
1872	*Elephas Mississippiensis*	Foster	Nature, VI, p. 443. Hab.: Indiana, exact locality unrecorded. Name changed from *Elephas Indianapolis* (see preceding item), without description or figure.	*Parelephas*(?) *mississippiensis*(?)
1873	*Mastodon proavus*	Cope	"Synopsis of New Vertebrata from Tertiary of Colorado," p. 10. Type loc.: Pawnee Buttes, Pawnee Creek, Weld County, Colorado. Type fig.: Cope, 1889, Amer. Naturalist, XXIII, No. 268, p. 202, fig. 6, as *Tetrabelodon angustidens proavus.*	*Serridentinus proavus*
1875	*Mastodon productus*	Cope	Proc. Acad. Nat. Sci. Phila., XXVI, pp. 221, 222. Type loc.: Santa Fé marls, New Mexico. Type figs.: Cope, 1877, Rept. U. S. Geogr. Surv. West of 100th Meridian (Wheeler), IV, Pt. II, Pls. LXX, figs. 1–3, LXXI, fig. 3. Neotype fig.: Frick, 1926, Bull. Amer. Mus. Nat. Hist., LVI, Art. II, fig. 7A.	*Serridentinus productus*
1875–1923	*Elephas Ausonius*	Major	(MS. labels). Name in Verri, 1886, Boll. Soc. geol. Ital., V, p. 453. Type loc.: San Romano, Val d'Arno inf., Italy. Type fig.: Depéret and Mayet, 1923, "Les Éléphants Pliocènes," Pl. x, figs. 1, 2. See Weithofer, 1890, p. 194, footnote, and p. 206; also Depéret and Mayet, 1923, p. 162.	*Hesperoloxodon antiquus ausonius*
1876	*Dinotherium pentapotamiæ*	Lydekker	Mem. Geol. Surv. India, Palæont. Indica, (X), I, Pt. II, pp. 72, 73. (Falc. Ex MS., *fide* Lydekker, 1885, "Catalogue of the Remains of Siwalik Vertebrata. . . Geological Department of the Indian Museum, Calcutta," p. 104.) Type loc.: Near Attock, Indus valley, India. Type fig.: Lydekker, 1876, *ibid.*, pl. IX, figs. 1, 2. Lydekker, 1876, pp. 72, 73: "Subsequently, the same naturalist [Falconer] identified two other molar teeth from near Attock ('Pal. Mem.,' vol. I, p. 414) as belonging to the same genus [*Deinotherium*]; in the note on these specimens in the 'Palæontological Memoirs' no specific name was assigned to them, though they were considered to be of too small a size to have belonged to *D.* (*perimense*) *indicum*; these specimens are now in the Indian Museum; they are ticketed with labels in Falconer's handwriting bearing the name of *D. pentapotamiæ*, which name I have accordingly adopted. . . The specimen is distinguished by its much smaller size from any of the European species; from the first premolar of *D. giganteum* and *D. cuvieri*, it is distinguished by the following points: the antero-posterior valley is very much deeper and wider in the Indian form, rendering thereby the inner tubercles more completely conical; the posterior tubercle is mammilliform in the Indian form, whereas it is elongated transversely in the European form." See Falconer, 1868, II, p. 5, footnote by Editor, in which he states that "A specimen of the third lower premolar of this species, from the 'Red Marl' at Noorpoor, found in Dr. Falconer's collection, is labelled in his hand-writing, '*Dinotherium Pentapotamicum*, Falc.' "	*Deinotherium indicum*
1877	*Mastodon* (*Trilophodon*) *Falconeri*	Lydekker	Rec. Geol. Surv. India, X, Pt. II, p. 83. Type loc.: Potwár district, Punjab, India. Supplementary description: Lydekker, 1880, Mem. Geol. Surv. India, Palæont. Indica, (X), I, Pt. V, p. 206. Type fig.: Lydekker, 1880, *ibid.*, Pl. XXXIII, figs. 1, 4.	*Tetralophodon* (*Lydekkeria*) *falconeri*
1877	*C.* [*Cænobasileus*] *tremontigerus*	Cope	Proc. Amer. Phil. Soc., XVI, pp. 584, 585. Type loc.: Probably Texas. No figure recorded. Genus and species withdrawn by Cope in 1889 (1889.2, p. 207).	

Year	Name	Author		Reference in Present Memoir
1878	*Tetralophodon campester*	Cope	Proc. Amer. Phil. Soc., XVII, p. 225. Type loc.: Republican River beds, Sappa Creek, Rawlins County, Kansas. Type figs.: Cope, 1889, Amer. Naturalist, XXIII, Pls. IX, X; also Cope and Matthew, 1915, "Hitherto Unpublished Plates of Tertiary Mammalia and Permian Vertebrata," Pls. CXX, CXXI, CXXII, CXXIII.	*Tetralophodon campester*
1879	*Mastodon affinis*	Jourdan	(Ex MS. 1859, labels in Lyons Museum), in Lortet and Chantre, Arch. Mus. hist. nat. Lyon, II, p. 308. Type loc.: (?)	*Zygolophodon borsoni affinis*
1879 1913	*Elephas primigenius comune*	Issel	Ann. Mus. Civ. Storia Nat. Genova, (1), XIV, p. 153 (as *Elephas primigenius*). In Zuffardi, 1913, Palæont. ital., XIX, p. 136. Type loc.: Camporosso, near Ventimiglia, Italy. Type figs.: Issel, *ibid.*, figs. 1–4.	*Mammonteus primigenius*
1879	*Elephas atlanticus*	Pomel	Bull. Soc. géol. France, (3), VII, p. 51. Type loc.: Ternifine, near Mascara, Algeria. Cotype fig.: Pomel, 1895, "Paléontologie Monographies, No. 6. Les Éléphants Quaternaires," Carte Géol. L'Algérie, Pl. VIII, figs. 1, 2.	*Palæoloxodon atlanticus*
1880	*Dinotherium sindiense*	Lydekker	Mem. Geol. Surv. India, Palæont. Indica, (X), I, Pt. V, p. 196. Type loc.: Sind, India. Type fig.: Lydekker, *ibid.*, Pl. XXXI, fig. 4. See Lydekker, 1879, Rec. Geol. Surv. India, XII, Pt. 1, p. 43, for first notice, but without name.	*Deinotherium sindiense*(?)
1880	*Elephas* (*Euelephas*) *antiquus* var. *nana*	Acconci	Atti Soc. Toscana Sci. Nat., V, Fasc. I, pp. 146–150. Type loc.: Cavern near Monti Pisani, Cucigliana, Tuscany, Italy. Type fig.: Acconci, *ibid.*, Tav. IV, figs. 6, 7.	*Hesperoloxodon antiquus nanus*
1882	*Notelephas australis*	Owen	Proc. Roy. Soc. London, XXXIII, p. 448; 1883, Phil. Trans. Roy. Soc. London, CLXXIII, Pt. III, p. 777. Type loc.: Drift deposit of ravine in district of Darling Downs, about 60 miles from Moreton Bay, Queensland, Australia. Type fig.: Owen, 1883, *ibid.*, Pl. LI. Jack and Etheridge, 1892, p. 683: "*Notoelephas* [*Notelephas* of Owen, 1882] *australis* Owen . .This genus and species were founded on portions of a tusk indicating a mammal larger than *Diprotodon*, in fact the largest fossil mammal yet foreshadowed amongst the extinct Australian forms. Sir Richard Owen appears to regard it as a Proboscidian Placental. . . He does not appear to apprehend any connection between this tusk and the molar tooth [*Mastodon australis* Owen, 1844] formerly described by him, and forming a portion of the late Count P. E. de Strzelecki's Collection. Prof. Owen remarks that this molar is too large to be associated with the tusk, supposing the latter to have come from the upper jaw of a full-grown individual of its species. . . Grave doubts have been expressed by several Writers as to the probability of this tooth as an Australian fossil, and it would perhaps be better to expunge it from the list."	*Diprotodon australis*
1883	*Mastodon Zaddachi*	Jentzsch	Schrift. phys.-ökonom. Ges. Konigsb., Jahrg. XXIII, Abth. 2, p. 202. Type loc.: Thorn, West Prussia. Type fig.: Jentzsch, *ibid.*, Taf. v, figs. 6*a*, 6*b*.	*Zygolophodon borsoni zaddachi*
1883	*Leptodon minor*	Gunn	Geol. Mag., Dec. II, N. S., X, p. 458. Type loc.: Forest bed, Norfolk, England. Type fig.: New Edition of Gunn's "Sketch of Geology of Norfolk, Pl. I, letter I" (*fide* Gunn, 1883, *loc. cit.*). This edition does not seem to have been published (cf. "Memorials of John Gunn," 1891, p. v).	*Hesperoloxodon antiquus*
1883	*Leptodon giganteus*	Gunn	*Loc. cit.* Type loc.; Forest bed, Mundesley, Norfolk, England. Description and type figure: Gunn, 1891, "Memorials of John Gunn," Pl. IV, fig. 2. Same as *E. Gunnii* Lartet, 1883, and *Elephas giganteus intermedius* Gunn, 1891 (see below, this list).	*Hesperoloxodon antiquus*
1883	*E. Gunnii*	Lartet	(In Gunn, 1883, *loc. cit.*) Type loc.: Forest bed, Mundesley, Norfolk. Type ramus No. 361, Gunn Coll., Norwich Castle Mus. 1703. Description and type fig.: Gunn, 1891, "Memorials of John Gunn," Pl. IV, fig. 2. It will be observed in this quaint description of 1883 that Gunn designates as the type of *E. Gunnii* Lartet the very same specimen and figure selected as the type of *Leptodon giganteus*. A revision of these types and specific names applied to the collection of Gunn may be found in F. Leney's "Type-specimens in the Norwich Castle Museum," 1902, Geol. Mag., p. 169.	*Hesperoloxodon antiquus*

Year	Name	Author		Reference in Present Memoir
1883	*Elephas Lamarmorae*	Major	Kosmos, XIII, Jahrg. VII, p. 6. Type loc.: Morimentu b. Gonnesa, Sardinia. No figures published.	*Palæoloxodon lamarmorae*
1884	*Elephas africanus fossilis*	Thomas, Philippe	Mém. Soc. géol. France, (3), III, No. 2, p. 46. Cited by Trouessart, 1897–1899, p. 708, as found in Algeria.	*Palæoloxodon atlanticus*
1884	*Mastodon (Trilophodon) angustidens* Cuv. var. *palæindicus*	Lydekker	Mem. Geol. Surv. India, Palæont. Indica, (X), III, Pt. I, p. 19. Type loc.: Near Kamlial, northern Punjab, India. Type fig.: Lydekker, *ibid.*, Pl. IV, fig. 3.	*Trilophodon palæindicus*
1884	*M.* [*Mastodon*] *euhypodon*	Cope	Amer. Naturalist, XVIII, p. 525. Type loc.: Trail Cañon, south fork of Driftwood Creek, Hitchcock County, Nebraska. Type figs.: Cope, 1889, *ibid.*, XXIII, p. 203, fig. 7, and Pl. XIII (erroneous drawing) figured as *Tetrabelodon euhypodon*.	*Blickotherium euhypodon*
1884	*M.* [*Mastodon*] *serridens*	Cope	*Loc. cit.* Type loc.: Texas, probably Clarendon formation. Type fig.: Cope, 1889, *ibid.*, p. 205, fig. 8, figured as *Tetrabelodon serridens*.	*Serridentinus serridens*
1884	*Dibelodon tropicus*	Cope	Proc. Amer. Phil. Soc., XXII, p. 7. Type loc.: State of Michoacan, Valley of Mexico. Type fig.: von Meyer, 1867, Palæontogr., XVII, Pl. VI, as *M. humboldtii*. Uhde Coll. See discussion of this species (*Dibelodon tropicus* Cope) by Freudenberg, 1922, pp. 128, 129, in which he reproduces the original type figure of Cope from von Meyer and places it at the summit of an ascending series ending with *Mastodon oligobunis progressa* Freudenberg.	*Cordillerion tropicus*
1885	*Mastodon perimensis* var. *sinensis*	Koken	Geol. u. Pal. Abh., III, Heft II, p. 34. Type loc.: Yunnan, China. Type fig.: Koken, *ibid.*, Pl. XII, fig. 1.	*Tetralophodon (Lydekkeria) sinensis*
1885 1887	*Elephas trogontherii*	Pohlig	Zeitschr. deutsch. geol. Ges., XXXVII, Heft IV, p. 1027. *Elephas (primigenius* bezw. *meridionalis) trogontherii* Pohlig, 1887, Sitz.-Ber. niederrhein. Ges. Bonn, p. 274. *Elephas (primigenius) trogontherii* Pohlig, 1887 [1888?], Zeitschr. deutsch. geol. Ges., XXXIX, Heft IV, p. 799. Type loc.: Süssenborn, near Weimar, northern Germany. Type figs.: Pohlig, 1888, Nova Acta Leop. Carol., LIII, p. 193, fig. 79, and p. 195, fig. 82. Cf. *Elephas intermedius* Jourdan, 1861, above, this list.	*Parelephas trogontherii*
1886	*Mastodon cautleyi*	Lydekker	Mem. Geol. Surv. India, Palæont. Indica, (X), III, pp. xiv-xix. Type loc.: Perim Island, India. Lectotype fig.: Lydekker, *ibid.*, p. xv, fig. 6. Cotype figs.: Lydekker, 1880, *ibid.*, (X), I, Pt. V, Pl. XL [subsequently referred by the present author to *Tetralophodon punjabiensis*]; 1884, *ibid.*, (X), III, Pt. V, Pl. XVI, fig. 2; 1886, *ibid.*, (X), III, p. xv, fig. 5; Falconer and Cautley, 1847, "Fauna Antiqua Sivalensis," Pl. XL, figs. 2, 2*a*, 3, 3*a*.	*Stegolophodon cautleyi*
1886	*Mastodon punjabiensis*	Lydekker	"Cat. Foss. Mamm. Brit. Mus.," p. 60. Type loc.: Siwalik Hills, Punjab, India. Lectotype fig.: Lydekker, 1880, Mem. Geol. Surv. India, Palæont. Indica, (X), I, Pt. V, Pl. XLII. Originally referred to *Mastodon (Tetralophodon) perimensis*.	*Tetralophodon punjabiensis*
1886 1896	*Mastodon (Trilophodon) floridanus*	Leidy	Proc. Acad. Nat. Sci. Phila., XXXVIII, p. 12. Type loc.: Alachua clays, Mixson's bone bed, near Williston, Levy County, Florida. Type fig.: Leidy and Lucas, 1896, Trans. Wagner Free Inst. Sci., IV, Pl. VI, figs. 1, 2.	*Ocalientinus (Serridentinus) floridanus*
1887	*E.* [*Elephas*] *antiquus* var. *minor*	Pohlig	Verh. natur. Vereins preuss. Rhein., Jahrg. 44, p. 115. Type loc.: Seville, Spain.	
1887	*Stegodon trigonocephalus*	Martin	Sammlung. Geolog. Reichs-Museums, Leiden, 1te Serie, Beiträge z. Geolog. Ost-Asiens u. Australiens, IV, Heft II, pp. 27, 36. Type loc.: Probably vicinity of Surakarta, Java. Type figs.: Martin, *ibid.*, Tab. II, figs. 1, 1a, and Tab. III, fig. 1.	*Stegodon trigonocephalus*

Year	Name	Author	Reference in Present Memoir
1887 [1888?]	*Elephas* (*primigenius*) *trogontherii*	Pohlig See *Elephas trogontherii* Pohlig, 1885, 1887, above, this list.	
1888	*E.* [*Elephas*] (*primigenius*) *Leith-Adamsi*	Pohlig Nova Acta Leop. Carol., LIII, No. 1, pp. 229, 232. Type loc.: Dornap (Fuhlrott), Thuringia, Germany. Type fig.: Pohlig, *ibid.*, p. 229, fig. 101 *c-d*.	*Mammonteus*(?) *primigenius leith-adamsi*
1888	*Mastodon bonaerensis*	Moreno "Informe Prelim. progresos Mus. La Plata," pp. 17, 18 (nomen nudum). See Ameghino, 1889, Acta Acad. Nac. Cien, Córdoba, VI, p. 641. Type loc.: Arrecifes, Province of Buenos Aires, Argentina. Not figured by Moreno, but Eduardo Carette figured it in his article "Los Proboscideos Fósiles Argentinos," 1919, Lám. XI, fig. 2, as *D.* [*Dibelodon*] *platensis*.	*Cuvieronius bonaerensis* (= *superbus*)
1888	*Mastodon argentinus*	Ameghino "Rápidas Diagnosis," p. 7. Type loc.: Valley of Tarija River, northern part of Argentina, exact locality not recorded. Type fig.: Ameghino, 1889, Actas Acad. Nac. Cien. Córdoba, VI, p. 644.	*Notiomastodon argentinus*
1888	*Mastodon platensis*	Ameghino *Loc. cit.* Type loc.: San Nicolás de los Arroyos, Province of Buenos Aires, Argentina. Type fig.: Ameghino, 1889, *ibid.*, p. 641.	*Cuvieronius platensis*
1888	*Mastodon superbus*	Ameghino *Loc. cit.* Type loc.: Pergamino, Province of Buenos Aires, Argentina. Type fig.: Ameghino, 1889, *ibid.*, p. 647.	*Cuvieronius superbus*
1889	*Mastodon rectus*	Ameghino Actas Acad. Nac. Cien. Córdoba, VI, p. 643. Type loc.: From the Ensenada, near La Plata, Argentina. Type fig.: Ameghino, *ibid.*, p. 643.	*Cuvieronius rectus*
1889	*Elephas* (*primigenius*) *Leith-Adamsi*	Pohlig var. *minor* (In Trouessart, 1897–1899, "Cat. Mamm. Viv. Foss.," p. 711). Search in Pohlig's contributions of 1889 does not disclose a definition of this variety, and a letter from Doctor Pohlig (Sept. 10, 1924) does not authenticate var. *minor* as a subspecific term (cf. p. 1150 of the present Memoir).	
1889	*Tetrabelodon brevidens*	Cope Amer. Naturalist, XXIII, pp. 198–202. Type loc.: Smith River, Meagher County, Montana. Type fig.: Cope, *ibid.*, p. 201, fig. 5.	*Rhynchotherium brevidens*
1889	*E.* [*Elephas*] *primigenius americanus*	Cope *Ibid.*, pp. 207, 209. Hab.: North America.	
1889	*Elephas primigenius columbi*	Cope *Ibid.*, pp. 208, 209. Type loc.: "Orange sand," city of Dallas, northeastern Texas. Type figs.: Cope, *ibid.*, Pl. XIV and text fig. 9.	
1889	*Elephas lyrodon*	Weithofer Jahrb. Geol. Reichsanst., XXXIX, pp. 79, 80. Type loc.: Val d'Arno supérieur, Italy. Type figs.: Weithofer, 1890, Beitr. Pal. Österr.-Ung., VIII, Taf. III, fig. 2, Taf. IV, fig. 2, Taf. V, fig. 1. Compare observations of Pohlig (1891, pp. 314, 334).	*Archidiskodon meridionalis* (female)
1890	*Stegodon Mindanensis*	Naumann Zeitschr. deutsch. geol. Ges., XLII, Heft I, pp. 166, 167. Type loc.: Mindanao, Philippine Islands. Type fig.: Naumann, 1887, Abh. Ber. k. Zool.-Anthrop.-Ethnog. Mus. Dresden, No. 6, Taf. I, figs. 1 and 2, as *S. trigonocephalus*.	*Stegodon* (*Archidiskodon*?) *mindanensis*
1890	*Stegodon Airâwana*	Martin Verh. Kon. Akad. Wetensch. Afdeel. Natuurk., Amsterdam, XXVIII, p. 4. Type loc.: Alas-Tuwa, Trinil, Java. Type figs.: Martin, *ibid.*, Tab. I, figs. 1 and 2, Tab. II, figs. 3 and 4.	*Stegodon airâwana*
1890	*Mastodon rugosidens*	Leidy Proc. Acad. Nat. Sci. Phila., XLII, p. 184. Type loc.: Santee beds, Beaufort County, South Carolina. No type figure recorded (see Fig. 115 of present Memoir drawn from cast, Amer. Mus. 14445). Original in Academy of Natural Sciences, Philadelphia.	*Mastodon americanus rugosidens*
1891	*E.* [*Elephas*] *primigenius* Blum. var. *hydruntinus*	Botti Boll. Soc. geol. Ital., IX, p. 709. Type loc.: La Grotta Ossifera di Cardamone, Terra d'Otranto, Italy. Type fig.: Botti, *ibid.*, Tav. XXVI, figs. 1, 1a, 2, 2a.	*Mammonteus primigenius hydruntinus*

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1891	*E.* [*Elephas*] *giganteus intermedius*	Gunn	Same as *Leptodon giganteus* Gunn, 1883, subsequently named by Lartet (in Gunn, 1883) *E. gunnii* (see above, this list).	*Hesperoloxodon antiquus*
1891	*E.* [*Elephas*] *Nestii*	Pohlig	Nova Acta Acad. Leop. Carol., LVII, pp. 303, 304. *Elephas antiquus Nestii* n.f., Pohlig, *ibid.*, p. 465. Type loc.: Happisborough, Forest bed (Norfolk), Walton (Essex), Southwold (Suffolk), England. Cotype figs.: None. See Figs. 941, 1041 of present Memoir.	*Parelephas*(?) *trogontherii nestii*
1891	*Mastodon maderianus*	Ameghino	Revista Argent. Hist. Nat., I, p. 243. Type loc.: Puerto Madero in Buenos Aires, Argentina.	*Cuvieronius* (?)*maderianus*
1892	*D.* [*Dinotherium*] *gigantissimum*	G. Stefănescu	Bull. Geol. Soc. Amer., III, pp. 81, 82. Type loc.: Găiceana, Tecuciŭ, Rumania. See Stefănescu, 1878, pp. 101–104, giving an account of discovery, also 1895, p. 173, Tab. IV and V (referred molars).	*Deinotherium gigantissimum*
1892	*Mastodon successor*	Cope	Proc. Acad. Nat. Sci. Phila., XLIV, pp. 227, 228. Type loc.: Blanco beds, Texas. Type figs.: Cope, 1893, 4th Ann. Rept. Geol. Surv. Texas, Pl. XVI, figs. 1, 1*a*, Pl. XVII, fig. 1, as *Dibelodon tropicus*.	*Stegomastodon successor*
1892 1893	*D.* [*Dibelodon*] *præcursor*	Cope	Amer. Naturalist, XXVI, p. 1059 (name only). Type loc.: Mt. Blanco, Llano Estacado, Texas. Type description: Cope, 1893, 4th Ann. Rept. Geol. Surv. Texas, pp. 64, 65. Type figs.: Cope, 1893, *op. cit.*, Pls. XVIII, XIX.	*Serbelodon*(?) *præcursor*
1893	*T.* [*Tetrabelodon*] *serridens cimarronis*	Cope	4th Ann. Rept. Geol. Surv. Texas, pp. 18–20. Type loc.: East of Llano Estacado, Texas, north of south fork of Red River. Type fig.: Cope, *op. cit.*, Pl. III, figs. 2 and 3.	*Serridentinus serridens cimarronis*
1893	*Mastodon oligobunis*	Cope	*Op. cit.*, p. 59. Type loc.: Tequixquiac, Valley of Mexico. Type fig.: After Villada, 1903, Ann. Mus. Nac. Mexico, VII, Lám. VII (as *Dibelodon Shepardi*, Cope).	*Cordillerion oligobunis*
1893	*M.* [*Mastodon*] *chilensis*	Philippi	Zeitschr. deutsch. geol. Ges., XLV, p. 88. Type loc.: Near Lake Tagua-Tagua, Chile. Type fig.: Philippi, *ibid.*, p. 89, fig. 4.	*Cuvieronius chilensis*
1893	*Mastodon bolivianus*	Philippi	*Ibid.*, p. 89. Type loc.: Ulloma, Bolivia. Type fig.: Philippi, *ibid.*, p. 89, fig. 2.	*Cordillerion bolivianus*
1894	*Mastodon Sahendi*	Pavlow	(MS. labels Hofmuseum in Wien), Mém. Acad. Imp. Sci. St. Pétersb., (8), I, No. 3, p. 16. Type loc.: Maragha, Persia. See Kittl, 1887, p. 320, for associated fauna of Maragha.	*Tetralophodon* sp.
1895	*Elephas jolensis*	Pomel	Paléontologie Monographies, No. 6, Carte Géol. L'Algérie, pp. 32, 39. Hab.: Algerian seacoast, downward from Krober-Roumia. Type fig.: Pomel, *op. cit.*, Pl. V, figs. 3 and 4.	*Palæoloxodon jolensis*
1896 1913	*Elephas meridionalis antiquitatis*	Portis	"Contribuzioni alla Storia fisica del Bacino di Roma, . ." Torino, II, p. 272. Portis' original description of 1896 was not seen by the present author. In the Rivista Italiana di Paleontologia, II, of the same year, the name appears in a phylogenetic chart on page 331. Zuffardi in Palæontologica Italica, 1913, XIX, p. 155, includes this subspecies in the synonymy of *Elephas antiquus* Falc. var. *trogontherioides*.	
1897	*Mastodon angustidens* Cuv. mut. asc. *pygmæus*	Depéret	Bull. Soc. géol. France, (3), XXV, p. 519. Type loc.: Kabylie, near Isserville, Algeria. Type fig.: Depéret, *ibid.*, Pl. XIX, figs. 1–3.	*Phiomia pygmæus*
1897	*Elephas platyrhynchus*	Graells	Mem. Real. Acad. Cien. Exactas, Fis. nat., Madrid, XVII, p. 569. Type loc.: San Isidro del Campo, near Madrid, Spain. Type fig.: Graells, *ibid.*, Lám. XVIII, figs. 9*a*, 10.	*Hesperoloxodon antiquus platyrhynchus*

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1897	*Mastodon aureliense*,	Cuv.	(In Graells, *ibid.*, p. 573.) Hab.: Madrid.	[Not determined by the present author]
1899	*Mastodon angustidens* var. *latidens*	Lankester	Geol. Mag., Dec. IV, N. S., VI, pp. 289–292, Pl. XI. Type loc.: Suffolk Crag, England. Figured as a trilophodont Mastodon in Quart. Journ. Geol. Soc., 1870, Pl. 34, figs. 1–4.	*Zygolophodon* sp.
1900	*Elephas maximus sumatranus*	Lydekker	"Great and Small Game of India . . . ," p. 11. Living form. See *Elephas sumatranus* Temminck, 1847, above, this list; also Lydekker, 1916, p. 83.	*Elephas indicus sumatranus*
1900	*Elephas cyclotis*	Matschie	Sitz.-Ber. Ges. naturf. Freunde Berlin, No. 8, p. 194. Type loc.: Mwelle district, S. Cameroon. Type fig.: Heck, 1899, "Lebende Bilder aus dem Reiche der Tiere, Berlin," Pl. CXLVI (original not seen by the present author). Formerly in Berlin Zoological Garden. Living form.	*Loxodonta capensis cyclotis*
1900	*Elephas* (*Loxodonta*) *oxyotis*	Matschie	*Ibid.*, p. 196. Type loc.: Upper Atbara, Sudan. Living form.	*Loxodonta africana oxyotis*
1900	*Elephas* (*Loxodonta*) *knochenhaueri*	Matschie	*Ibid.*, p. 197. Type loc.: Barikiwa, Tanganyika Territory. Living form.	*Loxodonta africana knochenhaueri*
1901	*Palæomastodon Beadnelli*	Andrews	Zoologist, (4), V, August 15, pp. 318, 319 (name only); Tageblatt V Internat. Zool.-Congr., Berlin, No. 6, August 16, p. 4; Geol. Mag., Dec. IV., N. S., VIII, September, p. 401. Type loc.: Fayûm, Egypt. Type fig.: Andrews, 1901, Geol. Mag., Dec. IV, N. S., VIII, p. 401, fig. 1, A, B.	*Palæomastodon beadnelli*
1901	*Mœritherium Lyonsi*	Andrews	Tageblatt V Internat. Zool.-Congr., Berlin, No. 6, August 16, p. 4; Geol. Mag., Dec. IV, N. S., VIII, September, pp. 403, 404. Type loc.: Fayûm, Egypt. Type fig.: Andrews, 1901, Geol. Mag., Dec. IV, N. S., VIII, p. 404, fig. 2.	*Mœritherium lyonsi*
1902	*Phiomia serridens*	Andrews and Beadnell	"A Preliminary Note on Some New Mammals from the Upper Eocene of Egypt," p. 3. Type loc.: Fayûm, Egypt. Type figs.: Andrews and Beadnell, *loc. cit.*, figs. 1 and 2.	*Phiomia serridens*
1902	*Mœritherium gracile*	Andrews	Geol. Mag., Dec. IV, N. S., IX, p. 292. Type loc.: Fayûm, Egypt. Type figs.: Andrews, 1906, "A Descriptive Catalogue of the Tertiary Vertebrata of the Fayûm, Egypt," p. 127, and Pl. XVII, figs. 1 and 2.	*Mœritherium gracile*
1902	*Mastodon tarijensis*	Ameghino	An. Mus. Nac. Buenos Aires, VIII (Ser. 3ª, I), p. 2 (name only). Hab.: Valley of Tarija, Bolivia.	*Cordillerion tarijensis*
1903	*Mastodon Lydekkeri*	Schlosser	Abh. bayer. Akad., II Cl., XXII, Abth. 1, pp. 46, 47. Type loc.: North China. Type fig.: Schlosser, *ibid.*, Taf. XIV, fig. 8.	*Serridentinus lydekkeri*
1903	*Elephas cypriotes*	Bate	Proc. Roy. Soc. London, LXXI, pp. 498–500. Type loc.: Cave, Kerynia Hills, Cyprus. Cotype figs.: Bate, 1904, Phil. Trans. Roy. Soc. London, CXCVII, B, Pls. XXI, XXII.	*Palæoloxodon cypriotes*
1904	*Mœritherium trigodon*	Andrews	Geol. Mag., Dec. V, N. S., I, p. 112. Type loc.: Fayûm, Egypt. Type fig.: Andrews, 1906, "A Descriptive Catalogue of the Tertiary Vertebrata of the Fayûm, Egypt," Pl. IX, fig. 5. Supplementary description: Andrews, 1906, *op. cit.*, p. 128, name changed to *trigonodon*.	*Mœritherium trigodon*
1904	*Palæomastodon minor*	Andrews	*Ibid.*, p. 115. Type loc.: Fayûm, Egypt. Type figs.: Andrews, 1906, "A Descriptive Catalogue of the Tertiary Vertebrata of the Fayûm, Egypt," Pl. XIV, figs. 1, 1A, text fig. 50D. Supplementary description: Andrews, 1906, *op. cit.*, p. 168.	*Phiomia minor*
1905	*Palæomastodon minus*	Andrews	*Ibid.*, II, p. 562. Error, the author had reference to *Palæomastodon* [= *Phiomia*] *minor*.	*Phiomia minor*
1905	*Palæomastodon parvus*	Andrews	*Loc. cit.* Type loc.: Fayûm, Egypt. Type figs.: Andrews, 1906, "A Descriptive Catalogue of the Tertiary Vertebrata of the Fayûm, Egypt," p. 143, text fig. 50C, and p. 163, text fig. 55.	*Palæomastodon parvus*

Year	Name	Author	Reference in Present Memoir
1905	*Palæomastodon wintoni*	Andrews *Ibid.*, p. 563. Type loc.: Fayûm, Egypt. Type fig.: Andrews, 1906, "A Descriptive Catalogue of the Tertiary Vertebrata of the Fayûm, Egypt," p. 157, text fig. 53. Originally referred to *Palæomastodon*; transferred by Matsumoto (1922, p. 3) to *Phiomia*.	*Phiomia wintoni*
1906	*Mœritherium trigonodon*	Andrews *Op. cit.*, p. 128. See *Mœritherium trigodon* Andrews, 1904, above.	
1906	*Elephas africanus albertensis*	Lydekker Field (London), CVII, p. 1089. Type loc.: South end of Lake Albert, Africa. Type fig.: Lydekker, 1907, Proc. Zool. Soc. London, text fig. 121. Living form.	*Loxodonta africana albertensis*
1906	*Elephas africanus pumilio*	Noack Zool. Anz., XXIX, pp. 631–633. Type loc.: French Congo. Type fig.: Hornaday, 1905, Bull. New York Zool. Soc., October, pp. 237, 238. Living form.	*Loxodonta africana pumilio*
1907	*Elephas africanus toxotis*	Lydekker Proc. Zool. Soc. London, p. 385. Type loc.: Mossel Bay, western Cape Colony. Type fig.: Lydekker, *ibid.*, text fig. 106. Living form.	*Loxodonta africana toxotis*
1907	*Elephas africanus selousi*	Lydekker *Ibid.*, p. 387. Type loc.: Mashonaland, Rhodesia. Type fig.: Lydekker, *ibid.*, text fig. 108. Living form.	*Loxodonta africana selousi*
1907	*Elephas africanus peeli*	Lydekker *Ibid.*, p. 393. Type loc.: Aberdare Mts., Kenya Colony. Type fig.: Lydekker, *ibid.*, text fig. 114. Living form.	*Loxodonta africana peeli*
1907	*Elephas africanus cavendishi*	Lydekker *Ibid.*, p. 395. Type loc.: Lake Rudolf district. Type fig.: Lydekker, *ibid.*, text fig. 115. Living form.	*Loxodonta africana cavendishi*
1907	*Elephas africanus orleansi*	Lydekker *Ibid.*, p. 398. Type loc.: North Somaliland. Type fig.: Lydekker, *ibid.*, text fig. 118. Living form.	*Loxodonta africana orleansi*
1907	*Elephas africanus rothschildi*	Lydekker *Ibid.*, p. 399. Type loc.: French Sudan. Type fig.: Lydekker, *ibid.*, text fig. 119. Living form. Lydekker states that he takes as type the statuette of "Jumbo" in the British Musuem. Professor Osborn (1931.846, p. 21) referred "Jumbo" to the subspecies *Loxodonta africana oxyotis*, which would make *rothschildi* a synonym of *oxyotis*.	*Loxodonta africana oxyotis*
1907	*E.* [*Elephas*] *a.* [*africanus*] *cottoni*	Lydekker *Ibid.*, II, p. 783. Type loc.: Northeastern Congo. Type fig.: Lydekker, *ibid.*, text fig. 111. Living form.	*Loxodonta africana cottoni*
1907	*Elephas maximus zeylanicus*	Lydekker "Game Animals of India," p. 15. Living form.	*Elephas indicus ceylanicus*
1907	*Elephas creticus*	Bate Proc. Zool. Soc. London, pp. 238–250. Type loc.: Near Cape Maleka, Crete. Cotype figs.: Bate, *ibid.*, Pl. XII, figs. 1–3, Pl. XIII, figs. 1, 2.	*Palæoloxodon creticus*
1907	*Paleomastodon Barroisi*	Pontier Ann. Soc. géol. du Nord, XXXVI, pp. 150, 151. Type loc.: Fayûm, Egypt. Type figs.: Pontier, *ibid.*, text figs. 1 and 2. Synonym, in part (*fide* Matsumoto, 1922) of *Phiomia wintoni* and *P. minor* (cf. Vol. I, p. 61, this Memoir, where the present author confirms Matsumoto's reference).	
1907	*Elephas* (*Loxodon*) *zulu*	Scott 3d Rept. Geol. Surv. (?)Natal and Zululand, pp. 259–262. Type loc.: Zululand, southeast coast of Africa. Type figs.: Scott, *op. cit.*, Pl. XVII, fig. 6, and Pl. XVIII, fig. 1.	*Loxodonta zulu*
1908	*Dinotherium náricum*	Pilgrim Rec. Geol. Surv. India, XXXVII, Pt. II, p. 156. Name abandoned by the author and the subspecific term *gajense* substituted in 1912, pp. 16 and 17. See below under *Dinotherium indicum* Lyd. var. *gajense* Pilgrim, 1912.	*Deinotherium indicum gajense*
1908	*Tetrabelodon crepusculi*	Pilgrim *Ibid.*, p. 157. See *Hemimastodon crepusculi* Pilgrim, 1912, below, this list.	

Year	Name	Author	Reference in Present Memoir
1908	*Stegodon javanoganesa*	Dubois Tijdschr. Nederl. Aardr. Genoots Amsterdam, (2), XXVB, No. 6, p. 1245. Von Koenigswald, 1933.1, p. 105: "Im grossen Ganzen scheint *Stegodon trigonocephalus* im Habitus von *Stegodon ganesa* nicht sehr verschieden gewesen zu sein. Dubois dachte sogar daran, die javanische Art nur als eine Varietät der indischen zu betrachten; ganz klar wird man über seine Auffassung nicht, da er die Art einmal als *Stegodon javanoganesa*, (1908, pg. 1245), einige Seiten weiter als *Stegodon ganesa* var. *javanicus* bezeichnet (1908, pg. 1257).	
1908	*Stegodon Ganesa* var. *javanicus*	Dubois *Ibid.*, p. 1257. Type loc.: Kendeng-Schichten, Trinil, Java. Figure not found by the present author.	*Stegodon airâwana* [*or S. trigonocephalus*]
1908	*Elephas hysudrindicus*	Dubois *Loc. cit.* Type loc.: Kendeng-Schichten, Java. Type fig.: First published figure of cotypes is in the present Memoir (Fig. 1160).	*Palæoloxodon hysudrindicus*
1909	*Elephas Wüsti*	Pavlow Annuaire Géol. Min. Russie, XI, pp. 171–174. Type loc.: Tiraspol (gouv. Kherson), southern Russia. Cotype figs.: Pavlow, *ibid.*, Pl. v, figs. 1 and 2; 1910, Nouv. Mém. Soc. Imp. Nat. Moscou, XVII, Livr. 2, Pl. i, figs. 1–12 (Figs. 10 and 12 being the same as 1909, Pl. v, figs. 1 and 2).	*Parelephas wüsti*
1909	*Gomphotherium conodon*	Cook Amer. Journ. Sci., XXVIII, p. 183. Type loc.: Near Agate, Sioux County, Nebraska. Type fig.: Cook, *ibid.*, p. 183.	Not a proboscidean, but *Dinohyus petersoni* Holland
1909	*Tetrabelodon dinotherioides*	Andrews Geol. Mag., Dec. V, N. S., VI, p. 347. Type loc.: "Loup Fork beds," northwestern Kansas. Type fig.: Andrews, *ibid.*, p. 348.	*Trilophodon dinotherioides*
1911	*Elephas primus*	Schlesinger Monatsbl. Ver. Landeskunde v. Niederöster., V, p. 244.	[Not determined by the present author]
1911	*Mœritherium Andrewsi*	Schlosser Beitr. Pal. Geol. Österr.-Ung., XXIV, p. 130. Type loc.: Fayûm, Egypt. Type figs.: Andrews, 1906, "A Descriptive Catalogue of the Tertiary Vertebrata of the Fayûm, Egypt," Pls. viii, ix.	*Mœritherium andrewsi*
1911	*Dinotherium hobleyi*	Andrews Abstract, Proc. Zool. Soc. London, (May), p. 35; Proc. Zool. Soc. London, (December), p. 943. Type loc.: Near Karungu, east side of Victoria Nyanza, Africa. Type fig.: Andrews, *ibid.*, Pl. xlviii, figs. 1, 1a.	*Deinotherium hobleyi*
1912	*Dinotherium indicum* Lyd. var. *gajense*	Pilgrim Mem. Geol. Surv. India, Palæont. Indica, N. S., IV, Mem. 2, p. 16. Type loc.: Gaj beds of Bugti Hills, Baluchistan. Type fig.: Pilgrim, *ibid.*, Pl. iv, figs. 1–4. Same type specimen as *Dinotherium náricum* Pilgrim, 1908, above, this list.	*Deinotherium indicum gajense*
1912	*Hemimastodon crepusculi*	Pilgrim *Ibid.*, p. 17. Type loc.: Gaj zone of Kumbhi, Bugti Hills, Baluchistan. Type fig.: Pilgrim, *ibid.*, Pl. iv, fig. 5; see also Pl. iv, figs. 6–9, and Pl. iii, fig. 4. Same as *Tetrabelodon crepusculi* Pilgrim, 1908, above, this list.	Suina
1912	*Elephas primigenius Fraasi*	Dietrich Jahresh. Ver. Naturk. Württemb., LXVIII, pp. 42–106. Type loc.: Steinheim a.d. Murr, Germany. Type figs.: Dietrich, *ibid.*, Taf. i and ii, also text figs. 2, 4, 11–14, 16–21, 24–26.	*Mammonteus primigenius fraasi*
1912	*Mastodon arvernensis* Croiz. et Job. var. *progressor*	Khomenko Annuaire Géol. Min. Russie, XIV, Livr. 6, pp. 159–165. Type loc.: Near Gavanosy, district of Ismaïl, southern Bessarabia, Russia. Type fig.: Khomenko, *ibid.*, Pl. i.	*Anancus arvernensis progressor*
1912	*Mastodon arvernensis* Croiz. et Job. var. *conservativus*	Khomenko *Ibid.*, p. 165. Synonym of *Mastodon arvernensis* Croiz. et Job. var. *progressor* Khomenko, 1912, above.	
1912	*Elephas antiquus* var. *insularis*	Soergel Palæontogr., LX, p. 1. Type loc.: Carini, Sicily.	Nomen nudum
1913	*Mastodon angustidens* var. *austro-germanica*	Wegner Palæontogr., LX, pp. 255–263. Type loc.: Near Oppeln, eastern Germany. Type fig.: Wagner, *ibid.*, Taf. xv, fig. 2.	*Trilophodon angustidens* var. *austro-germanicus*

Year	Name	Author	Reference in Present Memoir
1913	*Tetrabelodon corrugatus*	Pilgrim Rec. Geol. Surv. India, XLIII, Pt. IV, p. 293. Type loc.: Hasnot, India. Type fig.: Lydekker, 1880, Mem. Geol. Surv. India, Palæont. Indica, (X), I, Pt. V, Pl. xxxv, fig. 4, as *Mastodon* (*Trilophodon*) *pandionis*; see also Pl. xxxvi, fig. 1.	*Synconolophus corrugatus*
1913	*Mastodon hasnoti*	Pilgrim *Loc. cit.* Type loc.: Near Bhimbar, northwest of Jammu, India. Type fig.: Lydekker, 1880, *ibid.*, Pl. xliv, fig. 3, as *Mastodon* (*Tetralophodon*) *sivalensis*.	*Synconolophus hasnoti*
1913	*Mastodon stegodontoides*	Pilgrim *Ibid.*, p. 294. Type loc.: Lehri, Punjab, India. Type fig.: Lydekker, 1880, *ibid.*, Pl. xxxix, as *Mastodon* (*Tetralophodon*) *latidens*.	*Stegolophodon stegodontoides*
1913	*Tetrabelodon macrognathus*	Pilgrim *Ibid.*, p. 309. Type loc.: Near Chinji, India. No published type figure found by the present author. See figure 219 of the present Memoir.	*Trilophodon macrognathus*
1913	*Tetrabelodon angustidens* var. *chinjiensis*	Pilgrim *Ibid.*, p. 316 (name). Holotype of Osborn (Amer. Mus. 19421) found two miles west of Chinji Bungalow, India (see Fig. 218 of the present Memoir).	*Trilophodon chinjiensis*
1913	*Elephas antiquus* Falc. var. *trogontherioides*	Zuffardi Palæont. Ital., XIX, pp. 130, 155. Type loc.: Piedmont, Italy; lectotype from Nizza della Paglia (Astésan); cotypes from near San Paolo de Villafranca. Figures: Zuffardi, *ibid.*, Tav. ix, figs. 3*a*-6*b*.	*Parelephas trogontherioides*
1913	*Elephas primigenius* Blum. var. *trogontherii* Pohl.	Zuffardi *Ibid.*, p. 167. Cf. *Elephas primigenius* mutation *astensis* Depéret and Mayet, 1923, below, this list.	
1914	*Elephas africanus Fransseni*	Schouteden Rev. Zool. Africaine, III, Fasc. 2, p. 396. Type loc.: M'Paa near Bongo, northwest of Lake Leopold II. Type fig.: Schouteden, *ibid.*, Pl. xi, figs. 1, 2. Living form.	*Loxodonta africana fransseni*
1914	*Elephas maximus hirsutus*	Lydekker Abstract, Proc. Zool. Soc. London, I, p. 20 (name only). Type loc.: Kuala Pila district of the Negri Sembilan province, Malay Peninsula. Type fig.: Lydekker, 1914, Proc. Zool. Soc. London, I, text fig. 1, p. 285; 1916, "Catalogue Ungulate Mammals in British Museum," text fig. 25, p. 84. Formerly in the Gardens of the Zoological Society of London.	*Elephas indicus hirsutus* [of doubtful validity—see footnotes on page 1332 of Chapter XX above.—Editor.]
1914	*Tetrabelodon willistoni*	Barbour Univ. Studies, Univ. Neb., XIV, No. 2, pp. 192–194. Type loc.: Devil's Gulch, Niobrara River, Brown County, Nebraska. Type figs.: Barbour, *ibid.*, Pls. v, vi, viii.	*Trilophodon* (*Genomastodon*) *willistoni*
1914	*Eubelodon morrilli*	Barbour *Ibid.*, pp. 194–197. Type loc.: Devil's Gulch, Niobrara River, Brown County, Nebraska. Type figs.: Barbour, *ibid.*, Pls. ix–xii.	*Eubelodon morrilli*
1914	*Tetrabelodon lulli*	Barbour Neb. Geol. Surv., IV, Pt. 14, p. 217. On this same page, in a footnote, the subgenus *Megabelodon* was suggested. Type loc.: Exposures bordering Snake River, Cherry County, Nebraska. Type figs.: Barbour, *ibid.*, Pls. iii–vi. See also Barbour, 1917.1, p. 512.	*Megabelodon lulli*
1914	*Mammut progenium*	Hay Iowa Geol. Surv., Ann. Rept. for 1912, XXIII, pp. 368–373. Type loc.: Cox gravel pit, Missouri Valley, Harrison County, Iowa. Type fig.: Hay, *ibid.*, Pl. xliv, figs. 1 and 2 (specimen first described and figured by Calvin, 1911, Bull. Geol. Soc. Amer., XXII, p. 213, Pls. xx, xxi, under the name *Mastodon americanus*).	*Mastodon progenius*
1914	*Rhabdobunus mirificus*	Hay *Ibid.*, p. 374. Pohlig in 1912 chose *Mastodon mirificus* Leidy, 1858 (see above, this list), as the genotype of *Stegomastodon* (see Generic List above, p. 1379). In 1914 Hay made Leidy's *M. mirificus* the type of his new genus *Rhabdobunus*, which, however, is invalid because preoccupied by Pohlig's *Stegomastodon* (cf. Hay, 1930, p. 633).	*Stegomastodon mirificus*
1915	*Elephas hysudricus primitivus*	Soergel Centralb. Min. Geol. Pal., No. 8, p. 250, No. 9, p. 283.	[Not determined by the present author]
1915	*Dinotherium styriacum*	Hilber Mitt. Naturwiss. Ver. Steiermark, LI, pp. 113–117. Type loc.: Oberdorf bei Weiz, Styria. Type fig.: Hilber, *ibid.*, Taf. i, fig. 1.	[Not determined by the present author]

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1915	*Elephas hayi* Barbour Amer. Journ. Sci., (4), XL, pp. 129–134. Type loc.: Crete, Saline County, Nebraska. Type figs.: Hay, *ibid.*, p. 130, fig. 1; p. 133, fig. 3; p. 134, fig. 5*d*.	*Archidiskodon hayi*
1915 1918	*Elephas auroræ* Matsumoto Scientific Gazette, Tokyo, III, No. 5, pp. 308–315 (Japanese only); 1918, Sci. Rept. Tôhoku Imp. Univ., (2), Geol., III, No. 2, p. 52. Type loc.: Mt. Tomuro, Kaga, Japan. Type fig.: Matsumoto, 1918, *ibid.*, Pl. xx, figs. 1–3. Subsequently (1924, Journ. Geol. Soc. Tokyo, XXXI, No. 371, pp. 256, 257, 262) made the genotype of *Parastegodon.*	*Stegodon auroræ*
1915	*Mastodon pirayuiensis* Gez "Generalidades sobre paleontologia argentina: El *Mastodon platensis*—Amegh. de Corrientes," 2ª edición, p. 35.	*Cuvieronius pirayuiensis*
1915	*Mastodon "ligoniferus"* Cope and Matthew "Hitherto Unpublished Plates of Tertiary Mammalia and Permian Vertebrata," Amer. Mus. Monograph Series No. 2. Type loc.: Black Hills, South Dakota. Type figs.: Cope and Matthew, *op. cit.*, Pl. cxxiv, figs. 1 and 2.	*Trilophodon ligoniferus*
1916	*Elephas maximus maximus* Lydekker "Cat. Ungulate Mammals, British Museum," V, p. 82.	*Elephas indicus bengalensis*
1916	*Elephas antiquus Recki* Dietrich Arch. Biontol., IV, Heft I, p. 22. Type loc.: Oldoway-Tuffe, Serengetisteppe, northern Tanganyika Territory, Africa. Lectotype fig.: Dietrich, *ibid.*, Taf. i, fig. 2; cotypes, Taf. i–viii (in part).	*Palæoloxodon recki*
1916	*Tetrabelodon osborni* Barbour Amer. Journ. Sci., (4), XLI, pp. 522–529. Type loc.: Near Bristow, Boyd County, Nebraska. Type figs.: Barbour, *ibid.*, p. 523, fig. 1; p. 524, fig. 2; p. 526, fig. 3; p. 528, fig. 4.	*Trilophodon* (*Genomastodon*) *osborni*
1917	*Mastodon* (*Bunolophodon*) *angustidens* Cuv. f. *subtapiroidea* Schlesinger Denk. Naturhist. Hofmus., I, Geol.-Pal. Reihe I, pp. 30, 31, 35, 37. Type loc.: Wies, near Eibiswald (Styria), Austria. Cotype figs.: Schlesinger, *ibid.*, Taf. iii, fig. 2; Taf. iv, fig. 1; Taf. vii, fig. 3; Taf. viii, figs. 1 and 2, and p. 31, text fig. 3.	*Serridentinus subtapiroideus*
1917	*Mastodon* (*Bunolophodon*) *longirostre* Kaup *forma sublatidens* Schlesinger *Ibid.*, pp. 101, 102. Type loc.: Near Teschen (Schlesien), Austria. Type fig.: Schlesinger, *ibid.*, Taf. xvii, fig. 2.	*Stegolophodon sublatidens*
1917	*Mastodon* (*Bunolophodon*) *grandincisivum* Schlesinger *Ibid.*, p. 119. Type loc.: Maragha, Persia. Type fig.: Schlesinger, *ibid.*, Taf. xxxiv, figs. 1 and 2. Paratypes: Taf. xv, figs. 1 and 2, Mannersdorf near Angern, Austria.	*Tetralophodon grandincisivus*
1917	*Gomphotherium gratum* Hay Bull. Univ. Texas, No. LXXI, pp. 18–21. Type loc.: Pittbridge, Burleson County, Texas, on the Brazos River. Type figs.: Hay, *ibid.*, Pl. iii, figs. 3 and 4, Pl. iv, figs. 1 and 2.	*Cordillerion gratum*
1917	*Gomphotherium elegans* Hay *Ibid.*, pp. 21, 22. Type loc.: McPherson, Kansas. Type fig.: Hay, 1917, Proc. U. S. Nat. Mus., LIII, No. 2198, Pl. xxvi, figs. 1 and 2.	*Tetralophodon elegans*
1918	*Mastodon angustidens*, Cuvier var. *libyca* Fourtau Ministry of Finance, Egypt, Surv. Dept., pp. 84–89. Type loc.: Moghara, northern Egypt. Type fig.: Fourtau, *op. cit.*, text fig. 58.	*Trilophodon angustidens libycus*
1918	[*Mastodon angustidens*] mut. *Pontileviensis* Mayet (In Fourtau, *op. cit.*, p. 88—name only.) Hab.: Chevilly, Pontlevoy, France. Cotype figs.: Mayet, 1908, Ann. Univ. Lyon, Nouv. Sér. I,—Sci., Méd., Fasc. 24, Pls. vii, figs. 5, 6, xi, fig. 2 (as *Mastodon angustidens*). See Vol. I, p. 283 and fig. 230 of the present Memoir.	*Trilophodon pontileviensis*
1918	*Mastodon Spenceri* Fourtau *Op. cit.*, pp. 89–91. Type loc.: Moghara Desert, northern Egypt. Type figs.: Fourtau, *op. cit.*, p. 89, fig. 60; p. 90, fig. 61.	*Rhynchotherium*(?) *spenceri*
1918	*Rhynchotherium tlascalæ* Osborn Bull. Geol. Soc. Amer., XXIX, pp. 134, 135. Type loc.: Tlascala, Valley of Mexico. Type fig.: Vol. I, fig. 448, of present Memoir. See *Rhynchotherium browni* Osborn, 1936, below, this list.	*Rhynchotherium tlascalæ*

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1919 1922	*Mastodon (Mammut) americanus* Penn. *forma praetypica*	Schlesinger Mitt. Geol. Ges. Wien, XI, p. 142. Cotype loc.: Szabadka (=Maria-Theresiopel), Batta Érd, Rákoskeresztúr, Szentlörincz, and Ajnácskö, Hungary. Original figures: Schlesinger, *ibid.*, 1919, Taf. VI, figs. 2–4. Supplementary description and figures: Schlesinger, 1922, Geol. Hungarica, Ed. Sep., II, Fasc. 1, pp. 115, 116, 227–230, Pls. XIV–XIX.	*Pliomastodon americanus praetypica*
1921	*Trilophodon giganteus*	Osborn Amer. Mus. Novitates, No. 1, pp. 6–10. Type loc.: Eastview, near Dallas, Gregory County, South Dakota. Type fig.: Osborn, *ibid.*, p. 9, fig. 4C.	*Trilophodon giganteus*
1921	*Tetralophodon barbouri*	Osborn *Ibid.*, pp. 9, 10. Type loc.: Cambridge, Furnas County, Nebraska. Type fig.: Osborn, 1924, Amer. Mus. Novitates, No. 154, fig. 1. See also figs. 308F, 329D, and 337 of the present Memoir.	*Morrillia barbouri*
1921	*Mastodon matthewi*	Osborn Amer. Mus. Novitates, No. 10, pp. 2–6. Type loc.: Snake Creek, Sioux County, Nebraska. Type fig.: Osborn, *ibid.*, p. 3, fig. 1A (Fig. 98A of the present Memoir). Osborn (1922.564, p. 4) referred this species to *Miomastodon matthewi*; finally (1926.706, p. 1) he made it the type of his new genus *Pliomastodon*.	*Pliomastodon matthewi*
1921	*Mastodon merriami*	Osborn *Ibid.*, pp. 4–6. Type loc.: Thousand Creek, Humboldt County, Nevada. Type figs.: Osborn, *ibid.*, p. 3, fig. 1B, and p. 5, fig. 2.	*Miomastodon merriami*
1921 1922	*Mastodon tapiroides americanus*	Schlesinger (In Osborn, Amer. Mus. Novitates, No. 10, p. 2; fig. 1, D and D1, p. 3.) Schlesinger, 1922, Geol. Hungarica, II, Fasc. 1, pp. 224–227, Taf. XIII, figs. 6 and 7, and Taf. XIV, figs. 1–4. Type loc.: Tasnád, Usztató Komitat, Hungary.	*Miomastodon tapiroides americanus*
1921	*Trilophodon (Tetrabelodon) shepardi edensis*	Frick Bull. Dept. Geol. Univ. Calif., XII, No. 5, pp. 405–409. Type loc.: Mt. Eden Hot Springs, San Bernardino County, southern California. Type figs.: Frick, *ibid.*, p. 406, figs. 160–165. In the original description of *Trilophodon (Tetrabelodon) shepardi edensis* Frick, 1921, the author described material which ultimately proved to belong to two different genera, namely, *Rhynchotherium*, and *Dibelodon* (=*Cordillerion*). The molars (Frick, 1921, figs. 160–165) are referable to *Rhynchotherium shepardi edense* (see Frick, 1926, Bull. Amer. Mus. Nat. Hist., LVI, Art. II, pp. 169–176); the premaxillæ and tusks (Frick, 1921, Pl. L, figs. 1, 2) to *Cordillerion edensis*, 1936 (see below, this list).	*Rhynchotherium shepardi edense*
1922	*Dibelodon edensis*	Osborn (in part) Amer. Mus. Novitates, No. 49, p. 2. Synonym of *Cordillerion edensis*, 1936 (see below, this list).	
1922	*Miomastodon matthewi*	Osborn *Ibid.*, p. 4. See note under *Mastodon matthewi* Osborn, 1921, above, this list.	
1922	*Loxodonta griqua*	Haughton Trans. Geol. Soc. S. Africa, XXIV, pp. 11–13. Type loc.: Griqualand West, Africa. Type fig.: Haughton, *ibid.*, Pl. I, figs. 1, 2.	*Metarchidiskodon griqua*
1922	*Palæomastodon intermedius*	Matsumoto Amer. Mus. Novitates, No. 51, p. 2. Type loc.: North of Lake Qurun, Fayûm, Egypt. Type fig.: Matsumoto, *ibid.*, text fig. 1.	*Palæomastodon intermedius*
1922	*Phiomia osborni*	Matsumoto *Ibid.*, pp. 3, 4. Type loc.: Alexandria Trail, Fayûm, Egypt. Type fig.: Matsumoto, *ibid.*, p. 4, fig. 3.	*Phiomia osborni*
1922	*Mastodon engelswiesensis*	Klähn "Die badischen Mastodonten," pp. x, 30. Type loc.: Engelswies, Baden, Germany. Type fig.: Klähn, *op. cit.*, p. 30, fig. 10.	*Trilophodon engelswiesensis*
1922	*Mastodon steinheimensis*	Klähn *Op. cit.*, pp. x, xi, 35, 76. Type loc.: Steinheim, Baden, Germany. Type fig.: Fraas, 1870, Jahresh. Ver. naturk. Württemb., XXVI, Hefte II, III, Taf. V, fig. 1 (as *Mastodon arvernensis*).	*Trilophodon steinheimensis*
1922	*Mastodon gigantorostris*	Klähn *Op. cit.*, pp. xi, 48, 50, 87, 131. Type loc.: Bermersheim, Rheinhessen, Germany.	*Tetralophodon gigantorostris*

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1922	*Mastodon esselbornensis* Klähn *Op. cit.*, pp. xi, 50, 73. Type loc.: Esselborn and Westhofen, Rheinhessen, Germany. Type fig.: Klähn, *op. cit.*, p. 92, fig. 24.	*Trilophodon esselbornensis*
1922	*Mastodon wahlheimensis* Klähn *Op. cit.*, pp. xi, 76. Type loc.: Wahlheim and Esselborn, Rheinhessen, Germany. Cotype figs.: Klähn, *op. cit.*, p. 77, fig. 17; p. 94, fig. 25.	*Turicius wahlheimensis*
1922	*Mastodon minutoarvernensis* Klähn *Op. cit.*, pp. xii, 102. Type loc.: Herbolzheim, Baden, Germany.	*Anancus minutoarvernensis*
1922	*Mastodon gigantarvernensis* Klähn *Loc. cit.* Type loc.: Herbolzheim, Baden, Germany.	*Anancus gigantarvernensis*
1922	*Trilophodon hicksi* Cook Proc. Colo. Mus. Nat. Hist., IV, No. 1, p. 5. Type loc.: Near Wray, Yuma County, Colorado. Type figs.: Cook, *ibid.*, p. 9, figs. 2, 3; p. 10, fig. 1; p. 11, fig. 2.	*Amebelodon* (*Trilophodon*) *hicksi*
1922	*Trilophodon paladentatus* Cook *Ibid.*, p. 6. Type loc.: Near Wray, Yuma County, Colorado. Type figs.: Cook, *ibid.*, p. 9, fig. 1; p. 13, fig. 5; p. 14, fig. 6.	*Amebelodon* (*Trilophodon*) *paladentatus*
1922	*Elephas jeffersonii* Osborn Amer. Mus. Novitates, No. 41, pp. 11–16. Type loc.: Near Jonesboro, Indiana. Type fig.: Osborn, *ibid.*, p. 11, fig. 10.	*Parelephas jeffersonii*
1922	*Elephas roosevelti* Hay Proc. Biol. Soc. Washington, XXXV, pp. 100, 101 (description without figure). Type loc.: Ashland, Cass County, Illinois. See figure 968, p. 1096, above, this Memoir.	*Parelephas jeffersonii*
1922	*Mastodon oligobunis* var. *antiquissima* Freudenberg Geol. u. Pal. Abh., XIV (XVIII), Heft III, pp. 118–120. Type loc.: Valley of Amajaque, Hidalgo, Mexico. Type fig.: Freudenberg, *ibid.*, Taf. IX, figs. 3, 3a.	*Cordillerion oligobunis antiquissimus*
1922	*Mastodon oligobunis* var. *Felicis* Freudenberg *Ibid.*, pp. 120–123. Type loc.: Puebla, Mexico. Type fig.: Freudenberg, *ibid.*, Taf. X, figs. 1, 1a.	*Cordillerion*(?) *oligobunis felicis*
1922	*Mastodon oligobunis* var. *intermedia* Freudenberg *Ibid.*, pp. 123–126. Type loc.: Mexico, exact locality not recorded. Type fig.: Freudenberg, *ibid.*, Taf. XII, figs. 1, 2.	*Cordillerion*(?) *oligobunis intermedius*
1922	*M.* [*Mastodon*] *oligobunis* var. *progressa* Freudenberg *Ibid.*, p. 127. Type loc.: Cannada [canyon] de Aculcingo, Mexico. Type fig.: Freudenberg, *ibid.*, Taf. XIV, figs. 1, 2.	*Cordillerion oligobunis progressus*
1922	*El.* [*Elephas*] *Columbi* var. *Felicis* Freudenberg *Ibid.*, pp. 147–152. Type loc.: Tecamachalco, Puebla, Mexico. Type fig.: Freudenberg, *ibid.*, Taf. XVI, fig. 4.	*Parelephas columbi felicis*
1922	*El.* [*Elephas*] *Columbi* var. *silvestris* Freudenberg *Ibid.*, pp. 152, 153. Type loc.: Ejutla, Oaxaca, Mexico. Type fig.: Freudenberg, *ibid.*, p. 146, fig. 19.	*Archidiskodon imperator silvestris*
1922	*El.* [*Elephas*] *Columbi* var. *Falconeri* Freudenberg *Ibid.*, pp. 153–160. Type loc.: Tequixquiac, Valley of Mexico. Paratype fig.: Freudenberg, *ibid.*, p. 154, fig. 21 (originally figured by Villada, 1903, Ann. Mus. Nac. Mexico, VII, Lám. VIII, as *El. primigenius* Blum.)	*Archidiskodon imperator falconeri*
1922	*El.* [*Elephas*] *Columbi* var. *imperator* Leidy, Freudenberg *Ibid.*, pp. 160–171. Typical example from Spokam Bar, near Helena, Montana. Fig.: Freudenberg, *ibid.*, p. 55, fig. 22.	*Archidiskodon imperator*
1923	*E.* [*Elephas*] *meridionalis* mutation *cromerensis* Depéret and Mayet Ann. Univ. Lyon, Nouv. Ser., I,-Sci., Méd., Fasc. 43, Deuxième Partie, pp. 150, 152, 157. Type loc.: Kessingland, Suffolk, England. Type fig.: Depéret and Mayet, *ibid.*, Pl. IX, fig. 1.	*Archidiskodon meridionalis cromerensis*
1923	*E.* [*Elephas*] *primigenius* mutation *astensis* Depéret and Mayet *Ibid.*, pp. 183, 184. Type loc.: San Paolo de Villafranca, northern Italy. Type fig.: Depéret and Mayet, *ibid.*, Pl. XI, fig. 5 (original in Musée du Palais Carignan, Turin). Paratype fig.: *Ibid.*, Pl. XI, fig. 6 (original in Mus. Géol., Turin); figured by Zuffardi, 1913, Palæont. ital., XIX, Tav. VI [XII], fig. 2a, and Tav. V [XI] fig. 8a, as *Elephas primigenius* Blum var. *trogontherii* Pohl.	*Mammonteus primigenius astensis*

Year	**Name Author**	**Reference in Present Memoir**
1923	*Mœritherium ancestrale* Petronievics Ann. Mag. Nat. Hist., (9), XII, p. 57. Type loc.: Fayûm, Egypt. Type fig.: Petronievics, *ibid.*, p. 56, fig. 1.	*Mœritherium ancestrale*
1923	*Anancus brazosius* Hay Pan-Amer. Geol., XXXIX, pp. 112–114. Type loc.: Brazos River, near San Felipe, Texas. Type fig.: Hay, *ibid.*, Pl. viii, figs. 1, 2.	*Trilophodon* (*?Tetralophodon*) *brazosius*
1923	*Serridentinus simplicidens* Osborn Amer. Mus. Novitates, No. 99, p. 2. Type loc.: Near Pierce, Polk County, Florida. Type fig.: Figure 231 of the present Memoir.	*Trilophodon simplicidens*
1923	*Trilophodon progressus* Osborn *Ibid.*, p. 3. Type loc.: Driftwood Creek, Hitchcock County, Nebraska. Type fig.: Cope, 1889, Amer. Naturalist, XXIII, p. 202, Pl. xi, first as *Tetrabelodon angustidens proavus*, then as *Tetrabelodon proavus* (see Figs. 360 and 361 of the present Memoir; also p. 403, text).	*Serridentinus progressus*
1923	*Tetralophodon precampester* Osborn *Loc. cit.* Type loc.: Harlan County, Nebraska. Type figs.: Figures 308E, 329E, and 339 of the present Memoir.	*Morrillia barbouri*
1923	*Rhynchotherium rectidens* Osborn *Loc. cit.* Type loc.: Eight miles west of Pawnee Buttes, Weld County, Colorado. Type figs.: Figures 461 and 481 of the present Memoir.	*Rhynchotherium rectidens*
1923	*Rhynchotherium falconeri* Osborn *Ibid.*, pp. 3, 4. Type loc.: Mt. Blanco, Llano Estacado, Texas. Type fig.: Figure 468 of present Memoir (originally figured as "*Tetrabelodon shepardii* Leidy" by Cope, 1893, 4th Ann. Rept. Geol. Surv. Texas, Pl. xv).	*Rhynchotherium falconeri*
1923	*Elephas washingtonii* Osborn *Ibid.*, p. 4. Type loc.: Pine Creek, Whitman County, Washington. Type figs.: Figures 972, 975, 893, B, B1, of the present Memoir.	*Parelephas washingtonii*
1924	*Harpagonotherium canadense* Fischer de Waldheim (In Sherborn, "Index Animalium," 1924, Pt. V, p. 1022.) Probably same as *Harpagmotherium canadense* Fischer, 1808, above, this list.	
1924	*Serridentinus mongoliensis* Osborn Amer. Mus. Novitates, No. 148, pp. 1–3. Type loc.: Loh, near camp, Mongolia. Type fig.: Osborn, *ibid.*, p. 2, fig. 1.	*Serridentinus mongoliensis*
1924	*Elephas antiquus rumanus* S. Stefănescu Compt. Rend. Acad. Sci. (Paris), CLXXIX, p. 1418. Type loc.: Tulucesti (Covurlui), Rumania. Type fig.: Athanasiu, 1912 [1915], Annuar. Inst. Geol. Românie i, VI, Pl. xvii, fig. 4 (as *Elephas* cfr. *meridionalis*). Refigured by Stefănescu, 1927, "30 Notes sur l'Organisation des Molaires et sur la Phylogénie des Éléphants et des Mastodontes" (see Fig. 857 of the present Memoir).	*Archidiskodon planifrons rumanus*
1924	*Elephas antiquus germanicus* S. Stefănescu *Loc. cit.* Type loc.: Tanganu (Ilfov), Rumania. Type figs.: Stefănescu, 1927, *op. cit.*, Figs. A, B (see Fig. 1089 of the present Memoir).	*Hesperoloxodon antiquus germanicus*
1924	*Elephas namadicus naumanni* Makiyama Chikyû—The Globe, I, p. 381 (in Japanese; *fide* Matsumoto, original not available to present author); 1924, Mem. College Sci. Kyôto Imp. Univ., (B), I, No. 2, pp. 255–264 (in English). Type loc.: Sahamma, Tôtômi Province, Japan. Type figs.: Makiyama, Chikyû, I, Pl. viii; Mem. College Sci. Kyôto Imp. Univ., (B), I, Pls. xii–xv, and xvi, fig. 1. The following is an excerpt from Dr. Makiyama's article on "Japonic Proboscidea," Mem. Coll. Sci. Kyôto Imp. Univ., Ser. B, Vol. XIV, No. 1, Art. 1, p. 40, giving certain of the results of his recent studies (May, 1938): "This is the most common fossil elephant in Japan. The name of subspecies was given to the stenocoronine form [which] came from Sahanma near Hamamatu in Sizuoka-ken (Tôtômi) covering the Naumann's *E. namadicus* from Yokosuka as it be different from the type *E. namadicus* Falconer & Cautley, 1846 which is eurycoronine. After that time, I have had a number of chances to make interesting observation about the different forms of teeth, and now I have a thought that all the Japonic forms are equally separated from the Indian *E. namadicus*. The names listed are the synonyms: *E. namadicus namadi* Pohlig, 1893 of Makiyama, 1924 *Parelephas protomammonteus* Matsumoto, 1924 *Loxodonta* (*Palaeoloxodon*) *namadica yabei* Matsumoto, 1929 *Elephas* (*Palaeoloxodon*) *namadicus setoensis* Makiyama, 1929 *E. indicus buski* Matsumoto, 1929 *Euelephas trogontherii* of Matsumoto, 1924, and Makiyama, 1924 *Palaeoloxodon yokohamanus* Tokunaga, 1934)" Also see note below under "1929 *Elephas* (*Palæoloxodon*) *namadicus setoensis* Makiyama."	*Palæoloxodon namadicus naumanni*

Year	Name	Author	Reference in Present Memoir
1924	*Elephas namadicus namadi*	Makiyama Chikyu, I, p. 381 (in Japanese); Mem. College Sci. Kyôto Imp. Univ., (B), I, No. 2, pp. 263, 264 (in English). Type loc.: Dredged off island of Shôdo, Sanuki Province, Japan. Type figs.: Makiyama, Chikyû, I, Pl. VIII; Mem. College Sci. Kyôto Imp. Univ., (B), I, Pl. XVI, fig. 2. See note above under "1924 *Elephas namadicus naumanni*," also note below under "1929 *Elephas (Palæoloxodon) namadicus setoensis* Makiyama."	
1924	*Euelephas protomammonteus*	Matsumoto Journ. Geol. Soc. Tokyo, XXXI, p. 262 (in Japanese); 1926, Sci. Rept. Tôhoku Imp. Univ., (2), Geol., X, No. 2, pp. 43–50 (in English). Type loc.: Nagahama, Town of Minato, Kimitsu District, Province of Kazusa, Japan. Type figs.: Matsumoto, 1926, *ibid.*, Pl. XVIII, figs. 1, 2 (as *Parelephas protomammonteus*); Pl. XIX, figs. 1–3 (the paratype, from same locality as type). See note above, 1924, under *Elephas namadicus naumanni* Makiyama.	*Palæoloxodon protomammonteus*
1924	*Loxodonta (Palæoloxodon) tokunagai*	Mastumoto *Ibid.*, p. 267 (in Japanese); 1929, Sci. Rept. Tôhoku Imp. Univ., (2), Geol., XIII, No. 1, pp. 7–11 (in English). Type loc.: Soyama, Gokayama, Hira-mura Higashi-Tonami Dist., Province of Etchû, Japan. Type figure not found by present author. Referred to *Archidiskodon tokunagai* by Teilhard de Chardin and Trassaert in 1937 (Pal. Sin, (C), XIII, Fasc. 1, p. 44).	*Palæoloxodon tokunagai*
1924	*Stegodon orientalis shodoënsis*	Matsumoto *Ibid.*, pp. 333–335 (in Japanese). Type loc.: Island of Mitsugo (Mitsugo-Shima) and island of Shôdo, Inland Sea, Japan. Type fig.: See Makiyama, 1938, Mem. Coll. Sci. Kyoto Imp. Univ., (B), XIV, No. 1, p. 18, fig. 7 (holotype palate).	*Stegodon orientalis shodoënsis*
1924	*Hemimastodon annectens*	Matsumoto *Ibid.*, pp. 401, 405 (in Japanese). Type loc.: Banjobora, Kaminogô-mura, Kani District, Province of Mino, Japan. Type figs.: Matsumoto, 1926, Sci. Rept. Tôhoku Imp. Univ., (2), Geol., X, No. 1, Pls. I, figs. 1 and 2, II, figs. 1–3.	*Serridentinus annectens*
1924	*Trilophodon sendaicus*	Matsumoto *Ibid.*, pp. 402, 408 (in Japanese). Type loc.: Kitayama, near Sendai, Province of Rikuzen, Japan. Type figs.: Matsumoto, 1926, Sci. Rept. Tôhoku Imp. Univ., (2), Geol., X, No. 1, Pls. III and IV.	*Trilophodon sendaicus*
1924	*Elephas africanus moçambicus*	Frade Bull. Soc. Portugaise Sci. nat., IX, Fasc. 3, pp. 131, 133. Hab.: Maputo, Mozambique. Type fig.: Frade, *ibid.*, text fig. 5. Female formerly in the Jardin de Zoologique, Lisbon.	*Loxodonta africana moçambica*
1924	*Loxodonta africana Zukowskyi*	Strand (In Zukowsky, Arch. Naturges., XC, Abth. A, Heft I, p. 68.) Hab.: Kaoko District, southwest Africa. Living form.	*Loxodonta africana zukowskyi*
1924	*Parelephas jeffersonii progressus*	Osborn Amer. Mus. Novitates, No. 152, pp. 1, 4, 7. Type loc.: Zanesville, Muskingum County, Ohio. Type figs.: Osborn, 1922, Amer. Mus. Novitates, No. 41, p. 13, fig. 11, and p. 14, fig. 12 (as paratypes of *Elephas jeffersonii*).	*Parelephas progressus*
1924	*Mammonteus primigenius compressus*	Osborn *Ibid.*, pp. 5–7. Type loc.: Rochester, Indiana. Type figs.: Osborn, 1922, Amer. Mus. Novitates, No. 41, p. 8, fig. 8 (as *Elephas primigenius*); 1924, Amer. Mus. Novitates, No. 152, p. 6, fig. 2. Paratype fig.: Osborn, 1922, Amer. Mus. Novitates, No. 41, p. 7, fig. 7 (from Eschscholtz Bay, Alaska).	*Mammonteus primigenius compressus*
1924	*Stegomastodon texanus*	Osborn Amer. Mus. Novitates, No. 154, p. 3. Type loc.: Blanco formation, Llano Estacado, Texas. Type figs.: Figures 639, 642, 644A, 645D, of the present Memoir.	*Stegomastodon texanus*
1924	*Stegomastodon aftoniæ*	Osborn *Loc. cit.* Type loc.: About two miles east of Akron, Plymouth County, Iowa. Type r.M^3 originally figured as *Mammut mirificum* by Calvin, 1909, Bull. Geol. Soc. Amer., XX, Pl. XXVII; refigured as *Rhabdobunus mirificus* by Hay, 1914, Iowa Geol. Surv., XXIII, Pl. L. Type l.M^3, see figure 650 of the present Memoir.	*Stegomastodon aftoniæ*

Year	Name	Author	Reference in Present Memoir
1924 1926	*Stegomastodon arizonæ* Gidley	(In Osborn, Amer. Mus. Novitates, No. 154, p. 4—from Gidley MS.); Gidley, 1926, U. S. Geol. Surv., Profess. Paper 140–B, p. 86. Type loc.: Curtis Flats, Cochise County, Arizona. Type figs.: Gidley, *ibid.*, Pls. XXXIII–XXXV, Pl. XXXVIII, figs. 1–3, Pl. XXXIX, figs. 1–3.	*Stegomastodon arizonæ*
1924	*Stegomastodon nebrascensis* Osborn	*Ibid.*, p. 5. Type loc.: Snake Creek, Sioux County, western Nebraska. Type fig.: Osborn, *ibid.*, p. 4, fig. 2 B.	*Serridentinus* (*Ocalientinus?*) *nebrascensis*
1925	*Mammonteus primigenius americanus* Osborn	Proc. Amer. Phil. Soc., LXIV, No. 1, p. 33. See *E. americanus* DeKay, 1842, above, from near Rochester, New York.	*Mammonteus primigenius americanus*
1925	*Elephas scotti* Barbour	Neb. State Mus., Bull. 2, I, pp. 21–24. Type loc.: Five miles south of Staplehurst, Seward County, Nebraska. Type figs.: Barbour, *ibid.*, text figs. 7–10. [On page 1025, of the present Memoir, appears the following statement by Professor Osborn: "Awaiting further evidence, Osborn is inclined to regard the type of '*Elephas scotti*' as representing a young individual of *Archidiskodon imperator*." Nevertheless he treated this species under the heading *Archidiskodon imperator scotti*.]	*Archidiskodon imperator scotti*
1925	*Tetrabelodon abeli* Barbour	Neb. State Mus., Bull. 9, I, pp. 91–94. Type loc.: Devil's Gulch, Brown County, Nebraska. Type figs.: Barbour, *ibid.*, pp. 92, 93, figs. 52–56.	*Trilophodon abeli*
1925	*Elephas maibeni* Barbour	Neb. State Mus., Bull. 10, I, pp. 95–118. Type loc.: About sixteen miles north of Curtis, Lincoln County, Nebraska. Type figs.: Barbour, *ibid.*, text figs. 58–60, 63–70, 72, 74, 76–87. In 1926 described by Barbour as *Archidiskodon maibeni*.	*Archidiskodon imperator maibeni*
1926	*Archidiskodon maibeni* Barbour	Neb. State Mus. Bull. 11, I. See *Elephas maibeni* Barbour, 1925, preceding item.	
1926	*Mammut francisi* Hay	Journ. Wash. Acad. Sci., XVI, No. 2, pp. 35–39. Type loc.: Brazos River, Pittbridge, Burleson County, Texas. Type figs.: Hay, *ibid.*, p. 36, fig. 3; p. 37, fig. 4.	?*Rhynchotherium francisi*
1926	*Mammut oregonense* Hay	*Ibid.*, pp. 39, 40. Type loc.: Rye Valley, Dixie Creek, Baker County, Oregon. Type figs.: Hay, *ibid.*, p. 36, figs. 1, 2.	*Mastodon oregonensis*
1926	*Mastodon americanus plicatus* Osborn	Amer. Mus. Novitates, No. 238, p. 1. Type loc.: Walnut, Bureau County, Illinois. Type fig.: Osborn, *ibid.*, p. 2, fig. 1.	*Mastodon americanus plicatus*
1926	*Zygolophodon pyrenaicus aurelianensis* Osborn	*Ibid.*, p. 2. Hab.: Chevilly(?), Cassegrain, Avaray, France. No type figure available to the present author.	*Zygolophodon pyrenaicus aurelianensis*
1926	*Turicius turicensis simorrensis* Osborn	*Ibid.*, pp. 3, 4. Type loc.: Near Simorre (Gers), France. Type figs.: Lartet, 1859, Bull. Soc. géol. France, (2), XVI, Pl. XV, fig. 3 (as *Mastodon tapiroides*); Osborn, 1926, *ibid*, p. 4, fig. 2.	*Turicius turicensis simorrensis*
1926	*Serridentinus browni* Osborn	*Ibid.*, p. 4. Type loc.: Near Chinji Bungalow, India. Type figs.: Osborn, *ibid.*, p. 5, fig. 3; p. 6, fig. 4.	*Serridentinus browni*
1926	*Serridentinus republicanus* Osborn	*Ibid.*, p. 6. Type loc.: Republican River formation, northwestern Kansas. Type figs.: Osborn, *ibid.*, p. 7, fig. 5; p. 8, fig. 6.	*Ocalientinus* (*Serridentinus*) *republicanus*
1926	*Serridentinus obliquidens* Osborn	*Ibid.*, p. 9. Type loc.: Phosphate beds near Charleston, South Carolina. Type fig.: Osborn, *ibid.*, p. 9, fig. 7.	*Ocalientinus* (*Serridentinus*) *obliquidens*
1926	*Serridentinus anguirivalis* Osborn	*Ibid.*, p. 10. Type loc.: South-central Sioux County, western Nebraska. Type fig.: Osborn, *ibid.*, p. 10, fig. 8.	*Serridentinus anguirivalis*
1926	*Serridentinus brewsterensis* Osborn	*Ibid.*, p. 11. Type loc.: Brewster, Polk County, Florida. Type fig.: Osborn, *ibid.*, p. 11, fig. 9.	*Serridentinus brewsterensis*

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1926	*Serridentinus guatemalensis*	Osborn	*Ibid.*, p. 12. Type loc.: Chinautla, Guatemala, Central America. Type fig.: Osborn, *ibid.*, p. 12, fig. 10.	*Serridentinus guatemalensis*
1926	*Rhynchotherium anguirivalis*	Osborn	*Ibid.*, p. 13. Type loc.: Sioux County, western Nebraska, Quarry 3 (Olcott Hill). Type fig.: Osborn, *ibid.*, p. 13, fig. 11.	*Rhynchotherium anguirivale*
1926	*Anancus falconeri*	Osborn	*Ibid.*, pp. 13, 14. Type loc.: Red or Norwich Crag of Suffolk, England. Type fig.: Originally described and figured by Falconer as *Mastodon* (*Tetralophodon*) *arvernensis* (1857, Quart. Journ. Geol. Soc. London, XIII, Pl. XII, figs. 3, 4; 1868, "Palaeont. Mem.," II, Pl. IV, figs. 3, 4). Osborn, *ibid.*, p. 14, fig. 12.	*Anancus falconeri*
1926	*Parelephas protomammonteus* (Matsumoto) *typicus*	Matsumoto	Sci. Rept. Tôhoku Imp. Univ., (2), Geol., X, No. 2, pp. 43–48. Originally named *Euelephas protomammonteus* by Matsumoto in 1924, p. 262 (published in Japanese). See above, this list. [According to Shikama (1937, p. 164) this species is synonymous with the species *antiquus*.—Colbert-Simpson, letter, July 12, 1939.—Editor.]	*Palæoloxodon protomammonteus*
1926	*Parelephas protomammonteus proximus*, mut. nov.	Matsumoto	*Ibid.*, pp. 48–50. Type loc.: Isone, Kokubo, Onuki-mura, Kimitsu District, Province of Kazusa, Japan. Type fig.: Matsumoto, *ibid.*, Pl. XXIV, figs. 1, 2. [If *protomammonteus*, according to Shikama, is a synonym of *antiquus* (see preceding note under *Parelephas protomammonteus typicus* Masumoto), then Shikama was justified in emending the name of Matsumoto's second species to read *Parelephas proximus proximus*.—Colbert-Simpson, letter, July 12, 1939.—Editor.]	*Palæoloxodon protomammonteus proximus*
1926	*Elephas eellsi*	Hay	Journ. Wash. Acad. Sci., XVI, No. 6, pp. 154–159. Type loc.: Port Williams, Clallam County, Washington. Type figs.: Hay, *ibid.*, p. 156, figs. 1, 2.	*Parelephas*(?) *eellsi*
1926	*Anancus orarius*	Hay	Proc. U. S. Nat. Mus., LXVIII (1927), No. 2625, Art. XXIV, pp. 8–14. Type loc.: West bank of Aransas River, San Patricio County, near town of Sinton, Texas. Type figs.: Hay, *ibid.*, Pl. II, fig. 1; Pl. III, fig. 1; Pl. IV, fig. 1; Pl. V, figs. 1–3.	*Cordillerion orarius*
1926	*Anancus defloccatus*	Hay	*Ibid.*, pp. 14–16, 18. Type loc.: West bank of Aransas River, San Patricio County, near town of Sinton, Texas. Type figs.: Hay, *ibid.*, Pl. VII, and Pl. VIII, fig. 1.	*Cordillerion defloccatus*
1926	*Anancus bensonensis*	Gidley	U. S. Geol. Surv., Profess. Paper 140-B, pp. 85, 86. Type loc.: Near Benson, Cochise County, west side of San Pedro Valley, Arizona. Type fig.: Gidley, *ibid.*, Pl. XXXII.	*Cordillerion bensonensis*
1926	*Trilophodon* (*Serridentinus*) *pojoaquensis*	Frick	Bull. Amer. Mus. Nat. Hist., LVI, Art. II, pp. 125, 142–150, 161, 162–165. Type loc.: About twenty-four miles north of Santa Fé, Santa Fé County, near Pojuaque, New Mexico. Type figs.: Frick, *ibid.*, p. 148, fig. 26, and p. 144, fig. 22A. Amer. Mus. 21115 (type skull). The skull (F.: A. M. 21125), originally considered by Frick as a paratype of *Trilophodon* (*Serridentinus*) *pojoaquensis*, proved on subsequent examination to be referable to his new genus and species *Ocalientinus ojocaliensis*.	*Trilophodon pojoaquensis*
1926	?*Trilophodon* (*Serridentinus*) *leidii*	Frick	*Ibid.*, pp. 137, 140, 141, 155, 169. Type loc.: Alachua clays, Mixson's bone bed, near Williston, Levy County, Florida. Type figs.: Leidy and Lucas, 1896, Trans. Wagner Free Inst. Sci., IV, Pl. IV, figs. 9–11; Frick, 1926, *ibid.*, figs. 20A,B.	*Ocalientinus* (*Serridentinus*) *floridanus leidii*
1926	?*Rhynchotherium* (*Dibelodon*) *edensis*	Frick	*Ibid.*, pp. 169–176. See note under *Trilophodon* (*Tetrabelodon*) *shepardi edensis* Frick, 1921, above, this list.	*Rhynchotherium shepardi edense*
1927	*E.* [*Elephas*] *primigenius Matsumotoi*	Dietrich	Neues Jahrb. Min., I, Abth. B, Referate, p. 314. [The specimen considered as the type of *Elephas primigenius matsumotoi* by Dietrich, 1927, is regarded by Shikama (1937, pp. 164, 165) as belonging to *Parelephas proximus* (see above, this list, under *Parelephas protomammonteus proximus* mut. nov. Matsumoto, 1926); therefore the former of these names becomes a synonym of the latter.—Colbert-Simpson, letter, July 12, 1939.—Editor.]	[Not determined by the present author]

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1927	*Amebelodon fricki* Barbour Neb. State Mus., Bull. 13, I, pp. 131–134. Type loc.: Freedom, Frontier County, Nebraska. Type figs.: Barbour, *ibid.*, text figs. 89–91.	*Amebelodon fricki*
1927	*Archidiskodon transvaalensis* Dart Supplement, Nature, No. 3032, pp. 41–48. Type loc.: Near Bloemhof, South Africa. Type figs.: Dart, *ibid.*, p. 47, fig. 6 (right); p. 48, fig. 7 (left).	*Palæoloxodon transvaalensis*
1927	*Archidiskodon Sheppardi* Dart *Loc. cit.*. Type loc.: Near Bloemhof, South Africa. Type figs.: Dart, *ibid.*, p. 47, fig. 6 (left); p. 48, fig. 7 (right).	*Palæoloxodon sheppardi*
1927	*Elephas indicus Buski* Matsumoto Sci. Rept. Tôhoku Imp. Univ., (2), Geol., X, No. 3, pp. 57, 58. Type loc.: Ninohe District, Province of Mutsu, Japan. Type fig.: Matsumoto, *ibid.*, Pl. xxvii, figs. 2, 3.	?*Palæoloxodon buski*
1927	*Leith-Adamsia siwalikiensis* Matsumoto Japanese Journ. Geol. and Geog., V, No. 4, Art. XII. Type loc.: India. Type figs.: Falconer and Cautley, 1845, "Fauna Antiqua Sivalensis," Pl. xi, fig. 4; 1847, Pl. xiv, fig. 8 (as *Elephas planifrons*).	*Archidiskodon planifrons*
1928	*Elephas primigenius* Blumenbach var. n. *pachyganalis* Schroeder Jahrb. preuss. geol. Landesanstalt, XLVIII, pp. 701, 702, 718. Type loc.: Rixdorf, Germany. Type fig.: Schroeder, *ibid.*, Taf. xxxvi, figs. 1a, 1b.	[Not determined by the present author]
1928	*Trilophodon* (*Serridentinus?*) *inopinatus* Borissiak and Belĭaeva Bull. Acad. Sci. U. S. S. R., Cl. Sci., Phys.-Math., pp. 241–252. Type loc.: Jilančik beds of the Turgai region, U. S. S. R. Type figs.: Borissiak and Belĭaeva, *ibid.*, Pls. i, ii.	*Trilophodon inopinatus*
1928	*Archidiskodon subplanifrons* Osborn Nature, CXXI, No. 3052, pp. 672, 673. Type loc.: Sydney-on-Vaal, Vaal River, South Africa. Type fig.: Osborn, *ibid.*, p. 672, fig. 1.	*Archidiskodon subplanifrons*
1928	*Archidiskodon broomi* Osborn *Ibid.*, pp. 672, 673. Type loc.: The Bend, Vaal River, near Kimberley, South Africa. Type fig.: Osborn, *ibid.*, p. 672, fig. 2.	*Archidiskodon broomi*
1928	*Elephas exilis* Stock and Furlong Science, N. S., LXVIII, No. 1754, p. 140. Type loc.: Santa Rosa Island, California. Type fig.: Stock, 1935, Sci. Monthly, XLI, September, p. 210, fig. 6 (see also Figs. 920 and 921 of the present Memoir).	*Archidiskodon exilis*
1928	*Elephas haroldcooki* Hay Proc. Colo. Mus. Nat. Hist., VIII, No. 2, Pt. I, p. 33. Type loc.: Frederick, Oklahoma. Type figs.: Hay and Cook, 1930, *ibid.*, IX, No. 2, Pl. iii, fig. 1, Pl. v, fig. 1, Pls. xiii and xiv.	*Archidiskodon haroldcooki*
1928	*Trilophodon phippsi* Cook Proc. Colo. Mus. Nat. Hist., VIII, No. 4, pp. 37–43. Type loc.: Near Ainsworth, Brown County, Nebraska. Type figs.: Cook, *ibid.*, Pls. i–iii. [In a footnote on page 329 of Volume I of the present Memoir *Trilophodon phippsi* is included among the species referable to *Megabelodon*, the "Spoonbill Mastodonts." While on page 707 Professor Osborn mentions *Megabelodon lulli*, *M. cruziensis*, and *M. joraki*, we fail to find anywhere the use of the term *Megabelodon phippsi*. However, it was evidently his intention to assign *phippsi* to *Megabelodon* because of its tuskless mandible, the distinctive character of this genus. Therefore on page 738 it has been listed under *Megabelodon* with the three above-mentioned species.—Editor.]	*Megabelodon phippsi*
1928	*Serridentinus fricki* Peterson Mem. Carnegie Mus., XI, No. 2, pp. 111–121. Type loc.: Northern flanks of Douglas Mountain on Weller Ranch, Moffat County, Colorado. Type figs.: Peterson, *ibid.*, Pls. xi–xiv, and text figs. 21, 22; also restoration by A. Avinoff (Pl. xv).	*Trilophodon fricki*
1928	*Loxodonta africana angolensis* Frade "Títulos e trabalhos cientificos (Curriculum vitae)," p. 15. Type loc.: Region of Cunene, southern Angola, Africa. Living form.	*Loxodonta africana angolensis*
1928	*Mastodon andium Kraglievichii* Berro "Un nuevo Mastodon en la R. O. del Uruguay." *Fide* Cabrera, 1929, Rev. Mus. La Plata, XXXII, pp. 119, 141; not seen by the present author.	*Cordillerion andium kraglievichii*
1928	Mastodonte de Alangasi. See "1931 *Bunolophodon postremus* Spillmann," below, this list.	

Year	Name	Author	Reference in Present Memoir
1928	*Platybelodon Danovi*	Borissiak Ann. Soc. Paléont. Russie, VII, pp. 105–120. Type loc.: Kuban region, North Caucasus, Russia. Type fig.: Borissiak, *ibid.*, Taf. VIII, figs. 1–4.	*Platybelodon danovi*
1928 1931	*Tetrabelodon* (*Bunolophodon*) *Ayora*	Spillmann El Ecuador Comercial, Año VI, No. 57. Type loc.: Quebrada [canyon] of Chalang, near Punin, southeast of Riobamba, Province of Chimborazo, Ecuador. Type fig.: Spillmann, *ibid.*, fig. 2 (see also figures 548 and 549 of the present Memoir). Supplementary description: Spillmann, 1931, "Die Säugetiere Ecuadors im Wandel der Zeit," Erster Teil, p. 67.	*Cuvieronius ayoræ*
1929	*Elephas* (*Palæoloxodon*) *namadicus setoensis*	Makiyama Chikyû—The Globe, XII, No. 5, pp. 364, 365 (in Japanese). Type loc.: Seto, Japan. [Dr. Jirô Makiyama in a letter to the editor, dated Kyoto, August 26, 1937, stated that the name *Elephas* (*Palæoloxodon*) *namadicus setoensis* Makiyama appears on page 365 of his article of 1929 in Chikyû, without diagnosis or figure, but by "designation points, as an example, to the specimen given in his paper 'Notes on Fossil Elephant from Sahamma, Tôtômi' (Mem. Coll. Sci. Kyoto Imp. Univ., Ser. B, Vol. I, No. 2, 1924, pp. 263, 264, Pl. XVI, fig. 2, as *Elephas namadicus namadi*)." This was an outline in English of the note subsequently given by him in Japanese in the publication Chikyû—The Globe, XII, No. 5, pp. 364, 365, November, 1929, with the translated title "Scientific Names of Fossils and the International Rules of Zoological Nomenclature," pp. 358–366. Doctor Makiyama further stated that during the intervening years he had changed his opinion somewhat and that he hoped to publish the results of his studies in the near future. This article has since appeared under the title "Japonic Proboscidea," Mus. Coll. Sci. Kyôto Imp. Univ., Ser. B, Vol. XIV, No. 1, Art. 1, May, 1938.—Editor.]	[Not determined by the present author]
1929 1931	*Amebelodon grangeri*	Osborn Nat. Hist., XXIX, No. 1, pp. 12–16. Type loc.: Tairum Nor Basin, Mongolia. Type fig.: Osborn, *ibid.*, p. 15 (plate). Supplementary description: Osborn and Granger, 1931, Amer. Mus. Novitates, No. 470, pp. 6, 7, text figs. 1 and 3A, A1. Transferred to genus *Platybelodon*, owing to fundamental differences in the structure of the tusks, e. g., the presence of dentinal rod-cones in *Platybelodon* (characteristic of *grangeri*), but which are absent in *Amebelodon*.	*Platybelodon grangeri*
1929	*Torynobelodon loomisi*	Barbour Neb. State Mus., Bull. 16, I, pp. 147–150. Type loc.: Sand Canyon, two and a half miles southwest of Republican City, Harlan County, Nebraska. Type figs.: Barbour, *ibid.*, text figs. 98–100.	*Torynobelodon loomisi*
1929	*Trilophodon angustidens gaillardi*	Osborn Amer. Mus. Novitates, No. 393, p. 1. Type loc.: Villefranche d'Astarac (Gers), France. Type fig.: Osborn, *ibid.*, p. 1, fig. 1.	*Trilophodon angustidens gaillardi*
1929	*Serridentinus bifoliatus*	Osborn *Ibid.*, p. 2. Type loc.: Brewster, Polk County, Florida. Type fig.: Osborn, *ibid.*, p. 2, fig. 2.	*Ocalientinus* (*Serridentinus*) *bifoliatus*
1929	*Serridentinus hasnotensis*	Osborn *Loc. cit.* Type loc.: Near Hasnot, India. Cotype figs.: Osborn, *ibid.*, p. 3, fig. 3.	*Serridentinus hasnotensis*
1929	*Serridentinus metachinjiensis*	Osborn *Ibid.*, pp. 4, 5. Type loc.: One mile northwest of Chinji Bungalow, India. Type fig.: Osborn, *ibid.*, p. 3, fig. 4.	*Serridentinus metachinjiensis*
1929	*Serridentinus chinjiensis*	Osborn *Ibid.*, p. 5. Type loc.: One mile and a half west of Chinji Bungalow, India. Type fig.: Osborn, *ibid.*, p. 4, fig. 5.	*Serridentinus chinjiensis*
1929	*Serridentinus prochinjiensis*	Osborn *Ibid.*, p. 6. Type loc.: Two miles west of Chinji Bungalow, India. Type fig.: Osborn, *ibid.*, p. 5, fig. 6.	*Serridentinus prochinjiensis*
1929	*Serridentinus florescens*	Osborn *Ibid.*, p. 6. Type loc.: Kholobolchi Nor region, Mongolia, five to eight miles north of camp. Type fig.: Osborn, *ibid.*, p. 7, fig. 7.	*Ocalientinus* (*Serridentinus*) *florescens*
1929	*Rhynchotherium paredensis*	Osborn *Ibid.*, pp. 6–8. Type loc.: Mt. Eden Hot Springs, San Bernardino County, California. Type fig.: Osborn, *ibid.*, p. 7, fig. 8. Originally figured by Frick, 1926, Bull. Amer. Mus. Nat. Hist., LVI, Art. II, figs. 2, 8, 9 as (?)*Rhynchotherium* (*Dibelodon*) *edensis*. In the present Memoir (Vol. I, p. 496, also fig. 474) *R. paredensis* is regarded as a synonym of *R. shepardi edense*.	*Rhynchotherium shepardi edense*

Year	Name	Author	Reference in Present Memoir
1929	*Rhynchotherium chinjiensis*	Osborn *Ibid.*, p. 8. Type loc.: Two miles west of Chinji Bungalow, India. Type fig.: Osborn, *ibid.*, p. 8, fig. 9.	*Rhynchotherium chinjiense*
1929	*Synconolophus dhokpathanensis*	Osborn *Ibid.*, pp. 10–12. Type loc.: Three miles west of Dhok Pathan, India. Type fig.: Osborn, *ibid.*, p. 9, fig. 10.	*Synconolophus dhokpathanensis*
1929	*Synconolophus ptychodus*	Osborn *Ibid.*, p. 12. Type loc.: Four miles west of Chinji Bungalow, India. Type fig.: Osborn, *ibid.*, p. 11, fig. 12.	*Synconolophus ptychodus*
1929	*Synconolophus propathanensis*	Osborn *Ibid.*, pp. 12, 13. Type loc.: Three miles east of Dhok Pathan, India. Type fig.: Osborn, *ibid.*, p. 13, fig. 13.	*Synconolophus propathanensis*
1929	*Stegolophodon nathotensis*	Osborn *Ibid.*, pp. 13–15. Type loc.: Near Nathot, India. Type fig.: Osborn, *ibid.*, p. 14, fig. 14.	*Stegolophodon nathotensis*
1929	*Stegolophodon cautleyi progressus*	Osborn *Ibid.*, p. 15. Type loc.: Twelve miles east of Chinji Bungalow, India. Type fig.: Osborn, *ibid.*, p. 14, fig. 15.	*Stegolophodon cautleyi progressus*
1929	*Stegodon insignis birmanicus*	Osborn *Ibid.*, pp. 15, 16. Type loc.: Mingoon, opposite Mandalay, Burma. Type fig.: Osborn, *ibid.*, p. 16, fig. 16.	*Stegodon insignis birmanicus*
1929	*Stegodon orientalis grangeri*	Osborn *Ibid.*, pp. 16, 17. Type loc.: Yenchingkou, near Wanhsien, Province of Szechuan, China. Type fig.: Osborn, *ibid.*, p. 16, fig. 16.	*Stegodon orientalis grangeri*
1929	*Stegodon pinjorensis*	Osborn *Ibid.*, p. 18. Type loc.: Three miles north of Siswan, India. Type fig.: Osborn, *ibid.*, p. 17, fig. 17.	*Stegodon pinjorensis*
1929	*Archidiskodon sonoriensis*	Osborn *Ibid.*, p. 18. Type loc.: One mile east of Arizpe, northern Sonora, Mexico, on the Sonora River. Type fig.: Osborn, *ibid.*, p. 18, fig. 18.	*Archidiskodon sonoriensis*
1929	*Parelephas floridanus*	Osborn *Ibid.*, p. 20. Type loc.: Manatee County, Florida, two miles south of Bradenton. Type fig.: Osborn, *ibid.*, p. 19, fig. 19.	*Parelephas floridanus*
1929	*Parelephas columbi cayennensis*	Osborn *Ibid.*, pp. 20, 21. Type loc.: Cayenne, French Guiana, South America. Type fig.: Osborn, *ibid.*, p. 21, fig. 20.	*Parelephas columbi cayennensis*
1929	*Elephas platycephalus*	Osborn *Ibid.*, pp. 21, 22. Type loc.: Near Siswan, bed of Amilee Creek, Simla Hills, India. Type fig.: Osborn, *ibid.*, p. 22, fig. 21.	*Platelephas platycephalus*
1929	*Elephas platycephalus angustidens*	Osborn *Ibid.*, pp. 22, 23. Type loc.: Three miles west of Chandigarh, Siwalik Hills, India. Type fig.: Osborn, *ibid.*, p. 23, fig. 22.	*Hypselephas hysudricus*
1929	*Loxodonta (Palæoloxodon) namadica (Yabei)*	Matsumoto Sci. Rept. Tôhoku Imp. Univ., (2), Geol., XIII, No. 1, pp. 4, 5. Type loc.: Inland Sea, Japan. Type figs.: Matsumoto, *ibid.*, Pl. III, fig. 2, Pl. IV.	*Palæoloxodon namadicus yabei*
1929	*Lox. (Pal.) Tokunagai junior*, mut. nov.,	Matsumoto *Ibid.*, p. 10. Type loc.: Japan, precise locality unknown. Type fig.: Matsumoto, *ibid.*, Pl. VII, figs. 1, 2.	*Palæoloxodon (?Archidiskodon) tokunagai* mut. *junior*
1929	*Notiomastodon ornatus*	Cabrera Rev. Mus. La Plata, XXXII, p. 91. Type loc.: Monte Hermoso, Province of Buenos Aires, Argentina. Type figs.: Cabrera, *ibid.*, p. 91, fig. 2; p. 93, fig. 4.	*Notiomastodon ornatus*
1929	*Archidiskodon vanalpheni*	Dart So. Afr. Journ. Sci., XXVI, p. 704. Type loc.: Sydney-on-Vaal, South Africa. Type figs.: Dart, *ibid.*, p. 704, figs. 8, 9.	*Archidiskodon vanalpheni*
1929	*Archidiskodon milletti*	Dart *Ibid.*, pp. 706–708. Type loc.: Sydney-on-Vaal, South Africa. Type figs.: Dart, *ibid.*, p. 706, figs. 10, 11.	*Archidiskodon milletti*
1929	*Archidiskodon loxodontoides*	Dart *Ibid.*, pp. 709–711. Type loc.: Sydney-on-Vaal, South Africa. Type fig.: Dart. *ibid.*, p. 709, fig. 13.	*Archidiskodon loxodontoides*

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1929	*Archidiskodon andrewsi*	Dart *Ibid.*, pp. 711–713. Type loc.: Gong-Gong, Vaal River, South Africa. Type fig.: Dart, *ibid.*, p. 711, fig. 14.	*Palæoloxodon*(?) *andrewsi*
1929	*Archidiskodon hanekomi*	Dart *Ibid.*, pp. 713–715. Type loc.: Delport's Hope, Vaal River, South Africa. Type figs.: Dart, *ibid.*, p. 713, figs. 15, 16.	*Palæoloxodon hanekomi*
1929	*Archidiskodon yorki*	Dart *Ibid.*, pp. 715, 717. Type loc.: Vanasswegenshoek—Bloemheuvel, near Christiana, South Africa. Type fig.: Dart, *ibid.*, p. 717, fig. 19.	*Archidiskodon yorki*
1929	*Pilgrimia yorki*	Dart *Ibid.*, pp. 719, 720. Type loc.: Below Christiana, Vaal River, South Africa. Type figs.: Dart, *ibid.*, p. 719, figs. 20, 21.	*Palæoloxodon yorki*
1929	*Pilgrimia wilmani*	Dart *Ibid.*, pp. 720–722. Type loc.: Below Christiana, Vaal River, South Africa. Type fig.: Dart, *ibid.*, p. 721, fig. 22.	*Palæoloxodon wilmani*
1929	*Pilgrimia kuhni*	Dart *Ibid.*, pp. 723, 724. Type loc.: Pniel Estate, South Africa. Type fig.: Dart, *ibid.*, p. 725, fig. 24.	*Palæoloxodon kuhni*
1929	*Loxodonta prima*	Dart *Ibid.*, pp. 724–726. Type loc.: Pilandsberg, Transvaal, South Africa. Type figs.: Dart, *ibid.*, p. 725, figs. 25, 26.	*Loxodonta prima*
1929	*Loxodonta africana* var. *obliqua*	Dart *Ibid.*, pp. 726–728. Type loc.: Valley of Steelport River, tributary of Oliphants River, northeast Transvaal, South Africa. Type figs.: Dart, *ibid.*, p. 726, figs. 27, 28.	*Loxodonta africana* var. *obliqua*
1930	*Gomphotherium*? *emmonsi*	Hay "Second Bib. and Cat. of Fossil Vertebrata of North America," II, p. 636. Type loc.: Halifax County, North Carolina. Type figs.: Emmons, 1858, "Rept. North-Carolina Geol. Surv.," p. 199, fig. 23; Emmons, 1860, "Manual of Geology," p. 218, fig. 186.	*Ocalientinus emmonsi*
1930	*Gomphotherium serpentirivale*	Hay *Op. cit.*, p. 639.	NOMEN NUDUM
1930	*Amebelodon sinclairi*	Barbour Neb. State Mus., Bull. 17, I, pp. 155–158. Type loc.: Freedom, Frontier County, Nebraska. Type fig.: Barbour, *ibid.*, fig. 101.	*Amebelodon sinclairi*
1930	*Pliomastodon sellardsi*	Simpson Bull. Amer. Mus. Nat. Hist., LIX, Art. III, pp. 203–206. Type loc.: Brewster, Florida. Type figs.: Simpson, *ibid.*, p. 204, fig. 30; p. 205, fig. 31.	*Pliomastodon sellardsi*
1930	*Gomphotherium priestleyi*	Hay and Cook Proc. Colo. Mus. Nat. Hist., IX, pp. 31, 32. Type loc.: Near Frederick, Tillman County, Oklahoma. Type fig.: Hay and Cook, *ibid.*, Pl. XII, figs. 1, 2.	*Stegomastodon priestleyi*
1930	*Prodinotherium hungaricum*	Éhik Geol. Hungarica, Ser. Palæont., Fasc. 6, pp. 1–14. Type loc.: Kotyháza (Dep. Nógrád), Hungary. Type figs.: Éhik, *ibid.*, Pl. I, figs. 1–3; Pls. II–IV.	*Deinotherium hungaricum*
1930	*Pliomastodon vexillarius*	Matthew Bull. Dept. Geol. Univ. Calif., XIX, No. 16, pp. 335–341. Type loc.: Southeast of Coalinga, Fresno County, California. Type figs.: Matthew, *ibid.*, Pl. XLI–XLIV, text figs. 1, 2.	*Pliomastodon vexillarius*
1931	*Bunolophodon postremus*	Spillmann "Die Säugetiere Ecuadors im Wandel der Zeit," Erster Teil, pp. 73–107. Type loc.: Quebrada [canyon] of Cachihuayco, near Alangasi, Province of Pichincha, east of Quito, Ecuador. Type figs.: Spillmann, 1929, Natur und Museum, LIX, Heft II, text figs. 3, 4, and associated skeleton, fig. 1. Material first described in "El Ecuador Comercial," 1928, Año VI, No. 57, p. 75, as "Mastodonte de Alangasi."	*Cuvieronius postremus*
1931	*Teleobunomastodon* Revilliod, 1931, *bolivianus* Philippi, 1893.	Revilliod, Mém. Soc. Paléont. Suisse, LI, pp. 1–21. Type loc.: Exact locality unknown, probably from the vicinity of Calacoto, valley of the Rio Desaguadero, Bolivia, south of Corocoro, or from Concordia. Type figs.: Revilliod, *ibid.*, Pls. I, II, and fig. 3, p. 9.	*Cordillerion* (?)*bolivianus*

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1931	*Torynobelodon barnumbrowni*	Barbour Neb. State Mus., Bull. 22, I, pp. 191–198. Type loc.: Snake River, Cherry County, southwest of Valentine, Nebraska. Type figs.: Barbour, *ibid.*, figs. 123, 124.	*Torynobelodon barnumbrowni*
1931	*Mastodon moodiei*	Barbour Neb. State Mus., Bull. 24, I, pp. 203–210. Type loc.: West Blue River, southwest of Milford, Seward County, Nebraska. Type figs.: Barbour, *ibid.*, figs. 130, 131, 132*b*.	*Mastodon moodiei*
1931	*Parelephas protomammonteus* (Matsumoto) *matsumotoi*	Saheki Japanese Journ. Geol. and Geog., VIII, No. 3, pp. 125–129. Type loc.: Mishima, Kimitsu district, Chiba Prefecture, Province of Kazusa, Japan. Type fig.: Saheki, *ibid.*, Pl. xv, figs. 1–3. [*Parelephas protomammonteus matsumotoi* Saheki, 1931, is invalid, since *matsumotoi* in this case is a homonym of *matsumotoi* Dietrich, 1927 (see above, this list, under *E.* [*Elephas*] *primigenius Matsumotoi* Dietrich, 1927). If the material described by Saheki is distinct, as he thought it was, it is material at present without a name.—Colbert-Simpson, letter, July 12, 1939.—Editor.]	[Not determined by the present author]
1931	*Palæoloxodon antiquus italicus*	Osborn Amer. Mus. Novitates, No. 460, pp. 1–24. Type loc.: Pignataro Interamna, near Cassino, Italy. Type figs.: Osborn, *ibid.*, figs. 1, 4–16.	*Hesperoloxodon antiquus italicus*
1931	*Palæoloxodon antiquus* (*andrewsi*?)	Osborn *Ibid.*, pp. 1, 19, 21, 23. Type loc.: Upnor on the banks of the Medway, Kent, England. Type fig.: Osborn, *ibid.*, p. 21, fig. 15; also Andrews and Cooper, 1928, "On a Specimen of Elephas antiquus from Upnor," Pls. i–viii, text figs. 1–5, and figs. 1079–1082 and 1084 of the present Memoir.	[*Hesperoloxodon antiquus* (*fide* Simpson, see p. 1222 above)]
1932	*Pilgrimia archidiskodontoides*	Haughton Trans. Roy. Soc. So. Africa, XXI, Pt. I, pp. 4–8. Type loc.: Sydney-on-Vaal Breakwater, bed of Vaal River, South Africa. Type figs.: Haughton, *ibid.*, Pls. i–iii.	*Palæoloxodon archidiskodontoides*
1932	*Pilgrimia subantiqua*	Haughton *Ibid.*, pp. 8–10. Type loc.: Delport's Hope, half a mile from Vaal River, South Africa. Type fig.: Haughton, *ibid.*, Pl. iv, figs. 1, 2.	*Loxodonta subantiqua*
1932	*Serridentinus gobiensis*	Osborn and Granger Amer. Mus. Novitates, No. 537, pp. 11–13. Type loc.: About forty miles southeast of Iren Dabasu, Inner Mongolia. Type fig.: Osborn and Granger, *ibid.*, p. 12, fig. 8.	*Serridentinus gobiensis*
1932	*Archidiskodon meridionalis nebrascensis*	Osborn Proc. Colo. Mus. Nat. Hist., XI, No. 1, pp. 1–3. Type loc.: Near Angus, Nuckolls County, Nebraska. Type figs.: Osborn, *ibid.*, figs. 1, 2.	*Archidiskodon meridionalis nebrascensis*
1932	*Trilophodon cooperi*	Osborn Amer. Mus. Novitates, No. 585, pp. 1–6. Type loc.: Dera Bugti, Baluchistan. Type fig.: Osborn, *ibid.*, p. 2, fig. 1; paratype, p. 3, fig. 2 (described by Forster Cooper, 1922, Proc. Zool. Soc. London, p. 610, as referable to *Bunolophodon angustidens*).	*Trilophodon cooperi*
1932	*Tetralophodon bumiajuensis*	van der Maarel "Contribution to the Knowledge of the Fossil Mammalian Fauna of Java," pp. 2, 3, 108–121. Type loc.: Bumiaju, central Java. Type figs.: van der Maarel, *op. cit.*, Pls. viii, ix, x, and text figs. 17–21.	*Tetralophodon bumiajuensis*
1932	*Stegodon bondolensis*	van der Maarel *Op. cit.*, pp. 158–164. Type loc.: Bondol near Kuwung, District Randublatung, Regency Blora, Residency Rembang, Java. Type figs.: van der Maarel, *op. cit.*, Pl. xiv, figs. 1, 4, 5, and text figs. 24, 25.	*Stegodon bondolensis*
1933	*Blickotherium blicki*	Frick Bull. Amer. Mus. Nat. Hist., LIX, Art. IX, pp. 509, 515, 527–531. Type loc.: Near Tapasuma, Gracios, Honduras. Type figs.: Frick, *ibid.*, figs. 3, 4.	*Blickotherium blicki*
1933	*Aybelodon hondurensis*	Frick *Ibid.*, pp. 527, 528, 532. Type loc.: Near Tapasuma, Gracios, Honduras. Type figs.: Frick, *ibid.*, figs. 5, 13, 18.	*Aybelodon hondurensis*

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1933	*Serridentinus filholi*	Frick *Ibid.*, pp. 509, 535. Type loc.: Gers, France. The mandible (Mus. d'Hist. Nat. Paris AC 2058, 2062) of this species was referred to in the article by Frick, 1926, Bull. Amer. Mus. Nat. Hist., LVI, Art. II, pp. 177, 178, but the name *Serridentinus filholi* was not assigned until 1933.	*Serridentinus filholi*
1933	*Trilophodon cruziensis*	Frick *Ibid.*, pp. 505, 579. Type loc.: Santa Cruz, New Mexico. Type figs.: Frick, *ibid.*, figs. 10, 12A, 17, 23A, 25.	*Megabelodon cruziensis*
1933	*Ocalientinus ojocaliensis*	Frick *Ibid.*, pp. 509, 576, 579. Type loc.: Ojo Caliente, New Mexico. Type figs.: Frick, *ibid.*, figs. 7, 18.	*Ocalientinus ojocaliensis*
1933	*Trobelodon taoensis*	Frick *Ibid.*, pp. 505, 580. Type loc.: Santa Cruz, New Mexico. Type figs.: Frick, *ibid.*, figs. 2, 13, 18.	*Trobelodon taoensis*
1933	*Tatabelodon riograndensis*	Frick *Ibid.*, pp. 505, 581. Type loc.: Battleship Mountain, New Mexico. Type figs.: Frick, *ibid.*, figs. 6, 13.	*Trilophodon* (*Tatabelodon*) *riograndensis*
1933	(?)*Amebelodon joraki*	Frick *Ibid.*, pp. 505, 582. Type loc.: Santa Cruz, New Mexico. Type fig.: Frick, *ibid.*, fig. 18. This type (a tuskless mandible) was first referred by the present author (Vol. I, p. 326, this Memoir) to the genus *Trilophodon*, but finally in the Appendix to Volume I, pp. 707, 738, he definitely assigned it to *Megabelodon*.	*Megabelodon joraki*
1933	*Serbelodon barbourensis*	Frick *Ibid.*, pp. 506, 592, 594. Type loc.: Christmas quarry, near Ainsworth, Nebraska. Type figs.: Frick, *ibid.*, figs. 14, 16, 27.	*Serbelodon barbourensis*
1933	*Tatabelodon gregorii*	Frick *Ibid.*, pp. 506, 597. Type loc.: Vicinity of Ainsworth, Nebraska. Type figs.: Frick, *ibid.*, figs. 13, 27A.	*Trilophodon* (*Tatabelodon*) *gregorii*
1933	(?)*Trilophodon barstonis*	Frick *Ibid.*, pp. 506, 607. Type loc.: Mohave Desert, California. Type figs.: Frick, *ibid.*, figs. 33, 36.	*Serridentinus barstonis*
1933	*Mastodon raki*	Frick *Ibid.*, pp. 506, 630. Type loc.: Hot Springs, New Mexico. Type figs.: Frick, *ibid.*, figs. 25A, 29A.	*Mastodon raki*
1933	*Mastodon americanus alaskensis*	Frick *Ibid.*, pp. 506, 631. Type loc.: Vicinity of Fairbanks, Alaska. Type fig.: Frick, *ibid.*, fig. 29A.	*Mastodon americanus alaskensis*
1933	*Elephas primigenius alaskensis*	Osborn (In Frick, *ibid.*, pp. 631, 632.) Type loc.: Vicinity of Fairbanks, Alaska. Type figs.: Osborn, this Memoir, Vol. II, figs. 1025, 1026.	*Mammonteus primigenius alaskensis*
1933	*Serbelodon burnhami*	Osborn Amer. Mus. Novitates, No. 639, pp. 1–5. Type loc.: Near Ricardo, San Bernardino County, California. Type figs.: Osborn, *ibid.*, figs. 1, 2.	*Serbelodon burnhami*
1933	*Stegodon trigonocephalus praecursor*	von Koenigswald Wetenschappelijke Mededeelingen, Dienst Mijnbouw Nederl.-Indië, I Teil, No. 23, pp. 104, 105. Type loc.: Bumiaju, Java. Type fig.: von Koenigswald, *ibid.*, Taf. xxvii, fig. 2.	*Stegodon trigonocephalus praecursor*
1933	*Cryptomastodon martini*	von Koenigswald *Ibid.*, pp. 111–119, Taf. xxviii, figs. 1–3, and text figs. 8, 9.	?SIRENIAN
1934	*D.* [*Dinotherium*] *Bozasi*	Arambourg Compt. Rend. Soc. géol. France, No. 6, pp. 86, 87. Type loc.: Valley of the Omo, Abyssinia. Type fig.: Arambourg, 1935, Bull. Soc. géol. France, (5), IV, Pl. xviii (mandible). Supplementary description: Arambourg, *op. cit.*, pp. 305–310.	[Not determined by the present author]
1934	*Mastodon grangeri*	Barbour Neb. State Mus., Bull. 35, I, pp. 287–290. Type loc.: Pender, Thurston County, Nebraska. Type fig.: Barbour, *ibid.*, p. 289, fig. 170.	*Mastodon grangeri*
1934	*Palæoloxodon yokohamanus*	Tokunaga Journ. Geog. (Tokyo), XLVI, No. 546, pp. 363–371 (in Japanese). Type loc.: Mouth of Tsurumi-gawa, Yokohama, Japan. Type fig.: Tokunaga, *ibid.*, Pl. viii, figs. 1, 2.	[Not determined by the present author]

Year	Name	Author		Reference in Present Memoir
1934	*Parastegodon? kwantoensis*	Tokunaga	*Ibid.*, pp. 365–369 (in Japanese). Type loc.: Kakio, Kanagawa Prefecture, Japan. Type fig.: Tokunaga, *ibid.*, Pl. IX, figs. 1–3.	[Not determined by the present author]
1934	*Archidiskodon proplanifrons*	Osborn	Amer. Mus. Novitates, No. 741, pp. 10–12. Type loc.: Gong-Gong, near the Vaal River, South Africa. Type fig.: Osborn, *ibid.*, p. 5, fig. 2.	*Archidiskodon proplanifrons*
1935	*Palæoloxodon priscus* var. *bosei*	Chakravarti	Proc. 22nd Indian Sci. Congress, Calcutta, p. 209. Type loc.: Parkalta near Jammu, India. Type fig.: Bose, 1929, Quart. Journ. Geol. Min. and Metallurg. Soc. India, II, No. 3, Pl. V, fig. 10, as *Stegodon bombifrons*. Supplementary description: Chakravarti, 1937, Quart. Journ. Geol. Min. and Metallurg. Soc. India, IX, No. 2, pp. 39–42, Pl. VI (figured as *Palæoloxodon* sp.).	[Not determined by the present author]
1935	*Gnathabelodon thorpei*	Barbour and Sternberg	Neb. State Mus., Bull. 42, I, pp. 395–404. Type loc.: Near Ogallah, Trego County, western Kansas. Type figs.: Barbour and Sternberg, *ibid.*, figs. 187–191.	*Gnathabelodon thorpei*
1935	*Stegodon yüshensis*	Young	Pal. Sinica, (C), IX, Fasc. 2, pp. 26–28. Type loc.: Yüshe, China. Type fig.: Young, *ibid.*, Pl. V, figs. 1, 1a.	[Not determined by the present author]
1935	*Stegodon zdanskyi*	Hopwood	(In Young, *ibid.*, p. 28); Hopwood, Pal. Sinica, (C), IX, Fasc. 3, p. 75. Type loc.: Unknown. Type fig.: Hopwood, *ibid.*, Pl. VII, fig. 5.	*Stegodon zdanskyi*
1935	*Stegodon officinalis*	Hopwood	(In Young, *ibid.*, Fasc. 2, pp. 27, 30.) Hopwood, *ibid.*, Fasc. 3, p. 73. Type loc.: (?)Szechuan, China. Type fig.: Hopwood, *ibid.*, Pl. VII, fig. 3.	*Stegodon officinalis*
1935	*Trilophodon connexus*	Hopwood	*Ibid.*, p. 14. Type loc.: Kansu, Sining Fu, SW 20 li, Shui Ch'üan, P'u, SE 5 li, Tiao Kou, China. Type fig.: Hopwood, *ibid.*, Pl. V, figs. 1, 2.	*Trilophodon connexus*
1935	*Trilophodon wimani*	Hopwood	*Ibid.*, p. 19. Type loc.: Pa P'an Shan, China. Type fig.: Hopwood, *ibid.*, Pl. V, fig. 3.	*Serridentinus wimani*
1935	*Trilophodon spectabilis*	Hopwood	*Ibid.*, p. 30. Type loc.: Said to have come from Sian, China. Type fig.: Hopwood, *ibid.*, Pl. VI, fig. 2.	*Trilophodon spectabilis*
1935	*Tetralophodon exoletus*	Hopwood	*Ibid.*, p. 35. Type loc.: Shansi, China. Type fig.: Hopwood, *ibid.*, Pl. VI, fig. 3.	*Tetralophodon exoletus*
1935	*Pentalophodon sinensis*	Hopwood	*Ibid.*, p. 57. Type loc.: Yü She Hsien, Shansi, China. Type fig.: Hopwood, *ibid.*, Pl. VII, fig. 2.	*Anancus sinensis*
1935	*Parastegodon sugiyamai*	Tokunaga	Proc. Imp. Acad. Tokyo, XI, p. 434. Type loc.: Iruhi, in Saida village, Shikoku, Japan. Type fig.: Tokunaga, *ibid.*, p. 433, text fig. [Not determined by the present author, but regarded by Dr. E. H. Colbert as referable to *Stegodon* rather than to *Parastegodon* (which was considered by Professor Osborn as possibly equal to *Archidiskodon* Pohlig or to a progressive *Stegodon*). Consequently this species is described in the *Stegodon* chapter, pp. 899 and 900 above.—Editor.]	[*Stegodon*(?) *sugiyamai*]
1936	*Mastodon atavus*	Borissiak	Travaux de l'Institut Paléozoologique de l'Académie des Sciences de l'U.S.S.R., V, pp. 171–234. Type loc.: Dschilantschik River, Turgai, Russia. Type figs.: Borissiak, *ibid.*, Taf. I–V, VIII, and Taf. VI, VII (in part), also text figs. 1–16. Pal. Inst. No. 2280, Leningrad.	[Not determined by the present author]
1936	*Pliomastodon nevadanus*	Stock	Publ. Carnegie Instn. Wash., No. 473, p. 37. Type loc.: Thousand Creek basin, about four miles northwest of the Hot Spring and on east side of Railroad Ridge, Humboldt County, northwestern Nevada. Type fig.: Stock, *ibid.*, Pl. I (incomplete skull representing most of the palate, second and third superior molars of each side, and a complete right tusk—Calif. Inst. Tech. Coll. Vert. Pal. No. 1922).	[Not determined by the present author]

Year	Name Author	Reference in Present Memoir
1936	*Palæoloxodon aomoriensis* Tokunaga Journ. Geog. (Tokyo), XLVIII, No. 564, February, pp. 67–70 (in Japanese). Type loc.: Tenjinbayashi, on the Shichinohe-gawa, near entrance to town of Shichinohe, Kamikita-gun, Aomori Prefecture, Japan. Type fig.: Tokunaga, *ibid.*, Pl. I. Supplementary description: Tokunaga and Takai, 1936, Journ. Geol. Soc. Japan, XLIII, No. 511, April 20, pp. 254–258 (in English).	[Not determined by the present author]
1936	*Deinotherium hopwoodi* Osborn This Memoir, I, p. 117. Type loc.: Olduvai, near southeast shore of Lake Victoria, Tanganyika Territory, Africa. Type fig.: Osborn, *op. cit.*, p. 104, fig. 68a. Regarded by Doctor Hopwood as a synonym of *Dinotherium Bozasi* Arambourg, 1934. See above, this list.	*Deinotherium hopwoodi*
1936	*Trilophodon hasnotensis* Osborn *Op. cit.*, p. 279. Type loc.: Near Hasnot, India. Type fig.: Osborn, *op. cit.*, p. 454, fig. 417.	*Trilophodon hasnotensis*
1936	*Tetralophodon fricki* Osborn *Op. cit.*, p. 375. Type loc.: Near Clarendon, northern Texas. Type figs.: Frick, 1933, Bull. Amer. Mus. Nat. Hist., LIX, Art. IX, fig. 12 (lower) and fig. 23B (upper).	*Tetralophodon fricki*
1936	*Rhynchotherium browni* Osborn *Op. cit.*, p. 494. Type loc.: San José de Pimas, Sonora, Mexico. Type fig.: Osborn, 1921, Amer. Mus. Novitates, No. 1, fig. 2C, as neotype of *Rhynchotherium tlascalæ*. See also this Memoir, I, fig. 467. On locating the type cast of *Rhynchotherium tlascalæ* in the Geneva Museum, the neotype mandible was found to be quite different; consequently the present author made it the type of a new species, *Rhynchotherium browni*.	*Rhynchotherium browni*
1936	*Cordillerion edensis* Osborn This Memoir, I, p. 560. Type loc.: Mt. Eden Hot Springs, San Bernardino County, California. Type fig.: Frick, 1921, Bull. Dept. Geol. Univ. Calif., XII, No. 5, Pl. L (as *Trilophodon shepardi edensis*); Osborn, 1922, Amer. Mus. Novitates, No. 49, fig. 1, A1, A2 (as *Dibelodon edensis*). See also this Memoir, I, figs. 522, 523. Cf. notes under *Trilophodon* (*Tetrabelodon*) *shepardi edensis* Frick, 1921, and *Dibelodon edensis* Osborn, 1922, above, this list.	*Cordillerion edensis*
1936	*Anancus properimensis* Osborn This Memoir, I, p. 647. Type loc.: Near Chinji Bungalow, India. Type figs.: Osborn, *op. cit.*, figs. 609, 613.	*Anancus properimensis*
1936	*Pentalophodon falconeri* Osborn *Op. cit.*, p. 653. Type loc.: Siwalik Hills, India. Type figs.: Falconer and Cautley, 1847, "Fauna Antiqua Sivalensis," Pls. XXXII, and XXXIII, figs. 1, 2 (as *Mastodon sivalensis*).	*Pentalophodon falconeri*
1936	*Miomastodon depereti* Osborn *Op. cit.*, p. 693. Type loc.: Chevilly, France. Type fig.: Mayet, 1908, Ann. Univ. Lyon, Nouv. Sér., I, Sci., Méd., Fasc. 24, Pl. VII, fig. 3 (as *Mastodon angustidens*).	*Miomastodon depereti*
1936	*Mastodon pavlowi* Osborn *Op. cit.*, p. 694. Type loc.: Pestchana, Podolia, Russia. Type fig.: Pavlow, 1894, Mém. Acad. Imp. Sci. St. Pétersb., (8), I, No. 3, Pl. I, figs. 1, 2, 3 (as *Mastodon ohioticus*).	*Mastodon pavlowi*
1936	*Mastodon acutidens* Osborn *Op. cit.*, p. 696. Type loc.: Rochester, Indiana. Type figs.: Osborn, *op. cit.*, figs. 131, A1–A4, 135, 656, and Pl. I, L.	*Mastodon acutidens*
1936	*Stegolophodon lydekkeri* Osborn *Op. cit.*, p. 700. Type loc.: Vicinity of Bruni, northwest coast of Borneo. Type fig.: Lydekker, 1885, Proc. Zool. Soc. London, Pl. XLVIII (as *Mastodon latidens*); Lydekker, 1886, "Cat. Foss. Mamm. Brit. Mus.," fig. 19 (as *M. latidens*).	*Stegolophodon lydekkeri*
1936	*Stegomastodon primitivus* Osborn *Op. cit.*, p. 726. Type loc.: Northeast of Ainsworth, Nebraska. Type figs.: Osborn, *op. cit.*, figs. 674, 675.	*Stegomastodon primitivus*

Year	**Name**	**Author**	**Reference in Present Memoir**
1936	*Parastegodon akashiensis*	Takai Proc. Imp. Acad. Tokyo, XII, No. 1, pp. 19–21. Type loc.: "Shore of the cliffy coast," west of Nishiyagi, Okubo-mura, Akashi-gun, Hyogo Prefecture, Japan. Type figs.: Takai, *ibid.*, p. 20, figs. 1, 2.	[Not determined by the present author]
		[Both Mr. Fuyuji Takai and Mr. Tokio Shikama simultaneously studied the same fossil material from the Akasi District, neither being aware of the description of the other. Mr. Takai chose a molar as his type, naming the species *Parastegodon akashiensis*, while Mr. Shikama extended his studies on this material, including two skulls with molars, a lower jaw with molars, and some other isolated teeth from the same locality, choosing as his type one of the skulls, and naming the species *Parastegodon nipponicus* in his manuscript. Meanwhile Mr. Takai had announced his species in a lecture delivered at the meeting of the Palæontological Society of Japan, November 30, 1935. While this announcement did not constitute priority of description, Mr. Shikama very generously withdrew his unpublished manuscript name in favor of Mr. Takai's species name *Parastegodon akashiensis*. (Cf. footnote by H. Yabe, in Takai, 1936, *ibid.*, p. 19).—Editor.]	
1937	*Pentalophodon cuneatus*	Teilhard de Chardin and Trassaert Pal. Sinica, (C), XIII, Fasc. 1, p. 11. Type loc.: Southeastern Shansi (Yushê Basin), China. Type fig.: Teilhard de Chardin and Trassaert, *ibid.*, Pl. III, fig. 4.	[Not determined by the present author]
1937	*Mastodon intermedius*	Teilhard de Chardin and Trassaert *Ibid.*, p. 22. Type loc.: Southeastern Shansi (Yushê Basin), China. Type fig.: Teilhard de Chardin and Trassaert, *ibid.*, Pl. III, fig. 2 a-c.	[Not determined by the present author]
1937	*Stegodon licenti*	Teilhard de Chardin and Trassaert *Ibid.*, p. 27. Type loc.: Southeastern Shansi (Yushê Basin), China. Type figs.: Teilhard de Chardin and Trassaert, *ibid.*, Pl. VIII, figs. 1a, 1b, 2, and text fig. 3.	[Not determined by the present author]
1937	*Parastegodon infrequens*	Shikama Japanese Journ. Geol. Geogr., XIV, pp. 127–131. Type loc.: Near Akasi (precise locality unknown). Type fig.: Shikama, *ibid.*, Pl. IX. Type: Anterior portion of left ramus with M_2 *in situ*. Collection of Takikawa Middle School in Kôbe.	[Not determined by the present author]
1937	*Parelephas proximus uehataensis*	Shikama *Ibid.*, p. 165.	[Not determined by the present author]
		If the name *Parelephas protomammonteus typicus* is synonymous with *antiquus*, then Shikama was justified in giving a new name, *Parelephas proximus uehataensis*, to include secondary specimens of *P. protomammonteus typicus* plus those of *E. primigenius matsumotoi*.—Colbert-Simpson, letter, July 12, 1939. (See notes under *Parelephas protomammonteus typicus* Matsumoto, 1926, and *E.* [*Elephas*] *primigenius Matsumotoi* Dietrich, 1927, above, this list.)	
1937	*E.* [*Elephas*] *antiquus* mut. *ruthenensis*	Astre Bull. Soc. Hist. Nat. Toulouse, LXXI, p. 30. Type loc.: Salles-la-Source (Aveyron), France. Type fig.: Astre, *ibid.*, Pl. I (incomplete molar), figured as "*Elephas antiquus*, de Salles-la-Source."	[Not determined by the present author]
1938	*Bunolophodon yokotii*	Makiyama Mem. Coll. Sci. Kyoto Imp. Univ. (B), XIV, No. 1, pp. 12–14. Type loc.: Upper Banko Sandstone of the Meisen series, at Senkaibō in the Meisen district, North Kankyō-dō, Japan. Type figs.: Makiyama, *ibid.*, text figs. 5a and 5b.	[Not determined by the present author]
1938	*Stegodon shodoensis akashiensis*	(Takai, 1936) Makiyama *Ibid.*, pp. 21–27. Cotype loc.: Eigasima near Akasi, and under the sea off Hayasi-zaki, Japan. Cotype figs.: Makiyama, *ibid.*, figs. 10–12.	[Not determined by the present author]
1939	*Palæoloxodon darti*	Cooke and Clark Trans. Roy. Soc. So. Africa, XXVII, Pt. 3, pp. 296-302. Type loc.: Victoria Falls, northern Rhodesia. Type figs.: Cooke and Clark, *ibid.*, Pls. XII and XIII.	[Not determined by the present author]
1939	*Archidiskodon paramammonteus*	Matsumoto Zool. Mag. (Tokyo), LI, No. 10, p. 704 (in Japanese), p. 716 (English résumé). Type loc.: Nagahama, Minato Town, Province of Kazusa, Japan. Type fig.: Matsumoto, *ibid.*, fig. 3. Type: Fragment of molar.	[Not determined by the present author]

CHAPTER XXII

THE GEOLOGIC SUCCESSION OF THE PROBOSCIDEA

By Edwin H. Colbert

I. INTRODUCTION

At the time of Professor Osborn's death, in 1935, certain portions of Volume II of the Proboscidea Memoir were left uncompleted. As the editorial work on the second volume progressed, it became particularly evident that the chapter on the stratigraphic relationships of Proboscidea-bearing beds throughout the world would necessitate a considerable amount of work to bring it to completion, for although voluminous notes had been assembled, representing a great deal of work on the part of Professor Osborn and the several persons assisting him, virtually no text had been written. Therefore it became apparent that a complete text for this chapter would have to be prepared, and for various reasons this task fell to the lot of the present author.

For several years preceding Professor Osborn's death I had been associated with him as his research assistant on the Proboscidea Monograph and during that association an appreciable amount of my time had been devoted to the assembling of data as to the geologic succession and occurrences of the numerous species of fossil proboscideans. Thus I had the opportunity to become familiar with Professor Osborn's views as to geologic ages and correlations, and to learn, to some extent, the manner in which he planned to write and present this chapter on the geologic succession of the fossil Proboscidea.

A detailed presentation of the geologic succession, such as Professor Osborn would have written, is not now considered practicable. The original author is not here to write this chapter or to supervise its writing, and it is not considered feasible to imitate his style or his method of presentation. Therefore this chapter will be more or less in the form of a running narrative, describing the distribution, development, and correlation of the various Proboscidea-bearing horizons of the world. Charts and faunal lists will be included only where it is thought necessary to clarify the text.

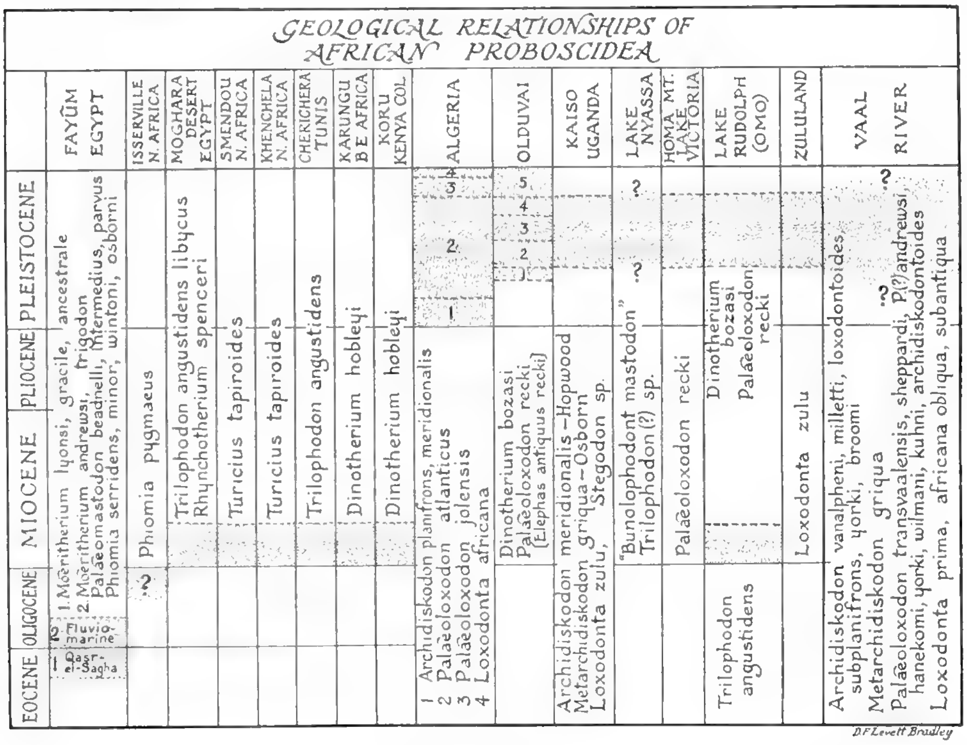

Figure 1220

In writing this chapter, an attempt will be made to set forth the various viewpoints—often very divergent—regarding the geologic age and the relationships of the horizons being considered. In all cases, Professor Osborn's views will be stressed (when known), and his opinions will be compared with the opinions of other palæontologists, including those of the present author.

This chapter will be divided into six large divisions, dealing with Africa, the Oriental region (India, Java, Borneo, etc.), Europe, Asia, North America, Central and South America. These divisions correspond in a general way to the modern zoogeographic realms or regions of the world, but for various reasons there will be no attempt made to follow slavishly the zoogeographical divisions as they are usually recognized. Thus, in considering Africa, the whole of the continent will be included—even that portion which at the present time is considered as belonging to a part of the Palæarctic region. Within each of the above divisions, the Proboscidea-bearing beds will be discussed according to their age, beginning with the earliest horizons and ending with the latest ones. Within this general stratigraphic arrangement of the subject matter, a regional plan will be followed, whereby sediments are compared according to their local developments in each continent.

II. AFRICA

1. INTRODUCTION

It would seem logical to begin our discussion of the geologic succession of the Proboscidea with a study of the Tertiary and Quaternary beds in Africa, because the earliest known proboscideans are found on this continent. Whether or not Africa was the original center for the adaptive radiation of the Proboscidea is a question beyond the scope of the present discussion; suffice it to say that at the present time there is considerable evidence, especially if one adheres to the theories of the late W. D. Matthew regarding the origin and distribution of the orders of mammals, supporting the idea that these animals had a northern, Palæarctic origin, rather than an Ethiopian origin as postulated by Professor Osborn.

North Africa, where the earliest known proboscideans are found, is at the present time in the Palæarctic zoogeographic region. Consequently, upon the basis of the present-day distribution of mammals, the first proboscideans and the sediments in which they occur might logically be considered in connection with the discussion of Eurasiatic horizons. It has been thought best, however, to include the whole of Africa in this one section, so that the Eocene and Oligocene sediments of the Egyptian Fayûm, containing the ancestral types of proboscideans, will be taken up at this place.

2. THE EOCENE AND OLIGOCENE OF NORTH AFRICA

Fayûm District, Egypt.—The Fayûm District is a circular depression in the Libyan Desert, located to the west of that portion of the Nile River between Kafr el Ayat and Feshn. Its central portion is occupied by a lake known as Birket el Qurun—the remnants of a once much larger lake known as Moeris, which in the time of the ancient Egyptian dynasties served as a reservoir that controlled the Nile irrigation system. A series of marine and fluviatile deposits, ranging in age from the Middle Eocene through the Lower Oligocene, form the escarpments around this depression; these are the Fayûm deposits in which several distinct and characteristic early Tertiary faunas have been discovered.

The Fayûm sediments, ranging from the lower to the upper beds, represent a succession of facies beginning with marine sediments, passing through a series of mixed marine and fluviatile beds and finally developing at the top into fluviatile deposits. As Andrews and Beadnell have shown, this gradual change in the character of the Fayûm deposits from the lower to the upper beds is to be attributed to an uplift of the Ethiopian region progressing from the south to the north.

The succession of sediments in the Fayûm District, and their correlation by different authors, is as follows.

Pliocene and Pleistocene and Recent		Sands and Terraces
(1)	(2)	
Lower Oligocene	Lower Oligocene	Jebel el Qatrani beds
		Basalt Flow
Upper Eocene		Fluvio-marine beds
Middle Eocene	Upper Eocene	Qasr el Sagha beds
		Birket el Qurun beds Ravine beds Wadi Rayan Series

[1] Andrews, Beadnell.
[2] Stromer, Osborn, Schlosser.

In the succession of Fayûm deposits, the Qasr el Sagha and the Fluvio-marine series are of interest to us, since these are the beds containing ancestral proboscideans. The beds below the Qasr el Sagha series contain strictly marine vertebrates—notably very primitive cetaceans among the mammals—while the sediments above the Fluvio-marine series are virtually unfossiliferous so far as mammals are concerned.

In the original descriptions of the Fayûm mammals by Andrews, the ages of the Qasr el Sagha and the Fluvio-marine beds were established as Middle Eocene and Upper Eocene respectively. Subsequently several authors, notably Stromer (1907), Osborn (1910) and Schlosser (1911) designated the Qasr el Sagha beds as of Upper Eocene age, thereby shifting the Fluvio-marine beds up into the lowest part of the Oligocene period. These differences of interpretation of the Fayûm sediments may be attributed to divergent opinions as to the affinities of the contained faunas.

Andrews'[1] views as to the age and affinities of the Fayûm mammals were expressed in 1906 as follows:

> The Mammals may be divided into three sections:—(1) the land-mammals which seem to be truly endemic to the Ethiopian region; these occur both in the Upper and Middle Eocene beds, and include such genera as *Mœritherium*, *Palæomastodon*, *Arsinoitherium*, *Barytherium*, *Megalohyrax*, *Saghatherium*, and perhaps *Geniohyus*: (2) forms of which close allies occur in other regions in approximately contemporary deposits; these, so far as at present known, occur only in the Upper Eocene beds, and include such genera as *Ancodon*, *Rhagatherium*, *Hyænodon*, *Pterodon*, *Apterodon*, and *Sinopa*: (3) the aquatic mammals so far not found in the Upper Eocene beds, and comprising *Eosiren*, *Zeuglodon*, and *Prozeuglodon*. It seems probable that some of these last, like the genera included in section 1, are of endemic origin, having originated from land-mammals inhabiting the region.

In 1907 Stromer[2] suggested that the fauna of the Fluvio-marine beds might properly be placed in the Oligocene.

> Nachdem nun jener ausgezeichnete Kenner tertiärer Wirbelloser zu dem Schlusse kam (1906, S. 347), dass sie ganz oder doch zum Teil dem Bartonien, also dem Obereocän entspreche, würde der unmittelbar auflagernden Fluviomarinstufe mit ihren verkieselten Hölzern und Reptil- und Landsäugetier-Resten (Andrews, 1906) unteroligocänes Alter zuzuschreiben sein.

In 1910, Osborn indicated the Fluvio-marine beds as of Lower Oligocene age, and this same interpretation was followed by Schlosser in 1911, in his monograph on the "Oligozänen Landsäugetiere aus dem Fayûm."

It may be well to review briefly at this place the evidence in favor of these differing interpretations as to the age of the Qasr el Sagha and of the Fluvio-marine series.

Qasr el Sagha Series

The four genera of importance in the Qasr el Sagha beds are:

Barytherium
Mœritherium
Eosiren
Zeuglodon

Of these the first two genera are autochthonous to northern Africa and therefore are of no value for correlative purposes. The other two genera, *Eosiren* and *Zeuglodon*, are decidedly of Eocene age. It is difficult to say whether these forms should be placed in the Middle or in the Upper Eocene, but comparisons with related genera in other parts of the world (particularly the wide-spread *Zeuglodon*) would seem to indicate that their affinities might be with Upper Eocene forms.

Fluvio-marine Beds

In reviewing the Fluvio-marine fauna, it is well to remember Andrews' separation of the various mammalian genera into endemic African types and mammals common not only to Africa but to other parts of the world as

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[1] Andrews, C. W., 1906. "A Descriptive Catalogue of the Tertiary Vertebrata of the Fayûm, Egypt," pp. xii-xiii.

[2] Stromer, E., 1907. Abhandl. Senckenbergischen Naturforschenden Gesellschaft, XXIX, p. 144.

well. Schlosser, in 1911, lists nine orders of mammals from the Fluvio-marine deposits of the Fayûm. Of these, three—the Hyracoidea, Proboscidea, and Embrithopoda—were at that time probably indigenous to North Africa, and hence should be excluded from any consideration of intercontinental correlations.

Of the remaining orders, the following genera are important. Their relationships, both zoologic and geologic, are indicated.

PRIMATES

Parapithecus	Generally more advanced toward the anthropoid habitus than the Burmese genus, *Amphipithecus*, which latter is of uppermost Eocene age. Therefore the evidence would be in favor of an Oligocene age for the Fayûm genus.
Propliopithecus	Related to *Pliopithecus*. *Propliopithecus* is definitely so far advanced as an anthropoid as to warrant its position in the Oligocene.

INSECTIVORA

Metoldobotes	Schlosser has compared this genus with the North American *Oldobotes* (*Mixodectes*), of Paleocene age. Insectivores are, however, notoriously persistent primitive forms in all mammalian faunas.

CREODONTA

Ptolemaia	Regarded by Schlosser as a specialized descendant of the Phosphorite genus, *Cynohyænodon*.
Metasinopa	Closely related to "*Sinopa*" *aethiopica* of the Fayûm.
Sinopa	An Eocene genus.
Apterodon	Originally described from the Phosphorites of Quercy.
Pterodon	An advanced type of hyænodont.
Hyænodon	Typically an Oligocene genus.

RODENTIA

Phiomys	Schlosser has compared these two genera with *Theridomys* of the Lower Oligocene, and *Trechomys* of the Upper Eocene of France.
Metaphiomys	

ARTIODACTYLA

Ancodon	This is typically an Oligocene genus in Europe and America.
Brachyodus	Schlosser referred to this genus the species that Andrews placed in *Ancodon*. *Brachyodus* first appears in the Oligocene and continues into the Miocene.

Considering the possibilities offered by the above review of certain diagnostic genera, it would seem likely that the fauna of the Fluvio-marine beds is of Lower Oligocene age. Of course this fauna contains various Eocene types, but these may very well be holdovers from an earlier period—a phenomenon that is very common in the development of faunal assemblages. On the other hand, the presence in the fauna of numerous typically Oligocene forms, particularly among the hyænodonts and the anthracotheres, would argue strongly for the Oligocene age of the Fluvio-marine sediments. It is the presence of these newcomers that is important in determining the age of a fauna.

Proboscideans:

Phiomia osborni Matsumoto *Phiomia wintoni* (Andrews) *Phiomia minor* (Andrews) *Phiomia serridens* Andrews and Beadnell *Palæomostodon parvus* Andrews *Palæomostodon intermedius* Matsumoto *Palæomastodon beadnelli* Andrews *Mœritherium trigodon* Andrews *Mœritherium andrewsi* Schlosser	Fluvio-marine Beds Lower Oligocene
Mœritherium lyonsi Andrews *Mœritherium gracile* Andrews *Mœritherium ancestrale* Petronievics	Qasr-el-Sagha Beds Upper Eocene

3. THE MIOCENE OF NORTH AFRICA

Isserville, North Africa.—In 1897 Charles Depéret[1] published a short notice descriptive of a single proboscidean tooth found near Isserville in North Africa. This tooth he regarded as representing a very small race of *Trilophodon angustidens*, and he gave it a subspecific name, making its designation *Mastodon angustidens pygmæus*. Comparing this specimen with the typical Miocene *Trilophodon angustidens* of Europe, Depéret came to the conclusion that the African specimen represented a more primitive and an earlier race of the *T. angustidens* stock. Consequently he considered its age as Cartennien, which in turn he regarded as representing the beginning of the Miocene.

> Je terminerai en faisant remarquer l'intérêt qui s'attache à la constatation précise de la présence du genre Mastodonte en Afrique à l'époque cartennienne, c'est-à-dire dès le début du Miocène, exactement comme en Europe, sans que, dans l'état actuel de nos connaissances, on puisse dire de quelle région du globe proviennent ces premiers Proboscidiens, ni quelle forme animale a pu leur donner naissance.

Subsequently Professor Osborn came to the conclusion that the tooth that Depéret had compared with *Trilophodon angustidens* might be more properly placed in the genus *Phiomia*. Because of this apparent relationship between the specimen under consideration and the advanced mastodonts of the Fayûm, Osborn placed the beds at Isserville as questionably of Upper Oligocene age, rather than as of Lower Miocene affinities.

Proboscidean: *Phiomia pygmæus* (Depéret).

Moghara Desert, Egypt.—The most abundant remains of Miocene proboscideans in Africa were discovered in northern Egypt, in the desert between the Nile Delta and the boundary of Tripoli. These specimens were described by Fourtau[2] in 1918 and 1920, in his publication "Contribution a l'Étude des Vertébrés Miocènes de l'Égypte."

The mammalian fauna of the Moghara deposits consists of certain genera of cetaceans, a brachypodine rhinoceros designated by Fourtau as "*Teleoceras*," several species of anthracotheres referred to the genera *Brachyodus* and *Masritherium*, two types of proboscideans, assigned by Professor Osborn to the genera *Trilophodon* and *Rhynchotherium*, and two primates, *Prohylobates* and *Dryopithecus* (?). The complexion of this fauna is distinctly Miocene. In addition to the mammals, the deposits at Moghara contain numerous and various crocodilians, chelonians, and fish.

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[1] Depéret, C., 1897. Bull. Soc. géol. France, (3), XXV, pp. 520, 521.

[2] Fourtau, R., 1918. Ministry of Finance, Survey Dept., Cairo, p. 98.

It is quite evident that such a fauna represents a region in the vicinity of a shoreline a strand crossed by rivers and bordered by the sea. This fact was recognized by Fourtau, who differentiated three categories of mammals in the Moghara deposits.

1. Aquatic mammals. The cetaceans, of which two types are recognizable, one inhabiting the open water and the other an estuarine form.
2. Semiaquatic mammals. The anthracotheres and the brachypodine rhinoceros. Living along the rivers and in the marshes.
3. Land mammals. The proboscideans and the primates.

This fauna was compared by Fourtau with the Burdigalian, Lower Miocene, assemblages of Europe, particularly those of the Orléanais sands and the Eggenburg deposits (Fourtau, 1918, *op. cit.*, p. 98):

"Quant à son âge, les affinités des vertébrés nous amènent à synchroniser ce gisement avec ceux des sables de l'Orléanais, en France, et avec celui d'Eggenburg, en Autriche, et à en faire un dépôt datant du Burdigalien."

This author differed from Haug, who placed the deposits under consideration in the Aquitanian a division that has been variously interpreted as either of Upper Oligocene or of Lower Miocene age.

The evidence of the mammalian fossils strongly supports Fourtau's conclusion that the Moghara deposits are of Lower Miocene age. The anthracotheres, *Brachyodus* and *Masritherium*, and the proboscideans, *Trilophodon* and *Rhynchotherium*, are particularly significant in fixing the age of the deposits as Lower Miocene.

PROBOSCIDEANS:
Trilophodon angustidens libycus (Fourtau)
Rhynchotherium spenceri (Fourtau)

Osborn (Vol. I of this Memoir) designated *Trilophodon angustidens libycus* as of Lower (?) Miocene age, while he placed *Rhynchotherium spenceri* in the Middle Miocene. However, Fourtau's description of the fauna from Moghara would indicate that this is a single assemblage of mammals coming from one horizon. Consequently it would seem likely that the age of both proboscideans is Lower Miocene, as indicated by Fourtau.

Hopwood, in a personal communication to the present author, states that he has an unrecorded tooth of *Dinotherium* from Moghara.

SMENDOU.—Gervais (Zoologie et Paléontologie Francaises) described a single tooth which was found at Smendou in the Province of Constantine in northern Africa, as a form closely related to if not identical with *Zygolophodon borsoni*. This identification was revised by Depéret in 1897, who referred the specimen to *Turicius tapiroïdes*, a change of considerable significance since the former species is of Upper Pliocene age while the latter is characteristic of the Miocene. In speaking of the specimen, Depéret[1] made the following statement: "Il résulte de cette description fort claire que la molaire du Smendou appartenait à un Mastodonte du groupe à molaires tapiroïdes, et vraisemblablement au *Mastodon turicensis* Schinz (= *tapiroïdes* Cuv.), espèce répandue dans toute la hauteur du Miocène européen."

In discussing the beds in which this particular specimen was discovered, Depéret said that: "M. Ficheur dans un important travail sur les terrains tertiaires de ce bassin (*B. S. G. F.*, 3e sér., t. 22, p. 544), a été amené à considérer ces couches comme un équivalent lacustre du Miocène inférieur ou *Cartennien*."

PROBOSCIDEAN: *Turicius tapiroides* (Cuvier).

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[1] Depéret, C., 1897. Bull. Soc. géol. France, (3), XXV, p. 518.

Khenchela.—This deposit is probably correlative with certain other North African localities considered in these pages, namely, those of Isserville and Smendou, which are of Lower Miocene age. A proboscidean tooth was found at this locality, and Depéret[1] made the following statement concerning it: "Cette molaire, remarquable par ses dimensions très petites, ressemble, dit M. Gaudry, aux dents du *Mastodon turicensis* et provient sans doute du terrain miocène."

Proboscidean: *Turicius tapiroides* (Cuvier).

Cherichera.—In Tunis, at Cherichera, are deposits that would seem to be somewhat later in age than the beds exposed near Isserville and at Khenchela. Here was found a jaw referable to *Trilophodon angustidens*, typically a Middle Miocene species: "Enfin, dans le même Memoire, M. Gaudry a décrit et figuré ... une belle moitié de mandibule droite d'un Mastodonte d'un autre groupe, le *Mastodon angustidens* Cuv. aux molaires pourvues de mamelons arrondis, non tapiroïdes; cette belle pièce provient du Miocène moyen (probablement Helvétien) du Cherichera, près Kairouan (Tunisie)."[2]

Proboscidean: *Trilophodon angustidens* (Cuvier).

4. THE MIOCENE OF CENTRAL AND EAST AFRICA

Several localities are known in Central and East Africa where Miocene proboscideans have been discovered. These will be discussed briefly in the following pages.

Karungu, British East Africa.—In 1911 C. W. Andrews described a new species of *Dinotherium* that was found on the east side of Lake Victoria.

In a subsequent paper (1914)[3] on the fauna from Karungu, Andrews made the following remarks as to the age of the deposits.

> The general character of the fauna indicates that the age of the deposits is probably Lower Miocene (Burdigalien) and that it was contemporary with the faunas of the Sables de l'Orléanais and of Moghara, and probably also with the recently-discovered fauna of the Bugti Hills in British Baluchistan. In all these localities Anthracotheres of similar type appear as an important constituent of the fauna; and, although at present the characteristic small form of *Dinotherium* has not yet been found at Moghara, nevertheless a primitive *Tetrabelodon*, closely similar to *T. angustidens*, which elsewhere accompanies the *Dinotherium*, has been found in that locality.

In discussing the Karungu fauna, Andrews notes particularly the presence of a peculiar hyracoid, probably descended from the Eocene hyracoids of northern Africa, and a rodent seemingly a direct descendant of the Fayûm genus, *Phiomys*. The mammalian fauna of Karungu is as follows.

Pseudælurus africanus Andrews
Creodont(?)
Dinotherium hobleyi Andrews
Myohyrax oswaldi Andrews
Paraphiomys pigotti Andrews
Rhinoceros
Merycops africanus Andrews
Tragulids

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[1] Depéret, C., 1897. Bull. Soc. géol. France, (3), XXV, pp. 518, 519.

[2] Depéret, C., 1897. Bull. Soc. géol. France, (3), XXV, p. 519.

[3] Andrews, C. W., 1914. Quart. Journ. Geol. Soc., London, LXX, p. 163.

Osborn (Volume I, p. 111, of this Monograph) placed the Karungu deposits in the Lower Miocene. This would seem to be as satisfactory a correlation as may be made at the present time.

PROBOSCIDEAN: See faunal list, above.

KORU, KENYA COLONY.—This deposit, the fossil fauna of which has been described by Hopwood, is very important because of the presence in it of several primitive dryopithecoids. The Proboscidea are represented by *Dinotherium hobleyi*, which leads Hopwood to think that these beds are closely related to and correlative with the Karungu deposits—that is, Lower Miocene.

In 1933, Hopwood[1] described the fauna (exclusive of the higher primates) as follows: "The fauna consists of two or three genera, which may prove to be lemuroids, *Dinotherium hobleyi*, three genera of Creodonts, an amphicyonine carnivore, several Rodents, two Insectivores one very close to *Potamogale*,—as well as small pigs and ruminants."

PROBOSCIDEAN: *Dinotherium hobleyi* Andrews.

Hopwood's detailed study of fossil vertebrates from Kenya is now in the course of preparation.

LAKE RUDOLPH, EAST AFRICA.—Closely related to the fauna of Kenya is that recently reported by Arambourg as coming from beds of Burdigalian age, along the western border of Lake Rudolph. This fauna was discovered in tuffs interstratified between heavy basalts and other eruptive rocks of that vicinity. According to Arambourg,[2] the constitution of the fauna is as follows:

> Proboscidiens: *Mastodon* af. *angustidens* Cuv.
> Perissodactyles: *Aceratherium*? sp.
> Hyracoïdes: *Pliohyrax* nov. sp.
> Artiodactyles: *Brachyodus* sp.
>
>   *Listriodon* nov. sp.
>   Suidé indeterminé, voisin de Palaeochœrus.
>   *Dorcatherium* nov. sp.
>   Antilope indeterminée.
>
> Par sa composition, cette faune s'apparente étroitement à celles qui ont été reconnues déjà en quelques points de l'Afrique et attribuées au Miocène inférieur: celles de Moghara, dans le désert Libyque, de Karungu près du Lac Victoria en Afrique orientale et du Namib, dans les Diamantenwüste de l'ancien Sud-Ouest africain allemand.

PROBOSCIDEAN: See faunal list, above.

5. THE PLEISTOCENE OF NORTH AFRICA

The Pleistocene is perhaps the most difficult period to summarize of any of the geological ages included in this consideration of Proboscidea-bearing beds. Even in Europe and North America, where our knowledge of the Pleistocene has been advanced to its greatest degree of perfection, the problems of correlation—particularly where evidences of glaciation are missing—are extraordinarily difficult. Therefore it becomes evident that in the more southerly portions of the world, particularly the African, Oriental, and South American regions, correlations within the Pleistocene must of necessity be at the present time very questionable, since they are based for the most part on the development of river terraces or the expression of faunas, and in many cases there is no possibility of connecting them with the comparable Eurasiatic and American stages. In this discussion of the Pleistocene of Africa, the continent will be more or less arbitrarily divided into a North, a Middle, and a South section, and the deposits in each of these sections will be in turn listed and discussed.

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[1] Hopwood, A. T., 1933. Journ. Linnean Soc. Zool., London, XXXVIII, p. 437.

[2] Arambourg, C., 1933. C. R. Soc. géol. France, No. 14, pp. 221, 222.

	Terraces	Age	Cultures	Climate	Faunal Aspects	Proboscideans
Recent	Present level	Post-Würm	Aurignacian and later cultures	Progressive desiccation Hot and dry	Reduction of fauna, especially Ethiopian types	*Loxodonta africana*
Pleistocene IV	15-20 meter terraces	Würm glacial U. Monastirian	Mousterian; beginning of Aurignacian	Relatively cold and humid		*Palæoloxodon jolensis*
3	Negative movement	Riss-Würm interglacial L. Monastirian	Acheulean: beginning of Mousterian		Europe N. Africa Africa Ethiopian elem. Eurasiatic elements	
III	30 meter terraces, shorelines	Riss glacial U. Tyrrhenian	Chellean; beginning of Acheulean	Hot and humid	Influx of Eurasiatic mammals, giving the North African fauna a "European" aspect	
2	Negative movement	Mindel-Riss interglacial L. Tyrrhenian			Europe N. Africa Africa Ethiopian elements Eurasiatic	*Palæoloxodon atlanticus*
II	55-60 meter terraces	Mindel glacial U. Milazzian			Fauna distinctly African in character contrasted with European fauna due to withdrawal of Ethiopian elements from the latter	
1	Negative movement	Günz-Mindel interglacial L. Milazzian			Europe N. Africa Africa Ethiopian elements Eurasiatic	
I	90-100 meter terraces, shorelines	Günz glacial U. Sicilian-Cromerian			Faunas similar, due to wide spread of Ethiopian forms Appearance of progressive Pleistocene mammals Persistence of many Pliocene forms	
	Negative movement	L. Sicilian				*Archidiskodon planifrons* *Archidiskodon meridionalis*
	130-150 meter terraces, shorelines	St. Prestian				
	Negative movement	Villafranchian				
Pliocene	200 meter terraces, shorelines			Hot and humid	Upper Pliocene mammals Distinctly African	Mastodont

ALGERIA.—In a very succinct account of the Pleistocene of Algeria, Romer (1928)[1] summarizes the work of previous authors, notably Thomas, Pomel, Tournouer, Pallary, Joleaud, Boule, Stromer, Lamothe, Depéret, and Solignac, by showing that in North Africa a division of the Pleistocene must of necessity be based on the sequence of mammalian faunas, the sequence of cultures, and the development of shorelines and river terraces. As Romer has remarked, the development of correlations by the use of the above methods is very apt to lead into a "vicious circle," whereby each line of evidence depends upon and in turn supports every other line of evidence; consequently the application of these several methods of correlative attack must needs be accomplished with the greatest of circumspection. When, however, such studies are carried out with a great deal of care, and when all modifying factors have been accounted for, the following facts as to the Pleistocene sequence would seem to be evident.

Romer, following Depéret and Mayet, placed the base of the Pleistocene in North Africa above the Villafranchian and the St. Prestian and below the Lower Sicilian. In this he followed the general practice of European palæontologists. Recently (Matthew, 1929,[2] Hopwood, 1935,[3] Colbert, 1937[4]) it has been argued that the Villafranchian is truly of Pleistocene age, for it contains certain immigrant types that may be taken as diagnostic of the beginning of the Pleistocene. These are particularly the true elephants of the genus *Archidiskodon* and the true horse of the genus *Equus*. If this correlation holds good, then the Pleistocene in North Africa would open with the negative movement of the Villafranchian, followed by the establishment of the high 150 meter terraces, and this in turn followed by the Lower Sicilian negative movement.

The Pleistocene succession of Algeria is characterized by some very interesting faunal developments, of which brief notice may be taken here.

The close of the Pliocene in the North African region was a period of warmth, with a rather humid climate. The fauna was distinctly African in its character, and it contained such typically Pliocene genera as *Machairodus*, *Hipparion*, a mastodont, a primitive hippopotamus, *H. hipponensis*, and a gigantic giraffid, *Libytherium*. According to Romer, *Equus stenonis* was present at this time—a slightly earlier occurrence of this horse than its more characteristic Villafranchian appearance. It is to be noted in this connection that *Equus stenonis* may not belong to the genus *Equus*, but rather may show relationships with the Upper Pliocene American equid, *Plesippus*.

The beginning of the Pleistocene, here regarded as the advent of the Villafranchian, was marked by the continuation of the warm, moist climate of the Upper Pliocene, and concomitantly by the continuation of many characteristic Upper Pliocene mammals. In this period, however, certain new and immigrant forms appeared; these were the true elephants, particularly *Archidiskodon planifrons*, the true *Equus*, the modern type of *Hippopotamus*, and a varied array of bovids—antelope and cattle. These immigrant types that set the Villafranchian apart as the opening of a new era in mammalian history continued for the most part to the end of the Pleistocene and on into recent times, while the holdover Pliocene forms that give to the Villafranchian its rather Pliocene appearance died out sooner or later in the Pleistocene. Yet some of these characteristic Pliocene mammals, particularly *Hipparion*, persisted well into the Pleistocene in Algeria—a telling demonstration of the fact that mammals are prone to continue beyond the period of their "typical" expression in geologic time. So it is that new and immigrant types are much more reliable as diagnostic time markers in the study of faunal successions than are the "characteristic" or "typical" forms, which may persist from one period to the next.

The development of the Pleistocene in Algeria was marked by a long period of warm, to hot, humid climates, beginning in the Pliocene and lasting to the opening of Upper Pleistocene times. During a portion of the Upper

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[1] Romer, A. S., 1928. Bull. Logan Mus., I, No. 2.

[2] Matthew, W. D., 1929. Bull. Amer. Mus. Nat. Hist., LVI, pp. 437-500.

[3] Hopwood, A. T., 1935. Proc. Geol. Assoc., XLVI, Pt. 1, p. 46.

[4] Colbert, E. H., 1937. "The Pleistocene Mammals of North America and Their Relations to Eurasian Forms," in Early Man as Depicted by Leading Authorities at the International Symposium The Academy of Natural Sciences Philadelphia, March, 1937. 8vo, J. B. Lippincott Company, Philadelphia, pp. 173–184.

Pleistocene, the Monastirian, there would seem to have been an interval of relatively cold, but humid weather, which in turn was followed by a rise in temperature and a final desiccation of the entire North African region.

At the beginning of the long warm, humid period, the fauna of North Africa was quite similar to that of Europe, due in large part to the northward extension of many Ethiopian types of mammals. But during the development of the Pleistocene there were differential changes in the relationship between the North African, Eurasiatic, and Ethiopian faunas, due to the "de-Africanization" of the European fauna and the "Europeanization" of the North African fauna. In other words, there was a succession of faunal movements with results somewhat as follows.

1. Similarity between North African and European faunas, due to extension northwardly of African types of mammals. Africanization of Europe.

2. Withdrawal of African forms from Europe, causing a dissimilarity between this region and North Africa. De-Africanization of Europe.

3. Influx of European types into North Africa again establishing a similarity between the North African and European faunas, but causing the former to be different from the lower African fauna or faunas. Europeanization of North Africa.

This history would seem to have been complicated in its end stages by the fluctuations in the desiccation of North Africa. According to Romer, there was a period of aridity following the Mousterian, causing the more tropical elements in the North African fauna to migrate southwardly. This period was followed by a humid period during the Neolithic, at which time these warmth loving animals reëstablished themselves in the North African region, where they continued, but in gradually diminishing strength, until recent times. The final, slow diminution of the North African fauna has been due largely to the post-Pleistocene desiccation of the region, which has been quite marked during historic times.

PROBOSCIDEANS: See table, above.

6. THE PLEISTOCENE OF CENTRAL AND EAST AFRICA

Fossiliferous mammal localities are known in Central Africa from Kenya Colony, Uganda, Tanganyika Territory, Nyasaland, and northern Rhodesia. The occurrences and geologic ages of these Central African faunas have been excellently summarized by Hopwood (1929).

Hopwood has shown that the fossil mammals of Central Africa are, for the most part, immigrant types that have migrated into this region from the north and from the east. Here, protected in something of an ecological "backwash," there has been a tendency for primitive forms to persist to relatively late geologic dates, thereby giving to the African faunas a somewhat less advanced aspect than is consistent with their real ages. In this respect, there is a close similarity between the fossil faunas of Africa and India, in which latter region there is a tendency for the fossil mammals to be homotaxially related to assemblages of earlier ages in other portions of the world. And it is an interesting fact that India, like Africa, was more or less separated from the rest of the world during late Tertiary times—the one by the high Himalaya Mountains, the other by the developing Mediterranean Sea and the expansive waste of northern Africa.

Of the Pleistocene faunas of Central Africa, by far the most important and the most complete is the Oldoway or Olduvai fauna. This assemblage Hopwood considers to be no older than Middle Pleistocene in age. The other Pleistocene faunas of Central Africa are those of Lake Rudolph, Karungu, Homa Mountain, Kaiso, and Lake Nyasa—all related to the Oldoway fauna and all essentially equivalent to it in age.

In the following pages the Oldoway fauna will be considered in some detail, while the other Pleistocene faunas named above, since they are essentially similar to the Oldoway fauna, will be treated more briefly.

OLDUVAI (OLDOWAY).—The Olduvai (or Oldoway) locality in Tanganyika Territory, along the southeastern shore of Lake Victoria, was first explored for fossil vertebrates in 1913, by an expedition under the leadership of Dr. H. Reck, and more recently in 1931, by an expedition led by Dr. L. S. B. Leakey, who had as one of his coworkers Dr. A. T. Hopwood. The principal contributors to the problem of the age of the Olduvai fauna have been Dr. W. O. Dietrich, working on the basis of the material collected by Dr. Reck and his associates, and Dr. Hopwood, basing his studies on his own personal observations of the region and on material that he collected there.

The deposits at Olduvai are of volcanic origin, being composed of fine volcanic tuffs that seemingly were accumulated in shallow lake basins. Lithologically the Olduvai beds are divisible into five horizons or layers, which have been described by Hopwood[1] as follows:

> Exposed in the cliffs of the gorge are four main beds, lying on a thick flow of lava. The first, or bottom bed is known as Bed I. It consists of silvery grey tuffs, with yellow pumiceous layers and concretionary bands. It is the thickest of the four, with very little earthy contamination, and its deposition, although discontinuous, was very rapid. To the east it is practically barren of fossils, but to the west it yielded crocodiles, antelopes, elephants, *Dinotherium*, the three-toed horse (*Hipparion*), and zebras.
>
> Bed II is mainly buff-coloured. It is more massive and earthy than Bed I, with which it is entirely conformable. At the time it was deposited, the rainfall was of varying intensity, and extra wet seasons are represented by beds of pebbles. The fossils from this bed are much the same as those from Bed I, but we did not find *Dinotherium*, and in 1913 Professor Reck recovered a human skeleton from here.
>
> Bed III is the most useful for stratigraphical purposes owing to its bright red colour. It is conformable to Bed II, but dies out to the west. This suggests that the volcanoes were dormant, and their reddened decomposition products were washed into the lake from the east. The bed itself is hard and close grained, with occasional layers of pebbles and gravel.
>
> Conformable to the last is Bed IV, a grey or brown bed, with a reddish phase in its western extension. It reflects in its structure and composition the gradual drying up of the lake. In a pebbly layer near the top we found an incomplete skeleton of a hippopotamus with over a hundred quartzite hand-axes lying on or among the bones.
>
> Next comes a marked unconformity, followed by a complex series of deposits of wind-blown dust known collectively as Bed V.

Recently (1933) Dietrich[2] has published his conclusions as to the age of the beds at Olduvai. The sequence of deposits, according to Dietrich, range throughout the extent of the Pleistocene: Horizon 1 is of Lower Pleistocene age, Horizons 2, 3, and 4 are of Middle Pleistocene age, and Horizon 5 may be assigned to the Upper Pleistocene. Dietrich bases his conclusions on the supposed restriction of the Pliocene elements, *Dinotherium* and *Stylohipparion* to the lowest horizon, on the general Middle Pleistocene character of the bulk of the fauna, found in Horizons 2 to 4 inclusive, associated with Chellean and Acheulean industries, and on the supposed discordance between the topmost horizon and the bed beneath it, together with the presence of Mousterian and Aurignacian cultures in this uppermost layer.

Horizont 5	Steppenkalk ('Löss'). Moustier? Aurignac. Recente Fauna.
	Diskordanz
Horizont 4	Graue Tuffite mit Geröllagen. *Elephas antiquus recki*, *Hippopotamus gorgops*, *Pelorovis oldowayensis*, Fische, Muscheln. Acheul-Industrie.
Horizont 3	Grellrote harte Tuffite mit eingelagerten Schottern ('Rote Bank'), Fauna wie in 2. Jüngeres Chelles.
Horizont 2	Stumpffarbige, erdige Tuffite mit Geröllagen. Fauna wie in 1, aber ohne *Dinotherium*. Chelles-Industrie.
Horizont 1	Graue Tuffite mit Praechelles-Industrie. Fauna mit *Dinotherium*, *Elephas antiquus recki*, dreizehigen Pferden, Zebras, Antilopen, Krokodilen, Schildkröten.
	Lava.

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[1] Hopwood, A. T., 1932. "The Olduvai Expedition, 1931." Nat. Hist. Mag., III, pp. 219, 220.

[2] Dietrich, W. O., 1933. Centralblatt f. Min., etc., Jahrg. 1933, Abt. B, No. 5, p. 300.

Somewhat opposed to Dietrich's conclusions are Hopwood's final conclusions as to the age of the Olduvai deposits. This author, as a result of his field work at Olduvai and his subsequent studies of the fauna, has decided that the four lower successive beds represent a more or less continuous series, all of Middle Pleistocene age, for he found that the lowest bed contained a large representation of Olduvai mammals, in all respects similar to the forms from the beds above. This was in contrast to Dietrich's conclusion that Horizon 1 is relatively barren of fossils.

Therefore, in speaking of the Olduvai fauna, Hopwood[1] said that: "Die fauna von Oldoway muss daher als einheitlich, und zwar als mitteldiluvial, betrachtet werden."

As to the uppermost bed, Horizon 5, Hopwood makes no comment in this latest contribution of his. Since it is separated from the underlying sediments by a distinct disconformity and since its origin is entirely different from that of the beds preceding it (this bed is composed of a complex series of wind-blown dust) the evidence would seem to be strongly in favor of a later age for this uppermost bed.

Therefore, the sequence of deposits at Oldoway might be represented in the following manner.

Horizon 5—Late Pleistocene

4
3 Middle Pleistocene
2
1

Lava

A complete list of the Olduvai fauna as known at the present time is presented below. An examination of this fauna will show at once that it is decidedly African in its constitution, and for the most part the various genera and species comprising the fauna are rather closely related to the modern African mammals of the same or nearby regions. There are, however, some curious associations in the Olduvai fauna, and since these have considerable bearing on the age of the assemblage, they will be commented on at this place.

First of all, it is to be noted that the Olduvai fauna contains a number of really primitive holdovers—mammals that are not generally considered as being of Pleistocene age. These are, specifically, an *Hipparion* (*Stylohipparion albertensis*) and a dinothere (*Dinotherium hopwoodi*[2]), mammals that are to be expected in the Pliocene rather than in the Pleistocene. The *Stylohipparion* is found at Olduvai associated with true *Equus* of the zebra type. A similar association of *Hipparion* and *Equus* has been noted in North Africa (above), so it would seem that the Pleistocene persistence of *Hipparion* and its relatives is a phenomenon restricted to Africa.

As against this occurrence of primitive Tertiary types in the Olduvai beds there is the presence of certain very advanced forms. Most notable of these is *Hippopotamus gorgops*, a species that must be considered as the most specialized member of the Hippopotamidæ. Its extremely elevated orbits and constricted muzzle, with widely flaring canines and long face, mark this form as being structurally more advanced than the modern *Hippopotamus amphibius*.

The bulk of the fauna is, as indicated above, closely related to the modern African fauna of the same general locality. This is particularly apparent among the carnivores, the pigs, and the antelopes. It might be well to say

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[1] Hopwood, A. T., 1937. "Die Fossilen Pferde von Oldoway." Wissenschaftliche Ergebnisse der Oldoway-Expedition 1913, heraus. v. H. Reck, N. F., Heft 4, p. 135.

[2] *Dinotherium bozasi* (Osborn's *D. hopwoodi* is a synonym). Hopwood, A. T.—Personal communication.

that certain members of the Olduvai fauna are undoubtedly immigrants from the north and from the east, and these forms have been used to advantage in correlating the assemblage with contemporaneous Eurasiatic faunas. Characteristic of these immigrant forms are '*Elephas*' *antiquus recki*, closely related to *Hesperoloxodon antiquus* of the European Pleistocene, and *Sivatherium olduvaiensis*, a link with *Sivatherium giganteum* of the Upper Siwalik beds of India.

The Olduvai Fauna

Canis africanus Pohle
Lupulella mesomelas latirostris Pohle
Prototocyon recki Pohle
Hyæna aff. *brunnea* Thunberg
Felis aff. *caffra* Desmarest
Deinotherium hopwoodi Osborn (a synonym of *Dinotherium bozasi* Arambourg—Hopwood)
Hesperoloxodon antiquus recki (Dietrich) = *Palæoloxodon recki* (Dietrich)—Osborn (p. 1275 of the present memoir)
Papio sp. Remane
Simopithecus leakeyi Hopwood
Stylohipparion albertensis (Hopwood)
Equus oldowayensis Hopwood
Rhinoceros simus germano-africanus Hilzheimer
Koiropotamus majus Hopwood
Koiropotamus sp. Dietrich
Notochoerus dietrichi Hopwood
Notochoerus sp. Dietrich
Phacochoerus sp. Dietrich
Hippopotamus gorgops Dietrich
Sivatherium oldowayensis Hopwood
Giraffa sp. Dietrich
Pelorovis oldowayensis Reck
Philantomba monticola (Thunberg)
Tragelaphus scriptus (Pallas)
Tragelaphus speckii stromeri Schwarz
Tragelaphus strepsiceros (Pallas)
Thaleroceros radiciformis Reck
Taurotragus oryx pachyceros Schwarz
Nesotragus moschatus von Duben
Gazella gazella praecursor Schwarz
Gazella granti Brooke
Phenacotragus recki Schwarz
Beatragus hunteri Sclater
Damaliscus angusticornis Schwarz
Pultiphagonides africanus Hopwood
Parmularius altidens Hopwood

It might be well at this place to present the following citation from a recent paper by Hopwood.[1]

> Neither did big faunal changes take place in Africa until late in the Pleistocene. For example, the lower Pleistocene deposits of Kenya Colony and Uganda contain primitive elephants, mastodonts, *Stegodon*, *Deinotherium*, *Sivatherium*, *Stylohipparion*, *Equus oldowayensis*, *Hippopotamus gorgops*, *H. imaguncula*, and large pigs of the *Notochoerus-Metridiochoerus* group. In the Middle Pleistocene of Kenya Colony and Tanganyika Territory the primitive elephants, *Stegodon* and *Hippopotamus imaguncula*, have become extinct, but the other species continue. *Deinotherium* and a mastodont are both known from Bed II at Olduvai; they have not yet been found in the higher beds (III, IV). The most striking newcomer is the elephant, *E. antiquus recki*, which replaces the primitive forms of the lower Pleistocene. . . .
>
> The upper Pleistocene fauna, so far as we are at present acquainted with it, contains nothing but Recent species. All the forms mentioned in the list of the lower and middle Pleistocene faunas appear to have become extinct.

PROBOSCIDEANS: See list of Olduvai fauna, above.

KAISO.—The Kaiso bone beds are located on the eastern shore of Lake Albert, Uganda. These deposits have yielded a fairly extensive series of vertebrate remains, of both aquatic and terrestrial types, associated with freshwater Mollusca. The vertebrates include such mammals as "*Rhinoceros*," two kinds of equids, various pigs, *Hippopotamus*, and proboscideans, aquatic reptiles, namely turtles and crocodiles, and fish. The association of these varied vertebrates with the Mollusca, coupled with the physical expression of the sediments, shows clearly that the Kaiso deposits contain two facies—one freshwater, the other terrestrial, which intergrade laterally each into the other.

In his description of the Kaiso deposits, Wayland[2] made the following remarks:

> Lithologically the bone beds are ironstones ranging in composition from extremely ferruginous sandstones to moderately pure limonite in which oölitic structure is locally developed. . . . They are not uniformly fossiliferous, but very few, if indeed any, are entirely without organic remains. . . .
>
> It was thought at one time that the different ferruginous horizons were characterized by different types of fossils, but within the limits of the investigation this view has proved erroneous, for the transition of lacustrine to terrestrial types of organisms, of

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[1] Hopwood, A. T., 1940. Proc. Geol. Assoc., LI, Pt. 1, pp. 86, 87.

[2] Wayland, E. J., 1926, "The Geology and Palæontology of the Kaiso Bone-Beds." Uganda Protectorate, Geol. Surv. Dept., Occasional Paper, No. 2, pp. 9–11.

> which this faunistic difference consists, is found to be lateral rather than vertical. Indeed it appears probable that, could one trace an ironstone patch completely to its limits, and study in detail the variation of its fossil contents, the purely lacustrine organisms would, in general, be found grouped toward the centre, the terrestrial forms round the periphery, and a graduated mixture of aquatic and land-frequenting species between. At any rate the evidence so far gathered points that way. It would appear then that the ironstone patches of any one horizon represent, singly or severally, a number of pools that constituted the remains of a desiccated Albertine lake of Plio-Pleistocene days.

Hopwood, who described the mammals from the Kaiso deposits, identified the forms given in the list below.

Machairodus sp.
Rhinoceros scotti
Hipparion albertensis
Equus zebra
Chalicothere
Sus limnetes
Hylochœrus euilus
Hippopotamus amphibius kaisensis
Hippopotamus imaguncula
Elephas zulu (*Loxodonta zulu* of this Memoir)
Elephas aff. *meridionalis* (*Archidiskodon meridionalis* of this Memoir)

Hopwood's original conclusions were that this fauna is for the most part typically African in its complexion, that it contains certain immigrant forms from the northeast, namely, *Hipparion* and *Archidiskodon meridionalis,* that the small hippopotamus, *H. imaguncula*, is closely related to the Pleistocene Mediterranean form, *H. madagascariensis,* and that the fauna is of Pliocene age. Subsequently (1929), he decided that the Kaiso fauna, like the other related faunas of Central Africa, is certainly of Pleistocene age, a conclusion thoroughly justified by the facts of the case. The presence of *Machairodus, Hipparion,* and a chalicothere in the Kaiso fauna is certainly due to the persistence of these forms into the Pleistocene.

In a recent communication to the author Hopwood makes the following statement: "Additional material seems to show that only one elephant occurs at Kaiso, namely '*Loxodonta griqua*' Haughton. An undescribed *Stegodon* has also been found there."

PROBOSCIDEANS: See faunal list, above.

LAKE NYASA.—The fossils from Lake Nyasa come from the Chiwondo Beds of Uraha Hill. The specimens are extremely fragmentary and scanty, being broken proboscidean teeth identified by Hopwood as belonging to a "*Bunolophodont Mastodon*," and several bones referred to *Hippopotamus*. The age is probably Pleistocene.

HOMA MOUNTAIN.—At Homa Mountain, near the eastern shore of the Victoria Nyanza, there have been found various fossil remains of antelopes, *Phacochœrus, Hippopotamus,* and a baboon, described by Andrews as *Simopithecus oswaldi*. In 1926 Hopwood described additional mammals from Homa Mountain, as follows:

Hippopotamus amphibius Linn.
Metridiochœrus andrewsi Hopwood
Phacochœrus æthiopicus Linn.
Bos sp.
Elephas antiquus recki Dietrich[1]

The complexion of this fauna is distinctly Pleistocene, and since the primate is closely related to the *Papio* from Oldoway, described by Remane, while there is complete identity between the proboscideans of these two regions, there is every reason to think that the Homa Mountain deposits are contemporaneous with those of Oldoway. This would make the age Middle Pleistocene.

PROBOSCIDEANS: See faunal list, above.

LAKE RUDOLPH.—Fossils from this area, which may be designated as belonging to the Omo fauna, were first described by Haug in 1911. In recent years the Omo fauna has been made a subject of special investigation by Arambourg,[2] who has shown that:

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[1] "Kanjera *Elephas antiquus recki*. This locality includes Homa Mountain." Hopwood, A. T.—Personal communication.

[2] Arambourg, C., 1935. Bull. Soc. géol. France, (5), IV, pp. 306, 307.

1. The Omo fauna closely resembles that of Olduvai
2. Like the Olduvai fauna it contains:
    a. Many typically African genera similar to the modern forms in the same area.
    b. Certain persistent types, that would seem to be holdovers from Tertiary times.

> Les gisements de Vertébrés de l'Omo n'ont point livré d'industries humaines. Leur association faunique paraît correspondre en partie à celle que Leakey a observée dans le ravin d'Oldoway (Tanganyika) immédiatement au-dessous des niveaux à industries de faciès chelléen; il paraît donc logique de les considérer comme appartenant à cette période de transition qui sépare, en Europe, la fin du Pliocène de l'apparition des industries humaines, si tant est que l'on puisse admettre le synchronisme de celles-ci entre des régions aussi éloignées.

It is a foregone conclusion, therefore, that since the mammalian assemblage at Omo would seem to be virtually identical with that of Olduvai, it is contemporaneous with the latter and consequently is of approximate Middle Pleistocene age (compare faunal list on page 1435).

PROBOSCIDEANS:

Dinotherium bozasi Arambourg (*D. hopwoodi* Osborn a synonym—Hopwood)
Palæoloxodon antiquus recki (Dietrich)

7. THE PLEISTOCENE OF SOUTH AFRICA

ZULULAND.—The fauna described by Scott (1907)[1] from Zululand has a decidedly advanced aspect. It is doubtful whether this fauna is any older than the Middle Pleistocene and it might be even later than this in age. Hopwood,[2] by inference, would make this assemblage more or less contemporaneous with the Middle Pleistocene faunas of Central Africa.

"The fossil mammals of South Africa are all of comparatively recent date. They have been described by various authors, . . . and the general assemblage differs from those of the same date in Central Africa only in matters of detail."

In a recent letter to the author, Hopwood states that the Zululand fossils are, in his opinion, equivalent in age to the Olduvai fauna. The fauna as described by Scott, is as follows.

Opsiceros simplicidens Scott
Loxodonta zulu Scott
Hippopotamus ponderosus Scott
Bubalus andersoni Scott

The fossils from Zululand were placed by Scott in the Upper Pliocene, because of the seeming presence of marine beds with Tertiary molluscs *above* the sediments in which the mammals were found. On the other hand, Scott recognized the obvious Pleistocene character of the mammalian remains, admitting that they might be more properly placed in the Pleistocene than in the Pliocene.

> Concerning the position and mode of occurrence of these fossils Mr. Anderson writes as follows: 'The fossils were scattered over a large flat outcrop of shales, which occurs below the level of ordinary low-water mark, and is only exposed under the exceptional circumstances of a strong south-easterly gale and a neap tide, when the large covering of sand is removed. Overlying this bed are a series of shales with a few scattered bones and crustacean and fish remains. Above these a thin layer containing Foraminifera, and then a foot or so containing marine Mollusca, which Mr. Etheridge referred to the Tertiary period; above this a thick series (probably over 100 feet) of false bedded sands of various colours covered by the Recent sand dunes.'
>
> Seeing that these mammals all belong to existing genera, and that, with the exception of the elephant, they differ but comparatively little from Recent Ethiopian species, it is obvious that the fossils cannot have any very great geological antiquity, and probably they should be referred to the later Pliocene. So far, however, as the mammals themselves are concerned, they might almost equally well be regarded as early Pleistocene.

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[1] Scott, W. B., 1907. Third Report of the Geological Survey of Natal and Zululand, pp. 253, 254.

[2] Hopwood, A. T., 1929. Amer. Journ. Sci., (5), XVII, p. 103.

Due to the conditions under which these fossils were found, it is indeed doubtful whether they were in place beneath marine Tertiary sediments.

Proboscidean: See faunal list, above.

Vaal River.—From the Vaal and Limpopo rivers (principally the former) of the Transvaal, South Africa, a bewildering array of fossil elephants has been described during the course of the past fifteen years. The first descriptions were made by Haughton (1922), supplemented in more recent years by the rather prolific creation of species by Dart (1927, 1929), with additional contributions by Osborn (1928). These fossils for the most part come from various localities and from different stratigraphic positions along the Vaal River, and since there exists a considerable amount of confusion as to their stratigraphic positions and geologic ages, the problem of their deposition and associations must be approached with a great deal of caution.

Essentially, the condition along the Vaal River, south of Johannesburg and in the vicinity of Bloemhof, is as follows.

There are three terraces exposed along the river, a high terrace some 200 to 300 feet above the river bed, a middle terrace at approximately 60 to 80 feet above the water, and a low terrace grading into river-bed gravels contiguous to or within the present river. The high terrace is, so far as known at present, unfossiliferous. It is from the middle terrace and the low terrace and river gravels that the several types of fossil elephant teeth have been found. It might be added, too, that in the middle and low terraces and the river gravels several distinct stone cultures have been discovered and have been used for the stratigraphic differentiation of the sediments.

Dart concluded that the Vaal River terraces represent successive phases of aggradation by the early Vaal River, the high terrace being of Pliocene age, the middle terrace very probably containing two levels, one of Pliocene age, above which is a later Pleistocene level, and the low terrace being of late Pleistocene age, containing, as suggested by van Riet Lowe, two distinct gravel layers.

In 1932 Haughton[1] raised the question as to the validity of this sequence. He pointed out the very important fact that "the earliest date that can be assigned to any undisturbed river-gravel is the date at which the lowest beds in a continuous sequence were deposited; and that comparisons between gravels at varying distances from a river or at various places along a river valley should be based upon the altitude of the bottom-bed of each deposit with respect to the present river-level, and not upon that of the top of the gravel."

Haughton then went on to show that the middle terrace of the Vaal River is very close to the present river channel, and that at each of the places where fossils or flint implements were discovered in this middle terrace, the *base* of the terrace is only a few feet above the present river-bed level. With this consideration in mind, Haughton presents the possibility that the middle terrace beds and the river gravels or low terrace beds are in reality part of a single, continuous series of deposits. If such be the case, the conclusions of Dart would be greatly modified, since there would be no time-gap between the fossils found in the middle terrace and those of the river gravels. Essentially, the specimens from the middle terrace beds would therefore become much younger in their geologic age than they were considered by Dart or by Osborn.

Which conclusion as to the sequence of the Vaal River deposits is valid, Dart's or Haughton's, is a question that cannot be answered at the present time. As Haughton has pointed out, "Much detailed investigation is necessary before the true sequence of events can be elucidated." It might be mentioned, however, that the

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[1] Haughton, S. H., 1932. Trans. Roy. Soc. S. Afr., XXI, Pt. 1, p. 15.

evidence in favor of Haughton's views is very strong. In this connection Hopwood, in a personal communication to the author, expresses his opinion that Haughton's work is at the present time the most satisfactory interpretation of the Vaal River deposits.

Stratigraphic Relationships of the Vaal River Proboscidea

High Terrace
    Loxodonta subantiqua (Haughton)

Middle Terrace
  Upper level (Lower Pleistocene—Dart; Pleistocene—Haughton)
    Metarchidiskodon griqua (Haughton)
    Archidiskodon yorki Dart

  Lower level (Pliocene—Dart; Pleistocene—Haughton)
    Bunolophodont mastodont
    Palæoloxodon(?) andrewsi (Dart)—from a depth of 80 feet within terrace
    Archidiskodon vanalpheni Dart
    Archidiskodon milletti Dart
    Archidiskodon loxodontoides Dart
    Archidiskodon subplanifrons Osborn—washed in from High Terrace?

Level not specified
    Palæoloxodon archidiskodontoides (Haughton)

Lower Terrace (River Bed Gravels)—Pleistocene
    Archidiskodon broomi Osborn—washed in from Middle Terrace?
    Palæoloxodon transvaalensis (Dart)
    Palæoloxodon sheppardi (Dart)
    Palæoloxodon hanekomi (Dart)—more recent than *P. transvaalensis*?

River Gravels—possibly related to the Lower Terrace gravels
    Palæoloxodon yorki (Dart)
    Palæoloxodon wilmani (Dart)
    Palæoloxodon kuhni (Dart)

Recent
    Loxodonta prima Dart
    Loxodonta africana obliqua Dart

III. THE ORIENT

1. INTRODUCTION

The Oriental region as here defined is that portion of Asia south of the Himalaya Mountains and the Tibetan Plateau, namely, India and Burma and adjacent countries, South China, Indo-China, and the East Indian Islands. Thus the Oriental region as used in this chapter coincides with the *Oriental Region* or *Realm* as used by the zoogeographers. In this case it is practicable to make the zoogeographical term and the term as used herein equal in value—whereas in Africa, as we have seen above, the strict utilization of the zoogeographic division was not convenient for our purposes.

By far the most important part of the Oriental region is northern India, where the tremendous thickness of the Siwalik Series constitutes one of the most remarkable and productive sequences of fossil-bearing beds in the world. Here, through a vertical extent of some twenty thousand feet of sediments, the development of the Upper Tertiary and Quaternary mammalian faunas of India can be traced with the greatest of detail. And throughout this long and virtually unbroken series of fossiliferous beds the remains of fossil proboscideans are of major importance.

But for the earliest Proboscidea-bearing sediments of the Oriental region it is necessary to go outside of the Siwalik area, to Baluchistan and Sind, where the early Miocene continental beds have yielded a considerable fauna.

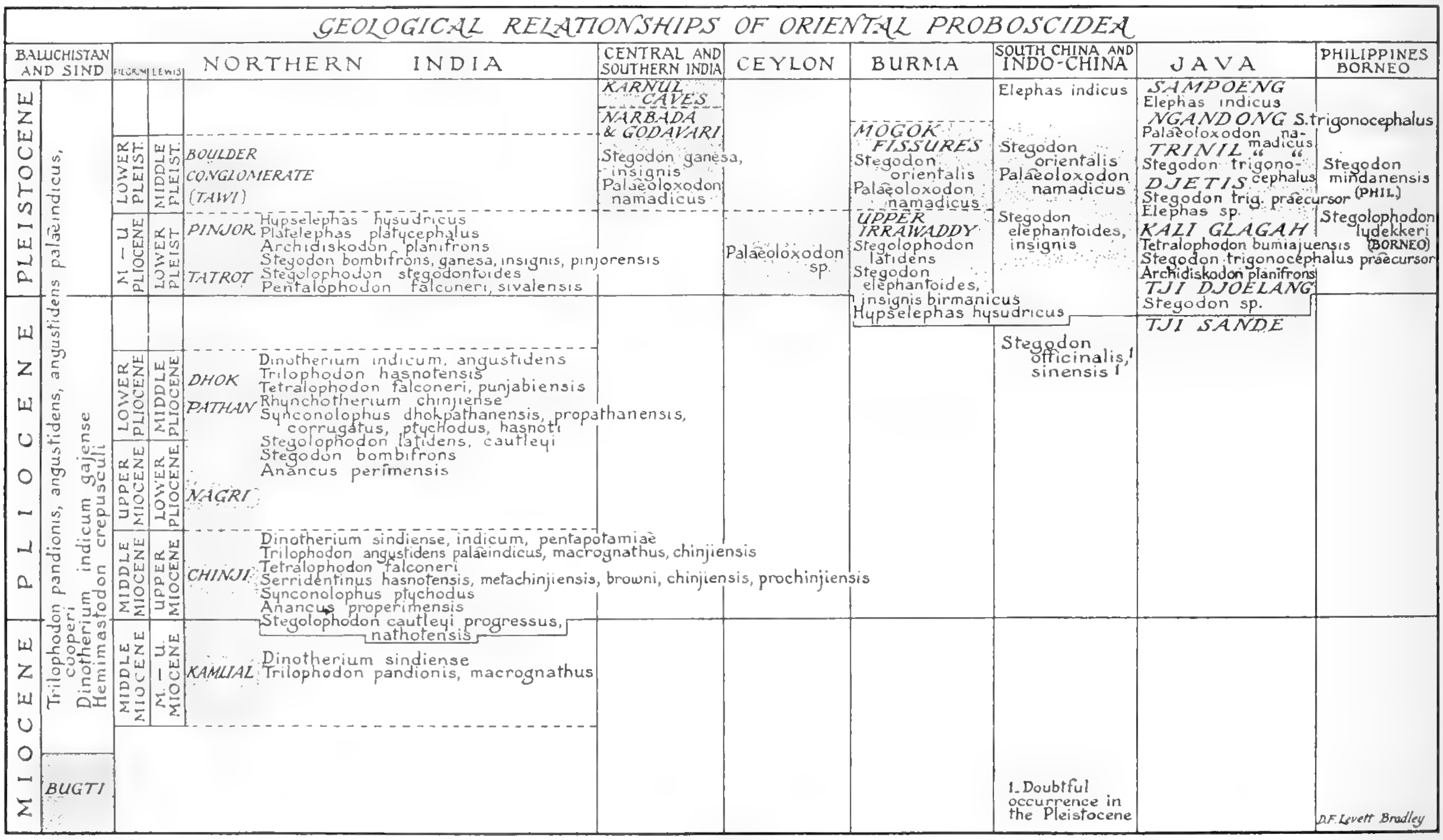
2. THE MIOCENE OF BALUCHISTAN AND SIND

Baluchistan, Bugti Beds.—Fossil vertebrates were found in Baluchistan as long ago as 1846 by Vicary, but it was not until 1882, when Blanford visited the region, that serious attempts at collecting were made. Blanford brought back a few anthracothere remains, which were subsequently described by Lydekker.

But the mammalian fauna of Baluchistan remained virtually unknown until the years 1907–1910, when Pilgrim and Forster Cooper independently conducted several expeditions to that region, particularly to the area of the Bugti Hills, in the vicinity of Dera Bugti, Kumbhi, and Chur Lando, with the result that a large mammalian fauna was discovered.

The mammal-bearing beds of the Bugti Hills have been described by Pilgrim[1] in part as follows:

> The ossiferous Upper Nári series [these beds were subsequently correlated by Pilgrim with the Gaj series, rather than with the older Nári series] of the Bugti country attains a thickness of 1,000 feet, the rocks are subject to considerable lateral variation, and it is often difficult to trace any particular bed for more than a short distance. As it happens, the same fossil species occur at different horizons, so that it has been found impracticable to regard the series otherwise than as a whole. . . .
>
> Fossil bones and teeth are met with at various horizons, from the base of the series up to within 100 feet of the top, on either side of the Zen range south of Dera Bugti and the Sihaf valley, particularly near Gandoi and Kumbhi which are situated on the same meridian on exactly opposite sides of the range. . . Unfortunately, though well preserved, they are for the most part isolated fragments of small size.



GEOLOGICAL RELATIONSHIPS OF ORIENTAL PROBOSCIDEA

	BALUCHISTAN AND SIND	PILGRIM	LEWIS	NORTHERN INDIA	CENTRAL AND SOUTHERN INDIA	CEYLON	BURMA	SOUTH CHINA AND INDO-CHINA	JAVA	PHILIPPINES BORNEO
PLEISTOCENE	Trilophodon pandionis, angustidens, angustidens palaeindicus, cooperi Dinotherium indicum gajense Hemimastodon crepusculi				KARNUL CAVES			Elephas indicus	SAMPOENG Elephas indicus NGANDONG S.trigonocephalus Palaeoloxodon namadicus	
		LOWER PLEIST.	MIDDLE PLEIST.	BOULDER CONGLOMERATE (TAWI)	NARBADA & GODAVARI Stegodon ganesa, insignis Palaeoloxodon namadicus		MOGOK FISSURES Stegodon orientalis Palaeoloxodon namadicus	Stegodon orientalis Palaeoloxodon namadicus	TRINIL " " Stegodon trigonocephalus DJETIS Stegodon trig. praecursor Elephas sp.	Stegodon mindanensis (PHIL.)
		M – U PLIOCENE	LOWER PLEIST	PINJOR Hypselephas hysudricus Platelephas platycephalus Archidiskodon planifrons Stegodon bombifrons, ganesa, insignis, pinjorensis TATROT Stegolophodon stegodontoides Pentalophodon falconeri, sivalensis		Palaeoloxodon sp.	UPPER IRRAWADDY Stegolophodon latidens Stegodon elephantoides, insignis birmanicus Hypselephas hysudricus	Stegodon elephantoides, insignis	KALI GLAGAH Tetralophodon bumiajuensis Stegodon trigonocephalus praecursor Archidiskodon planifrons TJI DJOELANG Stegodon sp.	Stegolophodon ludekkeri (BORNEO)
PLIOCENE								Stegodon officinalis,[1] sinensis [1]	TJI SANDE	
		LOWER PLIOCENE	MIDDLE PLIOCENE	DHOK PATHAN Dinotherium indicum, angustidens Trilophodon hasnotensis Tetralophodon falconeri, punjabiensis Rhynchotherium chinjiense Synconolophus dhokpathanensis, propathanensis, corrugatus, ptychodus, hasnoti Stegolophodon latidens, cautleyi Stegodon bombifrons Anancus perimensis						
		UPPER MIOCENE	LOWER PLIOCENE	NAGRI						
		MIDDLE MIOCENE	UPPER MIOCENE	CHINJI Dinotherium sindiense, indicum, pentapotamiae Trilophodon angustidens palaeindicus, macrognathus, chinjiensis Tetralophodon falconeri Serridentinus hasnotensis, metachinjiensis, browni, chinjiensis, prochinjiensis Synconolophus ptychodus Anancus properimensis Stegolophodon cautleyi progressus, nathotensis						
MIOCENE		MIDDLE MIOCENE	M.–U. MIOCENE	KAMLIAL Dinotherium sindiense Trilophodon pandionis, macrognathus						
	BUGTI									

1. Doubtful occurrence in the Pleistocene

D.F. Levett Bradley

Fig. 1221

In 1912, as the result of more detailed and considered studies of the Bugti fauna, Pilgrim[2] came to the conclusion that it should be correlated with the Gaj series, of Aquitanian-Burdigalian age, rather than with the Nári beds.

In his discussion of the Bugti fauna, Pilgrim shows first that it is separated by considerable differences from the Lower Siwalik fauna of Sind and the Punjab. He therefore concludes that there is a great hiatus between these faunas, a conclusion that is substantiated by the stratigraphic evidence. Continuing, with a comparison between the Bugti fauna and like faunas in Europe and northern Africa, Pilgrim finally concludes that "it seems improbable that the bone beds of the Bugti hills are younger than uppermost aquitanian."

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[1] Pilgrim, G. E., 1908. Rec. Geol. Surv. India, XXXVII, Pt. 2, pp. 141, 143.

[2] Pilgrim, G. E., 1912. Pal. Indica, N. S., IV, Mem. No. 2, pp. 2, 5.

Both Pilgrim and Forster Cooper, as the result of their independent studies on the fossils of the Bugti beds, decided that these remains represent a unit fauna of essentially Lower Miocene age.

In preparing preliminary manuscript and notes for this chapter, Professor Osborn came to the conclusion that the fossiliferous beds at Dera Bugti and at Chur Lando might be assigned to two stratigraphic horizons. This determination was based on the supposed presence of *Baluchitherium* at Chur Lando and its absence at Dera Bugti, denoting in his opinion the fact that the beds at the former locality were older than those at the latter place.

"Upper level: Dera Bugti bone beds; no remains of *Paraceratherium* or *Baluchitherium*. Lower level: Chur-Lando bone beds; *Baluchitherium* or *Paraceratherium* life zone." (Osborn, H. F., Notes.)

In his most recent notes, Professor Osborn marked the "Chur-Lando bone bed" as of Lower Miocene age and the "Dera Bugti bone bed" as of Lower to Middle Miocene age.[1]

Since Professor Osborn's supposition of two zones or levels in the Bugti beds was quite contrary to the published opinions of both Pilgrim and Forster Cooper, it was thought advisable at the time to secure statements from these authorities as to the probabilities of such a division. I take the liberty of quoting from their letters, written in reply to the request.

> Personally I am not convinced of the necessity for erecting a stage for the Chur Lando bone bed with *Baluchitherium*, separate from the rest of the Bugti stage of the Gaj, but in any case it seems impossible that any part of the Bugti stage can be newer than the Burdigalian. This is proved by the fact that 4000 feet or more of Murrees north of the Salt Range intervenes between the Kamlial stage (Helvetian) and the *Fatehjang stage* which contains *Baluchitherium*, *Anthracotherium* cf. *bugtiense*, *Brachyodus* cf. *africanus*, *Hemimeryx*, *Palaeochoerus pascoei* and *Brachypotherium fatehjangense*. Thus even if the Kumbhi and Gandoi beds are the equivalent of a stage in the Murree a considerable way above the Fatehjang, they must still fall into the Burdigalian.
>
> If the Chur Lando bone bed is earlier than the oyster beds with which presumably the Kumbhi fauna is associated, there is much more to be said for Professor Osborn's view, but this seems hardly likely, nor apparently does Cooper suggest anything in support of this conjecture.
>
> *Baluchitherium* may of course have died out suddenly before the bulk of the Bugti beds was deposited, but it seems to me as reasonable that the Chur Lando bone bed was a sort of cemetery for that particular species, and may have been contemporaneous with the Kumbhi beds.
>
> If one is determined to invent stratigraphical possibilities, then I should say that the Chur Lando bone bed may be of any age later than the Stampian, that an unconformity separates it from the Kumbhi and Khajuri beds, which through the associated oysters must be at any rate Burdigalian, probably Lower Burdigalian. At the same time I do not see why *Baluchitherium bugtiense* should not be Burdigalian just as much as *Cadurcotherium indicum*, since the latter genus elsewhere occurs in the Oligocene. Cooper alone is in a position to estimate the stratigraphical value of the Chur Lando bone bed, and if he thinks that both it and the Kumbhi beds are later than the oyster beds then both Professor Osborn's stages must lie in the Burdigalian. (Pilgrim, G. E., September, 1931. Personal communication to E. H. Colbert.)

> A good number of my specimens were picked up on the ground washed out by rains so that their precise level must remain in doubt. *Personally I cannot feel that there are sufficient grounds for establishing two horizons*, and it is pretty clear that *Paraceratherium bugtiense* is not confined to the Churlando deposit as a number of large lower molars were found scattered in other parts. This is sufficiently clear when you remember that Pilgrim was the first to describe the species and that the *Churlando bone bed was not discovered and opened up until I went to Baluchistan some time later.* No one of Pilgrim's specimens therefore can be considered as coming strictly from this bed. (Cooper, C. Forster, 1932. Personal communication to E. H. Colbert.)

PROBOSCIDEANS:

Trilophodon pandionis Falconer
Trilophodon angustidens palæindicus (Lydekker)
Trilophodon angustidens (Cuvier)
Trilophodon cooperi Osborn
Dinotherium indicum gajense Pilgrim
Hemimastodon crepusculi Pilgrim [SUINA of Osborn]

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[1] In Volume I of this Monograph (page 275, caption to figure 221) the "Chur-Lando" horizon is designated as being of Upper Oligocene age. Professor Osborn was inclined at times to regard this correlation as the correct one, thereby making the "Dera Bugti" beds of Lower Miocene age. In this discussion his later views, as presented above, are followed.

Sind.—Any remarks as to the Bugti beds in Baluchistan apply equally well to the contemporaneous deposits of Sind. Pilgrim[1] discussed the Lower Miocene of Sind as follows.

> I have elsewhere remarked upon the close similarity to the Bugti bone beds presented by certain unfossiliferous sands and conglomerates at Bhagathoro in Lower Sind. These also rest upon Lower Nari limestones and were referred by Blanford to the Upper Nari. Mr. Vredenburg, however, considers that a shell bed, which overlies them, is Upper Gaj. There seems, therefore, little doubt that these, like the Bugti beds, represent a fresh water facies of the Gaj. . . . Generally, these beds do not contain more than mere fragments of vertebrates, but near Fatehjang, *Anthracotherium bugtiense, Brachyodus* cf. *africanus, Teleoceras fatehjangense,* a species very closely allied to *Teleoceras blanfordi,* and a species of *Hemimeryx* have been found. Across the Indus, in the Kohat district, there occurs in similar beds a ribbed *Unio,* which may be the same as one of the curious ribbed species found in the Gaj series of the Bugti hills.

3. THE SIWALIK SERIES (MIOCENE—PLEISTOCENE) OF NORTH INDIA

Punjab, Northwestern India.—In the northern Punjab district, along the Siwalik Hills and in the Salt Range are found tremendously thick deposits of continental sediments, constituting the Siwalik Series, the most important mammal-bearing beds in the Oriental region and likewise, one of the most important mammal-bearing series in the world. Here are exposed more than twenty thousand feet of sediments, deposited as a more or less unbroken sequence ranging from the Miocene through the Lower or Middle Pleistocene periods. Since the Siwalik Series is a continuous sequence of sediments, it will be convenient to discuss the various divisions of the series together.

The Siwalik Series has been divided in its larger aspects into three main divisions or groups, namely, the Lower Siwalik, the Middle Siwalik, and the Upper Siwalik beds. Each of these three principal groups of the Series has again been divided into formations or zones, as follows.

Upper Siwalik	Boulder Conglomerate (Tawi of Lewis)	
	Pinjor	(Tatrot of Lewis)
	Tatrot	
Middle Siwalik	Dhok Pathan	
	Nagri	
Lower Siwalik	Chinji	
	Kamlial	

The establishment of this detailed sequence of deposits is the result of studies that began with the pioneer work of Hugh Falconer, a century ago, and which have continued up to the present time. Numerous authors have contributed to the Siwalik problem, notably Falconer, Cautley, Lydekker, Pilgrim, Matthew, Colbert, Lewis, and de Terra and Teilhard. Naturally opinions have differed as to the proper correlation of the several zones or formations within the Siwalik Series, but generally speaking it may be said that the lowest Siwalik horizons are of Miocene age, while the highest ones are located within the Pleistocene. The intervening beds cover the period of time between the Miocene and the Pleistocene.

Proboscideans appear in the Kamlial formation and they form a very important portion of each fauna through all of the succeeding beds.

Lithologically the Siwaliks show the results of alluvial sediments accumulating in a region closely adjacent to a rapidly uplifting mountain mass. The Lower Siwaliks are sands and clays, with occasional beds of heavier material. These deposits, particularly those of the Chinji zone, are bright red in color and contain what Pilgrim has called "pseudo-conglomerates"—bands of concretionary beds. Passing up into the Middle Siwaliks, the

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[1] Pilgrim, G. E., 1912. Pal. Indica, N. S., IV, Mem. No. 2, p. 2.

sandstones become somewhat coarser, with clay beds less frequent. These Middle Siwalik beds are light gray in color—not red—and they often contain large amounts of relatively unweathered minerals. In the Upper Siwaliks there are sands and clays, often heavily cemented, and capping the series is a very heavy conglomerate made up of extremely coarse gravels and large stones.

These sediments pass upward from the lower to the higher beds with but few apparent breaks. Recent work has shown that there is a distinct angular unconformity between the Dhok Pathan horizon and the overlying Tatrot zone, while the Upper Siwalik Pinjor zone is separated from the capping Boulder Conglomerate by another unconformity.

Although fossils range throughout the extent of the Siwalik Series, three main faunas characterize the sequence. These are the Lower, Middle, and Upper faunas, characteristic of the three groups to which these names are applied. The Lower Siwalik fauna is typically developed in the Chinji formation, the Middle Siwalik fauna in the Dhok Pathan formation, and the Upper Siwalik fauna in the Pinjor formation. The fossils of the Kamlial formation are genetically related to those of the Chinji, while the Nagri fossils are transitory between the Chinji and Dhok Pathan faunas. The Tatrot fossils may be either transitional between the Dhok Pathan and the Pinjor or identical with the latter fauna.

Falconer, who knew only the Upper Siwalik fauna, regarded it as of Miocene age. Lydekker, who described a greater portion of the Middle Siwalik fauna, placed the two faunas with which he was acquainted in the Pliocene. It remained for Dr. Pilgrim to discover the Lower Siwalik fauna, and to show the true relationships of these faunas to each other and to point out their probable ages.

After many years of intensive study of the Siwalik mammals, Pilgrim came to the conclusion that the Lower Siwaliks, Kamlial and Chinji, are of Middle Miocene age (Helvetian and Tortonian, respectively), while the Nagri horizon is to be placed in the Sarmatian or Upper Miocene. Furthermore, he argued that the Dhok Pathan should most properly be placed in the Pontian, and the Tatrot and Pinjor in the middle and upper portions of the Pliocene, respectively. The Boulder Conglomerate was placed by Pilgrim in the Lower Pleistocene. Pilgrim's views,[1] which have been recently epitomized in a short paper on the correlation of the Siwaliks (1934), may be shown to advantage as follows.

Lower Pleistocene	Boulder Conglomerate
Upper Pliocene (Val d'Arno)	Pinjor
Middle Pliocene (Montpellier)	Tatrot
Lower Pliocene—Pontian	Dhok Pathan
Upper Miocene—Sarmatian	Nagri
Middle Miocene—Tortonian	Chinji
Middle Miocene—Helvetian	Kamlial

Pilgrim's views as to the correlation of the Siwaliks were based on his comparison of the several Siwalik faunas with what seemed to be their equivalents in the European sequence. The outstanding characteristics of the Siwalik faunas, on this basis, would be the close resemblance of the Chinji fauna to the typical Tortonian fauna of La Grive-St.-Alban, similarly the resemblance of the Dhok Pathan fauna to the wide-spread Pontian faunas of Pikermi, Samos, and Maragha, and finally the close comparison between the Pinjor fauna and the so-called Upper Pliocene fauna of Val d'Arno.

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[1] Pilgrim, G. E., 1934. Amer. Mus. Novitates, No. 704.

In 1929 Dr. Matthew,[1] having studied the Siwalik fossils in London and Calcutta, attempted to modify Pilgrim's correlation by stepping the whole Siwalik Series up in the geologic column from the position assigned to it by Pilgrim. In doing this Matthew was guided by two main considerations.

> 1. The appearance of new invading elements in a fauna is a safer guide to its correlation than the disappearance of old elements or the average composition of the fauna as a whole. The appearance of these new elements must be interpreted in the light of what is known of their origin and dispersal. When this is as directly recorded and fully documented as it is in the case of Tertiary Equidæ or Camelidæ, the evidence appears not open to any effective challenge. But more often the appearance of new elements in a fauna may be explained in several ways, the relative probability of which is not easy to test.
>
> 2. India and the Oriental region generally are today characterized by the survival of many primitive types of mammals as well as by the absence, scarcity, or recent appearance of some of the most progressive and specialized mammals. It compares in these respects with West Africa and tropical America. While it does not necessarily follow that this was true during the later Tertiary, yet it should be so considered until evidence proves the contrary; and so far from proving the contrary I believe that all of the evidence conforms with this assumption and much of it is difficult to explain in any other way.

Matthew argued that since *Hipparion* in India first appears in the Chinji beds, these deposits cannot be older than the oldest *Hipparion*-bearing beds of North America, which latter mark the first appearance of *Hipparion* as a direct descendant of the North American *Merychippus*. In other words, *Hipparion* arose in North America and subsequently migrated to the Old World—consequently its appearance in the eastern hemisphere must of necessity be later than its first appearance in North America. And Matthew regarded the appearance of *Hipparion* as indicative of the faunal change that marked the transition from the Miocene into the Pliocene.

Likewise, Matthew postulated that *Equus* arising in North America at the beginning of the Pleistocene, did not reach Eurasia until after its first appearance in the New World. Consequently, the Upper Siwalik beds containing *Equus* would of necessity be of Pleistocene age. In this respect, it might be said that Matthew placed the Val d'Arno and Villafranchian faunas of Europe in the Lower Pleistocene because of the presence of *Equus* in these horizons a decision differing from the traditional European practice of assigning this stage to the Upper Pliocene.

It might be said that Matthew's correlation of the Siwaliks was not based on the evidence of the Equidæ alone. He showed that the Chinji giraffes are comparable to the Pontian giraffes, while the Dhok Pathan giraffes are more advanced than any giraffes of the Pontian. And in the Upper Siwaliks, he cited the appearance of the camel as additional evidence of the Pleistocene age of these beds.

Therefore, he argued, the general resemblances of the Siwalik faunas show their homotaxial but not their correlative identities. These are relict faunas, in which the influx of new types from the outside furnish the real clews as to their age.

Pilgrim,[2] in 1931, answered Matthew's argument as follows:

> Matthew (1929) has recently sought to replace my correlation of the Dhok Pathan stage with the Pontian by another which, to judge from his diagram on p. 441, puts both it, as well as the earlier Nagri stage, later than Pikermi; assumes a gap, which does not exist, between the Middle and Lower Siwalik, and makes the Chinji and Kamlial stages start in the Vindobonian and end at an horizon which is the equivalent of Pikermi. His argument is mainly based on the first occurrence of *Hipparion* in India at the top of the Chinji stage, but he considers that the remainder of the fauna, including the Carnivora, support it. Apparently, while admitting in part the occurrence in the Dhok Pathan of species allied to those of Pikermi, he regards these as relics of an earlier age. . . If this is so, we have the choice of alternatives: (1) either such forms must have migrated from the Holarctic region in Pikermi times and lingered on in India to a much later epoch; or (2) such migration did not take place until post-Pikermi times. If we adopt the first alternative we ought to find that the Nagri fauna and that of the uppermost Chinji, which by hypothesis are the equivalent of Pikermi, contain Pikermi species or species at a similar stage of development; but if the second, neither the Nagri nor Chinji fauna ought to contain any immediately ancestral types of the Pontian fauna of the Holarctic region. Actually, however, neither is true of the Carnivora, nor it may be said of other mammalian orders. We do

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[1] Matthew, W. D., 1929. Bull. Amer. Mus. Nat. Hist., LVI, pp. 442, 443.

[2] Pilgrim, G. E., 1931. Catalogue of the Pontian Carnivora of Europe, Brit. Mus. (Nat. Hist.), pp. 151, 152.

not find Pikermi species at any earlier stage than the Dhok Pathan (the Perim Island beds I now regard as belonging to the Dhok Pathan stage); while the Nagri and, still more so, the Chinji stages contain species that are quite definitely ancestral to (or at any rate more primitive than) those of the Dhok Pathan and the Pontian of Europe alike.

Matthew's argument from *Hipparion* is more difficult to answer. If *Hipparion* originated in North America in Pontian times it obviously could not have reached India before the Pontian. But his premises lack absolute proof. First, although badly preserved equid teeth do occur at the top of the Chinji, are these certainly *Hipparion* and what stage of development do they represent? Secondly, did *Hipparion* originate in North America and not in Central Asia? Thirdly, if it did, is the age of the Valentine, in which *Hipparion* first appears in America, demonstrably contemporaneous with and not earlier than, say, the Sebastopol fauna of the Black Sea region in Europe? The discovery of a fauna which contains the immediate ancestors of the hitherto described 'Hipparion fauna' of China will settle the question definitely. Personally, I anticipate that such a fauna will be comparable to some extent with that of the Chinji stage of India.

In 1935 the present author, as the result of protracted studies on the Siwalik collection in the American Museum of Natural History, came to a conclusion essentially similar to Dr. Matthew's views as to the age of the Siwaliks, in short, that the Chinji fauna is equivalent to the "Valentine" or transitional Miocene-Pliocene of North America and is slightly pre-Pontian, or Pontian, in age, that the Dhok Pathan fauna is definitely post-Pontian and that the Pinjor fauna is definitely of Lower Pleistocene age. There were a few slight differences between my interpretations and those of Matthew, namely, the raising of the Chinji into the Lower Pliocene and the consideration of the Siwaliks as a continuous series rather than as separated by two major breaks, the view taken by Matthew.

Consequently the correlation adopted by the present author is as follows:

Lower Pleistocene.	Boulder Conglomerate Pinjor
Transitional	Tatrot
Middle to Upper Pliocene.	Dhok Pathan Nagri
Lower Pliocene	Chinji
Upper Miocene	Kamlial

Subsequently (1937) G. E. Lewis[1] published still another opinion as to the ages of the several Siwalik faunas. On the basis of new evidence, especially his stratigraphic field studies, he adopted the following correlation of the beds forming the Indian sequence.

Middle Pleistocene	Tawi (new name for Boulder Conglomerate)
Lower Pleistocene	Tatrot (including Tatrot and Pinjor)
Upper Pliocene	Break
Middle Pliocene	Dhok Pathan
Lower Pliocene	Nagri
Upper Miocene	Chinji
Middle Miocene	Kamlial

This correlation differs from those of Matthew and of Colbert by placing the Lower Siwaliks even lower than was granted by these two authors, but not so far down as they were placed by Pilgrim, and by extending the Upper Siwaliks higher into the Pleistocene than had previously been done.

Lewis' views as to the age of the Chinji beds are based to a great extent on the supposed *Upper Miocene* appearance of *Hipparion* in North America, in the Mint Canyon beds of the Pacific coast. He points out that this *Hipparion mohavense* is very close to the Siwalik *Hipparion*, that it is probably close to the ancestor of the Asiatic species, and that the Mint Canyon formation in which it appears is topped by marine beds carrying Miocene invertebrates.

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[1] Lewis, G. E., 1937. Amer. Journ. Sci., (5), XXXIII, p. 197.

As Lewis has remarked, it is probable that *Hipparion mohavense* is as close or closer to the Asiatic *Hipparion* than are any other North American species of this genus, while *Merychippus sumani* is very likely ancestral to these *Hipparion* types. Consequently *Merychippus sumani* and *Hipparion mohavense* are the forms that should be compared with the Asiatic *Hipparion.* The real crux of Lewis' argument is the question as to whether the Mint Canyon formation is of Upper Miocene age. This is the interpretation given by Maxson, who described the mammalian fauna from these beds. It should be pointed out here, however, that Stirton (1933)[1] has disputed the Miocene age of the Mint Canyon, linking this formation with the Ricardo of Lower Pliocene age, rather than with the Barstow of Upper Miocene age—as was done by Maxson, and placing it above the Barstow but below the Ricardo in the geologic column.

One important point in this discussion of the Mint Canyon is, of course, the age of the overlying marine beds. It should be noted that the invertebrate fossils are not well preserved, and that Woodring's correlation of the deposits with the Cierbo formation was more or less tentative. Stirton places the Mint Canyon assemblage as equivalent in age to the Cierbo and regards both of these formations as being about as close in their time relationships to the Ricardo as they are to the Barstow.

Lewis regards the Nagri as the Pontian equivalent in the Siwalik Series, and places the Dhok Pathan in the Middle Pliocene, as did Matthew and Colbert.

Finally Lewis shows a great stratigraphic break between the Dhok Pathan and the Upper Siwaliks, a fact of which the present author was unaware when his work was carried forward. The Tatrot, which the present author considered as possibly transitional between the Upper Pliocene and the Lower Pleistocene, is regarded by Lewis as an equivalent of the Pinjor horizon. Lewis chooses the name Tatrot for this level, a choice that may not be generally followed, due to the long-established use of the term "Pinjor." Likewise, Lewis' designation of the Boulder Conglomerate as "Tawi" may not be generally accepted.

In 1936 de Terra and Teilhard placed the Tatrot and Pinjor in the Lower Pleistocene and the Boulder Conglomerate in the Middle Pleistocene, as did Lewis. Since these two authors were concerned only with the Pleistocene of India, their conclusions are not discussed here.

In several recent papers (1939, 1940)[2], Pilgrim has defended his views as to the correlation of the Siwaliks, and has offered rebuttals to the arguments of Matthew, Colbert, de Terra and Teilhard, and Lewis. While admitting as proven fact the North American origins of *Hipparion* and *Equus,* Pilgrim nevertheless maintains that the general characters of the Chinji and Dhok Pathan faunas prove their pre-Pontian and Pontian relationships, respectively. This author holds that Matthew's and Colbert's idea that the Siwalik faunas are homotaxially similar to but correlatively later than comparable faunas in Europe is untenable. Therefore, in order to explain the presence of *Hipparion* in the Chinji and to retain this formation at a pre-Pontian level, Pilgrim suggests that the various Lower Pliocene formations of North America may be actually older than has hitherto been admitted by American palæontologists.

Pilgrim disagrees with Lewis' procedure of making the Dhok Pathan an equivalent of Roussillon and Montpellier and placing these latter in the Plaisancian. As he shows by his arguments, these European faunas are of Astian age, while the Plaisancian represents a general faunal gap between the Lower and the Upper Pliocene in

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[1] Stirton, R. A., 1933. Amer. Journ. Sci., (5), XXVI, p. 570.

[2] Pilgrim, G. E., and A. T. Hopwood, 1939. Rec. Geol. Surv. India, LXXIII, Pt. 4. Pilgrim, 1939.1. Pal. Indica, N. S., XXVI; 1940.1, Geol. Mag., LXXVII, pp. 1–27.

Europe. Pilgrim further maintains that the Tatrot is a truly distinct horizon, not closely related to the Pinjor as considered by de Terra and Teilhard, or identical with it as claimed by Lewis.

In the light of these recent discussions, Pilgrim presents his latest correlation of the Siwalik Series as follows:

Pleistocene	Post-Cromerian	Boulder Conglomerate
	Villafranchian	Pinjor
Pliocene	Astian	Tatrot
	Pontian	Dhok Pathan
Miocene	Sarmatian	Nagri
	Tortonian	Chinji
	Tortonian	Kamlial

In conclusion, it may be said that the Siwalik Series of India represent a period of deposition ranging from the middle or upper part of the Miocene well into the Pleistocene. The lowest Siwalik horizon, the Kamlial formation or zone, is definitely of pre-Pontian age. Above this is the Chinji formation, carrying *Hipparion*, which may be correlated as either Pontian or as representing a period of time immediately preceding the Pontian, according to the manner in which the origin and migrations of *Hipparion* from North America are interpreted. Following the Chinji is the Nagri formation, transitional between the underlying Chinji and the overlying Dhok Pathan. The Dhok Pathan is Pontian or post-Pontian, according to the manner in which the Siwalik faunas are interpreted in relation to Eurasiatic and North American faunas. Between the Dhok Pathan and the succeeding Upper Siwaliks is a break, representing an Upper Pliocene interval during which no sediments were deposited. The Upper Siwaliks are composed of two horizons of Lower Pleistocene age (Tatrot plus Pinjor) separated by an erosional break from the uppermost Boulder Conglomerate (Tawi of Lewis), possibly of Middle Pleistocene age.

PERIM ISLAND.—The fauna from Perim Island was originally considered by Dr. Pilgrim to be equivalent to the Lower Siwalik fauna. Subsequently, however, he changed his opinion and placed the Perim Island assemblage in the Dhok Pathan stage. This latter procedure would seem to express correctly the true relationships of the Perim Island beds.

4. THE PLEISTOCENE OF CENTRAL INDIA

NARBADA-GODAVARI ALLUVIUM.—Extensive deposits of Pleistocene age are exposed in Central India in the Narbada and the Godavari valleys. These sediments are approximately contemporaneous with each other (Pilgrim, 1905) and they represent, at least in part, the final stages of the Pleistocene in India.

The alluvial deposits of the Narbada and the Godavari rivers have been known for many years, and from time to time fossil mammals, definitely related to the Upper Siwalik fauna, have been found in them. Consequently various papers have been published in which these sediments and their contained fossils are discussed. One of the latest contributions is that of de Terra and Teilhard (1936), in which the problem of the Upper Siwalik and later Pleistocene deposits of India is considered.

These authors find that in northern India the Boulder Conglomerate stage is followed by a long erosion interval, after which there comes the *Potwar silt*, a fine deposit, partly of fluviatile, partly of eolian origin, of Upper Pleistocene age. The Potwar silt is succeeded by another long erosion interval, while finally, at the top of the section, are redeposited Potwar sediments and loesses.

Turning now to the Narbada valley, de Terra and Teilhard[1] make the following remarks as to the Narbada alluvium.

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[1] Terra, H. de, and P. Teilhard de Chardin, 1936. Proc. Amer. Philos. Soc., LXXVI, No. 6, pp. 820–822.

PROBOSCIDEA:	Kamlial	Chinji	Dhok Pathan	Tatrot	Pinjor
Dinotherium sindiense Lydekker	×	×			
Dinotherium indicum Falconer		×	×		
Dinotherium pentapotamiæ Lydekker		×			
Dinotherium angustidens Koch			×		
Trilophodon pandionis Falconer	×				
Trilophodon angustidens palæindicus (Lydekker)		×			
Trilophodon macrognathus (Pilgrim)	×	×			
Trilophodon chinjiensis (Pilgrim)		×			
Trilophodon hasnotensis Osborn			×		
Tetralophodon falconeri (Lydekker)		×	×		
Tetralophodon punjabiensis (Lydekker)			×		
Serridentinus hasnotensis Osborn		×			
Serridentinus metachinjiensis Osborn		×			
Serridentinus browni Osborn		×			
Serridentinus chinjiensis Osborn		×			
Serridentinus prochinjiensis Osborn		×			
Rhynchotherium chinjiensis Osborn			×		
Synconolophus dhokpathanensis Osborn			×		
Synconolophus propathanensis Osborn			×		
Synconolophus corrugatus (Pilgrim)			×		
Synconolophus ptychodus Osborn		×	×		
Synconolophus hasnoti (Pilgrim)			×		
Anancus perimensis (Falconer and Cautley)			×		
Anancus properimensis Osborn		×			
Pentalophodon sivalensis (Cautley)					×
Pentalophodon falconeri Osborn				×	
Stegolophodon latidens (Clift)			×		
Stegolophodon cautleyi (Lydekker)			×		
Stegolophodon cautleyi progressus Osborn		×			
Stegolophodon nathotensis Osborn		×			
Stegolophodon stegodontoides (Pilgrim)					×
Stegodon bombifrons (Falconer and Cautley)			×	×	
Stegodon cliftii (Falconer and Cautley)			×		
Stegodon elephantoides (Clift)			×		
Stegodon ganesa (Falconer and Cautley)					×
Stegodon insignis (Falconer and Cautley)					×
Stegodon pinjorensis Osborn					×
Archidiskodon planifrons (Falconer and Cautley)					×
Hypselephas hysudricus (Falconer and Cautley)					×
Platelephas platycephalus (Osborn)					×

> The formation consists here [Narbada valley] of two different horizons, each of which begins with a basal gravel overlain by brown and pinkish or orange coloured concretionary clays and silts. In the lower zone the conglomerate is coarser and more cemented, the clay is more intensely coloured and also richer in concretions than in the upper zone.
>
> Fossils occur chiefly near the disconformity which separates both zones. . .
>
> The 'lower zone' of the Narbadda Pleistocene can be equated with the Upper Siwalik 'Boulder Conglomerate' on faunistic, archæological and lithological grounds. The association of advanced *Elephas* with *Hippopotamus* and large *Bos* suggests a stage slightly younger than the older Upper Siwaliks. In harmony with this is the appearance of an early Paleolithic culture in the basal gravel, clearly calling to one's mind the picture of heavy accumulation of river deposits during the glacio-pluvial stage of late Siwalik times in the Punjab. It follows that on these grounds a further correlation between the 'Upper Zone' and the 'Potwar silt' becomes rather plausible. Both are separated by a long erosion interval from the underlying beds and both contain implements of Soan type. The cotton soil might then well represent the latest Pleistocene which possibly is homotaxial with the redeposited Potwar silt and the second loess in the Punjab.

According to these authors, the relationships of the Narbadda alluvium might be represented in the following manner.

	Narbada valley	Punjab
	Cotton soil	Re-deposited Potwar and second loess
	Erosion interval	
U. Pleist.	Narbada alluvium upper zone	Potwar silt
	Erosion interval	
M. Pleist.	Narbada alluvium lower zone	Boulder conglomerate

The mammalian fauna of the Narbada alluvium is as follows:

Helarctos namadicus (Falconer and Cautley)
Stegodon insignis (Falconer and Cautley)
Stegodon ganesa (Falconer and Cautley)
Palæoloxodon namadicus (Falconer and Cautley)
Rhinoceros unicornis Linnæus
Equus namadicus Falconer and Cautley
Sus namadicus Pilgrim
Hippopotamus palæindicus Falconer and Cautley
Hippopotamus namadicus Falconer and Cautley
Cervus duvaucelli Cuvier
Bubalus palæindicus Falconer
Leptobos fraseri Rütimeyer
Bos namadicus Falconer

Closely related to the Narbada alluvium is the Godavari alluvium, exposed also in peninsular India, but on the eastwardly flowing drainage system. Pilgrim,[1] in 1905, made a study of the Godavari deposits, and below are given certain remarks that he made with regard to this formation.

> As compared with the alluvial deposits of the Narbada, which flows in a contrary direction, and enters the sea on the west coast of India, our knowledge of those of the Godávari is very limited, both as regards the fossil contents, and even as to the nature, thickness and superficial extent of the alluvium itself. . .
>
> Comparing the fauna of the Godávari alluvium with that of the older Narbada deposits, we shall see that the only three mammalian species found in it up to now are identical with Narbada forms. Of these *E. antiquus* (*namadicus*) Falc. et Caut., and *Hippopotamus palæindicus* F. et C., are quite absent from the older deposits of the Siwalik beds, while *Equus namadicus* F. and C. comes up from below. We are therefore justified in regarding the two series of alluvia as of approximately the same age, and any conclusion we arrive at with respect to the Narbada deposits must apply equally to those of the Godávari.

Proboscidean: See faunal list, above.

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[1] Pilgrim, G. E., 1905. Rec. Geol. Surv. India, XXXII, Pt. 3, pp. 199, 213.

5. THE PLEISTOCENE OF CEYLON

CEYLON.—During the years 1935 and 1936 Upper Siwalik fossils were discovered in Ceylon, and described by Deraniyagala.[1] These fossils are extremely fragmentary but are sufficiently complete to show that they are true Upper Siwalik forms. The faunal list is as follows.

Palæoloxodon
Rhinoceros
Hexaprotodon ?sivalensis

6. THE PLEISTOCENE OF BURMA

IRRAWADDY VALLEY (IRRAWADDY SERIES).—The Cenozoic history of Burma may be summed up by saying that there was continuous subsidence accompanied by continuous deposition. Consequently the sediments have accumulated to a great thickness, with but minor breaks in the series. Of course there were variations in the rate of subsidence and deposition, causing a considerable amount of interfingering of marine and continental deposits, but on the whole since Middle Eocene times a gradual encroachment of the continental beds from the north to the south took place, thereby causing the Burmese gulf to retreat southwardly.

A series of deposits represent the Tertiary in Burma, of which the Pondaung sandstone of Upper Eocene age and the Pegu beds of Oligocene to Pliocene age are the continental, mammal-bearing facies. Correlative with the upper portions of the Pegu beds are the lower phases of the Irrawaddy series. These Irrawaddy beds constitute the upper part of the sedimentary section in Burma, ranging from the Lower Pliocene up through the lower phases of the Pleistocene.

Fossils are fragmentary and scarce in the Pegu beds, and it is only in the Irrawaddy series that proboscideans are found.

Two faunas have been identified in the Irrawaddy beds, a lower one of Pliocene age, probably correlative with the Dhok Pathan fauna of the Siwaliks, and an upper one of Pleistocene age, correlative with the Pinjor fauna of the Siwaliks. The two faunas are separated from each other by a vertical range of about 4500 feet of sediments.

There is some question as to the actual presence of proboscideans in the Lower Irrawaddy beds. Pilgrim, in 1910, listed the mastodont, *Stegolophodon latidens*, as belonging to the Lower Irrawaddy fauna, but this occurrence was questioned by Stamp in 1922.[2] Subsequent work in Burma would seem to indicate that this animal is a member of the Upper Irrawaddy fauna; certainly a number of discoveries made in recent years establish it as definitely belonging in the Lower Pleistocene of Burma. Therefore, since its presence in the Lower Irrawaddy beds is very doubtful, it will be considered here as limited to the Pleistocene in Burma.

The Upper Irrawaddy fauna is in all respects an eastward extension of the typical Upper Siwalik fauna of India. In numerous cases there is a specific identity between elements constituting the Burmese faunas and those elements in the Pinjor fauna of northwestern India. Where species are not identical in the two regions, they are so closely related as to leave little doubt as to their derivation from common ancestral types. Therefore there is no reason to regard the Upper Irrawaddy fauna as other than of Lower Pleistocene age, strictly correlative with the Pinjor fauna to the west.

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[1] Deraniyagala, P. E. P., 1935. Journ. Roy. Asiatic Soc. (Ceylon), XXXIII, No. 88; 1936, Geol. Mag. (London), LXXIII, No. 865.

[2] Stamp, L. Dudley, 1922. Geol. Mag. (London), LIX, No. XI, pp. 481–501.

That there was an extension of the Upper Siwalik fauna eastwardly throughout a considerable portion of the Oriental region, is shown by the presence of characteristic Siwalik types in various East Indian Islands, to the south and east of Burma. This extension of the Upper Siwalik fauna has been designated by von Koenigswald[1] as the "Siva-Malayan" fauna, having its origin in northern India, pushing into Burma and reaching Java and adjacent regions in Lower Pleistocene times.

PROBOSCIDEANS:

Stegolophodon latidens (Clift)
Stegodon elephantoides (Clift)
Stegodon insignis birmanicus Osborn
Hypselephas hysudricus (Falconer and Cautley)

SHAN PLATEAU (MOGOK FISSURES).—The Irrawaddy faunas of Burma are found in the Irrawaddy River valley, in stream and flood-plain deposits. As contrasted with this, is the fauna found in the limestone caverns or fissures of the Shan Plateau. This fauna is distinguished by *Stegodon orientalis*, *Palæoloxodon namadicus*, *Ailuropoda baconi*, and *Hystrix*. These are essentially the very forms that characterize the mammalian assemblages found in limestone caverns and fissures to the east of Burma, in Yunnan, Shansi, and Szechwan. There are other mammals also in the Burma caverns that show the close relationships of these deposits to the cave deposits of China, animals such as *Rhinoceros*, *Sus*, and various ruminants. But it is upon the basis of the first four forms enumerated that the affinities of this cavern fauna in various regions may be established.

Of late years, particularly because of the work of Teilhard and de Terra, Pei, Bien, von Koenigswald, and others, there is a tendency to regard the cave faunas of China as belonging to a Middle Pleistocene stage of development. In Burma there is the Upper Irrawaddy fauna which seems to be definitely older than the mammals from the Mogok caves, while in China there are such assemblages as those of Nihowan and Ma-Kai, which would seem to precede the cave faunas. In short, the cave faunas represent a post-Villafranchian development throughout the Orient.

So far as Burma is concerned, the Mogok fauna may be compared with the Narbada assemblage on the west, as well as with the cave faunas to the east. But an analysis of such a comparison will show that although certain Narbada elements are to be found in the Mogok fauna, the bulk of the assemblage is closely related to, if not identical with the cave faunas of China.

Of course the most important correlations are with the Choukoutien fauna of North China, containing *Sinanthropus*, and the Trinil fauna of Java, containing *Pithecanthropus*.

Von Koenigswald, recognizing the continuity over a broad area in the Orient of this Middle Pleistocene fauna, designated it as the "Sino-Malayan" fauna. Seemingly having had its origin in the southern part of China, the Sino-Malayan fauna spread to the south to the East Indian Islands, and to the west to Burma. Consequently the two Pleistocene faunas of Burma represent invading assemblages, the Lower Pleistocene or Upper Irrawaddy fauna coming in from the west, and the Middle Pleistocene or Mogok fauna coming in from the east.

PROBOSCIDEANS:

Stegodon orientalis Owen
Palæoloxodon namadicus (Falconer and Cautley)

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[1] Koenigswald, G. H. Ralph von, 1938–1939. Peking Nat. Hist. Bull., XIII, Pt. 4, pp. 293–298.

7. THE PLEISTOCENE OF SOUTH CHINA

Szechwan Province, China.—In southwestern China, in the province of Szechwan, are numerous pits and fissures developed in the limestone that forms the surface outcrops, and many of these pits contain rich deposits of fossil mammals. They have been worked by the Chinese since ancient times for their "dragon bones," which constitute one of the staples of the Chinese drug trade.

The fossils from the Szechwan pits were first described by Owen, who regarded them as of Pliocene age. Subsequently various authors, notably Koken, Schlosser, and Matsumoto, described fossils from the Szechwan pits. Finally, in 1923, Matthew and Granger[1] described a new and a very complete series of fossils from Szechwan (collected by the latter author). At the time, these authors retained the older viewpoint of an Upper Pliocene age for the material with which they were working. Subsequently, however, Matthew came to the conclusion that the Szechwan fauna is more properly to be placed in the Lower Pleistocene, a view that was never published, but clearly stated in manuscript notes.

Perhaps the most important mammals in the Szechwan fauna are *Stegodon orientalis*, a large stegodont with very long grinding teeth, a gibbon, *Bunopithecus*, a langhur monkey, a large *Hystrix*, a dhole related to the modern Indian dhole, a giant panda, a gigantic tapir, *Megatapirus*, a chalicothere, *Nestoritherium sinense*, a *Rhinoceros*, and an extremely large gaur, *Bibos geron*.

The generally modern character of this fauna places it as definitely of Pleistocene age, for there are too many advanced elements in it to allow its inclusion in the Pliocene. The association of *Stegodon orientalis*, *Hystrix*, and the giant panda at once establishes a strong resemblance to the Mogok fauna of Burma, discussed on a preceding page. Indeed, upon the basis of the entire faunal assemblage at Mogok and in the Szechwan fissures, there is every reason to think that they are contemporaneous, representing essentially a single fauna stretching from Burma through southern China. As has been pointed out in the discussion of the Mogok fauna, there is good reason to think that these cave faunas are of Middle Pleistocene age since they are preceded both in Burma and in China by faunas having a Villafranchian aspect.

I take the liberty to quote at this place from Matthew's unfinished manuscript on the Szechwan fauna:

> This is a fairly typical fauna of southeastern Asia, plus a number of species now extinct or limited in their range. Marked features are the presence of *Stegodon*, but no mastodons or mammoths,[2] the giant tapir, and a rhinoceros, but no horses, a single tooth of *Chalicotherium*. Among the Carnivora is a hyæna related to the spotted hyænas, *Cyon* but no *Canis*, a very large marten as big as the American fisher *Martes pennanti*, and a tiger, civet, particolored bear and true bear not very different from modern survivors. The artiodactyls include muntjac and sambhur gazelle, serow, gaur and yak, also some other species which we have not yet succeeded in identifying; they may be extinct species. The rodents are almost wholly a large bamboo rat allied to the Chinese species but as big as the Malayan.
>
> Altogether this fauna appears to be the fauna of South Chinese forests and mountain valleys, as we may suppose it to have been before civilized or semicivilized man cut down the forests, cultivated the valleys, and brought about the extinction of the larger and more specialized animals, driving the remainder of the fauna into the hills.
>
> The absence of horses, of true dogs, of mammoths and of mastodons is in marked contrast to the Pliocene fauna of North China, where all those animals had already appeared. The latter was apparently a plains fauna.

Teilhard, Young and others,[3] in 1933, indicated the fissure deposits of Szechwan and adjacent localities as extending over a period of time in the Lower Pleistocene that embraced both the Sanmenian and the Choukoutien deposits. In another part of this same paper, they indicated that the fissure deposits of South China might be limited to a period of time contemporaneous with the Choukoutien deposits. This is their latest opinion, and is now generally held by authorities on the Pleistocene mammals of Asia.

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[1] Matthew, W. D., and Walter Granger, 1923. Bull. Amer. Mus. Nat. Hist., XLVIII, Art. XVII, pp. 563–598.

[2] *Palæoloxodon namadicus* has recently been discovered in Szechwan, and described by Young.

[3] Black, Teilhard de Chardin, Young and Pei, 1933. Mem. Geol. Surv. China, Ser. A, No. 11, Table III, p. 158; Map III, opposite page 164.

The mammalian faunas from other caverns in southern China are so similar to that of the Yenchingkou pits as to need no particular consideration at this place. It is quite evident that all of these occurrences represent a single fauna that was rather widely spread during Middle Pleistocene times.

Mention should be made of the caves in Kwangsi, the fauna of which has been described by Teilhard, Young, Pei and Chang, and the Hoshangtun Cave in Yunnan, described by Bien and Chia. Also there should be mentioned the isolated occurrence of a stegodont said to have been found near Shanghai and described by Owen as *Stegodon sinensis.* This is probably of the same age as the other South Chinese Stegodonts.

PROBOSCIDEANS:

Stegodon orientalis Owen
Palæoloxodon namadicus (Falconer and Cautley)

8. THE PLEISTOCENE OF INDO-CHINA

FRENCH INDO-CHINA.—There are cavern deposits in northern French Indo-China, seemingly quite similar to those of southern China, described above. Since they contain the same fauna as the Chinese caverns, they must be considered as correlative with the latter, representing a southern extension of the characteristic Middle Pleistocene cave fauna of the Orient. Mansuy,[1] who described the mammalian fossils from Indo-China, identified the stegodont material as belonging to *Stegodon "clifti"* and *Stegodon insignis.* A comparison of his excellent plates with material on hand suggests the possibility that the *Stegodon* from Indo-China is of the species *orientalis.* In fact, Mansuy regarded *S. orientalis* as probably synonymous with *S. insignis*, and this view undoubtedly influenced him in his identification of the material.

PROBOSCIDEANS:

Stegodon orientalis Owen.—(*S. insignis* according to Mansuy.)
Stegodon elephantoides (Clift).—(This species? probably *orientalis.*)
Palæoloxodon namadicus (Falconer and Cautley)

9. THE PLEISTOCENE OF THE EAST INDIES

JAVA.—Since the discovery of *Pithecanthropus* in 1892, Java has assumed a position of great importance to the students of human prehistory and the evolution of life. Consequently numerous contributions have appeared during the course of the past forty years, discussing the phylogenetic relationships and the probable geologic age of *Pithecanthropus.* It has been only recently that detailed geological investigations have been carried on in Java, with a view to clarifying some of the hitherto obscure points as to the succession of upper Cenozoic sediments in Java.

For many years it was supposed that the beds at Trinil, in which *Pithecanthropus* was discovered, might be placed in the Upper Pliocene or the Lower Pleistocene, thereby allocating to *Pithecanthropus* the honored position of being the oldest known hominoid. But recent studies by various authors have shown that the upper Cenozoic stratigraphy of Java is much more complex than it was originally thought to be—therefore our ideas as to the age of *Pithecanthropus* and the associated fauna have necessarily undergone considerable revision.

In 1931 van Es published a detailed geologic study entitled "The Age of Pithecanthropus," in which he showed that there was a volcanic boulder breccia and beneath it a sand and conglomerate underlying the Trinil beds. Both of these older horizons he regarded as of Pleistocene age.

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[1] Mansuy, H., 1916. Mem. Surv. Geol. Indochine, V, Fasc. II, pp. 1–26.

In 1932 van der Maarel[1] described a new fauna from Bumiaju, in Central Java, and came to the following conclusions as to the stratigraphic relationships of the Javanese strata:

> "1. The Bumiaju fauna is older than the Trinil fauna.
>
> 2. The Trinil fauna is certainly of Pleistocene age, more particularly either Lower [or] Middle Pleistocene, but not Upper Pleistocene.
>
> 3. Accordingly the Bumiaju fauna is of upper pliocene or lower pleistocene age."

In recent years von Koenigswald[2] has carried on a series of careful studies regarding the upper Cenozoic mammal-bearing sediments in Java, and he has distinguished a number of successive horizons within the Pleistocene. These and correlative horizons in India may be listed as follows:

	JAVA	INDIA
Pleistocene	Sampoeng zone (Neolithic) Ngandong zone Trinil zone Djetis zone Kali Glagah zone Tji Djoelang	Potwar Narbadda Boulder Conglomerate Pinjor Tatrot
Pliocene	Tji Sande zone	

Incidentally von Koenigswald placed the Kali Glagah and the Tji Djoelang zones in the Upper Pliocene, since he regards the Pinjor fauna as a transitional Pliocene-Pleistocene assemblage and the Tatrot fauna as of Upper Pliocene affinities.

The Tji Djoelang and Kali Glagah faunas contain Lower Pleistocene elements, e. g., *Tetralophodon*, *Stegodon*, *Merycopotamus*, and *Hippopotamus*, such as are found in the Tatrot and Pinjor faunas of India. While these animals may also be found in Upper Pliocene sediments, the general resemblance of the two Javanese faunas listed above to the Tatrot and Pinjor faunas of India justifies their inclusion in the Pleistocene according to the definition of the period adopted in this work.

The Djetis fauna is more advanced, although it contains a few persistent remnants of the Siwalik fauna—notably *Nestoritherium sivalense*. There are, however, various characteristic Oriental elements in this fauna, such as *Rhinoceros* cf. *sondaicus*, tapir, *Paradoxurus*, pangolin, and *Symphalangus*. Von Koenigswald was fully justified in placing the Djetis fauna fully as late as or probably later than the Pinjor assemblage of India.

The Trinil fauna is directly comparable with the Choukoutien fauna of China, and both of these are now regarded as definitely post-Villafranchian in age. According to the definitions adopted in the present work the Trinil beds may therefore be regarded as approximately of Middle Pleistocene age. There are numerous elements in the Trinil fauna correlating it with the cave faunas of China, such as *Stegodon*, *Viverra*, *Felis*, *Hystrix*, *Muntiacus*, *Cervus*, *Bubalus*, and *Simia*.

Finally, the Ngandong fauna of Java is a very late Pleistocene assemblage, with a few new elements, but distinguished mainly from the older Trinil fauna by the presence of a Neanderthal type of man.

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[1] Van der Maarel, F. H., 1932. "Contribution to the Knowledge of the Fossil Mammalian Fauna of Java," p. 199.

[2] Koenigswald, G. H. R. von, 1935. Proc. Akad. Wet. Amsterdam, XXXVIII, No. 2, pp. 188–198; 1939, Quartär, Zweiter Band, pp. 28–53.

The faunas of the several Javanese Pleistocene horizons are too extensive to list here, so only the proboscideans will be enumerated.

PROBOSCIDEANS:

Sampoeng zone
    Elephas indicus Linnæus

Ngandong zone
    Stegodon trigonocephalus Martin
    Palæoloxodon cf. *namadicus* (Falconer and Cautley)

Trinil zone
    ?*Cryptomastodon martini* von Koenigswald [=Sirenian? (Osborn)]
    Stegodon trigonocephalus Martin
    Palæoloxodon cf. *namadicus* (Falconer and Cautley)

Djetis zone
    Stegodon trigonocephalus praecursor von Koenigswald
    Elephas sp.

Kali Glagah zone
    Tetralophodon bumiajuensis Maarel
    Stegodon trigonocephalus praecursor von Koenigswald
    Archidiskodon planifrons (Falconer and Cautley)

Tji Djoelang zone
    Stegodon sp.

BORNEO.—In 1885 Lydekker[1] described a tooth that he identified as *Mastodon latidens*, from the northwest coast of Borneo.

> The specimen forming the subject of the present notice was forwarded from Borneo to the Secretary of this Society by Mr. A. H. Everett, C.M.Z.S., who stated that it was found during the early part of the present year by a Kadayan in the jungle in the vicinity of Bruni, on the north-west coast of Borneo. Owing to the country being in a disturbed state Mr. Everett could not visit the locality to make further inquiries; but there seems no doubt that the history of the specimen is a true one.

Comparing this tooth with the many teeth of *Mastodon latidens* from Burma and India, Lydekker came to the conclusion that the tooth from Borneo was specifically identical with the Burmese-Indian forms, and therefore he decided that the deposits in Borneo from whence this tooth was recovered might be questionably of Pliocene age.

Subsequently (1936, Volume I of this Monograph, p. 700) Professor Osborn made the tooth from Borneo the type of a new species, *Stegolophodon lydekkeri*.

Stegolophodon latidens from Burma, where the type was discovered, would seem to be restricted to the Upper Irrawaddy beds of Pleistocene age, while in India the species ranges down into the Pliocene Dhok Pathan horizon. It is an interesting fact that Lydekker emphasized the close mineralogical comparison between the Borneo tooth and those teeth of *M. latidens* from Burma. With this fact in mind, and remembering that the *Stegolophodon latidens* in Burma is found in the Pleistocene level, there would seem to be some reason for thinking that the

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[1] Lydekker, R., 1885. Proc. Zool. Soc., London, 1885, p. 777.

Borneo specimen might be of Pleistocene age. It should be pointed out, however, that Professor Osborn placed this specimen in the Pliocene (but with a query) as did Lydekker.

PROBOSCIDEAN: *Stegolophodon lydekkeri* Osborn.

PHILIPPINE ISLANDS.—On the basis of published records it would seem that fossil proboscideans from the Philippine Islands are represented by a single tooth from the island of Mindanao. This specimen was described many years ago by E. Naumann, under the name of *Stegodon mindanensis*. Naumann compared it with *Stegodon trigonocephalus* of Java, pointing out the fact that there were great similarities between the species. Therefore it would seem possible that the beds containing these two forms in Java and Mindanao are geologically more or less equivalent to each other. In this connection it may be pointed out that *Stegodon trigonocephalus* in Java is found typically in the Ngandong beds, above the Trinil zone of probable Middle Pleistocene affinities. It is an interesting fact, however, that stegodonts closely related to *S. trigonocephalus* are found in lower beds in Java, ranging down to the basal Pleistocene. Therefore it would seem that the Mindanao deposits might be representative either of Lower or of Middle Pleistocene times in the Philippine region.

PROBOSCIDEAN: *Stegodon mindanensis* Naumann.

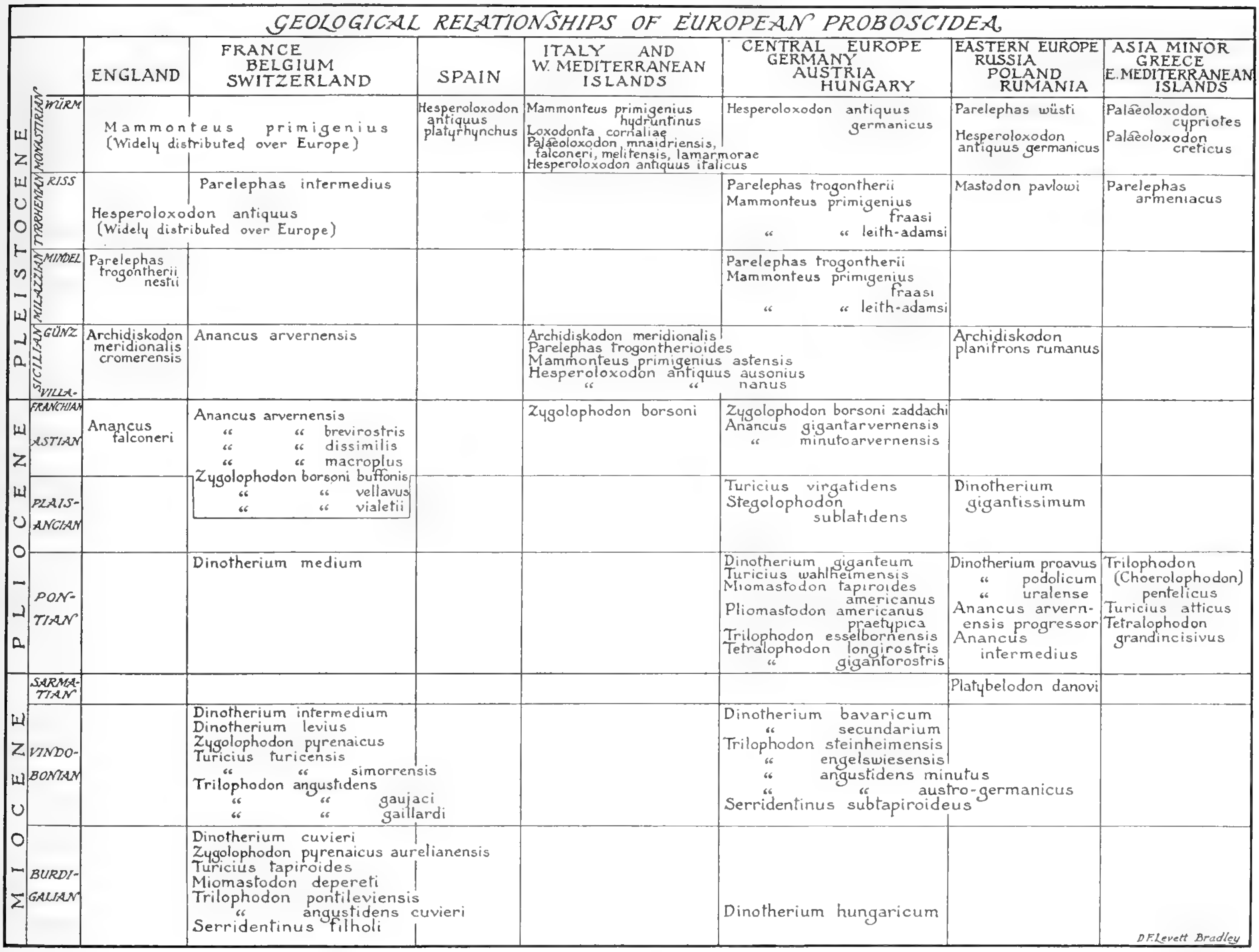
IV. EUROPE

1. INTRODUCTION

It may be said that the Proboscidea entered Europe at the beginning of the Miocene—considering the Burdigalian to be the opening stage of this period. From that time until the final stages of the Pleistocene, these animals were prominent in the extinct mammalian faunas of the European region; therefore, a consideration of the Proboscidea-bearing beds of Europe is virtually a discussion of the continental stratigraphy of the Miocene, Pliocene, and Pleistocene of that region.

A thorough discussion of the continental Tertiary and Quaternary sediments of Europe is indeed a large order, too much to be included within the scope of this present work, and beyond the capabilities of one who does not have an intimate first-hand knowledge of the complex relationships of these Old World mammal-bearing horizons. Therefore, it is proposed to discuss very broadly the general succession of upper Tertiary and Pleistocene continental deposits in Europe, giving particular attention to the more typical localities at which the several stages are best developed. In doing this the localities at which proboscidean types were discovered will, of course, be especially stressed.

In dealing with the Tertiary mammalian faunas of Europe one general consideration must be kept in mind, namely, that this was primarily a mediterranean area—particularly during the earlier phases of the Tertiary period—interspersed with numerous islands and peninsulas. In this respect, the European region is to be contrasted with America and Asia, which from the end of the Cretaceous were, generally speaking, broad continental platforms, with the shallow sea borders lapping over the edges, but not in the main encroaching materially beyond their present limitations. It was not until late Tertiary times that Europe underwent a general emergence so that most of its present area was permanently lifted above sea level. Naturally, the broken-up character of the land areas of Europe in earlier Tertiary times had a distinct influence on the development of the mammalian faunas, and similarly the final emergence of this region as a continental mass also is reflected in the expression of the assemblages of land animals. So it is that the earlier separated faunas are finally replaced by associations of mammals that become more and more cosmopolitan, with an eventual culmination in the appearance of the almost world-wide *Hipparion* faunas and subsequent assemblages that are so characteristic of the last phases of Tertiary times.



GEOLOGICAL RELATIONSHIPS OF EUROPEAN PROBOSCIDEA

			ENGLAND	FRANCE BELGIUM SWITZERLAND	SPAIN	ITALY AND W. MEDITERRANEAN ISLANDS	CENTRAL EUROPE GERMANY AUSTRIA HUNGARY	EASTERN EUROPE RUSSIA POLAND RUMANIA	ASIA MINOR GREECE E. MEDITERRANEAN ISLANDS
PLEISTOCENE	MONASTIRIAN	WÜRM	Mammonteus primigenius (Widely distributed over Europe)		Hesperoloxodon antiquus platyrhynchus	Mammonteus primigenius hydruntinus Loxodonta cornaliae Palaeoloxodon mnaidriensis, falconeri, melitensis, lamarmorae Hesperoloxodon antiquus italicus	Hesperoloxodon antiquus germanicus	Parelephas wüsti Hesperoloxodon antiquus germanicus	Palaeoloxodon cypriotes Palaeoloxodon creticus
	TYRRHENIAN	RISS	Hesperoloxodon antiquus (Widely distributed over Europe)	Parelephas intermedius			Parelephas trogontherii Mammonteus primigenius fraasi " " leith-adamsi	Mastodon pavlowi	Parelephas armeniacus
	MILAZZIAN	MINDEL	Parelephas trogontherii nestii				Parelephas trogontherii Mammonteus primigenius fraasi " " leith-adamsi		
	SICILIAN VILLA-	GÜNZ	Archidiskodon meridionalis cromerensis	Anancus arvernensis		Archidiskodon meridionalis Parelephas trogontherioides Mammonteus primigenius astensis Hesperoloxodon antiquus ausonius " " nanus		Archidiskodon planifrons rumanus	
PLIOCENE	FRANCHIAN ASTIAN		Anancus falconeri	Anancus arvernensis " " brevirostris " " dissimilis " " macroplus		Zygolophodon borsoni	Zygolophodon borsoni zaddachi Anancus gigantarvernensis " minutoarvernensis		
	PLAISANCIAN			Zygolophodon borsoni buffonis " " vellavus " " vialetii			Turicius virgatidens Stegolophodon sublatidens	Dinotherium gigantissimum	
	PONTIAN			Dinotherium medium			Dinotherium giganteum Turicius wahlheimensis Miomastodon tapiroides americanus Pliomastodon americanus praetypica Trilophodon esselbornensis Tetralophodon longirostris " gigantorostris	Dinotherium proavus " podolicum " uralense Anancus arvernensis progressor Anancus intermedius	Trilophodon (Choerolophodon) pentelicus Turicius atticus Tetralophodon grandincisivus
MIOCENE	SARMATIAN							Platybelodon danovi	
	VINDOBONIAN			Dinotherium intermedium Dinotherium levius Zygolophodon pyrenaicus Turicius turicensis " " simorrensis Trilophodon angustidens " " gaujaci " " gaillardi			Dinotherium bavaricum " secundarium Trilophodon steinheimensis " engelswiesensis " angustidens minutus " " austro-germanicus Serridentinus subtapiroideus		
	BURDIGALIAN			Dinotherium cuvieri Zygolophodon pyrenaicus aurelianensis Turicius tapiroides Miomastodon depereti Trilophodon pontileviensis " angustidens cuvieri Serridentinus filholi			Dinotherium hungaricum		

D.F. Levett Bradley

Fig. 1222

2. THE LOWER MIOCENE: BURDIGALIAN

It is not the purpose in this exposition to go into the question as to whether the Aquitanian is more properly to be considered as the closing stage of the Oligocene or the opening stage of the Miocene, for this horizon precedes the appearance of proboscideans in Europe, and its consideration here would be fruitless. Suffice it to say, therefore, that the Miocene may be considered for the purposes of convenience to have opened with the Burdigalian.

The development of Burdigalian mammals in Europe is perhaps best exemplified by the fauna of the Sables de l'Orléanais of central France. This fauna, known since the time of Cuvier, has long been regarded as typifying the Burdigalian stage in the European region, but in recent years as knowledge of the stratigraphy and palæontology of these beds has become more exact, there have arisen the inevitable differences of opinion as to the exact relationships of the several horizons and their contained mammalian faunas within the Sables de l'Orléanais each to the other. The problem was stated by Mayet[1] in 1908 as follows.

> Les sables de l'Orléanais ne sont pas une formation géologique ayant la remarquable unité qu'on lui a longtemps atribuée. *A priori*, il était à supposer que cette masse énorme d'alluvions granitiques qui couvre encore actuellement une partie du centre de la France, avait exigé un temps fort long pour être formée, charriée, déposée. Les renseignements stratigraphiques et les données paléomammalogiques me paraissent confirmer cette induction. On peut distinguer dans le Burdigalien de l'Orléanais, dont l'expression 'Sables de l'Orléanais' est pour ainsi dire synonyme, plusieurs facies locaux, d'âge trés probablement différent.

It is Mayet's contention, and in this he follows the lead of his illustrious countryman, Professor Depéret, that the Burdigalian of central France is inaugurated by the Calcaire de Montabuzard, underlying the Sables de l'Orléanais, and between these two horizons he would place the Sables de Chitenay. Thus, his Burdigalian section would be, generally speaking, as follows:

Sables de la Sologne
Marnes de l'Orléanais
Sables de l'Orléanais
Marnes du Blesois
Sables de Chitenay
Calcaire de Montabuzard

Mayet has envisaged the Burdigalian in central France as beginning with the deposition of sediments in a vast lake, the "lac de Beauce." The Calcaire de Montabuzard is a local facies of this deposition, and as such contains a mammalian fauna which Mayet finds to be essentially more primitive than the typical Sables de l'Orléanais fauna. The Sables de Chitenay are also regarded by Mayet as constituting a local facies of the basal Burdigalian, deposited by a large Miocene river which flowed from the Central Plateau into the lac de Beauce at about the time the deposition of the Calcaire was coming to an end. Either contemporaneous with or immediately succeeding the sands of Chitenay are the Marnes du Blesois. Then come the Sables de l'Orléanais in the strict sense of the word, with the large mammalian fauna typical of these sands. And finally at the top of the section are unfossiliferous beds, the Marnes de l'Orléanais and the Sables de la Sologne.

A much different interpretation of the Burdigalian and associated faunas of central France was put forward by Stehlin in 1908.[2] A decade or so before this time, Depéret had called attention to the very important fact that the fauna of the Sables de l'Orléanais contains two elements, one consisting of indigenous mammals, derived directly from the Aquitanian mammals of the same region—the other being composed of immigrant forms coming in from African, Asiatic, and American centers of origin. Stehlin elaborated on this thesis and attempted to show that the relative abundance of immigrant forms as compared with indigenous types is indicative to a certain extent of the general advancement in age of the several faunas within which they are contained.

Following this line of thought, Stehlin came to the conclusion that the fauna of Chitenay is the most archaic of the Burdigalian mammalian assemblages, because it contains the smallest percentage of immigrant forms. Thus, he would designate the Chitenay fauna as lower Burdigalian, intermediate in position between the upper Aquitanian faunas, such as Saint Gerand-le-Puy and the characteristic *middle* Burdigalian fauna of the true Sables de l'Orléanais.

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[1] Mayet, L., 1908. Ann. Univ. Lyon, N. S., I, Fasc. 24, p. 313.
[2] Stehlin, H. G., 1908. Bull. Soc. géol. France, (4), VII, p. 545.

Perhaps the greatest discrepancy between the views of Stehlin and those of Depéret, Mayet and others, is his assignment of the Calcaire de Montabuzard to a position not below the Sables de l'Orléanais, but rather to an elevated place considerably above the Sables. Here again Stehlin has based his views on the fact that there is a very large immigrant element in the Montabuzard fauna, as compared with the indigenous mammals. Thus, this authority would regard the Montabuzard assemblage as being perhaps equivalent to or slightly later than the typical Sansan fauna. Stehlin admits, however, that:

> Si, un jour, on découvre une faunule de Mammifères dans quelque lambeau de calcaire de l'Orléanais indubitable, c'est-à-dire directement recouvert par des sables fluviatiles burdigaliens fossilifères, la question de Montabuzard sera tranchée.

The localities at which Burdigalian faunules have been found in central France are numerous and are listed by Depéret, by Mayet, and by Stehlin, to which authors the reader is referred. Mayet, particularly, has given detailed discussions of the important localities at which Sables de l'Orléanais deposits containing mammalian remains have been discovered.

As to the fauna of the Sables de l'Orléanais, the following forms might be accorded particular attention:

Pliopithecus—according to Stehlin present in the Faluns de Pontlevoy and not in the Sables de l'Orléanais, strictly speaking. But Mayet placed this genus in the Sables, as well as in the Faluns. Certainly an advanced anthropoid, that might be of Middle rather than of Lower Miocene affinities.

Amphicyon—typically Miocene.
Pseudælurus—also typically Miocene.
Steneofiber—a characteristic Lower Miocene form.
Proboscideans—all essentially primitive—Lower to Middle Miocene.
Brachyodus—a persistent type from the Oligocene.
Palæochœrus—another persisting Oligocene form.
Listriodon—characteristic of the Miocene. *L. lockharti* of the Sables is a very primitive member of the genus, and might be considered as indicative of the beginning of the Miocene.
Palæomeryx, Amphimoschus, Procervulus, Dicrocerus—all primitive Miocene cervulines.
Anchitherium—the earliest appearance of this genus in Europe.
Macrotherium—quite characteristic of the Miocene, and it may occur as early as the beginning of the period.
Diceratherium—this genus?
Aceratherium, Teleoceras—again typical Miocene forms.

It might be well to mention here some important localities in addition to those discussed, namely, Chitenay, Chevilly, Eggenburg in Lower Austria, and Brüttelen in Switzerland, at which latter place a shoreline facies has been discovered, with an association of marine forms.

In a recent paper (1934) by Roman and Viret,[1] a Burdigalian fauna from La Romieu is described. This fauna is found to be contemporaneous with the *upper* Burdigalian of the Sables de l'Orléanais, particularly as characterized by the faunas of Baigneaux and of Chevilly. In this connection, it might be said that these authors make some interesting comments as to the characters of the upper Burdigalian fauna in general, as compared with

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[1] Roman, F., and J. Viret, 1934. Mem. Soc. géol. France, N. S., IX, No. 21.

the lower Burdigalian assemblage below, and the Helvetian fauna above. In short, the conclusions of Roman and Viret as to the characters of the upper Burdigalian fauna or faunas of Central Europe are as follows:

The upper Burdigalian fauna differs from the older lower Burdigalian fauna in that:

There are more of *Brachyodus onoideus, Amphitragulus, Palæomeryx garsonnini,* and typical *Brachypotherium aurelianense.*

The following forms appear for the first time:

Listriodon lockharti, Hemicyon, near *H. göriachensis, Pseudælurus quadridentatus, Lagomeryx* of small size, *Dorcatherium, Dinotherium,* as characterized by the small *D. cuvieri,* and a large *Brachypotherium.*

The upper Burdigalian differs from the younger Helvetian in that:

There have not as yet appeared such forms as *Pliopithecus, Machairodus, Ursavus, Micromeryx, Potamotherium,* and above all the antelopes, which latter appear suddenly in the Middle Miocene of Sansan.

Anchitherium aurelianense is present but as a small mutation—that is, it has not attained the size of the typical later Miocene *Anchitherium.* The same is true of *Steneofiber. Palæochœrus* is present but not *Hyotherium.*

The proboscideans of the Burdigalian are as follows:

Dinotherium cuvieri Kaup Type—Chevilly
Turicius tapiroides (Cuvier) Type—Calcaire de Montabuzard
Turicius turicensis (Schinz) (According to Mayet, type from Sarmatian)
Dinotherium bavaricum von Meyer (According to Mayet, type from Helvetian)
Miomastodon depereti Osborn Type—Chevilly
Trilophodon pontileviensis Mayet and Fourtau Type—Pontlevoy
Trilophodon angustidens cuvieri (Pomel) Type—Gers
Serridentinus filholi Frick Type—Gers
Zygolophodon pyrenaicus aurelianensis Osborn Type—Chevilly
Dinotherium hungaricum Éhik Type—Kotyháza, Hungary

3. THE MIDDLE MIOCENE: HELVETIAN AND TORTONIAN = VINDOBONIAN

HELVETIAN.—The Middle Miocene of Europe, the Vindobonian, may be divided into two stages, the Helvetian and the Tortonian, each typified by distinctive mammalian faunas. The characteristic Helvetian fauna is that of Sansan.

The Sansan fauna, discovered by Lartet, and studied by this same authority and by Milne-Edwards, and later by Filhol, comes from a hill near the little village of Sansan in southern France. At this place there is a succession of freshwater sediments, beginning with a clay bed at the bottom, followed by a calcareous layer, which in turn is capped by a series of marls containing freshwater molluscs and numerous fossil vertebrates—particularly mammals and birds.

In contradistinction to the preceding Burdigalian fauna, as developed in the Sables de l'Orléanais, the Sansan assemblage is definitively a more modernized fauna, with no important persisting Oligocene types, which were so common in the Burdigalian faunas. Indeed, the Sansan fauna is characterized by the appearance of many mammalian forms indicative of the beginning of evolutionary developments that culminated in the modernized faunas of uppermost Cenozoic and Recent times.

The origin of the Sansan deposits was discussed by Lartet, whose conclusions were substantiated by Filhol. Lartet had the following to say about the genesis of these beds:

> Toutes ces circonstances m'avient porté à penser que l'accumulation successive des fossiles organiques qui constitue le dépôt de Sansan se serait effectuée au fond d'un marais, ou si l'on veut d'un petit lac où auraient vécu les espèces aquatiques dont on retrouve des débris; tandis que les eaux torrentielles auraient pu entraîner dans ce bas-fond, soit des ossements dispersés, soit les cadavres entiers des animaux terrestres établis à demeure ou du moins se montrant passagèrement sur les terres environnantes, émergées pour un temps plus ou moins long.[1]
>
> L'hypothèse de Lartet paraît bien justifiée. Il y a eu à Sansan un lac, dont la plus grande partie a disparu, a été emportée à l'epoque du creusement des vallées. Dans ce lac venaient se déverser différents cours d'eau, susceptibles de déborder à certains moments et de couvrir probablement d'assez vastes espaces, d'où ils emportaient les animaux y vivant au moment de leurs crues subites, pour les déposer en un point où existait un remous.[2]

Depéret has discussed at length the composition and relationships of the Sansan fauna, consequently the fauna in its entirety will not be listed here. But the following important genera contained within the fauna may be given some consideration.

Pliopithecus—here we see the continuation of a relatively advanced anthropoid, which already has appeared in the Burdigalian fauna of the Sables de l'Orléanais and the Faluns de Pontlevoy.
Insectivores—several genera, such as *Erinaceus, Sorex, Talpa,* which are similar to the modern forms.
Rodents—like the insectivores, genera leading to modern types. There should be mentioned particularly:
Steneofiber—a characteristic Lower to Middle Miocene castoroid. This, or a related type, is found in the Lower Miocene of North America.
Amphicyon—a typical Miocene canid, showing advanced characters.
Hemicyon—one of the more advanced "bear-dogs," distinctly later than Lower Miocene, and found at various Middle to Upper Miocene localities in Europe, Asia, and North America.
Machairodus and *Pseudælurus*—Miocene Felidæ.
Other carnivores are distinctly leading to more modern types.
Anchitherium—the typical Miocene equid of the Eastern Hemisphere.
Macrotherium—similarly, the typical Old World Miocene chalicothere.
Aceratherium—continuation of a form that first appeared in the Burdigalian.
Listriodon—typical Miocene suid.
Palæomeryx—a very typical element in the Miocene faunas of Europe.
Trilophodon.
Turicius.

Of the European deposits correlative with those of Sansan, perhaps the most important are those of Engelswies and Georgensgmünd in Germany, and Eibiswald and Göriach in Austria.

Klähn (1922) describes the Engelswies deposits as chalky, brackish water sediments, probably deposited in an estuary or the mouth of a river that flowed out into the Middle Miocene mediterranean of Central Europe. These beds contain a typical Middle to Upper Miocene fauna, characterized notably by *Dinotherium, Barchypotherium, Aceratherium, Anchitherium, Macrotherium,* and *Hyotherium.* Klähn would correlate this fauna with the Steinheim assemblage, which would place it somewhat higher than it is regarded in the present work.

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[1] Lartet, E., quoted by H. Filhol, 1891, pp. 5, 6.
[2] Filhol, H., 1891, p. 6.

The fauna from Göriach, described by various authors but particularly by Toula and by Hofmann, would seem to be a typically Middle Miocene mammalian assemblage. The presence in this fauna of characteristic Miocene genera, the lack of truly advanced Miocene forms, and the persistence of certain types from the Lower Miocene seem to favor the correlation of Göriach as approximately of Sansan age. There might be noted here such genera as *Amphicyon, Dinocyon, Hemicyon, Trilophodon, Anchitherium, Steneofiber, Aceratherium, Hyotherium, Palæomeryx, Dicrocerus* and other primitive deer, all of which relate this fauna very closely with the Sansan assemblage. The genus *Cebochœrus*, described by Hofmann as from Göriach, is at best of doubtful reference, for the material is very fragmentary. One would hardly expect this form in the Miocene.

Others faunas of Helvetian age will compare with the Sansan fauna in about the same way as these, as considered above.

PROBOSCIDEANS: See list of Vindobonian proboscideans (p. 1464 below).

TORTONIAN.—Of the Tortonian deposits in which fossil mammals have been found, none is perhaps better known than La Grive-Saint-Alban, Isère, in southern France. This locality has been known for many years, and has been studied extensively by Depéret, who published several large papers dealing with the fauna and the stratigraphic relationships of that deposit.

Depéret has shown that the mammal-bearing beds of La Grive-Saint-Alban are in reality fissure deposits, formed during Middle Miocene times, in pits, fissures, and caves that were eroded out of Mesozoic limestones. In similar pockets at Mont-Ceindre, near Lyons, Depéret discovered such a wealth of bat remains that he was led to think that perhaps some of the deposits in this general complex or series were formed in Miocene bat caves.

Some fifty years ago this author[1] described the typical deposits at La Grive-Saint-Alban, as follows (Depéret, 1887, p. 60):

> Ces fentes sont toutes ouvertes vers le haut, et pénètrent plus ou moins profondément dans l'épaisseur du terrain jurassique; la plupart cependant atteignent le niveau du sol de la carrière. Le remplissage de ces fentes, s'est opéré, il me semble, par le haut, et sous l'influence d'un simple ruissellement à la surface du calcaire; la faible vitesse des eaux pluviales sur ce plateau horizontal, et la lenteur du phénomène de remplissage me paraissent suffire à expliquer l'absence si remarquable, dans les matériaux charriés, de cailloux roulés et même de graviers, qui pourraient faire penser à un charriage opéré par un cours d'eau de quelque importance. Les seuls éléments étrangers à l'argile que j'ai observés sont des cristaux spathiques, qui paraissent résulter de l'évaporation répétée d'eaux riches en acide carbonique. Quant à l'argile rouge, je pense qu'elle n'est ici que le simple résidu de la lente dissolution du calcaire, opérée d'une manière continue par les eaux pluviales, pendant la longue émersion du continent mayencien, et accumulée dans les fentes par les eaux de ruissellement.

A few years later (1892) Depéret[2] had the following to say as to the age and relationships of the fauna from La Grive-Saint-Alban.

> Ainsi que je l'ai déjà indiqué en 1887, la présence à la Grive du *Rhinoceros brachypus* et du *Dinotherium*, qui manquent à Sansan, mais se retrouvent dans l'horizon un peu plus élevé *de Simorre* (Gers) annonce des affinités importantes entre la faune de la Grive et celle de cette dernière localité, sur laquelle nos connaissances sont malheureusement fort incomplètes. Ce dernier parallélisme est d'autant plus probable que, ainsi que je l'ai déjà indiqué, les animaux de la Grive, tels que le *Pliopithecus*, le *Machairodus Jourdani*, la *Lutra Lorteti*, le *Cricetodon Rhodanicum*, le *Protragocerus Chantrei* paraissent représenter dans leur ensemble un degré d'évolution légèrement plus avancé que celui des espèces représentatives dans le gisement de Sansan. . . .
>
> Le gisement des *sables de Steinheim* (Wurtemberg) doit être considéré comme l'équivalent exact de celui de la Grive. En effet, sur les quarante-sept espèces de la Grive, dix-sept se trouvent aussi à Steinheim. . . .
>
> Les autres gisements de Suisse, d'Allemagne ou d'Autriche que l'on peut considérer comme à peu près synchroniques de celui de la Grive-Saint-Alban sont: les lignites de *Göriach* (Styrie); *Georgensgmünd*; *Günsburg* et *les sables à Dinotherium* de Bavière; *Ellg, Kapfnach*; *Ries* (Nordlingen); *Vermes* (Jura Bernois); mais la faune de ces diverses localités est beaucoup plus pauvre que celle des autres gisements précités.

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[1] Depéret, C., 1887. Arch. Mus. hist. nat. Lyon, IV, p. 60.

[2] Depéret, C., 1892. Arch. Mus. hist. nat. Lyon, V, Pt. 2, pp. 4, 5.

Subsequently, in 1899, Gaillard[1] published a paper supplementing the studies of Depéret, and describing new or little known mammals from La Grive-Saint-Alban. Gaillard's conclusions as to the age of this deposit were essentially the same as those of Depéret. Since the time that Depéret and Gaillard made their detailed studies of the fauna of La Grive, the general trend has been to substantiate and strengthen the conclusions of these authors as to the age of this mammalian assemblage.

That the Helvetian and Tortonian stages are very closely related is shown by a comparison of their respective faunas. Thus, the Sansan and La Grive faunas may be compared, by genera, as follows.

Sansan	La Grive-Saint-Alban
Pliopithecus	*Pliopithecus*
Vespertilio	*Vespertilio*
Rhinolophus	*Vesperugo*
Erinaceus	*Erinaceus*
Galerix	*Galerix*
Lanthanotherium	
Mygale	*Dimylus*
Sorex	*Sorex*
Talpa	*Talpa*
Sciurus	*Sciurus*
Cricetodon	*Cricetodon*
Myoxus	*Myoxus*
Meriones?	
Arvicola?	
Steneofiber	
	Lagopsis
	Prolagus
Hemicyon	*Hemicyon*
Pseudocyon	
Amphicyon	*Amphicyon*
Trochitis	*Trochitis*
Mustela	*Plesictis*
Putorius?	*Martes*
Proputorius	*Lutra*
Viverra	*Viverra*
	Herpestes
	Progenetta
Machairodus	*Machairodus*
Pseudælurus	*Pseudælurus*
	Aelurogale
Trilophodon	*Trilophodon*
Turicius	*Dinotherium*
Anchitherium	*Anchitherium*
Aceratherium	*Aceratherium*
	Macrotherium
Chæromorus	*Chæromorus*
Chærotherium	
Listriodon	*Listriodon*
	Hyotherium
Hyæmoschus	*Hyæmoschus*
Micromeryx	*Micromeryx*
Palæomeryx	*Palæomeryx*
Morphelaphus	*Dicrocerus*
Strogulognathus	
Palæocervus	
Cervus	
Antilope	*Protragocerus*

From this comparative list it may be seen that there is little definitive evidence that enables one logically to separate the typical Helvetian faunas from those of Tortonian age. Indeed many of these faunas are considered as of one or the other of these two stages, by different authors, and no two authorities will correlate the Middle Miocene deposits of Central Europe in exactly the same way. Therefore there is much to be said in favor of lumping the several Middle Miocene faunas within one time division, the Vindobonian.

Of the other so-called Tortonian faunas, some of the most important are those of Simorre and Villefranche d'Astarac in France, of Steinheim, Mösskirch, and Oppeln in Germany.

The Steinheim fauna, preserved in an impure chalky ooze, or mud, contains the following diagnostic genera: *Amphicyon*, *Viverra*, *Chalicomys*, *Aceratherium*, *Macrotherium*, *Anchitherium*, *Listriodon*, *Dicrocerus*, and *Palæomeryx*. This assemblage is generally regarded as of Middle to Upper Miocene age, equal to the La Grive fauna and perhaps younger than the typical Helvetian faunas. Klähn[2] speaks of it as follows:

> In Begleitung des unten zu beschreibenden *Mast. steinheimensis* deutet die Fauna auf obermiozänes Alter hin. Diese ist dieselbe wie die von Kgl. Neudorf bei Oppeln und Grive-St. Alban.

The fauna of Simorre is in all respects correlative with that of La Grive-Saint-Alban, and for this reason is often considered as typical of the Tortonian in Europe. The remarks as to the age and relationships of the fauna of La Grive apply equally well to that of Simorre.

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[1] Gaillard, Claude, 1899. Arch. Mus. hist. nat. Lyon, VII.

[2] Klähn, H., 1922. "Die badischen Mastodonten, etc.," p. 33.

Certain other European faunas, representing the final stages of the Vindobonian or Tortonian, may be considered here. Of these, particular mention should be made of Œningen, Saint Gaudens, Elgg, and Monte Bamboli; Käpffnach, Günsburg, and San Isidro.

The Œningen fauna, and flora preserved in fine-grained calcareous beds near Zurich, Switzerland, has long been famous for the excellence and diversity of the fossils comprising it. It is especially characterized by numerous plants, insects, reptilian and amphibian remains, as well as those of fossil mammals. Incidentally, it was here that the type of *Andrias scheuzeri* was discovered. De Lapparent[1] makes the following remarks concerning the Œningen fossils:

> On attribue au sommet du tortonien les couches d'Œningen, sur les bords du lac de Constance, calcaires en minces plaquettes, extraordinairement riches en fossiles, insectes, poissons (*Leuciscus*), reptiles, etc. Mais c'est surtout par sa flore que le gîte d'Œningen est célèbre. Heer en a décrit près de 500 espèces, parmi lesquelles bon nombre de formes européennes sont mêlées à des types asiatiques, africains, australiens ou même américains. L'assise inférieure ou *couche* à *insectes* d'Œningen est composée d'environ 250 feuillets, où l'on distingue jusqu'aux saisons successives: les fleurs de camphrier annonçant le printemps, les fruits d'orme et de peuplier l'été, ceux de camphrier et de *Diospyros* l'approche de l'automne. . .
>
> Heer pense qu'il régnait à Œningen un climat analogue à celui de Madère, du Japon méridional et de la Géorgie, soit une moyenne annuelle de 18 à 19 degrés.

The numerous faunas contemporaneous with or correlative with Œningen and Saint Gaudens were listed by Depéret in 1906.

PROBOSCIDEANS: See list of Vindobonian proboscideans, below.

VINDOBONIAN PROBOSCIDEANS

Dinotherium levius Jourdan	T. La Grive-Saint-Alban
Dinotherium intermedium Blainville	Type locality? France
Dinotherium bavaricum Meyer	H. Gmünd
Dinotherium secundarium Kaup	T. Simorre
Zygolophodon pyrenaicus (Lartet)	T. Ile-en-Dodon
Zygolophodon borsoni affinis (Jourdan)	Type locality?
Trilophodon angustidens (Cuvier)	T. Simorre
Trilophodon angustidens minutus (Cuvier)	Saxony
Trilophodon angustidens gaujaci (Lartet)	Lombez
Trilophodon angustidens austro-germanicus Wegner	Oppeln
Trilophodon angustidens gaillardi Osborn	T. Villefranche d'Astarac
Trilophodon engelswiesensis Klähn	H. Engelswies
Trilophodon steinheimensis Klähn	T. Steinheim
Serridentinus subtapiroideus (Schlesinger)	H. Wies
Turicius turicensis (Schinz)	T. Elgg
Turicius turicensis simorrensis Osborn	T. Simorre

T.—Tortonian
H.—Helvetian

4. THE UPPER MIOCENE: SARMATIAN

The close of the Miocene and the opening of the Pliocene in Eurasia was inaugurated by a new cycle of sedimentation. This was, in brief, the beginning of the regression of Miocene seas, with a consequent inauguration of extended continental sedimentation, characterized at first by littoral deposits, and then, in a progressive fashion,

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[1] De Lapparent, A. de, 1906. Traité de Géologie, p. 1615.

by lake beds and river channels. The change from a predominantly mediterranean and island type of landscape, typical of the European Miocene, to a truly continental type of landscape, so characteristic of the Pliocene, may be said to have begun in the Upper Miocene, progressing with increasing rapidity through the Sarmatian and finding its culmination in the Pontian.

The question of the correlation of Sarmatian deposits and faunas, which are characteristically of marine, shallow-water facies, with the continental mammalian faunas of the same period is indeed difficult. This problem is chiefly concerned with the query as to just what may be considered as truly Sarmatian or equivalent mammalian faunas.

Certain deposits, such as Saint Gaudens, Œningen, Monte Bamboli and related beds, listed by Osborn in 1910 (p. 257) as of Sarmatian age, are more properly to be considered as representing the uppermost phases of the Vindobonian or Tortonian in Europe, as shown in preceding pages of this chapter. This would seem to be the general consensus of opinion of authorities on the matter and need not be discussed at any greater length here.

Yet the question of whether or not any mammalian faunas can be truly correlated with the marine Sarmatian stage is an important one, and it has been recently considered by von Koenigswald and by Tobien.

Borissiak, in 1914 and 1915, described a mammalian fauna that was found at Sebastopol, on the borders of the Black Sea, in beds containing unmistakable Sarmatian molluscs. According to this author, the fossils were found as a "breche ossifere" in a small calcareous lens, intercalated within the upper zone of the middle Sarmatian of that region. Naturally, the occurrence of this fauna led the author, and numerous subsequent writers, to believe that the Sebastopol fauna was in truth a mammalian assemblage of Sarmatian age.

Yet it is a very curious fact that the mammalian fauna of Sebastopol is typically Pontian in its characters. It contains *Achtaria*, a giraffid quite similar to *Palæotragus*, *Tragoceras*, *Aceratherium*, and *Hipparion*; all in all an assemblage that recalls Pikermi and Samos. Naturally, if this fauna is of true Sarmatian age, then it offers undoubted proof of the pre-Pontian occurrence of *Hipparion*—a fact of prime importance. For, if as some authors think, *Hipparion* appears in Eurasia before the beginning of the Pontian, the most important of the several criteria definitive of the Pontian loses much of its diagnostic value.

The idea that the Sebastopol fauna is truly of Sarmatian age, or that *Hipparion* occurs in the Old World prior to the advent of the Pontian, has recently been disputed by von Koenigswald. This author believes that rather than a pre-Pontian appearance of what seems to be a typically Pontian fauna, the Sebastopol deposit represents a cave, or possibly a fissure deposit, in which animals of a later age have been intruded into sediments older than the period during which they lived. This explanation of the Sebastopol occurrence, if valid, goes a long way towards clearing up what has always been a stumbling block in the correlation of Eurasiatic mammalian horizons. Von Koenigswald[1] says that: "Das sarmatische Alter der *Hipparion*-Fauna von Sebastopol kann bei der Art der Einlagerung und der Erhaltung der Reste nicht als unbedingt erwiesen angesehen werden."

Von Koenigswald goes on in the same contribution to dispute the idea that *Hipparion* is present as a pre-Pontian form in any of the several localities where it has been reported as of an age preceding the characteristic Pontian fauna.

As opposed to this view is the recent work of Tobien (1938), in which it is maintained that not only at Sebastopol, but at various other localities, particularly in eastern Europe, there are beds of true Sarmatian age,

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[1] Koenigswald, G. H. R. von, 1931. Sonderabdruck aus dem Centralblatt f. Min., etc., Abt. B, No. 1, p. 45.

[2] Tobien, H., 1938. Zeits. deutsch. Geol. Ges., XC, Heft 4.

bearing *Hipparion.* The localities other than Sebastopol cited by Tobien are the trans-Caucasian region (Alekseev, 1930), Linz (Gümbel, 1894), Bavarian Flinz (Freudenberg, 1928), Odessa (Andrussow, 1905), Constantinople (Dietrich, 1933), Taraklia in Bessarabia (Khomenko, 1913, 1914), Thrace (von Arabu, 1916, 1919), Rumania (Krejci-Graf, 1932). And in addition, Tobien describes some teeth and astragali of *Hipparion* from Œningen (Ohningen).

So the problem stands at the present time. If these localities are truly of Sarmatian age, then they represent what might be considered as the final stage of the continental Miocene in Europe, a stage during which *Hipparion* and other Pontian types appear, foreshadowing the tremendous spread of the *Hipparion* faunas of the true Pontian. If, on the other hand, these localities are of Pontian age (at least those in which *Hipparion* is present) then it may be said that for practical purposes there are no continental mammalian faunas that may be proven as the exact equivalents of the marine Sarmatian, and that the continental Miocene of Europe comes to a close with such upper Vindobonian or Tortonian assemblages as those of Saint Gaudens and the like. At best the problem works down to one of definitions, and as such is a difficult one to settle satisfactorily.

5. THE LOWER PLIOCENE: PONTIAN

The new faunal and sedimentation cycle that had its beginnings in the Sarmatian continued with increased momentum into the following Tertiary subdivision in Europe, the Pontian. The mediterranean sea, so characteristic of the Middle Miocene of Central Europe, became increasingly restricted, continental flood-plain and lacustrine deposits replaced marine beds, and mammalian faunas became exceedingly wide-spread and characteristic.

In this connection, there need only be repeated the well-known fact that the Pontian was the time during which the characteristic *Hipparion* fauna spread throughout Eurasia. This fauna, which all in all was remarkably uniform throughout the extent of its range, stretched from Spain and western Europe to China, from the shores of the Mediterranean as it was at that time into northern Europe. It was a wide-spread assemblage of mammals living in a plains or steppe environment, and showing a great preponderance of grazing perissodactyls and artiodactyls, accompanied by the carnivores that might be expected with an ecological and faunal association such as this.

The presence of the *Hipparion* fauna in the Oriental and the Asiatic areas, and its significance with regard to the correlation of the upper Tertiary beds of these regions, has been discussed in other sections of this chapter. At the present time the discussion will be limited to the occurrence and significance of the Pontian *Hipparion* fauna in Europe.

In a discussion of the continental Pontian faunas, the fact must be kept in mind that these mammalian assemblages mark the beginning of a new period in the history of mammalian faunas. This was the time when truly modernized types of advanced mammals made their first appearance, and particularly when immigrant forms suddenly became conspicuous in the Eurasiatic faunas, to characterize these faunas wherever they might be developed.

Of course, as the name implies, the most characteristic of the immigrant genera is *Hipparion.* That this genus is of undoubted North American origin can no longer be questioned by anyone who has made a careful study of the succession of the Equidæ. Consequently, as has already been pointed out in other sections of this chapter, the appearance of *Hipparion* in the Old World must be subsequent to the time at which it arose in North

America—whatever that time may be. Certainly *Hipparion* did not become a genus distinct from its ancestor *Merychippus,* before the uppermost part of the Miocene in North America. And even though some evidence would seem to indicate that *Hipparion* might have made its first appearance in North America during Upper Miocene times, other evidence has been interpreted to indicate the fact that the genus did not appear in the New World until the beginning of the Pliocene.

Turning now to a consideration of other Pontian types, we see numerous immigrant and specialized forms appearing for the first time in Eurasia.

Among the carnivores it is interesting to note that true bears such as *Indarctos* and *Ursavus*—as distinguished from the ancestral "bear-dogs," such as *Hemicyon*—first appear in the Pontian.

Likewise, the hyænas, of Asiatic and Oriental origin, become well-established elements in the Tertiary faunas in Pontian times. True enough, these animals first appear in Upper Miocene times, in the immediately pre-Pontian deposits, but it is in the Pontian that the hyænas become widely distributed throughout the European region.

A conspicuous element in the Pontian faunas of Europe, particularly along the eastern border of the Mediterranean, is the aardvark, *Orycteropus.* The tubulidentates, though now of African distribution, did not necessarily originate or evolve on that continent; indeed, all of the fossil aardvarks of pre-Pleistocene age come from the Eurasiatic and Oriental regions, so that the group may well have originated somewhere in the north.

In a different category is the gigantic hyracoid, *Pliohyrax*—a conspicuous member of the Pikermi fauna. We know quite definitely that the hyracoids originated in Africa in Eocene times, and so the presence of a member of this group in the European Pontian implies an immigration into the fauna from a southerly source.

The most conspicuous elements of the Pontian fauna, with the exception of *Hipparion,* are the numerous ruminants. Here is an advanced group of mammals, appearing for the most part as newly evolved elements in the mammalian assemblage. Our evidence points rather strongly to the fact that the ruminants of advanced type are relatively recent developments in the mammalian world. That is, the common ancestor of the deer, of the giraffids, and of the bovids is probably to be found in the Miocene.

In the European Pontian is a very primitive giraffe, *Palæotragus,* not greatly different in most of its characters from the modern African okapi. With *Palæotragus* is *Samotherium,* which is nothing more nor less than an enlarged type of *Palæotragus,* and *Helladotherium,* a gigantic giraffid belonging to a group that was to become widely spread during Upper Pliocene and Pleistocene times. It would seem probable that the origin of the giraffids might have been Oriental—that they were immigrants into Europe and into Africa, and that the modern okapi represents a persistent primitive form, pushed to the periphery of the range for this family by more specialized types developing at or near the center of origin.

This was the age of the first flowering for the gazelles and the antelopes, and these animals are to be found in great profusion throughout the Eurasiatic and Oriental Pontian. There is a host of forms (recently monographed by Pilgrim) that give to the *Hipparion* fauna a very African appearance. It would seem, however, that these various gazelles, sheep, antelopes, and pre-cattle were of northern origin and migrated in Pontian or post-Pontian times to the southern continent.

With these considerations in mind, what is the age of the Pontian? Among French scholars the European Pontian has been generally accepted as of Upper Miocene age, while many Germans would place the Pontian at the beginning of the Pliocene. Many years ago, as pointed out elsewhere in this chapter, Matthew suggested the desirability of making the continental Pliocene throughout the world coincident with the appearance of *Hipparion*. This definition for the beginning of the Pliocene is, on the whole, as satisfactory a designation as has ever been proposed. Consequently, the Pontian is here considered as of Lower Pliocene age, corresponding in Europe to those stages in Asia, the Orient, and North America at which *Hipparion* first becomes a definitely identifiable element in the mammalian faunas.

The outstanding Pontian localities of Europe are listed below, taken from the list as presented by Pilgrim in his "Pontian Carnivora of Europe." These localities, stretching from Spain on the west to the Black Sea region and Asia Minor on the east, are characterized and correlated by the uniformity and the similarity of their faunas.

Spain	Aragon, Catalonia, La Mancha
France	Montredon, Orignac, Cerdagne, Mont Léberon, Cucuron, Croix Rousse
Germany	Eppelsheim, Salmendingen, Melchingen, Trochtelfingen
Sicily	Gravitelli
Greece	Pikermi
Macedonia	Salonica, Veles
Samos	Samos
Hungary	Baltávar, Polgardi, Csakvar, Baroth-kopecz
Black Sea	(Sebastopol), Novo Elisavetovka, Taraklia Kischinev, Grebeniki, Tschobrotschi
Persia	Maragha

Of these, perhaps the best known from their faunas, are: Mont Léberon, Cucuron, Eppelsheim, Pikermi, Samos, and Maragha.

Of course, the presence of typical Pontian faunas characterized by *Hipparion* at the above localities affords strong evidence as to their general unity and contemporaneity. Yet it is quite possible, as Pilgrim has pointed out, that all of these faunas may not be exactly equivalent, each to the other, in age. That is, homotaxial factors may play a certain part in the spread and delimitation of the Pontian complex in Europe—just as they most probably did (as shown in another section of this paper) in India. Indeed, certain authorities would subdivide the Pontian, particularly on the basis of the geology of the Black Sea area, into at least three zones. But in spite of these considerations it is to be remembered that the Pontian faunas represent essentially a definite phase in the evolution of mammalian faunas, and as such are for all practical purposes to be considered together as a unit, even though there may not be exact time identities between them—due to homotaxial lags dependent upon migrations or other causes. This whole question has been no better stated than by Pilgrim (1931),[1] as follows:

> At the same time, there is no doubt that the 'Hipparion fauna' does occur at different levels, of which the lowest, including perhaps the Sebastopol fauna described by Borissiak [but see remarks in the discussion preceding this on the Sarmatian problem] (1915), has been referred to the Upper Sarmatian; the fauna of Taraklia (Khomenko, 1914) and Novo-Elisavetovka (Alexejew, 1916) are classed as Maeotic, or intermediate between the Sarmatian and the Pontian, while the remaining localities are truly Pontian.
>
> It is hardly conceivable that these three stages should not be represented among the so-called 'Pontian' deposits of the rest of Europe. It may be that increased material, and intensive study of what is already in our museums, may one day render such a correlation possible, but in my opinion the state of our knowledge does not permit of it at present...
>
> However this may be, there can be no doubt that we are dealing with a definite faunistic unit. Its homogeneous character is specially striking when we compare it with the Vindobonian fauna of La-Grive-Saint-Alban which preceded it or that of Monte Olivola, Rousillon and Montpellier, which followed it. The question, however, arises as to whether such a fauna, which includes both Sarmatian and Pontian elements, can strictly be called Pontian. These names were definitely applied to certain marine strata in the Black Sea region, and their application should not be either restricted or extended. Many writers, seeing this, have written of this fauna as the 'Hipparion fauna', but since the genus *Hipparion* seems to have a wider range even in Europe and still more so in Asia and North America than the fauna we are considering, that term does not meet the need, and we seem therefore bound to speak of the Sarmato-Pontian fauna.

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[1] Pilgrim, G. E., 1931. Catalogue of the Pontian Carnivora of Europe. Brit. Mus. (Nat. Hist.), pp. 147, 148.

PONTIAN PROBOSCIDEA

Trilophodon (*Choerolophodon*) *pentelicus* (Gaudry and Lartet)	Pikermi
Turicius atticus (Wagner)	Pikermi
Tetralophodon grandincisivus (Schlesinger)	Maragha
Tetralophodon longirostris (Kaup)	Eppelsheim
Dinotherium medium Kaup	Eppelsheim
Dinotherium giganteum Kaup	Eppelsheim
Trilophodon esselbornensis (Klähn)	Esselborn
Turicius wahlheimensis (Klähn)	Wahlheim
Tetralophodon gigantorostris (Klähn)	Bermersheim
Miomastodon tapiroides americanus (Schlesinger)	Tasnád
Pliomastodon americanus praetypica (Schlesinger)	Batta-Érd
Dinotherium proavum Eichwald	Podolia, Russia
Dinotherium podolicum Eichwald	Podolia
Dinotherium uralense Eichwald	Ural Mts.
Anancus arvernensis progressor Khomenko	S. Bessarabia
Anancus intermedius (Eichwald)	Volhynia
Platybelodon danovi Borissiak (Sarmatian)	Kuban, N. Caucasus, Chokrak Beds

6. THE MIDDLE PLIOCENE: PLAISANCIAN

Following the expansion of Pontian mammals in Europe, there would seem to be a gap in the succession of mammalian faunas—perhaps the result of extensive marine inundations. This fact has been pointed out by numerous authors, notably by Depéret, who was the first student to recognize and elucidate this distinct break in the sequence of Pliocene mammalian faunas in Europe. Osborn (1910)[1] emphasized the importance of Depéret's conclusions, as quoted below, and more recently Pilgrim (1939)[2] pointed out the reality of a Middle Pliocene hiatus in the European fossil mammal faunas.

> As this is chiefly a marine phase, the terrestrial mammalian fauna is imperfectly known. The typical deposits are those of the lignites of Casino (Tuscany) which are correlated by Depéret with the lacustrine deposits of Autrey in the valley of the Saône, France. On the east coast of England is a marine formation, the Coralline Crag of Suffolk, containing a mastodon and a rhinoceros (*Dicerorhinus*).

Of course this gap is not complete, for there are scattered mammalian remains known from deposits of Plaisancian age, but generally speaking the continental facies in this stage are of little importance. And it is interesting to note that in many cases the fossil mammals of Plaisancian age are found in littoral deposits, sometimes associated with diagnostic marine invertebrates. All of these facts were made clear by Depéret, in his classic studies of some fifty years ago.

Depéret[3] considered the Plaisancian and the succeeding Astian as closely related, and together they constituted his "older Pliocene" which he distinguished from the "new Pliocene" or Sicilian. In the older Pliocene, according to this author, were numerous holdovers from the Pontian fauna, while the Sicilian is marked by the influx of a new and modernized fauna, quite distinct from those preceding it. According to the chronology adopted in this

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[1] Osborn, H. F., 1910. "The Age of Mammals," pp. 311, 312.

[2] Pilgrim, G. E., and A. Tindell Hopwood, 1939. Rec. Geol. Surv. India, LXXIII, Pt. 4, pp. 445, 446.

[3] Depéret, C., 1893 (1894). Bull. Soc. géol. France, (3), XXI, pp. 529, 530.

present work, the Pontian, of course, represents the beginning of the Pliocene, while the Plaisancian and the Astian, still showing mammalian types of Pontian origin, constitute the middle and upper phases of the Pliocene, respectively. The Sicilian, with the influx of new and modernized types, such as *Equus* and *Archidiskodon*, represents the beginning of the Pleistocene (Depéret, 1894, *op. cit.*, pp. 529, 530):

> On distingue nettement dans le faciès marin du Pliocène trois étages: le *Pliocène inférieur* ou *Plaisancien*, dont le type est dans les argiles bleues subapennines; ensuite le *Pliocène moyen* ou *Astien*, fondé sur les sables jaunes très fossilifères du pays d'Asti où ils surmontent avec évidence l'étage des argiles bleues.
>
> Ces deux étages marins . . . . sont étroitement unis l'un à l'autre par leur distribution géographique et même par leur faune (qui dénote une mer assez chaude), de sorte que l'on pourrait à la rigueur, avec MM. de Rouville, de Stefani, Welsch, etc., les considérer comme les deux phases successives, la seconde plus littorale, d'un même dépôt, sur un fond de mer en voie d'exhaussement graduel.

Depéret then goes on to show that in Italy mammalian remains are rare in the marine facies of the Plaisancian, and in the Astian as well, while to the north, especially in France, the Plaisancian deposits constitute a series of blue clays with invertebrate remains, underlying or antecedent to the mammaliferous Astian sediments.

Pilgrim has recently restated Depéret's arguments, and has particularly emphasized the Plaisancian faunal gap by demonstrating that the succeeding Astian fauna shows closer resemblances to the Sicilian fauna above it, than to the older Pontian fauna.

> Very little of the Roussillon and Montpellier fauna became extinct between that stage and that of the Val d'Arno, Perrier and Senèze, as compared with the multitude of families and genera which appear for the last time in the Pontian. I can see no grounds for regarding the two faunas as very different in age, while on the contrary a great zoological gap is suggested between Roussillon and the Pontian. Two littoral or marine stages, the Plaisancian and the Astian, intervene between the Villafranchian and the stage which corresponds to the mammaliferous lignites of Casino. The fauna of the Casino lignites is perhaps slightly younger than that of the Pontian. Depéret, therefore, most reasonably considered that the Roussillon fauna corresponded with the Astian, while the Plaisancian filled the faunal gap between the Pontian and Roussillon faunas. *There is no mammal fauna known in Europe which can be said to correspond with certainty to the Plaisancian.* [Italics my own.]

Three proboscideans have been referred very questionably to the Plaisancian. These are:

Turicius virgatidens (von Meyer)	Fulda, Germany
Stegolophodon sublatidens (Schlesinger)	Teschen, Austria
Dinotherium gigantissimum Stefănescu	Găiceana, Rumania

7. THE UPPER PLIOCENE: ASTIAN

The final Tertiary stage in Europe is that of the Astian, typified by the deposits of Villanova, Asti, in Italy, and characterized by the very rich mammalian faunas of Roussillon and Montpellier in France. Depéret demonstrated very ably, as already shown above, the fact that the Astian fauna or faunas are essentially modernized—much closer to the Pleistocene and Recent faunas of the Holarctic region than to the Pliocene faunas preceding this stage. This point has been strongly emphasized by Pilgrim, in a recent paper, and it was more generally stated by Osborn in 1910,[1] as follows:

> Surveying this. . . Pliocene fauna as a whole we are struck by the great predominance of animals closely related to existing forms. If the living zoölogist should imagine himself in France at this period, he would see only four animals which would appear entirely novel and unknown, namely, the saber-tooth tiger, the mastodon, the hipparion, and the hyænarctos; all the rest of the fauna would seem to be a very strange commingling, or congress, of African, European, and Asiatic mammals of the present day. Not a single North American element would be observed in this assemblage, unless we except those elements of more remote migration, such as the hares, the tapirs, and possibly the hipparions and the foxes.

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[1] Osborn, H. F., 1910. "The Age of Mammals," p. 317.

One of the chief deposits of Astian age, perhaps the most important one in Europe, is that of Roussillon, fully described by Depéret in his classic monograph of 1890.[1] According to this author, after the retreat of the Plaisancian sea, the Roussillon basin was filled with a considerable thickness of argillaceous and silicious sandstones, and in addition calcareous muds, all having a fluviatile origin. It is in these latter beds that the characteristic Roussillon fauna was deposited.

> En revanche, ces limons sont le gisement d'une riche faune de vertébrés terrestres et fluviatiles, dont les débris charriés par les courants, se retrouvent aujourd'hui dans quelques points privilégiés, qui correspondent sans doute à des remous ou à des parties plus stagnantes du cours des anciennes rivières. Les pièces osseuses sont presque toujours isolées, souvent brisées et même un peu roulées; il est assez rare de rencontrer plusieurs os en connexion. Cependant diverses parties d'un même squelette se retrouvent quelquefois dans un rayon peu étendu; même le squelette de la *Testudo Perpiniana* a pu être déterré tout entier grâce à la protection efficace de la boîte osseuse, et à l'habitude qu'ont les Tortues de rétracter leurs membres et leur tête dans l'intérieur de la carapace.
>
> Les ossements se rencontrent dans les limons d'eau douce sur presque toute l'étendue du bassin du Roussillon; les localités les plus riches sont: Villemolaque, Trouillas, le mas Belrich dans la vallée du Réart; Thuir, Millas, le Soler, le Serrat d'en Vacquer, la citadelle et les briqueteries des portes Canet et St-Martin, à Perpignan, dans la vallée de la Têt; les briqueteries de Rivesaltes dans la vallée de l'Agly.

Pilgrim[2] (1939) has presented a very helpful review of the Roussillon fauna, particularly with regard to its relationships with European assemblages below and above it. Some of his remarks are as follows:

> The character of the European fauna altered considerably between the Pontian and the stage of Roussillon. Numerous families and genera have disappeared. . . .
>
> There are very few surviving genera from the Pontian, and almost all of these differ specifically. . . .
>
> On the other hand numerous species from Roussillon are identical or nearly so with Villafranchian forms.
>
> The differences which the fauna of the Villafranchian displays from that of Roussillon are mainly due to what are invading forms, which does not necessarily imply any great difference in age. . . .
>
> When we observe that the comparable forms are either specifically the same or differ very little from one another, we are forced to conclude that little development took place between the two levels. Very little of the Roussillon and Montpellier fauna became extinct between that stage and that of the Val'Arno, Perrier and Senèze, as compared with the multitude of families and genera which appear for the last time in the Pontian. I can see no grounds for regarding the two faunas as very different in age, while on the contrary a great zoological gap is suggested between Roussillon and the Pontian.

The Astian fauna, as known from the assemblages of Roussillon and Montpellier, is large and varied and shows a composition somewhat as follows:

Among the primates are *Dolichopithecus*, *Semnopithecus*, and *Macacus*, the first of which failed to survive into Pleistocene times.

The carnivores display a considerable variety, including *Vulpes*, *Ursus* (both appearing for the first time in Europe), *Agriotherium*, *Lutra*, *Viverra*, *Hyæna*, *Megantereon*, *Epimachaerodus*, and *Felis*.

A large group of rodents, including *Hystrix*, and one form, *Ruscinomys*, which became extinct at the end of the Pliocene.

The proboscidean genera, *Zygolophodon* and *Anancus*.

Among the perissodactyls, *Hipparion* as found in the Astian represents a long-persistent survivor from Pontian times. This genus, which generally became extinct at the end of the Pliocene, did persist in some regions into the Lower Pleistocene. Also there is to be noted *Tapirus* and *Dicerorhinus*.

Among the artiodactyls *Potamochœrus* and *Capreolus* appear here for the first time. There are also various bovids, such as *Palæoryx* and *Gazella*.

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[1] Depéret, C., 1890. Mém. Soc. géol. France, III, p. 9.

[2] Pilgrim, G. E., and A. Tindell Hopwood, 1939, *op. cit.*, pp. 443–445.

There is also *Orycteropus*, a large species as compared with the characteristic Pontian forms—although smaller than the recent types.

Of particular significance is the *absence* of certain diagnostic genera from the Astian faunas, notably *Equus*, *Elephas* (*Archidiskodon*), and bovines, such as *Leptobos*. It is the absence of these types that gives conclusive proof of the distinction of the Astian fauna from the succeeding Villafranchian, where these animals as immigrant forms appear for the first time in Europe. This difference was noted by Depéret, and has been emphasized by later authors.

In addition to the characteristic Astian mammalian faunas of France, and to a lesser extent of Italy, there are limited occurrences of mammals of this age in other parts of Europe, notably along the eastern coast of England. Here is found the Red Crag deposit, a marine sediment containing occasional mammals. The mammals, when found in the Red Crag, prove to be of the same types as those found at Montpellier and Roussillon.

The occurrences of the types of Astian proboscideans are given by Osborn as follows. In this connection it might be mentioned that Pilgrim (1939) denies the presence of *Zygolophodon borsoni* at Roussillon, although Depéret in his monographic study lists this species among the Roussillon fauna.

ASTIAN PROBOSCIDEANS

Zygolophodon borsoni (Hays)	Villanova, Asti, Italy
Zygolophodon borsoni buffonis (Pomel)	Auvergne, France
Zygolophodon borsoni zaddachi (Jentzsch)	Thorn, Germany
Zygolophodon borsoni vellavus (Aymard)	Velay, France
Zygolophodon borsoni vialetii (Aymard)	Vialette, France
Anancus arvernensis (Croizet and Jobert)	Perrier, France
Anancus arvernensis brevirostris (Gervais and de Serres)	Montpellier, France
Anancus arvernensis dissimilis (Jourdan)	Saône Basin, France
Anancus arvernensis macroplus Aymard	Mt. Coupet, Puy-en-Velay, France
Anancus gigantarvernensis (Klähn)	Herbolzheim, Germany
Anancus minutoarvernensis (Klähn)	Herbolzheim, Germany
Anancus falconeri Osborn	Suffolk, England

8. THE PLEISTOCENE

There was no abrupt change from the Pliocene to the Pleistocene in Europe, a condition which was generally true for the other parts of the World. Consequently the boundary between the two epochs is difficult to define, with the result that there are manifest differences of opinion as to what event or events in geologic history may be properly regarded as significant of the opening of Pleistocene times in this region. In a general way, the Pleistocene is the Great Ice Age, when portions of the northern hemisphere were partially covered by several successive glaciations, and it might be supposed that the advance of the first continental glacier would serve to mark the beginning of Pleistocene history. But some of the European authorities, notably Boule, would place the first glaciation in the Upper Pliocene. Moreover a great portion of the Earth's surface was not affected by glacial phenomena, so that other criteria must be used, no matter what may be the opinion as to the time of the first glacial advance. The sequence of pluvial and dry periods, the development of marine and river terraces and other geological phenomena have been widely studied and variously used as aids in Pleistocene chronology in the nonglaciated regions of the Earth, yet even these evidences, useful as they are in establishing the succession of diastrophic, climatic or sedimentary events within the Pleistocene period, have not been generally satisfactory in an attack upon the problem of the beginning of the Pleistocene. Therefore the evidences of wide-spread changes in the mammals are perhaps the most significant and the most useful of the criteria studied, in establishing the opening of Pleistocene times. The mammals were rapidly evolving animals, able to migrate quickly over most of the Earth's surface, so that changes in mammalian faunas necessitated by the adaptations required by the development of new and unusual environmental conditions would almost instantly (from a geological point of view) be reflected throughout wide areas. The problem has been excellently stated by Hopwood,[1] as follows:

> Apparently the boundary between the Pliocene and Pleistocene is difficult to determine on purely geological evidence, so that it is necessary to approach the problem in some other way, preferably by means of the fossil mammals since they furnish the raw material for the rest of the inquiry. There are many factors involved, but two of them are far more important than the others. First of these is the proposition that the best boundaries in time are those expressed by a change in fauna, which means in practice the incursion of new types, rather than the disappearance of old ones. The second proposition is, that the time necessary for the distribution of new types of active quadrupeds, e.g., horse or bison, over a very wide area is negligible from the geological point of view.

At the beginning of the so-called Sicilian or Villafranchian time division in Europe and Asia, there was a sudden appearance of new and modernized types of mammals, part of which were the descendants of indigenous ancestors, part of which were immigrants. Notable among these new types were the modern forms of horses (*Equus*), of cattle (*Bos*), and of elephants (*Archidiskodon*, *Elephas* and related genera). As long ago as 1911, Haug suggested that the appearance of these key types, the first an immigrant from the New World, the others of Old World origin, should mark the beginning of the Pleistocene in Europe. In recent years this view has been reiterated, notably by Matthew and by Hopwood. If accepted, then the typical Sicilian or Villafranchian faunas of the European region are to be regarded as of Lower or Basal Pleistocene age, and it is the influx of these new types that marks the beginnings of the period.

As opposed to this, many European authorities are inclined to regard the Villafranchian fauna, containing *Equus*, *Bos*, and *Elephas*, as marking the summit of the Pliocene. In the present chapter the former interpretation will be favored.

Granting that the opening of the Pleistocene is marked by the appearance of numerous modernized mammals, especially *Equus*, *Bos*, and *Elephas* (in the broad sense of the term), we may now consider the problem of dating the sequence of events within Pleistocene times. This has occupied the attention of many students over a long period of years. In Europe the criteria most generally used for establishing dates within the Pleistocene are those of the glacial succession, as delineated especially by Penck and by Geikie, and of the sequence of marine and river terraces, as described by de Lamothe, Depéret, and others.

In northern Europe there are evidences of four major glaciations, with interglacial periods between them. In the Mediterranean region there are the remains of four marine terraces, which may be traced in part around the Atlantic coast and into the North Sea. In 1919, Depéret indicated the relationships between the European glaciations and marine terraces in the following tabular form.

	NORTHERN EUROPE	ALPS	MEDITERRANEAN	
Fourth glaciation	Mecklenburgian	Würm	Monastirian	18–20 meter terrace
Third glaciation	Polonian	Riss	Tyrrhenian	30 meter terrace
Second glaciation	Saxonian	Mindel	Milazzian	55–60 meter terrace
First glaciation	Scanian	Günz	Sicilian	90–100 meter terrace

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[1] Hopwood, A. T., 1935. Proc. Geol. Assoc., XLVI, Pt. 1, p. 46.

It must not be supposed that this compilation represents an exact correlation, since it is known that the marine terraces may be correlated with the river terraces, while these latter *underlie* the moraines of the glaciations to which they are most closely related. Therefore, it is probable that the terraces are more or less of interglacial age, and immediately precede the glaciations with which they may be roughly correlated. The important fact is that there is a fourfold division of the Pleistocene in Europe, as based either upon the development of marine and river terraces, or upon the sequence of glaciations. And each glaciation may be considered as occupying the latter portion of the general terrace stage, as shown below.

IV	Upper Monastirian Lower Monastirian	IV Würm
III	Upper Tyrrhenian Lower Tyrrhenian	III Riss
II	Upper Milazzian Lower Milazzian	II Mindel
I	Upper Sicilian Lower Sicilian	I Günz

Many students, following particularly the work of Penck, have envisaged a succession of "warm" and "cold" mammalian faunas in Europe that might be correlated more or less closely with the successive advances and retreats of the great ice sheets. According to Penck's scheme, the four glaciations were more or less equally developed, but separated from each other by unequal intervals, of which the median one, the Mindel-Riss interglacial, was by far the most protracted, and the last one, the Riss-Würm, the shortest. He also distinguished the Würm glaciation from the others by his supposition that it terminated in a series of minor fluctuations, rather than by a single and steady decline. This idea of alternating faunas controlled by glacial phenomena has been expressed by Osborn[1] in the following words:

> The principal contributors to the theory of northward and southward migrations and to the succession of faunas are Nehring, Woldrich (1882), and more recently Penck. In considering the distribution and migration of the mammals throughout the Glacial Period, we must constantly keep in mind the differences of latitude. . .
>
> Penck also observes that we cannot hope to trace a continuous evolution of forms during Pleistocene times, because we are not dealing with a development of one successive series in one locality, but with the cyclical alternation of a number of different faunas compelled to migrate through the alternations in the temperature and in the floras, the mammals disappearing and returning at intervals too brief to allow of any marked evolutionary changes. Herein lies our difficulty when we attempt to distinguish between the tundra faunas of the late glaciations and the forest faunas of the late interglacial epochs, because the faunas return not only with the same generic but the same specific types, as especially illustrated in the case of the mammoth (*E. primigenius*) and the giant deer (*Cervus megaceros*).

A considerably different picture has been presented recently (1933) by Stehlin,[2] who thinks that the glacial periods were not only separated each from the other by interglacial periods of varying lengths, but also that they were in themselves much more different from each other in intensity than was admitted by Penck. Thus Stehlin, basing his conclusions upon the development of the mammalian faunas, supposes that the glaciation at the beginning of the Pleistocene was relatively much less intense than the two glaciations coming after the long Middle Pleistocene interglacial period. (Incidentally, this author, like Boule, recognizes only three glaciations in the Pleistocene.) According to Stehlin, the maximum of glacial activity was reached towards the end of the Würm

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[1] Osborn, H. F., 1910, *op. cit.*, pp. 388, 389.

[2] Dubois, A., and H. G. Stehlin, 1933. Mem. Soc. Pal. Suisse, LII–LIII, p. 272.

glacial period, a conception based upon the sequence of European Pleistocene faunas and which regards the "warm" or temperate types of mammals as prevailing through a great part of the Pleistocene, to be followed in Würm and then in post-Würm times by an invading arctic assemblage: ". . . la plus grand invasion des animaux arctiques dans les latitudes moyennes et méridionales ne coïncide avec le développement maximal des glaciers würmiens, mais lui succède. . ."

This view is somewhat in accord with the recent tendency to discount to a large degree the reality of alternating "cold" and "warm" faunas, and to regard the development of the Pleistocene mammals as a rather continuous process, with minor fluctuations due to the alternation of mild and severe temperature conditions.

Hopwood (1939, 1940), for instance, has the following to say on this subject:

> At this stage it may be useful to discuss some of the points which govern the use of mammalian faunas as indices of the age of Pleistocene deposits. It should be self-evident that the composition of a fauna will, in the main, depend on the climate as well as on the environment; the literature is full of reference to 'cold' and 'warm' faunas, and also to faunas of 'forest,' 'parkland,' or 'plains' type . . . Moreover, one cannot be absolutely certain that any particular species indicates a particular type of climate. . . . When 'warm-climate' mammals are considered it is well to keep in mind the wide range of climate acceptable to such animals as the leopard and tiger, and to remember that even a hippopotamus can survive an English winter with a minimum of extra shelter and warmth.
>
> Except with the aid of a long series of fossils, even an approximation to the true date is all but impossible in the absence of such easily recognisable species as *Equus robustus* Pomel, *Rhinoceros etruscus* Falconer, *Elephas meridionalis* Nesti, or *Rangifer tarandus* (Linn.)[1]
>
> Geographical changes of this magnitude [uplift of Alps, etc.] might be expected to have influenced the climate and the fauna in some way or another, but this does not seem to have happened. Admittedly, much has been written about alternating 'warm' and 'cold' faunas, particularly in Germany, where the teachings of Penck were most influential, but in fact there is very little evidence to support the more extreme expositions of this view. . .[2]

It has been the practice among many European palæontologists to recognize three general mammalian faunas in the Pleistocene of Europe, corresponding roughly to the lower, middle, and upper phases of the period. Although, as de Lapparent has stated, the various individual animals constituting these faunas extend beyond the vague limits of each assemblage to mingle with each other, nevertheless associations of certain mammals are characteristic of the early, middle, and late portions of Pleistocene times. Thus he would recognize an early warm fauna, typified by *Elephas antiquus*, a middle cool and humid period with *Elephas primigenius* and *Rhinoceros tichorhinus*, and finally a late cold fauna with the woolly mammoth and reindeer predominating. This was the general succession recognized by Osborn in his "Age of Mammals" in 1910, and described in a somewhat similar form recently (1935) by Boule and Piveteau.[3]

While this conception of the succession of Pleistocene faunas in Europe may be true in a general way, it is probably oversimplified. In the first place, it seems evident from recent work in various parts of the world that many if not most of the Pleistocene mammals appeared at an early stage in the history of the period, to continue with but little change through its extent. With the exception of certain rapidly developing types, such as the hominids and the proboscideans, there was probably but little evolution of a super-specific nature occurring within the relatively short duration of Pleistocene times. There were some extinctions, it is true, and these, as much as anything else, serve to distinguish the characters of the faunas in successive phases of the Ice Age. As regards this, it would appear that the evidence for extinctions at various times within the Pleistocene is certainly much more convincing in Eurasia than it is in the Americas.

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[1] Hopwood, A. T., 1939. Proc. Prehist. Soc., N. S., V, Pt. 1, pp. 13, 14.

[2] Hopwood, A. T., 1940. Proc. Geol. Assoc., LI, Pt. 1, p. 85.

[3] Boule, Marcellin, and Jean Piveteau, 1935. "Les Fossiles."

Hopwood has outlined the relationships of the appearance and disappearance within the Pleistocene in Europe as follows.

Glacial IV.—Extinction of *Elephas primigenius, Rhinoceros tichorhinus, Hyæna spelæa, Ursus spelæus.*
    Interglacial—Extinction of *Elephas antiquus, Rhinoceros megarhinus, Felis leo spelæa.*
Glacial III.—
    Interglacial—First appearance of *Bos primigenius, Rangifer tarandus, Rhinoceros tichorhinus, Ursus spelæus, Hyæna spelæa.*
Glacial II.—Extinction of *Hyæna arvernensis, Canis nescherensis, Equus robustus, Equus stenonis, Rhinoceros etruscus, Elephas meridionalis.*
    Interglacial—
Glacial I.—

These were some of the principal changes that took place during the development of the Pleistocene faunas in Europe, and it is mainly by looking at them that we can see the progress of Pleistocene history reflected in the assemblages of Ice Age mammals. Compared with changes such as these, the influx or egress of mammals adapted to warm or cold climates was of relatively slight importance. As Hopwood states[1]: "Climatic variations may have favoured first one type and then the other, but neither type was completely expelled from the area."

The typical Basal or Lower Pleistocene proboscideans of Europe were *Archidiskodon planifrons, Archidiskodon meridionalis,* and *Hesperoloxodon antiquus. Parelephas trogontherii* and *Elephas primigenius,* perhaps not quite so ancient in their first appearance as the above mentioned forms, nevertheless were present in the European Pleistocene before the close of its lower phase. Seemingly there was an early extinction of the *Archidiskodon* group, specifically *A. planifrons* and *A. meridionalis,* probably in the interval marking the close of the first interglacial and the opening of the second glacial periods. *Hesperoloxodon antiquus* probably became extinct in middle or later Pleistocene times, perhaps near the end of the third interglacial period according to Hopwood. Finally, during or after the fourth glaciation there was an extinction of *Elephas primigenius.*

PROBOSCIDEANS:
- *Mammonteus primigenius* (Blumenbach)
- *Mammonteus primigenius hydruntinus* (Botti)
- *Mammonteus primigenius fraasi* (Dietrich)
- *Mammonteus? primigenius leith-adamsi* (Pohlig)
- *Mammonteus primigenius astensis* (Depéret and Mayet)
- *Loxodonta cornaliae* Aradas
- *Hesperoloxodon antiquus* (Falconer and Cautley)
- *Hesperoloxodon antiquus germanicus* (Stefănescu)
- *Hesperoloxodon antiquus italicus* Osborn
- *Hesperoloxodon antiquus platyrhynchus* (Graells)
- *Hesperoloxodon antiquus ausonius* (Major)
- *Hesperoloxodon antiquus nanus* (Acconci)
- *Palæoloxodon mnaidriensis* (Adams)
- *Palæoloxodon falconeri* (Busk)
- *Palæoloxodon melitensis* (Falconer)
- *Palæoloxodon lamarmorae* (Major)
- *Palæoloxodon cypriotes* (Bate)
- *Palæoloxodon creticus* (Bate)
- *Parelephas trogontherii* (Pohlig)
- *Parelephas trogontherii nestii* (Pohlig)
- *Parelephas trogontherioides* (Zuffardi)
- *Parelephas intermedius* (Jourdan)
- *Parelephas wüsti* (Pavlow)
- *Parelephas armeniacus* (Falconer)
- *Archidiskodon meridionalis* (Nesti)
- *Archidiskodon meridionalis cromerensis* (Depéret and Mayet)
- *Archidiskodon planifrons* (Falconer and Cautley)
- *Archidiskodon planifrons rumanus* (Stefănescu)
- *Mastodon pavlowi* Osborn
- *Anancus arvernensis* (Croizet and Jobert)

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[1] Hopwood, A. T., 1940, *op. cit.*, p. 86.

V. ASIA

1. INTRODUCTION

Asia, as here used, comprises that portion of the continent north and west of the Himalaya Mountains and the Tibetan Plateau. Thus there is included within it Siberia, Mongolia, North China, Japan, and Turkestan. This separation of the more northerly and westerly sections of Asia from the Oriental Region is logical and natural, being based in large part on the modern zoogeographic realms. That part of Asia delimited above constitutes at the present time the eastern moiety of the Palæarctic Realm, and the evidence would seem to be indicative of the fact that during the later stages of the Cenozoic, the Palæarctic portion of Asia was zoogeographically distinct from the more southerly and easterly Oriental section, just as it is today.

2. THE MIOCENE OF MONGOLIA AND CENTRAL ASIA

Mongolia: Loh Formation.—The Loh formation is exposed to the south of Uskuk Mountain in the Tsagan Nor basin of Mongolia, where it overlies the Upper Oligocene Hsanda Gol beds. The only fossils identified to date from the Loh formation are *Serridentinus mongoliensis* Osborn and *Baluchitherium mongoliensis* Osborn. (This latter form is probably not *Baluchitherium* but rather a rhinoceros of the *Coelodonta* group.) From the evidence of these fossils, and due to the fact that the Loh rests directly on the Upper Oligocene Hsanda Gol, it would seem very probable that the Loh formation represents a Lower Miocene or Burdigalian phase in the sedimentary history of Mongolia. It might be pointed out here that the fossils of the Loh beds might be placed in later phases of the Miocene, particularly the Middle Miocene, with as much justification as in the Lower Miocene. Indeed, this series was designated as "Lower to Middle Miocene" by Professor Osborn in Volume I of this Monograph.

GEOLOGICAL RELATIONSHIPS OF ASIATIC PROBOSCIDEA

	MONGOLIA	CENTRAL ASIA	NORTH CHINA		JAPAN
PLEISTOCENE			Mammonteus primigenius Palæoloxodon tokunagai Palæoloxodon namadicus Archidiskodon planifrons		Elephas indicus buski (Palæoloxodon?) Parelephas trogontherii Palæoloxodon namadicus naumanni namadicus setoensis namadicus yabei Stegodon orientalis, sinensis
PLIOCENE			(SHANSI) Archidiskodon planifrons Stegodon zdanskyi, orientalis Zygolophodon borsoni "Mastodon" intermedius		Parelephas protomammonteus (=Palæoloxodon)[1] Palæoloxodon tokunagai[1] Trilophodon sendaicus Stegodon aurorae bombifrons elephantoides
	KHUNUK Serridentinus (Ocalientinus) florescens		*HIPPARION CLAYS* Serridentinus wimani, lydekkeri Trilophodon spectabilis Tetralophodon exoletus, sinensis Pentalophodon sinensis, cuneatus Zygolophodon borsoni[1] "Mastodon" intermedius Stegodon licenti, zdanskyi		
MIOCENE	*TUNG GUR* Platybelodon grangeri Serridentinus gobiensis		Trilophodon connexus		Serridentinus annectens Trilophodon palaeindicus Stegolophodon latidens[2] Stegodon sp.[2]
	LOH Serridentinus mongoliensis	*JILANČIK* Trilophodon inopinatus atavus cf. angustidens			

1 Doubtful occurrence in the Pliocene
2 Doubtful occurrence in the Miocene

D. F. Levett Bradley

Fig. 1223

Berkey and Morris[1] described the Loh formation as follows:

> Directly overlying the Hsanda Gol clays, about five miles south of Uskuk Mountain, there is a group of olive green clays less than one hundred feet thick. No clearly defined physical break can be seen between the two formations, but the upper olive clays yielded fossils which Dr. W. D. Matthew correlates with the Lower Miocene of Europe.

Proboscidean: *Serridentinus mongoliensis* Osborn.

Tung Gur Formation.—The Tung Gur formation of Mongolia is typically exposed along a northeast to southwest trending escarpment in the immediate vicinity of Gur Tung Khara Usu, Inner Mongolia. This escarp-

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[1] Berkey, C. P., and F. K. Morris, 1927. Natural History of Central Asia, II, p. 365.

ment is part of a broad table-land situated to the northeast of the Kalgan-Urga trail and near the border between Inner and Outer Mongolia.

The Tung Gur formation was described by Spock in 1929[1] and again by the same author in 1930.[1] On the basis of geologic evidence alone Spock suggested that this formation might be of Pliocene age, which was the opinion first held by Professor Osborn as a result of his studies of *Platybelodon,* the most important and by far the most spectacular fossil mammal from this horizon.

Soon after the Tung Gur fauna was discovered, however, P. Teilhard de Chardin suggested (verbally) that the fauna might be of Miocene age—or more specifically of pre-Pontian affinities. Teilhard's conclusion was based upon his observations of the fossils as they were collected in the field. This correlation of the Tung Gur was subsequently verified by the detailed studies of the fauna by various authors including the present writer. Consequently, Professor Osborn came to regard the Tung Gur formation as of Upper Miocene age, thereby placing *Platybelodon* as an earlier stage of shovel-tusked mastodont than he had first considered it to be. (See Volume I, pages 463-466, of this Monograph.)

The Tung Gur fauna is too large for detailed consideration or listing at this place. Some of the important forms constituting the fauna, however, may be briefly considered.

As for the rodents, there is an *Amblycastor* closely related to Miocene species of the same genus occurring in North America. Among the carnivores, the giant canid or ursid, *Hemicyon,* may be linked with certain Miocene species referable to this genus, particularly as the Tung Gur form shows numerous relatively primitive, dog-like characters. There is a hyæna of the *Crocuta* group, which might, on the other hand, perfectly well be of Pliocene age. The same is true of *Platybelodon,* since it shows many specialized characters. Perhaps one of the most significant of the Tung Gur animals is *Anchitherium,* definitely a Miocene type. The presence of this forest horse and the complete absence of any trace of *Hipparion* constitute strong evidence in favor of a Miocene age for the Tung Gur formation. The rhinoceroses, too, would seem to be of Upper Miocene affinities. A pig, *Listriodon,* on the whole shows affinities with Miocene species, although this is a genus that persisted from the Miocene into the Pliocene in some localities. The deer, *Stephanocemas* and *Lagomeryx,* show definite relationships with comparable Upper Miocene forms from Europe and Asia. Of the bovids, one species, *Oioceras noverca* is, according to Pilgrim, a small form that might have been ancestral to certain Pontian species.

From this brief review it becomes evident that the Tung Gur fauna, although containing some possible Pliocene elements, is, in its general aspects, of Upper Miocene affinities, a conclusion that is greatly strengthened by the presence of *Anchitherium* and the absence of *Hipparion* in the assemblage, particularly since the absence of the latter form would seem to be real and not due to accidents of collecting. It would seem that the Tung Gur fauna, with a mixture of woodland and plains species, represents a borderland assemblage of mammals.

PROBOSCIDEANS:
- *Platybelodon grangeri* (Osborn)
- *Serridentinus gobiensis* Osborn

CENTRAL ASIA: JILANČIK BEDS, TURGAI REGION.—In a series of papers published between 1927 and the present time Borissiak has described a mammalian fauna from the Turgai region of Central Asia, discovered in the Jilančik (or Dschilantschik) beds of Miocene age. The Jilančik beds rest on a series of Oligocene deposits containing *Indricotherium,* and in turn are succeeded by a Pliocene horizon in which *Hipparion* is present. At the

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[1] Spock, L. E., 1929. Amer. Mus. Novitates, No. 394; *ibid,* 1930, No. 407.

present time the Jilančik fauna (excavated during a long period of years, beginning in 1914) would seem to be composed entirely of proboscideans and rhinoceroses, as follows.

Trilophodon inopinatus Borissiak and Beliaeva
Trilophodon cf. *angustidens* (Cuvier)
Trilophodon atavus (Borissiak)[1]
Brachypotherium aurelianense Nouel
Aceratherium depereti Borissiak

This fauna has a distinct Miocene aspect, and due to the determination of elements within it identical with or close to certain Lower Miocene species of Europe, Borissiak has referred the assemblage to the Burdigalian. With regard to the age of the Jilančik beds, the following remarks might be appropriate at this place.

Trilophodon inopinatus

Although Borissiak thought that this species was close to *Serridentinus mongoliensis* of the Loh formation, Osborn placed it definitely in the genus *Trilophodon.* Borissiak, as the result of his comparisons, considered the Loh formation to be virtually identical with the Jilančik beds in age. Osborn, on the other hand, compared *Trilophodon inopinatus* with the primitive *Trilophodon cooperi*, from the Bugti beds of Baluchistan. It is interesting to notice that both comparisons are with Lower Miocene horizons. This agrees with other evidence on the age of the Jilančik beds.

Trilophodon angustidens

If this identification is valid, the Jilančik beds may be correlated with the Lower Miocene or Burdigalian of Europe.

Trilophodon atavus

This species is very close to *T. angustidens*. This again is a link with the Lower Miocene of Europe.

Brachypotherium aurelianense

According to Borissiak, this characteristic European Burdigalian form is present in the Jilančik sediments. He has shown, however, that the Jilančik form displays certain advanced traits in the direction of the Middle Miocene *B. brachypus* of Europe.

Aceratherium depereti

Placed by Borissiak between *A. lemanense* and *A. tetradactylum* in its evolutionary stage of development. This species shows certain specializations, notably the very much elongated nasals, which mark an advance beyond the typical Burdigalian forms.

PROBOSCIDEANS: See faunal list, above.

3. THE MIOCENE OF NORTH CHINA

CHINA.—The study of the fossil mammals of China dates from the middle of the last century, when Davidson published a short notice of some palæontological material gathered together in Shanghai by W. Lockhart. Among these first-known of the Chinese fossils was a tooth of an elephant. From that time until the present day a suc-

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[1] This form has been recently described by Borissiak, under the name of *Mastodon atavus.* It is closely related to *Trilophodon angustidens,* as Borissiak points out; consequently it is here referred to this latter genus.

cession of students, notably Owen, Gaudry, Koken, Schlosser, and in recent years the various authors describing the collections made by the Geological Survey of China, the Palæontological Institute of Upsala University, and the American Museum of Natural History, have added increasingly important and voluminous data concerning the palæontological history of northern China and Mongolia.

The history of Upper Cenozoic mammals in North China would seem to begin with the Middle or Upper Miocene and to continue almost uninterruptedly through the Pliocene into the Pleistocene. Through this stretch of geologic time two periods are marked by the expansion and the unusual abundance of fossil mammals. These are the Lower Pliocene or Pontian, in which the large, widely distributed "*Hipparion* fauna" occurs, and the Lower and Middle Pleistocene, in which there are several faunas, notably the "*Equus* fauna" or Villafranchian assemblages of the flood-plain deposits and the later Choukoutien cave faunas.

As to the beds preceding the almost universal *Hipparion* clays, there is little to be said. At best, these sediments are physically but slightly differentiated from the Pontian deposits, if they are at all distinguishable. There have been described, from time to time, certain fossils that would seem to be of definitely Upper Miocene rather than of Pontian affinities, and it is on the basis of these discoveries, as much as anything, that the presence of pre-Pontian sediments in North China is inferred.

Such is the case of *Trilophodon connexus,* which Hopwood regards as a very primitive stage in the bunodont mastodonts, closely comparable to the Miocene *Trilophodon cooperi* of Baluchistan. *Trilophodon cooperi* is a Lower Miocene species; whether, on the basis of this, *Trilophodon connexus* should be regarded as a very early Miocene form, or rather a structurally primitive species persisting into the Upper Miocene, is a question open to some doubt. It is possible that this species may represent a Sarmatian or an equivalent age in North China. On the other hand, there is no reason why the supposed pre-Pontian species in North China might not be structurally primitive forms persisting into the Lower Pliocene.

In this connection it might be noted that *Trilophodon wimani,* considered by Hopwood as possibly of Sarmatian age, was placed by Teilhard in the Pontian. Hopwood based his conclusions on the primitive structure of *Trilophodon wimani,* and also on the fact that it was associated with *Listriodon gigas*, a pig showing affinities, according to Miss Pearson, with certain Miocene forms of Europe. Yet Teilhard's conclusions as to the age of *Trilophodon wimani* were based on his thorough knowledge of the stratigraphic relationships of the Cenozoic deposits of China, and therefore they carry great weight.

PROBOSCIDEANS:

Trilophodon connexus Hopwood
Trilophodon wimani Hopwood (Pontian, according to Teilhard)

Andersson,[1] in his discussion of the Cenozoic of North China, describes the *Lu Tzŭ Kou* beds, exposed in the Pao Te Hsien area of Shansi. According to Andersson these beds, discovered by Zdansky, are of Upper Cenozoic age, but they underlie the *Hipparion* clay. Yet although the *Lu Tzŭ Kou* beds are exposed beneath the *Hipparion* beds, there is a strong possibility that the age difference between the two series is not great.

> As the *Hipparion* beds represent the transition from Miocene to Pliocene, the Lu Tzŭ Kou beds could eventually be supposed to represent the Miocene, but there are some facts at hand which indicate that they are in age nearly related to the *Hipparion* beds.

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[1] Andersson, J. G., 1923. Mem. Geol. Surv. China, Ser. A, No. 3, p. 107.

4. THE PLIOCENE OF MONGOLIA

KHUNUK FORMATION.—The Khunuk formation was described by Granger[1] as follows:

> In the Kholobolchi Nor region of Mongolia there are three areas of late deposits considered, in the field, as being of Pleistocene age; the geologists were of the opinion that these three exposures were of the same age, and the name 'Khunuk' was given to the formation. The three exposures mentioned in the Kholobolchi Nor region are respectively north, northeast, and east of the lake; the type of *Serridentinus florescens* comes from the northern exposure of the 'Khunuk' and represents the only specimen obtained in that particular locality.

As Osborn has shown, it is possible that the Khunuk formation is approximately correlative with the Hung Kureh beds of the Tsagan Nor region, which latter deposits contain a small mammalian fauna of Pliocene relationships. The single mastodont described from the Khunuk formation is an advanced type of serridentine, which would favor the assigning of a Pliocene age to these sediments.

It is not possible to say at what stage in the Pliocene the Khunuk and Hung Kureh formations should be placed, but it is very probable that they are in the main Pontian equivalents, representing a phase in the sedimentary history of Mongolia immediately subsequent to the period during which the very fossiliferous Tung Gur Upper Miocene sediments were deposited.

PROBOSCIDEAN: *Ocalientinus* (*Serridentinus*) *florescens* (Osborn).

5. THE PLIOCENE OF NORTH CHINA

LOWER PLIOCENE

The *Hipparion* clays of North China form a mantle covering extensive areas of valley and plateau country, dissected by streams. The localities at which fossils have been discovered in the *Hipparion* clays are so numerous that they cannot be listed here, nor can comparisons between them be attempted. It might be well, however, to quote Andersson's[2] description of the *Hipparion* clays at Chi Chia Kou in Pao Te Hsien, one of the most richly fossiliferous and best-known localities in this horizon.

> The Chi Chia Kou region is a plateau land dissected by an intricate system of ravines, in the bottom of which the substratum of the *Hipparion* clay is almost everywhere visible. The basement rock is formed by the Carboniferous coal series in nearly horizontal beds. The basal layer of the *Hipparion* series is a conglomerate bed, at most 4 meters thick with gray matrix. Above this basal conglomerate rests the red *Hipparion* clay with a maximum thickness of 65 meters. In the clay there are interbedded gravel beds of little persistence and occasionally also lenses of sand. In certain horizons there are also irregular lime concretions in the clay. Round the fossil mammal bones are seen infiltrations of lime.
>
> In the 65 meters of red, mostly entirely barren clay there is a well defined bone-carrying horizon 25 meters above the bottom and 35 meters underneath the top of the deposit. The bone layer is mostly less than a meter thick and so nearly horizontal that there is not more than 5 meters variation of altitude of the bone bed throughout the whole Chi Chia Kou area. In the bone horizon there are not bones everywhere, but rather pockets or nests rich in bones separated by some meters of barren clay...
>
> According to Dr. Wiman and Dr. Zdansky the *Hipparion* fauna indicates steppe conditions, but the occurrence of Giraffinæ and Suidæ points to the existence of groups of trees and of water pools spread over this steppe. As the clays are mostly barren over wide areas and rich in mammals only in the three areas mentioned, it might be inferred that in the otherwise very dry steppe there were locally oases with trees, water pools and occasionally also sheet floods after the rains. It seems as if these genial conditions prevailed only during a short, well defined period.

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[1] Granger, Walter, in H. F. Osborn, 1936. Volume I of this Monograph, p. 397.

[2] Andersson, J. G., 1923, *op. cit.*, pp. 107, 108, 110.

PROBOSCIDEANS: (Pontian of China)

Serridentinus wimani (Hopwood)
Serridentinus lydekkeri (Schlosser)
Trilophodon spectabilis Hopwood
Tetralophodon exoletus Hopwood
Tetralophodon sinensis (Koken) (This horizon?)
Pentalophodon sinensis Hopwood = *Anancus sinensis* (*fide* Osborn)
Pentalophodon cuneatus Teilhard and Trassaert
Zygolophodon borsoni (Hays) (This horizon?)
Mastodon americanus (Kerr) (This genus and species?)
"*Mastodon*" sp.
Mastodon intermedius Teilhard and Trassaert
Stegodon licenti Teilhard and Trassaert
Stegodon zdanskyi Hopwood (This horizon?)

MIDDLE PLIOCENE

Only within recent years has the Middle Pliocene been recognized in North China. The distinction of this stage has been difficult because it is lithologically closely related to the typical Pontian deposits, and particularly because the fauna is not well known. In their important contribution entitled "The Pliocene Lacustrine Series in Central Shansi," Licent and Trassaert[1] describe sediments overlying the Pontian beds but underneath the Sanmenian or Lower Pleistocene.

These authors have shown that the lacustrine sediments of Central Shansi occupy an extensive, shallow Permo-Triassic syncline. The beds representative of the Upper Cenozoic are 100 meters or more in thickness and entirely of a freshwater type. They are characterized by the "extremely deceptive recurrency of the same facies: rusty or reddish sands, green marls, etc.," thereby making the differentiation of the several horizons contained within the series extraordinarily difficult. Nevertheless, Licent and Trassaert recognize three zones within these lacustrine sediments. The lowest zone, designated as Zone 1, is of Pontian affinities. Above it is Zone 2, of Middle Pliocene age, succeeded by Zone 3, representing the Sanmenian. In addition it is pointed out that there is very likely a fourth zone, coming between zones 2 and 3, representative of a stage between the Middle Pliocene and the Sanmenian.

> *Zone 2.* In the following zone 2, better studied in the Changtsun basin, the deposits become less coarse, and a typical lacustrine condition is prevailing: green and bluish marls, containing many bird, turtle, fish-remains, freshwater shells (*Lymnæa*, *Planorbis*, thin-shelled *Unionidæ*) and carbonised plant-remains. A small *Hipparion*, the *Chilotherium*, a tapiroid *Mastodon* and the *Stegodon* are still present (as in zone 1). But a remarkable type of strepsiceros Antilope (cf. *Antilospira* T. & Y.) seems to appear for the first time, and also a special *Castor* (characteristic of the Ertemte fauna of Mongolia) *Dipoides majori* Schl. A middle Pliocene age seems to be indicated.
>
> *Suggestion of a fourth sedimentary zone.* The palæontological analysis of the fauna collected in the Yünchu basin suggests that, between zone 2 and zone 3 a fourth horizon might be eventually recognised in the Pliocene deposits. First, collected by country people, from such localities as Malan, we have, embedded in a characteristic matrix of a dark red hue, canon-bones of a big *Hipparion*, already associated with a Bison, but without any sure trace of *Equus*. Furthermore, amongst the best fossils purchased in the area, are several teeth of a thick lamelled Elephant (*Elephas* cf. *planifrons*), a form never observed in Nihowan, and yet too much advanced for being conveniently referred to the *Mastodon-Stegodon* fauna of zone 2.
>
> It would seem therefore that the lower part of zone 3 might have to be separated as a special unit, distinguishable from the true Nihowan beds by the absence of Horse and the presence of archaic Elephant.
>
> This point however is not yet supported by clear stratigraphical evidences.

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[1] Licent, E., and M. Trassaert, 1935. Bull. Geol. Soc. China, XIV, No. 2, pp. 214, 216.

UPPER PLIOCENE (?)

Teilhard and Trassaert,[1] in 1937, divided the Pliocene (as they considered the extent of its upper and lower limits) into three "zones," namely: (1) A lower zone comprising the Pontian *Hipparion* beds, (2) a middle zone of Pliocene age but subsequent to the Pontian, and (3) an upper zone comprising the Villafranchian, which these authors placed in the Upper Pliocene.

In addition to the characteristic "Middle Pliocene," as recognized by Teilhard and Trassaert, and as described by Licent and Trassaert (see above), there would seem to be an upper zone or subzone which is immediately antecedent to the base of the Villafranchian. Since the Villafranchian is considered as Lower Pleistocene (as will be shown below) it would seem logical to suppose that this upper portion of "Zone II" represents the uppermost Pliocene in North China. Teilhard and Trassaert made the following comments concerning it:

> But, near Chinglo (N. Shansi, cf. Teilhard and Young, 1931, p. 52, fig. 15), in an horizon representing clearly Zone II (rather large Deer and Hipparion, *Antilospira*, no *Equus* . .), Teilhard and Young have collected several years ago an isolated lamella of D_3 decidedly referable to a primitive Elephant, and not to a Stegodont. An upper horizon (*planifrons* subzone) might therefore have to be recognised some day at the top of Zone II.

PROBOSCIDEANS: (Middle and Upper Pliocene of China)

Zygolophodon borsoni (Hays)
Mastodon intermedius Teilhard and Trassaert
Stegodon zdanskyi Hopwood
Stegodon orientalis Owen (This zone?)
Archidiskodon planifrons (Falconer and Cautley) (Uppermost Pliocene)

6. THE PLEISTOCENE OF NORTH CHINA

The Pleistocene of China is of great importance, not only because it has yielded large and rich mammalian faunas that are directly ancestral to the modern faunas of northeastern Asia, but also because it has produced some of the most complete and the most significant remains of fossil man. For this reason, a rather complete and detailed discussion of the Quaternary beds of China will be necessary.

THE VILLAFRANCHIAN OF CHINA.—The Pleistocene succession of North China may be regarded as beginning with the Villafranchian deposits of Nihowan, and also possibly of Yushê. This assignment of the Villafranchian of China to the beginning of the Pleistocene is not entirely in accord with the views of Teilhard,[2] who recognizes the fact that there is a growing sentiment among vertebrate palæontologists to regard the appearance of *Equus*, elephants, and cattle as truly indicative of the beginning of the Pleistocene throughout the world, but who feels that in China it is most convenient to end the Tertiary sequence with the diastrophic movements that resulted in the cutting of the gorges, subsequent to the deposition of the typical Villafranchian sediments. Consequently, he would regard the accumulation of the Choukoutien deposits and the first appearance of man as indicative of the beginning of the Pleistocene in North China.

> In North China, the major period of gorges cutting (Fenho stage) first placed by Bailey Willis at the base of the Malan loess, and later transferred by Barbour and myself to a pre-Nihowan stage (2), would find its true place in an intermediate position, namely between the Sanmenian (Nihowan) and the Choukoutien stages of deposition. . . .

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[1] Teilhard de Chardin, P., and M. Trassaert, 1937. Palaeontologia Sinica, Ser. C, XIII, Fasc. 1, p. 53.

[2] Teilhard de Chardin, P., 1937. Bull. Geol. Soc. China, XVII, No. 2, pp. 173–175.

> In North China, again, (just as in France and also in North India), the first appearance of horse (more and more generally accepted by the palæontologists as indicating the base of the Pleistocene in the Old World) *antecedes* clearly the major diastrophisms which would be the best limit between the Tertiary and the Quaternary from a geological point of view.
>
> Therefore, the advantage of keeping the Villafranchian (first '*Equus-beds*') in the Pliocene, instead of referring it to the Pleistocene, should be re-considered. So far as North China is concerned, the most natural base of the Quaternary is given by the appearance of Man on a modernized topography, *after* the Villafranchian.

YUSHÊ.—According to Teilhard,[1] the basal portion of the Villafranchian of China is to be found in the Yushê basin, and consequently he has distinguished this part of the Pleistocene sequence as a separate subzone within the Villafranchian.

> Strangely enough, no *Archidiskodon* has been recorded up to now from the typical Villafranchian formation of Nihowan. In order to explain this difference (if it really does exist), we may suppose that the Nihowan beds represent only the top of the Villafranchian ('*namadicus* subzone?'), the base of the Villafranchian being on the contrary only present in Yushê, and characterized perhaps there by the latest *Archidiskodon* ('*tokunagai* subzone'?). . .
>
> In Yushê, as well as in Nihowan, the Stegodonts seem to have disappeared before the beginning of the Villafranchian. Yet, some new finds made in S. Shansi suggest that the group (represented by *Stegodon orientalis*) has lasted as far up as the Lower Pleistocene inclusively along the northern border of the Tsinling, as it did in Central and Southern China (Szechuan, etc.).

This definition of a basal zone of the Villafranchian would seem to be in accord with the evidence put forward by Licent and Trassaert for a distinct zone between the Middle Pliocene and the Villafranchian of Central Shansi. Since the relationships of this distinct subzone or horizon in Yushê is with the overlying Villafranchian, rather than with the underlying Pliocene sediments, it would seem best to place it as the first member of the Pleistocene group of sediments in North China.

PROBOSCIDEANS:

Palæoloxodon tokunagai (Matsumoto)
Palæoloxodon namadicus (Falconer and Cautley)

NIHOWAN (SANMENIAN).—The true Villafranchian of North China is best exemplified by the sediments and their contained fauna as exposed in Nihowan. Teilhard[2] has shown that originally only two distinct phases were recognized in the Upper Cenozoic of North China, namely, the Pontian *Hipparion* beds and the Pleistocene loess. Subsequently, as the result of more detailed work in the North China area, a series of post-Pontian, pre-Loess deposits came to light, occupying the interval between the levels originally known.

> But then again the first impression of the geologists was that they had to deal with a single polymorphous complex. On one hand, no internal disconformities were observed, at that time, in the newly recognised sedimentary block. And, on the other hand, the common occurrence in all these 'post-Pontian and pre-Loessic' deposits of closely related types of *Horse, Hyaena, Rhinoceros, Rodents* and Mollusca suggested for all of them a same general age.
>
> Thus was borne the conception of the '*Sanmenian*,' a single stratigraphical and faunistical unit, rather vaguely referred either to the Late Pliocene, or to the Lower Pleistocene.

As Teilhard has shown, there is a definite faunal and physiographic break between the Nihowan and Choukoutien phases, hitherto included in the Sanmenian. Consequently, he has felt it necessary to limit the term *Sanmenian* to the Nihowan deposits and their included fauna, thereby making the Choukoutien formation definitely post-Sanmenian in its relationships. In accordance with his views as to the Upper Pliocene age of the Villafranchian, Teilhard has placed the Sanmenian as the latest part of the Pliocene, relating it to the lacustrine Middle Pliocene sediments of North China, and separating it quite definitely from the overlying Choukoutien phase. It is proposed here to regard the Sanmenian as a lower phase of the Pleistocene sequence in China (preceded perhaps by the basal Villafranchian beds of Yushê) and related to the Choukoutien deposits. Of course, in

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[1] Teilhard de Chardin, P., and M. Trassaert, 1937. Palaeontologia Sinica, Ser. C, XIII, Fasc. 1, p. 53.

[2] Teilhard de Chardin, P., 1937. Bull. Geol. Soc. China, XVII, No. 2, p. 170.

following this line of procedure, the weight of the argument is being given to the faunal evidence, as based on the appearance of new and advanced Pleistocene genera, rather than to the physiographic evidence cited by Teilhard, as based on diastrophism and the rejuvenation of the streams.

It all comes down to a choice between two lines of evidence which do not coincide, as shown by the following diagram.

	Faunal Evidence		Physiographic Evidence	
Malan Loess Choukoutien		Pleistocene		Pleistocene
Sanmenian (Nihowan)			—Break— (Gorge Cutting)	Pliocene
Pliocene	—Break— (Influx of advanced fauna)	Pliocene		

Teilhard's[1] latest views as to the Nihowan fauna have been expressed as follows:

> In spite of the fact that some important physiographic changes have to be supposed (and have in fact been partly traced) in Shansi between the '*Equus-Camelus* beds' of Nihowan and their underlying Middle Pliocene beds (containing neither Horse nor Camel), it remains that both the Nihowan and the pre-Nihowan (Middle Pliocene) series have in common decided lithological and faunistical affinities. Both are dominantly lacustrine in facies, and both are characterized by a same 'sub-tropical Asiatic' fauna. . . . What I mean by this latter expression will only be clear when the description of the Yushê fauna has been given in *Palæontologia Sinica*. Anticipating however on the publication of these memoirs, I can already say that, from the material lately collected in SE Shansi, it appears now that, at the middle of the Pliocene, two different faunistical blocks were mixing in the forested steppes of North China:
>
> (1) A block of south-eastern affinities: abundance of Cervulids (several extinct genera of Munjack deer parallelizing in some way the living south-American deer), *Rusa* and *Axis*, associated with *Stegodon*.
>
> (2) A peculiar Central-Asiatic block, chiefly characterized by a harvest of beautiful, mostly strepsicere, antelopes (more than five new genera recognized so far). This was apparently a special 'Antelopes province,' parallelizing in many respects the modern African province, but separated from it since the base of the Pliocene.
>
> Now the important point bearing on our present subject is that, on the whole, the two above mentioned Cervine and Antilopine blocks were still thriving in North China *after* the appearance of such forms which (as horse, camel, bison, *Eucladoceros*) characterize the Villafranchian of Europe. In spite of many important differences in their respective faunas (disappearance of the *Stegodon*, Aceratherids, Giraffids, etc.) (cf. 2), the Middle Pliocene and the Villafranchian (Nihowan) of North China are marked by the same general topography (a rather mature surface), the same climate (rather warm), and the same fundamental types of deer and antelopes.

PROBOSCIDEAN: *Palæoloxodon namadicus* (Falconer and Cautley).

CHOUKOUTIEN.—The post-Villafranchian, pre-Loess Pleistocene deposits of North China have become of extreme importance within the last few years because of the discovery of the extinct man, *Sinanthropus*, at Choukoutien, southwest of Peking. The Choukoutien deposits were discovered by J. G. Andersson some twenty years ago, and as the result of many years of excavation a large and varied mammalian fauna has been taken out of these beds and described. The Choukoutien sediments are thick fillings in limestone caves or fissures, and as such need no stratigraphic description at this place.

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[1] Teilhard de Chardin, P., 1937, *op. cit.*, pp. 171, 172.

Various authors have described the several groups of mammals constituting the Choukoutien fauna, so that the detailed information as to this mammalian assemblage is voluminous, to say the least. Recently Teilhard has summarized the Choukoutien mammalian fauna by showing that from the standpoint of its geological significance the following classification may be formulated.

1. Forms that were present in the Sanmenian of Nihowan (Villafranchian), but which did not persist into Choukoutien times.
2. Nihowan forms present in the Choukoutien deposits, but absent in the subsequent Malan Loess.
3. Loess forms present in Choukoutien, but absent in Nihowan.
4. Loess forms absent from Choukoutien.
5. Forms that were present in all three formations.

The distribution of the significant mammalian types in the three formations enumerated above may be shown graphically in the following manner.

VILLAFRANCHIAN Sanmen-Nihowan	Choukoutien	LATE PLEISTOCENE Malan Loess
Mustela pachygnatha →		
Elasmotherium →		
Postschizotherium →		
Hipparion →		
Eucladoceros →		
Rusa →		
Ochotonoides →		
Siphneus tingi →		
Machairodus →	*Machairodus*	
Hyæna cf. *sinensis* →	*Hyæna* cf. *sinensis*	
Equus sanmeniensis →	*Equus sanmeniensis*	
Rhinoceros cf. *mercki* →	*Rhinoceros mercki*	
Ovibovids →	Ovibovids	
Nyctereutes →	*Nyctereutes* →	*Nyctereutes*
Meles →	*Meles* →	*Meles*
Camelus →	*Camelus* →	*Camelus*
Gazella →	*Gazella* →	*Gazella*
Spirocerus →	*Spirocerus* →	*Spirocerus*
Bison →	*Bison* →	*Bison*
Ovis →	*Ovis* →	*Ovis*
	Cyon →	*Cyon*
	Siphneus cf. *fontanieri* →	*Siphneus* cf. *fontanieri*
	Euryceros →	*Euryceros*
	Bubalus →	*Bubalus*
		Hyæna spelæa
		Equus hemionus
		Cervus elaphus
		Bos primigenius

From this it will be seen that the Choukoutien fauna is truly intermediate between the Villafranchian fauna of Nihowan and the late Pleistocene fauna of the Malan Loess. As to the relationships of the Choukoutien mammalian assemblage to the faunas either above or below it, Teilhard and Young[1] made the following statements.

> Taking the facts more in detail, the Choukoutien types in many cases are distinctly different from their corresponding Nihowan or Sjara-osso-gol forms, being less primitive than the former, and less advanced to some extent than the latter. For example: *Hyaena* cf. *sinensis*, *Rhinoceros* cf. *tichorhinus*, *Spirocerus wongi*, *Bison palaeosinensis*, *Ovis shantungensis*, from Nihowan are more primitive than *Hyaena sinensis*, *R. tichorhinus*, *Spirocerus peii*, *Bison* sp., *Ovis* cf. *ammon* from Choukoutien. On the contrary, *Hyaena sinensis*, *Euryceros pachyosteus*, *Bubalus teilhardi* from Choukoutien can be held as more archaic than *Hyaena spelaea*, *Euryceros ordosianus*, *Bubalus wansjocki* from the Loess.
>
> The conclusion is obvious. In full accordance with the stratigraphical facts which will be set forth subsequently below in section 5, the Choukoutien fauna fits so exactly between the Late Pliocene (Nihowan) and the Upper Pleistocene (Sjara-osso-gol) ages that it is not easy to decide to which of them it stands more closely related. The Choukoutien formation has consequently broadly to be considered as of Lower Pleistocene age.
>
> In order to account for the change between the Nihowan and the Choukoutien faunas, a long period of time must be allowed during which some climatic changes most probably took place. The fauna is still dominantly of a palaearctic type, but with a clearer tendency to break into a special east Asiatic type. Some southern migration, possibly along the sea coast, may be suggested by the appearance of the *Bubalus.*

Recently Teilhard has placed the Choukoutien deposits in the Middle Pleistocene, as a result of field work and correlative studies made throughout southeastern Asia. By following this procedure, the Choukoutien deposits are brought into line with the cave deposits of southern China and Burma, described in a preceding section of this chapter. On the basis of present evidence, this would seem to be the most logical correlation for the Choukoutien beds. There seems to be but little doubt that there was a widely spread Lower Pleistocene fauna in Asia and the Orient (Upper Siwalik, Upper Irrawaddy, Djetis, Nihowan) followed by an equally extensive Middle Pleistocene complex, which upon the mainland is commonly preserved in caves (Mogok, Hoshangtun, Trinil, Kwangsi, Szechwan, Choukoutien).

THE LOESS OF NORTH CHINA.—At the top of the Cenozoic succession in North China is the Loess, a characteristic and wide-spread deposit forming a prominent and easily-recognized capping layer over a large area north of the Yellow River. Fossils of an advanced type have been found in the Loess, and for this reason the deposit is generally regarded as of Upper Pleistocene age. The following remarks were made by Andersson,[2] in 1923, regarding the mammalian and avian fauna of the North China Loess.

> The most common mammal remains in the loess are tusks and molars of an *Elephas,* which according to Dr. Zdansky may possibly be *Elephas namadicus,* which was originally found in the Pleistocene alluvium of the Narbada valley of India, where it occurs together with two species of *Hippopotamus,* and several other mammals. The reappearance of this Indian species in the North China loess would be very surprising, especially in view of Richthofen's eolian theory. However, Dr. Zdansky's provisional determination has to be tested by a much closer study of the specimens. At any rate, it is beyond doubt that the common loess elephant is not the Mammoth as has formerly been suggested.
>
> Among the numerous isolated finds which have been made in loess-like material the following species can with fair safety be assigned to the loess: *Rhinoceros affinis simus, Ovis? sp., Hyena sp., Ursus sp.* A skull of a *Castorid* also was obtained from undoubted loess, and this is another find which tends to weaken Richthofen's eolian theory. The same applies to a recently found *Sus sp.*
>
> Only in a single case, have we ever come across what deserves the name of a small bone accumulation in the loess. This was in SE Shansi, in Yuan Chü Hsien, and the locality has been studied by Dr. Zdansky who has communicated the section fig. 39. In this place were found: *Hyena, Equus, Cervus* and *a turtle.* The deer, a forest animal, and the turtle, a water animal, are further finds which hardly agree with Richthofen's eolian theory.
>
> Lastly we have to mention a fossil which seems to conform better with the said theory, namely the egg shells of an *Ostrich,* a bird described under the name *Struthiolithus*. . . The modern ostrich is a steppe bird, and the mere mode of occurrence of these unbroken shells, often two or more together, seems to indicate that the nests were occasionally covered by a wind-drift deposit which prevented the eggs from maturing and preserved the shells in an unbroken state.

Earlier authors attributed a great thickness to the loess deposits of North China—in some cases as much as 1,500 feet. According to Andersson, however, the loess never exceeds a thickness of more than 50 or 60 meters.

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[1] Teilhard de Chardin, P., and C. C. Young, 1933. (In Black, Teilhard, Young and Pei), Mem. Geol. Surv. China, Ser. A, No. 11, pp. 48, 49.

[2] Andersson, J. G., 1923, *op. cit.*, p. 127.

Andersson's revised figures for the thickness of the loess are based on the fact that he differentiated the older beds, which the earlier students had confused with the loess and included in it.

The loess of North China, named the *Malan*, has been divided by Andersson into two beds or horizons. The lower deposit he has called the primary loess or the true loess. The upper bed is the secondary loess or the redeposited loess. As is indicated by the name, this secondary loess is merely material from the primary loess, reworked in very late Pleistocene times.

The redeposited loess, because of the taxonomic relationships and the slight mineralization of its contained fossils, has been defined by Andersson as a post-loessic deposit. Thus it may be considered as an horizon bridging the time between the latest Pleistocene and the beginning of Recent conditions in North China.

Lately Teilhard and Young have thrown new light on the problem of the post-loessic faunas of North China in their study entitled, "On the Mammalian Remains from the Archæological Site of Anyang." These authors show that in the ancient city of Anyang, capital of the Shang dynasty during the period between 1400 B.C. and 1100 B.C., there were numerous mammals similar to the post-loessic fossils found in other parts of China. In their analysis of the Anyang fauna, Teilhard and Young list three faunal divisions, namely:

1. The wild indigenous animals, such as the raccoon-dog, bear, badger, tiger, bamboo-rat, hare, water-deer and the sika.
2. The domesticated animals, including the pig, dog, sheep, goat, cattle, water-buffalo, and the macaque.
3. Imported mammals, the whale (probably bones collected along the seacoast), the elephant, tapir, and a small bear.

The presence of the elephant, which has been identified as *Elephas indicus*, in North China is interesting, to say the least. The evidence would seem to show, however, that this elephant was never wild here, but rather was imported (probably in the form of tribute) by the ancient peoples of this old city.

As Teilhard and Young[1] have remarked, "Such beds [the redeposited loess and similar deposits] are still, geologically, a 'no man's land'; more attention should be paid in [the] future to the redeposited loess, to peat-bogs and to subrecent cave deposits."

The difficulty in dealing with these redeposited loess and post-loessic beds is that they really do bridge the period between the Pleistocene and the present day. Consequently such beds are defined only in a most provisional manner. As Teilhard and Young have shown, if *Rhinoceros*, *Elephas namadicus* or *Elephas primigenius*, *Hyæna*, and *Euryceros* are present, the deposits may be called Pleistocene with some degree of assurance. On the other hand, there is no reason why some of these forms may not persist beyond the closing of the Pleistocene period—whenever that might have been. Therefore the problem resolves itself into a question of drawing an artificial line across a series of continuous events which are so close to us that it is not possible for us to gain a true perspective as to their importance or their interrelationships.

Proboscideans:

Palæoloxodon namadicus (Falconer and Cautley)	Loess
Elephas primigenius Blumenbach	Upper Pleistocene, North China, Mongolia
Elephas indicus Linn.	Sub-Recent, Anyang

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[1] Teilhard, P., and C. C. Young, 1936. Palaeontologia Sinica, Ser. C, XII, Fasc. 1, p. 57.

LIST OF THE FOSSIL LAND MAMMALS OF JAPAN AND KOREA

Specific Names[1]	Locality	Miocene	Pliocene	Pleistocene
Primates				
Macacus fuscatus Bly	Kyushu (Buzen)			×
Rodentia				
Sciurid	Honshu (Mino)	×		
Lepus brachyurus brachyurus Tem.	Kyushu (Buzen)			×
Carnivora				
Meles anakuma Tem.	Honshu (Shimotsuke), Kyushu (Buzen)			×
Proboscidea				
Hemimastodon annectens Mat. (*Serridentinus*)	Honshu (Mino)	×		
**Prostegodon latidens* (Clift) (*Stegolophodon*)	Honshu (Hitachi, Rikuzen)	×		
Trilophodon sendaicus Mat. (*Serridentinus*)	Honshu (Rikuzen)		×	
**Trilophodon palæindicus* Lyd.	Honshu (Mino)	×		
Parastegodon aurorae Mat. (*Stegodon*)	Honshu (Kaga)		×	
**Stegodon bombifrons* Falc. and Caut.	Honshu (Kazusa)		×	
**Stegodon clifti* Falc. and Caut.	Honshu (Ise)		×	
**Stegodon orientalis* Owen	Honshu (Kazusa, Shimotsuke, Echigo, Suo, Nagasaki), Inland Sea			×
**Stegodon sinensis* Owen	Inland Sea			×
Stegodon sp.	Kyushu (Hyuga)	×		
Parelephas protomammonteus Mat. (*Palæoloxodon*)	Honshu (Kazusa)		×	
Parelephas trogontherii Pohlig	Honshu (Kazusa, Mikawa, Omi, Shinano), Inland Sea.			×
Loxodonta tokunagai Mat. (*Palæoloxodon*)	Honshu (Etchu)		×	
Loxodonta namadica naumanni Mak. 1924 (*Palæoloxodon*)	Honshu (Musashi, Totomi, Sagami, Hitachi, Kazusa, Mikawa, Shimosa)			×
Elephas namadicus setoensis Mak. 1929 (*Palæoloxodon*)	Inland Sea			×
Loxodonta namadica yabei Mat.	Honshu (Ugo, Noto), Inland Sea, Shikoku, Hokaido (Ishikari)			×
Elephas indicus buski Mat.(*Palæoloxodon*)	Honshu (Musashi, Mino, Mutsu)			×
Mastodon sp.	Korea (Joshin)	?	?	
Perissodactyla				
Anchitherium hypohippoides Mat.	Honshu (Mino)	×		
**Equus caballus* Linné	Honshu (Hyogo, Korea (Keikido)			×
Palæotapirus yagii Mat.	Honshu (Mino)	×		
Teleoceras pugnator Mat.	Honshu (Mino)	×		
Rhinoceros (*Teleoceras*) *tokiensis* Tok.	Honshu (Mino)	×		
Rhinoceros (*Teleoceras?*) *kaniensis* Tok.	Honshu (Mino)	×		
Rhinoceros (*Aceratherium?*) *watanabei* Tok.	Honshu (Suo)	×		
Rhinoceros (*Aceratherium?*) *makii* Tok.	Korea (Kokaido)	×		
Rhinoceros sp.	Honshu (Suo)	×		
Rhinoceros shindoi Tok.	Honshu (Shimotsuke), Kyushu (Buzen)			×
Rhinoceros koreanicus Tok.	Korea (Keikido)			×
Rhinoceros sp.	Taiwan (Taikei)			×
Sus nipponicus Mat.	Honshu (Ugo)			×
Sus leucomystax Tem.	Honshu (Shimotsuke), Kyushu (Buzen)			×
Amphitragulus minoensis Mat.	Honshu (Mino)	×		
Dicrocerus tokunagai Mat.	Honshu (Iwaki)	×		
Cervavus oweni hirabayashii Tok.	Honshu (Shinano)	×		
Cervus nippon nippon Tem.	Honshu (Musashi, Shimotsuke, Ugo), Kyushu (Buzen), Inland Sea			×
Cervus kazusensis Mat.	Honshu (Kazusa)			×
Cervus riukiuensis Mat.	Loochoo Is.			×
**Cervus* cfr. *elaphus* Linné	Korea (Heian-nando)			×
Cervus sp.	Honshu (Shimoosa)			×
Cervus sp.	Honshu (Totomi)		?	
Cervus sp.	Honshu (Sagami)		?	
**Elaphurus davidianus* M–Edwards	Honshu (Kazusa)			×
Muntiacus astylodon Mat.	Loochoo Is.			×
Giraffa nipponica Mat.	Honshu (Kazusa)			×
Bubalina sp.	Honshu (Omi)		×	
**Bison occidentalis* Lucas	Inland Sea			×
**Bibos geron* Mat.	Inland Sea			×

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*Common to Japan and continental Asia.

[1] The proboscidean names in parentheses are the generic references used by Professor Osborn.

7. THE MIOCENE TO PLEISTOCENE OF JAPAN

JAPAN.—The fossil mammals of Japan, though for the most part very poorly preserved, have been found at numerous localities, showing that Cenozoic continental deposits, particularly those of the Upper Cenozoic, are widely distributed throughout the islands. Most of the mammal-bearing localities are on the island of Honshu, and a majority of these deposits are of Pleistocene age. In all of the Japanese deposits, whether of late Tertiary or of Pleistocene age, the proboscideans are the dominant elements in the faunas.

The evidence of the fossil mammals would seem to indicate that Japan was connected with Asia during Miocene, Pliocene, and early Pleistocene times. Certain elements of the Miocene fauna of Asia reached Japan, and in subsequent times there was likewise a constant infiltration of new migrants from the mainland. This influx from Asia into Japan reached its height seemingly during the early part of the Pleistocene, for at that time numerous proboscideans as well as certain other forms found in Japan were specifically identical with mainland types.

An interesting feature of the Japanese faunas is the dominance of the proboscideans, especially during Pleistocene times. Whether this dominance of the Proboscidea is real or illusory is a question difficult to decide on the basis of extant evidence. That is, there may be many proboscideans in the Japanese deposits because these fossils are large and more apt to be preserved than are more delicate, smaller mammalian types. Or it may be that the proboscideans actually effected a crossing from the mainland to the islands where other smaller, less adaptable mammals failed.

Recently Dr. Tokunaga[1] published a compendium of all the fossil land mammals found in Japan and Korea. His list of genera and species, with their horizons and localities, is repeated here (p. 1489) in so far as it bears on Upper Cenozoic forms.

VI. NORTH AMERICA

1. INTRODUCTION

It would seem that the Proboscidea first reached North America from the Old World in Upper Miocene times, and from that time until the end of the Pleistocene, these animals played an important rôle in the development of the mammalian faunas of the New World. Moreover, the evidence of recent discoveries shows that certain of the mammoths and mastodons did not become extinct until after man had crossed from Asia into America and was well established in his New World home.

In the following pages the relationships of the various Proboscidea-bearing formations of North America will be discussed. Only those beds in which proboscideans are actually recorded will be included in the discussion, and they will be grouped by their ages, according to whether they are of Miocene, Pliocene, or Pleistocene affinities. In considering the Miocene and Pliocene beds, the several formations as named according to prevalent American usage will be described and compared. To give the discussions a certain degree of order and comprehension, the formations will be grouped according to their occurrence in the eastern portion of North America, in the Great Plains region, and in the Mountain and Pacific Coast region respectively. The treatment of the Pleistocene must of necessity be somewhat different. Here the sequence of the glacial and interglacial periods in North America in relation to the occurrence of Pleistocene proboscideans will be discussed.

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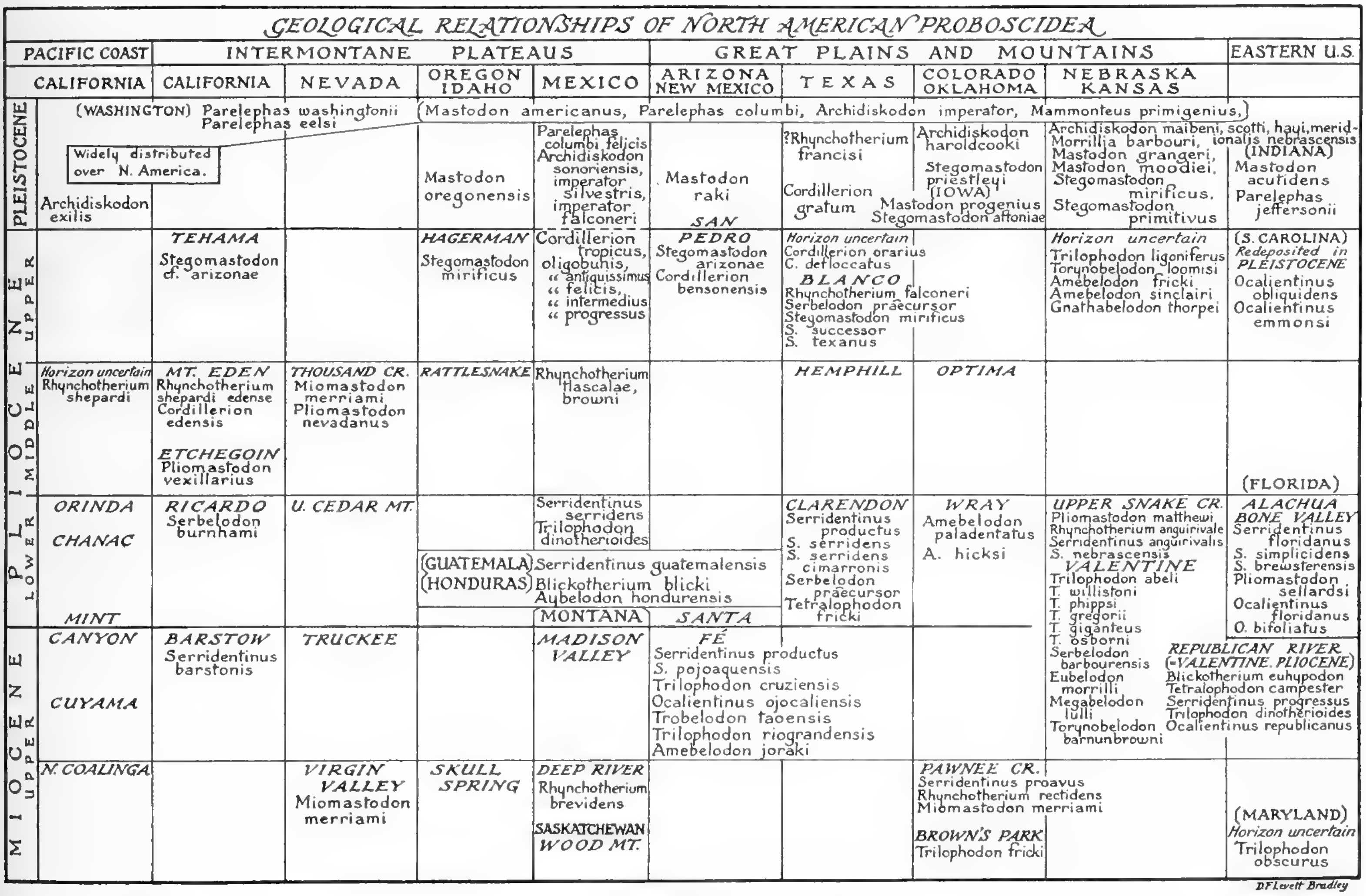
[1] Tokunaga, Shigeyasu, 1933. Amer. Mus. Novitates, No. 627, pp. 2–4.

2. THE UPPER MIOCENE: BARSTOVIAN

Pawnee Creek Formation, Colorado.—Dr. Matthew, in his first description of the Pawnee Creek beds of northeastern Colorado, recognized two fossiliferous layers or zones within the formation, but at that time he pointed out the fact that the separation between these zones, either stratigraphically or faunistically, was very inconstant, so he was inclined to regard the zoning of the Pawnee Creek beds as of little importance. Later, in 1909, in 1918, and in 1924, he regarded the Pawnee Creek formation as a unit, containing a single fauna.



GEOLOGICAL RELATIONSHIPS OF NORTH AMERICAN PROBOSCIDEA

		PACIFIC COAST	INTERMONTANE PLATEAUS				GREAT PLAINS AND MOUNTAINS				EASTERN U.S.
		CALIFORNIA	CALIFORNIA	NEVADA	OREGON IDAHO	MEXICO	ARIZONA NEW MEXICO	TEXAS	COLORADO OKLAHOMA	NEBRASKA KANSAS	
PLEISTOCENE		(WASHINGTON) Parelephas washingtonii Parelephas eelsi Archidiskodon exilis	Widely distributed over N. America.		(Mastodon americanus, Parelephas columbi, Archidiskodon imperator, Mammonteus primigenius,) Mastodon oregonensis	Parelephas columbi felicis Archidiskodon sonoriensis, imperator silvestris, imperator falconeri	Mastodon raki	?Rhynchotherium francisi Cordillerion gratum	Archidiskodon haroldcooki Stegomastodon priestleyi (IOWA) Mastodon progenius Stegomastodon aftoniae	Archidiskodon maibeni, scotti, hayi, meridionalis nebrascensis Morrillia barbouri, Mastodon grangeri, Mastodon moodiei, Stegomastodon mirificus, Stegomastodon primitivus	(INDIANA) Mastodon acutidens Parelephas jeffersonii
PLIOCENE	UPPER		TEHAMA Stegomastodon cf. arizonae		HAGERMAN Stegomastodon mirificus	Cordillerion tropicus, oligobunis, " antiquissimus " felicis, " intermedius " progressus	SAN PEDRO Stegomastodon arizonae Cordillerion bensonensis	Horizon uncertain Cordillerion orarius C. defloccatus BLANCO Rhynchotherium falconeri Serbelodon præcursor Stegomastodon mirificus S. successor S. texanus		Horizon uncertain Trilophodon ligoniferus Torynobelodon loomisi Amebelodon fricki Amebelodon sinclairi Gnathabelodon thorpei	(S. CAROLINA) Redeposited in PLEISTOCENE Ocalientinus obliquidens Ocalientinus emmonsi
	MIDDLE	Horizon uncertain Rhynchotherium shepardi	MT. EDEN Rhynchotherium shepardi edense Cordillerion edensis ETCHEGOIN Pliomastodon vexillarius	THOUSAND CR. Miomastodon merriami Pliomastodon nevadanus	RATTLESNAKE	Rhynchotherium tlascalae, browni		HEMPHILL	OPTIMA		(FLORIDA)
	LOWER	ORINDA CHANAC MINT	RICARDO Serbelodon burnhami	U. CEDAR MT.	(GUATEMALA) (HONDURAS) Serridentinus guatemalensis Blickotherium blicki Aybelodon hondurensis	Serridentinus serridens Trilophodon dinotherioides (MONTANA)	SANTA	CLARENDON Serridentinus productus S. serridens S. serridens cimarronis Serbelodon præcursor Tetralophodon fricki	WRAY Amebelodon paladentatus A. hicksi	UPPER SNAKE CR. Pliomastodon matthewi Rhynchotherium anguirivale Serridentinus anguirivalis S. nebrascensis VALENTINE Trilophodon abeli T. willistoni T. phippsi T. gregorii T. giganteus T. osborni Serbelodon barbourensis Eubelodon morrilli Megabelodon lulli Torynobelodon barnunbrowni	ALACHUA BONE VALLEY Serridentinus floridanus S. simplicidens S. brewsterensis Pliomastodon sellardsi Ocalientinus floridanus O. bifoliatus
MIOCENE	UPPER	CANYON CUYAMA	BARSTOW Serridentinus barstonis	TRUCKEE		MADISON VALLEY	FÉ Serridentinus productus S. pojoaquensis Trilophodon cruziensis Ocalientinus ojocaliensis Trobelodon taoensis Trilophodon riograndensis Amebelodon joraki				REPUBLICAN RIVER (=VALENTINE. PLIOCENE) Blickotherium euhypodon Tetralophodon campester Serridentinus progressus Trilophodon dinotherioides Ocalientinus republicanus
		N. COALINGA		VIRGIN VALLEY Miomastodon merriami	SKULL SPRING	DEEP RIVER Rhynchotherium brevidens SASKATCHEWAN WOOD MT.			PAWNEE CR. Serridentinus proavus Rhynchotherium rectidens Miomastodon merriami BROWN'S PARK Trilophodon fricki		(MARYLAND) Horizon uncertain Trilophodon obscurus

D.F.Levett Bradley

Figure 1224

Professor Osborn, however, held to the view that the Pawnee Creek formation consists of two levels, which he designated as "A" and "B," for the lower and upper divisions respectively. This view was expressed in 1918, in the monograph on the Tertiary Equidæ of North America, and will be found repeated in Volume I of the present Memoir.

In 1924 Matthew clearly demonstrated the virtual equivalence of the Pawnee Creek beds with the Lower Snake Creek beds of Nebraska. The correspondence of the two formations is indeed close, not only in the constitution of their mammalian faunas, but also in the fact that they are located only a hundred miles or so apart. Therefore there is every reason for regarding them as about contemporaneous with each other.

The Pawnee Creek formation and Lower Snake Creek would seem to be representative of the beginning of the Upper Miocene in North America. As Matthew has pointed out, certain elements in the faunas, particularly the horses, show the admixture of typically Middle Miocene types with more progressive forms that foreshadow to some extent Pliocene species.

Proboscideans in the Pawnee Creek formation are extremely scanty, and it is interesting to note that they are completely absent from the closely related Lower Snake Creek beds. Perhaps these beds were deposited soon after the proboscideans first reached America, so that the group had not had an opportunity to become widely spread.

PROBOSCIDEANS:
- *Serridentinus proavus* (Cope)
- *Rhynchotherium rectidens* Osborn
- *Miomastodon merriami* Osborn

BROWN'S PARK FORMATION, COLORADO.—The Brown's Park formation, located in the extreme northwest corner of Colorado, was fully described by Peterson in 1928, in his comprehensive memoir on the Brown's Park Fauna. According to Peterson, this formation consists of "soft, almost chalk-white sands and sandstones cemented with lime, sometimes intercalated with slightly argillaceous bands."

The lower part of the formation, consisting of a rather hard, resistant sandstone, was named the Weller sandstone by Peterson, and it is at this level that the fossil mammals representative of the formation were found.

At its earliest, the Brown's Park formation is possibly correlative with the Sheep Creek of Nebraska, of Middle Miocene age. The presence of a primitive procyonid, a chalicothere (chalicotheres extend upwardly into the Sheep Creek in Nebraska), and an oreodont probably related to *Ticholeptus*, would be evidence in favor of this correlation for the assemblage. The presence of *Trilophodon*, however, may be an argument in favor of a somewhat more advanced position for the fauna, that is, roughly equivalent to the Deep River, Pawnee Creek, and Lower Snake Creek formations.

PROBOSCIDEAN: *Trilophodon fricki* (Peterson).

SANTA FÉ BEDS, NEW MEXICO.—For many years the Upper Tertiary sediments around Santa Fé, New Mexico, have been known as the Santa Fé marls, and as a result of the early explorations and publications of Cope these beds have come to be regarded as of Upper Miocene age. In 1909 Matthew listed the Santa Fé as being more or less the equivalent of the "Fort Niobrara" and Little White River beds in Nebraska and Dakota, and of the Clarendon in Texas. This would indicate a possible position in the Lower Pliocene, rather than in the Miocene.

During recent years the expeditions sponsored by Mr. Childs Frick have made extensive collections in the Santa Fé beds, and much new material, far finer than any hitherto discovered, has been found. In an extensive paper on Tertiary proboscideans of North America Frick has described and figured some extraordinarily complete Santa Fé mastodonts, which are listed below.

Frick's work in New Mexico would seem to give evidence for the fact that the Santa Fé beds are not a unit horizon, but rather cover a considerable period of time, beginning in the Upper Miocene and extending throughout an appreciable portion of the Pliocene. The proboscideans discovered by Frick come from an intermediate horizon within the Sante Fé, which, because of the presence of *Hipparion*, is very probably of Lower Pliocene age, being more or less equivalent to the Republican River and Upper Snake Creek beds to the north. Above this zone carrying *Hipparion* and proboscideans are beds that Frick regards as of Upper Pliocene age. Frick's[1] remarks as to the age of the Santa Fé are as follows:

> The deposits of the Santa Fé basin of northeastern New Mexico, widely known in the literature as the Santa Fé marls, have been currently interpreted as of Upper Miocene age. More recent investigation indicates that the accumulations of this portion of the Rio Grande basin range from the Mid-Miocene to Pleistocene. The Pleistocene occurs in remnants of æolian origin that here and there cap the irregular Pliocene-Miocene surface... While no mastodonts have so far been encountered in limited exposures of probable Uppermost Pliocene facies, their remains are fairly common in the upper half of the earlier deposits. A possible time equivalent of the Little White River of South Dakota, the Republican River of Kansas and the Upper Snake Creek of Nebraska is indicated by the presence in certain localities of species of *Hipparion* and of advanced *Pliohippus*. . . .
>
> The mastodont forms of the Ojo Caliente and the Santa Cruz sections of the Santa Fé basin are tentatively interpreted as of the *Hipparion* zone.

More recently (1937) Frick[2] states that: "The Lower Snake Creek, Pawnee Creek, Santa Fé and Barstow ostensibly include a number of overlapping phases of the main Late Tertiary." According to this author's classification of Tertiary sediments, the formations named above might occur in the interval between Middle Miocene and about Middle Pliocene times.

Within the past year Charles S. Denny[3] has published a study of the Santa Fé formation in its type locality, principally in the Española Valley, north of the city of Santa Fé. This is strictly a geologic and sedimentation study, so that the question of the contained vertebrate fauna and its probable age is not considered. Denny concludes that the Santa Fé formation is made up of several sedimentary horizons, deposited as broad alluvial fans from rivers with low gradients arising in the relatively low ancestral Sangre de Cristo Mountains and associated highlands. He thinks that during the time these sediments were being deposited the climate was semi-arid to humid and that there were occasional showers of volcanic ash from nearby cones. There was a considerable amount of vegetation on the floodplain and along the bordering highlands.

It would be most desirable to have a supplementary study of the Santa Fé formation, based largely upon the contained vertebrate faunas, to determine as nearly as possible the zoologic and stratigraphic relationships of these mammalian assemblages.

PROBOSCIDEANS:

Serridentinus productus (Cope)
Trilophodon pojoaquensis Frick
Megabelodon cruziensis (Frick)
Ocalientinus ojocaliensis Frick
Trobelodon taoensis Frick
Trilophodon (*Tatabelodon*) *riograndensis* (Frick)
Trilophodon joraki (Frick)

DEEP RIVER BEDS, MONTANA.—Some confusion exists as to the name of this formation, for the term was originally applied by Scott to the sediments along the Smith River, which was once called Deep Creek. As originally described, two faunas were recognized from this series of deposits: a lower one of Upper Oligocene age, and an upper one of approximately Middle Miocene age. Consequently, Douglass in 1903[4] limited the name Deep River to the upper fauna, and applied a new name, Fort Logan, to the lower mammalian assemblage.

According to Douglass, the Deep River beds, in the strict sense of the word, consist of marl, volcanic dust, soft limestone, and fine sand, and they attain a thickness of approximately 400 feet.

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[1] Frick, Childs, 1933. Bull. Amer. Mus. Nat. Hist., LIX, Art. IX, pp. 549, 571.

[2] Frick, Childs, 1937. Bull. Amer. Mus. Nat. Hist., LXIX, p. 7.

[3] Denny, Charles S., 1940. Bull. Geol. Soc. Amer., LI, No. 5, pp. 677–693.

[4] Douglass, Earl, 1903. Ann. Carnegie Mus., II, No. 2, p. 150.

The fauna is of Middle or Upper Miocene affinities, and may be correlated with the faunas of the Pawnee, Virgin Valley, and Mascall formations. A new, detailed study of this formation and its contained fauna is now being made by H. A. Koerner, and when published will offer needed and valuable information on a long neglected subject.

PROBOSCIDEAN: *Rhynchotherium brevidens* (Cope).

VIRGIN VALLEY BEDS, NEVADA.—The Virgin Valley beds, which were thoroughly studied and described by Merriam (1910, 1911)[1] are located in the northwestern corner of Nevada in a high, intermontane basin. These sediments reach a thickness of about 1500 feet, and according to Merriam consist of three zones, the lower two of which constitute the Lower Virgin Valley and are separated from the upper zone, designated as the Upper Virgin Valley, by an unconformity. Most of the fossils come from a comparatively thin zone situated near the middle of the section.

An extensive fauna is known from the Virgin Valley beds, which is definitely of Middle or Upper Miocene relationships.

> The closest relationship of the Virgin Valley fauna seems to be with that of the Mascall Beds of Oregon and of the Pawnee Creek Beds of Colorado. The Snake Creek Beds of Nebraska contain a larger percentage of the Virgin Valley species than either the Mascall or Pawnee Creek, but there seems, nevertheless, good reason for considering the relationship with the other faunas as closer.

PROBOSCIDEAN:

Miomastodon merriami Osborn
"Mastodon (*Tetrabelodon* ?, sp.)"

BARSTOW FORMATION, MOHAVE DESERT, CALIFORNIA.—One of the characteristic Upper Miocene faunas of North America is that of the Barstow formation, named and described by Merriam. The Barstow beds are exposed in southern California, in the southwestern section of the Great Basin, and they form a part of the hot, dry Mohave Desert. According to Merriam five members (as defined by Baker) constitute the Barstow formation. These begin with a basal breccia at the bottom, and grade upward through a tuff-breccia, a fine ashy and shaly tuff, a resistant breccia, to a fossiliferous tuff constituting the topmost bed, and in which the vertebrate remains are found.

The fauna of the Barstow formation is extensive and closely comparable to the Santa Fé "fauna," as originally known. Thus the evidence would seem to be conclusively in favor of an uppermost Miocene age for the Barstow, slightly later than the Virgin Valley, Mascall, Pawnee, and Lower Snake Creek beds, but earlier than the Ricardo, which also is exposed in the Mohave Desert.

Merriam[2] has made the following remarks with regard to the Barstow formation, and its fauna:

> The fauna of the Barstow beds is as a whole that of an open country affording fairly abundant grass and herbage, and evidently better watered than the Mohave Desert at the present day. The abundance of remains of grazing horses of the *Merychippus* type, the presence of mastodons, oreodonts, abundant merycodonts, a considerable variety of camels, and a peccary all indicate that nutritious vegetation must have been more abundant than at present. The *Merychippus* forms would probably not have been present in such numbers unless grasses were well represented. . . .
>
> The fauna of the Barstow beds represents a stage in the evolution of Tertiary mammalian faunas not previously distinctly recognized in the Great Basin Province. It seems clearly later than the Middle Miocene stage of the Mascall and Virgin Valley; and is markedly older than Rattlesnake, Thousand Creek, and Ricardo, representing the next known stage following the

[1] Merriam, J. C., 1911. Bull. Dept. Geol., Univ. Calif., VI, No. 11, p. 206.

[2] Merriam, J. C., 1919. Bull. Dept. Geol., Univ. Calif., XI, No. 5, pp. 450, 451, 453.

Middle Miocene in the Great Basin. The fauna of the Barstow has few if any species in common with that of the Ricardo, and is of a distinctly older type. Its nearest relationships are with the faunal assemblage of the Cedar Mountain region of southwestern Nevada, from which it possibly differs somewhat in stage. . . .

The nearest relationships of the Barstow fauna outside the Great Basin are with the Santa Fé beds of New Mexico. Several types which are among the most important forms of the Santa Fé beds are similar to species in the Barstow fauna. These include *Aelurodon wheelerianus*, *Merychippus calamarius*, *Procamelus* near *gracilis*, and *Merycodus necatus*.

As a considerable distance separates the Barstow geographically from the Santa Fé some difference in fauna is to be expected. It is also possible that the Santa Fé beds represent more than one horizon, or may include beds ranging into stages older or younger than the Barstow.

PROBOSCIDEANS:

Serridentinus barstonis (Frick)
Tetrabelodon ? sp.

3. THE LOWER PLIOCENE; CLARENDONIAN

ALACHUA AND BONE VALLEY FORMATIONS, FLORIDA.—Two formations represent the Pliocene in Florida; these are the Alachua and Bone Valley beds exposed in the northwestern and central western portions of the State respectively. Although different from each other in their physical expression and the relations with underlying and overlying beds, these two formations are correlative in age and therefore may be considered together.

The Alachua formation consists of clays and phosphate rocks resting on the Eocene Ocala limestone and overlain by soft Pleistocene or Recent sands. Due to the action of ground waters there has been a great deal of solution and slumping, before, during, and after the deposition of the Alachua deposits, so that the relationships of the Alachua clays and their contained mammals with underlying and overlying deposits and faunas have been much confused. Simpson has shown that the Alachua formation contains a true, pure Pliocene fauna, not to be confused with the Eocene and Miocene vertebrates that are found in older beds below it, or with Pleistocene and Recent species from above.

The Bone Valley formation is made up of gravels, or more properly of "pebble phosphates" which grade upward into true sands. The Bone Valley everywhere rests upon the Miocene Hawthorn formation, and according to Simpson much of the material constituting it has been derived from the underlying Hawthorn sediments. Simpson believes that the Bone Valley is of estuarine origin. Although there is some false association of vertebrates from the older deposits in the Bone Valley beds, such association is readily interpreted, and does not lead to the confusion of various faunal elements as is the case with the Alachua formation. Fossil remains from overlying, younger beds also are apt to be included within the Bone Valley deposits.

It might be said at this place that the Peace Creek beds, often quoted in the older literature as representing in part the Pliocene of Florida, are in reality of Pleistocene age, containing an admixture of derived Pliocene species.

Various expressions of opinion have been made as to the age of the Alachua and the Bone Valley formations. Osborn and Matthew in 1909 considered these formations as equivalent to the "*Peraceras* zone" of Upper Miocene or Lower Pliocene affinities; Osborn in 1910 placed them in the Pliocene; Sellards in 1916 made the two formations correlatively equivalent to each other and placed them in the Pliocene; Kellogg in 1924 (on the basis of the marine mammals) regarded the Bone Valley as of pre-Pliocene age, while Hay in 1923 referred the two formations to the Pleistocene.

Simpson's recent work of 1930[1] is the most thorough that has been done on these formations. As the result of his studies, he has come to the following conclusions.

---

[1] Simpson, G. G., 1930. Bull. Amer. Mus. Nat. Hist., LIX, pp. 149–211.

1. The Alachua and Bone Valley formations are approximately equivalent in age, since their vertebrate faunas are essentially similar.

2. The land mammals found in these formations compare most closely with the Lower Pliocene faunas of western North America, more particularly with the faunas of the Upper Snake Creek and the Republican River beds.

3. The marine mammals of the Alachua and Bone Valley formations seemingly show definite pre-Pliocene affinities (perhaps as old as the Helvetian, according to Kellogg). However, this discrepancy between the evidence of the land and marine forms may be due to:

a. Derivation of the marine fossils from an older formation.

b. Survival of older marine types to a later period in Florida.

c. Tentative identifications, due to faulty material, that would result in the reference of the marine mammals to genera of older geologic age than they represent.

Stirton (1936)[1] places the Alachua in the Middle Pliocene, as about equivalent to the Hemphill.

PROBOSCIDEANS:

Serridentinus floridanus (Leidy)
Trilophodon simplicidens (Osborn)
Serridentinus brewsterensis Osborn
Pliomastodon sellardsi Simpson
Ocalientinus floridanus leidii (Frick)
Ocalientinus bifoliatus (Osborn)

VALENTINE BEDS, NORTH CENTRAL NEBRASKA.—The name "Valentine" was given by Barbour and Cook[2] in 1917 to a series of beds in northern Nebraska which these authors considered as representing a stratigraphic unit, containing a single fauna. Barbour and Cook, as a result of their study of the fossils from the Valentine beds, decided that these sediments are of Lower Pliocene age, below the Upper Snake Creek beds, as defined by Matthew.

Subsequently the name "Valentine" came into general acceptance for the lowermost Pliocene, or transitional Miocene to Pliocene phase of the Great Plains area—not only as a formation name, but also as a time term, due particularly to its usage by Matthew, Osborn, Simpson, and other students discussing general problems of correlation.

Stirton and McGrew, in 1935[3], as a result of their extensive field work in the Valentine area, divided the Valentine into three horizons, one of Upper Miocene age, one of Lower Pliocene age, and one of an age transitional between the Lower and Middle Pliocene. These authors restricted the name "Valentine" to the uppermost of these horizons, applying to the lowest horizon the name "Niobrara River" and to the middle one the name "Burge."

In an effort to modify the change in usage proposed by Stirton and McGrew, Johnson, in 1936,[4] suggested that the name "Valentine" be applied to the lowest of the three horizons in question, that a new name, "Cap Rock beds," be applied to the highest level, while the name "Burge" be retained for the middle horizon.

[1] Stirton, R. A., 1936. Amer. Journ. Sci., (5), XXXII, pp. 161–206.
[2] Barbour, E. H., and Harold J. Cook, 1917. Neb. Geol. Surv., VII, Pt. 19, p. 173.
[3] Stirton, R. A., and P. O. McGrew, 1935. Amer. Journ. Sci., (5), XXIX, pp. 125–132.
[4] Johnson, F. W., 1936. Amer. Journ. Sci., (5), XXXI, pp. 467–475.

Since then the relationships and nomenclature of the various horizons comprising the Upper Miocene and Lower Pliocene of northern Nebraska have been extensively discussed by several authors. Suffice it to say that at present several shades of opinion exist, so that the "Valentine Problem" has become rather complex and difficult to follow. There is a recent tendency among those interested in this problem, to regard the name "Valentine" as a rather inclusive term, designating the uppermost Miocene and the lowermost Pliocene in the north central Nebraska region. Such a view has been expressed by Lugn,[1] in a paper reviewing and redefining the entire Tertiary sequence in Nebraska. Lugn defines a large stratigraphic group of Pliocene age, which he calls the Ogallala—using a name that had long been more or less abandoned. In the lower portion of this group he includes the Valentine formation consisting of the original Valentine fauna, or Niobrara River assemblage at the base, contained in loose, white sands, with the Burge channel member above it. Above the Valentine is the Ash Hollow formation, the lower portion of which is formed by the hard cap rock, containing the "Valentine" fauna of Stirton and McGrew. Incidentally, this cap rock layer with its included fauna was renamed the "Minnechaduza" by Stirton,[2] in a paper that came out almost simultaneously with the above mentioned contribution by Lugn.

Several authors, notably Cook and Cook, Stirton and McGrew, Johnson, and McGrew, have given faunal lists in which the mammalian assemblages from the three zones or levels of the Valentine and lower Ash Hollow formations are defined. There is much disagreement among these authors as to the position of many genera and species in the three horizons, and due to the lack of knowledge as to the exact level at which most of the earlier collections were made, some well-known forms cannot be definitely placed. The important point brought out by the work of Stirton and McGrew is that in the lowest horizon *Merychippus* is the characteristic horse, while members of the *Hipparion* group are absent. This is the definitive argument for placing this fauna in the Upper Miocene. The *Hipparion* types, *Nannippus* particularly, appear first in the middle horizon, and this constitutes the most telling argument for considering this zone as of basal Pliocene age. Finally, in the upper horizon more advanced types of *Hipparion* appear, which would seem to connect this fauna with the progressive Lower Pliocene faunas of other parts of North America.

	Stirton and McGrew 1935	Johnson 1936	Lugn 1939	Stirton 1939
Upper Horizon				
Transitional Lower to Middle Pliocene	Valentine	Cap Rock	Ash Hollow (lower part)	Minnechaduza
Middle Horizon				
Lower Pliocene	Burge	Burge	Valentine (Burge channel sands)	Burge
Lower Horizon				
Upper Miocene	Niobrara River	Valentine	Valentine ("original" Valentine fauna)	Niobrara River

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[1] Lugn, A. L., 1939. Bull. Geol. Soc. Amer., L, No. 8, pp. 1245–1275. (In this paper there is a comprehensive bibliography, in which will be found listed all of the important articles published to date on the Valentine problem.)

[2] Stirton, R. A., 1939. Amer. Journ. Sci., CCXXXVII, pp. 429–433.

PROBOSCIDEANS:

Trilophodon abeli (Barbour)	Devil's Gulch
Trilophodon willistoni (Barbour)	" "
Trilophodon phippsi Cook	" "
Trilophodon (*Tatabelodon*) *gregorii* (Frick)	" "
Trilophodon giganteus Osborn	Oak Creek
Trilophodon (*Genomastodon*) *osborni* Barbour	Bristow
Serbelodon barbourensis Frick	Devil's Gulch
Eubelodon morrilli Barbour	" "
Megabelodon lulli Barbour	Valentine
Torynobelodon barnumbrowni Barbour	"

DEVIL'S GULCH, NORTH CENTRAL NEBRASKA.—The Devil's Gulch beds were named by Barbour in 1914,[1] for the Pliocene sediments as typically exposed in Devil's Gulch, north of Ainsworth, Nebraska. In his original description of this formation, Barbour considered it as of Pliocene age.

> As to the geological horizon, the faunal evidence suggests Pliocene equivalent to the Snake Creek beds of southern Sioux County. Possibly some Pleistocene may be represented. Further study will be necessary to determine accurately the geologic position of this newly explored fossil field. Faunal comparisons show this bed to be much earlier than that of Hay Springs, and later than that of the famous Agate Springs Quarries. It will not be far wrong to call the Devil's Gulch deposits, Pliocene.

Barbour, and Barbour and Cook, in the early work on the Devil's Gulch beds, definitely considered these sediments as being rather well up in the Pliocene, certainly later than the Valentine and probably later than the Upper Snake Creek.

In 1918 Osborn[2] listed two levels for the Devil's Gulch,a lower one more or less equivalent to the Valentine, and an upper one of much more advanced, post-Snake Creek affinities.

Recent field work (as yet unpublished) in the Ainsworth regions would seem to indicate that the Devil's Gulch beds probably are correlative with the Valentine formation to the west, and cover a fairly long period of time, ranging from late Miocene well into the Pliocene. It is very possible that there are several faunal zones here, corresponding to the zones of the Valentine area, as distinguished by Stirton and McGrew.

PROBOSCIDEANS: See preceding list.

OAK CREEK FORMATION, SOUTH DAKOTA.—The Oak Creek beds were named by Troxell, in 1916,[3] who described a new equine, *Pliohippus lullianus*, as coming from this horizon. Osborn, in 1918, placed the Oak Creek in the Lower Pliocene as an approximate equivalent of the Valentine beds, as then known.

In discussing *Trilophodon giganteus*, in Volume I of the present Monograph, Osborn[4] says:

> Whereas on the lower slopes of the Keyapaha there occur true Miocene beds, near the tops of the hills along the river Keyapaha, the upper zone on the north side of the river (near Dallas) corresponds to the Pliocene quarry near Springview, and to the beds near by in which was found the type of *Peraceras troxelli*. This whole formation seems to be as recent as the Oak Creek beds in which was found the type of *Pliohippus lullianus*; and all indicate an *early Pliocene age*.

The Oak Creek beds are undoubtedly the same as certain phases of the Devil's Gulch deposits to the south, and of the Valentine beds to the southwest. The strata in which *Trilophodon giganteus* was found are probably

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[1] Barbour, E. H., 1914. Neb. Geol. Surv., IV, Pt. XI, p. 183. (Reprint from the University Studies.)

[2] Osborn, H. F., 1918. Equidæ of the Oligocene, Miocene, and Pliocene of North America, Mem. Amer. Mus. Nat. Hist., N. S., II, Pt. I, p. 29.

[3] Troxell, E. L., 1916. Amer. Journ. Sci., (4), XLII, pp. 335–348.

[4] Osborn, H. F., 1936. Vol. I of this Monograph, p. 305.

correlative with the middle horizon of the Valentine beds, the Burge of Stirton and McGrew, in which *Megabelodon lulli* was discovered. Certainly, in view of the very close relationship that undoubtedly exists between the two above species, the contemporaneity of the beds in which they were found seems to be well established.

PROBOSCIDEANS: See preceding list.

UPPER SNAKE CREEK BEDS, NORTHWESTERN NEBRASKA.—The Snake Creek beds were named by Matthew and Cook in 1909,[1] who at the time considered them as constituting a stratigraphic unit containing a single fauna. This fauna was regarded as of Lower Pliocene age, but it was noted that there were Miocene species contained in the assemblage and these were thought to be persistent primitive forms, contemporaneous with the Lower Pliocene mammals. Merriam suggested that the seeming mixture of Miocene and Pliocene mammals in a single fauna might, in fact, be due to the stratigraphic mixing of two faunas. This same view was expressed by Matthew in 1918, but it was not until 1924[2] that he was able to define the stratigraphic horizons in the Snake Creek area.

Matthew has shown quite clearly that there are three principal horizons and faunas in the Snake Creek region. These are:

Upper Snake Creek beds	Lower Pliocene	*Hipparion affine*
Lower Snake Creek beds	Upper Miocene	*Merychippus paniensis*
Sheep Creek beds	Middle Miocene	*Merychippus primus*

In addition Matthew distinguished a fourth zone, which he called the *Pliohippus leidyanus* zone. This horizon is later than the Upper Snake Creek in age, but since it has a very fragmentary fauna it has not received a definite geographic name.

Proboscideans have been described only from the Upper Snake Creek beds, so this horizon in the Sioux County series will be the only one considered at this place. According to Matthew:

> The principal upper Snake Creek fauna is clearly distinct and of Pliocene age, comparable with that of the Republican River beds. There are some forms in it suggesting a later stage, but they are rare and imperfectly known, and their evidence is not weighty. The correspondence, however, is by no means so close as that between Pawnee Creek and lower Snake Creek. There are few species in common. *Teleoceras fossiger*, so abundant in Republican River, is not positively recorded from the Snake Creek. The Equidæ correspond fairly well as to genera, but not as to species. *Ælurodon* is the characteristic canid in both faunas.

Subsequently, in 1930,[3] Matthew suggested that the Upper Snake Creek fauna is nearly equivalent to the Hemphill fauna: "The Upper Snake Creek fauna is also rather nearly equivalent [to the Hemphill], including some species more advanced, others somewhat less so."

Generally speaking, the Upper Snake Creek may be regarded as representative of the upper portion of the Lower Pliocene in North America, probably approaching related Middle Pliocene deposits and faunas in its broad relationships.

There has been some tendency among recent students to assign the Upper Snake Creek to the Middle or Upper Pliocene (Lugn, 1939) or to spread it over a large extent of the Pliocene (Stirton, 1936), this latter correlation being made upon the basis of an apparent mixing of faunas in this horizon.

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[1] Matthew, W. D., and Harold J. Cook, 1909. Bull. Amer. Mus. Nat. Hist., XXVI, Art. XXVII, p. 363.

[2] Matthew, W. D., 1924. Bull. Amer. Mus. Nat. Hist., L, pp. 72, 73.

[3] Matthew, W. D., and R. A. Stirton, 1930. Univ. Calif. Publ., Bull. Dept. Geol. Sci., XIX, No. 17, p. 367.

PROBOSCIDEANS:

Pliomastodon matthewi Osborn
Rhynchotherium anguirivale Osborn
Serridentinus anguirivalis Osborn
Serridentinus nebrascensis Osborn

REPUBLICAN RIVER FORMATION, SOUTHERN NEBRASKA AND NORTHERN KANSAS.—Simpson,[1] in 1933, made the following remarks about the Republican River beds.

> Lower Pliocene of northwestern Kansas, and, by extension, the corresponding stage of the Pliocene generally. The beds were extensively explored, especially for Marsh, and a large fauna is known, but there is no recent faunal or stratigraphic revision aside from such syntheses as that of Osborn and Matthew (1909) or references in describing individual fossils or faunas of similar age. It was generally placed in the 'Loup Fork,' 'Upper Loup Fork,' or 'Ogalalla,' but the more definite local name has been consistently applied by Matthew and is now generally accepted. Matthew (in Osborn and Matthew, 1909) tentatively considered it as slightly later than the 'Nebraska' (Valentine), later reaffirming this more positively (1924). Most recently, Matthew and Stirton (1930) have, in passing, suggested that the Republican River may be in part composite, with the beds on Sappa Creek and elsewhere to the southwest later than those on Driftwood Creek and to the north. They continue to place the fauna, as a whole, as younger than the Valentine, adding that it seems to be slightly older than their Goodnight-Hemphill (and hence equivalent to Clarendon).

Lugn,[2] in his review of the Tertiary of Nebraska, makes the following remarks about the Republican River beds:

> Considering all available evidence, it seems certain that the 'Republican River' represents a composite of lithologic and faunal horizons and should be abandoned as a stratigraphic term. Furthermore, many of the fossil finds were obtained from the unconsolidated sands and gravels in pits under the lower slopes of the valleys west and southwest of McCook, Nebraska. Some fossils have been collected from higher beds, from the 'mortar beds' along the sides of the valleys. The sand and gravels belong to the upper part of the Valentine formation, and the 'mortar beds' levels contain the *Krynitzkia* fossil seed zone and the lowermost part of the *Biorbia* fossil seed zone, all in the lower part of the Ash Hollow formation. Therefore, the fauna is much mixed, and also the described and published sections do not include the lower (Valentine) beds in the exposures.

PROBOSCIDEANS:

Blickotherium euhypodon (Cope)
Tetralophodon campester (Cope)
Serridentinus progressus Osborn
Trilophodon dinotherioides Andrews
Ocalientinus republicanus (Osborn)

WRAY BEDS, NORTHEASTERN COLORADO.—A considerable fauna from the Pliocene of northeastern Colorado, near Wray, was described by Cook[3] in 1922. The fossils came from a relatively thin deposit of stream channel sands and gravels, resting directly on the Cretaceous Pierre shales. Cook regarded the Wray beds, as he designated them, as being very closely related to the Upper Snake Creek of northwestern Nebraska.

> This fauna from Yuma County, Colorado, which we may designate for local convenience, the 'Wray' beds, is a very close equivalent of the upper phases of the Snake Creek beds, but shows certain faunal differences. This may be partly due to the fact that we do not know both faunas completely and have found different representatives from each. . . . Some of the species from these beds are closely related to forms described by Merriam from California and Nevada, from beds slightly older or younger or of equivalent age.

Stirton (1936) regards the Wray as being somewhat later in age than it was originally designated by Cook, placing it in the Middle Pliocene as about an equivalent of the Hemphill.

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[1] Simpson, G. G., 1933. Bull. Amer. Mus. Nat. Hist., LXVII, p. 107.

[2] Lugn, A. L., 1939. Bull. Geol. Soc. Amer., L, pp. 1272, 1273.

[3] Cook, H. J., 1922. Proc. Colorado Mus. Nat. Hist., IV, No. 2, p. 4.

PROBOSCIDEANS:

Amebelodon paladentatus (Cook)
Amebelodon hicksi (Cook)

SANTA FÉ BEDS, NEW MEXICO.—As has been shown above (p. 1492), the Santa Fé beds seemingly contain more than one horizon and cover a time range including the Upper Miocene and the Lower Pliocene. Frick's work of the past few years in the Santa Fé region has given evidence of a definite Pliocene *Hipparion* level within this series of sediments.

LOUP FORK AND OGALALLA.—"Loup Fork" is an old term in the literature dealing with the continental Tertiary of North America, established through the early writings of Leidy and Cope. From the beginning, its meaning has been obscure and uncertain, so that it has no value as a stratigraphic name—and at the present time is for the most part ignored. Applied to Upper Tertiary beds in Nebraska of Miocene and Pliocene age, it was frequently confused with the "Loup River" of Meek and Hayden—a term applied to beds, mainly of Pleistocene age, along the Loup River in central Nebraska. Fossils described by the earlier writers as of "Loup Fork" age may be from almost any horizon between the Middle Miocene and the Upper Pliocene.

The name "Ogallala" was used by Darton in 1905[1] to designate the Upper Tertiary of Nebraska above the "Arikaree," and as such it included the Upper Miocene, Lower and Middle Pliocene of the Great Plains region. At the present time the Nebraska Geological Survey regards the Ogallala as a valid group name, containing Pliocene formations in Nebraska.

CLARENDON BEDS, NORTHWESTERN TEXAS.—The Clarendon beds were named by Gidley[2] in 1903 for Upper Tertiary deposits to the north of Clarendon, Texas, which he considered as being correlative with the "Loup Fork" of the Great Plains. At the time these sediments were considered as coming within the Miocene.

> The main body of the beds consists for the most part of cross-bedded sands and sandstones intermixing more or less and cross-bedding with the clays. These channels all take a direction nearly east and west, or approximately the same as that of the streams draining the country at the present time. Some of them are traceable for long distances. It is in these peculiar beds of sandy clays that all the fossils of this region occur.

According to Gidley, there are about 400 feet of thickness represented in the Clarendon horizon at its typical outcrops, and the fossiliferous stratum lies at the top of the section. Gidley included the Goodnight beds, as named by Cummins,[3] within the Clarendon, advancing a long argument to show why these Goodnight sediments are not separable. Subsequent data show that the Goodnight beds are distinct from and later than the Clarendon.

The Clarendon fauna is now generally recognized as representing a distinct phase in the Pliocene history of North America, older than the Hemphill-Goodnight and about equivalent to the Lower Pliocene of the Great Plains area.

"The typical Clarendon species are nearly allied to those from Hemphill, although more primitive, and they may well have been comparatively direct ancestral stages or mutations." Matthew, W. D., and R. A. Stirton, (*op. cit.*, 1930, p. 386).

PROBOSCIDEANS:

Serridentinus productus (Cope)
Serridentinus serridens (Cope)
Serridentinus serridens cimarronis (Cope)
Serbelodon praecursor (Cope)
Tetralophodon fricki Osborn

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[1] Darton, N. H., 1905. U. S. Geol. Surv. Profess. Paper No. 32, p. 178.

[2] Gidley, J. W., 1903. Bull. Amer. Mus. Nat. Hist., XIX, p. 633.

[3] Cummins, W. F., 1893. Texas Geol. Surv., Fourth Annual Report, Pt. I, pp. 201, 203.

RICARDO FORMATION, MOHAVE DESERT, CALIFORNIA.—The Ricardo beds are located in the southwestern corner of the Great Basin area, not far from the region where the typical Barstow Miocene sediments are exposed. Merriam, who studied both the Ricardo and the Barstow faunas, early recognized the fact that the former assemblage is of later age than the latter because of an almost complete specific separation between them and consequently he considered the relationships of the more advanced Ricardo fauna to be with certain Pliocene deposits of the Great Basin and the Plains regions. The Ricardo, typified by *Hipparion* and *Pliohippus*, is definitely of Lower Pliocene age, and is probably older than the Thousand Creek or the Rattlesnake deposits of the Great Basin region, since the Ricardo species, particularly among the Equidæ, are slightly more primitive than the forms from the Rattlesnake and Thousand Creek.

In its general age relationships the Ricardo, therefore, would seem to be more or less comparable with the Valentine and Clarendon of the Great Plains region.

PROBOSCIDEANS:

Trilophodon sp.
Serbelodon burnhami Osborn

4. THE MIDDLE PLIOCENE: HEMPHILLIAN

THOUSAND CREEK BEDS, NORTHWESTERN NEVADA.—The Thousand Creek beds, named from Thousand Creek in the northwestern corner of Nevada, consist of an alternation of tuffs, ashes, sands, gravels, and ancient soil accumulations. From these beds a distinctive Pliocene fauna has been described by Merriam.

As Merriam has shown, the Thousand Creek fauna contains advanced Tertiary carnivores, rodents, horses, camelids, and antilocaprids, yet in spite of the numerous progressive elements in the fauna, it must be regarded as a purely Pliocene assemblage. That is, none of the Thousand Creek mammals would warrant the inclusion of the beds within the Pleistocene. It might be mentioned, however, that Pleistocene terraces containing mammalian remains are found contiguous to the Thousand Creek exposures, and due to the difficulty of separating the sediments of the two epochs there is a possibility of mixing the faunal elements in making collections in this area.

The Thousand Creek beds are definitely much later than the Virgin Valley beds, which are exposed nearby, and are more nearly comparable to the Rattlesnake, and especially to the Upper Snake Creek of Nebraska. Merriam[1] made the following remarks with regard to the Thousand Creek beds:

> In so far as correlation with the American mammalian faunas is concerned the Thousand Creek fauna would seem necessarily to take a place later than that of the Snake Creek [Upper Snake Creek] and earlier than that of the Blanco.

In 1930 Matthew and Stirton suggested that the Thousand Creek fauna might be more or less equivalent to the Hemphill fauna.

PROBOSCIDEANS:

"*Tetrabelodon* ? sp."
Miomastodon merriami Osborn
Pliomastodon nevadanus Stock

MOUNT EDEN BEDS, SOUTHERN CALIFORNIA.—The Eden beds were named by Frick[2] in 1921 to distinguish a series of Lower Pliocene sediments exposed in the San Timoteo badlands in southern California. In his original

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[1] Merriam, J. C., 1911. Univ. Calif. Publ., Bull. Dept. Geol. Sci., VI, No. 11, p. 217.
[2] Frick, Childs, 1921. Univ. Calif. Publ., Bull. Dept. Geol. Sci., XII, pp. 283–288.

publication Frick placed the Eden beds in the middle portion of the Pliocene, as correlative with the Middle Etchegoin, Rattlesnake, and Snake Creek (Upper), but subsequently (1933) he stated that the Eden beds are of uppermost Pliocene age.

That the Eden beds are fairly well advanced in the Pliocene is made evident by certain progressive forms present in the faunal assemblage. These are particularly, two sloths, *Nothrotherium* or *Pronothrotherium* and *Megalonyx*, a sabre-toothed cat referred to *Smilodon*, a bear, *Hyænarctos*, and the advanced peccary, *Platygonus*. On the other hand there are many typical Lower Pliocene forms in the Eden fauna, such as *Pliohippus* among the horses, *Prosthennops*, *Pliauchenia* and *Procamelus*, *Merycodus*, and *Trilophodon*. Frick has called attention to the absence of *Hipparion* in the Eden fauna, which might argue for a relatively advanced age for the assemblage. Likewise, rhinoceroses are absent in this faunal assemblage as they are in post-mid-Pliocene deposits of North America, but the same is true of the Ricardo fauna, so that this line of evidence must not be accorded too much importance in the consideration of age relationships.

All in all, it would seem probable that the Eden fauna is a moderately advanced Pliocene assemblage, containing many progressive types of mammals that foreshadow the coming of the Pleistocene in North America, but the absence of truly advanced horses such as those characterizing the Hagerman of Idaho, would seem to preclude the assignment of the Eden to the uppermost Pliocene.

The Eden, as originally named by Frick, has been changed to "Mount Eden" by Fraser,[1] the name "Eden" being preoccupied by a Paleozoic formation.

PROBOSCIDEANS:

Rhynchotherium shepardi edense (Frick)
Cordillerion edensis Osborn

ETCHEGOIN, SOUTHERN CALIFORNIA.—Merriam recognized three horizons or zones in the Etchegoin area, on the western border of the San Joaquin Valley, which he named as follows:

Pliohippus proversus zone
Pliohippus coalingensis zone
?*Hipparion* zone.

Generally speaking these three zones cover a period of time extending from the upper part of the Lower Pliocene, comparable to the Rattlesnake or Upper Snake Creek, to the Upper Pliocene, comparable to the Blanco. Fragmentary mastodont remains have been found in the upper portion of the Etchegoin.

PROBOSCIDEANS:

"*Mastodon*"
Pliomastodon vexillarius Matthew

5. THE UPPER PLIOCENE: BLANCAN

BLANCO FORMATION, NORTHWESTERN TEXAS.—The Blanco beds have for many years been regarded as representative of one of the later phases of the Pliocene in North America. These deposits were first studied and described by Cummins and by Cope in 1893, the former author reporting on their stratigraphic relationships and the latter describing the contained fauna. Subsequently (1903) Gidley redescribed the Blanco, limiting its horizontal and vertical extent as compared with the original descriptions of Cummins and Cope.

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[1] Fraser, D. M., 1931. Mining in Calif., XXVII, No. 4, pp. 511–514.

According to Gidley, the Blanco beds consist of stream channel deposits—sands, clays, and diatomaceous earth—cut into the older Miocene sediments, and exposed in a relatively narrow belt trending in a northwesterly to southeasterly direction along either side of the Blanco River.

The Blanco fauna, though small, is well known due to the writings of Cope, Osborn, and Gidley, and therefore has become well established as one of the most characteristic later Pliocene faunas of America. It has always been recognized as of Pliocene age, although the earlier authors did not specify its exact position within the Pliocene. In 1909, however, Matthew definitely placed it as of Middle Pliocene age—a correlation that has been generally followed in subsequent publications.

Recent evidence favors the idea that the Blanco might be even later than Middle Pliocene in its age. Thus, Gazin, who has described the uppermost Pliocene Hagerman beds of Idaho, regards the fauna of these sediments as showing many close relationships to the Blanco fauna. Illustrative of the close relationships between the Blanco and the Hagerman, there might be mentioned the very advanced monodactyl horse *Plesippus*, which occurs in both formations. *Plesippus* is certainly directly ancestral to *Equus*, and its first appearance cannot antedate the Pliocene-Pleistocene transition by any great length of time.

PROBOSCIDEANS:

Rhynchotherium falconeri Osborn
Serbelodon praecursor (Cope)
Stegomastodon mirificus (Leidy)
Stegomastodon successor (Cope)
Stegomastodon texanus Osborn

SAN PEDRO VALLEY BEDS, ARIZONA.—On either side of the San Pedro valley, in southern Arizona, are fossiliferous localities at which Upper Pliocene vertebrates have been found. Gidley, who has described the mammals from the San Pedro deposits, has shown that the sediments, as interpreted by Bryan, consist of a considerable thickness of sand, conglomerate, and clay valley fill, deformed to a certain extent by subsequent diastrophic movements.

On the west side of the valley fossils were found near the town of Benson, while to the east the fossiliferous deposits are exposed on the Curtis Flats, near Curtis Ranch. The names Benson and Curtis Ranch have been assigned accordingly to the faunas from the two areas.

Although the beds at the Benson and Curtis Ranch localities seem to be much the same stratigraphically, the faunas from the two areas show decided differences. From the Benson horizon are *Cordillerion bensonensis*, *Neohipparion*, *Pliohippus*, and *Merycodus*, while the mammalian assemblage from Curtis Ranch, containing as it does such forms as *Stegomastodon arizonæ*, *Glyptotherium*, and *Plesippus*, would seem to be definitely later in age than the Benson fauna. Gidley[1] considered the Benson fauna to be fairly closely related to the Blanco fauna—perhaps somewhat earlier in age than the Texas assemblage, while he placed the Curtis Flats fauna in the Upper Pliocene as definitely later than the Blanco fauna.

> The bones occur for the most part in relatively small patches or layers of greenish tuffaceous clay, which, according to Bryan, interfinger on one side with arkosic gravel and conglomerate typical of deposition on alluvial slopes and on the other with the lake beds. This position seems to confirm Bryan's view that these bone-bearing patches of greenish clay represent the marginal and fresh-water springs that are characteristic of the borders of salt lakes in such basins. The localities thus probably constituted the chief watering places for the animals of the region, and here, naturally, occur their fossil remains.

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[1] Gidley, J. W., 1926. U. S. Geol. Surv., Profess. Paper 140–B, p. 84.

> . . . although the general process of sedimentation in the San Pedro basin was continuous, the marginal springs of the two localities may have belonged to lakes of slightly different levels. Thus the time interval between the active existence of the watering places on the west side of the salt lakes at the Benson locality and those on the east side of the lakes at Curtis Flats may well have been long.
>
> During this interval the faunas changed, but it does not necessarily follow that this change was greatly affected by evolution in this locality, for, although considered long as measured in years, the interval was probably in a geologic sense relatively short, and it may well be that the entire change was accomplished by migration. . . . though many of the species of the Curtis Flats locality are closely related to the species found in the Benson locality, the former are not descendant forms of the latter.

More recently, Dr. Gazin has expressed his opinion in conversations with the writer that the San Pedro beds at Curtis Ranch are of Lower Pleistocene, rather than of Pliocene age. He would regard the Benson deposits as approximately equivalent in age to the Blanco of Texas, a view that is coming to be generally accepted.

PROBOSCIDEANS:

Curtis Ranch	*Stegomastodon arizonæ* Gidley
Benson	*Cordillerion bensonensis* (Gidley)

HAGERMAN FORMATION, SOUTHWESTERN IDAHO.—The name "Idaho" has been used as a vague term indicative of a series of deposits of Upper Tertiary and Pleistocene age in southern Idaho. That the name is rather inclusive was recognized by Merriam in 1917, in his study of the Pliocene mammalian faunas of western United States. Certainly, the fauna, as he lists it, shows a mixture of Pliocene and Pleistocene types.

In recent years certain parts of the Idaho beds have been closely studied by Gazin,[1] who has shown that the deposits from which his collections were made are definitely of very late Pliocene age. These beds have been named by Gazin the Hagerman, or Hagerman lake beds, and are representative of the uppermost Pliocene of North America. They are characterized by an advanced horse, *Plesippus*, which is certainly the direct ancestor of the genus *Equus*. According to Gazin, the Hagerman beds are probably correlative with the Blanco of Texas.

Gazin states that the Hagerman lake beds, as he defines them, are probably somewhat older than other exposures identified as the Idaho, particularly at Sinker Creek and certain other localities. Merriam mentions that *Stegomastodon mirificus*, which he lists as from the Idaho formation, came from Sinker Creek. He then goes on to say that this is a Pliocene type of proboscidean. It would seem to be adequately proven that the type of *Stegomastodon mirificus* from Nebraska comes from beds definitely of Pleistocene age (see Lugn and Schultz, 1934). Therefore it is very possible that the portion of the Idaho beds from which the above species was obtained is of Pleistocene age, and later than the Hagerman, as was surmised by Gazin.

Gazin, in comparing the Hagerman beds with the Blanco, says that: "The Blanco shows a greater wealth of Proboscidea but fewer members of the microfauna."

At the present time proboscideans have not been described from the Hagerman beds.

PROBOSCIDEAN (Idaho): *Stegomastodon mirificus* (Leidy).

TEHAMA FORMATION, SACRAMENTO VALLEY, CALIFORNIA.—The Tehama formation, described by Russell and VanderHoof,[2] is a thick series of tuffaceous greenish gray to buff sandy clays, containing intercalated cross-bedded sands and gravels. A small fauna was discovered in this formation, which would seem to be indicative of a late Pliocene age, for it contains such advanced Tertiary genera as *Hyænognathus*, *Plesippus*, ?*Antilocapra*, *Odocoileus*, *Stegomastodon*, and a megalonychid sloth.

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[1] Gazin, C. L., 1936. Proc. U. S. Nat. Mus., LXXXIII, No. 2985, p. 287.

[2] VanderHoof, V. L., 1933. Amer. Journ. Sci., (5), XXV, p. 384.

> The horses are more advanced than those in the upper Etchegoin (*Plesippus proversus*) stage of evolution and there is an influx of forms which appear to be the forerunners of those reaching their maximum development in the lower Pleistocene. From this faunal evidence, the Tehama formation may be regarded as being uppermost Pliocene in age.

Proboscidean: *Stegomastodon* cf. *arizonæ* Gidley.

6. THE PLIOCENE OF MEXICO

The first proboscideans that reached Mexico would seem to have appeared in that region in Lower Pliocene times. These early forms, referred by Freudenberg to two species, *Trilophodon dinotherioides* and *Serridentinus serridens*, were seemingly contemporaneous with a fauna of general Lower or Middle Pliocene affinities.

Generally speaking, the proboscideans of Mexico range from the Pliocene throughout the extent of the Pleistocene. Whether their history, as well as that of the contemporaneous mammals, is a continuous story in this region, or whether it is a record broken by considerable gaps (particularly in Upper Pliocene times) is a point that cannot at the present time be definitely decided. Freudenberg[1] (1922) considered that there were, broadly speaking, just two mammalian faunas in Mexico. He distinguished an earlier one of Lower Pliocene age, which in fact may range into Middle Pliocene times, and a later one covering the extent of the Pleistocene. The Pleistocene "fauna" Freudenberg thought might be divisible into three successive mammalian assemblages, but the evidence for any such separation is admittedly uncertain.

> Es bleibt also bei zwei Säugetier-Faunen in Mexiko, einer unterpliocänen und einer diluvialen sensu lato. Die erstere ist wohl einer einzigen kürzeren Epoche zuzuweisen. Sie ist reich an Pferdeformen, die sämtlich auf der *Hipparion*-stufe stehen. Demgegenüber enthalten die Beckensedimente des Hochlandes nur die Gatung *Equus*, als Vertreter des Pferdestammes.

Lower and Middle Pliocene.—The Pliocene fauna described by Freudenberg is found in the states of Vera Cruz and Hidalgo, in freshwater and lake deposits in the vicinity of Zacualtipan and Tehuichila. In these sediments is a mastodont referred to *Serridentinus serridens*, an *Hyænarctos*, peccary, and *Procamelus*, as well as *Hipparion peninsulatum*, *Hipparion rectidens*, and *Protohippus castilloi*.

This mammalian assemblage is most certainly of Pliocene age, probably later than "upper Miocene or lower Pliocene" as it was thought to be by Freudenberg. The presence in it of *Serridentinus serridens* would point towards an approximate correlation with the Lower Pliocene Clarendon of Texas. In this connection it is to be noted that Freudenberg has also described material which he referred to *Trilophodon dinotherioides*, a Lower Pliocene form the type of which is from the Republican River beds of Kansas.

Proboscideans:

Serridentinus serridens (Cope)
Trilophodon dinotherioides (Andrews)

Middle and Upper Pliocene.—It is very difficult to be certain as to the presence of late Pliocene deposits in central Mexico. Two species of rhynchotheres, described by Osborn, may be indicative of sediments geologically younger than those in which the fauna listed by Freudenberg occurs. Osborn, in Volume I of this Monograph, considered these forms as questionably of Upper Pliocene age. It is, of course, quite possible that *Rhynchotherium tlascalæ* and *Rhynchotherium browni* are of Upper Pliocene affinities; certainly they are later than the lowest Pliocene of North America. On the other hand, there is no evidence against their contemporaneity with the Vera Cruz-Hidalgo fauna, which is of late Lower or Middle Pliocene age.

Proboscideans:

Rhynchotherium tlascalae Osborn
Rhynchotherium browni Osborn } These species may be from the Lower or Middle Pliocene

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[1] Freudenberg, W., 1922. Geol. und Pal. Abh., N. Folge, Band XIV, Heft III, p. 104.

7. PROBOSCIDEANS FROM UNDETERMINED LEVELS IN THE MIOCENE AND PLIOCENE OF NORTH AMERICA

A number of proboscideans from the Pliocene of North America have been described from horizons or levels that are at the present time either unknown or not definitely determined. In some cases the exact age of the types will never be known, for the species were described many years ago and precise data as to their levels or localities are not to be had. On the other hand, certain forms are known to have been found at definite localities and at well-determined geologic positions, but the uncertain knowledge as to the exact geological relationships of the beds within which these types were found makes their stratigraphic position for the time being somewhat uncertain. The species falling into these categories will be discussed below.

Trilophodon ligoniferus (Cope and Matthew)

This species is known from a type that was found in the Black Hills, according to Cope's original record. The horizon and locality for this species must be regarded as uncertain, to say the least.

Torynobelodon loomisi Barbour

In the type description, Barbour states that this form was found in "Sand Canyon, just east of Indian Hill, two and one-half miles southwest of Republican City, Harlan County, Nebraska, the formation being Late Pliocene to Early Pleistocene."

Amebelodon fricki Barbour

Amebelodon fricki was discovered near Freedom, Frontier County, Nebraska, in the southwestern portion of the state, some miles to the north of the Republican River. Barbour regarded its age as "late Pliocene or possibly early Pleistocene," on the basis of his observations of the type locality.

Amebelodon sinclairi Barbour

The type of this species was found only a few hundred yards distant from the place where *Amebelodon fricki* was discovered. Therefore it is very probable that it is contemporaneous with the above species in geologic age.

Gnathabelodon thorpei Barbour and Sternberg

According to Barbour,[1] "Professor Maxim K. Elias, of the University of Kansas, who has made special studies of Trego County, when consulted, pronounced this bed Late Pliocene in all probability, although he had not seen a section at this particular gravel pit, and based his opinion on neighboring exposures."

In a recent communication, Dr. C. Bertrand Schultz of the University of Nebraska tells me that the above four species "all come from deposits which appear to be late Pliocene in age. Perhaps it would be better to say 'middle to late Pliocene.' They do come from the upper part of the Ogallala."

Rhynchotherium shepardi (Leidy)

The horizon of the type of this species cannot be positively determined on the basis of evidence now at hand. The opinions of Stock and Buwalda with regard to this question are quoted on page 487 of Volume I of this Monograph. It might be pointed out that a subspecies described by Frick, namely, *Rhynchotherium shepardi edense*, comes from the Mount Eden formation of about Middle Pliocene age.

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[1] Barbour, E. H., and George F. Sternberg, 1935. Bull. Neb. State Mus., I, Bull. 42, p. 396.

Cordillerion orarius (Hay)
Cordillerion defloccatus (Hay)

These species were described from teeth and jaws found on the west bank of the Aransas River, near Sinton, Texas. Hay, who described them, evidently regarded the age as Lower Pleistocene. In Volume I of this Monograph Professor Osborn has assigned them provisionally to the Pliocene.

Stegomastodon priestleyi (Hay and Cook)

Although found in a deposit of Pleistocene gravels, the type of this species is possibly a derived fossil, of Upper Pliocene age.

Trilophodon obscurus (Leidy)

The type of *Trilophodon obscurus* was found at Greensboro, Caroline County, Maryland, which would mean that the probabilities are that it was found in the Choptank formation of Miocene age. The marine invertebrate fauna would seem to indicate that the Choptank is of approximately Middle Miocene age. (See Volume I of this Monograph, page 285.)

Ocalientinus obliquidens (Osborn)

The phosphate beds, near Charleston, South Carolina, are definitely of Pleistocene age, as is shown by the presence in them of numerous teeth referable to *Parelephas columbi.* It is notable, however, that the type tooth of *Ocalientinus obliquidens* is structurally a Pliocene type of mastodont. Since redeposition is common in the phosphate beds, and since remanié fossils of an earlier age are often found in younger sediments, the probabilities are strongly in favor of the species under consideration being of Upper Pliocene age.

Ocalientinus emmonsi (Hay)

It is very likely that the age of this form is similar to that of *Ocalientinus obliquidens,* discussed above. That is, it is an Upper Tertiary specimen redeposited in a Pleistocene sediment. Hay regarded this species as questionably of Pleistocene age.

8. NORTH AMERICAN TERTIARY HORIZONS CONTAINING FRAGMENTARY PROBOSCIDEAN REMAINS

A number of important mammal-bearing horizons of Upper Tertiary age have not been included in the foregoing discussion, since they contain but fragmentary remains of proboscideans which have not been specifically, and, for the most part, not even generically identified. Considering, however, the fact that there are indications of proboscideans in these horizons—even though the evidence is largely incomplete—it may be well to discuss very briefly these mammal-bearing sediments.

Wood Mountain Gravels, Southern Saskatchewan.—Described by Sternberg,[1] who records a very scanty and fragmentary fauna, including an indeterminate mastodont. The age is either Middle or Upper Miocene.

Madison Valley Beds, Montana. Originally described by Douglass, as the "Loup Fork of Madison Valley, Montana." The fauna indicates a close relationship in age to the Barstow and to the lower portions of the Santa Fé—hence of Upper Miocene affinities. Proboscidean: a "mastodon."

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[1] Sternberg, C. M., 1930. Trans. Roy. Soc. Canada, (3), XXIV, Sec. 4, pp. 29 and 30.

SKULL SPRINGS BEDS, SOUTHEASTERN OREGON.—Gazin, who described the fauna from this horizon, compared it with the faunas of Virgin Valley, Mascall, Payette, Lower Snake Creek, and Pawnee. The evidence therefore indicates an Upper Miocene age. A mastodont is known from this series.

CEDAR MOUNTAIN BEDS, WESTERN NEVADA.—Described by Merriam and compared with the Barstow and Santa Fé. Stirton divided the Cedar Mountain into two horizons, one of Middle Miocene, the other of Lower Pliocene age. "Tetrabelodon" is known from this series.

CUYAMA FORMATION, SOUTHERN CALIFORNIA.—This horizon with its contained fauna has been carefully studied by Gazin, who regards it as related in a general way to the Mint Canyon and to the Barstow beds, especially the latter. Gazin lists "mastodont sp." as from the Cuyama, now designated as the Quatal Canyon.

NORTH COALINGA BEDS, CALIFORNIA.—One of a series of sediments north of Los Angeles. Considered by Merriam, on the basis of a scanty fauna, to be related to the Mascall and the Virgin Valley; consequently of Middle or Upper Miocene age. *"Tetrabelodon"*(?)sp. is recorded.

MINT CANYON BEDS, CALIFORNIA.—An important mammal-bearing horizon, described by Maxson in 1930. The age of the Mint Canyon has been variously debated. Considered by Maxson as of Upper Miocene age perhaps later than the Barstow. Stirton, on the other hand, regards it as of Lower Pliocene age, closely related to the Ricardo. Perhaps this is a "boundary-line" horizon, representing the transition from the uppermost Miocene into the lowermost Pliocene. *Trilophodon* sp. is known from this horizon.

TRUCKEE BEDS, WESTERN NEVADA.—The back portion of a third molar from these sediments was described by Buwalda as *Tetrabelodon* (?), and on the basis of this specimen the beds were placed in the Upper Tertiary. The tooth appears to be referable to the genus *Miomastodon*; the age is probably Upper Miocene.

HEMPHILL BEDS, TEXAS.—An important horizon, containing a fauna of about Middle Pliocene age. Matthew and Stirton, who studied the Hemphill fauna, decided that it is somewhat later in age than the Clarendon but earlier than the Blanco. It is equivalent to the Goodnight assemblage described many years ago by Cope. The only known proboscidean is a fragment questionably referred to *Rhynchotherium.*

OPTIMA FORMATION, OKLAHOMA.—Described by Hesse, in 1936.[1] This author regards it as closely related to the Hemphill of Texas, both as to its fauna and as to its age. "A lower molar of a Proboscidean, the only indication of this family at Optima, was determined by the late W. D. Matthew as *Miomastodon.*"

RATTLESNAKE FORMATION, EASTERN OREGON.—Described in detail by Merriam, Stock, and Moody, in 1925.[2] These authors regard it as later than the Ricardo, and rather closely related to the Thousand Creek. Therefore of Middle Pliocene age. "Proboscidean remains" are recorded from the Rattlesnake.

CHANAC FORMATION, SOUTHERN CALIFORNIA.—Described by Merriam as closely related to the Ricardo and to the Middle Etchegoin of the Pacific Coast area. *Tetrabelodon* (?) sp. is known from this horizon.

ORINDAN AND SIESTAN FORMATIONS, BERKELEY HILLS; PINOLE TUFF, SAN PABLO BAY, CALIFORNIA.—These formations, in the San Francisco area, are closely related to each other. The scanty fossils may be compared with those of the Ricardo. *Tetrabelodon* (?) sp. has been recorded from the Orindan.

The formations discussed in the preceding pages of this section have been listed in detail by Wilmarth (1938),[3] to which the reader is referred.

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[1] Hesse, C. J., 1936. Univ. Calif. Publ., Bull. Dept. Geol. Sci., XXIV, No. 3, p. 66.

[2] Merriam, John C., Chester Stock, and C. L. Moody, 1925. Contributions to Palaeontology, III, Carnegie Inst. Washington, No. 347, pp. 43–92.

[3] Wilmarth, M. Grace, 1938. U. S. Geol. Surv. Bull. 896, Pts. 1 and 2.

9. THE PLEISTOCENE OF NORTH AMERICA

As in Eurasia, the Pleistocene in North America may be regarded as having commenced with the extension of the first continental glacier from the North, and with the appearance and spread of certain new and advanced types of mamals in all parts of the continent. Those mammals particularly diagnostic of the beginning of the Pleistocene in North America are the modern horse, *Equus*, the mammoth, *Archidiskodon*, and cattle, *Bison*. To these three types there may be added the modern camelids, as exemplified in the New World by *Camelops*. Of the foregoing enumerated forms, the first and last were autochthonous and their first appearance marks the actual beginning of Pleistocene times in the North American region. The other two forms, being immigrants from Asia, may not have arrived in North America until after the opening of the Pleistocene, but if such is the case, the time lag was not great.

An important clue to the changes that were taking place with the evolution of an Upper Pliocene fauna into one of Pleistocene aspects is to be seen in the evidence of the horse, *Plesippus*, characteristic of the uppermost Tertiary horizons of North America. This equid is in most of its characters much closer to the true *Equus* of the Pleistocene than it is to any other Pliocene horses, and for this reason it may be regarded as immediately ancestral to the horses of the Pleistocene. Thus we see in the appearance of *Plesippus* a near approach to the Pleistocene similar and parallel to that signalized in the Old World by the appearance of primitive, ancestral types of *Archidiskodon* in horizons of uppermost Pliocene age.

In North America, as in Europe and Asia, the Pleistocene may be divided according to the advance and retreat of continental glaciers. In Europe there is a difference of opinion as to the presence of three or four glacial advances during Pleistocene times, according to the manner in which the Pliocene-Pleistocene boundary is limited. In America, on the other hand, the argument is concerned with the presence of four or five glacial advances. The general trend of opinion is to recognize five glaciations in North America, separated from each other by four interglacial stages. But some students of Pleistocene chronology in the New World would limit the glaciations in North America to four, regarding one of the generally recognized glacial advances (Iowan) as a minor substage of the larger fourth glaciation.

The subdivision of the Pleistocene in North America has been arranged by Kay,[1] one of the outstanding authorities on this subject, as follows:

EPOCH	AGE
Eldoran	(Recent)* Wisconsin glacial Peorian interglacial Iowan glacial
Centralian	Sangamon interglacial Illinoian glacial
Ottumwan	Yarmouth interglacial Kansan glacial
Grandian	Aftonian interglacial Nebraskan glacial

*Included by Kay in the Pleistocene.

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[1] Kay, George F., 1931. Bull. Geol. Soc. Amer., XLII, pp. 425–466.

The question which concerns us at this place is, of course, the appearance, sequence, and extinction of mammals within the Pleistocene of North America. This subject has been variously investigated by numerous workers over a long period of years, with the result that two generally opposing views have been formulated. One of these concepts as to the relationships of the Pleistocene mammals of North America, developed particularly by Osborn, and elaborated in a much modified form by Hay, is that there was a succession of faunas within the Quaternary of North America distinguished by the gradual and progressive extinction of many mammalian types, and perhaps to a lesser extent by the influx of other types, as a result of changing environmental and climatic factors. The other theory, which has grown up in recent years among the later students of Pleistocene mammals, and which has been particularly well set forth by Romer, regards the Pleistocene mammals of North America as comprising essentially a unit fauna, appearing for the most part at the beginning of the period and persisting throughout its extent, to continue into Recent times. Such extinctions as have occurred, and it is largely by these that the Pleistocene fauna of North America can be distinguished from that of Recent times, took place for the most part at the "end" of Pleistocene times, which was at no very great date of geological antiquity.

Perhaps Cope was the first author to recognize a distinction of faunas within the Pleistocene, when he designated an *Equus* fauna characteristic of the western plains and a *Megalonyx* fauna typical of the eastern woodlands.

Osborn,[1] in 1910, recognized four faunal "zones" within the Pleistocene, basing them in part upon their supposed sequence in time and in part upon their geographic facies. In designating these divisions he admitted that the "lines of separation between these zones are by no means clearly defined at present, and will depend in the future upon the more accurate definition of species." They may be listed as follows:

IV. *Cervus* zone. Prehistoric fauna of the forests of eastern and western North America. Mammals entirely of modern types; "Pleistocene" forms extinct.

III. *Ovibos-Rangifer* zone. Plains and forest faunas. A "cold" fauna accompanying the last glaciation, and dominated by muskoxen, reindeer, American mastodon, and woolly mammoth.

II. *Megalonyx* zone. Temperate faunas of middle and late Pleistocene times. Some primitive early Pleistocene forms still survive, while certain of the "late" mammals, such as *Rangifer*, have not as yet appeared.

I. *Equus-Mylodon* zone. Lower and Middle Pleistocene faunas of the Plains regions. Many types surviving from Pliocene times. Certain advanced forms, such as true Eurasiatic deer, bear, mountain goats, sheep or bison have not as yet appeared.

"These zones are not sharply distinguishable chronologically at present; they partly overlap and are partly successive."

Hay,[2] who devoted a considerable portion of his life to the study of Pleistocene mammals in North America, also recognized a sequence of faunas dependent upon gradual extinction throughout the Pleistocene. But his theory as to mammalian succession within the Pleistocene period was widely divergent from that held by Osborn. According to Hay, there was an early Pleistocene fauna, usually designated by him as of Aftonian age, containing many genera of mammals, such as *Archidiskodon*, *Equus*, *Camelops*, and the like, which became extinct at the end

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[1] Osborn, H. F., 1910. "The Age of Mammals," p. 438, and succeeding pages.

[2] Hay, O. P., 1925. Journ. Wash. Acad. Sci., XV, No. 6, p. 128.

of "Lower" Pleistocene times. Thus he envisaged a sharp break between the Lower Pleistocene and succeeding times, due to the wide-spread elimination of forms with the advent of the second glaciation. Subsequently, during Middle and Upper Pleistocene times there were still more extinctions, so that only a few genera such as *Mastodon*, *Mammonteus*, and *Megalonyx* persisted to the end of the Quaternary.

> We know little from actual discovery about the vertebrate life of the first glacial stage, the Nebraskan; but it must have been made up of some species from South America, some from Asia, but principally of native species remaining over from the Pliocene. . . . The first glacial stage. . . . almost annihilated the descendants of the Pliocene mammals, not inured to a severe climate. The second glacial stage had nearly wiped out the South American contingent. The survivors were mostly of northern Asiatic origin, hardened to an inclement environment. *Elephas imperator* had probably reached North America from southern Asia and was a weakling. The faunal change that occurred during the first three stages appears to have been more profound than that of the rest of the Pleistocene. Hence I believe that the division of the Pleistocene into Earlier and Later expresses best the history of the North American vertebrate animals during the Pleistocene.
>
> Later Pleistocene (Yarmouth—Wisconsin)
> "Few edentates, few or no horses, no camels, no *Elephas imperator*, one or two mastodons, fewer large cats."
>
> Earlier Pleistocene (Nebraskan—Kansan)
> "Many edentates, many horses, many camels, *Elephas imperator*, several mastodons, many large cats."

Among the students who have been working in recent years upon the question of Pleistocene mammals in North America, there is strong support for the idea that the characteristic Quaternary fauna appeared at the beginning of that period, to persist throughout its extent, finally to be decimated by a wide-spread series of extinctions at a relatively recent date—seemingly *after* the entrance of man into the New World. According to the proponents of this view, there was very little gradual and progressive extinction during the extent of the Pleistocene.

This theory, although at first sight seemingly less logical than the theory of gradual extinctions occurring during the Pleistocene, is nevertheless based upon very strong evidence—the result of recent careful stratigraphic and palæontologic work in the field. And with the passing of time, each successive year of field work strengthens the theory of a continuous Pleistocene fauna. Hay's thesis depended upon his assumption that many of the extinct types of Pleistocene mammals in North America did not survive long after their period of greatest development, namely, the Aftonian or first interglacial period. Yet most of the supposed Aftonian faunas, cited by Hay in support of this theory, cannot be definitely proven as of Aftonian age, while as a result of careful work carried on in recent years, many of them can be definitely proven as later than Aftonian in age. Moreover, the work of recent years in the southwestern United States in caverns, and in such valley deposits as that at Clovis, has proven beyond doubt that practically all of the mammals supposed by Hay to be diagnostic of his Earlier Pleistocene were still living at a relatively recent date, and were associated with early man in America.

In Romer's[1] extremely valuable paper on this subject, the conclusions are summarized as follows:

> A hypothesis which implies that practically all the important fossil forms had existed until a comparatively Recent date and then become extinct in a geologically short period of time had seemed equally improbable to the writer; and yet it is to such a conclusion that a study of the evidence leads. A considerable proportion of the large Pleistocene forms now extinct in this country appear to have existed until post-glacial or sub-Recent time in either the north-east or south-west . . . . The overwhelming trend of the evidence is that very little extinction appears to have taken place among mammals during the Pleistocene proper, and that a vast amount of extinction, reducing the fauna to its present impoverished condition, has taken place in a comparatively short period which presumably cannot have had its initiation more than, roughly, 20,000 years or so ago.

Of course the idea of a continuous Pleistocene fauna in North America cannot be expressed as an unqualified fact. Undoubtedly there were some exceptions to the general rule that the Pleistocene mammals in this region continued from the beginning until the end of the period. For instance, there is every reason to believe upon the

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[1] Romer, A. S., 1933. Article II in "The American Aborigines." Edited by Diamond Jenness. Univ. Toronto Press, pp. 75, 76.

basis of available evidence, that certain immigrant forms, particularly some of the ground sloths and the capybara from South America and the woolly mammoth and the bisons from Eurasia, did not reach this continent until after the opening of Pleistocene times. And again certain forms, notably *Stegomastodon*, failed to persist into late Pleistocene times. But except for these few types, all of the Pleistocene mammals in North America lived from the beginning of the period until a few thousand years ago.

This picture of a generally continuous Pleistocene fauna in North America, while at variance with the earlier ideas of successive "warm" and "cold" faunas in Europe, corresponds in a general way to the more recent hypothesis of the European succession, as expressed by Stehlin, Hopwood, and other students and outlined on previous pages of this chapter. Even so, there would seem to be some real differences between Europe and North America in the development of their Pleistocene mammals. Thus in Europe the persistence of Pleistocene genera from the beginning until the end of the period does not seem to be so complete as is the case in North America. In other words, there was more extinction during the progress of Quaternary times in Europe, and less of a widespread suppression of types at the end or after the end of the last glaciation.

Of course it may be that this difference is illusory rather than real, due to the incompleteness of the knowledge in both regions. On the other hand, recent work tends to point to the reality of the difference as outlined above.

It is possible, although in the present state of our knowledge the contributing factors are difficult to envisage, that the difference between the extinction of large Pleistocene mammals in Eurasia and North America may have been due in part to the evolution of man as a potent force in the history of later Quaternary times. In Eurasia, man "grew up" with the Pleistocene faunas of that region, so that he was always more or less in a state of ecological balance with the mammals around him. In North America, on the other hand, he came in as a late, aggressive element, and it may have been the entrance of this destructive animal, even though not at first important, that caused the final extinction of so many great mammals in the New World. Not that man was directly responsible for the killing off of numerous and large herds of mammoths, horses, and camels, but rather by his entrance he may have upset an ecological balance, he may have introduced epidemics, or he may have contributed in other ways which from this distance are quite obscure, to the downfall of numerous seemingly successful mammalian lines. This fact we do know, that almost all of the large Pleistocene mammals of North America were still living when man entered this continent, and that they became extinct after his appearance in the New World.

Of course it is evident that with a continuous fauna inhabiting North America from the beginning until the end of the Pleistocene, there arise great difficulties in any attempt to date events within the Pleistocene upon the basis of mammalian evidence alone. Hopwood's statement with regard to the Pleistocene mammals of Europe that "Except with the aid of a long series of fossils, even an approximation to the true date is all but impossible...," holds to even a greater degree in North America. It may be possible at some future date, with numerous long series of fossils at hand, to arrive at approximate dates within the Pleistocene upon the basis of mammalian associations, yet even this method seems in the state of our present knowledge to be incapable of yielding any very positive results. For it is so subject to geographic and ecologic factors as to be almost abrogated without the most complete kind of evidence correlated in all possible ways.

Nor is there much hope for dating within the Pleistocene upon the basis of mammalian evolution, because generally speaking there was very little evolutionary progress made during the relatively short extent of this period. Certainly generic evolution was virtually nonexistent. And while it is widely held that many early Pleistocene species became extinct before the end of the period even this criterion is too vague and tenuous to be of much help in correlation studies. Moreover, we know that in many cases the same species continued from the beginning to the end of the Pleistocene and even into Recent times. Again, it is all too true that much Pleistocene material is not specifically identifiable, while many Pleistocene species are not valid.

As for the Pleistocene proboscideans of North America, it would seem to be quite certain that the mastodont genus *Stegomastodon* lived only through the earlier portion of the period. The same is very probably true of the genus *Cordillerion* in Mexico. Conversely, although the evidence is not definitive, it would seem that the woolly mammoth, "*Mammonteus*," was not present in the lowermost phases of the Pleistocene. The other genera, *Mastodon*, *Archidiskodon*, and *Parelephas*, seemingly lived pretty much throughout the extent of the Quaternary period, while there is very good evidence based upon recent work to show that *Mastodon*, *Parelephas*, and *Mammonteus* persisted until a relatively recent date and were contemporaneous with early Man in North America.

The stratigraphic position of the mastodont, *Morrillia*, is not certain. Although Osborn considered it as of Middle Pleistocene age, this is more probably a Pliocene form.

The range of proboscidean genera in the Pleistocene of North America may be indicated as follows:

	Pleistocene			
	Lower	Middle	Upper	"Post-Pleistocene"
Cordillerion	?			
Stegomastodon	x			
Mastodon	x	x	x	x
Archidiskodon	x	x	x	?
Parelephas	x	x	x	x
Mammonteus	?	x	x	x

PROBOSCIDEANS:
- *Cordillerion defloccatus* (Hay)
- *Cordillerion gratum* (Hay)
- *Cordillerion orarius* (Hay)
- *Mastodon americanus* (Kerr)
- *Mastodon americanus alaskensis* Frick
- *Mastodon americanus plicatus* Osborn
- *Mastodon americanus rugosidens* Leidy
- *Mastodon americanus rupertianus* Richardson
- *Mastodon oregonensis* (Hay)
- *Mastodon raki* Frick
- *Mastodon grangeri* Barbour
- *Mastodon moodiei* Barbour
- *Mastodon progenius* (Hay)
- *Mastodon acutidens* Osborn
- *Stegomastodon priestleyi* (Hay and Cook)
- *Stegomastodon primitivus* Osborn
- *Stegomastodon mirificus* (Leidy)
- *Stegomastodon arizonæ* Gidley
- *Stegomastodon aftoniæ* Osborn
- *Archidiskodon imperator* (Leidy)
- *Archidiskodon imperator maibeni* Barbour
- *Archidiskodon scotti* (Barbour)
- *Archidiskodon hayi* (Barbour)
- *Archidiskodon meridionalis nebrascensis* Osborn
- *Archidiskodon exilis* Stock and Furlong
- *Archidiskodon haroldcooki* (Hay)
- *Parelephas columbi* (Falconer)
- *Parelephas jeffersonii* Osborn
- *Parelephas washingtonii* Osborn
- *Parelephas eellsi* (Hay)
- *Parelephas francisi* (Hay)
- *Mammonteus primigenius* (Blumenbach)
- *Mammonteus primigenius compressus* Osborn

10. THE PLEISTOCENE OF MEXICO

Freudenberg (1921,[1] 1922[2]) has recognized in a general way three successive divisions in the Pleistocene of Mexico, as based on the occurrence of mammalian fossils. As he has pointed out, a precise subdivision of the Quaternary here is not as yet possible, for there remains much to be learned about the succession and relationships of the Pleistocene mammals south of the Rio Grande. Naturally, any attempts to correlate the Pleistocene mammals of Mexico with the several glacial or interglacial periods of northern United States and Canada are necessarily of the most provisional nature, particularly in view of the fact that such correlations in North America are anything but certain.

According to Freudenberg, the truest knowledge as to the succession of Pleistocene faunas in Mexico is to be had in Tequixquiac, where some fifty species of mammals have been discovered in Pleistocene sediments. The oldest fauna in this region Freudenberg would correlate approximately with the first interglacial or Aftonian of North America. This fauna is characterized by the presence of *Equus giganteus*, *Hyænognathus*[3] and *Preptoceras*, and by the fact that the bones composing it are of a dark brown color. Whether the correlation proposed by Freudenberg is valid is a debatable question for it may be that this author was unduly influenced by the work of Hay, who regarded many Pleistocene types demonstrably ranging through the period as being restricted to the Aftonian. The reader is referred to the discussion of the Pleistocene of North America, above, in which this problem is treated at some length.

From the younger Pleistocene, according to Freudenberg, come *Arctotherium simum*, *Smilodontopsis hyænoides* and many other typical Pleistocene genera. He considers *Parelephas columbi* as representative of the "jungdiluviale Steppenfauna" while he would place *Archidiskodon imperator* as somewhat older, in an interglacial age. He correlates a deposit in which a tapir, *Tapirus* cf. *tarijensis*, was found with the Illinoian to the north. Finally, he states that the *Megalonyx-Mylodon* fauna of Mexico is quite young, as it is in the United States, occurring in river gravels in Mexico that are correlative with the cave deposits to the north.

Freudenberg lists *Cordillerion oligobunis* and the four subspecies described by him, as well as *Cordillerion tropicus*, in his "Quartärfauna des Hochtals von Mexico."[2] Yet elsewhere in the same work (1922) he definitely places two of the subspecies, *C. oligobunis antiquissimus* and *C. oligobunis felicis*, in the Pliocene. It may be that *Cordillerion* in Mexico is of Pleistocene age, very possibly confined to the lower levels. On the other hand, one cannot be sure but that some of the *Cordillerion* may come from Upper Pliocene deposits—as it would seem evident that certain other genera, notably *Hyænognathus* and possibly *Rhynchotherium*, do represent the Upper Pliocene in Mexico.

On the basis of our present evidence, therefore, it must be recognized that most of the Pleistocene mammals of Mexico, as listed by Freudenberg, may with good reason range from the lower to the upper reaches of the period.

PROBOSCIDEANS:

Cordillerion tropicus (Cope) *Cordillerion oligobunis* (Cope) *Cordillerion oligobunis antiquissimus* (Freudenberg) *Cordillerion*(?) *oligobunis felicis* (Freudenberg) *Cordillerion*(?) *oligobunis intermedius* (Freudenberg) *Cordillerion oligobunis progressus* (Freudenberg)	Some of these forms may be of Pliocene age.

Parelephas columbi felicis (Freudenberg)
Archidiskodon sonoriensis Osborn
Archidiskodon imperator silvestris (Freudenberg)
Archidiskodon imperator falconeri (Freudenberg)

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[1] Freudenberg, W., 1921. Geologie von Mexiko, 8vo, Borntraeger, Berlin, pp. 134–145.

[2] Freudenberg, W., 1922. Geol. u. Pal. Abh., N. F., XIV (XVIII), Heft III, pp. 104, 105, 171–176.

[3] It might be said in this connection that *Hyænognathus*, listed by Freudenberg in the Pleistocene of Mexico, is probably of Pliocene age. This genus ranges from the Lower to the Upper Pliocene in the United States.

VII. CENTRAL AND SOUTH AMERICA

1. INTRODUCTION

Although proboscideans had migrated into Central America from the north by late Pliocene times, it would seem that the geographic conditions prevailing in the isthmus may have been sufficiently severe to serve as a barrier that prevented these great animals from reaching South America in appreciable numbers until the beginning of Pleistocene times. The world-wide depression of average temperatures, so characteristic of the Pleistocene, though making itself felt on the climate and the life of South America, did not cause in this region the formation of extensive continental glaciers, as in the northern hemisphere; in fact, glaciation in South America was confined to the Andean uplift and to Patagonia, in the southernmost tip of the continent. Over a major portion of the land, cool and dry conditions, perhaps alternating with warm, moist periods, were prevalent. Thus there were accumulated over a vast tract the extensive loess deposits designated as the Pampean beds, in which fossil mammals of Pleistocene age are abundant. Here and elsewhere in South America, in beds of related age, the proboscideans make their first appearance and follow the course of their characteristic Neotropical development.

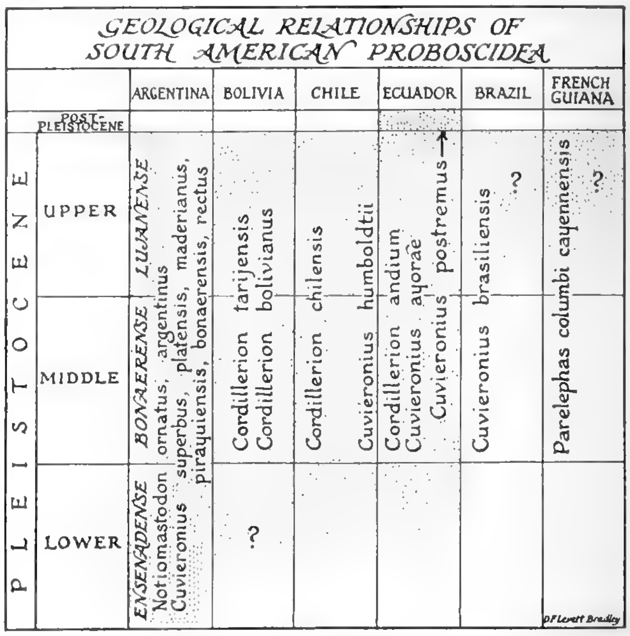

Figure 1225

2. THE PLIOCENE OF CENTRAL AMERICA

Osborn and Frick have separately described Pliocene mastodonts from Central America, but beyond a mere mention of the fact that these new types are probably of Upper Pliocene age, there has been no elucidation of their stratigraphic relationships. These are undoubtedly the oldest of the Neotropical proboscideans, being definitely older than the earliest of the Pampean forms.

In the original description of *Serridentinus guatemalensis*, Osborn listed this new species as doubtfully of Pleistocene age. In Volume I of the present Monograph, however, the age is listed as Upper Pliocene. Frick, in the type descriptions of *Aybelodon* and *Blickotherium*, states that they came from "an Honduras horizon of Upper Pliocene facies."

PROBOSCIDEANS:
  Chinautla, Guatemala
    Serridentinus guatemalensis Osborn

  Tapasuma, Gracios, Honduras
    Blickotherium blicki Frick
    Aybelodon hondurensis Frick

3. THE PLEISTOCENE OF ARGENTINA

The Pampean formation of Argentina may be described as a complex series of fluviatile, lacustrine, and eolian deposits, having for the most part the form of brown and yellow loesses. As might be expected from the mode of origin of these beds, lateral variations in their expression are numerous, and it is doubtful whether any particular sequence of Pampean deposits, as established at a given point, can be traced without change for any considerable distance. The Pampean loess, as typically exposed, is probably for the most part of eolian origin, but fluviatile and lacustrine facies are common, with their consequent variations in the composition of the sediments. Thus there are bands or zones of coarser materials, concretions, 'loesskindl,' limy deposits and the like. The loess itself, as is typical of this kind of sediment, is very fine-grained, compact, and rather well consolidated, forming a resistant mantle, and where erosion has cut through it, vertical cliffs. In many localities, particularly in the easternmost portions of the Pampean exposures, there are intercalated marine deposits, representing temporary incursions of the sea due to slight depressions of the land surface.

The first serious studies of the Pampean beds were made some hundred years ago by d'Orbigny and by Darwin, and subsequently by Bravard and by Burmeister. However it remained for Ameghino, the great Argentine palæontologist, to attempt a classification or stratigraphic subdivision of these deposits.

Ameghino, in 1880,[1] suggested the separation of the Pampean into three successive horizons, as follows:

Terreno pampeano lacustre
Terreno pampeano superior
Terreno pampeano antiquo.

Subsequently locality names were given to these horizons, so that they became:

Lujanense = Pampeano lacustre = Upper Pampean
Bonaerense = Pampeano superior = Middle Pampean
Ensenadense = Pampeano inferior = Lower Pampean.

Naturally in the course of time Ameghino greatly extended his division of the Pampean beds, and subsequent authors added to or modified the subdivision for the series that had been proposed. Consequently the views as to the proper stratigraphic classification of the several units comprising the Pampean deposits became diverse, and the system of classification for these subdivisions in many cases became complex. Suffice it to say at this point that the three divisions given above constitute the basic separation of the Pampean deposits, and the more refined or more complex systems of stratigraphic nomenclature for these sediments are based on the essentially tripartite plan first proposed by Ameghino.

Ameghino, who was inclined to regard all of the South American formations and their contained mammalian faunas as being much older than is justified by the facts, placed the entire Pampean sequence in the Pliocene. Needless to say, all other authorities have differed from this interpretation of the age of the Pampean. Roverto, in 1914, regarded the Pampean as essentially of Pleistocene age, but he included within it the Puelchense stage or division, which by most authors is assigned to the series antecedent to the Pampean (Uquiana or Araucana). Later, in 1934, Kraglievich regarded the Middle and Upper Pampean as of true Pleistocene age, but he designated the Lower Pampean, or Ensenadense, as "Upper Pliocene or Pliopleistocene." In 1937, Rusconi, like Kraglievich, placed the Middle and Upper Pampean in the Pleistocene, but regarded the Lower Pampean as of Upper Pliocene age, a view that seemingly is shared by Castellanos in his recent work on the Lower Pampean and Araucanean sediments of the Valle de Los Reartes.

A comparison of the several Pampean faunas, particularly on the bases as outlined elsewhere in this chapter, would seem to put a somewhat different interpretation on the age of the Pampean beds, than that outlined in the preceding paragraph. Briefly, the mammals of the Pampean, as compared with those of other portions of the

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[1] Ameghino, F., 1880. "La Antiqüedad del Hombre en El Plata," Tome I, p. III; 1881, Tome II, p. 334.

world, give every evidence for us to suppose that the entire Pampean sequence is of Pleistocene age. Thus, the Ensenadense, instead of being Upper Pliocene, as generally regarded by South American authorities, would seem to be, on the basis of faunal evidence, of *Lower Pleistocene age.*

The Pleistocene age of the Pampean was effectively set forth a number of years ago by the late W. D. Matthew, in his comprehensive essay "Climate and Evolution."[1] Matthew showed most clearly that the Holarctic genera in the Pampean of South America most certainly were immigrants from North America, and that their appearance in the Neotropical region must of necessity have been made subsequent to their origin in the north.

> The first appearance of true equines in South America is in the Pampean. The three best-known genera are *Equus, Hippidion* and *Onohippidion.* The first might be regarded as of Palearctic origin;[2] the second and third have no Old World predecessors, but may be directly derived from the North American *Pliohippus.* They are, however, much larger and more progressive than *Pliohippus*, and in size, reduction of the lateral digits, etc., are equivalent to *Equus.* We can hardly doubt that they came to South America from North America, nor can I see any practical alternative to believing that *Equus* arrived by the same route. Now, the first appearance of *Equus* in North America is at the base of the Pleistocene. In Argentina, it first appears in the middle Pampean. The middle Pampean cannot therefore be older and is presumably younger than Lower Pleistocene. *Hippidion* and *Onohippidion* are found (*fide* Roth) in somewhat older levels; but as they are much advanced over anything in our Middle Pliocene (Blanco), it would seem that their first occurrence in the Pampean must be placed at the top of the Pliocene or preferably in the Lower Pleistocene. I conclude that the Pampean formation approximately represents the Pleistocene epoch.
>
> . . . the genus *Arctotherium* of the true Pampean in South America, unknown in North America until the Pleistocene, indicates, like *Equus*, that the Pampean is a Pleistocene formation.
>
> The distribution of *Smilodon* in North and South America is in exact accord with that of *Arctotherium.* The relations of the South American Proboscidea to those of North America correspond to those of the Equidæ. The Camelidæ, Cervidæ, Canidæ, etc., also support the Pleistocene age of the true Pampean.

The differentiation of distinct, successive faunas within the Pampean is not so clear-cut or definitive as might be expected. For, as is typical of the Pleistocene in other parts of the world, modern genera appear at the base of the Pampean, and continue uninterruptedly throughout the sequence, from bottom to top. Therefore, the faunas of the Ensenadense, Bonaerense, and Lujanense show successive appearances of the same genera, with only specific changes to differentiate them. And specific differences are of little value in establishing time sequences within the Pleistocene, as has been shown by Romer in his illuminating paper on the Pleistocene of North America (1933).

Of course there are many relatively primitive forms, characteristically South American, which have persisted from older beds into the Pampean. But the presence of these conservative or holdover types in the Pampean does not argue for the antiquity of the beds in which they are found, but rather constitutes once again an example of the persistence of earlier types into a period later than that of their typical expression. Indeed, the very presence in the Ensenadense of a large group of thoroughly modern genera is one of the strongest arguments for the Pleistocene age of the base of the Pampean.

There would seem, however, to be certain differences that distinguish the Ensenadense from the overlying beds. One of these is the presence of the genus *Typotherium* in the lowest of the Pampean stages and its absence from the upper beds, for there seems to be valid proof that *Typotherium* persisted from the Tertiary into the Ensenadense, at the end of which stage it became extinct. Conversely, the absence of *Equus* in the Ensenadense and its presence in the Bonaerense and Lujanense also serve to distinguish this lower horizon from the upper ones.

But, for the most part, the Pampean mammals run through from the lowest to the highest phases of the formation. This is true not only of the autochthonous genera, such as the edentates and certain of the notoungulates, but also of the immigrant forms, such as *Arctotherium, Canis, Smilodon, Hippidion,* the artiodactyls, and the proboscideans.

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[1] Matthew, W. D., 1915. Ann. N. Y. Acad. Sci., XXIV, pp. 196, 198.

[2] Studies made subsequent to the writing of Matthew's paper have shown most conclusively that *Equus* is of North American origin, having been derived from the Upper Pliocene genus *Plesippus*, this latter a direct descendant of *Pliohippus.*

At the present time there is no evidence definitely confirming the fact that any of the South American proboscidean genera are limited to certain stages of the Pampean. Thus, it would seem that *Cuvieronius*, *Cordillerion*, and *Notiomastodon* range through the Pampean, although the last of these genera may be limited to the lower phases of the formation. With regard to this question the reader is referred to page 595 of Volume I of the present Monograph, where the geologic age of certain species of *Cordillerion* and *Cuvieronius* is discussed by Dr. G. G. Simpson. (Dr. Simpson considers among other things the supposed Lower and Middle Pampean age of *Cuvieronius platensis* and the Upper Pampean age of *Cuvieronius superbus* and shows that such restriction of these species rests upon unsatisfactory evidence.)

PAMPEAN PROBOSCIDEANS:

Notiomastodon ornatus Cabrera
Cuvieronius superbus (Ameghino)
Cuvieronius platensis (Ameghino)
Cuvieronius maderianus (Ameghino)
Cuvieronius perayuiensis (Gez)
Cuvieronius bonaerensis (Moreno)
Cuvieronius rectus (Ameghino)

4. THE PLEISTOCENE OF THE ANDEAN VALLEYS

TARIJA, BOLIVIA.—During the time that the diverse loesses of the Pampean formation were being deposited on the broad plains of Argentina, sediments of somewhat different origins but of a similar age were being accumulated in the high mountain valleys of the western Cordilleras. These were the sandstones, clays, and gravels of fluviatile origin, which were laid down by mountain streams to form discontinuous but locally extensive deposits in the numerous valleys at the bases of the ever-uplifting Andean mountains.

Typical of these mountain valley deposits are the sediments exposed in the valley of Tarija in southern Bolivia, the fauna of which has been thoroughly monographed by Boule and Thevenin. These deposits consist of sand and clays, which in many areas have been extensively eroded to form small areas of badlands.

The fauna from the valley of Tarija is closely comparable to the Pampean fauna, an indication of the virtual contemporaneity of the mammals in the two regions. Of particular interest in the Tarijan fauna are *Cordillerion andium*, *Macrauchenia*, *Toxodon*, *Equus*, *Hippidion*, *Onohippidium*, *Smilodon*, and various ground sloths. One difference is to be noted between the Pampean assemblage and that of Tarija, namely, the presence of *Typotherium* in the former and its absence in the latter. As has been shown above, this genus presumably is found only in the Lower Pampean beds of Argentina, having become extinct before the deposition of the Middle and Upper Pampean deposits. Therefore, its absence from the Tarija fauna may mean one of two things, either that these beds are later than Lower Pampean, being generally correlative with the Middle and Upper Pampean of the plains, or that the ecological conditions were such as to prevent the genus *Typotherium* from venturing into the elevated areas of the mountains.

Enrico de Carles divided the Tarija beds into two horizons, a lower level containing among other things *Cordillerion*, *Hippidion*, *Macrauchenia*, and *Equus*, and an upper level with *Glyptodon*, *Mylodon*, *Megatherium*, and again *Equus*. But, as Boule and Thevenin have shown, this division will not hold -rather the fauna seems to continue throughout the extent of the beds.

It has been the opinion of many authors that the Tarija deposits are in part at least of Upper Tertiary age. Ameghino even went so far as to place these beds in the Lower Pliocene. Yet as Boule and Thevenin have most amply demonstrated, the Tarija deposits are fully correlative with the Pampean to the east, and as such are to be regarded *entirely as of Pleistocene age.*

PROBOSCIDEANS:
- *Notiomastodon argentinus* (Ameghino)
- *Cordillerion tarijensis* (Ameghino)

What has been said about the Tarija deposits applies, for the most part, to other mountain valley beds of the Andes. That is, they are essentially of Pampean age, and therefore come within the Pleistocene.

ULLOMA, BOLIVIA.—Philippi, in 1893, described a small mammalian fauna from Ulloma, which in most respects is similar to the Tarija fauna and likewise to the Pampean fauna. This assemblage from Ulloma is characterized by *Hippidion, Cordillerion,* and various ground sloths.

PROBOSCIDEAN: ULLOMA, BOLIVIA
- *Cordillerion bolivianus* (Philippi)

PROBOSCIDEAN: LAKE TAGUA-TAGUA, CHILE
- *Cordillerion chilensis* (Philippi)

ECUADOR.—The localities and ages of Cuvier's types of *Cordillerion andium* and *Cuvieronius humboldtii.*

The type of *Cordillerion andium,* described by Cuvier, was found by von Humboldt near the volcano of Imbaburra, at Quito, Ecuador. This specimen came from an elevation of some 7,600 feet—undoubtedly from mountain valley beds contemporaneous in some degree with the sediments of Tarija, and with some portion of the Pampean series of Argentina. Consequently the age of this species is Pleistocene, and it is very probable that *Cordillerion andium* persisted into very late Pleistocene times. It is the typical notorostrine of the high cordilleran valleys of South America.

Although *Cuvieronius humboldtii,* described by Cuvier, is the typical Pampean plains form of Argentina, the type of this species was found in the Andean region. The locality is near Concepcion, either in Chile or in Ecuador. Whatever may be the locality for the type, there would seem to be little doubt that it was found in one of the high mountain valleys, in beds that were probably more or less equivalent to the Tarija deposits and to the Pampean of the plains. Therefore the age of this form is Pleistocene.

PROBOSCIDEANS:
- *Cordillerion andium* (Cuvier)
- *Cuvieronius humboldtii* (Cuvier)

In a notable study of the fossil mammals of Ecuador, Spillmann in 1931 presented a detailed description of the geologic relationships of the various extinct mammals of that region. The facts are somewhat as follows.

During Pleistocene times an extensive tuff or volcanic ash deposit was built up throughout the mountain valleys of the region. This deposit, which in places reached a considerable thickness, is of the nature of an eolian accumulation and therefore forms a wide-spread mantle through the numerous mountain valleys. It would seem to be indicative of deposition under dry conditions, not only by reason of the nature of the sediments themselves, but also because the contained fauna shows adaptations to such a habitat.

In the Quebrada of Chalang, a canyon tributary to the Rio Colorado valley and opposite Punin, Spillmann found a fairly extensive fossiliferous deposit in the tuffaceous beds, known locally as the Cangahua. The fossils were in the basal portion of the tuff at this locality, which may be rather high up in the tuff as it is generally developed. The fauna includes certain characteristic South American Pleistocene genera, such as *Mylodon, Megatherium, Protauchenia, Neohippus, Hippidion,* and *Cuvieronius*; consequently it is to be considered as of Pleistocene age, probably equivalent to some part of the Pampean assemblage. Such was the opinion of Spillmann, who described the material.

In Volume I of this Monograph, page 567, will be found a map and a stratigraphic diagram, showing the location and the geological occurrence of the Chalang fauna.

PROBOSCIDEAN: *Cuvieronius ayorae* (Spillmann).

Near the town of Alangasi, in the Quebrada Cachihuayco, Spillmann discovered a rather complete skeleton of *Cuvieronius* in a superficial layer, associated with man. This remarkable find is clearly indicative of the fact that some of the South American proboscideans persisted until a very recent date—certainly to within a few thousands of years ago.

The Alangasi specimen was found in a fine, bluish clay, which rests on the tuff or Cangahua. Evidently the clay is a late, post-Pleistocene deposit, originally a soft mud in which the animal was trapped and finally perished. As Spillmann has shown, the very nature of this deposit not only was responsible for the death of the proboscidean but also for its exceptional preservation. These sediments form a locally developed terrace at the place where the fossil was discovered.

The specimen shows certain marks that may be due to the inflicting of wounds by arrows or spears. With it were pottery fragments and other clear signs of human workmanship. Thus the age probably is "post-Pleistocene," contemporaneous with some of the early South American Indians.

For further details as to the occurrence of this specimen, the reader is referred to Volume I of this Monograph, pages 571–574.

PROBOSCIDEAN: *Cuvieronius postremus* (Spillmann).

5. THE PLEISTOCENE OF BRAZIL AND FRENCH GUIANA

BRAZIL.—One of the notable discoveries of a South American proboscidean is *Cuvieronius brasiliensis*, first described by Lund almost a hundred years ago. This specimen was found in a limestone cave, in association with sloths, carnivores, and other typical South American mammals. The age is difficult to determine, but probably is late Pleistocene.

PROBOSCIDEAN: *Cuvieronius brasiliensis* (Lund).

FRENCH GUIANA.—A fragment of a tooth constitutes the only record, known at the present time, of the extension of the elephantines into South America. This specimen was found in Cayenne, French Guiana, and is listed by Osborn as "probably Upper Pleistocene." Nothing more can be said as to its age.

PROBOSCIDEAN: *Parelephas columbi cayennensis* Osborn.

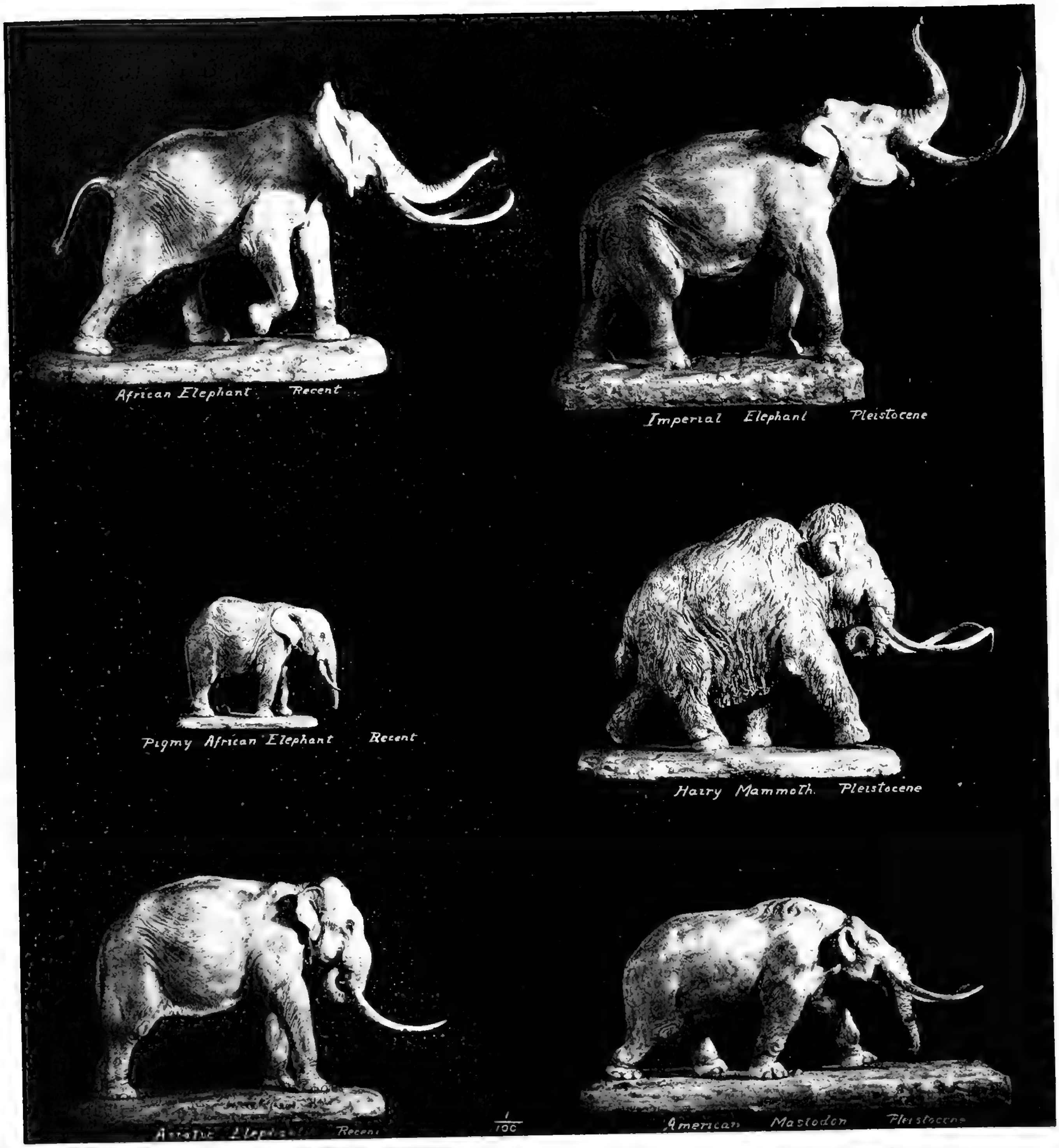

Fig. 1226. Models of Recent and extinct Mammoths and Mastodons, all reduced to a uniform scale of one one-hundredth natural size. Executed under the direction of Henry Fairfield Osborn by Charles R. Knight in 1914, to show the external characters and proportions. See Osborn, "Restoration of the World Series of Elephants and Mastodons" (1914.411).

African Elephant (Recent) = *Loxodonta africana.*
"Pigmy" African Elephant (Recent) = *Loxodonta africana cyclotis* (*Elephas cyclotis* of Matschie).
Asiatic Elephant (Recent) = *Elephas indicus ceylanicus.*
Imperial Elephant (Pleistocene) = *Archidiskodon imperator.*
Woolly Mammoth (Pleistocene) = *Mammonteus primigenius.*
American Mastodon (Pleistocene) = *Mastodon americanus.*

CHAPTER XXIII

AFFINITIES, MIGRATIONS, AND PHYLOGENY OF THE PROBOSCIDEA: A SUMMARY

1. Introduction together with lists of:
    - Superfamilies.
    - Families.
    - Subfamilies.
    - Genera.
    - Species (with horizons).
2. Explanation of terms used throughout the text of the present Memoir.
3. Characters, affinities, and migrations of the Proboscidea: Mœritheres, Deinotheres, Longirostrines, Gnathabelodonts, Amebelodonts, Tetralophodonts, Notorostrines, Rhynchorostrines, Brevirostrines, Humboldtines, Serridentines, Platybelodonts, Notiomastodonts, Palæomastodonts, Mastodonts, Zygolophodonts, Stegolophodonts, Stegodonts, Mammontines, Loxodontines, Elephantines.
4. Skeletal material.
5. Heights of proboscideans, estimated and actual.

1. INTRODUCTION

During a period of fifteen years, namely, from 1920, when intensive work on the present Memoir was inaugurated, to 1935, Professor Osborn collected notes, articles, and illustrations for his proposed chapter on the affinities, migrations, and phylogeny of the Proboscidea, in which he intended to summarize the results of his own researches as well as those of the palæontologists of the world. It is a regrettable fact that this chapter was never written, and in the following attempt to present his conclusions, it cannot be too strongly impressed upon the mind of the reader that in no respect is there any deviation from the views expressed by him in his various publications, especially those in his final articles of 1934 and 1935, and in Volume I of the present Memoir. Quite naturally certain of his earlier writings have become obsolete owing to the advance in knowledge of these interesting animals, and for this reason modifications in some of the citations have had to be made, such alterations being indicated by the use of dots (to show the omission of statements regarded as erroneous at the present time), or by square brackets (embodying his final conclusions). For the sake of clarity and ease of presentation, however, there is in general purposive avoidance of exact quotations; rather is this a paraphrased narrative of proboscidean evolution since Eocene time, as revealed in the fossil remains unearthed over a period of more than three hundred years and as interpreted by Professor Osborn in his writings and illustrations.

The accompanying phylogenetic charts by Mrs. Margret Flinsch Buba, with migration maps by Miss D. F. Levett Bradley, while the conception of Professor Osborn, were not wholly prepared under his direction but (since the death of Professor Osborn in 1935) in consultation with the various curators of the American Museum conversant with the subject, and in consistent agreement with the text and illustrations of the Memoir, thus expressing his final views.

Perhaps no more fitting introduction to this chapter could be chosen than Professor Osborn's opening words in his article in NATURAL HISTORY of January-February, 1925 (Osborn, 1925.637):

> There are few joys in life comparable with that which the naturalist experiences when one of his predictions or prophecies happens to be fulfilled. In 1900 I predicted that Africa would prove to be the cradle of the Proboscidea; in 1903 this prophecy was verified by British explorers in Egypt. Naturally eager to visit the scene of this discovery at once, I refrained until my British friends had fully described and published this and other discoveries and gained the world-wide reputation therefor to which they were richly entitled. I then asked President Theodore Roosevelt for an introduction to Lord Cromer, at the time Viceroy of Egypt, and through the generosity of President Jesup of the American Museum an expedition was fitted out, carrying as credentials a thoroughly characteristic note from President Roosevelt to Lord Cromer . . . [whose] brief and simple diplomatic message opened the doors of Egypt to the American Museum party. On our arrival at Shepheard's Hotel on the morning of

> January 23 [1907], a card was sent up announcing Captain H. G. Lyons, then director of the Geological Survey of Egypt, who thereupon assured me that all the resources of the Survey would be placed at our disposal,—a camel caravan, a supply of the absolutely essential *fantasses* for carrying water, and, best of all, the guidance of a most intelligent and delightful member of the Survey staff, Mr. Hartley T. Ferrar. A personal caravan was also engaged. Thus, sixty camels strong, we wound our way past the pyramids of the eastern side of the Nile, skirted the fertile basin of the Fayûm, and struck southwest into the waterless desert until we reached the region that represented the ancient cradle of the elephant family. We at once set to work with a very superior force of Egyptian excavators from Kuft, under the direction of Mr. Walter Granger and Mr. George Olsen, two of the best fossil hunters of America, who stuck to their arduous post for nearly two months, until driven out by sandstorms and excessive heat. With their skilled aid, we soon discovered the burial sites of three of the early elephant dynasties; the MŒRITHERIUM, the abundant PHIOMIA, and finally the rare PALÆOMASTODON. The last-mentioned name is derived from the uncorrupted Greek words παλαιός, μαστός, and ὀδόυς, signifying 'the ancient nipple tooth.'
>
> The Fayûm Expedition . . . . aroused in the writer's mind the liveliest interest in these relatively small and primitive proboscideans, and a desire to compare them closely with the large proboscideans of France and South America, which were first described in 1806 by the famous Cuvier, also the wish to compare them with the proboscideans described and figured by the British explorers Falconer and Cautley in India between the years 1845 and 1847, and finally the hope to trace all these animals from their ancestral homes in Africa and Eurasia through their migrations to America.
>
> An insatiable *Wanderlust* has always possessed the souls of elephants as it has those of the tribes and races of man. Not only to overcome the changes and chances of this mortal life, but also to gratify their intelligent curiosity ever to explore afresh forests, pastures, fields, rivers, and streams, they have gone to the very ends of the earth and have far surpassed man in adapting their clothing and teeth to all possible conditions of life. Thus the romances of elephant migration and conquest are second only to the romances of human migration and conquest. Variety is the spice of elephant life, as it is of human life, and the very longing for a change of scene and of diet has been the indirect cause of what in scientific parlance we term *adaptive radiation*—the reaching out in every direction for every kind of food, every kind of habitat, in itself the *cause* of radiating or divergent evolution and adaptation. It is to this predisposition to local, continental or insular, and world-wide wanderings that we attribute the many branches and sub-branches which have been developed in this remarkable family.

The distinguishing feature of the present Memoir, as stressed by Professor Osborn (see Vol. I, p. 21) "is the separation of many direct phyletic lines of descent from each other and the recognition of many mastodonts and elephants which are very much alike in certain characters, but which are still more unlike in other characters and cannot possibly be descended one from the other."

It will be noted by comparing Plates x and xi of Volume I that the author in 1935 departed somewhat radically from his phylogenetic arrangement of 1934. The present treatment, therefore, will follow the author's 1935 chart. The reader is also referred to Chapter XXI of the present volume which gives a detailed history of proboscidean nomenclature.

Five Superfamilies

Four main divisions (suborders or superfamilies) of the Proboscidea were adopted in 1921 (Osborn, 1921.515, p. 2) as follows: "With the reservations, first, that we should not expect to find different orders of mammals subdivided into branches of equal rank and, second, that the subdivisions of the Proboscidea are either of subordinal or of superfamily value, we may adopt as the four primary divisions:

I. MŒRITHERIOIDEA typified by the *Mœritherium* in the Oligocene of North Africa
II. DINOTHERIOIDEA [Deinotherioidea] typified by the Miocene and Pliocene Dinotheres [Deinotheres] of Eurasia
III. MASTODONTOIDEA to include the Bunomastodontidæ, new family, and the Mastodontidæ
IV. ELEPHANTOIDEA to include the Elephantinæ, Stegodontinæ, and Mammontinæ"

This fourfold classification was retained by the author until the publication of Volume I of the present Memoir in which he withdrew the true *Stegodon*, subfamily Stegodontinæ, from the Elephantoidea, creating for this genus and subfamily a new superfamily, the

V. STEGODONTOIDEA (see Vol. I, pp. 22 and 25, also Vol. II, Chap. XIV, p. 807)

Thus the Proboscidea are now divided into five suborders or superfamilies.

EIGHT FAMILIES

The author's classification of 1933 included five families (see pp. 30 to 33 of Vol. I). While the family name Bunomastodontidæ Osborn is most appropriate as characterizing the dentition of its included genera and species, it is without a type genus. Of family names based on generic names, a choice between Trilophodontidæ (as in Simpson, 1931, p. 281) and Gomphotheriidæ (as in Cabrera, 1929, pp. 74, 75) would depend upon the acceptance of *Gomphotherium* Burmeister, 1837, as a valid genus, and its priority over *Trilophodon* Falconer and Cautley, 1846. Doctor Simpson (in a personal communication to the editor) now considers Gomphotheriidæ as preferable under the International Rules and common usage. Professor Osborn's judgment was that *Trilophodon* should be used rather than *Gomphotherium.* If, therefore, he had followed the ordinary rule for family names, he would have preferred Trilophodontidæ.

A similar condition exists in connection with the family name Humboldtidæ Osborn, i.e., it is without a type genus. In 1934 (see Pl. x, Vol. I), Professor Osborn withdrew *Stegomastodon* Pohlig, 1912 (which antedates both *Eubelodon* Barbour, 1914, and *Cuvieronius* Osborn, 1923) from the Brevirostrinæ and placed it in the Humboldtine group. Dr. William Berryman Scott in his revision of "A History of the Land Mammals of the Western Hemisphere," 1937, pp. 267, 281, 294, suggested the name Stegomastodontidæ for the name Humboldtidæ.

Professor Osborn did not accept the ordinary rule that a family or subfamily name must be based upon an already named genus. In giving names to new families and subfamilies he followed the precedents in naming suborders and orders from appropriate characters (e.g. Proboscidea) rather than from type genera. Consequently his names are used in the present chapter, which is a summary of his work.

1. MŒRITHERIIDÆ Andrews-Osborn (1906–1921)
2. CURTOGNATHIDÆ (Curtognati Kaup, 1833; Curtognathidæ Osborn, 1933)
3. MASTODONTIDÆ Girard, 1852; Osborn, 1918, including the Palæomastodontidæ of Andrews, 1906
4. BUNOMASTODONTIDÆ Osborn, 1921 (Gomphotheriidæ Cabrera, 1929, in part; Trilophodontidæ Simpson, 1931, p. 281)
5. ELEPHANTIDÆ Gray, 1821

In the Appendix to Volume I two new families are described (pp. 722 and 729 respectively):

6. HUMBOLDTIDÆ, to include *Eubelodon, Cuvieronius,* and *Stegomastodon,* as distinguished from *Cordillerion* of the family Bunomastodontidæ, subfamily Notorostrinæ, in which subfamily it was thought at one time (see p. 541) that these four genera should be included. Professor Scott in his new edition of "A History of the Land Mammals of the Western Hemisphere," 1937, has substituted the name Stegomastodontidæ for Humboldtidæ, based on the genus *Stegomastodon.*

7. SERRIDENTIDÆ, to include *Serridentinus* Osborn, typified by *S. serridens* Cope, *Ocalientinus* Frick, *Serbelodon* Frick, and *Trobelodon* Frick, all of the subfamily Serridentinæ; *Platybelodon* Borissiak and *Torynobelodon* Barbour of the subfamily Platybelodontinæ, and *Notiomastodon* Cabrera of the subfamily Notiomastodontinæ.

To these should be added the family recently (1935) described by Drs. Chung-Chien Young and A. Tindell Hopwood:

8. STEGODONTIDÆ, regarded by these authors as comprising two groups, one with "compressed, tectiform ridges" (*Stegodon* Falconer and Cautley), the other with ridges more blunt and "composed of rounded conules" (*Stegolophodon* Schlesinger)—see Hopwood, 1935, p. 72. According to the views of the present author, this family would embrace the true *Stegodon* only, the Stegolophodonts having been removed by him to the Mastodontidæ, subfamily Stegolophodontinæ (see p. 700 of Vol. I for definition).

Therefore, in the final classification of the present Memoir, there are eight families.

Twenty-one Subfamilies

In direct opposition to the morphological and horizontal system of classification of Cope, and despite the highly valued opinion of such colleagues as Dr. William Diller Matthew and Dr. William King Gregory, who differed with Professor Osborn as to the practicability of a phylogenetic system of classification, which phyla were designated as subfamilies, he held to the last the firm conviction that a subfamily division could be "properly applied to vertical lines of succession." Thus, beginning in 1910 ("Age of Mammals," pp. 558, 559), he adopted three subfamilies of the Proboscidea, namely, the Dinotheriinæ, Mastodontinæ, and Elephantinæ, the number increasing until in 1933 (see Vol. I, pp. 30–33) he had included seventeen, and in 1935 (his final classification) as many as twenty-one subfamilies, of more than half of which he was the author:

Mœritherioidea Mœritheriidæ	1.	MŒRITHERIINÆ Winge-Osborn (1906–1923)
Deinotherioidea Curtognathidæ	2.	DEINOTHERIINÆ Bonaparte-Winge-Osborn (1841, 1850–1906–1910)
Mastodontoidea Bunomastodontidæ [=Trilophodontidæ Simpson, 1931][1]	3.	LONGIROSTRINÆ Osborn, 1918
	4.	GNATHABELODONTINÆ Barbour and Sternberg, 1935
	5.	AMEBELODONTINÆ Barbour, 1929
	6.	TETRALOPHODONTINÆ van der Maarel, 1932
	7.	NOTOROSTRINÆ Osborn, 1921
	8.	RHYNCHOROSTRINÆ Osborn, 1918
	9.	BREVIROSTRINÆ Osborn, 1918
Humboldtidæ [=Stegomastodontidæ Scott]	10.	HUMBOLDTINÆ Osborn, 1934, 1936
Serridentidæ	11.	SERRIDENTINÆ Osborn, 1921
	12.	PLATYBELODONTINÆ Borissiak, 1928
	13.	NOTIOMASTODONTINÆ Osborn, 1936
Mastodontidæ [=Mammutidæ Cabrera, in part]	14.	PALÆOMASTODONTINÆ Osborn, 1936
	15.	MASTODONTINÆ Brandt-Osborn (1869–1910)
	16.	ZYGOLOPHODONTINÆ Osborn, 1923
	17.	STEGOLOPHODONTINÆ Osborn, 1936
Stegodontoidea Stegodontidæ	18.	STEGODONTINÆ Osborn, 1918
Elephantoidea Elephantidæ	19.	MAMMONTINÆ Osborn, 1921
	20.	LOXODONTINÆ Osborn, 1918
	21.	ELEPHANTINÆ Osborn, 1910

Forty-four Genera

Out of the more than ninety names (cf. Chap. XXI, pp. 1371–1382) applied generically or subgenerically to the Proboscidea since the time of Linnæus in 1735, Professor Osborn selected forty-four as valid. This will seem a surprisingly large number in view of the fact that for many years only two, *Elephas* and *Mastodon*, were accepted by the majority of scientists.

Elephas.—The name *Elephas* was first used by John Ray in his "Synopsis Methodica Animalium Quadrupedum et Serpentini Generis" of 1693, p. 131; in 1735 Linnæus in the first edition of the "Systema Naturæ," p. 10, placed *Elephas* in the same division as the rhinoceroses; in 1754 in his "Animalia Rariora, Imprimis, et Exotica," p. 11, he gave *Elephas indicus* as the type, for which he subsequently (10th edition of the "Systema Naturæ," 1758, p. 33) substituted *Elephas maximus*. This genus, together with other names appearing in the same edition, was officially adopted by the members of the Fifth International Zoological Congress of 1901; hence the genus *Elephas* dates from 1758.

[1] [See previous page where Doctor Simpson states that he now (October, 1940) prefers Gomphotheriidæ Cabrera, 1929.—Editor.]

Mastodon.—The name *Mastodon* in its original or French form was the "Mastodonte" of Cuvier, 1806. Ten years later (1816) Oken first used the form *Mastodon*, based on the five classic species of Cuvier of 1806, thus anticipating Cuvier by one year, who in 1817 in his "Le Règne Animal," p. 233, described *Mastodon giganteum* and *M. angustidens*. Inasmuch, however, as Cuvier was the author of *Mastodonte*, he has been given precedence over Oken in the use of the scientific form *Mastodon*.

Genera of the Mœritherioidea, Deinotherioidea, and Mastodontoidea Regarded as Valid by the Present Author

1. *Mœritherium* Andrews, 1901
2. *Deinotherium* Kaup, 1829
3. *Palæomastodon* Andrews, 1901
4. *Miomastodon* Osborn, 1922
5. *Pliomastodon* Osborn, 1926
6. *Mastodon* Cuvier, 1806, 1817
7. *Zygolophodon* Vacek, 1877
8. *Turicius* Osborn, 1926
9. *Stegolophodon* Schlesinger, 1917
10. *Rhynchotherium* Falconer, 1856 (MS.), 1863, 1868
11. *Blickotherium* Frick, 1933
12. *Aybelodon* Frick, 1933
13. *Trilophodon* Falconer, 1846, 1857
14. *Megabelodon* Barbour, 1914, 1917
15. *Gnathabelodon* Barbour and Sternberg, 1935
16. *Phiomia* Andrews and Beadnell, 1902
17. *Amebelodon* Barbour, 1927
18. *Tetralophodon* Falconer, 1847, 1857
19. *Morrillia* Osborn, 1924
20. *Cordillerion* Osborn, 1926
21. *Pentalophodon* Falconer, 1857, 1865
22. *Anancus* Aymard, 1855, 1859
23. *Synconolophus* Osborn, 1929
24. *Cuvieronius* Osborn, 1923
25. *Eubelodon* Barbour, 1914
26. *Stegomastodon* Pohlig, 1912
27. *Serridentinus* Osborn, 1923
28. *Ocalientinus* Frick, 1933
29. *Serbelodon* Frick, 1933
30. *Trobelodon* Frick, 1933
31. *Platybelodon* Borissiak, 1928
32. *Torynobelodon* Barbour, 1929
33. *Notiomastodon* Cabrera, 1929

Genera of the Stegodontoidea and Elephantoidea Regarded as Valid by the Present Author

34. *Stegodon* Falconer and Cautley, 1847, 1857
35. *Archidiskodon* Pohlig, 1888
36. *Metarchidiskodon* Osborn, 1934
37. *Parelephas* Osborn, 1924
38. *Mammonteus* Camper-Osborn, 1788–1924
39. *Loxodonta* F. Cuvier, 1825–1827
40. *Palæoloxodon* Matsumoto, 1924
41. *Hesperoloxodon* Osborn, 1931
42. *Elephas* Linnæus, 1735–1758
43. *Hypselephas* Osborn, 1934, 1936
44. *Platelephas* Osborn, 1934, 1936

Valid Species of Proboscidea

A complete list of the 552 species and subspecies of the Proboscidea described since 1754 will be found in Chapter XXI of the present Memoir, pages 1382 to 1420. A list of the valid species of the Mœritherioidea (5), Deinotherioidea (12), and Mastodontoidea (205), together with migration map (Fig. 1227) is repeated here from Volume I, pages 735–743, followed by a similar list of the valid species of the Stegodontoidea (19) and Elephantoidea (111), with migration map (Fig. 1228) —in all 352 valid species and subspecies as determined by the present author, of which at least 22 are existing species, subspecies, or geographical varieties. For a detailed treatment of the geologic succession of the Proboscidea, reference should be made to Chapter XXII above by Dr. Edwin H. Colbert.

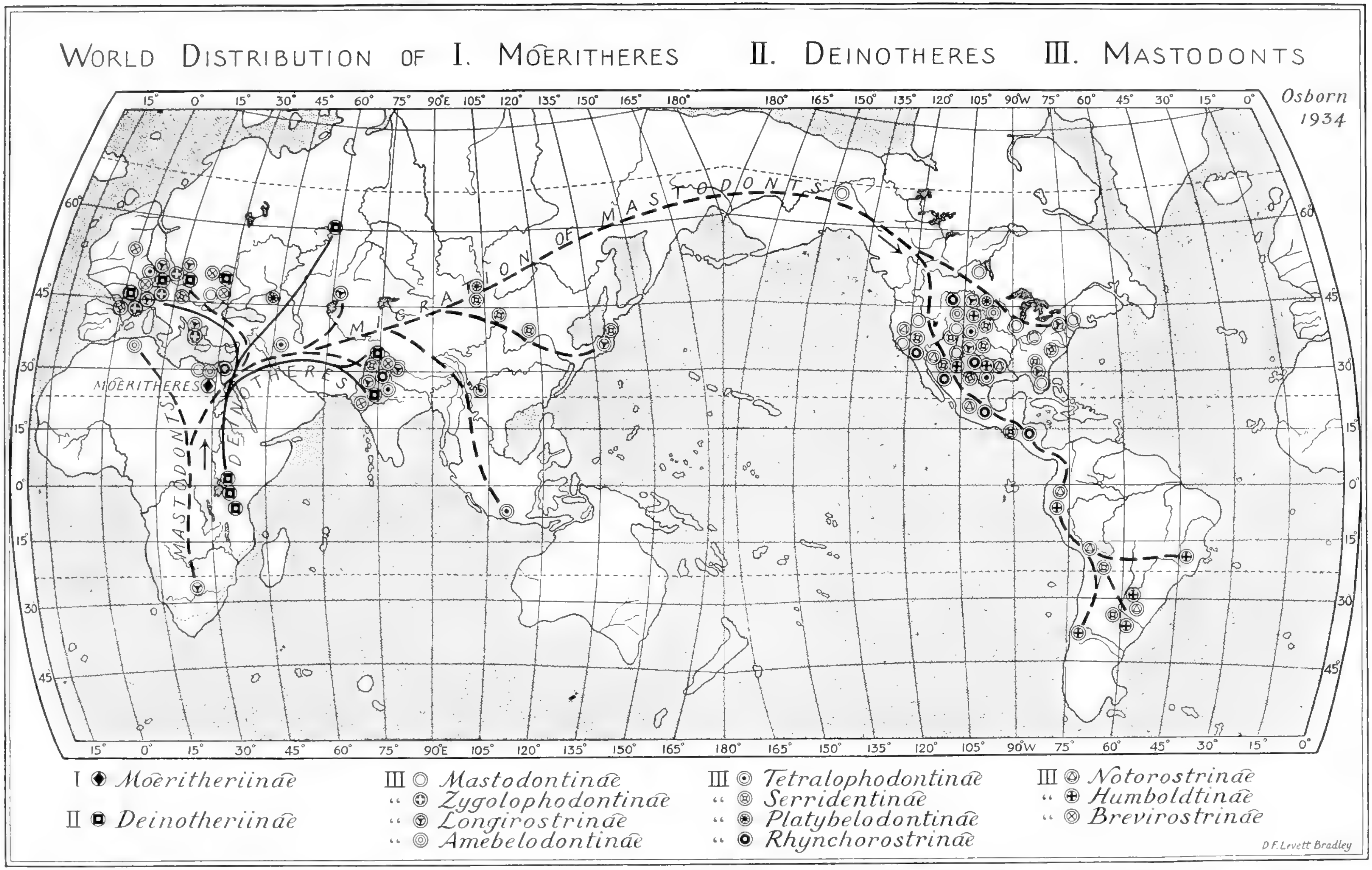

Fig. 1227. Geographic distribution of three of the great primary stocks of the Proboscidea, namely, the Mœritherioidea, Deinotherioidea, and Mastodontoidea. This map, the result of intensive research by the present author over a period of more than thirty years, illustrates the theory put forward in 1899–1900 by Tullberg, Stehlin, and Osborn that Africa was the continent on which the Proboscidea originated (see Vol. I, Chap. II, p. 34, also Fig. 6, and Vol. II, Fig. 1242).

OSBORN'S FINAL (1935)
CLASSIFICATION OF THE MŒRITHERIOIDEA, DEINOTHERIOIDEA, AND MASTODONTOIDEA

Superfamily: MŒRITHERIOIDEA

Fam.: MŒRITHERIIDÆ. Subfam.: MŒRITHERIINÆ

Genus: *Mœritherium*

Primitive aquatic Proboscideans, Hippopotamus-like, or Sirenian-like bodies

MŒRITHERIUM Andrews, 1901		Page
Mœritherium andrewsi Schlosser, 1911, Fayûm, Egypt, Fluvio-marine formation	Lower Oligocene	61, 74
Mœritherium trigodon Andrews, 1904, Fayûm, Egypt, Fluvio-marine formation	Lower Oligocene	57, 74
Mœritherium lyonsi Andrews, 1901, Fayûm, Egypt, Qasr-el-Sagha formation	Upper Eocene	54, 72
Mœritherium gracile Andrews, 1902, Fayûm, Egypt, Qasr-el-Sagha formation	Upper Eocene	56, 73
Mœritherium ancestrale Petronievics, 1923, Fayûm, Egypt, Qasr-el-Sagha(?) formation	Upper Eocene	65, 76

Superfamily: DEINOTHERIOIDEA

Fam.: CURTOGNATHIDÆ. Subfam.: DEINOTHERIINÆ

Genus: *Deinotherium*

Very large downturned inferior tusks, no superior tusks; [flat cranium], elephantine bodies

DEINOTHERIUM Kaup, 1829. Partial list of species		
Deinotherium hopwoodi sp. nov., Olduvai, southeast shore Lake Victoria, Africa	Middle Pleistocene	117
Deinotherium gigantissimum Stefănescu, 1892, Găiceana, Rumania	Lower or Middle Pliocene	95
Deinotherium indicum Falconer, 1845, Perim Island, India	Middle Pliocene	90, 105, 114
Deinotherium giganteum Kaup, 1829, Eppelsheim, Germany	Lower Pliocene	80, 84, 86, 114
Deinotherium uralense Eichwald, 1835, Ural Mountains	Lower Pliocene	85, 87, 114
Deinotherium podolicum Eichwald, 1835, Podolia, Russia	Pliocene (?)	85, 87
Deinotherium intermedium De Blainville, 1845, France	Upper Miocene (?)	85, 90, 115
Deinotherium bavaricum von Meyer, 1831, Gmünd, Bavaria	Upper Miocene	84, 99, 107, 115
Deinotherium hungaricum Éhik, 1930, Kotyháza, Hungary, Burdigalian (?)	Lower Miocene (?)	115, 116
Deinotherium indicum gajense Pilgrim, 1912, Bugti Hills, Baluchistan, Bugti beds	Lower Miocene	85, 105, 115
Deinotherium cuvieri Kaup, 1832, Chevilly, France	Lower Miocene	85, 87, 90, 107, 115
Deinotherium hobleyi Andrews, 1911, Karungu, British East Africa	Lower Miocene	104, 115

Superfamily: MASTODONTOIDEA

Fam.: MASTODONTIDÆ. Subfam. nov.: PALÆOMASTODONTINÆ

Genus: *Palæomastodon*

Superior tusks unknown; inferior tusks short, rounded. Progressive grinders, with six cones, proto- and metaconules closing the median sulcus. Not ancestral to Mastodontinæ

PALÆOMASTODON Andrews, 1901		
Palæomastodon beadnelli Andrews, 1901, Fayûm, Egypt, Fluvio-marine formation	Lower Oligocene	54, 147
Palæomastodon intermedius Matsumoto, 1922, Fayûm, Egypt, Fluvio-marine formation	Lower Oligocene	63, 146
Palæomastodon parvus Andrews, 1905, Fayûm, Egypt, Fluvio-marine formation	Lower Oligocene	59, 146

Fam.: MASTODONTIDÆ. Subfam.: Mastodontinæ

Genera: *Miomastodon, Pliomastodon, Mastodon*

Superior tusks and inferior tusks (when present) rounded, enamel disappearing; typical mastodontine bodies

Species of Eurasia and North America in approximate theoretic descending order, apparently monophyletic, directly ancestral to typical *Mastodon*

Mastodon Cuvier, 1806, 1817. Superior tusks without enamel; molars with median sulcus and progressively sharpened crests

		Page
Mastodon acutidens sp. nov., Rochester, Indiana	Pleistocene—Postglacial (IV)	696
Mastodon americanus alaskensis Frick, 1933, near Fairbanks, Alaska	Pleistocene	176
Mastodon oregonensis Hay, 1926, Rye Valley, Baker County, Oregon	Pleistocene(?)	173
Mastodon americanus plicatus Osborn, 1926, Walnut, Bureau County, Illinois	Late Pleistocene—Postglacial (IV) or post-Wisconsin(?)	173
Mastodon americanus rugosidens Leidy, 1890, Beaufort County, South Carolina	Pleistocene	171
Mastodon raki Frick, 1933, Hot Springs, New Mexico	Pleistocene	175
Mastodon americanus rupertianus Richardson, 1854, Lake Winnipeg basin, Manitoba, Canada	Pleistocene	137
Mastodon americanus Kerr, 1792, Big-Bone Lick, Boone County, Kentucky	Late Pleistocene (IV Glacial = Wisconsin time)	170
Mastodon grangeri Barbour, 1934, Pender, Thurston County, Nebraska	Pleistocene (*1st Interglacial,* Aftonian, or II Glacial)	175, 695
Mastodon moodiei Barbour, 1931, near Milford, Seward County, Nebraska	Pleistocene (II Glacial)	174
Mastodon progenius Hay, 1914, Missouri Valley, Harrison County, Iowa	Early Pleistocene	172
Mastodon pavlowi sp. nov., Pestchana, Podolia, Russia	Pleistocene	694

Pliomastodon Osborn, 1926. Superior tusks with enamel; molar crests intermediate in character (subhypsodont)

Pliomastodon vexillarius Matthew, 1930, near Coalinga, Fresno County, California	Late Pliocene	161
Pliomastodon americanus praetypica Schlesinger, 1919, 1922, Batta-Érd, Hungary	Middle Pliocene	159
Pliomastodon sellardsi Simpson, 1930, Brewster, Florida, Bone Valley formation	Lower Pliocene	160
Pliomastodon matthewi Osborn, 1921–1926, Snake Creek B ["Upper Snake Creek"], Sioux County, western Nebraska	Lower Pliocene	157

Miomastodon Osborn, 1922. Superior tusks with enamel; molars with rounded crests

Miomastodon tapiroides americanus Schlesinger, 1921, 1922, Tasnád, Hungary	Lower Pliocene	156
Miomastodon merriami Osborn, 1921, Thousand Creek, Humboldt County, Nevada, Virgin Valley formation (type)	Middle Miocene	154
Pawnee Creek horizon, Colorado (ref.)	Middle Miocene	155
Miomastodon depereti sp. nov., Chevilly, Sables de l'Orléanais, France	Lower Miocene	693

Fam.: MASTODONTIDÆ. Subfam.: Zygolophodontinæ

Genera: *Zygolophodon, Turicius*

Mastodontoid molar crowns, valleys open, conelets progressively added

Zygolophodon Vacek, 1877. Molars transversely crested, conelets 4–6, valleys open, median sulcus disappearing

Zygolophodon borsoni zaddachi Jentzsch, 1883, Thorn, west Prussia	Upper Pliocene	209
Zygolophodon borsoni Hays, 1834, near Villanova, Asti, Piedmont, Italy (type); western Eurasia (ref.)	Middle to Upper Pliocene	207
Zygolophodon pyrenaicus Lartet MS. (in Falconer, 1857), Lartet, 1859, Ile-en-Dodon (Haute-Garonne), France (type)	Middle Miocene	206
Zygolophodon pyrenaicus aurelianensis Osborn, 1926, Sables de l'Orléanais, Chevilly (?), France	Lower Miocene	207

Turicius Osborn, 1926. Molars transversely crested, conelets 4–25, valleys open, median sulcus disappearing

Turicius wahlheimensis Klähn, 1922, Wahlheim and Esselborn, Rheinhessen, Germany	Pliocene	282
Turicius virgatidens von Meyer, 1867, Fulda, northeast of Frankfort, Germany, 'Gelben Lehme'	Middle (?) Pliocene	221
Turicius atticus Wagner, 1857, Pikermi, Greece	Lower Pliocene	220
Turicius turicensis Schinz, 1824, Elgg, Canton Zurich, Switzerland, Tortonian	Upper Miocene	219
Turicius turicensis simorrensis Osborn, 1926, near Simorre (Gers), France	Upper Middle Miocene	219
Turicius tapiroides Cuvier, 1806, 1821–1824; (in Desmarest, 1820–1822), Calcaire de Montabusard, France	Lower Miocene	217

Fam.: MASTODONTIDÆ. Subfam. nov.: STEGOLOPHODONTINÆ

Genus: *Stegolophodon*

Stegodontoid rounded molar cones, valleys compressed; median sulcus persisting in anterior crests

STEGOLOPHODON Schlesinger, 1917. Molars transversely crested, conelets 4–5+.

		Page
Stegolophodon stegodontoides Pilgrim, 1913, Lehri, Punjab, India, Upper Siwaliks (?)	Upper (?) Pliocene	Pl. IV, I, 701
Stegolophodon cautleyi Lydekker, 1886, Perim Island, India	Middle Pliocene	Pl. IV, H, 701
Stegolophodon sublatidens Schlesinger, 1917, Teschen (Schlesien), Austria	Middle (?) Pliocene	Pl. IV, A
Stegolophodon lydekkeri sp. nov., Bruni, northwest Borneo	Pliocene (?)	Pl. IV, G, 700
Stegolophodon latidens Clift, 1828, near Yenangyaung, Irrawaddy River, Burma, Irrawaddy Series (fluviatile)	Lower Pliocene[1]	Pl. IV, D,E,F,701
Stegolophodon nathotensis Osborn, 1929, Nathot, Lower Middle Siwaliks, India, Lower Chinji horizon	Mio-Pliocene	Pl. IV, C
Stegolophodon cautleyi progressus Osborn, 1929, near Chinji Bungalow, summit of Lower Chinji, 2,000 feet above base of Lower Siwaliks, India	Mio-Pliocene	Pl. IV, B

Fam.: BUNOMASTODONTIDÆ. Subfam.: RYHNCHOROSTRINÆ

Genera: *Rhynchotherium, Blickotherium, Aybelodon*

Typical beak-jawed Mastodonts. Mandible strongly deflected; enamel band on superior and inferior incisive tusks (excepting *Aybelodon*), inferior tusks upturned; molars with variable central conules, enamel thick, few ridge-crests (4–5)

RHYNCHOROSTRINES OF THE WESTERN UNITED STATES AND MEXICO

RHYNCHOTHERIUM Falconer, 1856 (MS.), 1863, 1868

Rhynchotherium falconeri Osborn, 1923, Mt. Blanco, Staked Plains, Texas	Upper Pliocene	494
Rhynchotherium shepardi edense Frick, 1921, Mt. Eden Hot Springs, San Bernardino County, California	Upper Pliocene	496
Rhynchotherium browni sp. nov., San José de Pimas, Sonora, Mexico	Upper Pliocene	494
Rhynchotherium tlascalæ Osborn, 1918, 1921, Tlascala, Valley of Mexico	Upper(?) Pliocene	493
(?)*Rhynchotherium francisi* Hay, 1926, Brazos River, Pittbridge, Burleson County, Texas	Pliocene(?)	501
Rhynchotherium anguirivale Osborn, 1926, Snake Creek B, Sioux County, Nebraska	Lower Pliocene	491
Rhynchotherium rectidens Osborn, 1923, near Pawnee Buttes, Weld County, Colorado, Pawnee Creek horizon	Upper Miocene	488
Rhynchotherium shepardi Leidy, 1871, Dry Creek, Stanislaus County, California	Upper(?) Miocene	487
Rhynchotherium brevidens Cope, 1889, Smith River, Meagher County, Montana, Deep River horizon	Middle to Upper Miocene	485

RHYNCHOROSTRINES OF ASIA AND AFRICA

Rhynchotherium chinjiense Osborn, 1929, near Chinji Bungalow, India, 600 feet above base of Lower Siwaliks	Mio-Pliocene	502
Rhynchotherium spenceri Fourtau, 1918, Moghara Desert, northern Egypt	Middle Miocene	485

RHYNCHOROSTRINES OF CENTRAL AMERICA

BLICKOTHERIUM Frick, 1933. Mandible progressively slender; incisors with enamel

Blickotherium blicki Frick, 1933, near Tapasuma, Honduras	Pliocene	508
Blickotherium euhypodon Cope, 1884, Driftwood Creek, Hitchcock County, Nebraska, Republican River beds	Lower Pliocene	489

AYBELODON Frick, 1933. Mandible attenuate; inferior incisors without enamel

Aybelodon hondurensis Frick, 1933, near Tapasuma, Honduras	Pliocene	509

Fam.: BUNOMASTODONTIDÆ. Subfam.: LONGIROSTRINÆ

Genera: *Trilophodon, Megabelodon*

Intermediate molars trilophodont (3 crests); third molars with 4–5+ crests and *central conules*. Superior tusks flattened, recurved, with enamel band; inferior tusks rounded, triangular, flattened-horizontal, flattened-oblique, massive, sometimes absent. Mandible hyperlongirostral

TRILOPHODON OF EURASIA AND AFRICA

TRILOPHODON Falconer, 1846, 1857

Trilophodon hasnotensis sp. nov., near Hasnot, India, 1,000 feet below Bhandar bone bed (=Dhok Pathan horizon)	Middle Pliocene	279
Trilophodon esselbornensis Klähn, 1922, Esselborn, Westhofen, Rheinhessen, Germany	Pliocene	281
Trilophodon (*Choerolophodon*) *pentelicus* Gaudry and Lartet, 1856–1862, Pikermi, Greece (type)	Lower Pliocene	263
Samos Island (ref.)	Lower Pliocene	264

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[1] [See page 824 above where reasons are given for regarding this species as of Lower Pleistocene age.—Editor.]

		Page
Trilophodon sendaicus Matsumoto, 1924, Kitayama, near Sendai, Province of Rikuzen, Japan	Lower Pliocene	280
Trilophodon connexus Hopwood, 1935, Kansu, China	Miocene	702
Trilophodon spectabilis Hopwood, 1935, locality and horizon unknown		702
Trilophodon inopinatus Borissiak and Belïaeva, 1928, Jilančik beds, Turgai region, Central Asia	Miocene	278
Trilophodon angustidens var. *libycus* Fourtau, 1918, Moghara, northern Egypt, Africa	Lower(?) Miocene	260
Trilophodon macrognathus Pilgrim, 1913, near Chinji, India, Upper Chinji	Mio-Pliocene	274
Trilophodon chinjiensis Pilgrim, 1913, Osborn, 1932, near Chinji Bungalow, Lower Chinji	Mio-Pliocene	272
Trilophodon angustidens gaillardi Osborn, 1929, Villefranche d'Astarac (Gers), France	Upper(?) Miocene	259
Trilophodon engelswiesensis Klähn, 1922, Engelswies, Baden, Germany	Miocene	281
Trilophodon steinheimensis Klähn, 1922, Steinheim, Baden, Germany	Middle to Upper Miocene	281
Trilophodon angustidens var. *austro-germanicus* Wegner, 1908, 1913, Oppeln, eastern Germany	Middle Miocene	259
Trilophodon palæindicus Lydekker, 1884, near Kamlial, northern Punjab, India, Kamlial horizon	Middle Miocene	268
Trilophodon pandionis Falconer, 1857, Larkana district, Sind, India, Lower Manchhar	Middle Miocene	267
Trilophodon angustidens minutus Cuvier, 1806, 1824, Saxony	Middle Miocene	252
Trilophodon angustidens Cuvier, 1806, 1817, Simorre, France	Middle Miocene	252
Trilophodon angustidens cuvieri Pomel, 1848, Gers and Sables de l'Orléanais, France	Lower Miocene	250
Trilophodon angustidens gaujaci Lartet, 1851, Lombez, France	Middle(?) Miocene	250
Trilophodon cooperi Osborn, 1932, near Dera Bugti, Baluchistan, Bugti horizon	Lower Miocene	275
Trilophodon pontileviensis Mayet-Fourtau, 1918, Chevilly, Pontlevoy, Sables de l'Orléanais, France	Lower Miocene	283

TRILOPHODON (TYPICAL, CF. T. ANGUSTIDENS), 'PROD-TUSKERS' ('SCAPTOBELODONTS') OF AMERICA

Mandible slender, nearly horizontal or slightly decurved; tusks rounded, rodlike or oval, horizontal or directed upwards

Trilophodon pojoaquensis Frick, 1926, Santa Fé marls, New Mexico	Mio-Pliocene	320
Trilophodon (Genomastodon) osborni Barbour, 1916, Bristow, Boyd County, Nebraska	Lower Pliocene	298
Trilophodon abeli Barbour, 1925, Devil's Gulch, Brown Co., Nebraska	Lower Pliocene	311
Trilophodon (Genomastodon) willistoni Barbour, 1914, Devil's Gulch, Niobrara River, Brown County, Nebraska	Lower Pliocene	293
Trilophodon fricki Peterson, 1928, Brown's Park formation, flanks of Douglas Mountain, Moffat County, Colorado	Middle to Upper Miocene	312

TRILOPHODON (TATABELODON), 'ANCIENT-TUSKERS'

Mandible massive at symphysis, inferior incisors elongate, rounded or triangular, of massive cross-section

Trilophodon (Tatabelodon) riograndensis Frick, 1933, Santa Fé marls, Battleship Mountain, New Mexico	Mio-Pliocene	324
Trilophodon (Tatabelodon) gregorii Frick, 1933, Ainsworth, Nebraska	Lower Pliocene	324

TRILOPHODON, 'OBLIQUE-TUSKERS'

Mandible massive, laterally compressed, more or less strongly decurved; tusks oblique or laterally flattened, directed downwards

Trilophodon dinotherioides Andrews, 1909, northwestern Kansas (?Republican River)	Lower Pliocene	291
Trilophodon ligoniferus Cope and Matthew, 1915, Black Hills, South Dakota (?Republican River level)	Lower(?) Pliocene	298
Trilophodon giganteus Osborn, 1921, Eastview, near Dallas, Gregory County, South Dakota	Lower Pliocene	304

TRILOPHODON OF EASTERN COAST OF NORTH AMERICA

Trilophodon (?Tetralophodon) brazosius Hay, 1923, Brazos River, near San Felipe, Texas	Pliocene(?)	374
Trilophodon simplicidens Osborn, 1923, Bone Valley formation, near Pierce, Polk County, Florida	Lower Pliocene	285
Trilophodon obscurus Leidy, 1869, Greensburgh, Caroline County, Maryland (?Choptank formation)	Miocene(?)	285

MEGABELODON, 'SPOONBILL MASTODONTS'

MEGABELODON Barbour, 1914, 1917. Mandible tuskless, round in section, extremely elongate, straight or slightly deflected, slender

Megabelodon lulli Barbour, 1914, 1917, Snake River, Cherry County, Nebraska	Lower(?) Pliocene	294
Megabelodon joraki Frick, 1933, Santa Fé marls, Santa Cruz, New Mexico	Mio-Pliocene	326
Megabelodon cruziensis Frick, 1933, Santa Fé marls, Santa Cruz, New Mexico	Mio-Pliocene	323
Trilophodon phippsi[1] Cook, 1928, Ainsworth, Brown County, Nebraska	Lower Pliocene	315

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[1] [This species is included with *Megabelodon* because of its tuskless mandible. It was evidently the intention of Professor Osborn to place *Trilophodon phippsi* in the genus *Megabelodon*. See footnote on page 329 of Volume I.—Editor.]

Fam.: BUNOMASTODONTIDÆ. Subfam.: GNATHABELODONTINÆ

Genus: *Gnathabelodon*

Mandible tuskless, elongate, spreading broadly at edentulous rostrum, horizontal; no inferior tusks, superior tusks massive, rounded, without enamel, upcurved, elongate. Molars of bunomastodont type, with central conules

GNATHABELODON Barbour and Sternberg, 1935		Page
Gnathabelodon thorpei Barbour and Sternberg, 1935, Ogallah, Trego County, western Kansas	Middle(?) Pliocene	713

Fam.: BUNOMASTODONTIDÆ. Subfam.: AMEBELODONTINÆ

Genera: *Phiomia, Amebelodon*

PHIOMIA-AMEBELODON, 'SHOVEL-TUSKERS' OF NORTHERN AFRICA AND NORTH AMERICA

Mandible elongate, slightly upcurved; [lower] tusks elongate, broadened, appressed, alveolar portion concave. Conules large

AMEBELODON Barbour, 1927. Inferior incisors with concentric dentinal laminæ

Amebelodon fricki Barbour, 1927, Freedom, Frontier County, Nebraska	Middle Pliocene	335
Amebelodon (Trilophodon) hicksi Cook, 1922, Wray, Yuma County, Colorado	Middle Pliocene(?)	307
Amebelodon (Trilophodon) paladentatus Cook, 1922, Wray, Yuma County, Colorado	Middle Pliocene	309
Amebelodon sinclairi Barbour, 1930, Freedom, Frontier County, Nebraska	Middle Pliocene	337

ANCESTRAL AMEBELODONTINÆ OF NORTH AFRICA

PHIOMIA Andrews and Beadnell, 1902. [Inferior tusks with concentric dentinal laminæ]

Phiomia pygmæus Depéret, 1897, Cartennien de Kabylie, near Isserville, Algeria	Upper(?) Oligocene	246
Phiomia osborni Matsumoto, 1922, Fluvio-marine of the Fayûm, Egypt	Lower Oligocene	64, 244
Phiomia wintoni Andrews, 1905, Fluvio-marine of the Fayûm, Egypt	Lower Oligocene	60, 241
Phiomia wintoni (cf. *serridens*) Andrews ref., Quarry B, Fayûm, Egypt	Lower Oligocene	240, 241
Phiomia serridens Andrews and Beadnell, 1902, Fluvio-marine of the Fayûm, Egypt	Lower Oligocene	55, 239
Phiomia minor Andrews, 1904, Fluvio-marine of the Fayûm, Egypt	Lower Oligocene	58, 239

Fam.: BUNOMASTODONTIDÆ. Subfam.: TETRALOPHODONTINÆ

Genera: *Tetralophodon, Morrillia*

Second molars tetralophodont. Mandibles and inferior tusks of medium length (medilongirostral). Inferior tusks flattened, oval; superior tusks enamel banded

TETRALOPHODONTS OF EURASIA

(?)Subgenus LYDEKKERIA Osborn, 1924. Mio-Pliocene. Third molars four to five crested, brachyodont; single to rudimentary double trefoils

Tetralophodon (Lydekkeria) falconeri Lydekker, 1877, Potwár district, Punjab, India [Dhok Pathan horizon]	Middle Pliocene	354
Tetralophodon (Lydekkeria) sinensis Koken, 1885, Yunnan, China	Mio-Pliocene	355

TETRALOPHODON Falconer, 1847, 1857. Ridge-crests 5½–6, brachyodont; double trefoils

Tetralophodon punjabiensis Lydekker, 1886, Punjab, Siwaliks, India [Dhok Pathan horizon]	Middle Pliocene	362
Tetralophodon grandincisivus Schlesinger, 1917, Maragha, Persia	Lower(?) Pliocene	360
Tetralophodon bumiajuensis van der Maarel, 1932, Bumiaju, central Java	Pliocene	365
Tetralophodon gigantorostris Klähn, 1922, Bermersheim, Rheinhessen, Germany	Pliocene	282
Tetralophodon longirostris Kaup, 1832, Eppelsheim, Germany	Lower Pliocene	357
Tetralophodon exoletus Hopwood, 1935, Shansi, China, Pontian	Lower Pliocene	704

TETRALOPHODONTS OF NORTH AMERICA

MORRILLIA Osborn, 1924. Ridge-crests 7½–8⅓, hypsodont; double trefoils, thickly coated with cement

Morrillia barbouri Osborn, 1921, Cambridge, Furnas County, Nebraska	Middle Pleistocene	377

TETRALOPHODON

Tetralophodon elegans Hay, 1917, McPherson, Kansas	Middle(?) Pliocene	372
Tetralophodon campester Cope, 1878, Sappa Creek, Rawlins County, Kansas, Republican River horizon	Lower Pliocene	369
Tetralophodon fricki sp. nov., near Clarendon, northern Texas	Lower to Middle Pliocene	375

Fam.: BUNOMASTODONTIDÆ. Subfam.: NOTOROSTRINÆ

Genus: *Cordillerion*

True Notorostrines typified by '*Mastodon*' *andium*. Mandible brevirostral. Superior tusks spiral or horizontal, with broad enamel band. Inferior tusks wanting in adult stages; probably present in juvenile stages. Molars persistently brachyodont with single trefoils, paralleling *Trilophodon*; ridge-crests 4–4½–5½.

CORDILLERION Osborn, 1926		Page
Cordillerion andium Cuvier, 1806, 1824, near volcano of Imbaburra, Quito, Ecuador	Pleistocene	549
Cordillerion tarijensis Ameghino, 1902, Valley of Tarija, Bolivia	Pleistocene	550
Cordillerion bolivianus Philippi, 1893, Ulloma, Bolivia	Pleistocene	551

CORDILLERION OF MEXICO

Cordillerion tropicus Cope, 1884, State of Michoacan, Valley of Mexico	Pliocene or Pleistocene	553
Cordillerion oligobunis Cope, 1893, Tequixquiac, Valley of Mexico	Pliocene or Pleistocene	554
Cordillerion oligobunis antiquissimus Freudenberg, 1922, Valley of Amajaque, Hidalgo, Mexico	Pliocene	555
Cordillerion(?) *oligobunis intermedius* Freudenberg, 1922, Mexico, exact locality not recorded	Pliocene or Pleistocene	557
Cordillerion oligobunis progressus Freudenberg, 1922, Canada de Aculcingo, Mexico	Pliocene or Pleistocene	558
Cordillerion(?) *oligobunis felicis* Freudenberg, 1922, Puebla, Mexico	Pliocene	556

CORDILLERION OF SOUTHWESTERN UNITED STATES

Cordillerion edensis Osborn, 1922, Mt. Eden Hot Springs, San Bernardino County, California	Upper Pliocene	560
Cordillerion bensonensis Gidley, 1926, near Benson, Cochise County, Arizona, San Pedro formation	Upper Pliocene	565
Cordillerion gratum Hay, 1917, Brazos River, Pittbridge, Burleson County, Texas	Pliocene	559
Cordillerion defloccatus Hay, 1926, Aransas River, San Patricio County, near Sinton, Texas	Pliocene(?)	564
Cordillerion orarius Hay, 1926, Aransas River, San Patricio County, near Sinton, Texas	Pliocene(?)	562

Fam.: BUNOMASTODONTIDÆ. Subfam.: BREVIROSTRINÆ

Genera: *Pentalophodon, Anancus, Synconolophus*

Mandible rapidly abbreviating, in correlation with loss of lower tusks; completely brevirostral in Upper Pliocene time. Grinding teeth, originally short crowned, brachyodont, finally becoming subhypsodont with folded enamel, ptychodont; internal and external cones progressively alternating and proverted; central conules

PENTALOPHODON OF INDIA

PENTALOPHODON Falconer, 1857, 1865. Five-crested 'intermediate molars'		
Pentalophodon sivalensis Cautley, 1836, vicinity of Nahun, southeast India, Upper Siwaliks(?)	Upper Pliocene	650
Pentalophodon falconeri sp. nov., Upper Siwaliks, Tatrot (?), 1,000 feet above Middle Pliocene Dhok Pathan, India	Upper Pliocene	653

ANANCUS OF EURASIA

ANANCUS Aymard, 1855, 1859. Superior tusks straight, attaining great length. Four-crested intermediate molars		
Anancus falconeri Osborn, 1926, Red or Norwich Crag of Suffolk, England	Uppermost Pliocene	636
Anancus arvernensis Croiz. & Job., 1828, Perrier, Auvergne, France, Villafranchian-Astian	Upper Pliocene	632
Anancus arvernensis brevirostris Gervais and de Serres, 1846, Montpellier, Hérault, France	Upper Pliocene	634
Anancus perimensis Falconer and Cautley, 1847, Perim Island, India [=Dhok Pathan]	Middle Pliocene	643
Anancus minutoarvernensis Klähn, 1922, Herbolzheim, Baden, Germany	Pliocene	283
Anancus gigantarvernensis Klähn, 1922, Herbolzheim, Baden, Germany	Pliocene	283
Anancus intermedius Eichwald, 1831, Volhynia, Russia	Pliocene	639
Anancus arvernensis progressor Khomenko, 1912, southern Bessarabia, Russia	Pliocene	639
Anancus properimensis sp. nov., near Chinji Bungalow, Lower Chinji, 800 feet above base of Lower Siwaliks	Mio-Pliocene	647
Anancus sinensis Hopwood, 1935, Shansi, China	Pliocene(?)	721

SYNCONOLOPHUS OF INDIA

SYNCONOLOPHUS Osborn, 1929. Warped, compacted conelets and conules, no trefoils		
Synconolophus dhokpathanensis Osborn, 1929, Dhok Pathan, level of *Hipparion punjabiense* (?) ref. quarry, 500 feet below top of Middle Siwaliks, India	Middle Pliocene	661
Synconolophus hasnoti Pilgrim, 1913, near Bhimbar, India [=Dhok Pathan horizon]	Middle Pliocene	659
Synconolophus corrugatus Pilgrim, 1913, Hasnot, India [=Dhok Pathan horizon]	Middle Pliocene	658
Synconolophus propathanensis Osborn, 1929, near Dhok Pathan, India, *Hipparion* quarry level, 500 feet below top of Middle Siwaliks (Dhok Pathan horizon)	Middle Pliocene	665
Synconolophus ptychodus Osborn, 1929, near Chinji Bungalow, India, Lower Chinji, 800 feet above base of Lower Siwaliks	Mio-Pliocene	657

Fam. nov.: HUMBOLDTIDÆ. Subfam.: HUMBOLDTINÆ

Genera: *Cuvieronius, Eubelodon, Stegomastodon*

Superior tusks without enamel. Molars with single, double, or quadruple trefoils; ridge-crests 4½ to 7½; inferior ridge-crests proverted; superior ridge-crests transverse, centroverted, or retroverted. Central conules rudimentary or wanting.

All species below arranged in ascending order of the evolution of the grinding teeth. Geologic levels of South American species uncertain.

NORTH AMERICAN SPECIES

		Page
EUBELODON Barbour, 1914. Grinders broad, double trefoils		
Eubelodon morrilli Barbour, 1914, Devil's Gulch B, Brown County, Nebraska	Middle(?) Pliocene	602

SOUTH AMERICAN SPECIES

CUVIERONIUS Osborn, 1923. Grinders broad, double trefoils; single trefoils in primitive species		
Cuvieronius humboldtii Cuvier, 1806 (in Desmarest, 1818), near Concepcion, Chile [Ecuador?]	Pleistocene	576
Cuvieronius platensis Ameghino, 1888, San Nicolás de los Arroyos, Province of Buenos Aires, Argentina, Lower Pampean formation	Pleistocene	579
Cuvieronius superbus Ameghino, 1888, Pergamino, Province of Buenos Aires, Argentina, probably Superior Pampean	Pleistocene	580
Cuvieronius bonaerensis Moreno, 1888, Arrecifes, Province of Buenos Aires, Argentina, Lower Pampean	Pleistocene	579
Cuvieronius rectus Ameghino, 1889, Ensenada, near La Plata, Argentina	[Pleistocene]	580
Cuvieronius maderianus Ameghino, 1891, Puerto Madero in Buenos Aires, Argentina	[Pleistocene]	581
Cuvieronius chilensis Philippi, 1893, near Lake Tagua-Tagua, Chile	[Pleistocene]	581
Cuvieronius pirayuiensis Gez, 1915, Corrientes, Argentina	[Pleistocene]	582
Cuvieronius brasiliensis Lund (in Lesson, 1842), valley of the Velhas River, Province of Minas Geraes, Brazil, limestone cave	[Pleistocene]	578
Cuvieronius postremus Spillmann, 1928–1931, Quebrada of Cachihuayco, near Alangasi, Province of Pichincha, Ecuador	Superior Pleistocene	585
Cuvieronius ayoræ Spillmann, 1928–1931, Quebrada of Chalang, near Punin, Province of Chimborazo, Ecuador	Pleistocene	583

STEGOMASTODON OF NORTH AMERICA

STEGOMASTODON Pohlig, 1912. Grinders with quadruple to multiple trefoils completely blocking the valleys; inferior ridge-crests proverted; cones ptychodont, labyrinthodont, subhypsodont		
Stegomastodon priestleyi Hay and Cook, 1930, near Frederick, Tillman County, Oklahoma	[Pleistocene]	684
Stegomastodon primitivus sp. nov., near Ainsworth, Nebraska	Lower Pleistocene	726
Stegomastodon mirificus Leidy, 1858, "Loup Fork of Platte River," Nebraska [probably near Seneca, Thomas County, Nebraska (*fide* Hay, 1924, p. 100); Hooker County? (*fide* Lugn and Schultz, 1934, p. 372)]	Upper Pliocene(?)[1]	669
Stegomastodon successor Cope, 1892, Blanco formation, Texas	Upper Pliocene	671
Stegomastodon texanus Osborn, 1924, Llano Estacado, Texas, Blanco formation	Upper Pliocene	673
Stegomastodon arizonæ Gidley, 1924, 1926, Curtis Flats, Cochise County, Arizona, San Pedro beds	Uppermost Pliocene	678
Stegomastodon aftoniæ Osborn, 1924, near Akron, Plymouth County, Iowa	Lower Pleistocene[2]	682
INCERTÆ SEDIS		
Stegomastodon chapmani Hay, 1834, 1843, unrecorded locality in United States		669

Fam. nov.: SERRIDENTIDÆ. Subfam.: SERRIDENTINÆ

Genera: *Serridentinus, Ocalientinus, Serbelodon, Trobelodon*

Serrate-toothed mastodonts. Superior and inferior molars universally characterized by more or less perfectly developed and serrated crests springing from the ectoconelets of the inferior molars, from the entoconelets of the superior molars. Generic divergence chiefly in inferior incisors—horizontal oval in *Serridentinus*, oval, greatly enlarged in *Serbelodon*, flattened into a pair of broad shovels in *Platybelodon*, abbreviated and rounded in *Torynobelodon*, and entirely wanting, with brevirostral mandible, in *Notiomastodon*.

SERRIDENTINES OF EURASIA

SERRIDENTINUS Osborn, 1923		
Serridentinus hasnotensis Osborn, 1929, near Hasnot, India, Upper Middle Siwaliks (Dhok Pathan horizon)	Middle Pliocene	452
Serridentinus metachinjiensis Osborn, 1929, near Chinji Bungalow, India, Lower Chinji, 800 feet above base of Lower Siwaliks (cf. *S. productus*)	Mio-Pliocene	456

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[1] [Lower to Middle Pleistocene (see footnote on page 669 of Volume I).—Editor.]

[2] [Lower to Middle Pleistocene (see footnote on page 671 of Volume I).—Editor.]

		Page
Serridentinus prochinjiensis Osborn, 1929, near Chinji Bungalow, India, Lower Chinji, 600 feet above base of Lower Siwaliks, small, primitive (cf. *S. productus*)	Mio-Pliocene	457
Serridentinus chinjiensis Osborn, 1929, near Chinji Bungalow, India, Lower Chinji, 700 feet above base of Lower Siwaliks, sharp crested (cf. *S. serridens*)	Mio-Pliocene	456
Serridentinus browni Osborn, 1926, near Chinji Bungalow, India, Lower Chinji, 800 feet above base of Lower Siwaliks, blunt crested (cf. *S. productus*)	Mio-Pliocene	452
Serridentinus gobiensis Osborn and Granger, 1932, near Iren Dabasu, Inner Mongolia, Tung Gur	Upper Miocene	398
Serridentinus mongoliensis Osborn, 1924, Loh formation, Mongolia, blunt crested	Lower to Middle Miocene	396

Serridentines of China and Japan

Serridentinus lydekkeri Schlosser, 1903 (1906), Red Clays, North China	Lower Pliocene(?)	457
Serridentinus wimani Hopwood, 1935, Kansu, China	Miocene(?)	732
Serridentinus annectens Matsumoto, 1924, Province of Mino, Japan, Hiramaki formation, probably Burdigalian	Lower Miocene	457

Serridentines of Europe

Serridentinus subtapiroideus Schlesinger, 1917, Wies, near Eibiswald (Styria), Austria (Lower Helvetian)	Lower Middle Miocene	394
Serridentinus filholi Frick, 1926, 1933, Gers, France	Lower Miocene	473

Serridentines of North and Central America

Sharp-crested Forms

Serridentinus serridens cimarronis Cope, 1893, east of Llano Estacado, Texas, Clarendon formation, *Procamelus-Hipparion* zone	Lower Pliocene	429
Serridentinus serridens Cope, 1884, Clarendon formation, Texas	Lower Pliocene	423
Serridentinus anguirivalis Osborn, 1926, Snake Creek B, Sioux County, western Nebraska	Lower Pliocene	425
Serridentinus brewsterensis Osborn, 1926, Brewster, Polk County, Florida, Bone Valley formation	Lower Pliocene	430

Blunt-crested Forms

Serridentinus guatemalensis Osborn, 1926, Chinautla, Guatemala	Upper Pliocene	432
Serridentinus progressus Osborn, 1923, Driftwood Creek, Hitchcock County, Nebraska	Pliocene(?)	401
Serridentinus (*Ocalientinus*?) *nebrascensis* Osborn, 1924, Snake Creek B, Sioux County, Nebraska	Lower Pliocene	473
Serridentinus productus Cope, 1875, Santa Fé marls, New Mexico (type)	Upper Miocene	404
Clarendon formation, Texas (ref.)	Lower Pliocene	404
Serridentinus proavus Cope, 1873, Pawnee Buttes, Pawnee Creek B, Weld County, Colorado	Upper Miocene	403

Incertæ sedis

Serridentinus barstonis Frick, 1933, Mohave Desert, California, Barstow beds	Mio-Pliocene	447

Ocalientinus of Mongolia

OCALIENTINUS Frick, 1933. Trefoils florescent; mandible longirostral, deeply grooved above; inferior tusks of 'prod-tusk' type

Ocalientinus florescens Osborn, 1929, Kholobolchi Nor region, Khunuk formation, Mongolia	Pliocene	397

Ocalientinus of North America

Ocalientinus obliquidens Osborn, 1926, Charleston, South Carolina, phosphate beds	Upper Pliocene, redeposited in Lower Pleistocene	419
Ocalientinus bifoliatus Osborn, 1929, Brewster, Polk County, Florida, Alachua clays	Lower Pliocene	415
Ocalientinus floridanus Leidy, 1886, near Williston, Levy County, Florida, Alachua clays	Lower Pliocene	416
Ocalientinus floridanus leidii Frick, 1926, near Williston, Levy County, Florida, Alachua clays	Lower Pliocene	419
Ocalientinus republicanus Osborn, 1926, Republican River formation, northwestern Kansas	Lower Pliocene	414
Ocalientinus ojocaliensis Frick, 1933, Ojo Caliente, New Mexico, Santa Fé marls (upper)	Mio-Pliocene	435
Ocalientinus emmonsi Hay, 1930, marl beds of Halifax County, North Carolina	Miocene	733

Serbelodon of North America

SERBELODON Frick, 1933, 'sub-shovel-tuskers.' Mandible massive, inferior tusks concavo-convex, increasingly massive, without dentinal rod-cones

Serbelodon burnhami Osborn, 1933, near Ricardo, San Bernardino County, California	Upper Pliocene	444
Serbelodon barbourensis Frick, 1933, near Ainsworth, Nebraska, Christmas quarry	Lower Pliocene	443

Phyletic relationship uncertain

Serbelodon(?) *præcursor* Cope, 1892, 1893, Mt. Blanco, Llano Estacado, Blanco formation, Texas, sharp crested, trefoils simple, cement in valleys	Upper Pliocene	431

TROBELODON OF NORTH AMERICA

		Page
TROBELODON Frick, 1933, 'sub-shovel-tuskers.' [Inferior tusks moderately heavy, biconvex, pointed]		
Trobelodon taoensis Frick, 1933, Santa Cruz, New Mexico, Santa Fé marls (rare)	Mio-Pliocene	446

Fam. nov.: SERRIDENTIDÆ. Subfam.: PLATYBELODONTINÆ

Genera: *Platybelodon, Torynobelodon*

PLATYBELODONTS OF ASIA AND NORTH AMERICA

PLATYBELODON Borissiak, 1928, 1929, typical 'flat-tuskers.' Incisors solid with closely compacted rod-cones		
Platybelodon danovi Borissiak, 1928, Kuban region, North Caucasus, Chokrak beds	Upper Miocene	461
Platybelodon grangeri Osborn, 1929, Tairum Nor basin, Mongolia, Tung Gur horizon	Upper Miocene	463
TORYNOBELODON Barbour, 1929, 'dredge-tuskers.' [Inferior tusks with dentinal rod-cones]		
Torynobelodon loomisi Barbour, 1929, Sand Canyon, east of Indian Hill, vicinity of Republican City, Harlan County, Nebraska	Middle Pliocene	338
Torynobelodon barnumbrowni Barbour, 1931, Pliocene gravels on Snake River, Cherry County, Nebraska	Pliocene	470

Fam. nov.: SERRIDENTIDÆ. Subfam. nov.: NOTIOMASTODONTINÆ

Genus: *Notiomastodon*

SERRIDENTINES OF SOUTH AMERICA

NOTIOMASTODON Cabrera, 1929, [brevirostal mandible, tusks wanting].		
Notiomastodon ornatus Cabrera, 1929, Monte Hermoso, Province of Buenos Aires, Argentina	Lower Pleistocene(?)	590, 731
Notiomastodon argentinus Ameghino, 1888, Valley of Tarija, Argentina, exact locality unrecorded	Pliocene	550

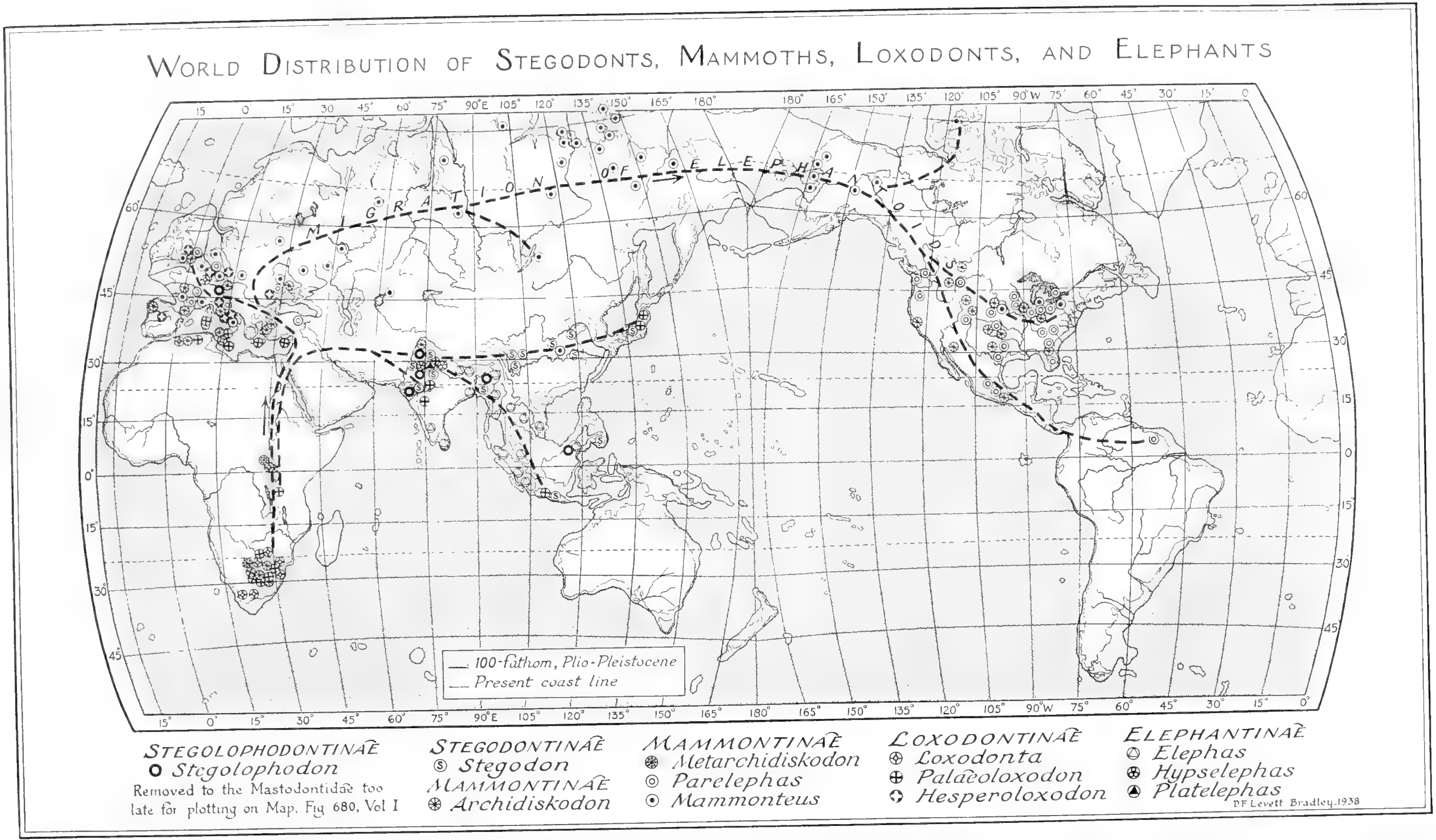

Fig. 1228. Geographic distribution of two of the five great primary stocks of the Proboscidea, namely, the Stegodontoidea and the Elephantoidea (cf. Fig. 680 of Vol. I, for similar distribution of the Mœritherioidea, Deinotherioidea, and Mastodontoidea). It will be observed that the Stegolophodontinæ appear on the accompanying map, inasmuch as Professor Osborn's decision to remove this subfamily to the Mastodontoidea, family Mastodontidæ, was arrived at too late for inclusion in figure 680 [Fig. 1227 of present chapter].

OSBORN'S FINAL (1935)
CLASSIFICATION OF THE STEGODONTOIDEA AND ELEPHANTOIDEA

The classification of the superfamilies, families, and subfamilies of the Proboscidea first adopted by Osborn (1933) will be found on pages 30 to 33 of Chapter II, Volume I, of the present Memoir. Osborn's final (1935) classification of the Mœritherioidea, Deinotherioidea, and Mastodontoidea immediately precedes this list, and, like the following list of the Stegodontoidea and Elephantoidea, embraces the genera and species regarded by him as valid.

Superfamily: STEGODONTOIDEA

Fam.: STEGODONTIDÆ Subfam.: STEGODONTINÆ

Genus: *Stegodon*

Phylum parallel to that of the true *Archidiskodon* and *Elephas*, not directly ancestral. Crania subelephantoid to extremely abbreviated (female?), to more elongated (male?), to triangular in form. Tusks attaining great dimensions. Molars generally more brachyodont than those of the Elephantoidea; ridge-crests increasing from nine to fifteen and a half in the third lower molars; conelets multiplying by binary fission to 20+. In section, the valleys separating the adjacent ridges are found to be closed or V-shaped, whereas in the elephantoid molars the valleys are open or U-shaped.

STEGODON Falconer and Cautley, 1847, 1857		Page
Stegodon insignis Falconer and Cautley, 1845, 1846, Siwalik Hills, India	Lower Pleistocene to Upper Pleistocene	836, 866, 874
Stegodon ganesa Falconer and Cautley, 1845, 1846, Siwalik Hills, India	Lower Pleistocene to Upper Pleistocene	836, 869, 874
Stegodon airâwana Martin, 1890, Alas-Tuwa, Trinil, Java, Kendeng-Schichten	Middle(?) Pleistocene	836, 885
Stegodon ganesa javanicus [=*S. airâwana* or *S. trigonocephalus*] Dubois, 1908, Trinil, Kendeng-Schichten, Java	Middle Pleistocene	836, 889
Stegodon orientialis shôdoënsis Matsumoto, 1924, island of Mitsugo (Mitsugo-shima) and island of Shôdo, Inland Sea, Japan	Middle Pleistocene	836, 893
Stegodon (*Archidiskodon?*) *mindanensis* Naumann, 1890, Mindanao, Philippine Islands	Lower(?) to Middle Pleistocene	836, 892
Stegodon trigonocephalus Martin, 1887, probably vicinity of Surakarta, Java	Lower(?) Pleistocene (*fide* Matsumoto)	836, 890
Stegodon pinjorensis Osborn, 1929, near Siswan, India, upper levels of Pinjor horizon	Lower Pleistocene	836, 883
Stegodon orientalis Owen, 1870, near Chungkingfoo, Szechuan, China	Lower(?) Pleistocene	836, 884
Stegodon orientalis grangeri Osborn, 1929, Yenchingkou, near Wanhsien, Province of Szechuan, China	Lower Pleistocene	836, 875
Stegodon auroræ Matsumoto, 1915, 1918, Mt. Tomuro, Kaga, Japan	Upper(?) Pliocene	836, 892
Stegodon insignis birmanicus Osborn, 1929, Mingoon, Burma, upper levels, Irrawaddy Series	Upper Pliocene[1]	836, 874
Stegodon bombifrons Falconer and Cautley, 1846, Siwalik Hills, India	Middle Pliocene	836, 863
Stegodon sinensis Owen, 1870, vicinity of Shanghai(?), China	Lower(?) Pliocene	836, 860
Stegodon elephantoides Clift, 1828, near Yenangyaung, Burma, Irrawaddy Series	Lower Pliocene[1]	836, 861
Stegodon elephantoides (=*cliftii*) Falconer and Cautley, 1846, near Yenangyaung, Burma, Irrawaddy Series	Lower Pliocene[1]	811, 814, 827 828, 831, 836

NOT DETERMINED BY THE PRESENT AUTHOR

Stegodon bondolensis van der Maarel, 1932, Bondol, near Kuwung, Java	894
Stegodon trigonocephalus praecursor von Koenigswald, 1933, Bumiaju, Schichten of Kali Glagah, Java	896
Parastegodon? kwantoensis Tokunaga, 1934, Kakio, Kanagawa Prefecture, Japan	897
Stegodon yüshensis Young, 1935, Yüshe, China, 'violet sands.'	897
Stegodon officinalis Hopwood, 1935, Szechuan(?), China. Horizon unknown.	898
Stegodon zdanskyi Hopwood, 1935, China. Horizon unknown	899
Parastegodon sugiyamai Tokunaga, 1935, Iruhi, in Saida village, Shikoku, Japan	899
Parastegodon akashiensis Takai, 1936, Okubo-mura, Akashi-gun, Hyogo Prefecture, Japan	1420
Stegodon licenti Teilhard de Chardin and Trassaert, 1937, southeastern Shansi (Yüshe Basin), China	1420
Parastegodon infrequens Shikama, 1937, near Akasi, Japan	1420
Stegodon shôdoënsis akashiensis (Takai, 1936) Makiyama, 1938, Eigasima, near Akasi, and under the sea off Hayasi-zaki, Japan	1420

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[1] [See page 824 above where reasons are given for regarding these species as of Lower Pleistocene age.—Editor.]

Superfamily: ELEPHANTOIDEA

Fam.: ELEPHANTIDÆ Subfam.: MAMMONTINÆ

Genera: *Archidiskodon*, *Metarchidiskodon*

Cranium brachycephalic, bathycephalic, hypsicephalic. Superior tusks large, incurved, crossing in old males. Primitive grinding teeth, subloxodont, subhypsodont; ridge-plates extremely broad, enamel borders thickened, more or less crenulate, cement usually thick.

ARCHIDISKODONTS OF EURASIA

Archidiskodon Pohlig, 1885, 1888

		Page
Archidiskodon meridionalis cromerensis Depéret and Mayet, 1923, Kessingland, Suffolk, England Cromerian or Norfolkian	Lower Pleistocene	946, 980
Archidiskodon meridionalis Nesti, 1825, Val d'Arno supérieure, northern Italy	Upper Pliocene[1] to Lower Pleistocene	946, 969
Archidiskodon planifrons Falconer and Cautley, 1845, Siwalik Hills, India. Pinjor horizon	Upper Pliocene and Lower Pleistocene	946, 950
Archidiskodon planifrons rumanus Stefănescu, 1924, Tulucesti (Covurlui), Rumania	Upper Pliocene	968

ARCHIDISKODONTS OF SOUTH AFRICA

ARCHIDISKODON Pohlig, 1885, 1888

Archidiskodon broomi Osborn, 1928, The Bend, Vaal River, near Kimberley, South Africa	Lower or Middle Pleistocene	946, 989
Archidiskodon vanalpheni Dart, 1929, Sydney-on-Vaal, South Africa	Lower(?) Pleistocene	990
Archidiskodon milletti Dart, 1929, Sydney-on-Vaal, South Africa	Lower(?) Pleistocene	991
Archidiskodon loxodontoides Dart, 1929, Sydney-on-Vaal, South Africa	Lower(?) Pleistocene	991
Archidiskodon yorki Dart, 1929, Vanasswegenshoek-Bloemheuvel, near Christiana, South Africa	Lower(?) Pleistocene	992
Archidiskodon subplanifrons Osborn, 1928, Sydney-on-Vaal, South Africa	Upper(?) Pliocene [Middle Pliocene]	946, 987
Archidiskodon proplanifrons Osborn, 1928, Gong-Gong, near Vaal River, South Africa	Middle(?) Pliocene	986

METARCHIDISKODON Osborn, 1934

Metarchidiskodon griqua Haughton, 1922, Griqualand West, South Africa	Lower(?) Pleistocene	946, 994

ARCHIDISKODONTS OF NORTH AMERICA

ARCHIDISKODON Pohlig, 1885, 1888

Archidiskodon imperator maibeni Barbour, 1925, near Curtis, Lincoln County, Nebraska	Upper Pleistocene	946, 1027
Archidiskodon meridionalis nebrascensis Osborn, 1932, near Angus, Nuckolls County, Nebraska	Lower to Middle Pleistocene	1033
Archidiskodon imperator Leidy, 1858, Platte River, Thomas County? (*fide* Hay, 1924), Hooker County? (*fide* Lugn and Schultz, 1934), Nebraska	Lower Pleistocene	946, 998
Archidiskodon exilis Stock and Furlong, 1928, Santa Rosa Island, California	Pleistocene	946, 1031
Archidiskodon haroldcooki Hay, 1928, Frederick, Oklahoma	Lower(?) Pleistocene	1029
Archidiskodon imperator scotti Barbour, 1925, Staplehurst, Seward County, Nebraska	Lower Pleistocene	946, 1025
Archidiskodon hayi Barbour, 1915, Crete, Saline County, Nebraska	Lower Pleistocene	946, 1023
Archidiskodon imperator falconeri Freudenberg, 1922, Tequixquiac, Valley of Mexico	Lower(?) Pleistocene	946, 1016
Archidiskodon imperator silvestris Freudenberg, 1922, Ejutla, State of Oaxaca, Mexico	Lower(?) Pleistocene	946, 1015
Archidiskodon sonoriensis Osborn, 1929, near Arizpe, northern Sonora, Mexico	Lower Pleistocene	1033

NOT DETERMINED BY THE PRESENT AUTHOR

Archidiskodon paramammonteus Matsumoto, 1939, Nagahama, Minato Town, Province of Kazusa, Japan		1420

Fam.: ELEPHANTIDÆ Subfam.: MAMMONTINÆ

Genus: *Parelephas*

Cranium intermediate in form between *Archidiskodon* and *Mammonteus*; frontals concave; occipital crest elevated. Tusks with remarkable incurvature. Molars with constantly increasing ridge formula in M 3.

EURASIATIC SPECIES

PARELEPHAS Osborn, 1924

Parelephas wüsti Pavlow, 1909, Tiraspol (gouv. Kherson), southern Russia	Upper Pleistocene	1048, 1065
Parelephas intermedius Jourdan, 1861, near Lyons, Rhone Valley, France	Pleistocene	1048, 1062
Parelephas armeniacus Falconer, 1857, near Khanoos, Province of Erzerum, Armenia	Pleistocene	1048, 1060
Parelephas trogontherii Pohlig, 1885, 1888–1891, Süssenborn, near Weimar, Germany	Middle Pleistocene	1048, 1056
Parelephas(?) trogontherii nestii Pohlig, 1891, Forest Bed (Norfolk), Walton (Essex), and Southwold (Suffolk), England	Lower Pleistocene	1048, 1059
Parelephas trogontherioides Zuffardi, 1913, Piedmont, northern Italy	Upper Pliocene[1]	1048, 1055

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[1] [Possibly Lower Pleistocene (see footnote 1 on p. 1049).—Editor.]

NORTH AMERICAN SPECIES

		Page
Parelephas progressus Osborn, 1924, Zanesville, Muskingum County, Ohio	Upper Pleistocene	1048, 1097
Parelephas jeffersonii Osborn, 1922, Jonesboro, Indiana	Upper Pleistocene	1048, 1083
Parelephas roosevelti Hay [=syn. *Parelephas jeffersonii*], Ashland, Cass County, Illinois	Pleistocene	1048, 1095
Parelephas jacksoni Mather, 1838, Jackson County, Ohio	Pleistocene	1048, 1068
Parelephas columbi cayennensis Osborn, 1929, Cayenne, French Guiana, South America	Upper(?) Pleistocene	1048, 1083
Parelephas floridanus Osborn, 1929, near Bradenton, Manatee County, Florida	Upper(?) Pleistocene	1048, 1108
Parelephas columbi felicis Freudenberg, 1922, Tecamachalco, Puebla, Mexico	Pleistocene	946, 1082
Parelephas columbi Falconer, 1857, 1863, 1868, Brunswick Canal, near Darien, Georgia	Upper(?) Pleistocene	1048, 1071
Parelephas washingtonii Osborn, 1923, Pine Creek, Whitman County, Washington	Pleistocene	1048, 1101
Parelephas? eellsi Hay, 1926, Port Williams, Clallam County, Washington	(?)	1104

NOT DETERMINED BY THE PRESENT AUTHOR

Parelephas proximus uehataensis Shikama, 1937, Japan		1420

Fam.: ELEPHANTIDÆ Subfam.: MAMMONTINÆ

Genus: *Mammonteus*

Cranium extremely acrocephalic, hypsicephalic, bathycephalic; frontals concave; occipital crest greatly elevated; occiput slightly convex. Superior tusks greatly incurved, crossing in old age. Molar crowns broad, with extreme compression and very high ridge-plate formula (M 3 $\frac{20-24-27}{20-24-27}$); enamel borders more or less crimped or sinuous.

EURASIATIC SPECIES

MAMMONTEUM CAMPER, 1788; MAMMONTEUS Osborn, 1924

Mammonteus primigenius Blumenbach, 1799, Europe and Asia	Late or Upper Pleistocene	1138, 1141
Mammonteus(?) *primigenius Leith-Adamsi* Pohlig, 1888, Thuringia, Germany	Upper-Lower Pleistocene	1137, 1150
Mammonteus primigenius hydruntinus Botti, 1891, Otranto, Italy	Upper-Lower Pleistocene	1137, 1150
Mammonteus primigenius fraasi Dietrich, 1912, Steinheim, Germany	Upper-Lower Pleistocene	1137, 1152
Mammonteus primigenius astensis Depéret and Mayet, 1923, San Paolo de Villafranca, Italy.	Upper Pliocene[1]	1138, 1154

NORTH AMERICAN SPECIES

Mammonteus primigenius compressus Osborn, 1924, Rochester, Indiana	Upper Pleistocene	1138, 1157
Mammonteus primigenius alaskensis sp. nov., vicinity of Fairbanks, Alaska	Pleistocene	1159
Mammonteus primigenius americanus De Kay, 1842, near Rochester, New York	Upper Pleistocene	1138, 1156

Fam.: ELEPHANTIDÆ Subfam.: LOXODONTINÆ

Genera: *Loxodonta, Palæoloxodon, Hesperoloxodon*

Cranium relatively primitive, platycephalic, brachycephalic (*Loxodonta*); somewhat more elevated or hypsicephalic (*Palæoloxodon, Hesperoloxodon*); prominent parietofrontal crest (*Palæoloxodon namadicus, P. melitensis, P. mnaidriensis*). Premaxillary rostrum broadened for insertion of widely divergent tusks; tusks relatively straight or slightly incurved. Molars moderately hypsodont, with strong 'loxodont sinus' (*Loxodonta*), rudimentary or absent (*Palæoloxodon, Hesperoloxodon*).

LOXODONTA F. Cuvier, 1825, 1827. Molar crowns low, broadly open 'loxodont sinus.'

Loxodonta prima Dart, 1929, Pilandsberg, Transvaal, South Africa	[?Recent (*fide* Dart)]	1287
Loxodonta africana var. *obliqua* Dart, 1929, valley of Steelport River, northeastern Transvaal, South Africa	[?Recent (*fide* Dart)]	1287
Loxodonta subantiqua Haughton, 1932, Delport's Hope, near Vaal River, South Africa	Level unknown—Pleistocene	1288
Loxodonta africana Blumenbach, 1797, probably from Cape region, South Africa	Upper Pleistocene to Recent	1197
Loxodonta zulu Scott, 1907, Zululand, South Africa	Pleistocene	1286
Loxodonta cornaliae Aradas, 1870, near monastery of Santa Chiara, Catania, Sicily	[Quaternary or post-Pliocene (*fide* Aradas)]	1204

PALÆOLOXODON (SYN. SIVALIKIA) OF INDIA

PALÆOLOXODON Matsumoto, 1924. Cranium with broad rugose parietofrontal crest.

Palæoloxodon namadicus Falconer and Cautley, 1846, 1847, valley of the Nerbudda, India.	Upper Pleistocene	1211

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[1] [Possibly Lower Pleistocene (see footnote 1 on p. 1049 above).—Editor.]

PALÆOLOXODON (SYN. PILGRIMIA) OF THE MEDITERRANEAN ISLANDS

		Page
Palæoloxodon mnaidriensis Adams, 1870, Mnaidra Gap, island of Malta	Pleistocene	1265
Palæoloxodon falconeri Busk, 1867, Zebbug Cave, island of Malta	Pleistocene	1263
Palæoloxodon melitensis Falconer, 1862, Zebbug Cave, island of Malta	Pleistocene	1262
Palæoloxodon lamarmorae Forsyth Major, 1883, Quaternary sands of Morimentu near Gonnesa, Sardinia	Pleistocene	1266
Palæoloxodon cypriotes Bate, 1903, Kerynia Hills, island of Cyprus	Pleistocene	1266
Palæoloxodon creticus Bate, 1907, near Cape Maleka, island of Crete	Pleistocene	1267

PALÆOLOXODON OF AFRICA

Palæoloxodon yorki Dart, 1929, near Christiana, Vaal River, South Africa	Middle(?) Pleistocene	1280
Palæoloxodon kuhni Dart, 1929, Pniel Estate, South Africa	Middle(?) Pleistocene	1281
Palæoloxodon wilmani Dart, 1929, below Christiana, Vaal River, South Africa	Middle(?) Pleistocene	1280
Palæoloxodon(?) andrewsi Dart, 1929, Gong-Gong, Vaal River, South Africa	Lower(?) Pleistocene	993, 1278
Palæoloxodon atlanticus Pomel, 1879, near Mascara, Algeria, North Africa	Pleistocene	1274
Palæoloxodon jolensis Pomel, 1895, Algerian seacoast, North Africa	Pleistocene	1274
Palæoloxodon recki Dietrich, 1916, Serengetisteppe, Tanganyika Territory, East Africa	Pleistocene	1275
Palæoloxodon transvaalensis Dart, 1927, near Bloemhof, Vaal River, South Africa	Pleistocene	946, 993, 1284
Palæoloxodon sheppardi Dart, 1927, near Bloemhof, Vaal River, South Africa	Pleistocene	946, 993, 1285
Palæoloxodon archidiskodontoides Haughton, 1932, Sydney-on-Vaal Breakwater, bed of Vaal River, South Africa	Level unknown—Pleistocene	1282
Palæoloxodon hanekomi Dart, 1929, Delport's Hope, Vaal River, South Africa	Level unknown—Pleistocene	1279

PALÆOLOXODON OF JAPAN

Palæoloxodon buski Matsumoto, 1927, Ninohe District, Province of Mutsu	Post-Pleistocene to Recent	1333
Palæoloxodon namadicus naumanni Makiyama, 1924, Sahamma, Tôtômi Province, Japan	Middle(?) Pleistocene	1289, 1295
Palæoloxodon namadicus namadi Makiyama, 1924, dredged off island of Shôdo, Sanuki Province, Japan	Middle(?) Pleistocene	1289, 1296
Palæoloxodon namadicus yabei Matsumoto, 1929, Inland Sea, Japan	Middle Pleistocene (*fide* Matsumoto)	1289, 1299
Palæoloxodon yokohamanus Tokunaga, 1934, Yokohama, Japan	[Lower(?) Pleistocene (*fide* Tokunaga)]	1301
Palæoloxodon protomammonteus Matsumoto, 1924, 1926, Nagahama, Town of Minato, Kimitsu District, Province of Kazusa, Japan	Upper Pliocene(?), Lower Pleistocene	1289, 1297
Palæoloxodon (?Archidiskodon) tokunagai mut. *junior* Matsumoto, 1929, precise locality unknown, Japan	Upper Pliocene(?) or Lower Pleistocene	1289, 1299
Palæoloxodon tokunagai Matsumoto, 1924, Soyama, Gokayama, Hiramura, Higashi-Tonami District, Province of Etchû, Japan	Upper Pliocene or Lower Pleistocene (so recorded)	1289, 1298
Palæoloxodon protomammonteus proximus Matsumoto, 1926, Kimitsu District, Province of Kazusa, Japan	Upper Pliocene(?)	1289, 1298

PALÆOLOXODON OF JAVA

Palæoloxodon hysudrindicus Dubois, 1908, Kendeng-Schichten, Java	Middle(?) Pleistocene	1289, 1302

NOT DETERMINED BY THE PRESENT AUTHOR

Parelephas protomammonteus (Matsumoto) *matsumotoi* Saheki, 1931, Mishima, Kimitsu District, Province of Kazusa, Japan	[See Chap. XXI, p. 1416, note under *matsumotoi*]	1300
Palæoloxodon priscus var. *bosei* Chakravarti, 1935, Parkalta, near Jammu, India		1418
Palæoloxodon aomoriensis Tokunaga, 1936, Tenjinbayashi, Aomori Prefecture		1289, 1419
Palæoloxodon darti Cooke and Clark, 1939, Victoria Falls, northern Rhodesia, Africa		1420

HESPEROLOXODON OF EUROPE

HESPEROLOXODON Osborn, 1931. Cranium domelike with flattened forehead. Premaxillaries extremely broad; tusks widely divergent, slightly upcurved and incurved. Grinders hypsodont, 'loxodont sinus' vestigial or absent.

Hesperoloxodon antiquus italicus Osborn, 1931, Pignataro Interamna, near Cassino, Italy	Upper Pleistocene	1245
Hesperoloxodon antiquus germanicus S. Stefănescu, 1924, Tanganu (Ilfov), Rumania	Upper Pleistocene	1233
Hesperoloxodon antiquus platyrhynchus Graells, 1897, San Isidro del Campo, near Madrid, Spain	(?)Lower or Middle Pleistocene	1231
Hesperoloxodon antiquus Falconer and Cautley, 1847, 1857, locality not recorded	Lower(?) Pleistocene	1217

Hesperoloxodon antiquus nanus Acconci, 1880, near Monti Pisani, Cucigliana, Tuscany, Italy	Geologic age unknown	1230
Hesperoloxodon antiquus ausonius Major, 1875, Verri, 1886, Depéret and Mayet, 1923, San Romano and San Paolo de Villafranca, Italy	Upper Pliocene[1]	1232

NOT DETERMINED BY THE PRESENT AUTHOR

E. [*Elephas*] *antiquus* mut. *ruthenensis* Astre, 1937, Salles-la-Source (Aveyron,) France	1420

Fam.: ELEPHANTIDÆ Subfam.: ELEPHANTINÆ

Genera: *Elephas, Hypselephas, Platelephas*

ELEPHAS OF INDIA, SUMATRA, AND THE MALAY PENINSULA

Cranium bathycephalic, cyrtocephalic, hypsicephalic, occipitofrontal dome more or less rounded; frontals gently concave. Superior tusks relatively straight, incurved. Mandibular rostrum extremely abbreviate. Molars with finely plicated enamel; not extremely hypsodont; ridge-plate formula: M 3 $\frac{24}{24\text{-}27}$.

ELEPHAS Linnæus, 1735–1758

Elephas indicus Linnæus, 1754, 1758,[2] Ceylon, India	Upper Pleistocene and Recent	1321, 1323
Elephas indicus ceylanicus de Blainville, 1845, Ceylon and mainland of India	Upper Pleistocene and Recent	1327
Elephas indicus bengalensis de Blainville, 1845, chiefly Bengal, India	Upper Pleistocene and Recent	1327
Elephas indicus sumatranus Temminck, 1847, District of Palembang, Sumatra	Upper Pleistocene and Recent	1329
Elephas indicus hirsutus Lydekker, 1914, Negri Sembilan province, Malay Peninsula	Upper Pleistocene and Recent	1332

HYPSELEPHAS OF INDIA

Cranium hypsicephalic; occiput elevated with broadly transverse frontal crest; frontals deeply concave. Tusks relatively straight, incurved, somewhat divergent at base. Molar crowns low; trace of median 'loxodont sinus.' Ridge-plate formula: M 3 $\frac{18+}{17\text{-}18\text{-}19}$.

HYPSELEPHAS Osborn, 1934 (*nomen nudum*), 1936

Hypselephas hysudricus Falconer and Cautley, 1845, 1846, Siwalik Hills, near Siswan, Chandigarh, Charnian, Kalka, as recorded by Barnum Brown	Lower Pleistocene	1340

PLATELEPHAS OF INDIA

Cranium relatively elongate, dolichocephalic, platycephalic. Tusks unknown. Molars imperfectly known; ridge-plates relatively low, directly transverse as in *Elephas*, no rudiment of a 'loxodont sinus.' Ridge-plate formula, as far as known: M 3 $\frac{16\frac{1}{2}}{}$.

PLATELEPHAS Osborn, 1934 (*nomen nudum*), 1936

Platelephas platycephalus Osborn, 1929, near Siswan, Simla Hills, India	Upper Pliocene or Lower Pleistocene	1359

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[1] [Possibly Lower Pleistocene, see footnote 1 on p. 1049 above.—Editor.]

[2] [*Elephas maximus* Linnæus, 1758, was adopted by the International Commission on Zoological Nomenclature at the meeting of the Fifth International Congress of Zoology, held at Berlin in 1901. The present author, however, thought it preferable to retain Linnæus' first designation, namely, *Elephas indicus*, for the reasons given above on pages 1308-1311 of Chapter XX.—Editor.]

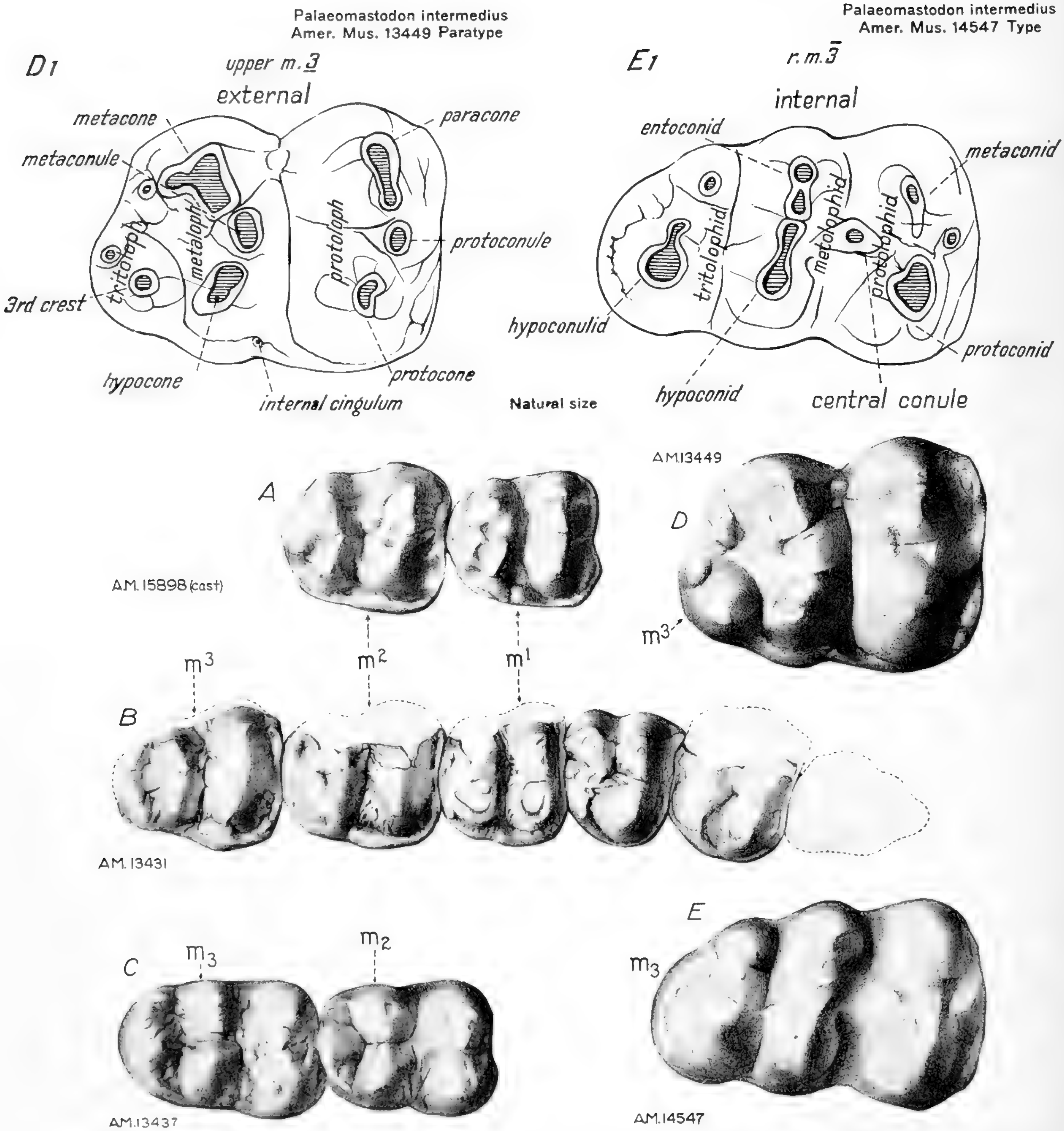


Fig. 1229. Four-coned ancestral grinders of the Proboscidea (e.g., *Mœritherium*) compared with the six-coned *Palæomastodon* molars (same as Figs. 93 and 94 of Volume I). All figures natural size.

(Upper) Key to the hexabunodont upper and lower molar crowns of *Palæomastodon intermedius*. Observe the relatively broad proportions; the hexabunodont crowns of M^3, namely, protocone, protoconule, paracone, hypocone, metacone, metaconule; the fundamental arrangement in two transverse crests, i.e., protoloph, metaloph; the two intermediate cusps, i.e., protoconule, metaconule; the lower molar, M_3, with rudimentary trilophodont crown; both the upper and lower molars wholly distinct in proportions from those of any species of *Phiomia*; a central conule rudiment in M_3; absence of median sulcus.

(Lower) Detailed studies of third superior and inferior hexabunodont (D, E) teeth, M^3-M_3, of the true *Palæomastodon intermedius*, as compared with the essentially tetrabunodont (A, B, C) *Mœritherium* teeth.

A, *Mœritherium lyonsi* ref., right M^{1-2} drawn from cast Amer. Mus. 15898.

B, *Mœritherium trigodon* ref., right superior grinders drawn from Amer. Mus. 13431.

C, *Mœritherium andrewsi* ref., left M_{2-3} drawn from Amer. Mus. 13437.

D, *Palæomastodon intermedius* paratype, third right superior molar, r.M^3, Amer. Mus. 13449.

E, *Palæomastodon intermedius* type, third left inferior molar, l.M_3, Amer. Mus. 14547 (reversed in drawing).

2. EXPLANATION OF TERMS USED THROUGHOUT THE TEXT OF THE PRESENT MEMOIR

All proboscidean molars are derived from four-coned ancestral grinding teeth, such as are found in *Mœritherium*. While the molar crowns in *Palæomastodon* are basically tetrabunodont, there being four principal cones in the two well-developed crests of each tooth, the retention of intermediate conules in the upper molars makes these teeth actually hexabunodont. In the last lower molar of this genus the development of a strong third crest leads to a hexabunodont condition. The main external and internal bunoid cones never unite transversely into a completed ridge-crest in the Mastodontinæ (*Miomastodon, Pliomastodon, Mastodon*), but remain separate or bunolophodont, never becoming fully zygolophodont or yoke crested, as in the Zygolophodontinae (*Zygolophodon, Turicius*). In general the cones are arranged transversely to the long axis of the crowns, but in the Brevirostrinæ (e.g., *Pentalophodon*) there is an alternation of both the external and internal cones—a distinctive character. There is also a slight alternation in the Humboldtine molar, *Stegomastodon*.

The numerical terminology of the superior (–loph) and inferior (-lophid) ridge-crests is as follows:

Pro-protoloph—id = One-half, anterior rudimentary ridge
Post-metaloph—id = One-half, posterior rudimentary ridge
Protoloph—id = First primary ridge = protocone and paracone of Ungulata
Metaloph—id = Second primary ridge = hypocone and metacone of Ungulata
Tritoloph—id = Third ridge
Tetartoloph—id = Fourth ridge
Pentaloph—id = Fifth ridge
Hexaloph—id = Sixth ridge
Heptaloph—id = Seventh ridge
Octaloph—id = Eighth ridge
Ennealoph—id = Ninth ridge
Decaloph—id = Tenth ridge
Endecaloph—id = Eleventh ridge
Dodecaloph—id = Twelfth ridge

Aristogenesis and Alloiometry.—A definition of aristogenesis (first known under the term "definite variation," then as "rectigradation") will be found on page 1580 of the present chapter together with figure 1239. See also page 1581 for figure and explanation of the term alloiometry.

Conules and Trefoils.—In the Bunomastodontidæ the very important coronal element or aristogene, known as a conule, which successively appears between the proto- and metalophs, then between the meta- and tritolophs, then between the trito- and tetartolophs, and so on, attaches itself to the external cones in the inferior molars, forming on wear the outer trefoil or ectotrefoil, and to the internal cones of the superior molars, forming the inner trefoil or entotrefoil. Molars of this structure are characterized by the term bunomastodont. Conules are highly characteristic of the Longirostrinæ and Amebelodontinæ and are more or less conspicuous in the Tetralophodontinæ and Notorostrinæ as well as in the Palæomastodontinæ and in certain of the Brevirostrinæ; they are absent, however, in the molars of the Mœritheriinæ (Mœritheres), the Deinotheriinæ (Deinotheres), the Mastodontinæ, the Stegolophodontinæ, the Stegodontinæ (genus *Stegodon*), and the Elephantidæ (Mammontinæ, Loxodontinæ, and Elephantinæ); vestigial or absent in the Zygolophodontinæ and Humboldtinæ; and functionally replaced in the Serridentidæ (Serridentinæ, Platybelodontinæ, Notiomastodontinæ) by lateral spurs which gradually arise on the internal and external cones of the superior and inferior molars respectively, which, in turn, subdivide into from two to six small conelets giving a serrated appearance to the spurs or crests, hence Serridentidæ. The absence in the Elephantoidea of conule development into trefoils, so characteristic of the mastodontoids, and the early tendency to form evenly transverse, more or less mammillate crests, is one of the distinctive features of this superfamily.

Conelets.—Another coronal element or aristogene is the conelet, which usually arises by binary fission, rarely by ternary fission. For example, the primary or paired cones in the protoloph, referred to in the first paragraph of this section, each splits into two making four (or 4+) conelets in the metaloph; each of these four conelets tends to split into two, tending to form from five to eight conelets. But the binary fission is not so regular as this. The newer anterior and posterior crests exhibit fewer conelets than the older mid-crests. To illustrate, the maximum number of cones and conelets in each crest runs as follows:

Molar cones and conelets: Primitive (*Palæomastodon*) 2–4–6–8–12–20+ progressive (*Stegodon airâwana*).

This conelet structure is also well illustrated in the *Zygolophodon* and *Turicius* molars (Pl. III, pp. 134-135) in which the conelets range from 4 to 25 in number. Professor Osborn in Chapter XIV of this volume, pages 809 to 812, has given a detailed explanation of this interesting transformation of the original crests or lophs by fission into conelets.

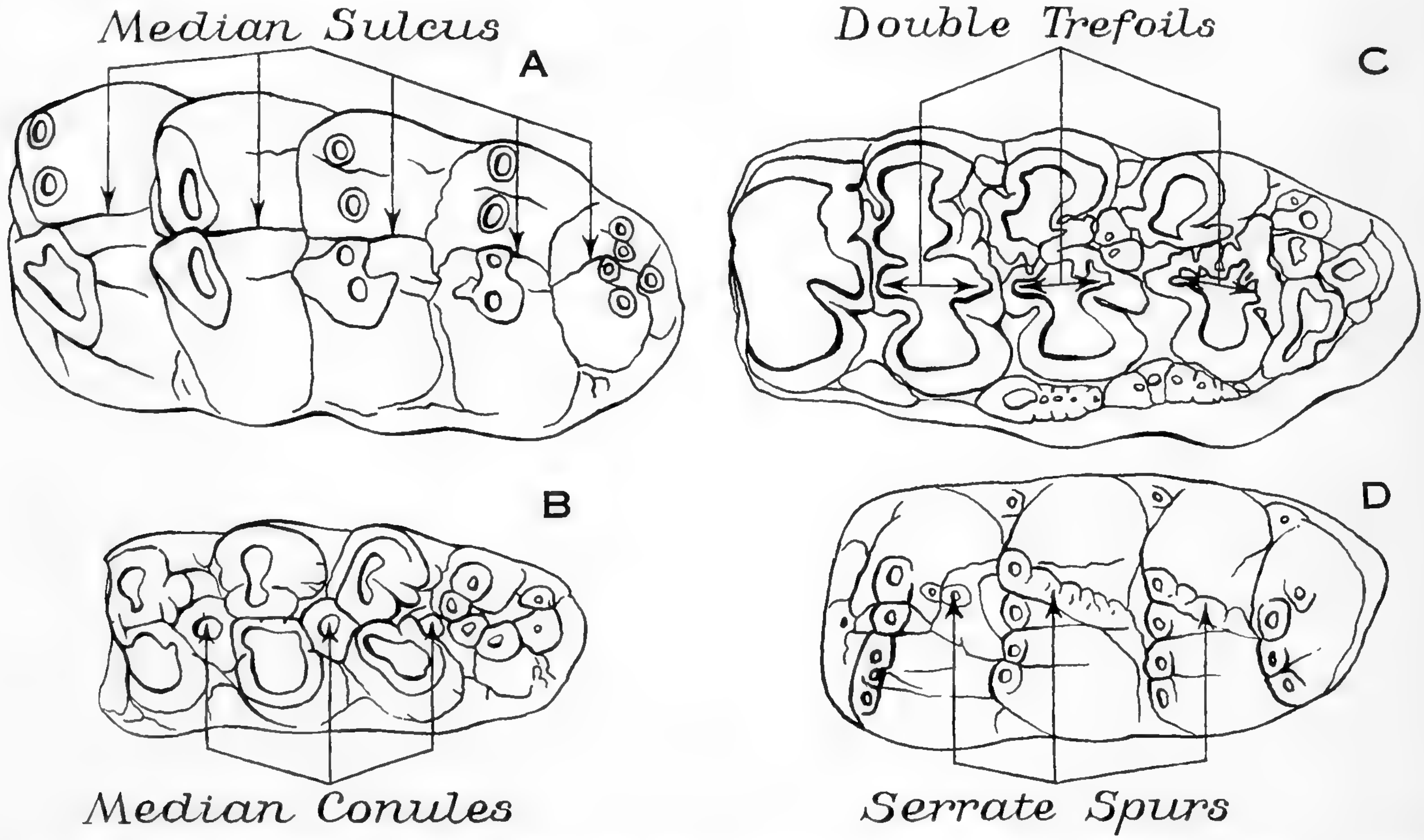


Fig. 1230. Molar diagrams showing typical crown pattern of M_3 of each of the four families (geologic range, Oligocene to late Pleistocene) of the Mastodontoidea. All figures reduced to a uniform one-half scale.

MASTODONTIDAE:	A, *Mastodon americanus* ref. (Amer. Mus. 14294), from Fulton, Indiana. Ridge-crests 4½; distinct median sulcus. Pleistocene. See figure 134 B of the present Memoir.
BUNOMASTODONTIDÆ:	B, *Trilophodon palæindicus* type (Ind. Mus. A.426; cast Amer. Mus. 9905), from northern Punjab, India. Ridge-crests 4½; prominent central conules. Middle Miocene. See figure 211 of the present Memoir.
HUMBOLDTIDÆ:	C, *Cuvieronius superbus* ref. (Buenos Aires Mus. 44; cast Amer. Mus. 27796). Ridge-crests 4½+, double trefoils; highly plicated. Probably Upper Pleistocene. See figure 672 of the present Memoir.
SERRIDENTIDÆ:	D, *Serridentinus productus* ref. (Amer Mus. 10582), from the Clarendon beds of Texas. Ridge-crests 4⅓; serrated crests or spurs springing from the ectoconelets. Lower Pliocene. See figure 369 C of the present Memoir.

MEDIAN SULCUS.—Also in dental structure the median longitudinal sulcus (the fissure or commissure of Hays) plays an important part (Fig. 1230, also Pl. I, p. 134); it is distinctive of the molars of the Mastodontinæ (e.g., *Miomastodon*, *Pliomastodon*, *Mastodon*), rapidly disappearing in the Zygolophodontinæ (*Zygolophodon* and *Turicius*), and persistent in the anterior ridge-crests only of the Stegolophodontinæ (*Stegolophodon*). This sulcus separates the external and internal cones both in the superior and inferior molars, further demonstrating that the ancestral proboscidean molar was tetrabunodont, as in *Mœritherium*, and not hexabunodont, as in *Palæomastodon;* in fact, the presence of proto- and metaconules blocking the median sulcus in the *Palæomastodon* molar forbids its direct ancestry to *Mastodon* in which the valleys between the crests are uninterrupted by either conules or trefoils.

Ganometry.—The ganometric method, from "ganos" signifying enamel, is, in brief, the measuring of the combined enamel foldings of the grinding teeth, which, when drawn out of their closely plicated arrangement for the finer comminution of the herbage on which these animals subsisted, steadily increase in length from Upper Pliocene time when *Eoanthropus* lived to closing Pleistocene time when the late Cro-Magnon man lived.

In Professor Osborn's experimentation with the elephantine molars, he was ably assisted by Dr. Edwin H. Colbert, who was careful to state that the measurements were approximate; that out of the thirty-six teeth studied, only two were unworn; consequently that there were large estimated factors in most of the measurements (cf. Osborn, with Colbert, 1931.858, p. 191). The accompanying figure (Fig. 1231) is inserted here to further demonstrate this method as a possible contributory factor in "estimating the duration of the sub-divisions of the age of man which have hitherto been dated chiefly by geologists calculating the length of the four glacial and three interglacial epochs," and, according to Professor Osborn's opinion, in ascertaining "just how long it took to produce a centimeter of enamel length" (*op. cit.*, p. 188).

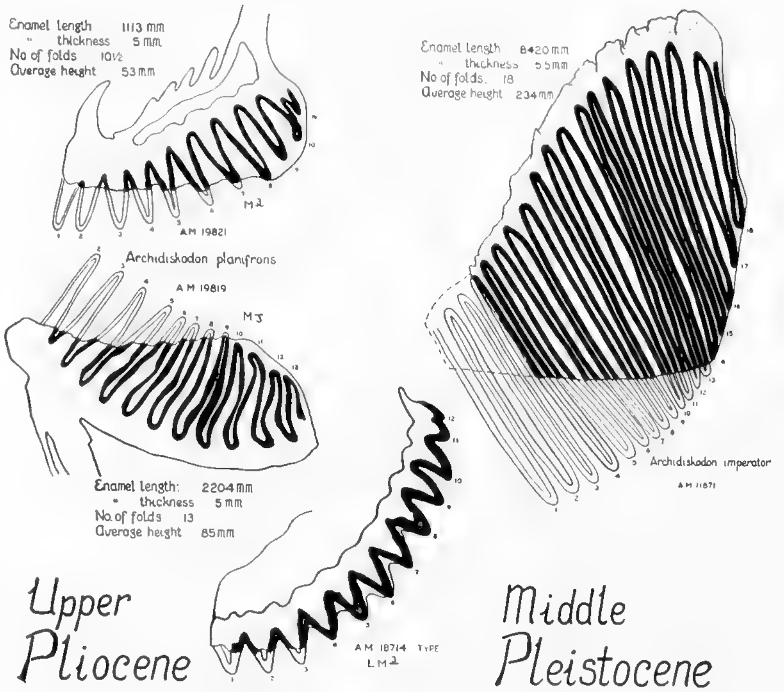


Fig. 1231. (Upper figures) Accelerated elephantine ridge-plates in *Archidiskodon*. Intensely accelerated evolution of the ridge-plates from the *Archidiskodon planifrons* of southern Eurasia into the *Archidiskodon imperator* of the United States and Mexico, all occurring from Upper Pliocene to Middle Pleistocene time. Length of enamel foldings:

Archidiskodon imperator of Texas = 8420 mm.
Archidiskodon planifrons of India = 2204
Archidiskodon planifrons of India = 1113

In these southern mammoths of Africa, Eurasia, and North America, gigantic size is attained in a relatively short period of geologic time.

(Lower figure) *Stegodon grangeri* of the Pliocene of Szechuan, China, type LM^3 with 11½ ridge-crests (Amer. Mus. 18714):

Enamel length	740 mm.
Enamel thickness	7.5
Average height of ridge-crests	31
Ridge-crests in 100 mm.	3–3½

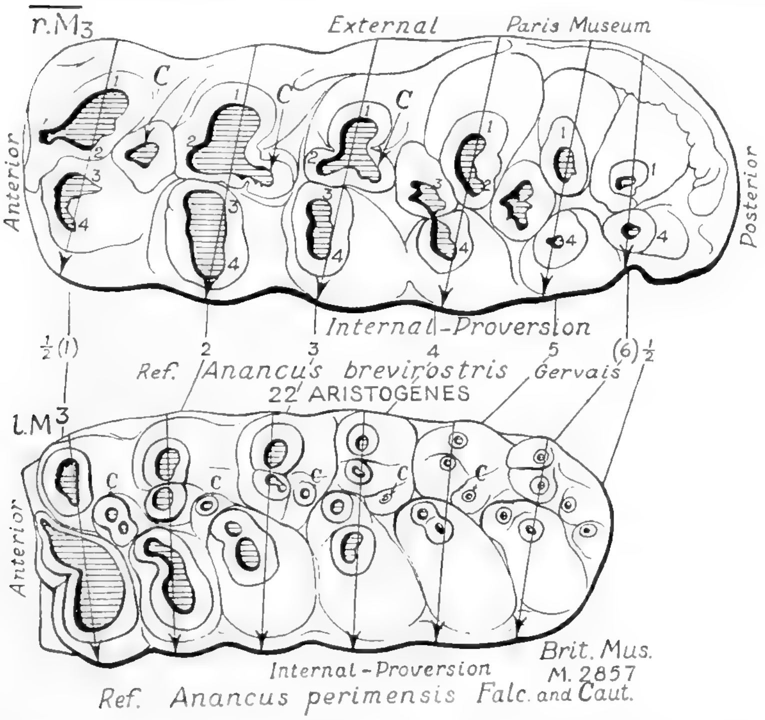
This figure illustrates one of the important differences between the stegodontoid and elephantoid molars. As will be observed, the valleys separating the adjacent molar ridges are closed or V-shaped at the bottom in the Stegodontoids, whereas in the Elephantoids they are U-shaped. Drawing modified after Osborn, 1934.926, fig. 4.

Dental Formulæ.—The canines are lacking in the Proboscidea, excepting in *Mœritherium*, in which the third superior canine is present but greatly reduced; nor are there any first deciduous premolars. The deciduous premolars (or deciduous molars as they are frequently called) consist of Dp 2, Dp 3, Dp 4. In *Mœritherium* and *Palæomastodon* P 2–4 are present; in *Deinotherium, Phiomia, Serridentinus, Ocalientinus*, and *Platybelodon* P 3–4 persist; in *Trilophodon, Pliomastodon, Miomastodon*, and possibly *Blickotherium*, P 4 only persists. In *Mastodon* the fourth true superior and inferior premolars, P^4, P_4, form in the jaw but do not erupt; in *Elephas* they are suppressed entirely, and, with the exception of *Archidiskodon* (of the Mammontinæ), there is also a complete suppression of this premolar in the Mammoths. Incisors present in *Mœritherium*, but I 2 enlarged. Only I 2 persisting in other proboscideans as tusks (cf. pp. 1550–1552 below).

Ridge Formulæ.—In certain of the Mastodontidæ and in all of the Elephantidæ the grinding teeth increase the number of their ridges by adding crests especially by the addition of crests posteriorly, for example, post-protolophid, post-metalophid, etc. The intermediate molars (Dp 4, M 1, M 2) vary in the number of their ridges from 3 to 5 in the Mastodontoidea (e.g., 3 in *Trilophodon*, 4 in *Tetralophodon*, and 5 in *Pentalophodon*). The count is much higher and apparently less uniform in the Stegodontoidea and Elephantoidea. In the Mastodontoidea the number of ridge-crests in the third molar (M 3) reaches 8½ in the Tetralophodontinæ (genus *Morrillia*); in the Stegodontoidea 15½ (*Stegodon airâwana*). In the Elephantoidea the number of ridge-plates reaches $\frac{27}{?27}$ (*Mammonteus*), $\frac{30}{26}$ (*Parelephas*). It is noteworthy that in *Parelephas* the ridge-plate count apparently is higher in the superior than in the inferior molars—a marked distinction from the ridge formula of other members of the Proboscidea, in which the inferior ridges exceed the superior ridges in number. If this character should prove to be constant, it would aid greatly in the determination of molars of the genus *Parelephas*.

Dolichodonty, Hypsodonty, and Brachyodonty.—Other terms illustrating the great variability in the molars of the Proboscidea are as follows:

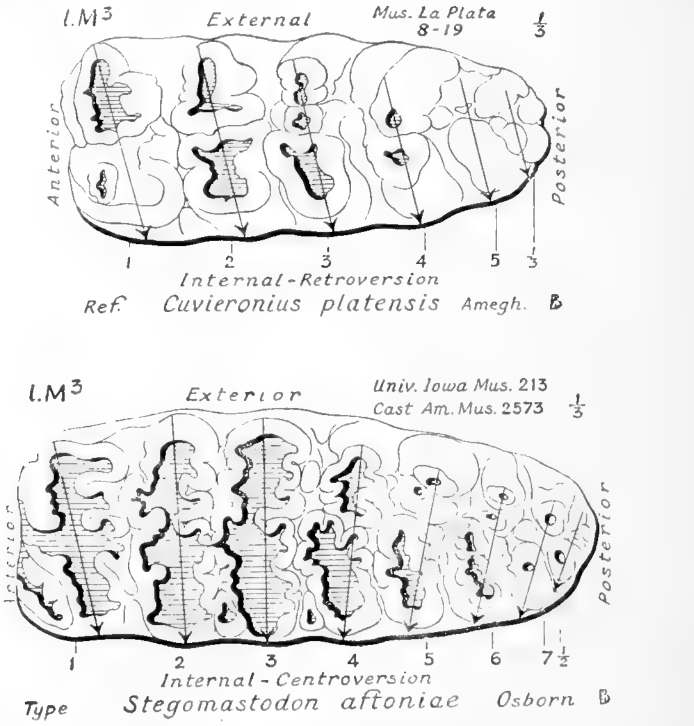
Dolichodonty, referring to the long and narrow proportions of the molar crowns.
Hypsodonty, descriptive of the elevation or heightening of the crowns.
Brachyodonty, which indicates the broad, short, low-crowned character of the molar crowns.



Brevirostrinæ: Proversion of Ridge-crests in Anancus. Four Conules on Each Crest (1, 2, 3, 4); Central Conules (CCC) between the Crests

Fig. 1232. Top: *Anancus brevirostris* ref. Third right inferior molar, r.M_3, strong internal proversion of 5½ ridge-crests.

Bottom: *Anancus perimensis* ref. Third left superior molar, l.M^3, internal proversion of 5½ ridge-crests.



Humboldtinæ: Retroversion and Centroversion of the Superior Ridge-crests in Cuvieronius and Stegomastodon

Fig. 1233. Top: Internal retroversion in 5+ridge-crested third left superior molar of *Cuvieronius platensis*.

Bottom: Internal centroversion in 7½ ridge-crested third left superior molar of *Stegomastodon aftoniæ*.

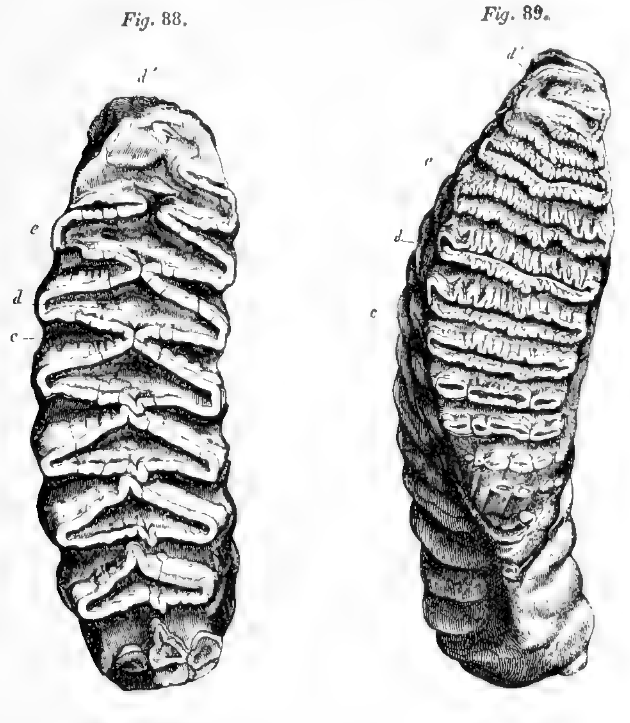
Chœrodonty and Ptychodonty.—Molar crowns covered with tubercles (chœrodonty), and plication or infolding of the enamel borders with grooving of the sides of the molars (ptychodonty) are variable characters of the proboscidean molar. The development of hypsodonty and chœrodonty among the mastodontoid (longirostrine and brevirostrine) browsers is analogous to that in the hippopotami and the hypsodont suillines. The elephantoid molars become hypsodont and polylophodont in the highest degree, in adaptation chiefly to grazing habits. The acme of hypsodonty is represented in the Mastodontoidea by the *Morrillia* molar, and in the Elephantoidea by the *Mammonteus* molar. *Synconolophus*, a brevirostral mastodont (see Fig. 623), and *Stegomastodon*, an humboldtine mastodont (Fig. 645), present the most labyrinthine crown pattern in the entire range of proboscidean molars.

PROVERSION, RETROVERSION, AND CENTROVERSION.—The following descriptive terms are used in the present Memoir in connection with the molars of certain of the Brevirostrines and Humboldtines (see Figs. 1232, 1233):

Ridge-crests extending obliquely from external to internal faces, toward anterior end of molars = Proversion
Ridge-crests extending obliquely from external to internal faces, toward posterior end of molars = Retroversion
Ridge-crests extending obliquely from external to internal faces, toward center of molars = Centroversion

LOXODONT SINUS. A mesial expansion of the ridge-plates of the grinding teeth into a broad lozenge-shaped sinus or cavity is especially characteristic of the genus *Loxodonta* (Fig. 1234); it is rudimentary or vestigial in *Palæoloxodon* and *Hesperoloxodon;* there is a trace of it in the molars of primitive species of *Archidiskodon,* also in *Elephas hysudricus;* in *Metarchidiskodon* there are prominent post-sinus folds instead of the median sinus expansion of the primitive *Archidiskodon.*

CEMENT.—The Proboscidea, as a whole, are progressive, consequently cement is present more or less abundantly in the molars of all the Elephantoidea, even in some of the most primitive species, as, for example, *Archidiskodon subplanifrons.* In the Mastodontoidea, however, this is not the case. There are indications of cement in the molars of such genera as *Pentalophodon* and *Eubelodon,* also it is present in the more progressive stages, e.g., *Cordillerion, Morrillia, Stegomastodon,* and *Synconolophus,* especially the last-mentioned genus, the molars of which are heavily cemented.



African Elephant. ⅓ nat. size. Asiatic Elephant.

Fig. 1234. Crown view of the third inferior molar of the right side of: Fig. 88, *Loxodonta africana;* Fig. 89, *Elephas indicus,* one-third natural size. Compare Owen, "History of British Fossil Mammals, and Birds," 1846, pp. 230–232, figs. 88, 89.

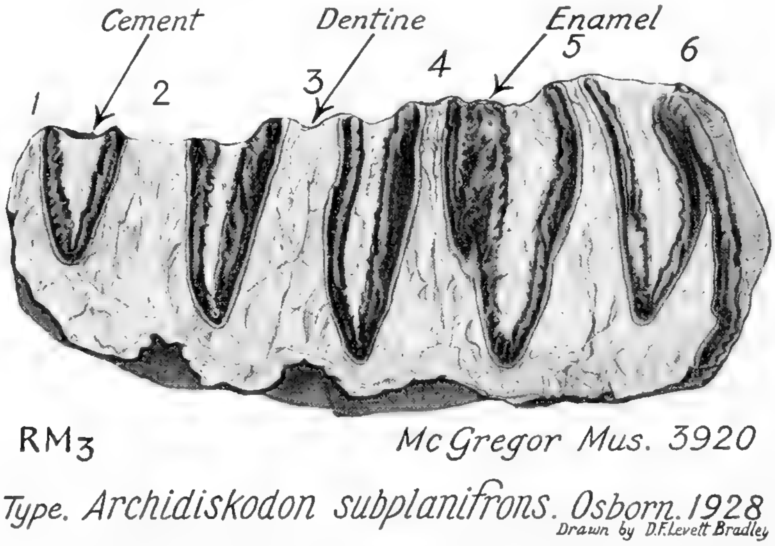
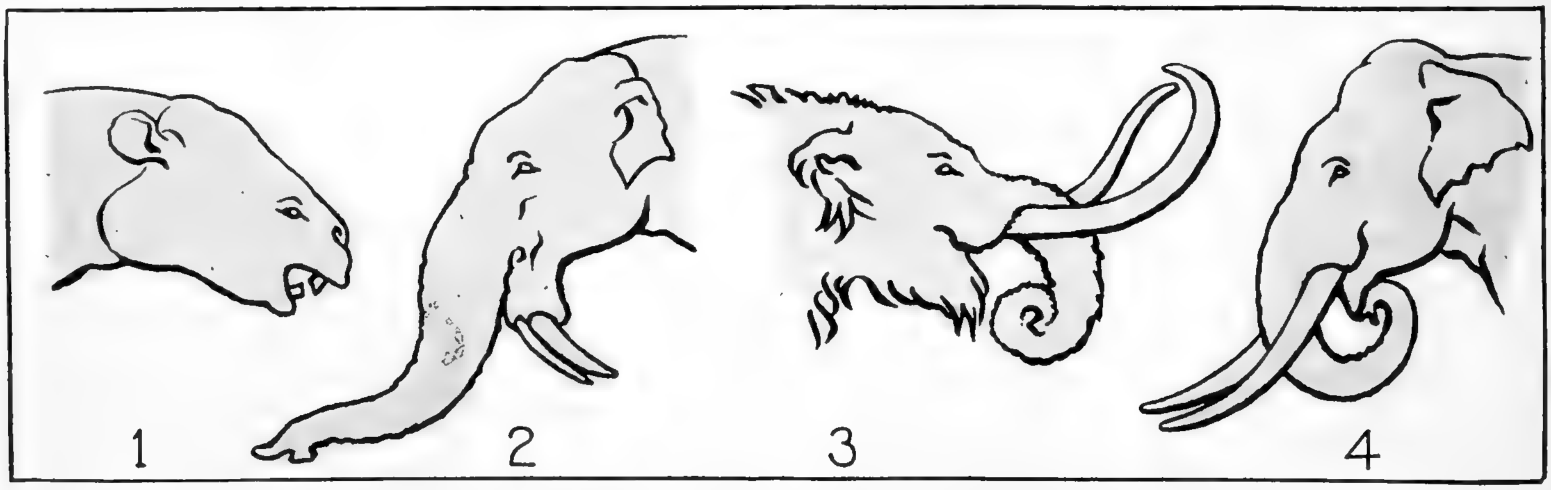


Fig. 1235. Section of third right inferior molar, r.M_3, of *Archidiskodon subplanifrons* type (McGregor Mus. 3920), with six ridge-crests. From Kimberley, South Africa. Drawn by Miss D. F. Levett Bradley, and reproduced herewith slightly more than two-thirds natural size.

CRANIUM.—In a comparison of the crania of the Proboscidea it will be observed that there is great variability, for example, the elongate (dolichocephalic), low cranium of the mastodonts as contrasted with that of the elephants, which is vertically high (hypsicephalic), peaked (acrocephalic), deep (bathycephalic), with great fore-and-aft compression (cyrtocephalic). In one respect, however, there is uniformity, for the skull bones surrounding the brain-case of all but the most primitive proboscideans are strongly cancellate to afford broad attachments for the heavy muscles necessary to support the weight of the tusks and of the trunk. As noted by Dr. C. W. Andrews (see p. 102 of Vol. I): "In the true Elephants and Mastodons the peculiar form of the skull is mainly due to the enormous development of cellular bone in the occipital region." With age there is apparently a shortening and deepening of the cranium in all species of elephants. In certain genera (e.g., *Phiomia*) the facial region lengthens more rapidly than the cranial (that is, it is dolichopic), in contrast to certain other genera (e.g., *Mœritherium*) in which the facial region shortens more rapidly than the cranial (that is, it is brachyopic).

TUSKS.—The Proboscidea are distinguished by a greatly enlarged pair of cutting teeth or incisors, which were originally opposed as feeding organs; this hypertrophy of I^2, I_2, through feeding function, resulted in the loss of both the first and third pairs of incisors; in the Mœritheres only does the first pair, I^1, I_1, persist, the third superior incisor being greatly reduced, the inferior wanting. In the Deinotheres the upper incisors, I^2, are entirely aborted; the inferior pair (probably I_2) is downturned and retroverted. In many of the Mastodontoidea and in all of the Stegodontoidea and Elephantoidea the lower tusks (I_2) are greatly reduced or completely suppressed.

Of the Mastodontoidea the most extraordinary tusks are those of: (1) The Amebelodonts, described as 'shovel-tusks' because of the high degree of specialization of the lower tusks for shoveling; these tusks with rounded tips are composed of concentric dentinal laminæ. (2) The Platybelodonts or 'flat-tuskers,' with broad, flat, square-tipped tusks, composed of dentinal rod-cones instead of dentinal laminæ as in the Amebelodonts, and in form like a coal shovel. (3) The Torynobelodonts or 'dredge-tuskers,' with broad, flat, chisel-like tusks, also composed of dentinal rod-cones. (4) The Andean mastodonts (*Cordillerion andium*) with long spirally-twisted tusks in which the enamel band follows the curved line of torsion. The Notorostrines, the Humboldtines, and the Brevirostrines were without inferior tusks. In the true *Mastodon* (*M. americanus*) the presence or absence of the inferior tusks varied with the individual.

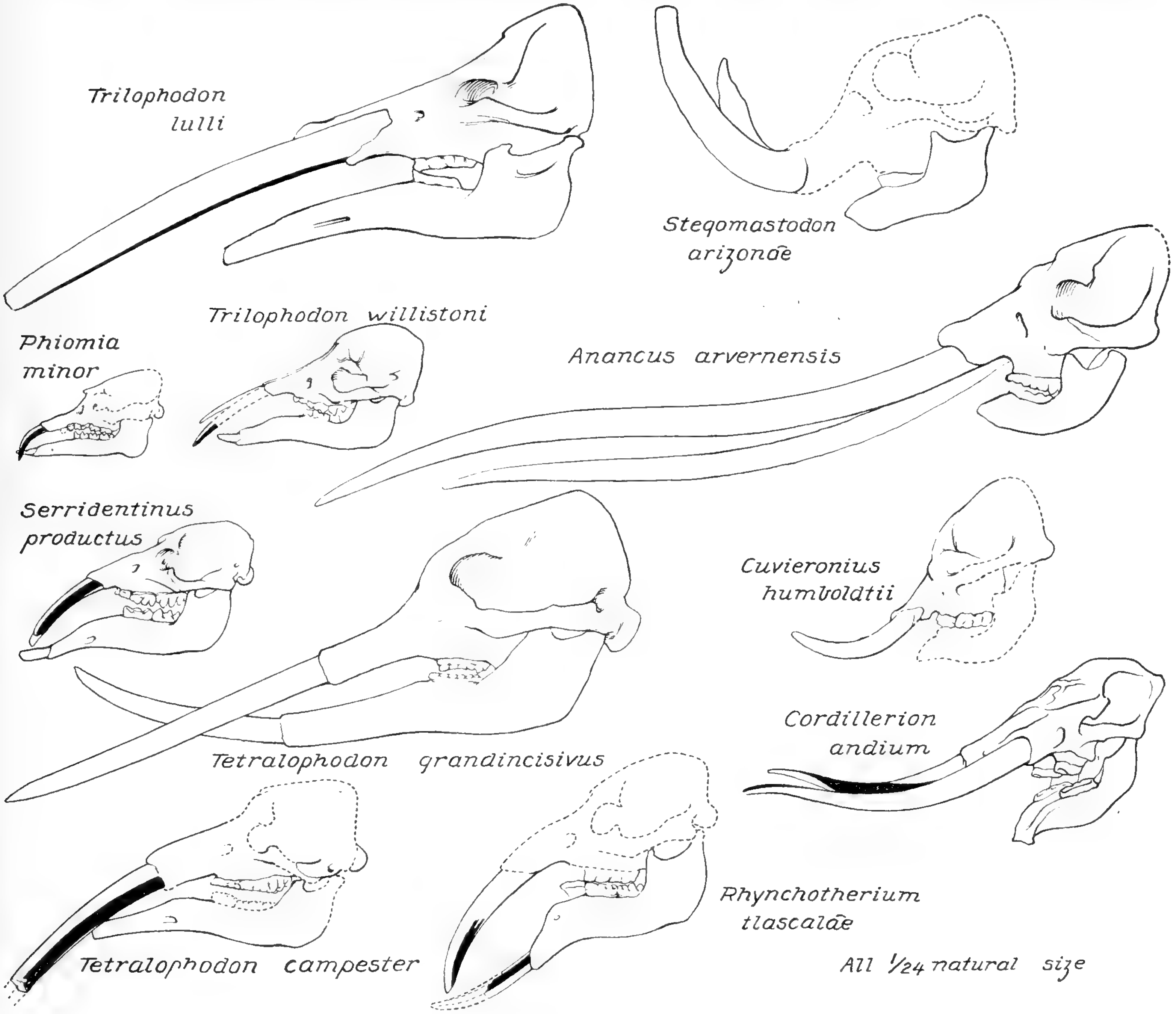


CHIEF HEAD AND DENTAL FORMS OF FOUR OF THE SUPERFAMILIES (I-IV) OF THE PROBOSCIDEA
Fig. 1236. (1) Mœritherioidea, one-twelfth natural size. (2) Deinotherioidea, (3) Mastodontoidea, and (4) Elephantoidea, all one-fiftieth natural size.

The famous *Stegodon ganesa* upper tusks are striking not only because of their great length and symmetry, but also because of the apparently impossible position in the jaw which left insufficient space for the pendant trunk. This is a moot question, however, and is fully treated in the present volume, p. 857, caption to figure 733.

Finally, in the Elephantoidea, especially in the Mammontinæ, the upper tusks attain gigantic size, e.g., the *Archidiskodon imperator* tusk from near Post, Texas, measuring 16+ feet in length, also the example formerly in the Geological Survey of Mexico with an estimated length of 13+ feet. In certain of the Mammontines (i.e., *Mammonteus primigenius*) the tusks cross in old age producing a striking wheel-like appearance. The very early loss of the lower tusks is one of the prime distinctions in the Elephantoidea and Stegodontoidea.

Tusk Enamel.—A dental characteristic of all primitive bunomastodonts is the presence of an enamel band on the superior tusks as opposed to the elongate, flattened inferior tusks which generally lack the enamel band. This betokens the primitive functional use of the upper and lower tusks in opposition, correlated with a grinding



Divergent Adaptive Radiation of Crania and Incisive Tusks in Six Bunomastodont Subfamilies. Scale uniform

Fig. 1237. Comparative outline illustrations, side view, to same scale, of the completely restored skulls, jaws, and tusks, in descending order, of:

Trilophodon (Megabelodon) lulli[1]
Trilophodon (Genomastodon) willistoni, juvenile
Phiomia minor
Serridentinus productus
Tetralophodon grandincisivus
Tetralophodon campester

Rhynchotherium tlascalæ, restored

Observe persistent enamel band on *inferior* tusks, also apposition of inferior and superior tusks. In contrast with superior enamel band only in *Trilophodon, Phiomia, Serridentinus,* and *Tetralophodon*, and absence of enamel band on inferior tusks.

Stegomastodon arizonæ
Anancus arvernensis
Cuvieronius humboldtii, juvenile
Cordillerion andium

(Osborn, 1934) *Serridentinus* belongs in the new family Serridentidæ; *Stegomastodon* and *Cuvieronius* in the new family Humboldtidæ.

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[1] The type mandible of *Trilophodon lulli*, originally restored by Barbour in 1914 with a pair of slender inferior incisive tusks (Fig. 244 of present Memoir), is now found to be tuskless. The rostrum is expanded at the tips. See Barbour, 1934.2.

and triturating molar action rather than the chopping motion characteristic of the true mastodonts. The important functional distinction of the Mastodontoidea is that for a very long period of time the upper tusks abraded the outer side of the lower tusks, which probably explains the retention of the superior enamel band (Mastodontinæ *fide* Schlesinger, and Notorostrinæ, *vide Cordillerion andium*). The Rhynchorostrines are an exception, in that the enamel band persists on the inferior tusks (see Fig. 1237). In all the mastodonts related to the classic *Mastodon* [*Trilophodon*] *angustidens* of Cuvier and the *M.* [*Tetralophodon*] *longirostris* of Kaup, as well as in certain of the Serridentines, the superior incisors are extremely formidable as weapons, sharp, down- and out-turned, the dentine or ivory being strengthened with a lateral enamel band. There seems to be no trace of an enamel band on the Stegodontoid tusks, and those of the Elephantoidea are devoid of enamel, except at the tips in the young stage.

SUMMARY OF PROPORTIONAL CHANGES

Cyrtocephaly: Fore-and-aft faciocranial abbreviation.
Cyrtodonty: Fore-and-aft molar-crown abbreviation.
Hypsicephaly: Vertical heightening of the cranium and jaws.
Hypsodonty: Vertical heightening of the molar crowns.
Brachyodonty: Vertical shallowness of the molar crowns.
Acrocephaly: Vertical heightening of the occipitofrontal apex.
Dolichocephaly: Lengthening of the cranium in proportion to breadth.
Brachycephaly: Broadening of the occiput or of the zygomatic arches.
Cyptocephaly: Downward flexure of the facial to the basicranial axes.
Orthocephaly: Lack of inclination of the basifacial to the basicranial axis.
Dolichopy: Lengthening of the face.
Brachyopy: Shortening of the face.
Bathycephaly: Vertical deepening of the basicranium, molar alveoli, and jaws.

3. CHARACTERS, AFFINITIES, AND MIGRATIONS OF THE PROBOSCIDEA

MŒRITHERIOIDEA

Superfamily: MŒRITHERIOIDEA Osborn, 1921. Family: MŒRITHERIIDÆ Andrews, 1906

Subfamily: MŒRITHERIINÆ Winge-Osborn (1906–1923)

Genus: *Mœritherium* Andrews, 1901–1906

(Cf. Vol. I, Chap. III, and Pls. x, xi, and Figs. 23 and 24; also Vol. II, p. 1529, and Figs. 1220, 1227, and Pl. xiv)

THE MŒRITHERES, named from Lake Mœris of the Greeks. Small amphibious quadrupeds of the North African rivers and lakes. Cranium primitive, elongated (dolichocephalic), tubular brain cavity, zygomatic arches slender. Face abbreviated (brachyopic); orbits very small, shallow, opening upward and outward. Eyes very far forward, well raised toward top of face. Auditory meatus elevated, an aquatic adaptation. Mandible and symphysis relatively short. Upper and lower lips opposing each other. First superior and inferior incisors partly functional; second greatly enlarged, directly opposed, tusk-like, curved, gliriform, partly sheathed in enamel; third superior incisors and superior canines greatly reduced; third inferior incisors and inferior canines entirely wanting. Superior premolars, $P^{3\text{-}4}$, tritubercular, tetartocones rudimentary or absent; last premolar not bilophodont. Molars tetrabunodont (quadritubercular), bilophodont, with incipient trilophodonty, quadrate or slightly elongate in proportion; superior molars, M^1, strictly bilophodont, M^2 with rudimentary third crest, M^3 with enlarged third crest; inferior molars, M_1, bilophodont, M_2, trilophodont, rudimentary, M_3, trilophodont, trilophodonty not pronounced—all three pairs of premolars and molars functioning at the same time. No trace of trefoil pattern or of intermediate conules. Skeleton partly known; vertebral structure indicating an ambulatory and amphibious habit; probably pentadactyl. Palustral, amphibious, and semi-aquatic, with ancestral genetic affinities to the Proboscidea in dentition, and analogies to the Sirenia and Hyracoidea in the skull, but much closer to the Sirenia than to the Hyracoidea.

Dental formula: $I\frac{1\text{-}2\text{-}3}{1\text{-}2\text{-}0}\ C\frac{1}{0}\ P\ \frac{2\text{-}4}{2\text{-}4}\ M\ \frac{1\text{-}3}{1\text{-}3}$

Ridge-crest formula: $P\ 2\frac{2}{2}\ P\ 3\frac{2}{2}\ P\ 4\frac{2+}{2+}\ M\ 1\frac{2}{2}\ M\ 2\frac{2+}{2+}\ M\ 3\frac{2+}{3}$

HORIZON.—Upper Eocene (Qasr-el-Sagha formation) to Lower Oligocene (Fluvio-marine formation).

Compare p. 1529, also figures 23, 24, and 1227.

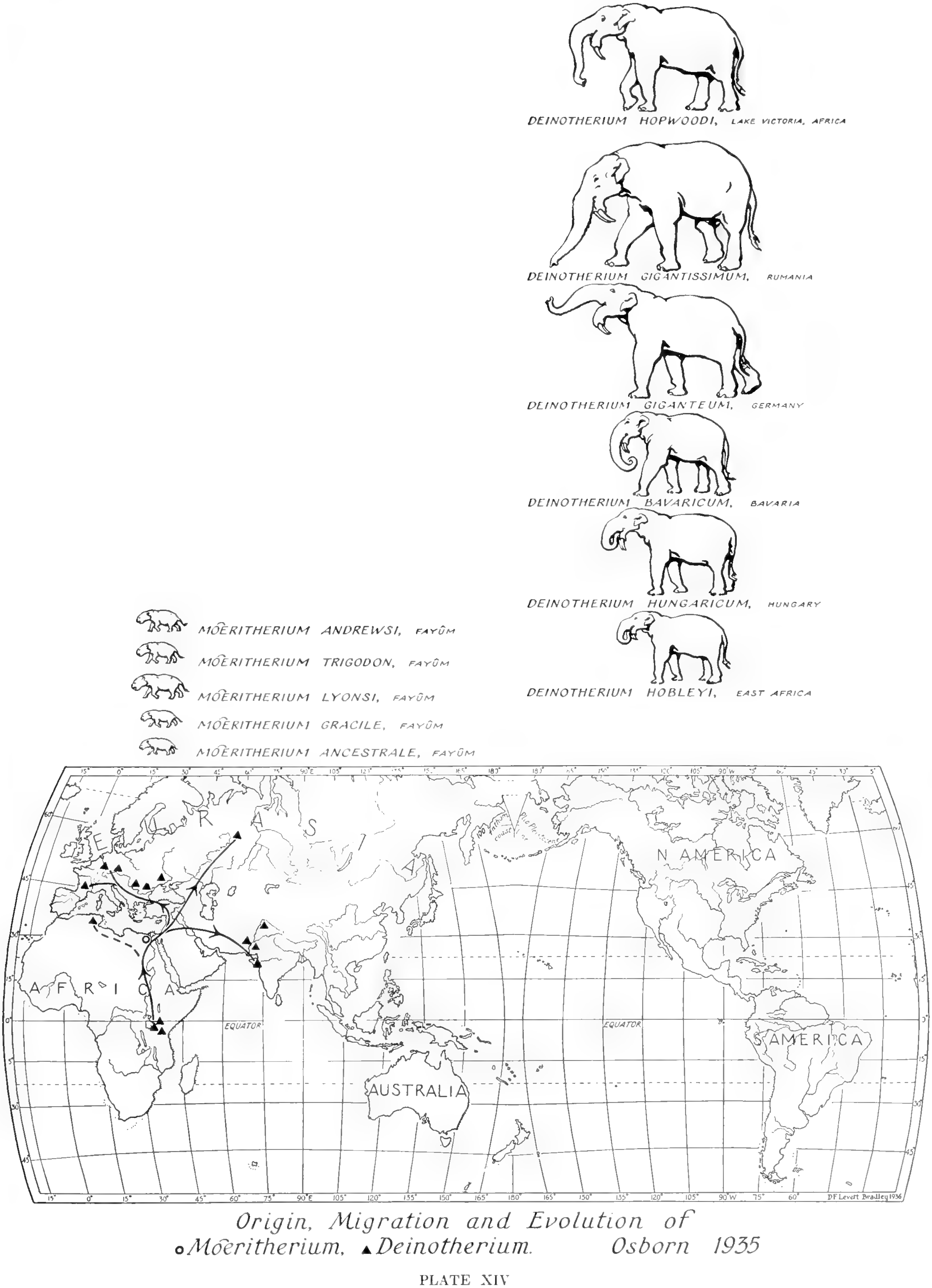

PLATE XIV

Geologic range: *Mœritherium*, Upper Eocene to Lower Oligocene. *Deinotherium*, Lower Miocene to Middle Pleistocene.

Habits and Affinities.—(Cf. Vol. I, p. 48): "The conclusions drawn from the front teeth, I^2- I_2, from the simple bunodont grinding teeth, from the very short face (brachyopy), from the long cranium (dolichocrany), and from the extremely small bony eye sockets, are that *Mœritherium* was a confirmed and continual river-living animal, feeding mainly under water and along the banks of rivers, more specialized for aquatic life than the hippopotamus, as proven by its feeble pelvic bones, but far less specialized for aquatic life in its limb structure than the Sirenia. This does not prove that *Mœritherium* is of the order Sirenia, as Osborn suggested in 1909; it is certainly an independent member of the Proboscidea, as Andrews originally maintained and as Matsumoto has stoutly contended. Its cranial *analogies* are with the sirenian skull; its cranial and dental *homologies* are with the Proboscidea. Its limbs and skeleton relate it to the primitive Proboscidea."

(*Op. cit.*, p. 39): "Recent studies by Gregory (1910–1920), Matsumoto (1923), and Simpson (1932) point towards the existence in Upper Cretaceous and Lower Eocene time in Africa of a common ancestral form of mammal which by adaptive radiation through ground-loving, shore-loving, and water-loving habits, may have given rise to the Sirenians . . ., the Mœritheres, and the Proboscideans. Widely different and profoundly divergent as the two great orders of Sirenians and Proboscideans are today, they still exhibit certain common characters in their internal anatomy, certain common characters in their cranial and labial structure, as well as one unique character in their grinding teeth, namely, *trilophodonty* or the evolution of three crests on the superior and inferior molars."

Professor Osborn considered that the structure of the muzzle proves that *Mœritherium* had heavy and fleshy lips capable of closing over the tusks when the mouth was shut; that it had no proboscis.

Migration.—So far as known at the present time *Mœritherium* was confined to the African continent. The *Mœritherium* sp. from Baluchistan, described by Pilgrim in 1912 (see Vol. I, p. 78), is provisionally referred to *Trilophodon pandionis*.

DEINOTHERIOIDEA

Superfamily: DEINOTHERIOIDEA Osborn, 1921. Family: Curtognathidæ Kaup-Osborn (1833–1936)
Subfamily: Dinotheriinæ Osborn, 1910
Genus: *Deinotherium* Kaup, 1829
(Cf. Vol. I, Chap. IV, also Fig. 56, and Pls. x, xi; Vol. II, p. 1529 and Figs. 1220–1222, 1227, also Pl. xiv)

The Deinotheres, implying proboscideans of terrifying size, existed in Europe and Asia in Miocene and Pliocene times, also in Africa in Middle Pleistocene time.

> Cranium abbreviate; proportions brachycephalic; summit flattened; occiput forwardly inclined.
>
> Probably long proboscis capable of reaching higher branches of trees as well as the ground. Lower jaw elongated (see Kittl's description on p. 99 of Vol. I, this Memoir, although on p. 112 it is described as abbreviate) and sharply bent downwards. Superior tusks early aborted; inferior tusks rounded, directly downcurved, and bent backwards. Primitive Deinotheres present simple, bilophodont grinders, similar to those of *Mœritherium*, and are progressively trilophodont; the upper grinders attain a stage which parallels the molar pattern of the tapir, but show a tendency to the trilophodont structure characteristic of the primitive mastodonts and elephants. As compared with other proboscideans, both mastodontoid and elephantoid, the dentition of the Deinotheres is relatively non-progressive; the fundamental pattern of the grinding teeth was established extremely early in geologic time, certainly during the unknown Oligocene stages, because in the Lower Miocene specific stages it is fully established, especially the number of ridges and the character of the crests of the upper and lower true molars, M1–M3. Grinding teeth sharply crested, persistently brachyodont, never hypsodont. Subdivision of

summit of crests into fourteen to sixteen conelets (*Deinotherium hopwoodi*[1]), a character not previously mentioned, so far as known, in connection with any other species of *Deinotherium*. Replacement of Dp 3–4 by P 3–4; no premolar replacement of Dp 2. Dp 4 and M 1 trilophodont; P 4, M 2, and M 3 bilophodont. All premolars and molars of both jaws functioning at same time. Pre- and postcingulum sometimes present. The ivory of the tusks "presents the fine concentric structure of those of the Hippopotamus, not the decussating curvilinear character which characterizes the ivory of the Elephant and Mastodon" (*fide* Owen, 1868, III, p. 359).

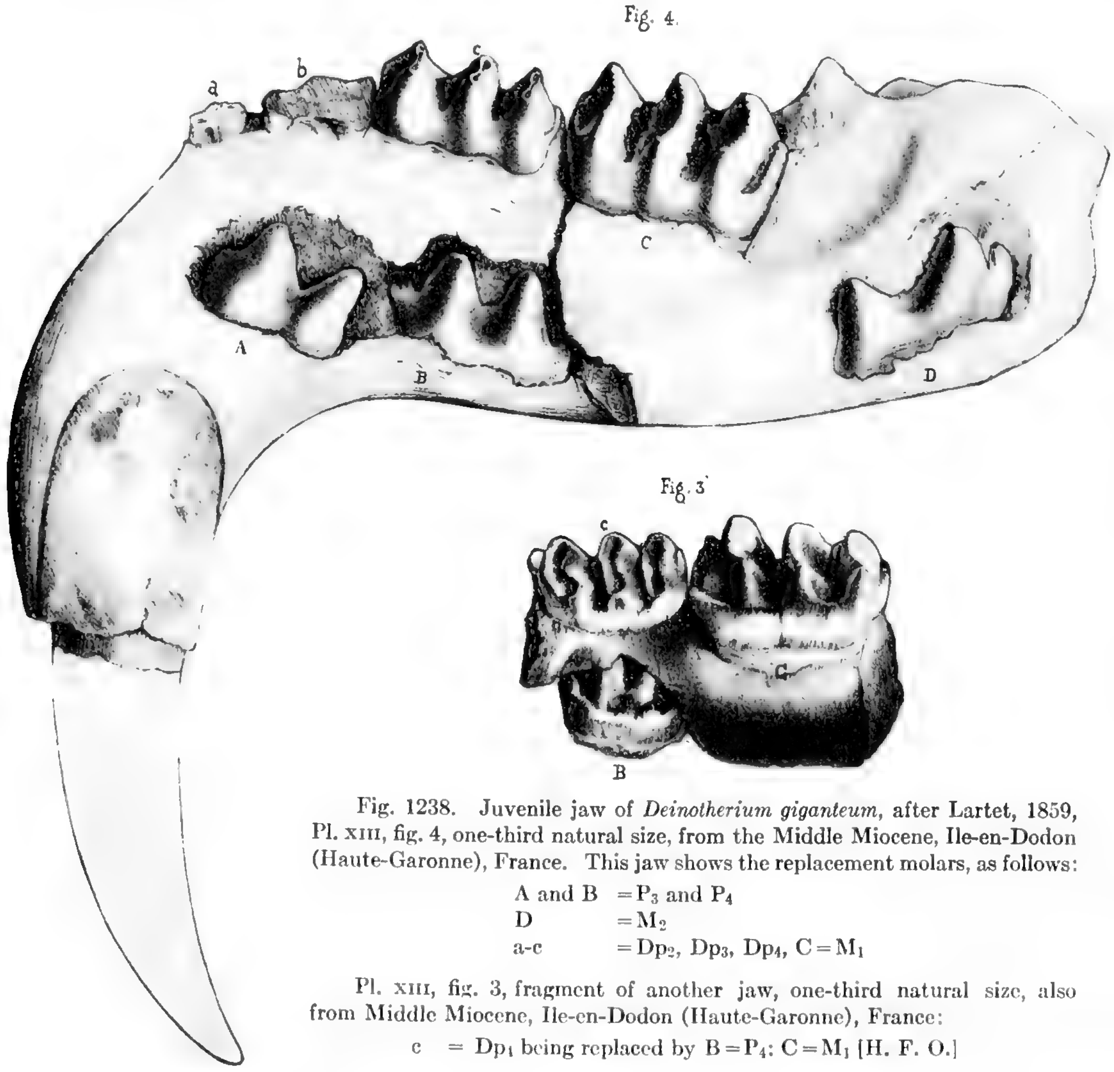

Fig. 1238. Juvenile jaw of *Deinotherium giganteum*, after Lartet, 1859, Pl. XIII, fig. 4, one-third natural size, from the Middle Miocene, Ile-en-Dodon (Haute-Garonne), France. This jaw shows the replacement molars, as follows:

A and B $= P_3$ and P_4
D $= M_2$
a-c $= Dp_2$, Dp_3, Dp_4, $C = M_1$

Pl. XIII, fig. 3, fragment of another jaw, one-third natural size, also from Middle Miocene, Ile-en-Dodon (Haute-Garonne), France:

c $=$ Dp_4 being replaced by $B = P_4$; $C = M_1$ [H. F. O.]

Limbs elongated, increasingly elephantoid, raising body well off the ground. Progressive increase in size from Lower Miocene stage to Pliocene stage. Digits II, III, IV; vestigial D.I in the pes. Dorsolumbar vertebræ abbreviate.

Dental formula: Di $\frac{0\text{-}0\text{-}0}{1\text{-}2\text{-}0}$ Dc $\frac{0}{0}$ I $\frac{0\text{-}0\text{-}0}{0\text{-}2\text{-}0}$ Dp $\frac{2\text{-}4}{2\text{-}4}$ P $\frac{3\text{-}4}{3\text{-}4}$ M $\frac{1\text{-}3}{1\text{-}3}$.
Ridge-crest formula: Dp $2\frac{2}{2}$ Dp $3\frac{2}{2}$ Dp $4\frac{3}{3}$ P $3\frac{2}{2}$ P $4\frac{2}{2}$ M $1\frac{3}{3}$ M $2\frac{2}{2}$ M $3\frac{2}{2}$.

HORIZON.—Lower Miocene to Middle Pleistocene. Compare Vol. I, p. 735, and figure 56; also Vol. II, p. 1529 and figures 1220, 1222, 1227.

HABITS AND AFFINITIES.—According to Weinsheimer (1883—see Vol. I, pp. 86–95), various authors during the long period of excavation and description of *Deinotherium* remains compared them to fossils (mastodonts) from the Ohio River, from Peru in South America, and from Asia, stating that they could not be distinguished from the Siberian mammoth; others ascribed them to Cuvier's "Tapirs gigantesques," still others believed them

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[1] [Regarded by Doctor Hopwood as a synonym of *Dinotherium bozasi* of Arambourg, 1934.—Editor.]

to be related to the hippopotamus and to the rhinoceros. Many of the early authors, e.g., Buckland (1835) and de Blainville (1837) were of the opinion that *Deinotherium* frequented freshwater lakes and rivers and was most nearly related to the tapirs.

The skeleton of *Deinotherium bavaricum* found at Franzensbad in 1883 fails to support the original theory that the Deinotheres were a fluviatile or water-loving animal which frequented streams and used its lower tusks for the prehension of food from the banks, although during the warm seasons it doubtless bathed in shallow waters, like the modern Indian elephant. On the contrary, one is inclined to conclude that it was a forest-living animal, subsisting upon leafage and tree boughs, to which its sharply crested grinding teeth were adapted like those of the tapir and of the tree- or shrub-browsing types of rhinoceroses. The very powerful trunk was eminently adapted to the collecting of tree boughs and leafage; the open supranarial space is enormous. The absence of large superior tusks, which are seen in all the Mastodontidæ and Elephantidæ, explains the relatively flattened form of the top of the cranium, and the forwardly inclined occiput. *Deinotherium* was neither mastodontoid nor elephantoid in profile but relatively flattened and depressed, and the body height and length of limb approximated that of the largest Proboscidea (see Figs. 63, 65 and 70).

It is not an unreasonable hypothesis of extinction that the brachyodont Deinotheres were unable to compete with the incoming Stegodonts with their very numerous transverse crests and tendency to hypsodonty. At all events, the climax of the series (*Deinotherium gigantissimum*) in southern Eurasia became extinct in Middle Pliocene time, just prior to the appearance of numerous species of *Stegodon*. In Africa the Deinotheres survived into Middle Pleistocene time (*Deinotherium hopwoodi*[1]).

MIGRATION.—The evidence available seems to point to an African origin of *Deinotherium*, where specimens have been found as far south as Tanganyika Territory, since there is no indication of ancestral forms of this genus in any Eocene or Oligocene horizon of Eurasia at present known. From Africa these animals spread northward through southern France, Germany, Hungary, Rumania, and as far east as Baluchistan and India; their most northerly range, so far recorded, is the Ural Mountain region.

MASTODONTOIDEA

Superfamily: MASTODONTOIDEA Osborn, 1921. Family: BUNOMASTODONTIDÆ Osborn, 1921
(Syn. TRILOPHODONTIDÆ Simpson, 1931)[2]
Subfamily: LONGIROSTRINÆ Osborn, 1918 (Syn. Trilophodontinæ Scott, 1937)
Genera: *Trilophodon* Falconer, 1846, 1857; *Megabelodon* Barbour, 1914, 1917
Subgenera: *Genomastodon* Barbour, 1914; *Choerolophodon* Schlesinger, 1917; *Tatabelodon* Frick, 1933
(Compare Vol. I, Chap. VIII, also Figs. 189, 277, 680, also Vol. II, p. 1531 and Figs. 1221, 1222, 1227, and Pl. xv)

THE LONGIROSTRINES, long-jawed bunomastodonts of Eurasia and North America, including *Trilophodon* and *Megabelodon*. Probably flood-plain and low savanna habitat.

The history of the subfamily Longirostrinæ is complex. While it was at first thought to embrace both the hyperlongirostral (*Trilophodon*) and the medilongirostral (*Tetralophodon*) mastodonts (see Vol. I, p. 231), it is now restricted to the former, the Tetralophodonts having been removed by van der Maarel in 1932 to his new subfamily Tetralophodontinæ, under which heading (pp. 343–379 of the present Memoir) they are treated. The ancestral form of the Longirostrinæ was believed to be *Phiomia* of the Oligocene of the Fayûm of Egypt, owing chiefly to the fundamental bunomastodont pattern of its molars, with 'central conules' conspicuous in *Phiomia*

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[1] [See footnote on opposite page.—Editor.]

[2] [See page 1525 above, where Doctor Simpson states that he now prefers Gomphotheriidæ Cabrera, 1929.—Editor.]

osborni (see p. 715), but subsequently, after comparing the sectioned tusks of *Phiomia*, *Trilophodon*, and *Amebelodon*, Professor Osborn came to the conclusion that the *Phiomia* tusk was more nearly like the tusk of *Amebelodon* than that of *Trilophodon*, and as a consequence he placed *Phiomia* in the direct line of ancestry of *Amebelodon* rather than of *Trilophodon* (see Amebelodontinæ below, also Pl. xv, opposite, indicated by interrupted line). The following is a citation from page 249 of Volume I:

> It has taken many years to establish the fact that a single generic phylum arose from an unknown ancestor in North Africa and gave rise to the series of long-jawed species in Europe, Asia, and North America, separated from other phyla by constant increment in the following distinctive characters, namely, the long, narrow teeth and the excessively long lower jaw. Typified by *Trilophodon angustidens* of Simorre. Jaws progressively elongating to an extreme; conules arising in the center of the molar valleys to form trefoils;... Inferior incisors scaptobelodont, rodlike (*Trilophodon angustidens, T. osborni, T. abeli, T. fricki*), more or less elongate or laterally compressed (*T. dinotherioides, T. giganteus*); sometimes tuskless (*T. phippsi, T. gaillardi, T. lulli*); subcylindrical ('prod-tuskers'); not spatulate or expanded as in the 'shovel-tuskers' (*Amebelodon, Platybelodon, Serbelodon*).

The principal generic characters of *Trilophodon* may be summarized as follows:

Trilophodon.—Cranium low, elongate (dolichocephalic). Lower jaws hyperlongirostral. Limited development of the proboscis, probably a prehensile upper lip, compensated for by great elongation of the jaw. Superior tusks flattened, recurved, with enamel band; inferior tusks rounded, triangular, flattened-horizontal, flattened-oblique, massive, without enamel band; sometimes absent. Grinding teeth persistently brachyodont, narrow; conules in center of valleys between crests, single mesotrefoils in superior and inferior molars; rudiments of double trefoils in late geologic stages. Cones and conelets regular, with simple, smooth enamel. Intermediate molars trilophodont. Third molars with four and a half to five plus crests. Cement in *T. dinotherioides*. Third molars only functional in extreme old age. Limbs mastodontoid; feet tetradactyl to pentadactyl; digits abbreviated. Low bodied; pelvis broad.

Dental formula: Di $\frac{0\text{-}0\text{-}0}{0\text{-}2\text{-}0}$ C $\frac{0}{0}$ I $\frac{0\text{-}2\text{-}0}{0\text{-}2\text{-}0}$ Dp $\frac{1\text{-}3}{1\text{-}3}$ P $\frac{0\text{-}0\text{-}4}{0\text{-}0\text{-}4}$ M $\frac{1\text{-}3}{1\text{-}3}$.
Ridge-crest formula: Dp $2\frac{1\frac{1}{2}}{1\frac{1}{2}}$ Dp $3\frac{2\frac{1}{2}}{2\frac{1}{2}}$ Dp $4\frac{3}{3}$ P $4\frac{?}{3}$ M $1\frac{3}{3}$ M 2 $\frac{3}{3\frac{1}{2}}$ M 3 $\frac{4\frac{1}{2}}{4\frac{1}{2}\text{-}5\frac{1}{2}}$
HORIZON.—Lower Miocene to Middle Pliocene. Compare Vol. II, p. 1531, also figures 1222–1224, 1227.

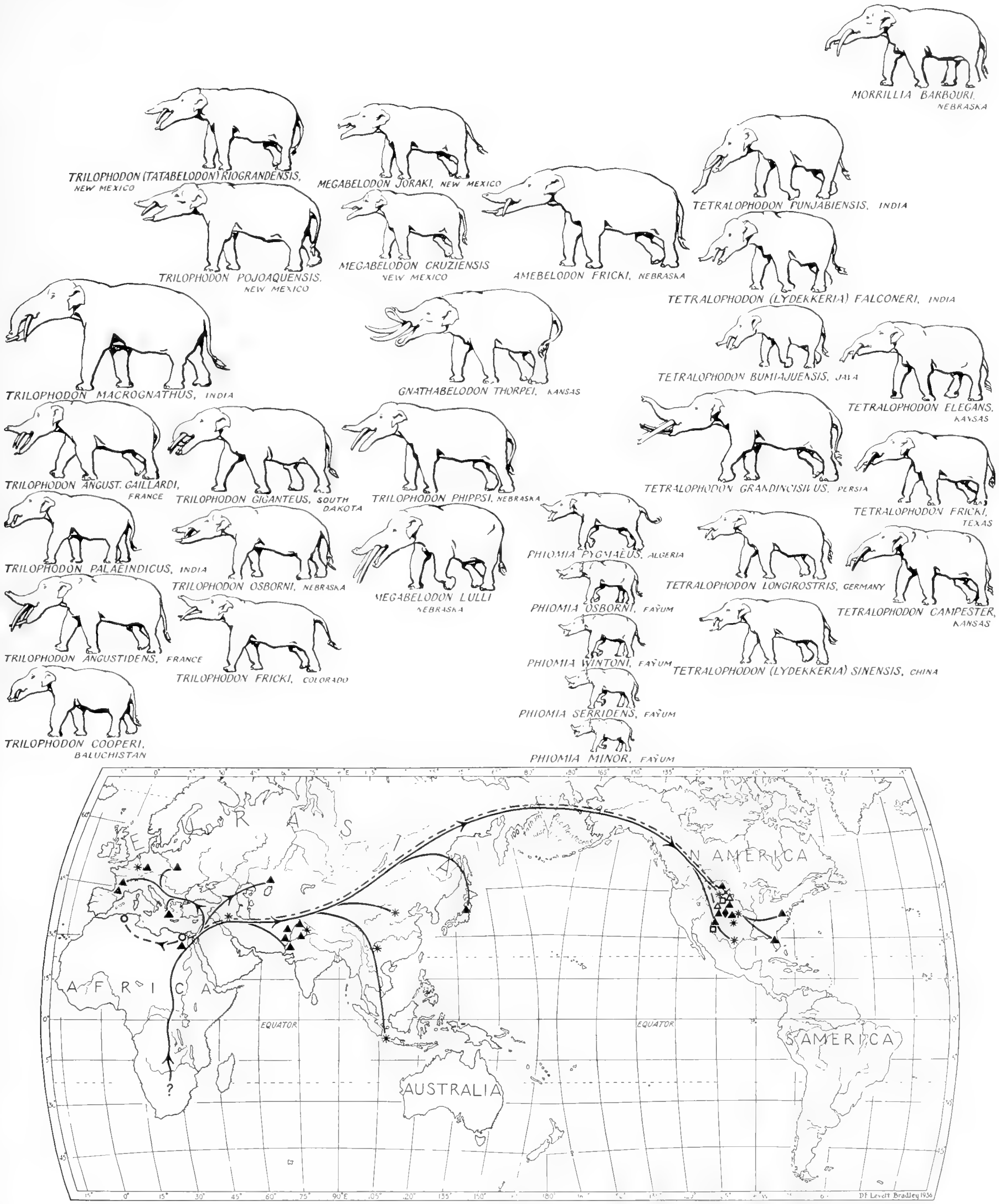
Megabelodon.—The genus *Megabelodon* Barbour was regarded by the present author as a synonym of *Trilophodon* until the discovery in Nebraska in 1935 by Professor Barbour and his field parties of two rostra, one of which was recovered at, or near, the type locality of *Tetrabelodon* [*Megabelodon*] *lulli*, which prove *Megabelodon* to be not only widely distinct from *Trilophodon*, but a member of an independent generic line characterized by the entire absence of the inferior tusks and by the broadening of the mandibular extremity into an obtuse, toothless digging expansion which varies in different species. *Megabelodon lulli* was originally restored with a pair of slender inferior tusks. Its possible relationship to *Gnathabelodon* has been suggested.

HORIZON.—Of Mio-Pliocene and Lower Pliocene age (cf. Vol. II, p. 1532, also Figs. 1224, 1227).

Hemimastodon.—In the case of *Hemimastodon* Pilgrim, 1912, type *Tetrabelodon crepusculi*, the present author was of the opinion that it was not a proboscidean; the triangular form and simple bunodont structure of the type molar appeared to him to relate it remotely to the Suina of the piglike Artiodactyla.

Choerolophodon (synonym of *Trilophodon*).—The subgenus *Choerolophodon* Schlesinger, 1917, type *Mastodon pentelicus* Gaudry, based entirely on juvenile skulls and jaws, was long under consideration by Professor Osborn, who finally concluded that its affinities were more nearly with *Trilophodon* than with *Tetralophodon*. He was led to this decision by the fortunate discovery in Samos by Dr. Barnum Brown of a palate of a young individual with molars Dp^3 to M^1 *in situ*, the latter exhibiting two large conules in the median valleys.

HORIZON.—Of Lower Pliocene age (cf. Vol. II, p. 1531, also Figs. 1222, 1227).



Origin, Migration and Evolution of ▲*Trilophodon,* □*Megabelodon,* ◆*Gnathabelodon,* ○*Phiomia,* △*Amebelodon,* ✳*Tetralophodon,* ×*Morrillia.* *Osborn 1935*

PLATE XV

Geologic range: *Trilophodon*, Lower Miocene to Middle Pliocene; *Megabelodon*, Mio-Pliocene and Lower Pliocene. *Gnathabelodon*, Middle(?) Pliocene. *Phiomia*, Lower Oligocene and Upper(?) Oligocene; *Amebelodon*, Middle Pliocene. *Tetralophodon*, Mio-Pliocene to Middle Pliocene; *Morrillia*, Middle Pleistocene.

Genomastodon and Tatabelodon.—As regards *Genomastodon* and *Tatabelodon*, Professor Osborn was unable to find clear generic distinctions to validate these terms. Of the latter he remarks on page 325 of Volume I that the "superiorly grooved and upcurved longirostral symphyses of these types [*Tatabelodon riograndensis* and *T. gregorii* of Frick] scarcely serve for generic distinction from *Trilophodon* to which they appear to be related both in length of jaw and in the dimensions of the 4½ ridge-crested third inferior grinding teeth." It will be noted, however, that both *Genomastodon* and *Tatabelodon* are retained as subgenera or synonyms of *Trilophodon* (see Vol. I, pp. 293, 298, and 324).

MIGRATION.—The classic *Trilophodon angustidens* of the Middle Miocene of France is now traced to the *T. angustidens libycus* of North Africa through the very primitive *T. pontileviensis* of the Lower Miocene of France and the *T. cooperi* of the Lower Miocene of Baluchistan; it passed through the Lower and Middle Miocene stages of Europe and Asia into the extremely long-jawed American types of the Upper Miocene and the Pliocene of Dakota, Nebraska, Colorado, and New Mexico, to which different generic names have been assigned, such as *Megabelodon* and *Genomastodon* (see migration map, Fig. 1227). Dr. Chester Stock lists *Trilophodon* sp. as occurring in the Ricardo deposits of the Mohave Desert, California (see Stock, 1928.1, pp. 43–47). Recently Doctor Hopwood has described members of this subfamily from China (see p. 702 of Vol. I of this Memoir). So far as known, *Trilophodon* became rare, or migrated from Eurasia to America, at the close of Miocene or beginning of Pliocene time both in Europe and Asia.

Superfamily: MASTODONTOIDEA Osborn, 1921. Family: BUNOMASTODONTIDÆ Osborn, 1921
(Syn. TRILOPHODONTIDÆ Simpson, 1931)[1]
Subfamily: GNATHABELODONTINÆ Barbour and Sternberg, 1935
Genus: *Gnathabelodon* Barbour and Sternberg, 1935
(Cf. Vol. I, Appendix, pp. 710–714, and Fig. 668; Vol. II, p. 1533, and Fig. 1227, also Pl. xv)

GNATHABELODONTS, typical "shovel-jawed longirostrines," of progressive bunomastodont type, with broad tuskless mandibular symphysis and very broad molars. The present author states on page 711 of Volume I that the "mandibular and dental characters widely separate *Gnathabelodon* from the shovel-tuskers, flat-tuskers, or any of the remaining genera of the Bunomastodontidæ and Serridentidæ and are in full accord with Barbour's conception of this as representing a distinct subfamily remotely related to the Amebelodontinæ."

Gnathabelodon.—Skull very large, the width across the occipital condyles being 294 mm. Lower jaws longirostral, expanding broadly towards the extremities with an elongated and longitudinally grooved symphysis—a broad, birdlike, toothless bill analogous to that of the duck-billed *Platypus* in the Monotreme order. Superior tusks massive, rounded, and outcurved, with upturned tips; no enamel. Inferior tusks wanting, replaced by a broadly expanded, sharpened bony border, probably sheathed with hardened epidermis. Superior and inferior grinding teeth tetralophoid to pentalophoid, ptychodont, with double entotrefoils and rudimentary ectotrefoils in superior molars, double ectotrefoils on inferior molars. In general, of progressive, bunomastodont type with central conules. Intermediate molars trilophodont. In old age reduced to a single pair above and below. Cement in valleys of third superior molars.

Dental formula incompletely known: I $\frac{0\text{-}2\text{-}0}{0\text{-}0\text{-}0}$ M $\frac{3}{2\text{-}3}$
Ridge-crest formula: M $2^{?}_{3?}$ M $3^{4\frac{1}{2}}_{4\frac{1}{2}}$.
HORIZON.—Middle(?) Pliocene. Compare Vol. II, p. 1533, and figures 1224, 1227.

MIGRATION.—The genotype *Gnathabelodon thorpei* is the only species of this genus thus far discovered, and was found near Ogallah, Trego County, western Kansas.

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[1] [See footnote 2 on page 1555 of this chapter.—Editor.]

Superfamily: MASTODONTOIDEA Osborn, 1921. Family: BUNOMASTODONTIDÆ Osborn, 1921

(Syn. TRILOPHODONTIDÆ Simpson, 1931)[1]

Subfamily: AMEBELODONTINÆ Barbour, 1929

Genera: *Amebelodon* Barbour, 1927; *Phiomia* Andrews and Beadnell, 1902

(Cf. Vol. I, pp. 333–338, 690, 715–719, Pls. v–vii, x, xi, Fig. 277; Vol. II, p. 1533, Figs. 1220, 1224, 1227, Pl. xv)

AMEBELODONTS, longirostral trilophodont mastodonts of North Africa and Central United States, differing from the typical Longirostrinæ in the high degree of specialization for the shoveling or digging functions of the inferior tusks, which are reinforced by internal dentinal laminæ. This tusk structure precludes the analogy of *Amebelodon* to *Platybelodon* in which the inferior tusks consist of closely compacted rod-cones. The postsymphyseal portions of the jaw and grinding teeth undergo little progressive evolution except in size; it is the anterior symphyseal and rostral region of the amebelodont shovel-tuskers that undergoes such an extraordinary specialization, while the grinding teeth remain substantially the same.

Amebelodon, typical 'shovel-tusker' of Nebraska, descendant of *Phiomia* of the Fayûm. Cranium and rostrum uniformly abbreviated and reduced in size. Mandibular rostrum relatively long and slender. Lower jaws elongated (longirostral), nearly horizontal, moderately expanded towards the extremities. Superior tusks reduced in size, downcurved, outcurved, with persistent outer enamel band; inferior tusks without enamel band, composed of concentric dentinal laminæ (1–9), instead of dentinal rod-cones as in *Platybelodon*, greatly elongated, somewhat broadened, closely appressed in the median line, tips rounded, alveolar portion plano-concave above. Mass of the *Amebelodon* tusk more than seventy times greater than that of the *Phiomia* tusk. Molars large, narrow, with double trefoils and central conules; inferior molars with five ridge-crests; cement present. From external cingulum rise many short, blunt cones.

Dental formula: Incompletely known.

HORIZON.—Middle Pliocene. Compare Vol. II, p. 1533, and figures 1224, 1227.

Phiomia, ancestral 'Fayûm shovel-tusker' of North Africa. Of medilongirostral type; cranium low, abbreviated; palate long and narrow; symphysis long; progressive dolichopy, also progressive dolichodonty and bunomastodonty, the latter character tending to place these animals in the direct line of ancestry of *Amebelodon fricki*. Superior tusks sharply pointed, downcurved, with enamel band on outer surface. Inferior tusks horizontal, spatulate, without enamel, composed of concentric dentinal laminæ (1–7); incisive alveoli elongate (*P. osborni*); Di_2 with straight inner border, convex outer border marked by crenulations or serrations, enamel confined to the tip. Molars typically bunodont, relatively long and narrow (progressive narrowing of M_3 prophetic of *Amebelodon fricki*), brachyodont, rudimentary or progressive conules; generally trilophodont, last inferior molar in *Phiomia osborni* subtetralophodont.

Dental formula: Di $\frac{}{0\text{-}2\text{-}0}$ C $\frac{0}{0}$ I $\frac{0\text{-}2\text{-}0}{0\text{-}2\text{-}0}$ Dp $\frac{2\text{-}4}{2\text{-}4}$ P $\frac{3\text{-}4}{3\text{-}4}$ M $\frac{1\text{-}3}{1\text{-}3}$

Ridge-crest formula: Dp $2\frac{1+}{1+}$ Dp $3\frac{2+}{2+}$ Dp $4\frac{3}{3}$ P $3\frac{?}{?}$ P $4\frac{2}{2+}$ M $1\frac{3}{3}$ M $2\frac{3}{3}$ M $3\frac{3}{3\frac{1}{2}}$

HORIZON.—Lower Oligocene (Fluvio-marine formation) and Upper(?) Oligocene. Compare Vol. I, figure 23; Vol. II, p. 1533, and figures 1220, 1224, 1227.

MIGRATION.—Up to the year 1934 the progressive species of *Phiomia* from the Fayûm of North Africa were believed by the present author to be broadly ancestral to the *Trilophodon angustidens* phylum of Europe, chiefly because of the fundamental bunomastodont pattern of the *Phiomia* molars with 'central conules' conspicuous in *Phiomia osborni*. Finally, however, he was of the opinion that *Phiomia* was the direct ancestor of *Amebelodon*, as stated in Volume I, p. 715: "Not only in external form but in the internal macroscopic and microscopic structure of the incisive tusks (see Pl. v, A–F3) *Phiomia wintoni* leads into *Phiomia osborni* and after an immense interval of geologic time[2] spanning the Upper Oligocene, the entire Miocene, and Lower Pliocene periods, the

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[1] [See footnote 2 on page 1555 of this chapter.—Editor.]

[2] ["Thirty million year evolution of the lower jaw and paired inferior tusks from the *Phiomia minor* of the Oligocene of North Africa into the *Amebelodon fricki* of the Pliocene of Nebraska" (cf. Osborn, 1935.937, p. 408, fig. 3; also Pl. v—with modifications—of Vol. I of the present Memoir).—Editor.]

Middle Pliocene *Amebelodon fricki* appears in Nebraska as the indubitable successor of *Phiomia osborni* of the Oligocene River Nile of Egypt." The abundance of *Phiomia* is attributable to its having a flood-plain habitat similar to that of *Trilophodon* and other longirostrines, which are by far the most numerous proboscideans throughout Oligocene, Miocene, and Lower Pliocene times.

Superfamily: MASTODONTOIDEA Osborn, 1921. Family: BUNOMASTODONTIDÆ Osborn, 1921
(Syn. TRILOPHODONTIDÆ Simpson, 1931)[1]
Subfamily: TETRALOPHODONTINÆ van der Maarel, 1932
Genera: *Tetralophodon* Falconer, 1847, 1857; *Morrillia* Osborn, 1924. Subgenus: *Lydekkeria*, Osborn, 1924

(Cf. Vol. I, pp. 342–379, 690, 703–705, Pls. x, xi, and Fig. 307; Vol. II, p. 1533, Figs. 1221, 1224, 1227, Pl. xv)

THE TETRALOPHODONTS, imperfectly known Medilongirostrines of Eurasia and North America, with four-crested or tetralophodont intermediate molars, single trefoils in the Miocene stage (*Lydekkeria*), rudimentary double trefoils in the Pliocene stage (*Tetralophodon*); brachyodont progressive to hypsodont, with cement and complete doubling of trefoils in Pleistocene time (*Morrillia*).

> Cranium brachycephalic, with rounded temporal region; moderate elongation of the rostrum. Palate contracted, with posterior nares directly opposite pentaloph of M^3. Lower jaw medilongirostral. Superior tusks with enamel band. Inferior tusks flattened, oval, retrogressive, absent(?) in females (*T. campester*), without enamel band (the exception being *T. grandincisivus*). Superior and inferior tusks straight (Fig. 320). Molars progressively brachyodont to subhypsodont (*Tetralophodon*), to hypsodont and covered with cement (*Morrillia*). Intermediate molars tetralophodont. Third molars long and narrow, with 5½ to 6⅓ ridge-crests (*Tetralophodon*), to 8½ superior crests (*Morrillia*); third superior molars in *T. fricki* exhibit forward inclination of the crests. Central conules variable, cones and conelets relatively smooth and regular; progressive doubling of the trefoils. Third grinders only in use in old age.
>
> Dental formula: $1\,\frac{0\text{-}2\text{-}0}{0\text{-}2\text{-}0}$ Dp $\frac{2\text{-}4}{2\text{-}4}$ M $\frac{1\text{-}3}{1\text{-}3}$
> Ridge-crest formula: Dp $2^{1\frac{1}{2}}$ Dp 3^{3} Dp $4^{4\frac{1}{2}}$ M $1^{4\frac{1}{2}}$ M $2\frac{4\frac{1}{2}}{4\frac{1}{2}}$ M $3\frac{5\frac{1}{2}\text{-}8\frac{1}{2}}{5\frac{1}{2}\text{-}8\frac{1}{2}}$
> HORIZON.—Mio-Pliocene to Middle Pliocene (*Tetralophodon*), to Middle Pleistocene (*Morrillia*). Compare Vol. I, figure 307; Vol. II, p. 1533, and figures 1221, 1224, 1227, also Pl. xv.

It has been erroneously assumed by some authors that animals of the *Trilophodon angustidens* type gave rise to animals of the *Tetralophodon* type by abbreviation of the jaw and by the addition of a fourth crest on the intermediate molars. This assumption is disproven by three facts: (1) The true *Trilophodon* persisted after the true *Tetralophodon* had appeared; (2) *Tetralophodon* is a Medilongirostrine, whereas *Trilophodon* is a Hyperlongirostrine; (3) a true ancestral species of *Tetralophodon* (*Lydekkeria*), e.g., *Mastodon* [= *Tetralophodon* (*Lydekkeria*)] *falconeri* Lydekker, is recorded in the Middle Pliocene, Dhok Pathan beds, of India. Consequently the separation by Maarel in 1932 of the Tetralophodonts from the Trilophodonts under the subfamily name Tetralophodontinæ has been adopted in the present Memoir.

These medilongirostral mastodonts arose independently from an ancestral Oligocene stage which might be comprised within the genus *Phiomia*. This stage was less specialized than *Phiomia osborni*, which leads directly into *Amebelodon fricki*, as mentioned above under the Amebelodontinæ (p. 1558). The distinctions between the genus *Trilophodon*, the typical genus *Tetralophodon*, and the genus *Morrillia* are entirely in progressive characters which developed from the Mio-Pliocene into Pleistocene times.

The subgenus *Lydekkeria* Osborn, 1924, genotype *Mastodon falconeri* Lydekker, 1877, of supposed Middle Miocene age by Lydekker, Pilgrim, and Osborn, now proves to be of Middle Pliocene age, according to Hopwood

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[1] [See footnote 2 on page 1555 of this chapter.—Editor.]

(see Vol. I, p. 353), and therefore a contemporary of '*Mastodon*' [*Tetralophodon*] *punjabiensis* Lydekker, 1886. This being the case, *Lydekkeria* may become a synonym of *Tetralophodon*, and *T. punjabiensis* may become a synonym of *T. falconeri*. This leaves the Miocene ancestry of *Tetralophodon* uncertain, but the primitive Mio-Pliocene stage (*Lydekkeria*) appears to be ancestral to the Lower Pliocene *Tetralophodon*.

MIGRATION.—By referring to figure 1227 of the present Memoir, also to Pl. XV, it will be noted that the general trend of migration is from the west to the east. A fragmentary molar of a member of the Tetralophodontinæ ('*M.*' *longirostris*?) is recorded from the lacustrine beds of Smendou north of Constantine, northern Africa. Professor Osborn in 1925 in his article in NATURAL HISTORY on "The Elephants and Mastodonts Arrive in America," pp. 12 and 13, states that the "Tetralophodonts are in all countries very rare, yet we can trace their long migration through eastern Europe into India and China, until finally they arrive in Kansas and Nebraska." Since that time *Tetralophodon bumiajuensis* of Java has been described by van der Maarel, and the present author, in the first volume of this Memoir, described *T. fricki* from northern Texas. From the limited evidence now at hand it would appear that *Tetralophodon* became rare in Eurasia early in Pliocene time but lingered until Middle Pleistocene time on the ancient flood-plains of Nebraska.

Superfamily: MASTODONTOIDEA Osborn, 1921. Family: BUNOMASTODONTIDÆ Osborn, 1921
(Syn. TRILOPHODONTIDÆ Simpson, 1931)[1]
Subfamily: NOTOROSTRINÆ Osborn, 1921 (syn. Cordillerioninæ Scott, 1937)
Genus: *Cordillerion* Osborn, 1926

(Cf. Vol. I, pp. 543–566, also Pls. X, XI, and Fig. 501; Vol. II, p. 1534, and Figs. 1224, 1225, 1227, Pl. XVI)

Cordillerion.—Cranium mastodontoid, of relatively low, simple character as in the primitive Trilophodonts; rostrum elongate. Jaws broad, deep, and abbreviated (brevirostral); symphysis is of medium length. Superior incisive tusks spiral or horizontal, down- and outcurved, around which is wound more or less spirally a broad enamel band. Inferior incisive tusks wanting, probably present in juvenile stages. Grinding teeth brachyodont, never hypsodont, moderately elongate, with single trefoils, parallel in this respect with *Trilophodon*, central conules more or less conspicuous, cement in progressive stages. Intermediate molars with tendency to tetralophodonty (subtetralophoid) in M 2. In final phyletic stages grinding tooth action concentrated on second and third superior and inferior molars. Adaptation chiefly to a mountain habitat, grinders adapted principally to a browsing habit, tusks probably used in the uprooting of plants for food.

Undoubtedly of Old World ancestry, although no member of the Notorostrinæ has as yet been found in the Eastern Hemisphere.

Dental formula: I $\frac{0\text{-}2\text{-}0}{}$ Dp $\frac{2\text{-}4}{2\text{-}4}$ M $\frac{1\text{-}3}{1\text{-}3}$
Ridge-crest formula: Dp $2\frac{?}{?}$ Dp $3\frac{?}{?}$ Dp $4\frac{?}{?}$ M $1\frac{3}{3}$ M $2\frac{3\text{-}3\frac{1}{2}}{3\text{-}3\frac{1}{2}}$ M 3 $\frac{4\frac{1}{2}}{4\text{-}4\frac{1}{2}\text{-}5\frac{1}{2}}$

HORIZON—Pliocene and Pleistocene. Compare Vol. I, figures 501 and 680; Vol. II, p. 1534, and figures 1224, 1225, 1227, also Pl. XVI.

THE NOTOROSTRINES.—The earliest member of the subfamily Notorostrinæ is the South American *Mastodonte des Cordilières* of Cuvier described in 1806 and later (1824) designated by him *Mastodon andium*, thus superseding the name *Mastodon cordillerarum* of Desmarest, 1820–1822. This species was for a long time confused with the *Mastodonte humboldien*, also of South America, described by Cuvier in the same publication of 1806.

In January of 1921—a century later—Professor Osborn reviewed (Osborn, 1921.515, p. 10) these two classic species, including also the *Dibelodon* [=*Cordillerion*] *tropicus* and *Mastodon* [=*Stegomastodon*] *successor* of Cope, designating them as the "Brevirostrines of South America," and in September of the same year he established

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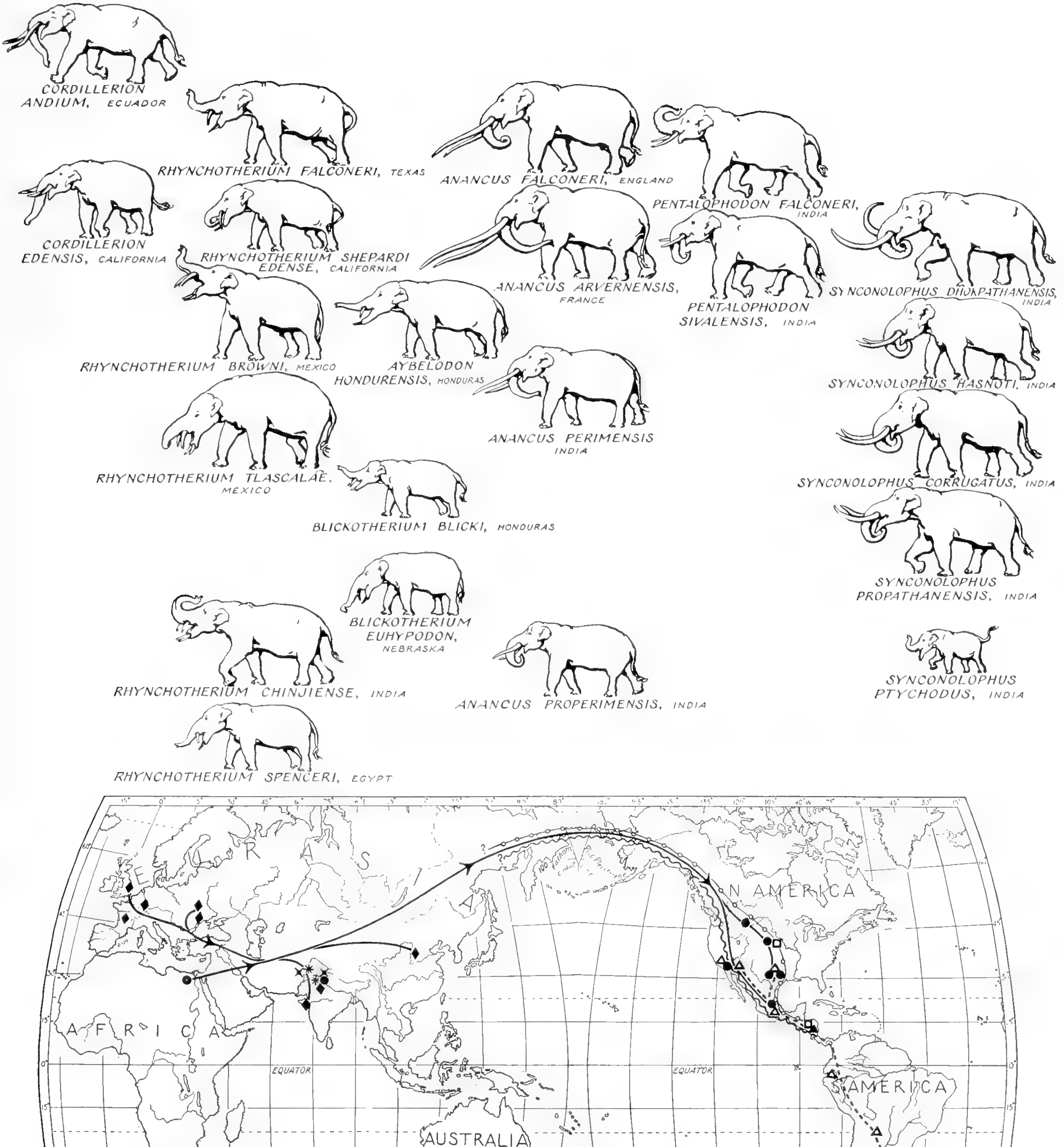
[1] [See footnote 2 on page 1555 of this chapter.—Editor.]



*Origin, Migration and Evolution of △Cordillerion, ●Rhynchotherium, □Blickotherium, ▲Aybelodon, ◆Anancus, *Pentalophodon, ×Synconolophus.* Osborn 1935

PLATE XVI

Geologic range: *Cordillerion,* Pliocene and Pleistocene. *Rhynchotherium,* Middle Miocene to Upper Pliocene; *Blickotherium,* Pliocene; *Aybelodon,* Pliocene. *Anancus,* Mio-Pliocene to uppermost Pliocene; *Pentalophodon,* Upper Pliocene; *Synconolophus,* Mio-Pliocene to Middle Pliocene.

his new subfamily, the Notorostrinæ (1921.526, p. 330) to embrace not only the four species just mentioned but six additional species, namely, *Mastodon bolivianus* and *M. chilensis* of Philippi, and *M. platensis*, *M. rectus*, *M. argentinus*, and *M. superbus* of Ameghino, on the ground that they were profoundly separated from other bunomastodonts by the progressive abbreviation of the jaw, and that they were the only members of the great order Proboscidea which, as far as known (1921), entered the South American continent. Professor Osborn's researches had not then revealed the fact that other mastodonts, namely, *Rhynchotherium* Falconer and *Notiomastodon* Cabrera, had also wandered into South America as well as one species of elephant belonging to the *Parelephas* phylum, i.e., *Parelephas columbi cayennensis* Osborn, of French Guiana.

Perhaps a still more important step was taken by Professor Osborn in 1923 (1923.601, p. 1) when he separated the *Mastodon humboldtii* group from the *M. andium* group, making *M. humboldtii* the type of his genus *Cuvieronius*, distinguished by double trefoils on the superior and inferior molars, and by simple, rounded, outwardly and upwardly curved superior tusks, lacking enamel band (see p. 540 of Vol. I), in contradistinction to *M. andium* with single trefoils, more or less conspicuous central conules in the molars, and broad, spirally enameled superior tusks, a peculiarity not observed in any other proboscidean, to which subsequently (1926.706, p. 15) he assigned the generic name *Cordillerion*. This subfamily of short-jawed bunomastodonts, therefore, is monophyletic, including the genus *Cordillerion* only.

MIGRATION.—As mentioned above, the Notorostrinæ probably originated in the Old World; fossil evidence of this fact, however, is lacking, for the earliest occurrence, as far as known, of the genus *Cordillerion* is the Upper Pliocene *C. edensis* Frick-Osborn, found at Mt. Eden Hot Springs, San Bernardino County, California; other discoveries are at Benson, Arizona, and near Sinton, Texas, also of the Pliocene. It would seem, therefore, that the trend of migration was southward, through Mexico, into South America, as far as Uruguay.

Superfamily: MASTODONTOIDEA Osborn, 1921. Family: BUNOMASTODONTIDÆ Osborn, 1921 (Syn. TRILOPHODONTIDÆ Simpson, 1931)[1]

Subfamily: RHYNCHOROSTRINÆ Osborn, 1918, 1921 (syn. Rhynchotheriinæ Cabrera, 1929)

Genera: *Rhynchotherium* Falconer, 1862, 1868; *Blickotherium* Frick, 1933; *Aybelodon* Frick, 1933

(Cf. Vol. I, pp. 475–513, 690, also Pls. x, xi, and Figs. 451, 483; Vol. II, p. 1531, and Figs. 1220, 1221, 1224, 1227, also Pl. xvi)

THE RHYNCHOROSTRINES, beak-jawed mastodonts, typified by *Rhynchotherium* Falconer, so named because of the sharply deflected rostrum. The subfamily Rhynchorostrinæ is the least known of any of the bunomastodonts. The genotype of *Rhynchotherium* is the cast of a lower jaw, the original of which was found at Tlascala, Valley of Mexico. It was at first characterized by Falconer (in a letter to Lartet of Sept. 12, 1856) as resembling "very much the figure in Alcide D'Orbigny's Voyage, described by Laurillard as *M. Andium*," but he stated that the "Genoese palæontologists had provisionally named it *Rhynchotherium*, from the enormous development of the beak, approaching Dinotherium." This letter was not published until 1868 (see Pal. Mem., Vol. II, pp. 74, 75). He further stated that he saw this cast in Genoa, an unfortunate substitution for Geneva (see Falconer, 1863, p. 56), an error to which Felix and Lenk called attention in 1891, but which was apparently unnoticed until Professor Osborn's researches for the present Memoir led him to make inquiry of Dr. Hans Georg Stehlin, who kindly located the cast in the Muséum d'Histoire Naturelle of Geneva. Through the courtesy of the Director, Dr. Pierre Revilliod, a duplicate cast was presented to the American Museum.

Professor Osborn was the first to use the specific name *tlascalæ* in 1918 (Osborn, 1918.468, table opposite p. 134); thus the genotype is *Rhynchotherium tlascalæ*. The discovery in 1911 by Dr. Barnum Brown near San

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[1] [See footnote 2 on page 1555 of this chapter.—Editor.]

José de Pimas, Sonora, Mexico, of a fine specimen of a lower jaw referable to *Rhynchotherium*—in fact, made the neotype by Professor Osborn in 1921 (1921.515, pp. 5, 6), owing to the supposed loss of the cast—served to confirm the presence of this genus in Mexico. On recovery of the cast in Geneva, it was found that the type and neotype differed sufficiently to warrant the naming of a new species; consequently Professor Osborn assigned to the neotype the name *Rhynchotherium browni* (see Vol. I of the present Memoir, p. 494). During the years following Falconer's description, specimens of *Rhynchotherium* were unearthed in California, Colorado, Montana, Nebraska, and Texas.

The Rhynchorostrinæ include the fewest and the least known species of the bunomastodonts. Tracing the phylum back into its Eurasiatic or Old World ancestry, we find a primitive lower jaw with downturned symphysis and laterally compressed incisive avleoli (Fig. 455) described by Fourtau in 1918 as *Mastodon spenceri* from Moghara, Egypt, but provisionally referred by Professor Osborn to *Rhynchotherium spenceri,* which may confirm the hypothesis of the African origin of the Rhynchorostrinæ. Also doubtfully referred by Professor Osborn to *Rhynchotherium* (*R. chinjiense*) is a left ramus, with M_2, M_3, *in situ,* found by Dr. Barnum Brown in 1922 in the Mio-Pliocene of India, near Chinji Bungalow. Dr. D. K. Chakravarti in 1935, p. 209, states that he sees no evidence of the downturning of the symphysis, and that the "warping of the alveolus of the tusk appears to the present author to be a case of distortion superinduced upon the specimen after its entombment"; he suggests that "it should be referred to *Trilophodon angustidens* (Cuvier) var. *chinjiensis* (a name proposed by Pilgrim in 1913 for a form discovered in the Salt Range. . .)."

Rhynchotherium.—No complete cranium known. Face of medium length, maxilla partly downturned. Mandible of medium length; symphyseal portion strongly deflected. Superior and inferior tusks, I^2, I_2, laterally compressed, bent downwards and outwards, with broad external enamel band; inferior tusks slightly upcurved. Grinding teeth of bunomastodont type, relatively broad, simple, brachyodont, single trefoils only, inferior 'central conules' variable, superior 'central conules' absent. Molar enamel thick. Third superior grinders with three and a half to four plus ridge-crests; third inferior grinders not exceeding four and a half to five ridge-crests; functional grinders in adults reduced to M 2–M 3, finally to M 3. Intermediate grinders trilophodont.

Dental formula: $\mathrm{I}\,\frac{0\text{-}2\text{-}0}{0\text{-}2\text{-}0}\ \mathrm{Dp}\,\frac{2\text{-}4}{2\text{-}4}\ \mathrm{M}\,\frac{1\text{-}3}{1\text{-}3}$

Ridge-crest formula: $\mathrm{Dp}\,\frac{2+}{2+}\ \mathrm{Dp}\,3\frac{3}{3}\ \mathrm{Dp}\,4\frac{3}{3}\ \mathrm{M}\,1\frac{3}{3}\ \mathrm{M}\,2\frac{3}{3+}\ \mathrm{M}\,3\frac{3\frac{1}{2}\text{-}4+}{4\frac{1}{2}\text{-}5}$

HORIZON.—Middle Miocene to Upper Pliocene. Compare Vol. II, p. 1531, and figures 1220, 1224, 1227, also Pl. XVI.

Up to the year 1929 the Rhynchorostrinæ had been considered as monophyletic. The discovery, however, near Tapasuma, Honduras, by Mr. John C. Blick of the Frick Expedition of 1929, of two long slender mandibles, one adolescent, the other mature, amplified our knowledge of these rare and probably forest-living animals, with the surprising result, as described by Mr. Childs Frick in 1933 in his article on "New Remains of Trilophodont-Tetrabelodont Mastodonts," that two new genera were added to this subfamily, namely, *Blickotherium,* genotype *Blickotherium blicki,* and *Aybelodon,* genotype *Aybelodon hondurensis.* The distinctive feature of *Aybelodon* is the enamel-less incisors, differing in this respect from other members of the Rhynchorostrinæ, but the profile of the type jaw reveals its rhynchotherine affinity and places it in a "distinct and unique line of succession."

Blickotherium.—No complete cranium known; see, however, figure 462 A for palate of *Mastodon euhypodon* Cope referred to *Blickotherium* by the present author. Mandible elongate, extremely slender, less deflected than in *Rhynchotherium.* Symphysis laterally compressed, downwardly curved. Inferior tusks upcurved, compressed laterally, broad external enamel band. Apparent presence of a replacement P_4 in the adolescent mandible.

Ridge-crest formula (Frick): $\mathrm{Dp}\,4\frac{}{2+}$ (possible replacement P_4) $\mathrm{M}\,1\frac{}{3}\ \mathrm{M}\,2\frac{}{3\frac{1}{2}}$

Ridge-crest formula (Osborn): $\mathrm{M}\,1\frac{}{2+}\ \mathrm{M}\,2\frac{}{3}\ \mathrm{M}\,3\frac{}{3\frac{1}{2}}$

HORIZON.—Pliocene. Compare Vol. II, p. 1531, and figures 1224, 1227, also Pl. XVI.

Aybelodon.—Cranium unknown. Mandibular rami of long, relatively slender type; vertical ramus, condyle and coronoid process low. Symphysis strong, very elongate, laterally and vertically compressed, upcurved, extremely narrow, transverse exceeding vertical diameter, as contrasted with *Blickotherium blicki.* Inferior tusks large, broad, closely appressed, upcurved, without trace of enamel band. Superior tusk (referred), possibly representing a distal section of upper left side, exhibits tendency toward inward and forward curvature, the presumed outer surface with remnants of enamel band. First and second inferior molars small; third inferior molars relatively broad and short; very thick enamel. Second inferior molars probably trilophoid; third inferior molars fully tetralophoid with rudimentary pentalophid.

Ridge-crest formula: $M\,2\frac{}{?\,3}$ $M\,3\frac{}{4\frac{1}{2}}$
HORIZON.—Pliocene. Compare Vol. II, p. 1531, and figures 1224, 1227, also Pl. XVI.

In summarizing the persistent primitive and progressive characters of the Rhynchorostrines, we may mention the following:

Persistent Primitive Characters.—(1) Grinding teeth persistently brachyodont or short crowned; (2) no evidence of hypsodonty or deposition of cement; (3) enamel unusually thick; (4) simple external trefoil spurs on inferior molars and internal trefoil spurs on superior molars, no trace of doubling of the trefoil spurs; (5) inferior 'central conules' variable, superior 'central conules' absent.

Progressive Characters.—Superior tusks progressive, elongated, and laterally flattened, with broad persistent enamel band. Inferior tusks progressive, compressed laterally, elongated, upturned, with persistent lateral enamel band. The tusks of *Aybelodon hondurensis,* however, are entirely without enamel.

MIGRATION.—From the Miocene of ?Egypt, through the Mio-Pliocene of ?India, to the Middle to Upper Miocene of Montana, Upper Miocene-Upper Pliocene of California, Nebraska, Texas, Colorado, Mexico, and Honduras. See especially figure 483 of Volume I of the present Memoir, and the accompanying Pl. XVI.

Superfamily: MASTODONTOIDEA Osborn, 1921. Family: BUNOMASTODONTIDÆ Osborn, 1921 (Syn. TRILOPHODONTIDÆ Simpson, 1931)[1]

Subfamily: BREVIROSTRINÆ Osborn, 1918 (syn. Pentalophodontinæ Scott, 1937)

Genera: *Anancus* Aymard, 1855, 1859; *Pentalophodon* Falconer, 1857, 1865; *Synconolophus* Osborn, 1929 (Cf. Vol. I, pp. 617–665, 690, Pls. X, XI, and Fig. 590; Vol. II, p. 1534, and figures 1221–1223, 1227, also Pl. XVI)

THE BREVIROSTRINES.—We now come to one of the mastodont divisions that never reached America, as far as is known at present, namely, the Brevirostrinæ, a subfamily provisionally named by Professor Osborn in 1918 (1918.468, p. 136) and fully defined by him in 1921 (1921.515, p. 11). In Volume I, p. 627, of the present Memoir, he summarizes the characters of this subfamily, as follows: "These short-jawed bunomastodonts are readily distinguished from all others by four principal characters: *First,* the skull and jaws short, as in the elephants; *second,* the grinding teeth finally reduced to one above and one below, as also in the elephants and in the Stegodonts; *third,* perhaps most distinctive and unique, the *alternation* of the main internal and external cones which are placed diagonally instead of transversely to the long axis of the crowns, a character first observed by Cautley in describing his species *Mastodon sivalensis* also by Falconer (1846, p. 50) in comparing the *Mastodon sivalensis* of the Siwaliks with *M. latidens,* and later (1868, II, pp. 29–31) with the *Mastodon arvernensis* of the British coast Upper Pliocene; the *fourth* distinctive character is the plication or folding (*Synconolophus*) of the enamel borders of the molar ridges, giving the hippopotamus- and piglike character termed 'chœrodont' by Schlesinger, the

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[1] [See footnote 2 on page 1555 of this chapter.—Editor.]

grinding action of the teeth being obviously as in pigs, and the hippopotami. The grinders, originally brachyodont, become subhypsodont; thus the single superior and inferior molar teeth become highly effective masticating organs, labyrinthodont in pattern and serving effectually in the comminution of food."

It appears that the Brevirostrinæ include three phyla, namely, *Anancus* Aymard, 1855, 1859, *Pentalophodon* Falconer, 1857, 1865, and *Synconolophus* Osborn, 1929. *Stegomastodon* Pohlig, 1912, at first regarded as belonging to the Brevirostrinæ, was removed by Professor Osborn to his new family Humboldtidæ, because of a "fundamental resemblace of the grinding teeth to those of '*Mastodon*' *humboldtii*."

Anancus, 'straight-tusked brevirostrine' of southern Eurasia. Aymard based his genus on *Anancus macroplus*, 1855, a generic and specific name applied to bones and teeth of an adult mastodont similar to the species described and figured by Croizet and Jobert as *Mastodon arvernensis* from Auvergne, based on the milk dentition. *Anancus macroplus* is therefore regarded as synonymous or identical with *A. arvernensis*, which latter becomes the genotype. The term *Anancus* signifies without bend, probably in allusion to the straight tusks or upper incisors. This phylum is purely Eurasiatic. *A. arvernensis* and *A. falconeri* may possibly be derived from *A. perimensis* or *A. properimensis* of India.

> *Anancus.*—Cranium approaching true elephantine type, with brachycephaly, hypsicephaly, and fore-and-aft abbreviation; relatively primitive elongation of the rostrum in front of the orbits, an adaptation to the presence of two grinding teeth in use at the same time, namely, M 2-M 3; frontal region relatively narrow or laterally compressed; summit also narrow, since the temporal fossæ are divided by a relatively narrow frontoparietal plate as compared with the very broad frontoparietal plate in *Pentalophodon falconeri*; occipital condyle very prominent and pedunculate—a unique feature in the Proboscidea. Anterior portion of symphyseal region abbreviate. Superior tusks straight, elongate. No ininferior tusks. True molars brachyodont to subhypsodont; cones simple, smooth, compressed fore and aft. Single external median conules in inferior molars; internal median conules in superior molars. Deciduous molars (premolars) grooved, ptychoid, or plicated, externally. No trefoils. Crowns brachyodont, cones erect (*Anancus macroplus* and related species); crowns subhypsodont, strongly inclined and alternating (*A. falconeri*). Internal proversion of superior and inferior ridge-crests. Intermediate molars tetralophodont.
>
> Dental formula: I $\frac{0\text{-}2\text{-}0}{}$ Dp $\frac{2\text{-}4}{2\text{-}4}$ M $\frac{1\text{-}3}{1\text{-}3}$
> Ridge-crest formula: Dp $2\frac{2}{2}$ Dp 3 $\frac{+3+}{+3+}$ Dp 4 $\frac{\frac{1}{2}\text{-}4\text{-}\frac{1}{2}}{?}$ M $1\frac{4}{4}$ M $2\frac{4\text{-}4\frac{1}{2}}{4\text{-}4\frac{1}{2}}$ M 3 $\frac{5\text{-}5\frac{1}{2}+}{5\frac{1}{2}\text{-}6\frac{1}{2}}$
> HORIZON.—Mio-Pliocene to uppermost Pliocene. Compare Vol. II, p. 1534, and figures 1221, 1222, 1227, also Pl. XVI.

Pentalophodon, 'five-crested straight-tusker' of the Siwaliks. Falconer in 1857 characterized this genus as having the intermediate molars divided upon a quinary ridge formula, evidently with *Mastodon sivalensis* of Cautley in mind at the time, for later (1865, p. 262) he clearly designated it as the genotype. His descriptions and definitions are also based on specimens of superior and inferior molars figured in plates XXXVI, XXXVII of the "Fauna Antiqua Sivalensis," as well as on a cranium figured in plate XXXIII, fig. 2, with altogether different and much more progressive grinding teeth. A close comparison of the molars shows that this referred cranium belongs to a much more progressive species, if not genus, than the type molar of '*Mastodon*' *sivalensis*, which Professor Osborn in Volume I, p. 653, of the present Memoir made the type of a new species, namely, *Pentalophodon falconeri*. This Indian form (*Pentalophodon sivalensis*) has a line of southern Asiatic ancestry of its own, branching from *Anancus perimensis* and distinct from the west European *A. arvernensis*.

> *Pentalophodon.*—Cranium lofty, hypsicephalic, brachyopic. Occipital condyles elevated. Symphysis abbreviate. Incisive tusks unknown. Intermediate molars pentalophodont. Molars subhypsodont; cones elevated, strongly alternating, inclined forwards in the lower molars; superior and inferior ridge-crests extending obliquely forwards from the external to the internal faces, that is, internal proversion; typically composed of three main irregular cones set widely apart (*P. sivalensis*), closely

compacted (*P. falconeri*); crown progressively chœrodont with twenty-two aristogenes in M_3 (*P. sivalensis*), twenty-seven in M^3 (*P. falconeri*); enamel smooth, not ptychoid; no ecto- and entotrefoils; central conules present in two anterior valleys. Small amount of cement sometimes present.

Dental formula: I $\frac{0\text{-}2\text{-}0}{0\text{-}2\text{-}0}$ Dp $\frac{2\text{-}4}{2\text{-}4}$ M $\frac{1\text{-}3}{1\text{-}3}$
Ridge-crest formula: Dp $4\frac{?}{?}$?M $1\frac{}{4\tfrac{1}{2}}$ M $2\frac{4\tfrac{1}{2}\text{-}5}{5}$ M $3\frac{5\text{-}6\tfrac{1}{2}\text{-}7\tfrac{1}{2}}{6\tfrac{1}{2}\text{-}7\tfrac{1}{2}?}$
HORIZON.—Upper Pliocene. Compare Vol. I, p. 648; Vol. II, p. 1534, Figs. 1221, 1223, 1227, and Pl. XVI.

Synconolophus, 'syncone-crested brevirostrine' of the Siwaliks. Falconer's plates or descriptions do not seem to show grinding teeth referable to this peculiar genus, but Lydekker in his memoir of 1880 on "Siwalik and Narbada Proboscidia" figures examples of teeth certainly referable to *Synconolophus*. The warping or dislocation of the cones and crests in the superior and inferior molars is much more extreme than in *Anancus* or in *Stegomastodon*, also the multiplication of separate intermediate conelets, originally springing from the trefoils, is quite distinct from the regular single or double trefoils of *Stegomastodon*. The whole surface of the crown becomes crowded with a labyrinthine pattern of cones, conelets, and more or less separate intermediate conelets, with warped or dislocated ridge-crests in apparent disorder, giving the appearance best expressed in the Greek generic term *Synconolophus*. The genotype is *Synconolophus dhokpathanensis*, based on a giant cranium found by Dr. Barnum Brown in 1922 in the Dhok Pathan horizon of India. The three-ridged second molar, M^2, suggested comparison with *Trilophodon*, but the broad four-ridged third molar, M^3, differed from that of *Trilophodon* and also from that of *Tetralophodon punjabiensis* which occurs in the same geologic horizon. It was not until perfect superior molars were found (see Fig. 631—paratype), also from the same horizon a pair of referred superior and inferior molars (Fig. 632), that the structural and phyletic key to this very aberrant genus could be determined (cf. Vol. I, pp. 654–665).

Synconolophus.—Cranium platycephalic, dolichopic, brachycranial (Vol. I, p. 649) [dolichocranial?—see p. 347], somewhat more elongate than in *Anancus* or *Pentalophodon*. Postnarial opening far back of grinders, a generic distinction from *Tetralophodon*. Mandibular symphysis broad, trough shaped, concave superiorly (*S. propathanensis*), indicating a large, fleshy lower lip. Superior tusks large, upturned, and out-turned, without enamel. Inferior tusks reduced or absent (*S. propathanensis*). Milk tusks with enamel. Grinders with ridge-crests strongly arched or dislocated; valleys blocked with warped, compacted conelets and conules, giving on wear a strongly chœrodont, ptychoid, crowded, compressed, enamel-bordered appearance; internal proversion. No trefoils. Cement strongly developed in *S. dhokpathanensis* and *S. propathanensis*. Cones smooth to deeply grooved. Intermediate molars with trilophodont ridge formula and small rudimentary half ridge-crests, representing pro-protoloph and tetartoloph.

Dental formula: Di $\frac{0\text{-}2\text{-}0}{}$ I $\frac{0\text{-}2\text{-}0}{?}$ Dp $\frac{2\text{-}4}{2\text{-}4}$ M $\frac{1\text{-}3}{1\text{-}3}$
Ridge-crest formula: Dp $4\frac{\tfrac{1}{2}\text{-}3}{}$ M $1\frac{\tfrac{1}{2}\text{-}3\text{-}\tfrac{1}{2}}{}$ M $2\frac{\tfrac{1}{2}\text{-}3\text{-}\tfrac{1}{2}}{3\text{-}\tfrac{1}{2}}$ M $3\frac{\tfrac{1}{2}\text{-}4\text{-}\tfrac{1}{2}}{\tfrac{1}{2}\text{-}5\text{-}\tfrac{1}{2}}$
HORIZON.—Mio-Pliocene to Middle Pliocene. Compare Vol. II, p. 1534, and figures 1221, 1227, also Pl. XVI.

GEOGRAPHIC RANGE.—(Vol. I, p. 629): "Armed with very powerful upper tusks, the enamel bands of which early disappear, propelled by massive limbs supported on a powerful frame, these animals appear to have been adapted to browsing on the succulent vegetation of the warm-temperate zones, chiefly of the 40th and 30th parallels, from France and the southeast coast of England, through northern Italy, then through India, but never reaching North America, so far as we know at present. Analogous but unrelated are the species of *Stegomastodon*." A step further must be taken in the migration of these animals, owing to the determination by Dr. A. Tindell Hopwood (1935.1, pp. 57–60) of molars from Shansi, China, as belonging to *Pentalophodon sinensis*. Professor Osborn accepted Doctor Hopwood's reference of these molars to a member of the Brevirostrinæ, but regarded them as referable rather to *Anancus* than to the more progressive *Pentalophodon* which has a greater number of ridge-crests than are present in the Chinese molars (see Appendix to Vol. I, p. 722).

Superfamily: MASTODONTOIDEA Osborn, 1921. Family: HUMBOLDTIDÆ Osborn, 1935, 1936
(Syn. STEGOMASTODONTIDÆ Scott, 1937)

Subfamily: HUMBOLDTINÆ Osborn, 1934, 1936 (syn. Stegomastodontinæ Scott, 1937)

Genera: *Cuvieronius* Osborn, 1923; *Eubelodon* Barbour, 1914; *Stegomastodon* Pohlig, 1912

(Compare Vol. I, Chap. XII, Chap. XIII, pp. 667–684, and Appendix, pp. 722–728, also Pls. x, xi, and figures 501, 590; Vol. II, p. 1535, and figures 1224, 1225, 1227, also Pl. xvii)

THE HUMBOLDTINES, 'hyperptychoid Humboldtine mastodonts' of the southern United States and South America. The decision of Professor Osborn in 1934 (Osborn, 1934.924, p. 183, fig. 2) to dismember his subfamily Notorostrinæ (which included the *Mastodon* [*Cordillerion*] *andium* and *M.* [*Cuvieronius*] *humboldtii* groups, as well as the *Eubelodon morrilli* of Barbour) was occasioned by his recognition of the differences in the crania and dentition of the members of these groups. For example, the *Cuvieronius* skull converges toward that of *Elephas* and of *Mastodon americanus,* while the *Cordillerion* skull retains the relatively low, simple character of the primitive Trilophodonts; furthermore, in *Cuvieronius humboldtii* the superior tusks are straight or upcurved without enamel band, and the superior and inferior molars are broad with typically double trefoils and central conules either inconspicuous or wanting; whereas in *Cordillerion andium* a broad enamel band winds more or less spirally around the elongated superior tusks and the molars are narrow with single trefoils on the internal side of the upper molars and on the external side of the lower molars, as in other bunomastodonts.

In the same article (1934, p. 183) Professor Osborn definitely placed *Eubelodon morrilli* in the direct ancestral line of the Humboldtines or Humboldtinæ (fig. 2, our Pl. x), and accepted Dr. Cabrera's inclusion of Leidy's *Mastodon* [=*Stegomastodon*] *mirificus*, 1858, as well as other Stegomastodonts, in the Humboldtinæ, which subfamily is defined on pages 575 and 615 of Volume I of the present Memoir.

Eubelodon.—From 1914, when Doctor Barbour described *Eubelodon morrilli,* until 1929, the type specimen was the single representative of this genus. The discovery of a superb cranium by the Frick Expedition of 1929, at Horsethief Canyon, near Ainsworth, Nebraska, and referred by Mr. Childs Frick in 1933 to this species, shed additional light on the dentition of *Eubelodon,* as both the second and third superior molars are present, the latter beautifully displaying the coronal pattern of 4½ ridge-crests with double trefoils, at once reminding one of Cuvier's type of '*Mastodon' humboldtii.*

> *Characters of Eubelodon*, 'ancestral Humboldtine mastodont' of Nebraska. Cranial and facial region primitive, subequal, less elevated than in *Cuvieronius humboldtii.* Occipital condyle low compared with elevated condyle and occipital crest of *Cuvieronius superbus.* Rostrum and inferior mandible elongate, somewhat downturned and pointed, with no trace of alveolus for tusks. Superior tusks relatively short, simple, rounded, out-turned, tips chisel shaped, slight downcurvature, conserving the primitive downcurvature of the paired superior incisors of all primitive mastodonts, divergent, without enamel band. No inferior tusks. Grinders broad with double trefoils, four ridge-crests and talon. Superior molars with strong entotrefoils, incipient ectotrefoils; indications of cement; broad internal cingulum; outer side more convex, inner side more plane or concave. Cingulum less distinct in inferior molars. Pelvis excessively broad; humerus robust; inferior in height and width to Warren Mastodon (*Mastodon americanus*).
>
> Ridge-crest formula: M $2^{?}_{?}$ M $3^{4\frac{1}{2}}_{4\frac{1}{2}}$
> HORIZON.—Middle(?) Pliocene. Compare Vol. II, p. 1535, and figures 1224, 1227, also Pl. xvii.

Cuvieronius.—In giving the history of the genotype of *Cuvieronius,* namely, the *Mastodonte humboldien* Cuvier, 1806 [=*Mastodon humboldtii* Cuvier in Desmarest, 1818, *Mastodon humboldii* Cuvier, 1824], Professor

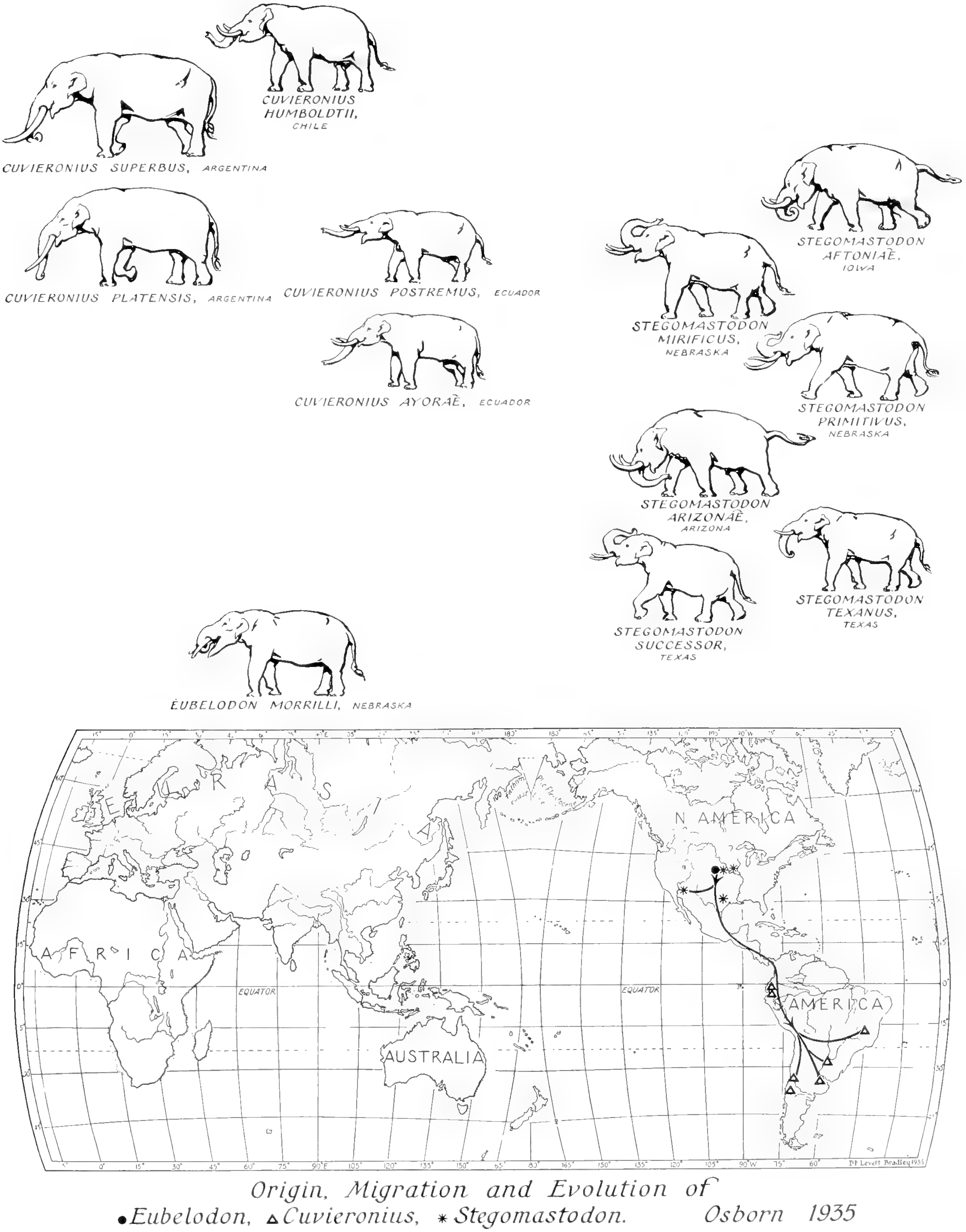


PLATE XVII

Geologic range: *Eubelodon*, Middle(?) Pliocene; *Cuvieronius*, Pleistocene, Upper Pleistocene (*C. postremus*); *Stegomastodon*, Upper Pliocene and Lower to Middle Pleistocene.

Osborn states in Volume I of the present Memoir, p. 575, as follows: "The weight of Cuvier's authority has been so great that since 1806 the generic name *Mastodon* was applied by all authors to *humboldtii*, until Cope proposed (1884.2, p. 2) the ill-fated generic name *Dibelodon*, signifying two-tusker, which he based upon the four-tusker *Mastodon shepardi* of Leidy. Cope's practice of including *Mastodon andium* and *M. humboldtii* also within the genus *Dibelodon* was followed by Lull and Osborn until Osborn discovered Cope's error and proposed the generic name *Cuvieronius* (1923.601). Meanwhile all the European authors continued to use Cuvier's name *Mastodon*, including Boule in his important Memoir of 1920."

Characters of Cuvieronius, 'Humboldtine mastodont' of the Pampean and Andean regions of South America. Cranium elevated, facial region prominent, expanded, with air-cell chambers as in *Mastodon* and *Elephas*. Rostrum of inferior mandible relatively abbreviate. Tusks relatively large, simple, rounded, upturned and out-turned or straight, without enamel band; relatively short, robust, upturned in primitive species (*C. ayoræ* and *C. postremus*). No inferior tusks. Molars broad with typically double trefoils; single trefoils in primitive species (*C. ayoræ, C. postremus*). Third superior and inferior molars tetralophodont to pentalophodont. Intermediate molars with rudimentary tetartoloph. Superior ridge-crests transverse or retroverted internally; inferior ridge-crests proverted internally. Superior and inferior crowns either plane or curved on external side. Central conules inconspicuous or absent.

Ridge-crest formula: M $1\frac{3+}{3+}$ M $2\frac{3+}{3+}$ M $3\frac{4\frac{1}{2}\text{-}5}{4\frac{1}{2}\text{-}5\frac{1}{2}}$

HORIZON.—Pleistocene. Upper Pleistocene (*C. postremus*). Compare Vol. II, p. 1535, and figures 1225, 1227, also Pl. XVII.

Stegomastodon.—This genus was first thought by Professor Osborn to be the American representative of his subfamily Brevirostrinæ, but it has recently been determined that the migration of the true Brevirostrines (*Anancus, Pentalophodon*, and *Synconolophus*) did not extend to the North American continent. We are still without knowledge of the Asiatic and possibly African forbears of *Stegomastodon*. The *Stegomastodon mirificus* group now proves to be closely related in its molar-tooth structure to the *Cuvieronius humboldtii* group of the subfamily Humboldtinæ. This observation was first made by Dr. Ángel Cabrera in 1929 and was confirmed by Professor Osborn (see Vol. I, p. 612, this Memoir) after a further "close comparison of the fundamental grinding-tooth pattern in *Stegomastodon*," which disclosed the fact that "both the superior and inferior ridge-crests of the true Brevirostrines of Eurasia are proverted, whereas in the Humboldtines of America the inferior ridge-crests are proverted and the superior ridge-crests are either retroverted or transverse (*Cuvieronius*) or centroverted (*Stegomastodon*)."

Characters of Stegomastodon, Pohlig's 'roof-toothed Humboldtine mastodont' of the southwestern United States. Cranium abbreviate; palate elongate, postnarial opening far back of grinders (*S. texanus*). Mandibular rostrum progressively abbreviated. Superior tusks short, massive, upcurved, outcurved, without enamel band. No inferior tusks. Tusks in *S. primitivus* first projected directly out from the alveoli after which they were simply outcurved and then by inward rotation the tips were finally incurved at the extremities. This peculiar tusk structure may remove it from the direct ancestry of the other species of *Stegomastodon* and place it in a line of its own. Juvenile tusks straight. Molars brachyodont to subhypsodont; cones slightly alternating, deeply plicated, ptychoid, folded, giving a labyrinthine pattern to the worn grinding surfaces; double to quadruple to multiple trefoils in both superior and inferior molars, completely blocking the valleys; enamel thick; no central conules; external pericones block the spaces between the five main crests (*S. texanus* ref.). Superior ridge-crests centroverted; inferior ridge-crests proverted internally as in *Anancus, Pentalophodon*, and *Snyconolophus*. Cement in transverse valleys. Intermediate molars with trilophodont to tetralophodont ridge formula, that is, 3½ ridge-crests.

Ridge-crest formula: Dp $4\frac{3}{3}$ M $1\frac{3\frac{1}{2}}{3\frac{1}{2}}$ M $2\frac{3\frac{1}{2}}{3\frac{1}{2}}$ M $3\frac{4\frac{1}{2}\text{-}5\frac{1}{2}\text{-}6\text{-}6\frac{1}{2}\text{-}7\frac{1}{2}}{4\frac{1}{2}\text{-}5\frac{1}{2}\text{-}6\text{-}6\frac{1}{2}\text{-}7\frac{1}{2}}$

HORIZON.—Upper Pliocene and Lower to Middle Pleistocene. Compare Vol. II, p. 1535, and figures 1224, 1227, also Pl. XVII.

The final step taken by Professor Osborn in 1935 was the creation of a new family, the Humboldtidæ (see Osborn, 1935.937, fig. 2, for name only; 1936, Vol. I, p. 722, for definition), to embrace the *Eubelodon-Cuvieronius-Stegomastodon* group, or Humboldtinæ.

MIGRATION.—(Vol. I, p. 611): "Putting together the important resemblances between specimens of *Eubelodon morrilli* of Nebraska and the relatively little-known primitive remains of tusks and grinding teeth from the Inferior Pampean of Argentina, we reach the very important conclusion that *E. morrilli* is a Middle Pliocene ancestral stage in the subfamily Humboldtinæ on its way from Eurasia through North America to South America. In the Andean region there appear the primitive short-limbed forms *Cuvieronius ayoræ* and *C. postremus*, and the primitive typical *C. humboldtii* of Bolivia, (?)Ecuador, and Chile, quadrupeds of smaller size and possibly of mountain habitat. Possibly a direct descendant of *Eubelodon* is the straight-tusked *Cuvieronius rectus* of the Inferior Pampean of the Argentine. Finally there appears in the Pampean the giant *Cuvieronius superbus* and the more specialized *C. platensis* as distinguished by Cabrera." On a subsequent page (p. 685) Professor Osborn states that we may be certain that at some future time we may trace *Eubelodon* back to northern or central Asia and ultimately perhaps to Africa.

Superfamily: MASTODONTOIDEA Osborn, 1921. Family: SERRIDENTIDÆ Osborn, 1935, 1936

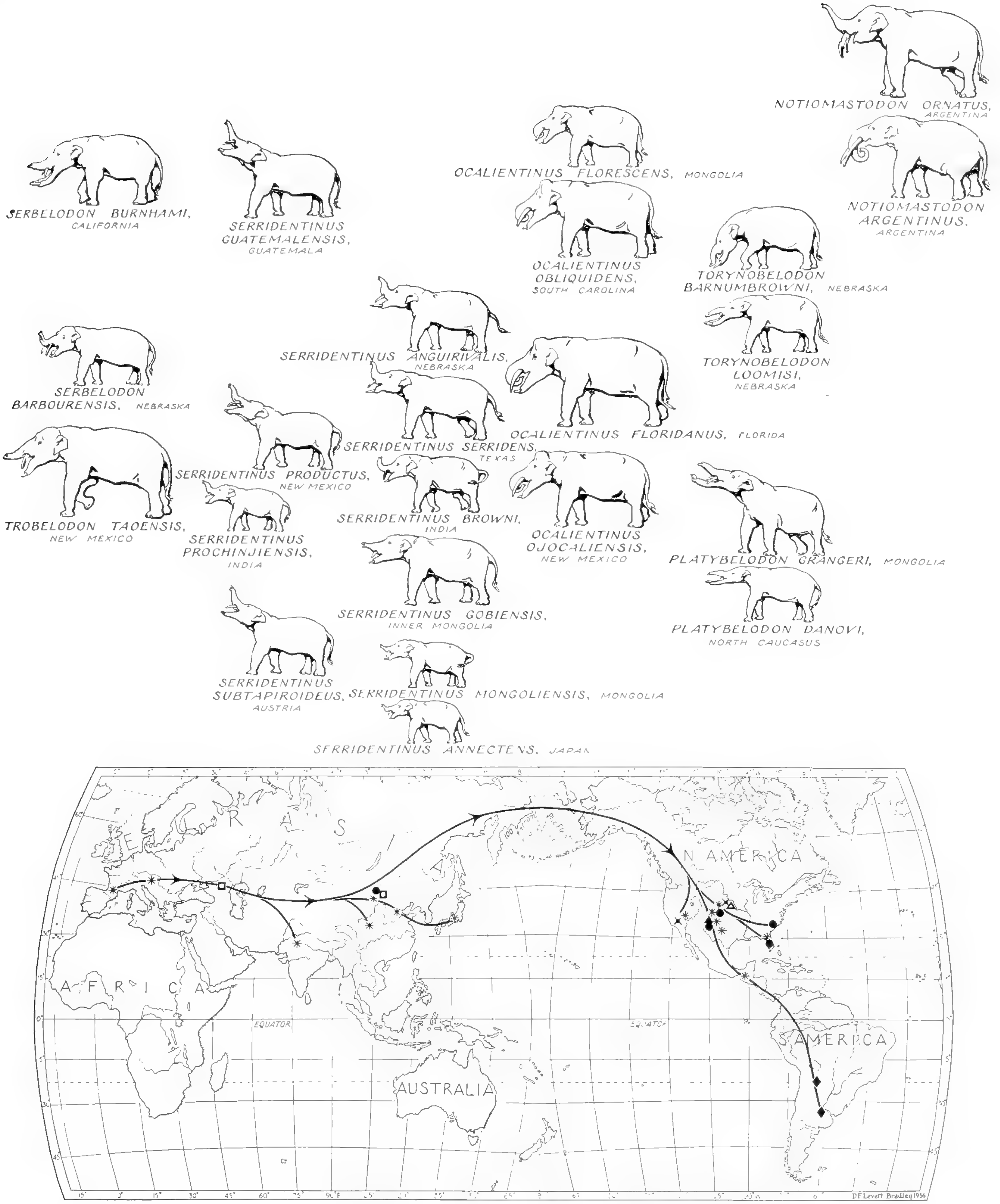
Subfamily: SERRIDENTINÆ Osborn, 1921

Genera: *Serridentinus* Osborn, 1923; *Ocalientinus, Serbelodon,* and *Trobelodon* Frick, 1933

(Cf. Vol. I, pp. 380–473, 729, also Pls. x, xi, and Figs. 344, 373; Vol. II, p. 1535, and figures 1221–1225, 1227, also Pl. xviii)

Perhaps in no other subfamily has there been such confusion in the determination of species as in the Serridentinæ, especially in the differentiation of the Trilophodont and Serridentine unworn molars, in fact, for a century these animals have been confused with *Trilophodon.* The salient features which clearly separate the subfamily Serridentinæ from the Longirostrinæ (or Trilophodonts) are: *First,* the central conules observed in all species of *Trilophodon* are entirely absent in the Serridentinæ; *second,* these central conules are functionally replaced in the Serridentinæ by crests or spurs which arise on the sides of the superior internal cones and on the inferior external cones; and *third,* these internal and external crests subdivide into two, three, four to six smaller conelets, which produce a serrated aspect, hence the term 'serrate-toothed mastodonts' or Serridentinæ.

By referring to Professor Osborn's first papers, it will be noted (Osborn, 1921.515, p. 8) that he designated as the "T. [Trilophodon] serridens Phylum" four species, namely, *Mastodon serridens* Cope, *Tetrabelodon serridens cimarronis* Cope, *Dibelodon præcursor* Cope, and questionably *Mastodon turicense* Schinz. Again in his definition of the new subfamily Serridentinæ (Osborn, 1921.526, p. 330) he stated that the "Serridentinæ apparently spring from *M. turicense* Schinz, 1824, of the Middle Miocene of France and Switzerland—a rare animal, probably because a forest dweller," and calls attention to the distinguishing spur or crest on the sides of the superior and inferior grinders of the Serridentinæ. Professor Osborn's final conclusions are given in Volume I, p. 382, of the present Memoir: "One of the most interesting results of the prolonged research in preparation for this Memoir is the discovery of two clearly distinguishable phyla of mastodonts (*Turicius* and *Serridentinus*) which by all previous investigators both in Europe and America had been confused with the phylum *Trilophodon*. . . In the present chapter [Chap. X] it is shown that the grinding teeth, e.g., of *Mastodon* (B.) *subtapiroidea* of the Lower Miocene lignites. . . widely differ from those of *Trilophodon* and strongly resemble those of *Serridentinus*. . . [see Figs. 350, 351, 352]; it is possible that *Turicius* [genotype *Mastodon turicense* Schinz] and *Serridentinus* arise from a similar stock not unlike *Serridentinus subtapiroideus.* The evolution of the true *Turicius* phylum, however, is entirely



*Origin, Migration and Evolution of ▲Trobelodon, ×Serbelodon, *Serridentinus. ●Ocalientinus. □Platybelodon, △Torynobelodon, ◆Notiomastodon.* Osborn 1935

PLATE XVIII

Geologic range: *Trobelodon*, Mio-Pliocene; *Serbelodon*, Lower Pliocene and Upper Pliocene; *Serridentinus*, Lower Miocene to Upper Pliocene; *Ocalientinus*, Miocene to Upper Pliocene (*O. obliquidens* redeposited in Lower Pleistocene). *Platybelodon*, Upper Miocene; *Torynobelodon*, Pliocene. *Notiomastodon*, Pliocene and Lower Pleistocene(?).

distinct, leading into sharply crested forms such as *T. virgatidens*, while the *Serridentinus* phylum is (A) increasingly Serridentine, ending in *Ocalientinus* (*Ser.*) *floridanus*, or (B) more crested, ending in *S. guatemalensis*." While, therefore, there is a strong resemblance in the Miocene stages between species of *Serridentinus* and species of *Turicius*, there is very little resemblance between final species in these two phyla which are very widely divergent.

The Serridentinæ are polyphyletic, embracing four genera—*Serridentinus* Osborn, 1923, and the *Ocalientinus*, *Serbelodon*, and *Trobelodon* of Frick, 1933. Professor Osborn's researches led him in 1935 (Osborn, 1935.937, fig. 2—see also Vol. I, p. 729, of the present Memoir) definitely to separate these 'serrate-toothed mastodonts' (the Serridentinæ), also the Platybelodontinæ (*Platybelodon, Torynobelodon*) and the Notiomastodontinæ (*Notiomastodon*) from all other mastodonts, thereby constituting a very large and highly diversified new family, the Serridentidæ, which at the present time includes no less than forty species (Vol. I, p. 741), united by the common character of the serrated crests arising from the ectoconelets in the lower molars and from the entoconelets in the upper molars, also by the enamel bands on the superior tusks, but generically separated by the widely radiating adaptations of the inferior tusks—horizontal oval in *Serridentinus*, oval, greatly enlarged in *Serbelodon*, flattened into a pair of broad shovels in *Platybelodon*, abbreviated and rounded in *Torynobelodon*, and entirely wanting, with brevirostral mandible, in *Notiomastodon*.

HABITS.—Members of the Serridentidæ, especially the true *Serridentinus*, rarely occur in the same fossil beds with members of the Bunomastodontidæ, hence it is inferred that they had different feeding habits. The more or less perfectly serrated crests on the inner side of the upper molars and on the outer side of the lower molars point to leaf-cutting and browsing habits, especially true of the typical Serridentines, which, it is thought, may have frequented forests and were principally browsers, while the typical flat-tuskers (*Platybelodon*), the cutting-tuskers (*Serbelodon*), and the sub-shovel tuskers (*Trobelodon*) frequented shallow lakes and river borders.

Characters of Serridentinus, typical 'serrate-toothed serridentine,' 'prod-tusker' or 'scaptobelodont,' of Eurasia and North America. Cranium low, dolichocephalic; undoubtedly rounded above like the skulls of *Trilophodon* and *Tetralophodon*; the chief difference between the skull of *Serridentinus* and that of *Trilophodon* is the abbreviation of the rostrum, maxillo-premaxillary above, and symphyseal portion of the mandible below. The symphysis in species of American *Serridentinus* is decurved and contains two large tusks of flattened oval section. Jaws moderately elongate (medilongirostral), relatively stout, tending to decurvature. Superior tusks laterally compressed, downcurved and outcurved, retaining broad lateral enamel band. Inferior tusks without enamel band, large, horizontally flattened, closely appressed, and never greatly elongated as in *Trilophodon*. Intermediate molars trilophodont from the beginning to the end of the phylum as in the *Trilophodon* phylum. Grinding teeth relatively broader than in *Trilophodon*, primitively brachyodont progressive to subhypsodont; prominent serrated trefoil spurs or crests arise from the anterior and posterior faces of the entocones in the superior molars, from the ectocones in the inferior molars; median conules absent in the valleys, unlike *Trilophodon* in which they are present. Three superior and inferior grinding teeth (M 1–M 3) in use at the same time; functional retention and usage of upper and lower second and third molars, in contrast to the Longirostrinæ (*Trilophodon*) and Tetralophodontinæ (*Tetralophodon*) in which the mastication is finally concentrated on the third upper and lower molars. Internal cingulum more or less crenulate on superior molars, extending as far back as the antero-internal border of third crest of the third molars; rudimentary external cingulum only in valley between first and second crests (*S. productus*).

Dental formula: I $\frac{0\text{-}2\text{-}0}{0\text{-}2\text{-}0}$ Dp $\frac{2\text{-}4}{2\text{-}4}$ P $\frac{3\text{-}4}{3\text{-}4}$ M $\frac{1\text{-}3}{1\text{-}3}$

Ridge-crest formula: Dp $2\frac{?}{2+}$ Dp $3\frac{?}{3}$ Dp $4\frac{3}{3}$ P $3\frac{}{2}$ P $4\frac{2+}{2+}$ M $1\frac{3}{3}$ M $2\frac{3}{3}$ M $3\frac{3\frac{1}{2}\text{-}5}{3\frac{3}{4}\text{-}5\frac{1}{4}}$

HORIZON.—Lower Miocene to Upper Pliocene. Compare Vol. II, p. 1535, and figures 1221–1224, 1227, also Pl. XVIII.

Characters of Ocalientinus, 'multiserrate-crested serridentine,' 'prod-tusker' or 'scaptobelodont,' of the United States and Mongolia, directly ancestral to '*Serridentinus*' *republicanus* of Kansas and to '*S.*' *floridanus* of Florida. Cranium tall, narrow. Mandible elongate, symphysis extremely narrow with deep superior longitudinal channel. Superior tusks as in *Serridentinus*, with latero-inferior enamel band. Inferior tusks without enamel, upcurved, relatively short. Molars with roundly blunted cones and conelets, trefoil spurs dominant, florescent. Relative breadth of molars correlated with foreshortening of cranium and heightening of occiput. Both superior and inferior ridge-crests sloping forward, slowly increasing in height.

Ridge-crest formula: Dp $4\frac{3}{3}$ P $3\frac{2}{-}$ P $4\frac{2}{2}$ M $1\frac{3}{3}$ M $2\frac{3}{3}$ M $3\frac{4\frac{1}{2}}{4\frac{1}{2}\text{-}5\frac{1}{4}}$

HORIZON.—Miocene to Upper Pliocene (*O. obliquidens* redeposited in Lower Pleistocene). Compare Vol. II, p. 1536, and figures 1223, 1224, 1227, also Pl. XVIII.

Characters of Serbelodon, Frick's 'sub-shovel-tusked serridentine' of the western United States. Cranium imperfectly known, probably more elongate than that of *Trobelodon*. Mandible extremely abbreviated and broadened, the length equaling that of *Serridentinus productus*. Symphysis short, symphyseal rostrum extremely short and relatively broad. Superior tusks heavy, downwardly and outwardly curved, with strong enamel band. Inferior tusks concavo-convex, relatively short, flattened, heavy, spatulate; distinguished from *Platybelodon* by total absence of dentinal rod-cones, the interior being composed of dentinal laminæ. Molars relatively long and narrow with serridentine pattern—superior molars with entoconelet spurs, inferior molars with ectoconelet spurs, but without serrated borders.

Ridge-crest formula: M $2\frac{3}{3}$ M $3\frac{4}{4}$

HORIZON.—Lower Pliocene, Upper Pliocene. Compare Vol. II, p. 1536, and figures 1224, 1227, also Pl. XVIII.

Characters of Trobelodon, Frick's 'brevidentate serridentine' of New Mexico, of 'sub-shovel-tusk' type. Cranium broad or brachycephalic. Mandible relatively decurved. Symphysis relatively elongate, narrow, slightly upcurved. Superior tusks with moderate enamel band; inferior tusks moderately heavy, biconvex, pointed, absence of dentinal rod-cones. Third superior molars short and broad, with blunt cones; expanded entotrefoils as in *Serridentinus*; third inferior molars also short and broad, with expanded ectotrefoils—trefoil structure of primitive serridentine type.

Ridge-crest formula: M $2\frac{3}{3}$ M $3\frac{3}{4}$

Horizon.—Mio-Pliocene. Compare Vol. II, p. 1537, and figures 1224, 1227, also Pl. XVIII.

MIGRATION.—The following is the geographic distribution of species of the Serridentinæ, the trend of migration being eastward from southwestern Europe to North America (see Pl. XVIII, also Figs. 373 and 1227): France, Austria, India, Mongolia, China, Japan, California, Nebraska, Kansas, Colorado, New Mexico, Texas, Guatemala, and eastward in the United States to North and South Carolina and Florida.

Superfamily: MASTODONTOIDEA Osborn, 1921. Family: SERRIDENTIDÆ Osborn, 1935, 1936

Subfamily: PLATYBELODONTINÆ Borissiak, 1928

Genera: *Platybelodon* Borissiak, 1928, 1929; *Torynobelodon* Barbour, 1929

(Cf. Vol. I, pp. 338, 339, 459–472, 729, 730, also Pls. X, XI, and Figs. 344, 373; Vol. II, p. 1537, and figures 1222, 1223, 1227, also Pl. XVIII)

The subfamily Platybelodontinæ was founded by Borissiak in 1928 on his *Platybelodon danovi* of the Chokrak beds, Kuban district, North Caucasus, the chief distinguishing character being the long and wide spoon-shaped symphysis with wide, flat incisors. Prior to this description, and wholly unknown to Professor Borissiak, a specimen found in Nebraska had been described by Dr. E. H. Barbour as *Amebelodon fricki* in 1927 and made the type of his family Amebelodontidæ (subsequently, 1929, modified to Amebelodontinæ). Professor Osborn assumed (1931) that the Amebelodontidæ Barbour, 1927, preoccupied the Platybelodontinæ Borissiak, 1928, especially as both possessed large shovel tusks *supposedly* penetrated by dentinal tubules or rod-cones; also at the time he was not aware of the highly progressive serridentine pattern of the *Platybelodon* molars, in widest contrast to the trilophodont pattern of the *Amebelodon* grinders, or of the fact that the second superior and inferior molars possessed four ridge-crests, unlike *Trilophodon* and members of the subfamily Serridentinæ with three ridge-crests.

As stated above under the subfamily Amebelodontinæ (p. 1558), the structure of the incisive tusks of *Amebelodon* and of its ancestral form *Phiomia* is that of progressively concentric dentinal laminæ, an observation made in 1934, 1935, when the inferior tusks of *Phiomia* were sectioned and carefully compared with those of *Amebelodon*. Likewise the inferior tusks of *Platybelodon* were sectioned, revealing compact interior dentinal rod-cones instead of concentric dentinal laminæ; also the tusk of the American related genus *Torynobelodon* was found to be composed of rod-cones, resulting in the reference of this genus to the Platybelodontinæ.

Quoting Dr. Edwin H. Colbert in Volume I, p. 715, of the present Memoir, "It would seem possible, then, that the presence or absence of these rods distinguishes the two subfamilies Platybelodontinæ and Amebelodontinæ respectively . . . It would seem likely, also, that in the Platybelodontinæ the tusks are square across the ends, whereas in the Amebelodontinæ the ends of the tusks are rounded. . . The origin of the rods constitutes a perplexing question. To me [Colbert] they appear to be derived from the lamellar ivory; perhaps they represent a secondary breaking down of the concentric cones of dentine that form the tusk. Perhaps they are structures developed in the pulp cavity independently of the lamellar ivory. . . A magnified cross-section of a dentinal rod of *Torynobelodon loomisi* shows that it is built up of concentric layers of dentine—presumably unvascular orthodentine. An examination of the tusk of *T. loomisi* shows that the rods occupy the central portion of the tusk, and that they are surrounded by typical ivory. The rods are quite variable as to size, ranging from one to five millimeters in diameter. Many of the rods branch. There are numerous nodules or egg-shaped excrescences on the sides of various rods, and on some rods the external surface is granular. The rods are of varying lengths. The rods are 'bundled' together, so to speak, in the tusk, but they are not compressed; consequently they are round and not hexagonal. The interstices between the rods were seemingly empty; if there was a filling of dentine it has been destroyed during the process of fossilization. In many places the rods seem to grade into the lamellar ivory."

Characters of Platybelodon, Borissiak's typical 'flat-tusker' of Mongolia. Cranium broad, low, dolichopic. Mandible with long and wide spoon- or shovel-shaped symphysis; extreme constriction and narrowing of mandibular groove (according to the theory of Dr. William K. Gregory, 1934, the lower surface of the tongue occupies this narrow groove which broadens out into the deeply hollowed suprarostral concavity). Low and massive rami (type). Superior tusks small, rounded, relatively short and slightly outturned and downturned; inferior tusks wide and flat, with regularly and sharply defined borders, composed of numerous and quite closely compacted dentinal rod-cones. Upper surface without enamel, with irregular longitudinal grooves, lower surface protected by enamel [?dentine] longitudinally striated (*fide* Borissiak). Anterior serration of the entocones in the superior molars and of the ectocones in the inferior molars, as distinguished from the double or anterior and posterior serration of the corresponding ento- and ectocones in the *Serridentinus* and *Ocalientinus* molars. Fourth superior and inferior deciduous premolars and second molars with four ridge-crests instead of three ridge-crests as in *Trilophodon*, *Amebelodon*, and members of the subfamily Serridentinæ, resembling *Tetralophodon* in this respect.

Dental formula: $\text{Di}\ \frac{0\text{-}2\text{-}0}{0\text{-}2\text{-}0}\ \text{I}\ \frac{0\text{-}2\text{-}0}{0\text{-}2\text{-}0}\ \text{Dp}\ \frac{2\text{-}4}{2\text{-}4}\ \text{P}\ \frac{3\text{-}4}{3\text{-}4}\ \text{M}\ \frac{1\text{-}3}{1\text{-}3}$

Ridge-crest formula (based on complete collection of *P. grangeri* in American Museum):

$\text{Dp}\ 1\frac{?}{?}\ \text{Dp}\ 2\frac{\text{not ridged}}{\text{peg-shaped tooth}}\ \text{Dp}\ 3\frac{2\frac{1}{2}}{2\text{-}2\frac{1}{2}}\ \text{Dp}\ 4\frac{3\frac{1}{2}}{3\frac{1}{2}}\ \text{P}\ 3\frac{\text{not ridged}}{\text{not ridged}}\ \text{P}\ 4\frac{2}{2}\ \text{M}\ 1\frac{3\text{-}3\frac{1}{2}}{3\frac{1}{2}\text{-}4}\ \text{M}\ 2\frac{4}{4\text{-}4\frac{1}{2}}\ \text{M}\ 3\frac{5\text{-}6}{5\frac{1}{2}\text{-}6\frac{1}{4}}$

HORIZON.—Upper Miocene. Compare Vol. II, p. 1537, and figures 1223, 1227, also Pl. XVIII.

Characters of Torynobelodon, Barbour's 'dredge-tusker' of Nebraska. Cranial characters not yet described by Doctor Barbour. Mandible thin, ladle shaped, with low ascending rami; abbreviated as compared with *Platybelodon grangeri*; symphysis relatively narrow with relatively broad bar between rostrum and rami. Tusks short, broad, ladle or spoon shaped, upcurved, roughly and deeply corrugated, composed of dentinal rod-cones.

Dental formula incompletely known: $\text{I}\ \frac{}{0\text{-}2\text{-}0}\ \text{M}\ \frac{}{2\text{-}3}$
Ridge-crest formula incompletely known: $\text{M}\ 2\frac{}{3}\ \text{M}\ 3\ \frac{}{4\frac{1}{2}}$
HORIZON.—Pliocene. Compare Vol. II, p. 1537, and figures 1224, 1227, also Pl. XVIII.

Migration.—Up to the present time members of this subfamily have been found in the North Caucasus and in the Gobi of Mongolia. A left lower incisor from Texas, in the Colorado Museum, may be referable to *Platybelodon*; also *Torynobelodon*, which appears to be a collateral branch, and somewhat less perfect mechanically, of the Platybelodonts of Central Asia, comes from the Pliocene of Nebraska.

Superfamily: MASTODONTOIDEA Osborn, 1921. Family: SERRIDENTIDÆ Osborn, 1935, 1936

Subfamily: Notiomastodontinæ Osborn, 1936

Genus: *Notiomastodon* Cabrera, 1929

(Compare Vol. I, pp. 541, 590–592, 691, 730, 731; also Pls. x–xii, and Fig. 501; Vol. II, p. 1537, and figures 1225, 1227, also Pl. xviii)

The third subfamily of the Serridentidæ is the Notiomastodontinæ Osborn, based on the *Notiomastodon ornatus* of Cabrera, 1929. The reasons set forth by the present author for his reference of this subfamily and genus to the Serridentidæ will be found on page 730 of Volume I of this Memoir, and are briefly as follows:

The inferior molars have prominent serrated ridges arising from the ectoconelets as in Serridentines, and the adjacent mesoconelets are reduced or wanting, in contrast to *Cuvieronius* and *Cordillerion* of South America, in which the trefoil spurs arise from the mesoconelets; it is radically different from the fundamental molar pattern of any of the Bunomastodontidæ, the trefoil structure of which invariably rises from the mesoconelet or is in close connection with it through the central conules. Also evidencing the Serridentine relationship are the laterally compressed, downcurved superior tusks, with broad external enamel band, all trace of which band is absent in the contemporary *Cuvieronius* of the Pampean region.

> *Characters of Notiomastodon,* Cabrera's 'short-jawed serridentine' of the Pampean. Mandible abbreviated, typically stout, lacking inferior tusks; symphysis strongly abbreviated with a transversely concave groove for the tongue; coronoid small and condyle elevated. Superior tusks down- and outturned, with broad enamel band as in Serridentines and Trilophodonts. Inferior molars bunolophodont, with prominent serrated ridges arising from the ectoconelets as in the Serridentines; mesoconelets reduced or wanting. Double series of trefoils on wear (genotype).
>
> Ridge-crest formula: $\mathrm{M}\ 1\frac{}{3+}\ \mathrm{M}\ 2\frac{}{4+}\ \mathrm{M}\ 3\frac{}{4\frac{2}{3}\ \text{(ref.)}}$
>
> Horizon.—Pliocene and Lower Pleistocene(?). Compare Vol. I, Pls. x and xi; Vol. II, p. 1537, and figures 1225, 1227, also Pl. xviii.

Migration.—The Notiomastodonts seem to have been confined to South America, as the genotype, *Notiomastodon ornatus* from Buenos Aires, and a tusk from the valley of the Tarija River, described by Ameghino in 1888 as *Mastodon argentinus*, referred by the present author to *Notiomastodon*, are the only specimens recorded up to the present time.

Superfamily: MASTODONTOIDEA Osborn, 1921. Family: MASTODONTIDÆ Girard, 1852

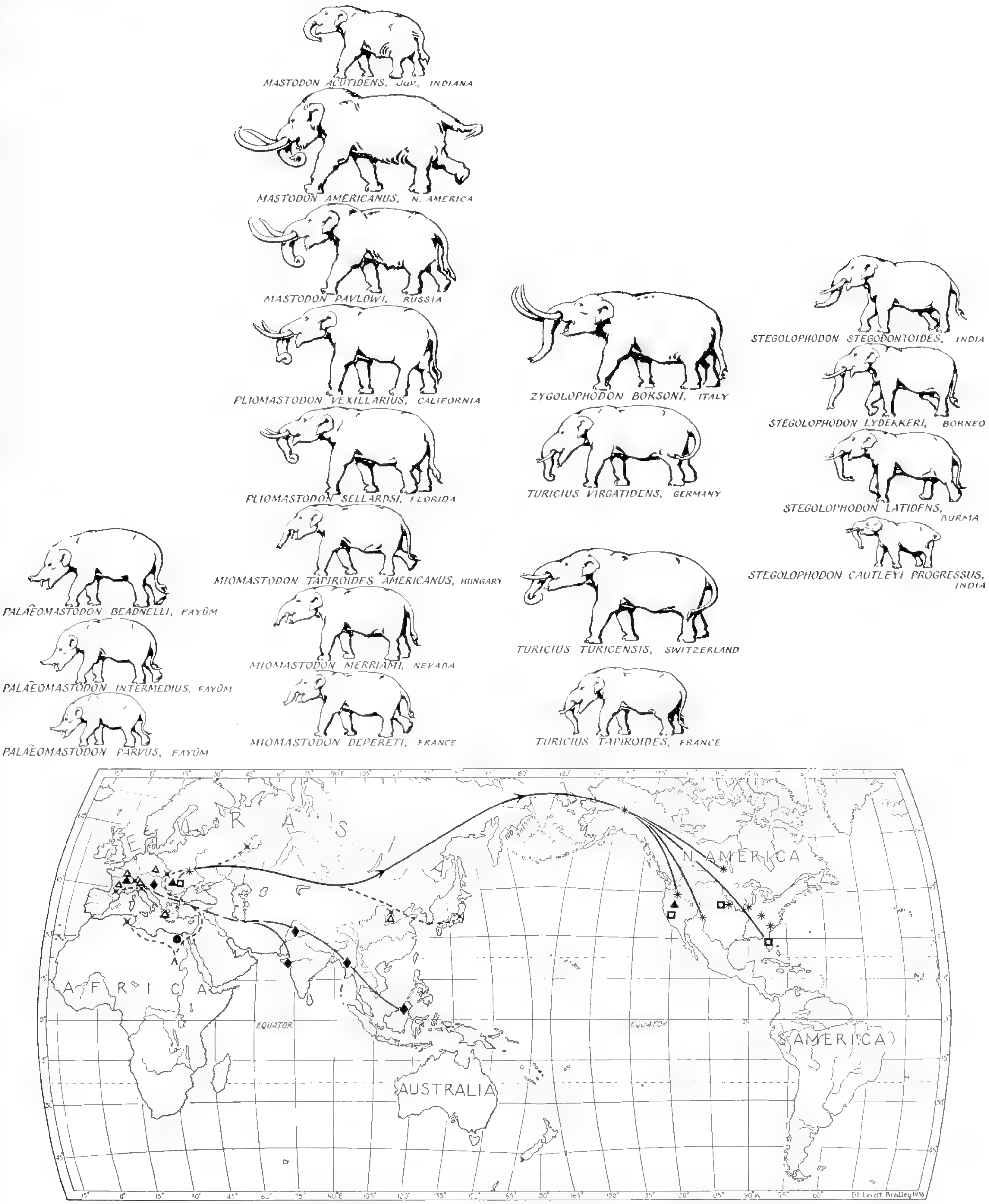
(syn. in part MAMMUTIDÆ Cabrera, 1929)

Subfamily: Palæomastodontinæ Osborn, 1936

Genus: *Palæomastodon* Andrews, 1901

(Cf. Vol. I, pp. 138, 139, 143–149, 689, 691, 692, also Pls. i, ii, x, xi, and Figs. 24, 86, 123a; Vol. II, p. 1529, and figure 1220, also Pl. xix)

The theory that *Mœritherium* gave rise to *Palæomastodon*, and that *Palæomastodon* gave rise to *Mastodon angustidens*, generally so interpreted from Dr. C. W. Andrews' Memoir of 1906, was not accepted by Professor Osborn, who, in 1909, even went so far as to separate *Mœritherium* from direct relationship to the Proboscidea. This opinion, however, he afterward (1921) modified, in fact, he definitely regarded *Mœritherium* as constituting



Origin, Migration and Evolution of ● *Palæomastodon,* ▲ *Miomastodon,* □ *Pliomastodon,* ✱ *Mastodon,* △ *Turicius,* × *Zygolophodon,* ◆ *Stegolophodon. Osborn 1935*

PLATE XIX

Geologic range: *Palæomastodon*, Lower Oligocene. *Miomastodon*, Lower to Middle Miocene, and Lower Pliocene; *Pliomastodon*, Lower to late Pliocene; *Mastodon*, early to late Pleistocene. *Turicius*, Lower Miocene to Middle(?) Pliocene; *Zygolophodon*, Lower Miocene to Upper Pliocene. *Stegolophodon*, Mio-Pliocene to Upper(?) Pliocene [Lower Pleistocene?].

one of the great primary stocks of the Proboscidea, namely, the Mœritherioidea. Doctor Andrews also (1909), while still regarding *Mœritherium* as a proboscidean, reconsidered the possibility of its not being in the direct line of ancestry of *Palæomastodon;* and Doctor Matsumoto (1924), while placing *Mœritherium* in a side line of its own, concluded that *Palæomastodon* appeared nearly to correspond to a theoretical ancestry of the *Zygolophodon-Mastodon* phylum, thus suggesting that it was related to the subfamily which the present author designated as the Mastodontinæ. This theory was immediately approved by Professor Osborn, although it must not be overlooked that in 1923 he had clearly separated the true *Mastodon americanus* from the *Zygolophodon* of Vacek, at which time he described a new subfamily, the Zygolophodontinæ.

In 1934 Professor Osborn became convinced that *Palæomastodon* should be removed from direct ancestry to the true *Mastodon,* because he observed that the progressive third superior and inferior molars of *P. intermedius* exhibited the presence of proto- and metaconules, thus blocking the median sulcus characteristic of all the Mastodontinæ. On page 139 of Volume I of the present Memoir we find the following: "In the carefully drawn Plates I, II, III, and IV, illustrating the evolution of the grinding teeth in *Mastodon, Zygolophodon, Turicius,* and *Stegolophodon,* a median longitudinal sulcus separates the external and internal cones both in the superior and inferior molars. This demonstrates that the ancestral proboscidean molar was *tetrabunodont,* as in *Mœritherium,* not hexabunodont, as in *Palæomastodon*. . . By close comparison of all the figures of the upper and lower grinding teeth of *Palæomastodon, Miomastodon, Pliomastodon,* and *Mastodon,* it is observed: (1) That the molar crowns in *Palæomastodon* are mainly tetrabunodont, i.e., each protoloph (superior) and each protolophid (inferior) is composed of a main external bunoid cone and a main internal bunoid cone; in the superior molars (Fig. 94D) where the conules persist the main crown is hexabunodont. The presence of proto- and metaconules blocking the median sulcus forbids the ancestry of *Palæomastodon* to *Mastodon.* (2) The vestigial intermediate protoconules and metaconules are observed in the hexabunodont superior molars of *Palæomastodon intermedius,* thus the crested upper grinders are hexabunodont or six coned, whereas the lower grinders are subtrilophodont (Fig. 93, M^3-M_3, Fig. 94). This primitive condition of the *cones* connects *Palæomastodon* with its undiscovered sexitubercular-quadritubercular ungulate ancestors; the *conules* observed in the third superior molar, M^3, of *P. intermedius* (Figs. 93 and 89) are not seen in M^2 of the same species (Fig. 92); the conules are vestigial or disappearing structures."

Accordingly Professor Osborn withdrew *Palæomastodon* from the subfamily Mastodontinæ and created a new subfamily, Palæomastodontinæ, for its reception (see Vol. I, Appendix, p. 691).

> *Palæomastodon,* the 'ancient mastodon' of North Africa, Eocene-Oligocene. Skull imperfectly known. Palate relatively short and broad. Mandible elongated anteroposteriorly (medium jawed) mandibular symphysis relatively short as compared with *Phiomia.* Superior tusks unknown. Inferior tusks rounded and relatively abbreviated. Molars brachyodont, of bunolophodont rather than of bunomastodont type, progressive in size and evolution from tetrabunodont cones (*Palæomastodon parvus*) to hexabunodont cones (*P. intermedius, P. beadnelli*); bilophodont superior molars, subtrilophodont inferior molars, in other words, the tritoloph and tritolophid are in a formative stage, tritoloph rudimentary even in M^3. Intermediate proto- and metaconules progressively developing to perfect the transverse crests, thus closing the median longitudinal sulcus characteristic of all the Mastodontinæ. Molars exhibiting central conules; trefoils rudimentary or absent. Basal cingula neither very strong nor very rough.
>
> Dental formula: $I_{\overline{0\text{-}2\text{-}0}}$ $C\,\frac{0}{0}$ $Dp\,\frac{?}{?}$ $P\,\frac{2\text{-}4}{3\text{-}4}$ $M\,\frac{1\text{-}3}{1\text{-}3}$
> Ridge-crest formula: $P\,2\frac{1}{0}$ $P\,3\frac{1\frac{1}{4}}{1\frac{1}{4}}$ $P\,4\frac{2}{2}$ $M\,1\frac{2\frac{1}{2}}{3}$ $M\,2\,\frac{2\frac{1}{2}}{3}$ $M\,3\frac{2\frac{1}{2}}{3}$
> HORIZON.—Lower Oligocene (Fluvio-marine formation). Compare Vol. II, p. 1529, and figure 1220, also Pl. XIX.

HABITS AND HABITAT.—Probably forest loving with transversely secant molar crests for cutting herbage. Up to the present time, however, specimens of *Palæomastodon* have been found in the Fayûm region only.

Superfamily: MASTODONTOIDEA Osborn, 1921. Family: MASTODONTIDÆ Girard, 1852

(Syn. in part MAMMUTIDÆ Cabrera, 1929)

Subfamily: MASTODONTINÆ Brandt, 1869—Osborn, 1910

Genera: *Mastodon* Cuvier, 1806–1817; *Miomastodon* Osborn, 1922; *Pliomastodon* Osborn, 1926

(Cf. Vol. I, pp. 132, 138, 150–190, 690, 693–697; also Pls. I, X, XI, and Figs. 86, 123a, 123b; Vol. II, p. 1530, and figures 1222, 1224, 1227, also Pl. XIX)

In Professor Osborn's article in NATURAL HISTORY of 1925 (Osborn, 1925.637), we find on page 10 the following statement: "The true mastodons of our American forests appear to have arisen from the diminutive *Palæomastodon* of the primordial river Nile. The reason these animals have left no trace of their 10,000-mile and 2,000,000-year journey from the Nile region to the forests bordering the Ohio and the Hudson rivers is that fossilization of forest-living fauna has always been rare. The ancestral *Palæomastodon* of the Nile region is itself very rare. . . not even fossilized teeth of this race were scattered in Europe to show the route."

During the ten-year interval from 1925 to 1935, Professor Osborn changed his views regarding *Palæomastodon* being the ancestor of the true *Mastodon*, as expressed in the foregoing paragraphs (p. 1573) on the Palæomastodontinæ and also on pages 138 and 139 of Volume I of the present Memoir: "While we are certain that the true *Palæomastodon* possesses a longer jaw but a broader and shorter skull than its Lower Oligocene contemporary *Phiomia*, while the superior grinding teeth are comparatively short and broad, and while in the crowns of the superior and inferior grinding teeth the proto- and metaconules forbid the ancestral relationship of *Palæomastodon* to *Pliomastodon*, *Miomastodon*, and *Mastodon*, we must await further knowledge of the cranium and of the cutting teeth, also of the incisors of *Palæomastodon*, before we can form a positive opinion on this very important and interesting question." Again, in the Appendix to Volume I, p. 692, he voices uncertainty as to the ancestral forms of the Mastodontinæ which embraced the four genera, *Palæomastodon*, *Miomastodon*, *Pliomastodon*, *Mastodon*, until he withdrew *Palæomastodon*, making it the type of a new subfamily Palæomastodontinæ: "Despite the extreme rarity of the remains of forest-loving and browsing mastodonts, exemplified by the rarity of *Palæomastodon* as compared with *Phiomia* in the Fayûm deposits, several discoveries of isolated grinding teeth have been made in the Tertiary deposits of Europe and North America which are now recognized as belonging to successors of still unknown true Mastodontinæ of Africa and ancestors of the true Mastodontinæ of North America."

The contrasting characters, so far as known, of the three genera now constituting the Mastodontinæ, are as follows:

> *Mastodon*, 'typical mastodon' of Eurasiatic and North American forests. Cranium brachycephalic, brachyopic. Mandible and symphysis abbreviated; progressive reduction of rostrum. Superior tusks large, rounded, upturned, with slightly indicated annular ring growths; inferior tusks straight, cylindrical, variable in old age; no enamel. Marked sexual disparity in female tusks. Grinders relatively elongate, bilobate, with strong median sulcus between inner and outer lobes; no conules; rudimentary trefoil spurs on superior inner lobes, on inferior outer lobes; summits of lobes simple or crowned with small conelets; extreme binary fission of summits of crests in *Mastodon acutidens*, in which as many as twenty-one conelets may be counted; progressive plication of the surface enamel. Ridge-crests lophodont, progressively elevated, subhypsodont. Progressive development of third crest (tritoloph and -lophid) in intermediate molars; progressive development of fifth crest rudiment (pentalophid) in third inferior molars. Permanent premolars suppressed, except P^4-P_4, which form in the jaw but do not erupt. Cingulum slightly stronger on inner side than on outer side.
>
> Dental formula: I $\frac{0\text{-}2\text{-}0}{0\text{-}2\text{-}0}$ Dp $\frac{2\text{-}4}{2\text{-}4}$ P $\frac{0\text{-}0\text{-}4}{0\text{-}0\text{-}4}$ (vestigial) M $\frac{1\text{-}3}{1\text{-}3}$
> Ridge-crest formula: Dp $2\frac{2}{2}$ Dp $3\frac{2}{2}$ Dp $4\frac{3}{3}$ M $1\frac{3}{3}$ M $2\frac{3}{3}$ M $3^{4\frac{1}{2}}_{4\frac{3}{4}}$
> HORIZON.—Early to late Pleistocene. Compare Vol. II, p. 1530, figures 1222, 1224, 1227, and Pl. XIX.

Pliomastodon, 'Pliocene mastodon' of Eurasia and North America, an ancestral stage of *Mastodon*. Distinctive, low browed, flat crested; abbreviated postnarial region and broadly divergent premaxillary region; approximation of condyles to superior molars (M^3), extreme backward recession of anterior nares and shortening of lower jaw, probably also an unusual width of the occipital crest, suggesting an exceptionally large development of the proboscis (characters based on *Pliomastodon vexillarius* Matthew, 1930—see Vol. I, pp. 161–163). Superior tusks suboval to rounded in section, upturned, enamel band vestigial or wanting; a "narrow strip of thin enamel" within the alveolar base of the tusk in *P. vexillarius*. Inferior tusks probably stout (as inferred from the alveoli—about 50 mm. in diameter near the posterior end—in *P. sellardsi* Simpson, 1930). Molars intermediate in hypsodonty between *Miomastodon* and *Mastodon*; a distinctive feature is the posterior narrowing of the crown of the third superior molars (*P. matthewi*). Ridge-crests with rudimentary trefoil spur extending from entocones of superior molars and from ectocones of inferior molars; expanded ectotrefoils (*P. matthewi*). No median conules. Persistent longitudinal sulcus; also persistent four conelets.

Dental formula incompletely known: $I\,\frac{0\text{-}2\text{-}0}{0\text{-}?\text{-}0}\ Dp\,\frac{?}{?}\ P\,\frac{?}{?}\ M\,\frac{1\text{-}3}{1\text{-}3}$

Ridge-crest formula: $P\,4\frac{3\,?}{3\,?}\ M\,1\frac{?}{3}\ M\,2\frac{3}{3}\ M\,3\frac{4\frac{1}{4}}{?\ 4\frac{1}{2}\text{-}5}$

Horizon.—Lower to late Pliocene. Compare Vol. II, p. 1530, and figures 1222, 1224, 1227, also Pl. xix.

Miomastodon, 'Miocene mastodon' of Eurasia and North America. Skull and skeleton unknown. Mandible and symphysis moderately elongated; rostrum laterally compressed, abbreviate as compared with *Trilophodon* or *Serridentinus*. Superior tusks downturned, broadly oval in vertical section; broad enamel band on concave external surface (*Miomastodon merriami*), on convex external surface (*M. tapiroides americanus*); inferior tusks rodlike, horizontal, vertically oval. Molars brachyodont to subhypsodont; internal and external lobes or cones of each loph separated by median or longitudinal sulcus; summit of each lobe or cone double or bifid, rounded; mesial expansion of rudimentary trefoils in ento- and ectoconelets, upper and lower; central conules absent; retarded binary fission of cones and conelets in proto- and metalophs; conelets never exceeding four in each loph or transverse ridge-crest. Persistent median sulcus.

Dental formula incompletely known: $I\,\frac{0\text{-}2\text{-}0}{0\text{-}2\text{-}0}\ Dp\,\frac{?}{?}\ P\,\frac{?}{?}\ M\,\frac{1\text{-}3}{1\text{-}3}$

Ridge-crest formula: $P\,4\frac{3\,?}{3\,?}\ M\,1\frac{3\,?}{3\,?}\ M\,2\frac{3}{3}\ M\,3\frac{4}{4\frac{1}{2}\text{-}5}$

Horizon.—Lower to Middle Miocene, Lower Pliocene. Compare Vol. II, p. 1530, and figures 1222, 1224, 1227, also Pl. xix.

Migration.—(Cf. Vol. I, pp. 132, 133): "Springing from unknown ancestors of the Eocene-Oligocene of North Africa, the true Mastodontinæ appear in the Lower Miocene *Miomastodon* [*M. depereti*] of western Eurasia [France] and soon find their way eastward into North America, appearing in the Middle Miocene species of Nevada, *Miomastodon merriami*, and in the Lower Pliocene species of western Nebraska, *Pliomastodon matthewi*, meanwhile leaving behind in Austria-Hungary their relatives, *Miomastodon tapiroides americanus* and *Pliomastodon americanus praetypica*, which give rise to the rare true *Mastodon* of southern Russia, referred to '*Mastodon ohioticus*' by Pavlow [and by the present author to *Mastodon pavlowi*]. Rarely found in northern and western North America, they multiply rapidly in the favorable forests of the middle and eastern United States in the typical form *Mastodon americanus*." Fossil remains are found even as far northeast as Nova Scotia and New Brunswick, as evidenced by a recent (1936) discovery at Hillsboro, N. B., and identified by Director William MacIntosh of the New Brunswick Museum as *Mastodon americanus*.

Superfamily: MASTODONTOIDEA Osborn, 1921. Family: MASTODONTIDÆ Girard, 1852
(Syn. in part MAMMUTIDÆ Cabrera, 1929)
Subfamily: ZYGOLOPHODONTINÆ Osborn, 1923
Genera: *Zygolophodon* Vacek, 1877; *Turicius* Osborn, 1926
(Cf. Vol. I, pp. 191–223, 282, 690, 697–699, also Pls. ii, iii, x, xi, and Figs. 137, 159; Vol. II, p. 1530, and figures 1222, 1227, also Pl. xix)

When in 1923 Professor Osborn created his subfamily Zygolophodontinæ, he had not observed the pronounced differences in the molar structure of species of *Zygolophodon* Vacek, 1877, which later (1926.706, p. 3) actuated him to describe a new genus, *Turicius*. Especially noticeable were (1) the strong subdivision of the main cones of certain species (*Zygolophodon*) into from four to six subequal conelets, whereas in other species (*Turicius*) the cones subdivided into from five to nine conelets, and even into twenty-five (see Pl. III, pp. 134, 135); also (2) the presence of strong 'trefoil spurs' on the supero-internal and infero-external cones of the latter (*Turicius*) in contrast to the absence (or vestiges) of these spurs in the former (*Zygolophodon*). The species included within *Turicius* show several resemblances to those included within the genus *Serridentinus* (e.g., the trefoil spurs just mentioned), but in many other characters *Turicius* is clearly separable from *Serridentinus* and more closely related to *Zygolophodon*.

The history of the Zygolophodontinæ will be found in detail in Volume I, Chapter VII, covering the period from 1770 to 1936, in which is set forth the grounds on which this subfamily is separable from the Mastodontinæ, to which it is most nearly related. In brief, the median longitudinal sulcus (Fig. 89) of *Mastodon americanus* disappears in *Zygolophodon* and transversely perfected crests evolve; in *Mastodon* the main cones feebly subdivide at the summits into two conelets,[1] progressive to four (*Miomastodon*), whereas in *Zygolophodon* there are four to six main conelets, and from five to nine and even twenty-five in certain specimens of *Turicius*. In other words, from the principal characters of the type grinding teeth we observe (cf. Vol. I, p. 199) "that the universal *generic* character both of *Zygolophodon* and of *Turicius* is the *absence* or *reduction* of the longitudinal sulcus, fissure, or commisure, which Hays pointed out as the chief character distinguishing his type (Fig. 154) of *M.* [*Zygolophodon*] *borsoni* from *M. americanus*. The absence or reduction of this sulcus distinguishes all the ascending species of *Zygolophodon* and of *Turicius*, from early Miocene to late Pliocene or early Pleistocene time, from all the ascending or ancestral stages of *Mastodon* in the corresponding period. We also observe that the fission of the cones into 'conelets' is rapidly progressive and distinct in *Zygolophodon* and in *Turicius*, whereas it is decidedly retarded in *Mastodon*. [The final stage of evolution, however, in the *Mastodon acutidens* molar (Fig. 656) converges towards the final evolution stage in the zygolophodont molar (*Turicius virgatidens*—Fig. 168).] In many other features . . . the progressive dental and skeletal evolution of *Zygolophodon* parallels that of *Mastodon*. . . . (1) the abbreviation of the jaws, (2) the suppression of the premolar dental succession, (3) the reduction of the lower incisive tusks, (4) the progressive abbreviation of the cranium. . . . From the fact that the *Zygolophodon molars* are relatively broader and shorter than those of *Mastodon*, it is probable that the cranium of *Zygolophodon* was more brachycephalic than that of *Mastodon*."

The collateral relationship of the Zygolophodontinæ to primitive species of Stegodonts (Stegolophodontinæ, Stegodontinæ) of Asia is treated in Volume I, p. 195, and in Chapter XIV of the present volume, p. 819. Such relationship was first adumbrated by Schlosser as early as 1903, and was followed in 1917 by the suggestion of Schlesinger that primitive European species may have given rise to primitive species of Stegodonts of Asia to which he gave the new generic name *Stegolophodon*—both of which suggestions Professor Osborn was inclined to favor. An excellent columnar presentation of the outstanding characters of the grinding teeth of the *Mastodon*, *Zygolophodon*, *Turicius*, and *Stegolophodon* phyla is given on page 211 of Volume I, supplemented by Plates I–IV (pp. 134–135) demonstrating the molar evolution. Reference is made in the last column to a description of the collateral ancestor of *Stegodon* in Chapter XV; this should read Chapter XIV, as in revising the present volume it was found desirable to rearrange the chapters somewhat (see pp. 819–822 above).

Professor Osborn made a further suggestion on page 202 of Volume I, to the effect that, owing to certain strong resemblances (e.g., supero-internal and infero-external trefoil spurs) between the grinding teeth of *Turicius* and *Serridentinus*, despite the entirely different lower tusks in the two genera, there might be an affinity of the

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[1] [See, however, *Mastodon acutidens* Osborn (described on pp. 696, 697 of Vol. I of the present Memoir) in which as many as twenty-one conelets may be counted on certain of the lophs.—Editor.]

genus *Turicius* to *Serridentinus* which a fuller knowledge would demonstrate. Among the distinguishing characters, in addition to the differences in the tusks, he mentions (p. 223) the development of a pure transverse crest in the molars of *Turicius*, as against the development of corresponding conelets and crests in the American *Serridentinus* in which the cones and conelets do not become connate and remain quite distinct at the summit, also the progressive strengthening of the trefoil spurs in *Serridentinus*, which become more and more prominent and conspicuous in progressive stages, surmounted with small conelets, whereas in progressive stages of *Turicius*, like *T. atticus* and *T. virgatidens*, the trefoil spurs are reduced to fine ridges accented with numerous small conelets. See, however, his final conclusions on pages 1568, 1569 above, namely, that the *Turicius* phylum is entirely distinct.

A condensed summary of the contrasting characters in the two genera *Zygolophodon* and *Turicius* is as follows:

Zygolophodon, typical 'yoke-crested mastodont' of Eurasiatic Miocene to Pleistocene. Cranium and skeleton relatively unknown, probably similar to *Mastodon americanus*. Symphysis more abbreviated than in *Turicius*. Superior tusks rounded, enamel band disappearing early, before Lower Miocene time. Inferior tusks reducing early; no enamel (*Z. pyrenaicus*). Grinders permanently blunt, brachyodont (*Z. borsoni*), not becoming subhypsodont. Ridge-crests or lophs directly transverse, not arched, each loph divided into four to six distinct subequal conelets. Conules or tubercles in median valleys disappearing in early stages (vestigial conules in anterior valley of *Z. pyrenaicus*). Trefoil spurs vestigial or absent. Median longitudinal sulcus disappearing, primitive, vestigial. Fifth inferior crest, i.e., pentalophid, slowly progressive. Intermediate molars trilophodont (*fide* Schlesinger). Suppression of the premolar dental succession.

Dental formula: I $\frac{0\text{-}2\text{-}0}{0\text{-}2\text{-}0}$ Dp $\frac{2\text{-}4}{2\text{-}4}$ M $\frac{1\text{-}3}{1\text{-}3}$
Ridge-crest formula: Dp $2\frac{?}{?}$ Dp $3\frac{?}{?}$ Dp $4\frac{3}{3}$ M $1\frac{3}{3}$ M $2\frac{3+}{3+}$ M $3\frac{4\text{-}4\frac{1}{2}}{4\text{-}4+}$
HORIZON.—Lower Miocene to Upper Pliocene. Compare Vol. II, p. 1530, and figures 1222, 1223, 1227, also Pl. XIX.

Turicius, sharp-crested 'Zurich mastodont' of the European Miocene and Pliocene. Cranium and skeleton relatively unknown. Symphysis progressively pointed and reduced in length, horizontal not decurved. Superior tusks oval in section, rodlike, with sharply defined enamel band except in *Turicius virgatidens*. Inferior tusks without enamel, straight, suboval in section, undergoing progressive reduction. Molar ridge-crests sharply transverse and elevated, with conelets progressive from four to twenty-five. Median longitudinal sulcus vestigial in early stages, completely disappearing in progressive stages. No median conules. Progressively strong trefoil spurs on superior internal cones and on inferior external cones. Conelets increasingly connate at summit, rising into sharp, subhypsodont transverse crests. Postero-inferior molars with four well-developed crests, the tetartolophid slowly progressive, the pentalophid rudimentary but progressive in the higher stages. Gradual repression of the premolar dental sucsession, as in *Mastodon americanus* and *Zygolophodon borsoni*.

Dental formula: Di $\frac{0\text{-}0\text{-}0}{0\text{-}2\text{-}0}$ I $\frac{0\text{-}2\text{-}0}{0\text{-}2\text{-}0}$ Dp $\frac{2\text{-}4}{2\text{-}4}$ M $\frac{1\text{-}3}{1\text{-}3}$
Ridge-crest formula: Dp $2\frac{2}{1+}$ Dp $3\frac{2+}{2+}$ Dp $4\frac{3}{3}$ M $1\frac{3}{3}$ M $2\frac{3+}{3+}$ M $3\frac{3\text{-}4}{4\text{-}4+}$
HORIZON.—Lower Miocene to Middle(?) Pliocene. Compare Vol. II, p. 1536, and figures 1220, 1222, 1227, also Pl. XIX.

MIGRATION.—The types of *Zygolophodon* and *Turicius*, as known up to the present time, occur in southern and central Europe. As will be seen by referring to figure 159 and Plate XIX, a referred specimen of *Turicius* comes from North Africa, also, according to Matsumoto, one of *Zygolophodon* from Japan. Recently (cf. pp. 698 and 699 of the present Memoir) Doctor Hopwood has described a juvenile mandible regarded by him as belonging to *Mastodon americanus* but according to Professor Osborn referable to *Turicius*, also a molar of *Zygolophodon borsoni*, both from China. *Zygolophodon borsoni* is relatively abundant in Siberia. Again consulting figure 159 and Pl. XIX, it would seem that the trend of migration was from North Africa, through southern and central Europe eastward to Siberia, China, and Japan. The Zygolophodontinæ apparently never reached America.

Superfamily: MASTODONTOIDEA Osborn, 1921. Family: MASTODONTIDÆ Girard, 1852

(Syn. in part MAMMUTIDÆ Cabrera, 1929)

Subfamily: STEGOLOPHODONTINÆ Osborn, 1936

Genus: *Stegolophodon* Schlesinger, 1917

(Cf. Vol. I, p. 700, Pls. IV, XI and Fig. 661; Vol. II, Chap. XIV, p. 837, also p. 1531, and Figs. 691, 1221, 1223, 1228, Pl. XIX)

The subfamily Stegolophodontinæ, type *Stegolophodon* Schlesinger, 1917, was defined by Professor Osborn as "transitional in molar tooth structure between the Mastodontoidea and the Stegodontoidea"—the latter a superfamily first created by him to embrace both *Stegolophodon* and *Stegodon* (see Osborn, 1935.937, fig. 2). On further study, however, the median sulcus characteristic of the Mastodontinæ was found to persist in the anterior ridge-crests of *Stegolophodon*, thus pointing toward a very remote relationship between the Mastodontoidea and the Elephantoidea—indeed, a comparison shows that the most primitive elephantoid molar known, that of *Archidiskodon proplanifrons* of South Africa (subfamily Mammontinæ), is, in section, very like the molar teeth of a *Mastodon* (subfamily Mastodontinæ), that is, without trefoils or central conules blocking the valleys. Professor Osborn, therefore, became convinced that *Stegolophodon* should be removed from the Elephantoidea and placed as a terminal member of the Mastodontoidea, leaving the genus *Stegodon* as the sole generic representative of the superfamily Stegodontoidea. The reader will find a detailed account of the phylogeny of the Stegolophodonts and Stegodonts in Chapter XIV of the present volume, wherein they are treated together according to Professor Osborn's original views, as unfortunately he had not reached this chapter in his final revision. We may summarize the distinctive characters of *Stegolophodon*, as follows:

> *Stegolophodon*, 'roof-crested pro-stegodont' parallel and collateral in evolution with the true *Stegodon* of eastern and southern Eurasia. Cranium low, dolichocephalic, suggesting the primitive type of skull and tusks seen in *Trilophodon* and *Serridentinus*. Mandibular symphysis not certainly known, but probably short and tuskless. Superior tusks straight with broad enamel band. Inferior tusks undiscovered. Lophs as in *Mastodon* and *Zygolophodon*, tendency to form from four to six transversely arranged cones and conelets (conelets somewhat irregular) and to consolidate into ridge-crests; molar pattern transitional between the *Zygolophodon* type and the *Stegodon* type; no median conules and no trefoil spurs. Closure of enamel in base of transverse valleys, that is, V-shaped; enamel thick; cement usually absent.
>
> Dental formula: I $\frac{0\text{-}2\text{-}0}{}$ Dp $\frac{2\text{-}4}{2\text{-}4}$ M $\frac{1\text{-}3}{1\text{-}3}$
> Ridge-crest formula (based largely on *Stegolophodon latidens*):
> Dp $2^?_?$ Dp $3^2_?$ Dp $4^4_?$ M $1\frac{¾\text{-}4\text{-}¼}{?}$ M 2 $\frac{4½\text{-}5}{4½\text{-}5}$ M 3 $\frac{5+\text{-}6+}{5\text{-}6½}$
> HORIZON.—Mio-Pliocene to Upper (?) Pliocene [Lower Pleistocene?]. Compare Vol. II, p. 1531, and figures 1221, 1223, 1228, also Pl. XIX.

ORIGIN AND MIGRATION.—It was doubtfully suggested by Schlosser in 1903 (1903, p. 191) that west European species, originally described as *Mastodon turicensis* [*M. tapiroides*, *M. pyrenaicus*, etc., separated as *Zygolophodon* by Vacek in 1877 and by Osborn in 1926 as *Turicius* (*M. turicensis*, *M. tapiroides*) and *Zygolophodon* (*M. pyrenaicus*)], may have given rise to primitive Asiatic species [such as *Stegolophodon cautleyi*]; also that *M. turicensis* [= *Turicius tapiroides*] of the Lower Miocene of Europe may have given rise to the *M.* [*Stegolophodon*] *latidens* of the Lower Pliocene [?Lower Pleistocene] of Asia from which in turn sprang off the true Stegodonts, such as *Stegodon insignis*. Professor Osborn's final opinion regarding the relationships of the Stegolophodontinæ (see pp. 197 and 819–822 above) would seem to be in favor of Schlosser's suggestion of 1903, also that of Schlesinger of 1917, that primitive species of Europe [*Mastodon* (*Stegolophodon*) *sublatidens*] may have given rise to primitive

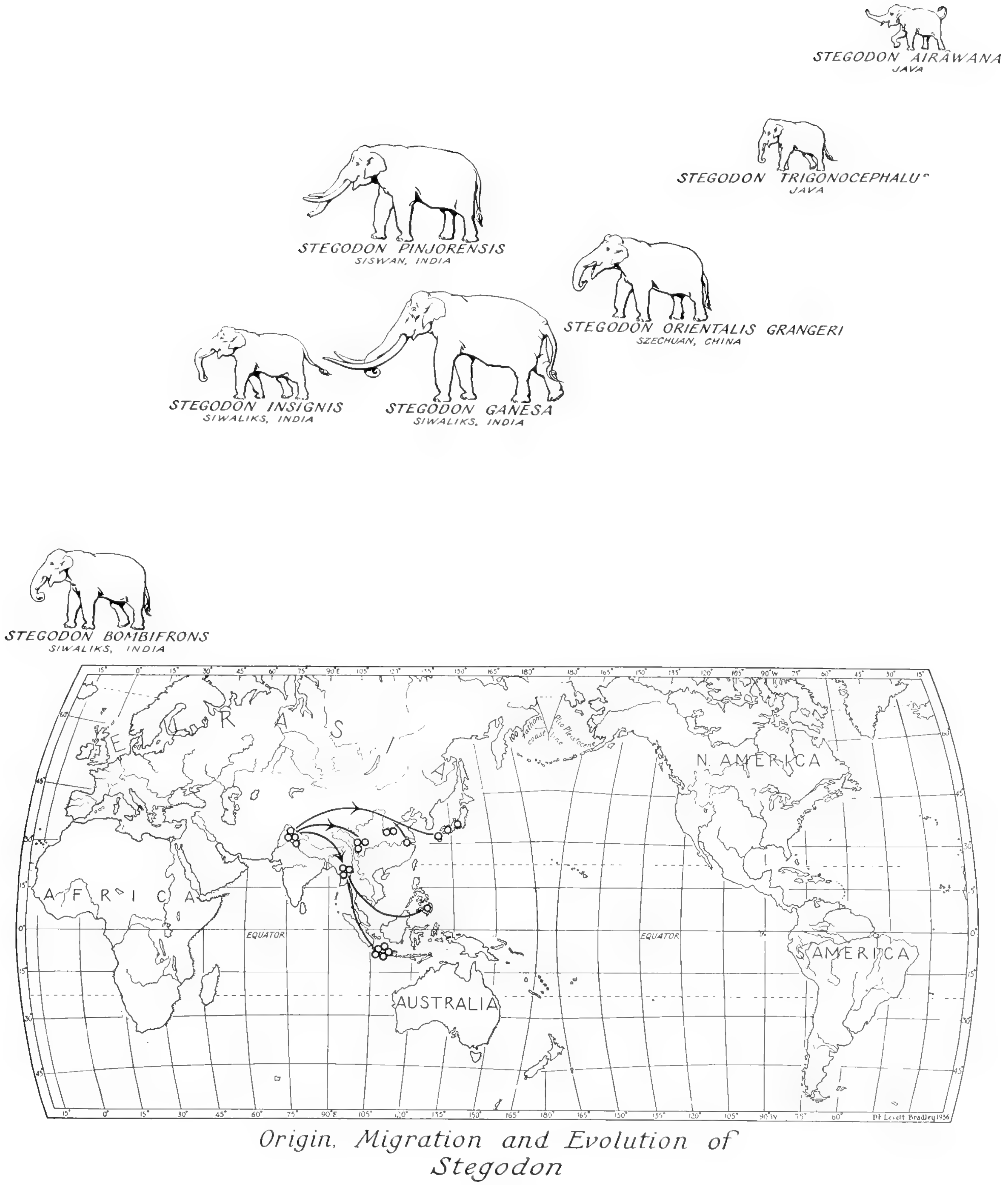

PLATE XX

Geologic range: *Stegodon*, Lower Pliocene [?Lower Pleistocene, see p. 824 above], Middle Pliocene to Upper Pleistocene. Since this map was prepared the range of *Stegodon* has been extended into Africa, as far south as Kaiso, on Lake Albert.

species of Asia to which Schlesinger has given the generic name *Stegolophodon* (cf. Vol. I, pp. 195, 197, and Pls. II–IV, also p. 700). The Stegolophodonts are not known to have reached America. Fossil remains have been found in Austria, in Perim Island, the Punjab and the Siwaliks of India, also in Burma, Japan, and Borneo. Their possible line of migration in indicated in figure 1228 and on the accompanying Plate XIX.

STEGODONTOIDEA

Superfamily: STEGODONTOIDEA Osborn, 1935, 1936. Family: STEGODONTIDÆ Young-Hopwood, 1935

Subfamily: STEGODONTINÆ Osborn, 1918, 1921

Genus: *Stegodon* Falconer and Cautley, 1847, 1857

(Cf. Vol. I, Pl. XI, and Chap. XIV of the present volume, pp. 807, 853, also Figs. 686–688, 691, 1221, 1223, 1228, and Pl. XX)

As fully stated in Chapter XIV above, Professor Osborn separated the true Stegodonts from the Elephantoidea, giving them a new superfamily name, Stegodontoidea, which includes the genus *Stegodon* only of the subfamily Stegodontinæ, the genus *Stegolophodon* having been removed by him to the Mastodontoidea, subfamily Stegolophodontinæ. The family Stegodontidæ, first mentioned by Dr. C. C. Young in 1935 and fully defined by Dr. A. Tindell Hopwood later in the same year, embraced both *Stegodon* and *Stegolophodon*. In the present Memoir this family is logically included in the superfamily Stegodontoidea, although Professor Osborn never indicated such reference other than in his chart of 1935 (Osborn, 1935.937, fig. 2), and even in this instance he also included both genera, *Stegodon* and *Stegolophodon*. The separation of the Stegodontoids from the Elephantoids was based chiefly on the fact that in section the molars of the former showed the valleys separating the adjacent ridges to be closed or V-shaped at the bottom and those of the latter to be open or U-shaped. Another determining factor was the extremely short face of the Stegodontoids which, in his opinion, could not have given rise to the longer face of the Elephantoids. With this classification in mind, the following characters have been compiled pertaining solely to the Stegodontinæ, genus *Stegodon*.

> *Stegodon*, so named because of the resemblance of the toothed ridges of the grinding teeth to a series of roof-gables; more primitive than the true elephants. Skull and tusks do not lead into either the Elephantinæ or the Mammontinæ types. Cranium brachycephalic, brachyopic, of mastodontoid (*Stegodon bombifrons*), to extremely abbreviated, female? (*S. insignis*), more elongated, male? (*S. ganesa*), more triangular (*S. trigonocephalus*) form; rostrum elongated to support the tusks; palate short, depressed well below the occipital condyles (bathycephalic); narial openings elevated. Jaws greatly abbreviated. Superior tusks horizontal or subhorizontal in direction, parallel, and slightly upcurved, without trace of enamel band, attaining great dimensions (*S. ganesa*). Inferior tusks disappearing very early. Grinding teeth short crowned; progressive heightening of ridge-crests (brachyodont to subhypsodont), the distinctive feature being the rapid multiplication of transverse crests by the addition of crests posteriorly; increasing curvature of the occlusal surface; enamel valleys closed or V-shaped at the bottom instead of U-shaped as in the elephantoids, filling with cement. Particularly interesting and significant is the transformation of the original cones by binary or rarely by ternary fission into conelets (maximum 20+ in *S. airâwana*). Ridge-crests intermediate between *Stegolophodon* and *Archidiskodon planifrons* types. Probably browsers rather than grazers.
>
> Dental formula: Di $\frac{0\text{-}2\text{-}0}{}$ I $\frac{0\text{-}2\text{-}0}{}$ Dp $\frac{2\text{-}4}{2\text{-}4}$ M $\frac{1\text{-}3}{1\text{-}3}$
>
> Ridge-crest formula: Dp $2\frac{2+}{2}$ Dp $3\frac{4\text{-}6}{4\text{-}6}$ Dp $4\frac{5\text{-}9}{6\text{-}7\frac{1}{2}}$ M $1\frac{6\text{-}9}{7\text{-}8}$ M $2\frac{6\text{-}11}{7\text{-}9+}$ M $3\frac{6\text{-}14}{7\text{-}15+}$
>
> HORIZON.—Lower Pliocene [?Lower Pleistocene, see p. 824 above], Middle Pliocene to Upper Pleistocene. Compare this chapter, p. 1539, and figure 1228.

ORIGIN AND MIGRATION.—Professor Osborn's views on the origin of the true Stegodonts are given on page 25 of Volume I of the present Memoir, as follows: "It has been assumed by practically all palæontologists that the Elephants were descended from the Stegodonts. . . . The Stegodonts were of independent origin and formed an independent parallel branch terminating in the highly specialized *Elephas* [*Stegodon*] *auroræ* Mastumoto from the Upper(?) Pliocene of Mt. Tomuro, Japan, now . . . separated by Osborn as the Stegodontoidea superfam. nov." Also on page 853 of the present volume, where the generic characters of *Stegodon* are enumerated, occurs the following, agreeing in substance with the above conclusions: "Phylum parallel to that of the true *Archidiskodon* and *Elephas*, not directly ancestral, readily distinguished by cranial and dental characters." It will be noted on page 819 above that Schlosser suggested the possible derivation of the true Stegodonts from certain Miocene species of western Europe since referred by the present author to the Zygolophodontinæ, that is to say, these may have given rise to the Lower Pliocene [?Lower Pleistocene] *M.* [*Stegolophodon*] *latidens* of Asia, from which in turn sprang off the true Stegodonts, such as *Stegodon insignis.* Professor Osborn regarded this phylogenetic problem as of such importance that he stated on page 197 of Volume I that it would be treated more fully in Volume II, under the Stegodontinæ [of the Stegodontoidea superfam. nov.]. It is with regret that we are unable to carry out his intention in this respect, as he left no record of his final views on the subject other than is given above.

The accompanying migration map (Pl. xx), therefore, omits the hypothetical European point of departure and indicates the Siwaliks of India as the center of dispersal, from which radiate three distinct routes, namely, to Burma and Java, to central China, and to the northern part of China onward to Japan. Up to the present time *Stegodon* has not been found in the Western Hemisphere. See Chapter XXII, p. 1436 above, where Dr. Edwin H. Colbert cites from a letter of January 14, 1938, from Dr. A. Tindell Hopwood, in which the range of *Stegodon* is extended into Africa as far south as Kaiso on the eastern shore of Lake Albert.

ELEPHANTOIDEA

It will be recalled that Professor Osborn long held the opinion that Africa was the center of adaptive radiation—or the "homeland"— of the Proboscidea. With this thought ever in mind, he pursued his researches over a period of nearly thirty-five years, and, happily, the results, so far as can be determined at the present time, have confirmed his views, as will be seen from the following citation from his last paper on the subject, "The Ancestral Tree of the Proboscidea. Discovery, Evolution, Migration and Extinction over a 50,000,000 Year Period," 1935.937, p. 410:

> In the Elephantoidea we have discovered a brilliant example of aristogenic growth and extensive migration in the evolution of *Archidiskodon proplanifrons*, a very primitive stage found in the Vaal River gravels of South Africa, into the *Archidiskodon maibeni* of Nebraska. *Archidiskodon proplanifrons* has a molar crown pattern like that of a mastodont, with an enamel length of 690 mm.; *Archidiskodon maibeni* has eighteen tall ridge plates and an estimated enamel length of 9000 mm. This is the first time that the evolution of the elephantoid molar from a theoretic mastodont prototype has ever been actually demonstrated . . . The 15,000 mile migration of *Archidiskodon*, from the Vaal River of South Africa through intermediate stages in North Africa, France, Italy, Britain, India, then the long geographic break to the Niobrara River in Nebraska where Leidy discovered these animals in 1858, is the most remarkable trek of any species of plant or animal thus far discovered in the life history of the earth. The by-product is the fact that these stages give us an unprecedented opportunity of measuring precisely the actual rate of evolution between Upper Pliocene and Middle Pleistocene time. The enamel length increasing from 690 mm. to an estimated 9000 mm. affords an evolution of approximately 15 mm. of enamel length per thousand years.

In this introduction to the subfamily members of the Elephantoidea it may not be amiss to give the present author's definitions of alloiometrons and aristogenes, as well as an outline of his "elephant enamel or ganometric method" of measuring Pleistocene time, particularly in view of the fact that reference has been made in the foregoing quotation to aristogenic and ganometric usage in his researches. Compare page 1582, also figure 300 of Vol. I, and figures 1231, 1239, 1240 of this chapter.

"Aristogenes are new adaptive units originating directly in the geneplasm and slowly evolving into important functional service." Hence aristogenesis (first known under the term "definite variation," then as "rectigradation") "is a creative process from the geneplasm of entirely new germinal biomechanisms; the process is continuous, gradual, direct, definite in the direction of future adaptation."

In time contrast to alloiometrons (that is, changes of proportion or intensity which may be expressed in measurements and indices, and which appear to be immediate and more or less temporal adaptive reactions to new habits), aristogenes are secular, appearing very slowly in the course of long periods of geologic time. Lines of ordinal, family, generic and specific descent may be distinguished by the potentiality of certain new geneplasmic aristogenes. (Modified from Osborn, 1934.922, pp. 202, 210.)

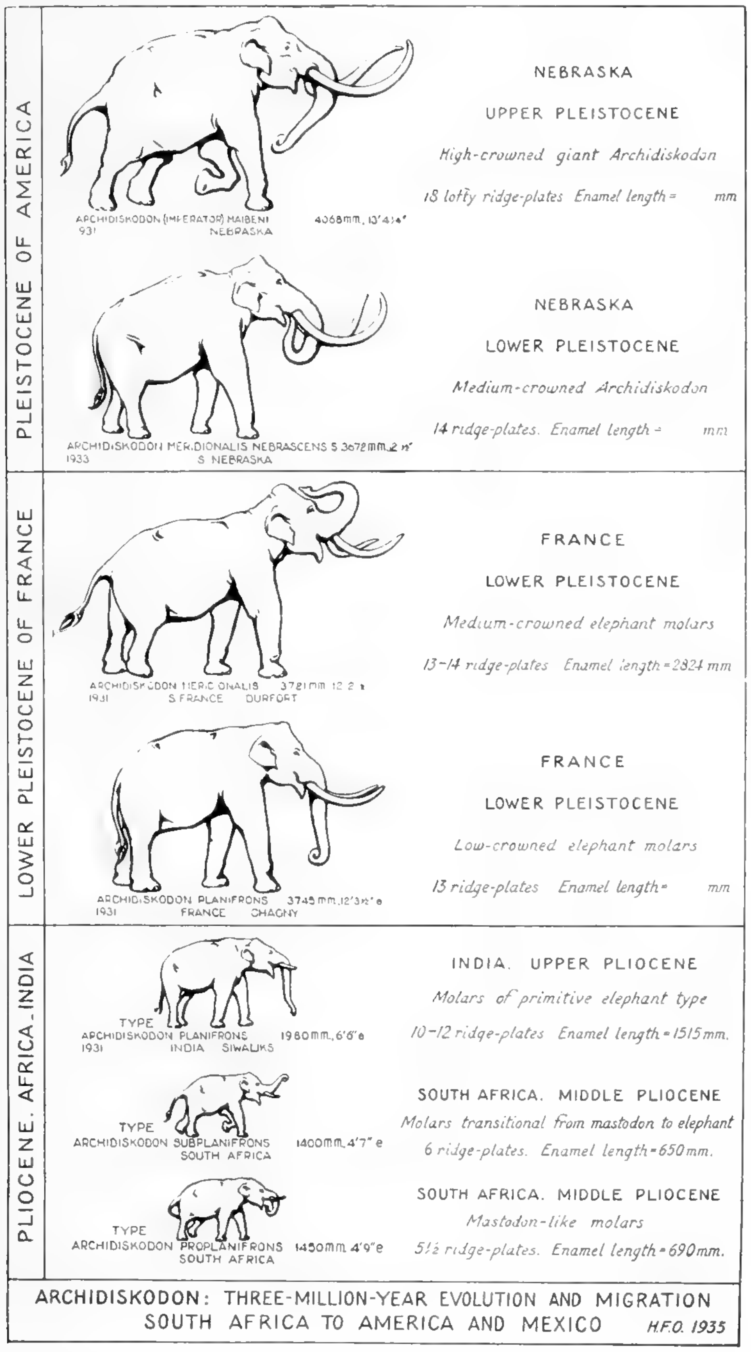

Fig. 1239. Geneplasmic evolution of the archaic-toothed mammoths during a three-million-year period so far as known to April, 1935.

Twenty-seven years of continuous exploration and research yielded all the ascending stages in the geneplasm of this archaic-toothed mammoth. After Osborn, 1938.1, fig. 11.

For example, compare Osborn, *op. cit.*, p. 221: "In the elephantoid division the low transverse ridge-crest is perfected in the upper Pliocene of the African ancestral elephants (*Archidiskodon*). The unique aristogenic

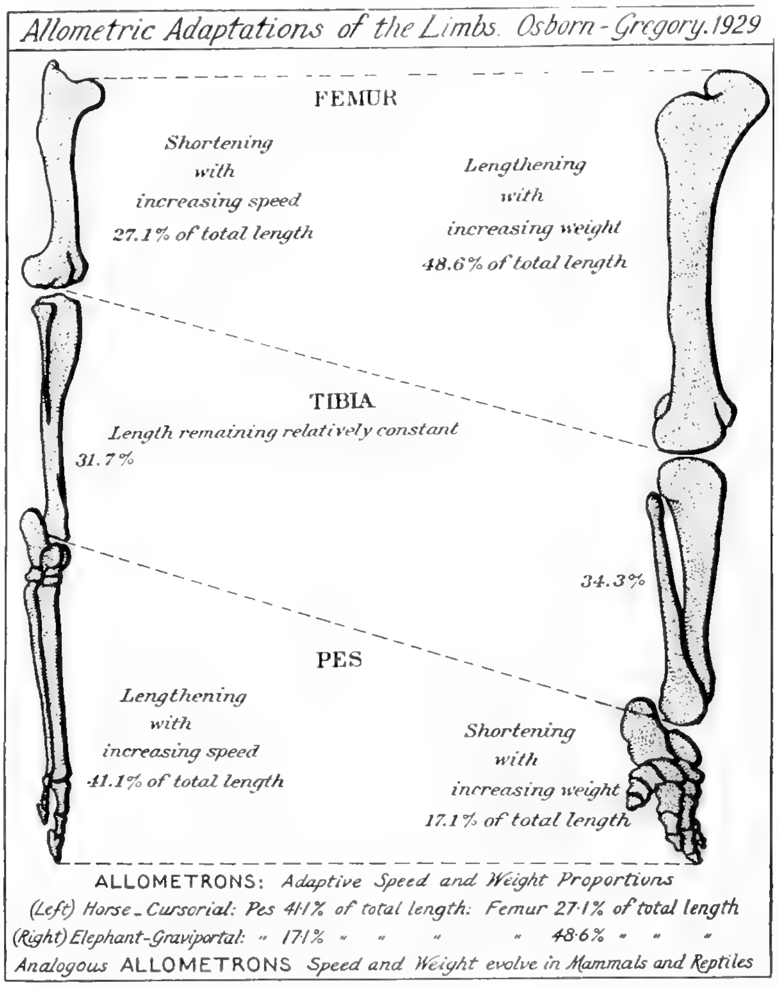

Fig. 1240. (Left) *Equus*: Alloiometrons of speed; (Right) *Elephas*: Alloiometrons of weight. After Osborn, 1938.1, fig. 6.

Abbreviating femur of the horse, 27.1 % of total length.
Elongating femur of the elephant, 48.6 % of total length.
Tibia of the horse relatively constant, 31.7 % of total length.
Tibia of the elephant relatively constant, 34.3 % of total length.
Elongating pes of the horse, 41.1 % of total length.
Abbreviating pes of the elephant, 17.1 % of total length.

Similar cursorial alloiometrons evolve in all quadrupeds attaining speed, irrespective of phyletic relationship. Similar graviportal alloiometrons evolve in quadrupeds irrespective of mammalian (Proboscidea) or reptilian (Sauropoda) affinity.

potentiality of the transverse ridge-crests to convert pairs of cones by transverse binary fission into transverse ridges is followed by the elevation of these ridge-crests into the elephantine ridge-plates, as first manifested in the roof-toothed *Stegodon* of southern Eurasia. It is paralleled in the distinct *Archidiskodon* ridge-plated stock of the upper Pliocene of South Africa. This dark continent gave rise to the world dominant elephantoid division of the Proboscidea . . . Aristogenesis combined with alloiometric extension is carried to the biomechanical extreme in the divergently adaptive grinders of the three mammoths [*Archidiskodon, Parelephas, Mammonteus*]. The contrasts in the total length of the enamel foldings of the gigantic *Archidiskodon* (8,000 mm), of the gigantic *Parelephas* (10,000 mm), of the relatively small *Mammonteus* (6,000 mm) are coordinated with the relative intensities of their struggle for existence." To summarize, in Professor Osborn's own words (*op. cit.*, p. 234):

> In biomechanical evolution there are two distinct processes. The one, long known, consists in the alloiometric modification of existing adaptations as in changes of proportion and of function. The other, discovered in course of researches on the phylogeny of the horses, titanotheres and proboscideans, consists in the gradual geneplasmic origin of new and distinct adaptations; it is to the latter originative and creative process that the term Aristogenesis is applied. Both processes become part of the hereditary equipment of the organism.

We may now proceed to epitomize the three subfamilies embraced within the superfamily Elephantoidea, family Elephantidæ, namely, the Mammontinæ, Loxodontinæ, and Elephantinæ, in uniformity with the fifteen subfamilies of the Mastodontoidea, and the single subfamily each of the Mœritherioidea, Deinotherioidea, and Stegodontoidea.

Superfamily: ELEPHANTOIDEA Osborn, 1921. Family: ELEPHANTIDÆ Gray, 1821

Subfamily: MAMMONTINÆ Osborn, 1921[1]

Genera: *Archidiskodon* Pohlig, 1885, 1888; *Metarchidiskodon* Osborn, 1934; *Parelephas* Osborn, 1924; *Mammonteus* Camper-Osborn, 1788–1924[1]

(Cf. the present volume, Chapters XVI, XVII, and XVIII, also Pls. XXI and XXII, and Figs. 815, 822, 933, 1006, 1221–1225, 1228)

The name Mammontinæ Osborn, 1921, was substituted for Euelephantinæ Osborn, 1918, owing to the fact that the genus *Euelephas* Falconer, 1857, was invalid (see Chap. XIX, p. 1175 above). Originally this subfamily, aside from the mammoths, doubtfully included *Elephas hysudricus* of India, subsequently found to belong to the Elephantinæ, genus *Hypselephas* Osborn, because of profound cranial and dental differences. A definition of this subfamily reads as follows on page 32 of Volume I:

> Subfamily Mammontinæ (Mammoths)—Osborn, 1921.515, p. 1. Of close original affinity to the Elephantinae, including (*a*) the southern mammoths *Archidiskodon planifrons* and *A. meridionalis* of southern Eurasia, *A. imperator* of North America, all with broad-plated teeth and few crests; also (*b*) the northern mammoths which apparently include *Parelephas trogontherii* of western Europe, *P. columbi* and *P. jeffersonii* of North America, and the widespread woolly mammoth (*Mammonteus primigenius*) of the northern steppes.

Great confusion had existed for years in the determination of species of *Elephas columbi, E. imperator*, and *E. primigenius*. Superficially these three species are so similar that Cope in 1889 referred the remains of a fine skull of *Archidiskodon* from Texas to *Elephas primigenius columbi*, and the present author also saw only resemblances to *Elephas columbi* in the fine Indiana skeleton (now the type of *Parelephas jeffersonii*), whereas Hay referred the same skeleton to *Elephas primigenius*. Consequently Professor Osborn made a careful comparison of

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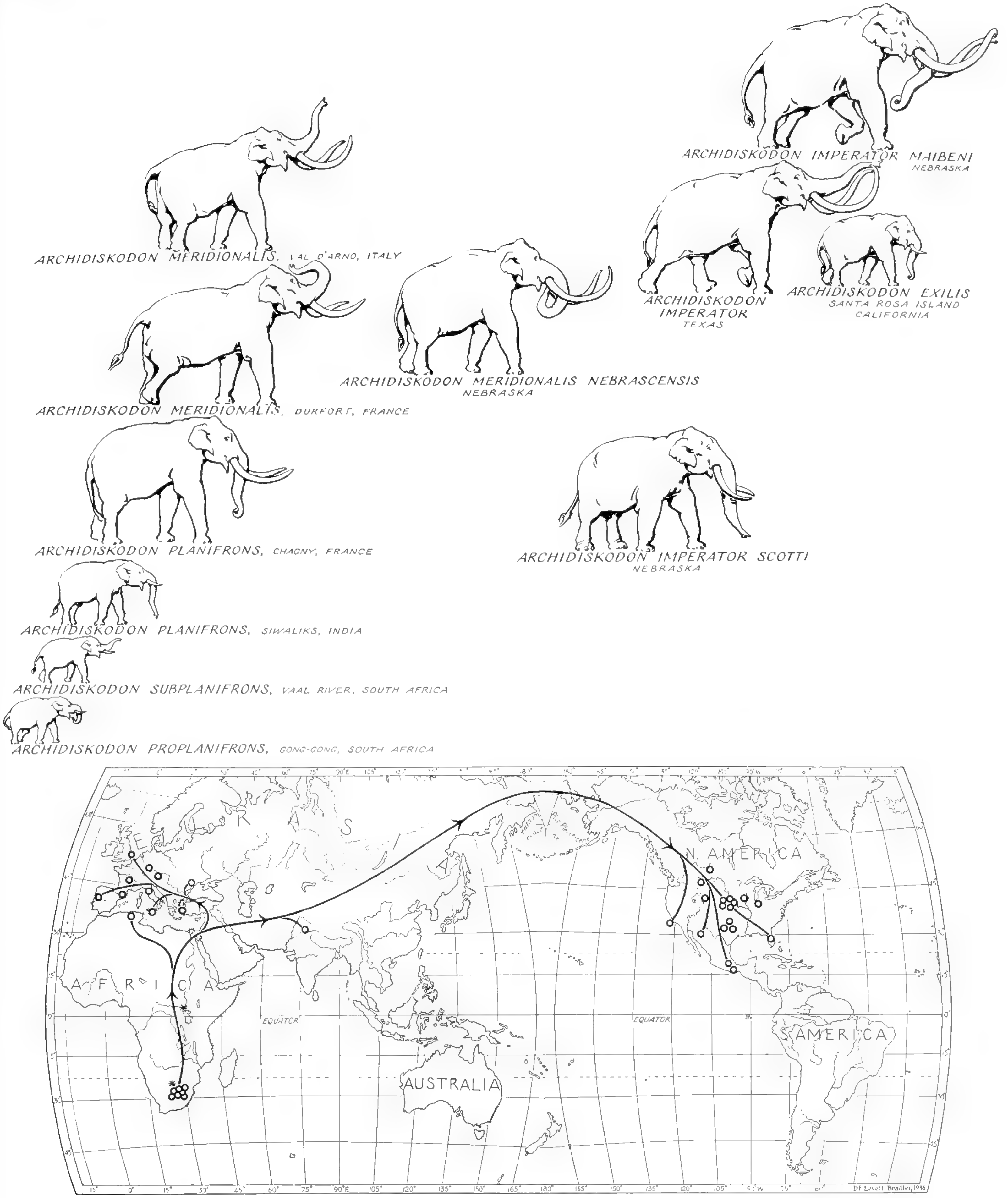
[1] [Should *Mammonteus* prove to be invalid, this would leave the subfamily Mammontinæ without a type genus.—Editor.]



Origin, Migration and Evolution of
○ Archidiskodon, * Metarchidiskodon

PLATE XXI

Geologic range: *Archidiskodon*, Middle Pliocene to Upper Pleistocene; *Metarchidiskodon*, Lower(?) Pleistocene.

both type and referred specimens of these three species, which he found were united by distinctive cranial characters but separated by various types of dental characters, resulting in their reference by him to the following genera (see his articles in Novitates, 1922.555, 1924.633, 1925.662):

Elephas columbi = *Parelephas columbi* and *P. jeffersonii*
Elephas imperator = *Archidiskodon imperator*
Elephas primigenius = *Mammonteus primigenius*

In the present Memoir the Mammontinæ embrace four genera, namely, *Archidiskodon* Pohlig, 1885, 1888, the most primitive member, with the genotypic species, *Elephas meridionalis* Nesti, 1825, of the Val d'Arno, Italy, and *E. planifrons* Falconer and Cautley, 1846 [1845] of India; *Metarchidiskodon* Osborn, 1934, genotype *Loxodonta griqua* Haughton, 1922, of the Vaal River, South Africa; *Parelephas* Osborn, 1924, genotype *Elephas jeffersonii* of Indiana, and *Mammonteus*[1] Camper-Osborn, 1788–1924, the history and outstanding characters of which are given in the following synopses.

Archidiskodon (referring to the archaic molar ridge-plates) of the southern and south temperate zones; also known as the Southern Mammoth, in reference to its remote relationship to the Northern Mammoth. Cranium foreshortened and broadened (brachycephalic), deepened (bathycephalic), heightened (hypsicephalic); through hypsicephaly, orbits and occipital condyles approximated, i.e., brachycranial (*A. meridionalis*), compressed fore and aft (cyrtocephalic), occipitofrontal apex vertically heightened (acrocephalic); far closer to *Mammonteus* and *Parelephas* than to either *Elephas* or *Loxodonta*. Nasals pointed. Forehead flattened (*A. planifrons*), concave (*A. meridionalis, A. imperator*). Mandible short; prolongation and beaklike depression of the symphysis (*A. planifrons*); without beak, blunt, obtuse (adult male *A. meridionalis*—*fide* Depéret and Mayet, 1923, p. 156); relatively long and shallow (*A. hayi*); symphysis prominent, ramus relatively slender (primitive stage). Superior tusks large (max. 13+ to 16+ feet in length), incurved, crossing in old males; no inferior tusks. Molars short, subhypsodont; subloxodont in primitive species; ridge-plates extremely broad, widely separated, enamel borders thickened, more or less crenulate; cement usually very thick; *A. planifrons* without cement outer coating. Ridge-plate formula slowly progressive from M 3^{6} (*A. proplanifrons*), to M $3\,\frac{10+}{11+}$ (*A. planifrons*), to M $3\frac{13}{13\text{-}14}$ (*A. meridionalis*), to M $3\frac{17\text{-}18}{18\text{-}20}$ (*A. imperator*); succession of premolars, P 4, P 4 (*A. planifrons*).

Dental formula (*A. planifrons*): I $\frac{0\text{-}2\text{-}0}{}$ Dp $\frac{2\text{-}4}{2\text{-}4}$ P $\frac{3\text{-}4}{3\text{-}4}$ M $\frac{1\text{-}3}{1\text{-}3}$. This premolar succession does not occur, so far as known, in any other species of the Elephantidæ.

Ridge-plate formula (*A. planifrons*): Dp 2^{4} Dp $3\frac{6+}{6+}$ P $3\frac{?}{?}$ P $4\frac{+3+}{}$ Dp $4\frac{6+}{7+}$ M $1\frac{7+}{7+}$ M $2\frac{8}{9}$ M $3\frac{10+}{11+}$

HORIZON.—Middle Pliocene to Upper Pleistocene. Compare this chapter, p. 1540, and figures 1221, 1224, 1239, also Pl. XXI.

Dr. Hans Pohlig, to the best of our knowledge, was the first to assign the name Archidiskodonten to elephant molars with archetypal ridge-plates, specifying *Elephas planifrons* Falconer and Cautley, 1846 [1845], and *E. meridionalis* Nesti, 1825, as types. This was in 1885. Subsequently (1888, p. 138) he supplemented his description, giving *E. meridionalis* only as the type, and on page 252 concluded with the introduction of three new generic names—*Archidiskodon*, *Polydiskodon*, and *Loxo(-disko)don*, of which Professor Osborn accepted *Archidiskodon* only as valid.

The first known species of this genus, therefore, was *Elephas meridionalis* Nesti. Leidy was the first to describe (1858) an American species belonging to the genus *Archidiskodon*, namely, *Elephas imperator* from Nebraska, regarded by the present author as a direct descendant of the *E. meridionalis* of Durfort, France—the

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[1] [See Chapter XXI, pp. 1363-1367 for the history of this genus, which is of doubtful validity. Should *Mammonteus* prove to be invalid, this would leave the subfamily Mammontinæ without a type genus.—Editor.]

last Eurasian representative. A comparison of the Durfort skeleton with that of the recently discovered *Archidiskodon meridionalis nebrascensis* of Nuckolls County, Nebraska, led him to this conclusion as to lineage. In 1915 Dr. Erwin H. Barbour described *Elephas hayi*, with a jaw almost as primitive in structure as that of *E. planifrons*, and a decade after appeared his description of the gigantic *E. maibeni*, both from Nebraska.

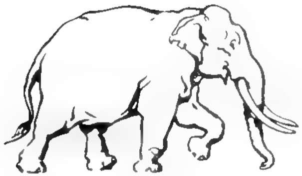
Through the courtesy of Director Wilman of the McGregor Museum at Kimberley, South Africa, two elephant's teeth were forwarded to Professor Osborn in 1926–1927 for description. Simultaneously Professor Raymond Dart described (Nature, 1927) two new species (*Archidiskodon transvaalensis* and *A. sheppardi*), which subsequently were found to belong to the genus *Palæoloxodon*. In 1928 Professor Osborn contributed an article to Nature in which he described the two molars from the McGregor Museum as *Archidiskodon subplanifrons* and *A. broomi*. Between 1929 and 1932 Professor Dart described several species from South Africa, which were reviewed by Professor Osborn in American Museum Novitates of August, 1934; certain of these species were found to be referable to *Palæoloxodon* rather than to *Archidiskodon*. In this article he described the new genus *Metarchidiskodon*, genotype *Loxodonta griqua* Haughton, 1922, also the new species *Archidiskodon proplanifrons* from Gong-Gong near the Vaal River, in his opinion the most primitive elephant tooth thus far discovered, even more primitive than *A. subplanifrons*, and indubitably an ancestral *Archidiskodon*.

MIGRATION.—The Archidiskodonts were widely distributed geographically, as will be seen from the accompanying Plate XXI, as well as from figures 815, 1228. Until the discovery of *Archidiskodon proplanifrons* and *A. subplanifrons* of South Africa, the *E.* [*Archidiskodon*] *planifrons* of India was thought to be geologically the earliest as well as the most primitive of all the members of this phylum. It is now believed that from the region of the Vaal River, South Africa, the Archidiskodonts radiated into all the continents except Australia (where up to the present time no proboscidean remains have been found) and South America. As stated above on page 1580, the 15,000-mile journey from the Vaal River, through North Africa, France, Italy, England, across to Rumania, onward to India, thence to North America (Saskatchewan, California, Montana, Wyoming, Nebraska, Kansas, Oklahoma, Texas, Mexico, and Florida) is one of the most remarkable instances of the migration of any species of animal or plant ever recorded in the life history of the earth.

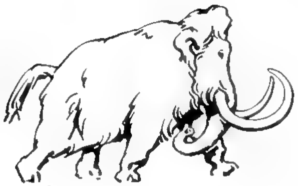
> *Metarchidiskodon*, genotype *Loxodonta griqua* Haughton, 1922, of Griqualand West, South Africa. A fragmentary molar with the following distinctive characters: Cement areas equal or exceed dentine areas; pre-sinus folds absent or inconspicuous; very prominent post-sinus folds; very deep U-shaped valleys extending to bottom of crown—a very important point; valleys filled to the summit with cement; enamel ridge-plates very deep, closely compressed with very narrow dentinal areas between.
>
> HORIZON.—Lower(?) Pleistocene. Compare this chapter, page 1540, and figures 1220, 1228, also Pl. XXI.

In reviewing the African material (see Osborn, 1934.925, p. 12) Professor Osborn observed that the fragmentary molar specimen described by Haughton in 1922 as *Loxodonta griqua* possessed characters (as enumerated above) distinguishing it not only from *Loxodonta*, but from *Archidiskodon* as well, and accordingly he made it the type of a new genus *Metarchidiskodon*. This group may also include certain relatively narrow grinders from the Val d'Arno now in the British Museum, namely, Brit. Mus. M12641 and M12642.

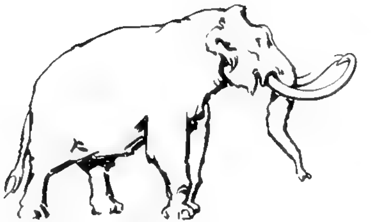
> *Parelephas*, in reference to the convergence or parallelism of the grinding teeth with those of the true *Elephas*; of the intermediate and north temperate zones. Cranium relatively broad, elongate, and rounded, intermediate in form between that of *Archidiskodon* and that of *Mammonteus*, namely, in bathycephaly and acrocephaly. Frontals concave, occipital crest elevated, occiput more or less convex, moderately compressed fore and aft (cyrtocephalic); moderately depressed molar-grinding area (bathy-



ELEPHAS INDICUS BENGALENSIS
BENGAL, INDIA



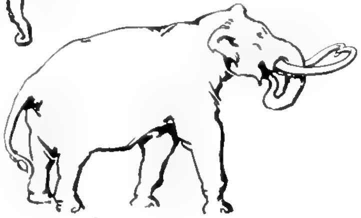
MAMMONTEUS PRIMIGENIUS
EURASIA



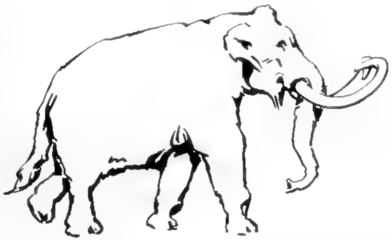
PARELEPHAS FLORIDANUS, FLORIDA

PARELEPHAS TROGONTHERII
MOSBACH, GERMANY

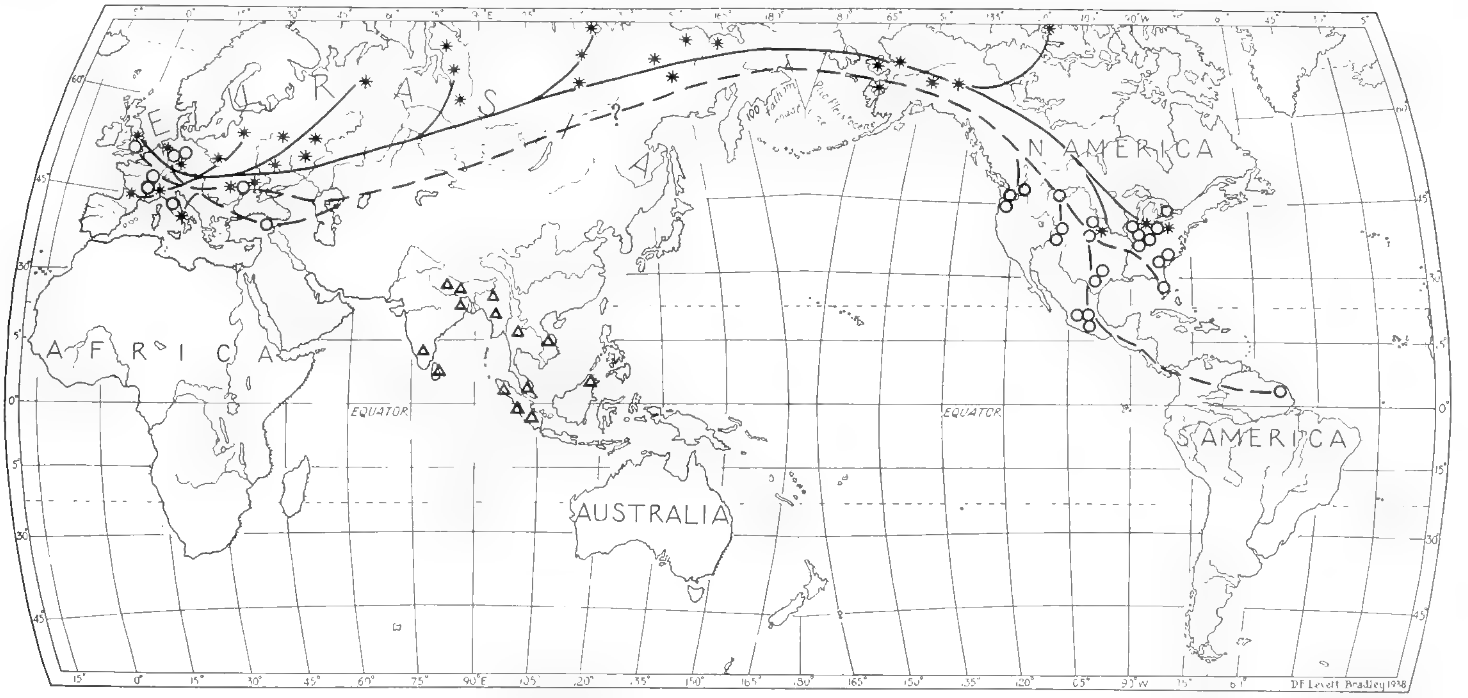
PARELEPHAS JEFFERSONII
GRANT CO., INDIANA



PARELEPHAS COLUMBI
GEORGIA



PARELEPHAS TROGONTHERII, TAUBACH, GERMANY



Origin, Migration and Evolution of
○ Parelephas, ✱ Mammonteus, △ Elephas

PLATE XXII

Geologic range: *Parelephas*, Upper(?) Pliocene [Lower(?) Pleistocene, see footnote 1 on p. 1049 above] to Upper Pleistocene. *Mammonteus*, Upper Pliocene to late Pleistocene. *Elephas*, Upper Pleistocene and Recent. Fossil representatives of the Elephantine phylum are *Hypselephas* of India (Lower Pleistocene) and *Platelephas* also of India (Upper Pliocene or Lower Pleistocene), restorations of which do not appear on the accompanying plate, nor elsewhere in this Memoir, as they were never prepared by Professor Osborn.

cephalic), space between condyle and orbit broader than in *Mammonteus primigenius*; anterior narial opening broad and widely open; divergent maxillo-premaxillary region, tusk sockets less elongate and less parallel than in *Mammonteus*. Mandible robust, short and deep (bathycephalic); ramus depressed with rounded inferior border; rostrum prominent. Superior tusks long, with remarkable incurvature, crossing in old age (*Parelephas jeffersonii*); shorter, more robust (*P. floridanus*). No inferior tusks. Molars relatively narrow as compared with those of *Archidiskodon*, with enamel of intermediate thickness, more or less crimped or sinuous. Ridge-plates arcuate, converging toward the summit; consequently the ridge-plate compression depends upon the level at which the count is taken—the count ranges in *P. jeffersonii* molars from 7 in 100 mm. (base) to 11½ (summit) in the inferior molars, from 7 (base) to 10 (summit) in the superior molars. Relatively few ridge-plates in the Upper Pliocene to Middle Pleistocene stages (M $3\frac{14+}{14+}$), progressive Upper Pleistocene stages (*P. progressus*) with multiple ridge-plates (M $3\frac{30}{26}$). Thin cement (*P. columbi*). Adapted to continental plains or steppe environment, grazing and browsing.

Dental formula: I $\frac{0\text{-}2\text{-}0}{}$ Dp $\frac{2\text{-}4}{2\text{-}4}$ M $\frac{1\text{-}3}{1\text{-}3}$
Ridge-plate formulæ:
P. columbi: Dp $2\frac{3}{3}$ Dp $3\frac{10}{}$ Dp $4\frac{}{13}$ M $1\frac{+11\frac{1}{2}}{13}$ M $2\frac{13\text{-}16}{12\frac{1}{2}}$ M $3\frac{18\text{-}19}{15\text{-}16+}$
P. jeffersonii: Dp $3\frac{8+}{}$ Dp $4\frac{12}{13}$ M $1\frac{11+}{}$ M $2\frac{18\text{-}19e}{19e}$ M $3\frac{25}{24}$

Comparative Ridge-plate Formulæ of M 3 in *Parelephas*

Parelephas progressus	M $3\frac{30}{26}$	*Parelephas columbi*	M $3\frac{19}{16+}$
Parelephas jeffersonii	M $3\frac{25}{24}$	*Parelephas intermedius*	M $3\frac{22}{20\text{-}21}$
Parelephas washingtonii	M $3\frac{23}{21}$	*Parelephas trogontherii*	M $3\frac{15+}{16+}$
Parelephas floridanus	M $3\frac{22+}{21\text{-}22}$	*Parelephas trogontherioides*	M $3\frac{\frac{1}{2}\text{-}14\text{-}\frac{1}{2}}{\frac{1}{2}\text{-}14\text{-}\frac{1}{2}}$

HORIZON.—Upper(?) Pliocene [Lower(?) Pleistocene, see footnote 1 on p. 1049 above] to Upper Pleistocene. Compare p. 1540, also figures 1222, 1224, 1225, and Pl. XXII.

Professor Osborn introduces his chapter on *Parelephas* (Chap. XVII) with the following statement:

> . . . it appears that *Parelephas* is linked with *Archidiskodon* and *Mammonteus* in its cranial resemblances and great incurved incisive tusks, while in its grinding teeth and ridge-plate formulæ it is so nearly intermediate between these two genera as to have been mistaken for an actual connecting link. In the present chapter [XVII] it is shown to be an entirely distinct generic phylum which during the more temperate interglacial periods . . . occupied the same geographic range as that of the true woolly mammoth (*Mammonteus*) during the glacial periods. [Compare Fig. 1241, below.]

While not sufficiently distinctive to preclude the subfamily unity of these three genera, there are certain cranial differences, such as the intensification of characters like hypsicephaly, bathycephaly, and acrocephaly. Their dental diversification, however, definitely separates them generically, for example, the broad, widely separated, thickly enamelled ridge-plates of *Archidiskodon*, as compared with the relatively narrow, more compressed and less thickly enamelled ridge-plates of *Parelephas*, and the narrow, extremely compressed, thinly enamelled, hypsodont ridge-plates of *Mammonteus*; also the multiplication of the ridge-plates of M 3, which in *Archidiskodon* increase from $\frac{10+}{11+}$ to $\frac{17\text{-}18}{18\text{-}20}$ and in *Mammonteus* from $\frac{19\text{-}20}{19\text{-}20}$ to $\frac{27}{?27}$, whereas in *Parelephas* the increment is from $\frac{\frac{1}{2}\text{-}14\text{-}\frac{1}{2}}{\frac{1}{2}\text{-}14\text{-}\frac{1}{2}}$ to $\frac{30}{26}$. It should also be stressed that, contrary to the normal ridge-plate structure, the superior count generally exceeds that of the inferior in *Parelephas*.

The principal characters by which *Parelephas* crania may be distinguished from *Mammonteus* crania are summarized by Professor Osborn (Chap. XVII, p. 1051) as follows:

> (1) In frontal aspect the crania of *Parelephas* are relatively broader, more spreading, and more brachycephalic than those of *Mammonteus*, which are deeper and more bathycephalic; (2) in lateral aspect (a) the orbit is more widely separated from the occipital condyle, (b) the occiput is much more convex, thus throwing the occipitoparietal apex farther forward, (c) the height from the occipital apex to the superior molar crowns is less deep, i.e., less bathycephalic, (d) the apex formed at the summit of the cranium is less acute, (e) the facial front is shorter and more deeply concave, (f) the maxillo-premaxillary sockets are less

vertical and the tusks emerge in a less vertical plane; (3) in frontal aspect (a) the premaxillary sockets are more expanded at the extremities, whereas in *Mammonteus* they are more elongate and more closely compressed, (b) the transverse diameter of the frontals is relatively broader than in *Mammonteus,* (c) the anterior nares are proportionately broader transversely and less deepened vertically; (4) in brief, the proportions of the cranium of *Parelephas* throughout are harmonious with those of the grinding teeth, i.e., less compressed anteroposteriorly, less bathycephalic and less hypsicephalic than those of *Mammonteus.*

This section would not be complete without some mention of Professor Osborn's clarification of the phyletic position of the true "*Elephas*" *columbi* of Falconer, 1857, from Georgia, and his own "*Elephas*" [*Parelephas*] *jeffersonii* from Indiana described in 1922. Falconer believed *E. columbi* to be identical with Leidy's *E.* [*Archidiskodon*] *imperator,* and the present author for several years treated it under the genus *Archidiskodon* but as a species quite distinct from *imperator.* Falconer was in error, as the two species are distinct, which will be seen by the following comparison; moreover, according to the views of Professor Osborn, they were not geologically contemporaneous, although the late Doctor Gidley [and many others] believed otherwise.

Elephas [=*Parelephas*] *columbi* Falconer, 1857–1868. Upper Pleistocene of southern United States and of Mexico. Smaller animal, with narrower grinders (Fig. 887), thin cement outer coating; maximum ridge-plate formula, M 3 $\frac{18\text{-}19}{15\text{-}16+}$. Enamel ridge-plates arcuate, converging at summit, giving the appearance in extremely worn grinding teeth of being as far apart in mid-section as in *A. imperator.*

Elephas [=*Archidiskodon*] *imperator* Leidy, 1858. Lower [Early and Middle Pleistocene, *fide* Lugn and Schultz, 1934, pp. 373–376] of southern United States and of Mexico. Larger animal in size, with broader grinders (Fig. 887), very broad enamel plates, and heavy cement outer coating; ridge-plate formula, M 3$\frac{17\text{-}18}{18\text{-}20}$. Enamel ridge-plates widely separated.

The present author was long misled by the widely separated ridge-plates seen in the types of both *Elephas columbi* and *E. imperator*, but with the opportunity for further study through the acquisition of new and rich materials from Florida and the phosphate beds of South Carolina, he perceived that the type of *E. columbi* belonged within the phylum *Parelephas.*

Again, the type of the true *Elephas* [*Parelephas*] *columbi* of Georgia, Florida, and South Carolina must not be confused with the *Elephas* [*Parelephas*] *jeffersonii* of the northern states, from which it is separable in its much more primitive ridge formula. The species *E. jeffersonii* first described by Professor Osborn in 1922 (Osborn, 1922.555, pp. 11–16) was based on a skeleton from Indiana referred to "*Elephas columbi*" by Cope and by Osborn, and to *E. primigenius* by Hay. In his description he gave the distinctive characters of the grinding teeth of each of the species *E. imperator*, *E. columbi*, and *E. primigenius*, remarking that these diagnoses left without a name the animal which previously had been described in all the literature (excepting Soergel's Memoir of 1921) as *Elephas columbi.* Unfortunately in his original description of *E. jeffersonii* Professor Osborn chose as paratypes a pair of upper and lower molars of both sides from Zanesville, Ohio, described by Warren in 1855 as *Elephas* "*primigenius,*" which he finally made the type of a new subspecies, *Parelephas jeffersonii progressus*, because of the large number of ridge-plates, namely, M 3^{30}_{26}. In the meantime the molars of the aged type specimen from Indiana were cut out of the jaw and sectioned, yielding a ridge-plate formula of M 3^{25}_{24}, still a much higher ridge-plate count than that of the true "*Elephas columbi,*" namely, M 3^{19}_{16+}. After the establishment, therefore, of *Elephas jeffersonii* as a species distinct from *E. columbi* and from *E. primigenius*, Professor Osborn (1924.633, p. 4) reached the conclusion that this species could be placed neither in the phylum of *Archidiskodon* nor in the phylum of *Mammonteus*; consequently he selected it as the type of a new genus, *Parelephas.*

In summation, *Elephas columbi* of Falconer, with a ridge-plate formula in M 3 of $^{19}_{16+}$ and an average specific ridge-plate frequency of 5–6½ in 100 mm., as compared with 7–9 (max. 11½) in *E. jeffersonii*, 5–7 in *E. imperator*, and 8–13 in *E. primigenius*, is to be regarded as a distinct species of *Parelephas*, namely, *P. columbi*;[1] *E. columbi* (previously described as the Columbian Mammoth) is now to be known as *Parelephas jeffersonii* or the Jeffersonian Mammoth. The skeleton from Brevard County, near Melbourne, Florida, now in the Amherst Museum, belongs to the true *Parelephas columbi*.

MIGRATION.—A very careful comparison of all the known characters of the *Elephas trogontherii* phylum of Europe and the *Elephas jeffersonii* of America, especially the cranial characters, established their close phyletic relationship, justifying the linking of the European and American species in the new and distinct genus *Parelephas*. The low ridge-plate formula of the true *Parelephas columbi* of Georgia and South Carolina suggested to Professor Osborn the possibility of the early geologic entrance into America of relatively primitive species of *Parelephas*, a theory which is supported by the primitive character of the lower jaw of *P. washingtonii* of Whitman County, state of Washington, the molar ridge-plate formula of which agrees quite closely with that of *P. intermedius* of southern France. Hence the evidence appears to indicate that the ancestors of *P. columbi* and of *P. washingtonii* may have passed across Europe and Asia[2] and migrated far southward in North America during the *2d* and even possibly during the *1st Interglacial* period, following the wave of migration into America of *Archidiskodon*. Professor Osborn was sanguine of the discovery (probably in northern Africa) of an ancestral stage more primitive than the *Parelephas trogontherioides* of the Upper Pliocene[3] of Italy. It will be noted from the accompanying Plate XXII that members of this *Parelephas* phylum are recorded from France, Italy, England, Germany, southern Russia, Asia Minor, Canada (Ontario), United States (Washington, Oregon, Montana, Colorado, Iowa, Kansas, Nebraska, Indiana, Illinois, Ohio, Kentucky, South Carolina, Texas), Mexico, and French Guiana—the only representative of the Elephantidæ that succeeded in reaching the South American continent, as far as we know at the present time. Thus we have an elephant phylogeny and migration second only to that of *Archidiskodon*.

> *Mammonteus*, the Northern or Woolly Mammoth, of the northerly and circumpolar zones. Cranium related to that of *Archidiskodon* and of *Parelephas*, with fore-and-aft compression, resulting in bathycephaly and hypsicephaly, which exceeds by far that of any other proboscidean or other mammalian skull known. Frontals concave, occipital crest greatly elevated, occiput slightly convex. Mandible with excessively short, deeply depressed ramus, terminating in a deflected and extremely narrow rostrum—in short, harmonic with the extreme hypsicephaly and bathycephaly of the cranium. Elevation of coronoid and of mandibular condyle. Anterior nares small. Superior tusks of large proportions, greatly incurved, crossing in old age; vertically placed tubular maxillo-premaxillary insertions of tusks, which are relatively longer, narrower, and deeper than those of any species of *Parelephas*. No inferior tusks. Molars with relatively numerous ridge-plates (polydiskodonty), Upper Pliocene stage (*Mammonteus primigenius astensis*), M $3\frac{19\text{-}20}{19\text{-}20}$; typical Upper Pleistocene stage (*M. primigenius*), M $3\frac{24}{24}$; final progressive stage (*M. primigenius compressus*), M $3\frac{27}{?27}$; broad, hypsodont, with enamel ridge-plates of minimum thickness, more or less crimped or sinuous, in fact, M 3 is the broadest and deepest proboscidean molar known (*compressus*). Ridge-plates compressed in typical superior molars to 10–11–12 in 100 mm., in highly progressive superior molars 13 in 100 mm.; in progressive inferior molars 8–9–10 in 100 mm. As in *Parelephas*, the molars are arcuate at base, more compressed at summit, consequently the ridge-plate count varies and as a rule should be taken at mid-section, both on the internal and external sides. Manus pentadactyl with five digital nails (*fide* Herz, 1902), manus and pes tetradactyl not pentadactyl (*fide* Salensky,[4] 1904, p. 86); four digits (*fide* Pfizenmayer, 1926, p. 239); total phalanges in

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[1] [Professor Osborn remarks (Osborn, 1930.837, p. 17): "It is not improbable that certain of the specimens found in Florida which hitherto have been referred to *Parelephas columbi* with its limited ridge formula, M $3\frac{19}{16+}$, actually belong nearer to *P. floridanus* stage with its more progressive ridge formula, M $3\frac{22+}{21+}$."—Editor.]

[2] [*Parelephas trogontherii* is reported by Tokunaga (Amer. Mus. Novitates, 1933, No. 627, p. 2) as occurring at Honshu (Kazusa, Mikawa, Omi, Shinano), Inland Sea, Japan. See figure 1223 in Chapter XXII above, by Dr. Edwin H. Colbert.—Editor.]

[3] [Possibly Lower Pleistocene, see footnote 1 on p. 1049 above.—Editor.]

[4] [See Zalensky, Vladimir Vladimirovich, in Bibliography of Volume I of the present Memoir.—Editor.]

each foot reduced to nine in number, e.g., $\frac{0\ 2\ 3\ 2\ 2\ \text{Phalanges.}}{0\ \text{II}\ \text{III}\ \text{IV}\ \text{V}\ \text{Digits.}}$ Dietrich (1912) records five digits in the manus and pes of the large and more primitive Upper(?) Pleistocene *M. primigenius fraasi.* Tail abbreviate, caudals 21.

Dental formula: I $\frac{0\text{-}2\text{-}0}{}$ Dp $\frac{2\text{-}4}{2\text{-}4}$ M $\frac{1\text{-}3}{1\text{-}3}$
Ridge-plate formula: Dp $2\frac{4}{4}$ Dp $3\frac{8}{8}$ Dp $4\frac{12}{12}$ M $1\frac{12}{12}$ M $2\frac{16}{16}$ M $3\frac{24}{24}$ (typical *M. primigenius*)
HORIZON.—Upper(?) Pliocene [?Lower Pleistocene] to late Pleistocene. Compare page 1541 of the present volume.

The true mammoth is the only extinct proboscidean of which the characters of the soft parts and of the hairy and woolly covering, as well as the nature of the food (with the exception of the *Mastodon*), are fully known. It is probable that these northerly or woolly mammoths were the first mammalian fossils of northern Eurasia to be discovered and recognized as extinct; the earliest descriptions are naturally lost in obscurity. The typical or true mammoth was found in Siberia long before it was recognized in western Europe. Blumenbach had in mind both Siberian and North German specimens in defining *Elephas primigenius* in 1799, also Cuvier had the Siberian mammoth in mind in defining *Elephas mammonteus* (1796 MS., 1799). Out of a host of names applied to the northern mammoth between the years 1696 and 1888, the species *Elephas primigenius* of Blumenbach alone survives and is accepted in the scientific literature of the entire world. As to the genus, nearly a century and a half of research since 1799 "demonstrates that the woolly mammoth belongs not to *Elephas,* but to a genus of its own, distinct by all the canons of nomenclature from the true modern *Elephas.*" In choosing, therefore, a new generic name for *E. primigenius,* Professor Osborn had under consideration the *Dicyclotherium* of Geoffroy, 1837, the *Cheirolites* of von Meyer, 1848, and the *Synodontherium* of Costa, 1850, also the *Polydiskodon* of Pohlig, 1888, which he regarded as the first really appropriate name. He selected, however, the name *Mammonteus* (see Osborn, 1924.633, p. 2), a term which he considered as most appropriate and as antedating the generic names just mentioned, but unfortunately this term was used by Camper in 1788 in an adjectival sense (*Mammonteum*) and applied to the remains of a Mastodon and not to a Mammoth. For a history of the nomenclature of this name and the substitution by Dr. A. Tindell Hopwood of the term *Mammuthus* Burnett, 1830, type *Mammuthus Borealis,* see pages 1363 to 1367 of Chapter XXI above.

The characters differentiating *Mammonteus* from *Archidiskodon* and *Parelephas* are given on the immediately preceding pages and are also observable by comparing the diagnoses accompanying these three genera, therefore they need not be repeated here. *Mammonteus,* in a word, is the most acrocephalic, hypsicephalic, bathycephalic, and cyrtocephalic of the Mammontines, with the greatest molar compression and an extremely high ridge-plate formula; also the contour of the body is distinctive, especially in the sloping hind quarters and the sharp notch behind the peaked skull, features brought out even in the drawings of Palæolithic age.

MIGRATION.—The geographic distribution of the Northern or Woolly Mammoth has proven to be a most difficult task, owing to the confusion that has existed in the separation of *Elephas* [*Mammonteus*] *primigenius* from *E.* [*Parelephas*] *trogontherii* and *P. jeffersonii* in the previous records (see pp. 1041, 1133, 1138, 1140); in fact, all the Pleistocene mammoths of western Europe and North America, including all the species of *Parelephas* as well as all the primitive and geologically ancient species and subspecies of the true mammoth, have been attributed, or referred, to the typical species *Elephas primigenius.* The ancestral relationship to *Mammonteus* of the Upper Pliocene [?Lower Pleistocene] *Mammonteus primigenius astensis* of Italy is problematic, as it shares characters of both *Mammonteus* and *Parelephas*; its ridge-plate formula, however, is higher (M $3\frac{19\text{-}20}{19\text{-}20}$) than that of the contemporary *Parelephas* species *P. trogontherioides* (M $3\frac{\frac{1}{2}\text{-}14\text{-}\frac{1}{2}}{\frac{1}{2}\text{-}14\text{-}\frac{1}{2}}$). "There can be no doubt," as stated by Professor Osborn, "that during late Pleistocene (IV GLACIAL and Postglacial) time there existed all over northern

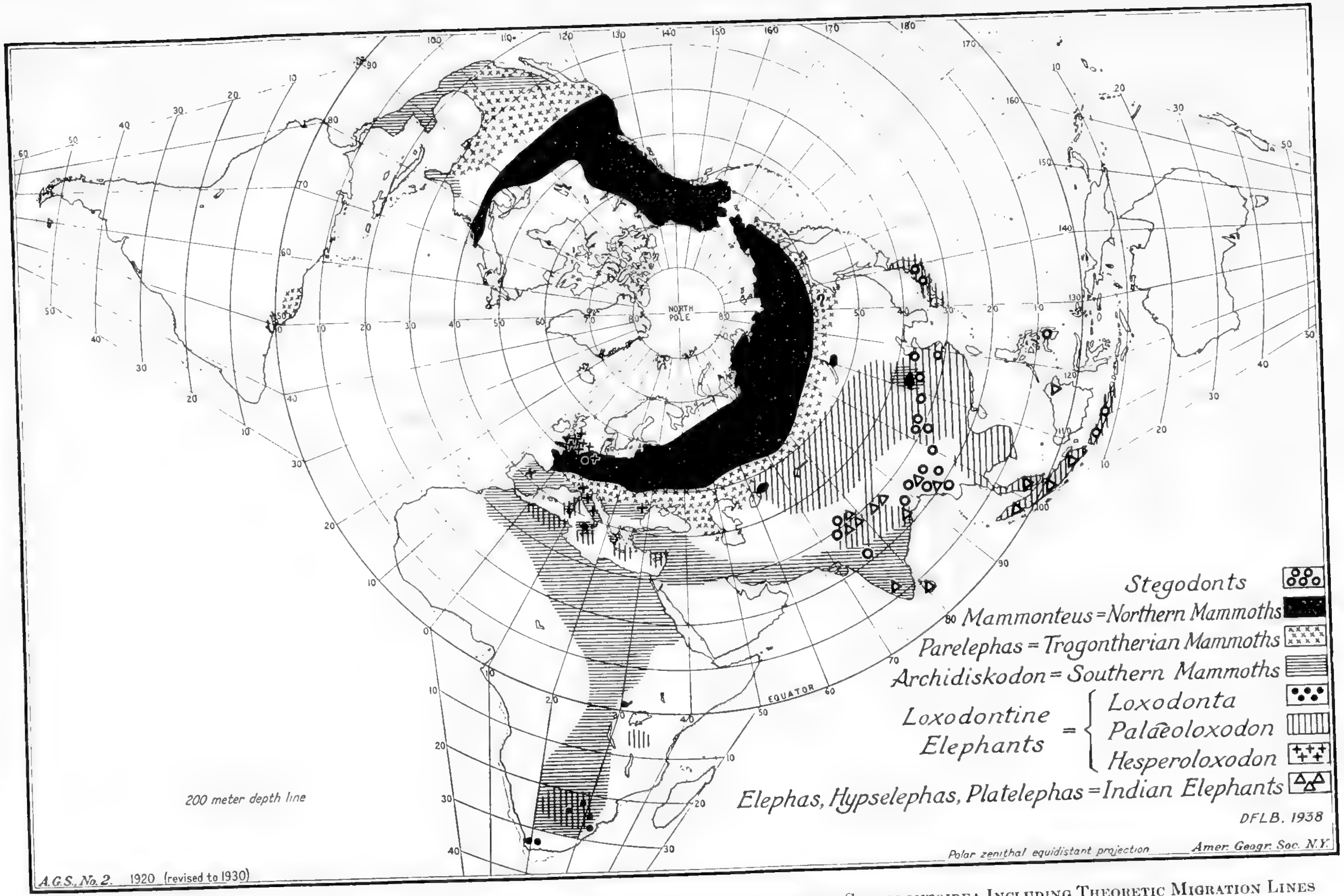


FIG. 1241. GENERAL CLIMATIC DISTRIBUTION OF THE SUBFAMILIES OF THE ELEPHANTOIDEA AND STEGODONTOIDEA INCLUDING THEORETIC MIGRATION LINES
North Polar projection prepared by the American Geographical Society in 1924

1. THE STEGODONTS (*Stegodon*): Southern and Eastern Asia, Japan, and the East Indies.
2. THE SOUTHERN MAMMOTHS (*Archidiskodon*): Africa, Southern Europe, England, Southern Asia, the United States, and Mexico.
3. THE NORTHERN MAMMOTHS (*Mammonteus*): Circumpolar distribution extending southward to the 40th parallel in late Pleistocene times.
4. TROGONTHERIAN MAMMOTHS (*Parelephas*): Southern and Eastern Europe, the United States, and Mexico; elsewhere theoretic (?) migration lines.
5. THE LOXODONTINE ELEPHANTS (*Loxodonta, Palæoloxodon, Hesperoloxodon*): Southern Europe, Asia, and the continent of Africa. See figure 1242 for living African elephants.
6. INDIAN ELEPHANTS (*Elephas, Hypselephas, Platelephas*), recent and fossil: Southern Asia and the East Indies. See figure 1242 for living Indian elephants.

Eurasia a single species of mammoth to which the name *Mammonteus primigenius* has been assigned, since it furnished the type to which the earliest as well as the original and later descriptions were applicable."

The accompanying plate (Pl. XXII) also figures 1228 and 1241 are of necessity theoretical, but they have been prepared with the utmost care, and only with a view to expressing Professor Osborn's latest determinations. It will be observed that the woolly mammoth ranged from Lat. 45° (northern France) to 75° (New Siberian Islands), according to Tolmachoff and Depéret and Mayet; in the Western Hemisphere from the 40th parallel (New York State on the east) to the western coast, northward to the 70th parallel (Melville Island, *fide* Sternberg) and Alaska.

Superfamily: ELEPHANTOIDEA Osborn, 1921. Family: ELEPHANTIDÆ Gray, 1821

Subfamily: LOXODONTINÆ Osborn, 1918

Genera: *Loxodonta* F. Cuvier, 1825, 1827; *Palæoloxodon* Matsumoto, 1924; *Hesperoloxodon* Osborn, 1931

Subgenera: *Sivalikia* Osborn, 1924; *Pilgrimia* Osborn, 1924, now regarded as synonyms of *Palæoloxodon*

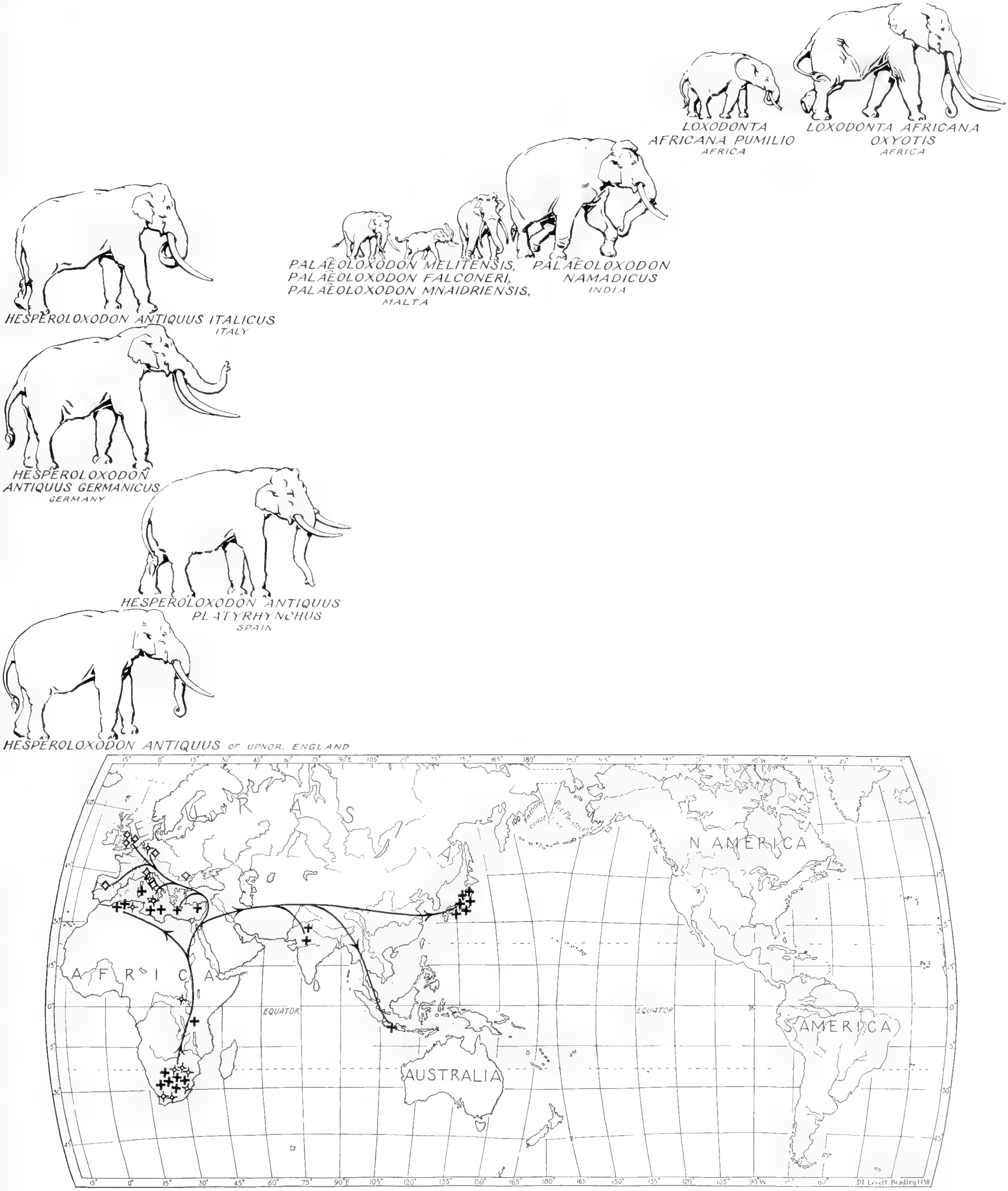
(Cf. Vol. I, Pls. X, XI, also Chap. XIX of the present volume, Figs. 1220–1223, 1228, and Pl. XXIII)

The subfamily Loxodontinæ (embracing three genera—*Loxodonta, Palæoloxodon*, and *Hesperoloxodon*), like the Elephantinæ, is distinctive in that certain of its members survive to the present day, namely, the *Loxodonta africana* of the African continent, the ancestry of which, in the opinion of the present author, is still in doubt, as will be seen by the following quotation from page 1273 above: "*L. africana* cannot be descended from any known typical species of *Palæoloxodon* but may have sprung from a more primitive ancestral form still to be discovered." While the *Loxodonta zulu* of Scott, 1907, and the recently described species of Dart (*Loxodonta prima*, 1929, *L. subantiqua*, 1929, and *L. africana obliqua*, 1932) may prove to be ancestral to the living African elephants, Professor Osborn was cautious in expressing his views on the subject (Osborn, 1934.925, pp. 7 and 6): "These occur only on the more recent levels and are clearly related to the existing African elephant, distinguished by the above [following] characters."

Loxodonta prima group

Crowns relatively narrow, 74 mm. (*L. prima*) to 92 mm. (*L. subantiqua*). Enamel relatively thin, coarsely crimped; conelets numerous. Cement thin in middle, thick at edge. Ridge plates per 100 mm. =4 (*L. africana obliqua*) to 5½ (*L. subantiqua*). Broad typical loxodont sinus expansion, double sinus foldings in contact. Total ridge plates 9 (*L. prima*) to 12–13 (*L. zulu*).

In Doctor Dart's description, however, of *Loxodonta prima* in 1929 (pp. 724–726) he states: "The outstanding character of this tooth (Figs. 25, 26 [Fig. 1149 of the present Memoir]) is its comparability with the living African species. It provides the first indubitable fossil evidence of a very close approximation to the distinctive lozenge-shaped lamellae of the living Loxodont grinding tooth. The absence of such a fossil type up to the present time according to Osborn 'is a striking circumstance.' . . . There can be no doubt that in this narrow-crowned, loxodont-simulating, few-plated, mountain-inhabiting specimen . . . we have a long-sought ancestral type from which the modern African elephant tooth might reasonably be derived by a progressive widening-out of the loxodont sinus, for which reason I have named it *Loxodonta prima*. This fossil is of importance not only in demonstrating an advancing, though still simple Loxodont tooth pattern in the Transvaal, but also in revealing Africa, and possibly South Africa as the evolutionary home of the true Loxodonta. Its habitat in the elevated and relatively waterless Pilandsberg suggests the possible reasons for Loxodont persistence, namely, their becoming inured to more arid conditions and more active movement, as compared with their more ponderous Archidiskodont relatives."



Origin, Migration and Evolution of
✧ Loxodonta, + Palaeoloxodon, ◇ Hesperoloxodon

PLATE XXIII

Geologic range: *Loxodonta*, Pleistocene to Recent; *Palæoloxodon*, Upper Pliocene(?) or Lower Pleistocene to Upper Pleistocene; *Hesperoloxodon*, Upper Pliocene [Lower(?) Pleistocene, see footnote 1 on p. 1049 above] to Upper Pleistocene.

Loxodonta, genotype probably the South African form *Elephas africanus* Blumenbach, 1797; the extreme South African form was distinguished by Cuvier in 1798 as *Elephas capensis*. Cranium relatively low, brachycephalic, platycephalic, mesocephalic, bathycephalic, and cyrtocephalic (foreshortened); cranial profile and section much more primitive, less hypsicephalic and bathycephalic than in the Mammontinæ or Elephantinæ; parietofrontal cranial vertex low, rounded, platycephalic to subacrocephalic, of persistent primitive form; rostrum short and extremely broad; premaxillaries diverging to the point where the tusks issue from the skull—thus the bases of the tusks are very far apart instead of being close together as in *Mammonteus*; nasals broad and rounded, narial openings hour-glass shaped; anterior position of suture separating malar from maxillary portion of zygoma. Mandibular ramus elongate; symphysis acute, relatively prominent and horizontal. Superior tusks elongate, widely divergent, relatively straight, slightly upcurved and incurved, resulting in a lyre-shaped arrangement; marked sexual disparity in tusks of females. No inferior tusks. Molars low crowned, relatively narrow and with comparatively few ridge-plates, total ridge-plates Dp 4–M 3 $\frac{32}{35}$: enamel borders thick and simple without foldings or plications: cement thin; distinguished by broadly open 'loxodont sinus' (lozenge-shaped median expansion) on wear. Ridge-plate formula constant and very conservative, since the M 3 ridge formula of the living African elephant closely corresponds with that of the primitive Upper Pliocene *Archidiskodon planifrons*.

Dental formula: I $\frac{0\text{-}2\text{-}0}{}$ Dp $\frac{2\text{-}4}{2\text{-}4}$ M $\frac{1\text{-}3}{1\text{-}3}$

Ridge-plate formula (typical): Dp $2\frac{3}{3}$ Dp $3\frac{6}{6}$ Dp $4\frac{7}{7}$ M $1\frac{7}{7}$ M $2\frac{8}{8\text{-}9}$ M 3 $\frac{10}{11\text{-}12}$

HORIZON.—Pleistocene to Recent. Compare page 1541, also figures 1220, 1222, and Pl. XXIII of the present volume.

COMPARISON OF LOXODONTA WITH THE GENERA ARCHIDISKODON, PARELEPHAS, MAMMONTEUS, AND ELEPHAS

Taking, for example, the middle-aged skull of "Jumbo," a Sudanese subspecies, we observe that "in the fully adult skull the dome is continuously rounded from the occipital condyles to the broad extremities of the nasals, presenting the widest contrast to the profiles of *Archidiskodon*, of *Parelephas*, of *Mammonteus*, and of *Elephas*; that while actually brachycephalic, the cranium of *Loxodonta* is also comparatively mesocephalic or elongate (shown in the relatively long mandibular ramus, [Fig. 1060]), as compared with the deeply depressed mandibular ramus of *Elephas indicus*, or with the extremely bathycephalic and abbreviate mandibular ramus of *Mammonteus primigenius*; that since both superior and inferior molars, M^3, M_3, are shorter and less hypsodont, the maxillary and mandibular dental cavities are much less deep, thus accounting for the less hypsicephalic proportions of this part of the skull; the superior aspect of the mandibular rami [Fig. 1060] also displays the relative prominence and horizontal distinction of the rostrum, again presenting a very wide contrast to the deep, hypsicephalic rostrum of the Mammontinæ and of the Elephantinæ"; the superior or frontal aspect of the cranium (Fig. 1061A) shows the short frontal bones, the massive orbital prominences, the broad narial openings, the widely separate maxillo-premaxillary sockets for the enormous incisive tusks, similar to those in *Palæoloxodon namadicus* and *Hesperoloxodon antiquus*. It will be observed in a comparison of the palatal aspect of the *Loxodonta* cranium with that of the *Elephas indicus* cranium (Fig. 800) that the former is relatively broader, more brachycephalic in all its dimensions (cf. Chap. XIX, p. 1200 above).

Palæoloxodon.—The origin of the Palæoloxodonts is obscure. Professor Osborn suggests on page 14 of his article in Novitates (Osborn, 1934.925) that the "problematic *A*. [=*Palæoloxodon*] *andrewsi*" of Dart, 1929, found at Gong-Gong, Vaal River, may be a "primitive or ancestral member of the *Palæoloxodon* group." In the present Memoir (cf. p. 1207 above) he also suggests that this generic phylum (which includes *Palæoloxodon* and its synonyms *Sivalikia* and *Pilgrimia*) may have sprung from the giant North African species *Elephas atlanticus* Pomel, 1879. In any event, there can be no question of its clear generic distinction from *Loxodonta*. In speaking of *Palæoloxodon* from the historic standpoint, he remarks (cf. p. 1207) that "It is not impossible that some elephants of the *Palæoloxodon* type survived into early historic times, but it is an open question whether the elephants described from Mesopotamia were of the ancient 'loxodontine' or of the modern 'elephantine' type, probably the latter: drawings and inscriptions will probably be found some day which will determine these relations." Pilgrim (1905) notes that *Elephas* [*Palæoloxodon*] *namadicus* is entirely absent from the Pliocene Siwalik strata and that there is no ancestral type from which it might arise.

> *Palæoloxodon*, genotype *Elephas namadicus naumanni* Makiyama, 1924. Cranium of genotype unknown, but compare the *Elephas* [*Palæoloxodon*] *namadicus* of Falconer and Cautley, 1846, 1847, from the Nerbudda, India, which is more hypsicephalic and bathycephalic, and relatively broader and more platycephalic than that of *Loxodonta*. Parietofrontal cranial vertex somewhat more progressive, acrocephalic, than in *Loxodonta*, with broad, smooth or rugose crest which in *Palæoloxodon namadicus* extends like a Phrygian cap down over the frontals almost to the nasals (seen also in the dwarfed *Elephas* [*Palæoloxodon*] *melitensis* and *E.* [*P.*] *mnaidriensis* of Malta). Narial openings very broad and shallow. Premaxillaries extremely broad, with widely divergent, relatively straight, slightly upcurved and incurved tusks toward the extremities. No inferior tusks. Molars moderately hypsodont; relatively narrow in primitive stages; superior molars progressively narrow to broad, with numerous ridge-plates composed of thin, plicated enamel foldings. Ridge-plates parallel, closely compressed. Loxodont sinus rudimentary or absent. Dentine areas equal or exceed cement areas by relatively close compression of the ridge-plates. Ridge-plate formula progressive from *Palæoloxodon atlanticus* ($\mathrm{M}\ 3\frac{12\text{-}?14}{12\text{-}?14}$), to *P. melitensis* ($\mathrm{M}\ 3\frac{12}{11\text{-}12}$), to *P. namadicus* ($\mathrm{M}\ 3\frac{15}{16}$), to *P. namadicus naumanni* ($\mathrm{M}\ 3\frac{19}{17}$).
>
> Dental formula: $\mathrm{I}\ \frac{0\text{-}2\text{-}0}{}\ \mathrm{Dp}\ \frac{2\text{-}4}{2\text{-}4}\ \mathrm{M}\ \frac{1\text{-}3}{1\text{-}3}$
>
> Ridge-plate formula (*fide* Falconer): $\mathrm{Dp}\ 4\frac{}{10\frac{1}{2}}\ \mathrm{M}\ 1\frac{}{\frac{1}{2}\text{-}13\text{-}\frac{1}{2}}\ \mathrm{M}\ 2\frac{}{?15}\ \mathrm{M}\ 3\frac{14\text{-}15}{15\text{-}16}$
>
> HORIZON.—Upper Pliocene(?) or Lower Pleistocene to Upper Pleistocene. Compare page 1541 of the present volume, also figures 1220–1223, also Pl. XXIII.

Sivalikia and Pilgrimia.—In 1924 both Matsumoto in Japan and the present author in America published almost simultaneously the results of their researches on the Loxodontines, neither being aware of the activities of the other. The genus *Palæoloxodon* of Matsumoto (described September 20, 1924) anticipated by three months Professor Osborn's description (December 20, 1924) of *Sivalikia* and *Pilgrimia*; hence technically it has priority over the last two genera, which become synonyms of *Palæoloxodon*. In Chapter XIX of the present Memoir Professor Osborn has explained the morphological reasons for regarding his *Sivalikia* and *Pilgrimia* as synonyms of *Palæoloxodon* Matsumoto.

Dwarfed Species of the Mediterranean Islands.—Before taking up the genus *Hesperoloxodon*, to which Professor Osborn referred members of the '*Elephas antiquus*' group, the dwarfed species of the Mediterranean Islands deserve some mention. It is interesting to note, that besides the pygmy elephants of Malta, a specimen of nearly normal size is also recorded from that island. Falconer and the older authorities related these insular species to the *Elephas antiquus* of the European continent, but subsequent discovery has shown that they are more probably derived from certain of the extinct ancestral African species described in the present Memoir as *Palæoloxodon* (syn. *Pilgrimia*); moreover, the cranium and jaw of *Elephas* [*Palæoloxodon*] *melitensis*,[1] with broadly overhanging parietofrontal crest, more closely resembles the *E.* [*Palæoloxodon*] *namadicus* of India than the *E.* [*Hesperoloxodon*] *antiquus* of western Europe. A comparison of the type grinding teeth of the dwarfed Mediterranean species with the type grinding teeth of the extinct African species reveals a striking general resemblance in the narrow proportions and in the rudiment or absence of the 'loxodont sinus,' characters which appear to relate these teeth to the *Palæoloxodon* (syn. *Pilgrimia*) of Africa rather than to the typical *Loxodonta africana* or to the broad-toothed *Palæoloxodon namadicus* of India. In Europe some of the narrow-toothed varieties of *Elephas* [*Hesperoloxodon*] *antiquus* may be related to the dwarfed insular elephants. After the discovery and description of the cranium from Pignataro Interamna, Italy, first referred by Professor Osborn to *Palæoloxodon antiquus italicus* and finally made the type of his genus *Hesperoloxodon*, he expressed himself as follows (see Chap. XIX, p. 1252): "The entire cranial and dorsal hump silhouette (Fig. 1092) is quite different from that of the African elephant (Fig. 1093)... The cranial profile of *Hesperoloxodon italicus* is also entirely different from that of *Palæoloxodon namadicus* (Fig. 1070) and of *P. melitensis*[1] (Fig. 1121), both of which are characterized by a very prominent transverse frontal ridge for the

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[1] [Subsequently (see p. 1260 above) referred by Professor Osborn to *Palæoloxodon mnaidriensis*.—Editor.]

attachment of the gigantic proboscis. . . . In both cranial and dental characters *H. italicus* differs profoundly from the African elephant, which is extremely conservative in its structure, in fact, much more conservative than any of the known fossil Pleistocene elephants of Eurasia. . . . *H. italicus* affords additional and positive evidence that the dwarfed elephants of the Mediterranean Islands (*P. falconeri*, *P. melitensis*, and *P. mnaidriensis*) were not derived from the '*Elephas antiquus*' phylum of Falconer, as hitherto universally believed, but sprang from some undiscovered phylum of elephants of African origin, which gave rise on the one hand to the dwarfed elephants of the Mediterranean Islands and on the other to the gigantic *P. namadicus* phylum of India and the Far East extending to Japan."

Thus, according to the views last expressed by Professor Osborn, we are able to make the following summary:

Elephas namadicus of India (Nerbudda), varieties and subspecies of which are abundant in Japan	= the true *Palæoloxodon* (syn. *Sivalikia* of Osborn)
Elephas atlanticus, *E. jolensis*, *E. recki*, etc. of Africa	= *Palæoloxodon* (syn. *Pilgrimia* of Osborn)
Mediterranean Island species (pigmy and normal size), possibly derived from the *Elephas atlanticus* group or the "*Elephas antiquus recki*" [= *Palæoloxodon recki*] of Dietrich. (Perhaps some of the narrow-toothed varieties of "*E. antiquus*" of Europe may be related to these dwarfed species.)	= *Palæoloxodon* (syn. *Pilgrimia* of Osborn)

Hesperoloxodon.—*Elephas antiquus* Falconer and Cautley, 1847, described one year after the naming of *E.* [*Palaeoloxodon*] *namadicus* Falconer and Cautley, 1846, is based on a molar, probably from England, although the locality is not recorded. To the best of our knowledge no complete cranium of the true *E. antiquus* has as yet been discovered, consequently the unearthing of a fine cranial specimen at Pignataro Interamna, Italy, in 1911–1912, and acquired by the American Museum of Natural History in 1929, was of signal importance. Professor Osborn immediately described the specimen, referring it first to *Palæoloxodon antiquus italicus*, but on comparing it more closely with the cranium of *P. namadicus*, he observed at once that it was more hypsicephalic and bathycephalic and that it lacked the prominent transverse frontal crest so characteristic of *P. namadicus* and *P. mnaidriensis*. On these grounds he provisionally made it the type of a new genus, *Hesperoloxodon*. Again the discovery in 1926 and 1928 at Steinheim on the Murr, Germany, of two crania referable to *Hesperoloxodon antiquus germanicus* convinced him more then ever of the distinction of the "*Elephas antiquus*" group from the *Palæoloxodon* group. Taken together, these crania furnished the basis for determining the evolutionary history and relationships of the classic *Elephas antiquus*, definitely assigned by Professor Osborn in the present Memoir to the genus *Hesperoloxodon*.

Hesperoloxodon, signifying 'loxodont of the west,' of the European continent. Cranium domelike with flattened forehead; more hypsicephalic and bathycephalic than that of *Palæoloxodon*; lacking the prominent parietofrontal crest so distinctive of *P. namadicus*. Occiput relatively narrow and high (broad and low in *P. namadicus*). Premaxillaries extremely broad, with widely divergent tusks, slightly upcurved and incurved. Mandibular rostrum abruptly truncated; symphysis wide. Molars hypsodont, 'loxodont sinus' vestigial or absent. Ridge formulæ progressive from $M\,3\,\frac{16\frac{1}{2}\text{-}17}{16\frac{1}{2}\text{-}17}$ (typical), to $M\,3\,\frac{17\text{-}19}{+18+}$ (*germanicus*), to $M\,3\,\frac{20}{18+}$ (*italicus*). Enamel plates relatively thick, more or less crimped or sinuous. Cement present.

Dental formula: $I\,\frac{0\text{-}2\text{-}0}{}\ Dp\,\frac{2\text{-}4}{2\text{-}4}\ M\,\frac{1\text{-}3}{1\text{-}3}$

Ridge-plate formula (*Hesperoloxodon antiquus*): $Dp\,2\frac{3}{3}\ Dp\,3\frac{6}{6}\ Dp\,4\frac{10}{10}\ M\,1\frac{10\text{-}12}{12}\ M\,2\,\frac{12}{12}\ M\,3\frac{16\frac{1}{2}\text{-}17}{16\frac{1}{2}\text{-}17}$

HORIZON.—Upper Pliocene[1] to Upper Pleistocene. Compare pages 1542, 1543 of the present volume, also figure 1222, and Pl. XXIII.

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[1] [Possibly Lower Pleistocene (see footnote 1 on p. 1049 above).—Editor.]

In a comparison of the crania of *Loxodonta africana*, *Palæoloxodon namadicus*, and *Hesperoloxodon antiquus*, we observe especially the following characters: Short and extremely broad rostrum; premaxillaries diverging to the point where the tusks issue from the skull thus the bases of the tusks are very far apart instead of being close together as in *Mammonteus primigenius* or relatively close as in *E. indicus*; whereas the premaxillary sockets are relatively of the same length in all three species, the divergence of the sockets in *P. namadicus* is about the same as in *L. africana*; the premaxillary sockets are relatively longer and diverge still more widely in *H. antiquus*; the crania of both *P. namadicus* and *H. antiquus* are distinguished from the cranium of *L. africana* by the greater development of the fronto-occipital crest which in *P. namadicus* engulfs the frontal bones so that there is a very short space between the lower border of this crest and the extremities of the nasals and the narial openings; the narial openings are extremely broad and shallow, they exhibit approximately the same hour-glass-shaped form in *L. africana*, *P. namadicus*, and *H. antiquus*; the skull of *P. namadicus*, moreover, is relatively broader and more flattened or platycephalic than the skull of *L. africana*; this broadening and flattening of the summit of the cranium reaches an extreme in the gigantic *P. namadicus* cranium (cf. Chap. XIX, p. 1209 above).

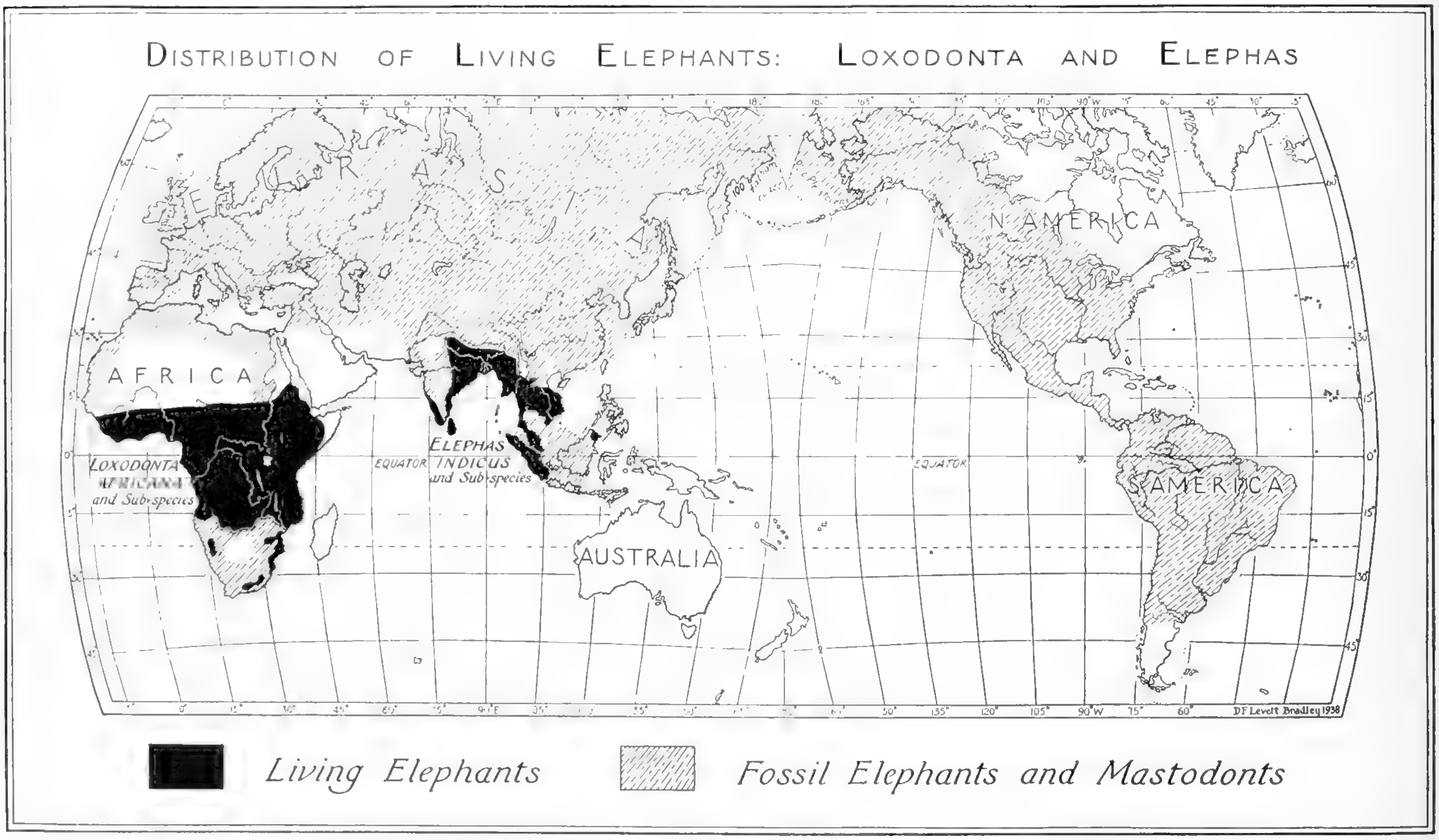


FIG. 1242. WORLDWIDE DISTRIBUTION OF THE PROBOSCIDEA IN PAST AND PRESENT TIME

This map on a larger scale constitutes the back end-paper of the present volume

AFRICAN ELEPHANT: After Blanc, 1897; Bocage, 1890; Buckley, 1876; Chapman, 1868; Chubb, 1909–1919; Claridge, 1915; Cox, 1900; Heilprin, 1887; Hippolyte, 1907; Johnston, 1907; Maydon, 1932; Roosevelt and Heller, 1914; Schultze, 1907; Sclater, 1900.

INDIAN ELEPHANT: After Bartholomew, 1911; Blanford, 1888–1891; Blyth, 1872; Bishop, 1921; Champion, 1928; Hornaday, 1885; Hunter, 1868; Jerdon, 1874; Laufer, 1925; Lydekker, 1900–1908; Sanderson, 1907; Sclater, 1899.

[Since Professor Osborn's intensive studies on the subject, recent observations by Père Teilhard de Chardin, Dr. C. C. Young, Dr. Glover Allen (letter of Dec. 24, 1938, to Dr. Pinkley), and Dr. George Pinkley have led to certain modifications of the map shown in Volume I, figure 6, namely, the area in Borneo, as well as that in southwestern China, has been reduced somewhat. See Chapter XX, p. 1362 above, for the views of Père Teilhard and Doctor Young regarding the existence in historical times of the wild Indian elephant in China.—Editor.]

MIGRATION OF THE LOXODONTINES

Loxodonta.—The eighteen existing species and subspecies or varieties of *Loxodonta africana* (partly distinguished by size, partly by geographic distribution, and partly by the shape of the ears) are found from the Cape northward to the southern border of the Sahara and the Sudan (see Fig. 1055). Fossil remains are principally of African provenance, that is, from Zululand (*L. zulu*) and the Transvaal (*L. prima*, *L. subantiqua*, and *L. obliqua*), although two or three localities in Europe have yielded types, e.g., Germany (*E. priscus* Goldfuss = *L. africana*) and Italy (*L. cornaliae*), as shown on the accompanying plate (Pl. XXIII).

Palæoloxodon.—The Palæoloxodonts, as we have just seen, are divided into two branches, (1) *Palæoloxodon* (syn. *Pilgrimia*), embracing such species as *atlanticus*, *jolensis*, and *recki* from the northern and east-central regions of Africa, and *transvaalensis*, *sheppardi*, *andrewsi*, *hanekomi*, *wilmani*, *kuhni*, *yorki*, and *archidiskodontoides* of South Africa, as well as the Mediterranean species—*melitensis*, *falconeri*, *mnaidriensis*, *lamarmorae*, *cypriotes*, and *creticus*; and (2) *Palæoloxodon* (syn. *Sivalikia*), embracing the *namadicus* of Falconer and Cautley, type locality the Nerbudda, India, the *hysudrindicus* of Java, and the various (possibly eight to ten) subspecies of Japan, represented by the genotype of *Palæoloxodon*, namely, *Elephas namadicus naumanni* Makiyama. It would appear, therefore, that the phylum *Palæoloxodon* originated in Africa, migrated northward into Europe, also northeastward, through the Mediterranean Islands, leaving dwarfed descendants resembling either the '*E. antiquus*' group or the '*E. namadicus*' group, finally arriving in southern and southeastern Asia developing into the '*Elephas namadicus*' group, thence eastward to Java and northward to Japan, but as far as we know never reaching America.

Hesperoloxodon.—Members of the '*Elephas antiquus*' group are recorded from Italy (*Hesperoloxodon antiquus nanus*, *H. antiquus ausonius*, *H. antiquus italicus*), from Spain (*H. antiquus platyrhynchus*), from England (the true *H. antiquus* especially), from Germany (represented by the *H. antiquus germanicus* of Steinheim), and from Rumania (by *H. antiquus germanicus* ref. from Ilfov). Professor Osborn states in Chapter XIX, p. 1258 that some of the narrow-toothed varieties of *Elephas* [*Hesperoloxodon*] *antiquus* in Europe may be related to the dwarfed insular elephants; and again on page 1252 he calls attention to the "lofty cranial dome" of *Hesperoloxodon antiquus italicus* which resembles that of the *Elephas indicus* of India and is in close agreement with the "Eléphant tracé en rouge" in the cavern of Pindal, also with the anterior dorsal hump of the Spanish and Algerian elephants (Fig. 1047).

Superfamily: ELEPHANTOIDEA Osborn, 1921. Family: ELEPHANTIDÆ Gray, 1821

Subfamily: ELEPHANTINÆ Osborn, 1910

Genera: *Elephas* Linnæus, 1735–1758; *Hypselephas* Osborn, 1934, 1936; *Platelephas* Osborn, 1934, 1936

(Cf. Chap. XX of present volume, also p. 1543, and figures 1173, 1221, 1228, and Pl. XXII)

The history of the elephant in art, industry, and science is fascinatingly told by Dr. George F. Kunz in his book on "Ivory and the Elephant." The early life phases, however, are so beclouded by superstition and myth that we are without positive knowledge of these interesting animals until the time of Homer. Strangely enough, also, the fossil ancestry of the living Asiatic elephant is still unknown, despite the untiring efforts of palæontologists and zoologists everywhere to solve this problem. Consequently the subfamily phylogeny of most of the elephantoids is better known than that of the Elephantinæ, or, as a matter of fact, of the Loxodontinæ, for, as noted in the preceding section, there is still uncertainty as to the ancestral forms of the living African elephant. Professor Osborn was of the opinion that "the conclusion is inevitable, that in some as yet unexplored region of

Asia the direct ancestors of *E. indicus* were slowly evolving, while in some unexplored area, probably west of central Africa, the very conservative ancestors of *L. africana* were also slowly evolving." As our knowledge stands at present, the Indian elephant suddenly appears fully formed during the Age of Man.

The nomenclatural problems in connection with the genotype of *Elephas* are no less complex. After long consideration Professor Osborn adopted *Elephas indicus* rather than *Elephas maximus* in the present Memoir, giving his reasons therefor in Chapter XX, pages 1308–1311 above.

Falconer, in his discussion of the unity or plurality of species among the existing Asiatic elephants, namely, types from Ceylon, Nepal, Bengal, and Sumatra, decided in favor of the unity of the species *Elephas indicus* (Falconer, 1868, Vol. II, p. 269): "the evidence in every aspect appears to fail in showing that the Elephant of Ceylon and Sumatra is of a species distinct from the Continental Indian form . . . The result of this range of observation, combined with long osteological study, has been to establish the conviction in my mind that there is but a single species of Asiatic Elephant at present known, modified, doubtless, according to his more northern or southern habitat, but not to an extent exceeding that of a slight geographical variety." He admits that the Ceylon elephants are occasionally imported into Bengal but does not admit, as claimed by Schlegel, that this is an explanation of the variation in the vertebral and rib formulæ of the Indian elephants. The present author expressed his belief (see p. 1315, Chap. XX above) that the "wide variations in cranial and vertebral characters as well as in dental and dermal characters and in the shape of the external ear support the subdivision of *Elephas indicus* into at least four out of the large number (12) of geographic varieties or subspecific forms," namely:

Elephas indicus ceylanicus (cf. Mukna var.)
Elephas indicus bengalensis (cf. Dauntela var.)
Elephas sumatranus
Elephas maximus hirsutus (=*E. indicus hirsutus*)

Professor Osborn left the question of the continental and insular races and subspecies for future investigation. He states on page 1329 that the "profound cranial differences which divide the Ceylon and Bengal elephants from each other as well as from the Sumatran elephant in all probability will be found to differentiate the Sumatran and other still undiscovered extinct types"; that by "comparison with the evolution of other Pleistocene ungulates it appears probable that a very long period of time separated these continental and insular subspecies and species from each other, a period of time equivalent perhaps to nearly half of Pleistocene time or 500,000 years, during which through isolation and segregation the subspecific and specific characters were thoroughly founded. Here again monographic research is essential before we can reach a final conclusion."

As to the extinct forms, it is remarkable that no fossil Pliocene ancestors of the recent Indian elephant have as yet been discovered. *Elephas hysudricus* found "below the conglomerates" in the upper Siwaliks of India, according to Dr. Barnum Brown, shows few resemblances in the cranium to the *E. indicus* (Dauntela var.) and no very marked resemblances in the grinding teeth; it appears to be unique, and in 1936 (see Vol. I, p. 12) it was made one of the types of the genus *Hypselephas* Osborn.

The third genus included within the subfamily Elephantinæ is the *Platelephas* of Osborn, genotype *Elephas platycephalus*, a very ancient and primitive animal. The inclusion by Professor Osborn of these three genera in the subfamily Elephantinæ was provisional, because *Elephas hysudricus* Falconer and Cautley and *E. platycephalus* Osborn are at present known chiefly by cranial characters, our knowledge of the dentition of *platycephalus* being confined to the third superior molar only; they appear, however, to represent generic or subgeneric phyla distinct from the true *Elephas*.

Characters of these three genera, as far as they are known:

Elephas	Hypselephas	Platelephas
Modernized elephant of India. Highly progressive and distinctive in cranial structure	Primitive elephant of India with elevated cranium	Elephant of India with flattened cranium, primitive
Typified by *Elephas indicus*	Typified by *Elephas hysudricus*	Typified by *Elephas platycephalus*
Cranium bathycephalic, cyrtocephalic, hypsicephalic, occipitofrontal dome more or less rounded, not acute, with expanding diploë, frontals gently concave	Cranium hypsicephalic, brachycephalic; condyles well raised above grinding surface of molars, occiput elevated with broadly transverse rugose frontal crest, relatively flat, sloping backward, frontals deeply concave	Cranium relatively elongate, dolichocephalic, platycephalic, occipital condyles not greatly elevated above level of grinding surface of molars; deeply indented supra-occipital border, without rugosity
Premaxillaries relatively narrow, subvertical. Orbits large, relatively elevated, i.e., directly opposite occipital condyle	Premaxillaries relatively narrow or laterally compressed. Orbits large, depressed, near maxillary rostrum, unlike *Loxodonta* or *Elephas*	Premaxillaries greatly elongated in front of superior third molars, somewhat divergent. Rostrum somewhat broad. Orbits large, elevated, near frontal profile, set widely apart. Posterior nares deeply indented
Superior tusks relatively straight, incurved, upcurved with bases of tusks relatively close together. No inferior tusks	Superior tusks relatively straight, incurved, somewhat divergent at base. No inferior tusks	Tusks imperfectly known
Mandible with extremely abbreviated symphysis. Ramus deeply depressed	Mandible with elongate, prominent symphysis; ramus shallow	
Molars of intermediate breadth, hypsodont (less extreme than in *Parelephas*, *Archidiskodon*, or *Mammonteus*); absence of 'loxodont sinus' (*E. indicus*); moderately compressed enamel ridges of intermediate thickness, extremely crimped or sinuous in *E. indicus*. Maximum number of plicated ridge-plates: M $3_{\frac{24}{24-27}}$	Molars low crowned, long, narrow; ridge-plates with plicated enamel, convexo-concave, reversed above and below; widely separated, with cement filled valleys (juvenile); trace of a median 'loxodont sinus.' Ridge-plate formula: M $3_{\frac{18+}{17-18-19}}$	Molars imperfectly known: relatively low, ridge-plates directly transverse, as in *Elephas*. No rudiment of 'loxodont sinus.' Ridge-plates broad, depressed, limited in number: M $3^{\underline{16\frac{1}{2}}}$

Dental formula: $\mathrm{I}\ \frac{0-2-0}{}\ \ \mathrm{Dp}\ \frac{2-4}{2-4}\ \ \mathrm{M}\ \frac{1-3}{1-3}$

Ridge-plate Formulæ:

Elephas (*E. indicus, fide* Falconer): $\mathrm{Dp}\ 2\frac{4}{4}\ \ \mathrm{Dp}\ 3\frac{8}{8}\ \ \mathrm{Dp}\ 4\frac{12}{12}\ \ \mathrm{M}\ 1\frac{12}{12}\ \ \mathrm{M}\ 2\frac{16}{16}\ \ \mathrm{M}\ 3_{2\frac{24}{4-27}}$

Hypselephas (*E. hysudricus*):

(Falconer, 1868): $\mathrm{Dp}\ 3^{\frac{5-5\frac{1}{2}}{7-9}}\ \ \mathrm{Dp}\ 4\frac{+7-8+}{9}\ \ \mathrm{M}\ 1\frac{10-12}{9+-12}\ \ \mathrm{M}\ 2_{\frac{13}{9+-12}}\ \ \mathrm{M}\ 3_{\overline{17-18}}$

(Osborn, 1930): $\mathrm{Dp}\ 3_{\overline{6\frac{1}{2}}}\ \ \mathrm{Dp}\ 4\frac{8+}{10}\ \ \mathrm{M}\ 1\frac{11}{11+}\ \ \mathrm{M}\ 2\frac{\frac{1}{2}-12-\frac{1}{2}}{\frac{1}{2}-12-\frac{1}{2}}\ \ \mathrm{M}\ 3\frac{18+}{19}$

Platelephas (as far as known): $\mathrm{M}\ 3^{\underline{16\frac{1}{2}}}$

HORIZON.—*Elephas*, Upper Pleistocene and Recent. *Hypselephas*, Lower Pleistocene. *Platelephas*, Upper Pliocene or Lower Pleistocene. Compare page 1543 of this volume, also figures 1221, 1228, and Pl. XXII.

Comparison of Hypselephas and Platelephas with Elephas

With the exception of the decidedly low position of the orbits, the front view of the *Hypselephas hysudricus* cranium bears a closer resemblance to the broad-narial variety *Elephas indicus bengalensis* than to the narrow-narial variety *E. indicus ceylanicus*; also the low, narrow grinding teeth of the type of *H. hysudricus* are entirely different in proportion from those of *E. indicus*, they exhibit some resemblance or analogy to the extinct *Palæoloxodon* of Africa both in their long, narrow proportions and in their 'loxodont sinus.' The juvenile cranium of *H. hysudricus* resembles somewhat closely the juvenile cranium of *E. indicus* at the time when the fourth deciduous molars are in use. From cranial and juvenile characters alone one would be inclined to regard *H. hysudricus* as an early offshoot in Lower Pleistocene times of the main stem which gave rise to *E. indicus* of recent times, but the less rugose orbits in a similarly depressed position as that seen in crania in the British and Amherst Museums referable to *H. hysudricus*, that is, lying directly upon the premaxillary sockets of the tusks instead of being raised above the tusk sockets, demonstrate afresh that *H. hysudricus* is not to be regarded as ancestral to the collective *Elephas indicus* type but that it belongs in a totally distinct phylum or line of descent. In short, *H. hysudricus* had a modernized cranium with a relatively primitive condition of the molars.

The *Platelephas platycephalus* cranium is of very primitive elephantine affinity—low and flattened—widely different from the elevated *Hypselephas hysudricus* or the greatly elevated *Elephas indicus* crania. Both in the cranium and the grinding teeth it is also profoundly distinct from those of *Archidiskodon planifrons*. Therefore, *Platelephas platycephalus*, in the opinion of the present author, was not ancestral to either *H. hysudricus* or *E. indicus*, nor was it related to *Archidiskodon;* it would seem to belong to a primitive stage in the evolution of the Elephantinæ. The specific name has reference to the highly characteristic and primitive lowering of the fronto-occipital profile and the placing of the occipital condyle only slightly above the horizontal level of the maxillary border of the superior grinders.

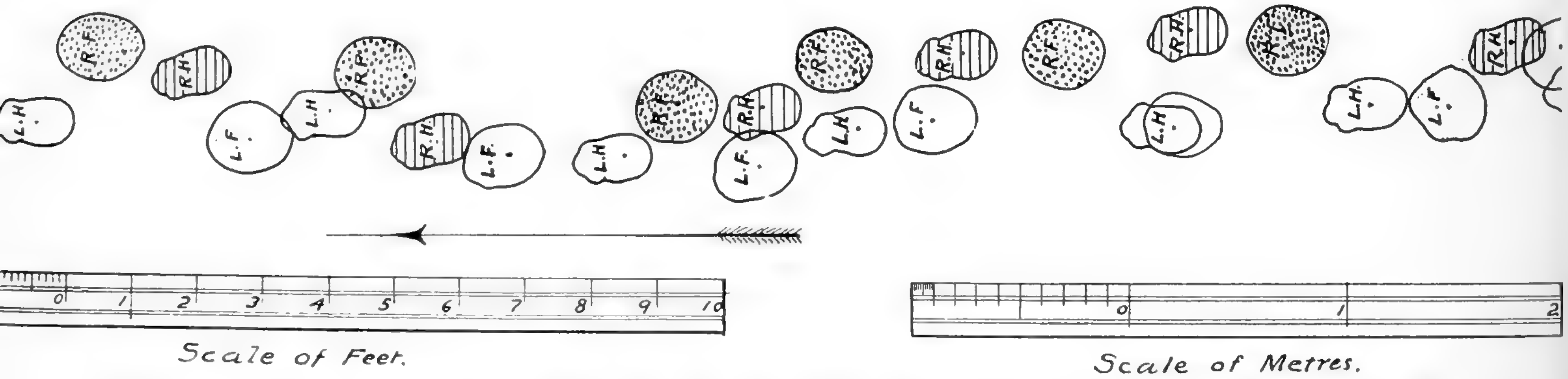


Fig. 1243. Foot trail of the Indian elephant "Gunda" in the New York Zoological Park, taken in sand by request of the author on April 14, 1906. Observe: (1) The marked contrast between the subround right fore foot (*R. F.*, dotted) and the narrow laterally compressed right hind foot (*R. H.*, crosslines); (2) that the trail of the right fore and hind feet does not impinge upon the trail of the left fore and hind feet; the two trails are parallel but not overlapping; (3) the height of "Gunda" when these measurements were taken was 7 ft. 2 in. = 218 cm.

Migration

In addition to the accompanying plate (Pl. xxii), compare also the excellent map on page 1594 of this chapter (Fig. 1242), showing the worldwide distribution of the Proboscidea in past and present time; it will be noted that *Elephas indicus* and its subspecies or varieties are confined to southeastern Asia, to be specific, Nepal, Punjab, Burma, Bengal, Siam, and Ceylon, also Sumatra, the Malay peninsula, and upper part of Borneo. Extinct species have been recorded from the Siwalik Hills of India, from Sumatra, and from Java.

In an article by Mr. George G. Goodwin in the Journal of Mammalogy, November, 1925, the date of the landing in the United States (at New York) of the first Asiatic elephant is given as April 13, 1796, on the ship "America" of Salem, Massachusetts.

Fig. 1244. Referred *Elephas indicus* showing contrast in proportions between adult and young. Mother, six months after capture, and her baby, one month old. Photograph reproduced through the courtesy of Underwood and Underwood of New York.

4. SKELETAL MATERIAL

Inasmuch as the axial and appendicular skeleton of the Proboscidea has been touched upon but briefly in the foregoing pages of this chapter, it may be helpful to summarize the skeletal material mentioned in the present Memoir, noting certain important observations made by Professor Osborn.

MŒRITHERIOIDEA

Mœritherium — Skeleton partly known (Fig. 43, and for restorations see Figs. 19, 41, 42, 51, also Pls. x and xiv). Vertebral structure indicates an ambulatory and amphibious habit. Limbs relatively short and stout. Vertebræ estimated: Cervicals 7, dorsals 19–20, lumbars 4, sacrals 4. Length of humerus 240–260 mm. (distally of primitive locomotor type). Femur straight with ligamentum teres pit, greater and lesser trochanter, absence of inner trochanter. Proportions of ulna and radius not fully known. Pelvis, scapulæ, and girdles primitive, with analogies to the sirenian type, not expanded as in the proboscidean graviportal type. Probably pentadactyl.

DEINOTHERIOIDEA

Deinotherium — Skeleton almost completely known in the Franzensbad and Rumanian specimens (pp. 99, 100, also 97 and 98 respectively; for restorations see Figs. 65, 66, 67, 70, 72, 73, and Pls. x and xiv). Limbs elongate, increasingly elephantoid, raising body well off the ground. Humerus 815 mm., ulna 800 mm., femur 1055 mm. (*D. bavaricum*—Franzensbad skeleton). *D. gigantissimum* ref. of Rumania, including two iliæ, two scapulæ (one measuring 1150 mm. in diameter), also vertebræ, four limbs, eighteen ribs, as well as tibia and pes, was probably double the size of *D. bavaricum*. Feet reduced to three short functional digits in manus and pes, with vestigial D.I in the pes. Dorso-lumbar vertebræ and trunk abbreviate.

MASTODONTOIDEA

Trilophodon — Referring to the mounted skeleton (Fig. 199) in the Paris Museum, Galerie de Paléontologie, there is some doubt as to the reference of this specimen to *Trilophodon* only; there is a possibility that some of the parts may be referable to *Serridentinus*. It is certainly an animal of larger size than *Serridentinus productus* in the American Museum, according to Dr. W. D. Matthew. There is, however, a fairly complete skeleton of *Trilophodon giganteus* in the American Museum (Figs. 257 and 372), the important measurements of which are as follows:

Humerus,	2 ft.	5½ in.	=750 mm.
Femur,	2	11½	=900
Ulna,	1	10	=560
Radius,	2		=610
Tibia,	1	9½	=547
Fibula,	1	9	=535
Scapula,	2	9	=840
Base to top of 3d dorsal,	7	9	=2365

The original material includes the left upper tusk, part of the summit of the cranium, left zygomatic arch and occipital condyles, entire lower jaw, cervical 2 to dorsal 12 inclusive, also dorsals 17 and 19, 3 lumbars, 2 caudals, nearly complete forelimbs, and scattered digits of manus and pes; complete sternum. Feet tetradactyl to pentadactyl (cf. Fig. 255). For restorations see figures 169, 234, 235, 268, and Pls. x and xv. Two scapulæ, 2 humeri (length 600 mm.), and partial hyoid of *Trilophodon* [*Megabelodon*] *cruziensis* were found at Santa Cruz, New Mexico.

Phiomia — Skeleton unknown. Restorations based on skull, mandible, tusks, and dentition (cf. Figs. 41, 185a, and Pls. vi, x, and xv). Certain skeletal parts referred by Dr. C. W. Andrews to *Palæomastodon beadnelli* and *P. parvus* may belong to *Phiomia wintoni* and *P. minor* respectively.

Amebelodon — Skeleton unknown. Restorations based on adult mandible in Nebraska State Museum (cf. Figs. 75, 284, 292, 293, 295, and Pls. vi, x, and xv).

Megabelodon — A fine skeleton of a young adult trilophodont, the finest and most complete known, probably referable to *Megabelodon phippsi* because of its tuskless mandible (see Fig. 269, also pp. 329 and 738). This skeleton includes, aside from the cranium, the scapula, humerus (772 mm.), femur (1022 mm.), radius (648 mm.), ulna, pelvis (composite), greatest width over all 1465 mm., tibia (602 mm.), fibula, and Mtc. III; also 7 cervicals, 11 articulated dorsals, 4 lumbars, complete sacrum, and four adjoining caudals, most of sternum, and ribs of more than one individual; it is somewhat superior in size to *Trilophodon giganteus*. See also pages 708, 709, and figure 667 for fine skeleton of *Megabelodon lulli* in the Nebraska State Museum, of which the following parts are present: Two upper tusks, mandible, axis, ribs, certain limb bones, a perfect pelvis with sacrum, and "elements of the left fore limb in articulation from the scapula to the tips of the toes with even the sesamoids in place." For restoration see Pl. xv.

Tetralophodon — The restorations of *Tetralophodon* are based on the skull. There are, however, fragmentary skeletal parts of *T. bumiajuensis*, i.e., limb bones, pelvis, in the collections of the Geological Survey at Bandung, Java. For restorations see figures 75, 301, 302, 339a, also Pls. x and xv.

Morrillia Skeleton unknown. For restoration see Pl. xv.

Cordillerion The restorations of *Cordillerion* are also based on the characters of the skull, especially the superior tusks, and on the lower jaw. For restorations see figures 75, 484, 498, 500, 502, 503, and Pls. x and xvi.

Rhynchotherium
Blickotherium
Aybelodon

The only skeletal parts known of the genus *Rhynchotherium* are those of the adolescent neotype of *Rhynchotherium shepardi edense,* consisting of the humerus (660 mm.), femur (860 mm.), radius (500 mm.), tibia (490 mm.); also metacarpals and metatarsals 1–5. The restorations of *Rhynchotherium, Blickotherium,* and *Aybelodon* are based on these fossil remains as well as on the lower jaws; no complete cranium is known. For restorations see figures 75, 447, and Pls. x and xvi.

Anancus
Pentalophodon
Synconolophus

Two skeletons of *Anancus arvernensis* from Italy are in the Turin Museum and Royal University of Bologna respectively. The Turin specimen (Fig. 584) is "deficient only in the cranial portion of the head, right hind-leg, part of the scapula and pelvis, and some of the bones of the carpus and tarsus. The upper and lower jaws, with the tusks entire to their tips, are preserved." Falconer says in regard to the Bologna specimen (Fig. 585) that it is nearly as perfect [as the Turin specimen].

Skeleton of *Pentalophodon* and of *Synconolophus* unknown.

For restorations see figures 75, 582, 583, 594, 595, 621, and Pls. x and xvi.

Cuvieronius

Skeletal remains of *Cuvieronius superbus* and *C. platensis* furnished the basis of the restorations in the present Memoir. The outlines of the crania and limbs in figure 566 rest entirely on the largest of these specimens in the La Plata Museum:

	C. superbus	*C. platensis*
Femur	970–1055 mm.	1030 mm.
Humerus	800	795
Tibia	633	750
Ulna		780

Other parts include the atlas, axis, and first and third dorsals. There is also a fine skeleton of *Cuvieronius postremus* from Ecuador in the Museos de la Universidad Central del Ecuador (Fig. 533): Femur (890 mm.), humerus (740 mm.), tibia (505 mm.), radius (630 mm.). For restorations see figures 75, 485, 498, 502, and Pls. x and xvii.

Stegomastodon

In the San Pedro valley of Arizona was found a portion of a young adult male skeleton of *Stegomastodon* (*S. arizonæ*) now in the U. S. National Museum, consisting of "the base portion of the skull with tusks and cheek teeth in place; the lower jaws; both fore limbs (one with nearly complete foot); parts of both hind limbs; the pelvis; and several of the more characteristic vertebræ and ribs." For skeleton (see Fig. 634), for restoration (Fig. 635). Humerus (850 mm.), femur (1010 mm.), scapula (765 mm.), width of pelvis (1475 mm.). For other restorations see figures 75, 498, 642, 648, and Pls. x and xvii.

Eubelodon

The following are measurements of the type pelvis and of referred specimens of *Eubelodon morrilli* in the Nebraska State Museum: Pelvis (type), extreme width 1424 mm.; referred femur (940 mm.), humerus (760 mm.), radius (610 mm.), fibula (545 mm.), ulna (685 mm.), scapula (760 mm.). See figures 573 (skeleton) and 577 (restoration); also figures 75, 498, and Pls. x and xvii (restorations).

Serridentinus

The reproductions of *Serridentinus productus* (Figs. 371, 372) give only an approximate idea of the complete skeleton. The original skull and jaws are mounted with the skeleton; also thirteen vertebræ, most of the ribs, pelvis and sacrum, the right hindlimb bones with the exception of the foot and some of the tarsals are original bone. The feet are all restored, excepting the left hind pes.

Measurements

Femur,	2 ft.	1¾ in.	=685 mm.
Tibia,	1	2⅜	=366
Fibula,	1	2½	=370

It is probable that it was inferior in size to *Trilophodon giganteus.* See restoration (Fig. 341). For other restorations see figures 347, 365 (model), 372a, and Pls. x and xviii.

Ocalientinus

This serridentine was of large size. The type of the genus (*O. ojocaliensis*) is a superb skull and jaws with tusks; the skeletal parts are an atlas, scapula, partial manus, pes, and series of vertebræ (see restorations of *O. ojocaliensis,* Fig. 347, and *O. floridanus,* Figs. 75, 340, and 347, also Pl. xviii).

Serbelodon Skeleton unknown. For restorations see figures 75, 406, and Pl. xviii.

Trobelodon Skeleton unknown. For restorations see figure 406 and Pl. xviii.

Platybelodon

The restorations of *Platybelodon grangeri* (Figs. 75, 285, and 423, also Pl. xviii) are founded on the remains of fifty individuals collected in Mongolia for the American Museum. All the essential parts of the skeleton are represented in the collection, together with numerous skulls and jaws.

Torynobelodon Skeleton unknown. Restoration based on mandible in the Nebraska State Museum (see Fig. 423 as *Platybelodon barnumbrowni*—finally believed by Professor Osborn to be referable to *Torynobelodon*). See also Pl. x, where it appeared as *Platybelodon barnumbrowni,* and Pl. xviii as *Torynobelodon barnumbrowni.*

Palæomastodon See figure 96 for limbs and vertebræ of *Palæomastodon beadnelli,* namely, axis vertebra, scapula, humerus, femur, and tibia. Important because of certain primitive, Mastodon-like characters. The restoration (Fig. 97) was based on these remains. See also figures 41, 41a, 110, and Pls. x and xix.

Mastodon The largest fully adult male skeleton of the true *Mastodon* (*M. americanus*) is the mount in the Ohio State University (Fig. 114), with a skeletal height of 2920 mm. or 9 ft. 7 in., and a height in the flesh of 3105 mm. or 10 ft. 2¼ in. This, together with the complete *M. americanus* skeleton (Fig. 124) in the American Museum, known as the "Warren Mastodon," with a skeletal height of 2780 mm., or 9 ft. 1½ in., and a height in the flesh of 2956 mm., or 9 ft. 9 in., furnished the measurements on which the restorations in the present Memoir were based. See also for skeleton, figures 82, 83, and 125; for restorations, figures 109, 110, 136, and 158, also Pls. x and xix. The following are the principal measurements of the "Warren Mastodon":

Humerus	950 mm.	Scapula	916 mm.
Femur	1060	Pes, extended	530
Tibia	710	Pelvis, width of ossa innominata	1826
Ulna-radius	658		

In an article by Professor Osborn on the "Mastodons of the Hudson Highlands" (Osborn, 1923.574, p. 3), he gives a table of the early discoveries of the mastodon (*M. giganteus* or *M. americanus*). As far as we know the first true Mastodon remains to be found in America (1705), near Albany, New York, consisted of a "very large Grinder, weighing 4 pounds and three quarters, with a Bone, suppos'd to be a Thigh-bone, 17 Foot long" (Phil. Trans., 1717, Vol. XXIX, No. 339, for April, May, and June, 1714, p. 62). Of especial interest are two skeletons unearthed in Orange County, New York, by Charles Willson Peale in the years 1799–1801 and 1802. A narrative of discovery was published by his son, Rembrandt Peale, in 1803, and subsequently (1852, 1855) both skeletons were figured by Dr. John Collins Warren in his memoir on "The Mastodon Giganteus of North America" (Pl. i). While incomplete, these were important in that early period before the discovery in 1845 of the "Warren Mastodon." On the same plate Doctor Warren figures Koch's "Missourium," a composite of several specimens found near Kimmswick, Missouri, and now in the British Museum. [There are several other *Mastodon* skeletons known in addition to those listed here.]

Pliomastodon The type femur (Fig. 108) was the basis for the restoration (Fig. 110) of *Pliomastodon vexillarius* of California. See also Pls. x and xix for restorations.

Miomastodon Skeleton unknown. For restorations, based chiefly on the upper tusks, mandible, and dentition, see Pls. x and xix.

Zygolophodon
Turicius As the skull and skeleton of the Zygolophodontinæ are relatively unknown or undescribed, the restorations were based chiefly on the grinding teeth and tusks (Figs. 110, 143a, 158, and Pls. x and xix).

Stegolophodon Cranium, tusks, and dentition only known. For restorations, see Pl. xix.

STEGODONTOIDEA

Stegodon Skeletal material relatively unknown. Restorations based on crania, tusks, and dentition of the various species; skeleton conjectural throughout. See figures 681 and 682 especially, also figures 731, 743, 755, 756, 768, 775, and Pl. xx.

ELEPHANTOIDEA

Archidiskodon The primitive species *Archidiskodon planifrons* is known chiefly by the cranium, jaws, and dentition; a femur found in the Red Crag of England is possibly referable to this species. Skeletal material, however, of *Archidiskodon* in more advanced stages is fully known both from the continent of Europe (Durfort, France—*A. meridionalis*) and from North America (Nebraska and Texas—*A. imperator*, and Nebraska—*A. imperator maibeni*). The following are the measurements of *A. imperator* and of *A. imperator maibeni*, also of the recently described *A. meridionalis nebrascensis* from Nebraska.

	A. imperator	*A. imperator maibeni*	*A. meridionalis nebrascensis*
Scapula	1017 mm.	1066+mm.	1020 mm.
Humerus	1095	1251	1220
Femur			1390

The frontispiece to Chapter XVI (Fig. 815), as well as other restorations of *Archidiskodon* in the present Memoir, was based chiefly on these measurements (see Figs. 856, 867, 909, also Pl. xxi).

Archidiskodon maibeni, the giant of the phylum, is represented by the skull, mandible, one tusk, the atlas, axis, and four other cervicals, several thoracics, lumbars, and the sacrum, ribs, and *double ribs,* both forelimbs, and parts of the hindlimbs, also parts of the pelvis, the shaft of a femur, and the major portion of a fibula. For skeleton, see figure 911; for restorations, figures 815, 824, and Pl. xxi).

Parelephas	Well represented both in Europe and America by skeletal remains. *P. intermedius* in the Lyons Museum (Fig. 944) is a complete skeleton and the beautiful frontispiece to Chapter XVII (*P. trogontherii*) is partly based on this skeleton, but chiefly on the superb *P. jeffersonii* in the American Museum (Figs. 931, 966, and 988), the following parts of which, however, are missing and restored in plaster: Radius and ulna of both sides, right tibia and fibula, and both fore- and hindfeet. The length of the femur is 1250–1255 mm., of the humerus 1085–1120 mm. A record humerus is that of *P. trogontherii* of Germany which measures 1480 mm. A fine skeleton of *P. columbi* from Florida is in the Amherst Museum; it lacks four dorsals, parts of the limb bones, ilium, manus and pes; otherwise largely original (Fig. 955). Finally, the *P. floridanus* skeletal remains are among the most important; this material, with measurements, is enumerated in Chapter XVII, pp. 1111–1114. For other restorations see figures 930, 936, and Pl. xxii.
Mammonteus	There is an abundance of skeletal material of the woolly mammoth, namely, from the Kolyma-Beresowka River, Siberia, Steinheim on the Murr, Württemberg, and Borna, Germany, also Lierre, Province d'Anvers, Belgium (p. 1130); the Moravian skeleton from Brünn, Czechoslovakia (Fig. 1007), and the fine skeleton of *M. primigenius fraasi* at Stuttgart (Fig. 1018); finally, and perhaps the most important skeleton discovered (as it included a piece of the hide with hair in place) is the Lena River specimen, known as the "Adams skeleton," which is mounted in the Zoological Museum of the Academy of Sciences, Leningrad (Fig. 1014). In 1929 a splendid lot of cranial and skeletal material was unearthed in the vicinity of Fairbanks, Alaska. This material is listed on page 1160 above. Length of the humeri 980–750 mm., of the femora 1130–965 mm., of the tibiæ 680–440 mm., of the radii 610–560 mm. For restorations see figures 990, 994, 1000–1002, 1013, 1034, and Pl. xxii.
Loxodonta	As one of the living genera of the Proboscidea there is endless skeletal material. In the American Museum is the skeleton of "Jumbo" (*Loxodonta africana oxyotis*) and the Akeley mount of two geographical varieties of *Loxodonta africana*, namely, *albertensis* and *peeli*. A table at the close of this section gives the maximum height and other measurements of the African elephant, so that it is not necessary to enumerate the extensive materials, excepting to mention the length of the humerus (1078 mm.—see Fig. 912) and of the femur (1246 mm.—see p. 1230) of "Jumbo," and to call attention to the comparative figure (Fig. 1084) of the vertebral columns of *L. africana*, *Elephas indicus*, *Mammonteus primigenius*, *Parelephas jeffersonii*, and *Hesperoloxodon antiquus*. According to Falconer (cf. p. 931 above) the African elephant varies in the number of dorsal vertebræ from 20 to 21.
Palæoloxodon	The extinct branches of the Loxodontinæ are not well represented by skeletal material. Doctor Dietrich gives the length of the humerus of *Palæoloxodon recki* of East Africa as 1235 mm., of the femur as 1470 mm. Professor Osborn suggested that the dwarfed elephants of the Mediterranean Islands might be descended from such forms as *P. recki*, *P. atlanticus*, etc. Dwarfed Palæoloxodonts of the Mediterranean Islands. These animals vary in size; observe particularly figures 1118 and 1119, in which the large stage (*Palæoloxodon mnaidriensis*) has a humeral length of 573 mm.; the intermediate stage (*P. melitensis*) has a humeral length of 478 mm., and the small stage (*P. falconeri*) has a humeral length of 270 mm. The skeleton of *P. falconeri* is fragmentary, and *P. lamarmorae* from Sardinia is represented by carpal and tarsal bones only. The heights of these insular species vary from 2 ft. 6 in. to 6 to 7 feet. The *Palæoloxodon* phylum culminates in the *P. namadicus* of the Nerbudda of India, the cranium of which has been used as a basis for the restorations in the present Memoir (Fig. 1068). Pilgrim, 1905, pp. 211, 212, gives the measurements of certain skeletal material which he recovered from the Godávari beds and regarded as referable to this species, but it is somewhat fragmentary; it consists of portions of a femur and of the pelvic bones; the cranium and tusks are very fine. For other restorations, see figure 1127, and Pl. xxiii.
Hesperoloxodon	The most complete skeleton of *Elephas* [*Hesperoloxodon*] *antiquus* is in the British Museum, although it lacks the cranium (Fig. 1080). It is important to note that since the discovery of this Upnor specimen, there have been several crania described, among them that of *Palæoloxodon* [*Hesperoloxodon*] *antiquus italicus* from Italy (Figs. 1105–1108) and two of *Hesperoloxodon antiquus germanicus* from Steinheim (Fig. 1114), affording the much-needed knowledge regarding the skull and tusks of this ancient elephant of Europe. The Upnor and Pignataro specimens furnished the necessary data for the restoration (Fig. 1074). The skeleton of the Upnor *H. antiquus* is shown in figure 1079; as noted in the caption, the backbone lacks two vertebræ, the radius of the left fore leg is restored in plaster, the right radius is complete. Fortunately the humerus, although not quite complete, was present and measures 1290 mm. Of the Pignataro Interamna specimen (*H. ant. italicus*) the right scapula is preserved. A femur of the large Taubach skeleton of *H. ant. germanicus* measures 1600e mm., and another from Rome of *H. ant. italicus* measures 1500e mm., according to Pohlig (cf. p. 1251 above). See figures 1068, 1083, 1092, and Pl. xxiii for restorations.
Elephas	Like *Loxodonta* the skeleton of the living Indian elephant (*Elephas indicus*) is well known. The average length of the humerus varies from 816 mm. to 895 mm. in three individuals (Fig. 1194). According to Falconer (cf. p. 931 above) *E. indicus*, including the continental and insular varieties, varied in the number of dorsal vertebræ from 19 to 20.
Hypselephas	The cranium, dentition, and tusks only of *Elephas* [*Hypselephas*] *hysudricus* are known.
Platelephas	Up to the present time the skeleton of *Platelephas* is unknown. It is represented by the type cranium and imperfectly known grinding teeth. The tusks also are unknown.

5. HEIGHTS OF PROBOSCIDEANS, ESTIMATED AND ACTUAL

In a recent monograph (1936) on "The Physiology of the Elephant," by Dr. Francis G. Benedict, Director of the Nutrition Laboratory, Carnegie Institution of Washington, much accurate and important information is given regarding the heights and weights of the elephant, especially of the Indian elephant. It is stated on page 290 that the weight of a "large" elephant is over 8,000 pounds or 3630 kilograms. The weight of "Jap" (the female Indian elephant used in the physiological experiments on which much of Doctor Benedict's conclusions are based) is given as 8095 lbs. or 3672 kg. (see p. 104). The weight of "Khartum" (a gigantic male African elephant formerly living in the New York Zoological Park), on which an autopsy was made by Dr. W. Reid Blair and Dr. C. V. Noback, was about 10,040+ lbs. or 4710 kg. (see p. 106).

The following is a list of the heights (in millimeters and feet, estimated and actual) of the Proboscidea, as recorded in the present Memoir.

	SKELETAL HEIGHT		HEIGHT IN FLESH		
Mœritherium					
lyonsi			699e mm.	2 ft.	3½ in.
andrewsi			650e	2	1½
trigodon			625e	2	½
gracile			500e	1	7¾
ancestrale			500e	1	7¾
Deinotherium					
gigantissimum			3900e	12	9½
giganteum			3000e	9	10
bavaricum			2500	8	2⅜
Phiomia					
pygmæus			1700e	5	7
osborni			1345e	4	5
wintoni			1200e	3	11¼
serridens			1030e	3	4½
minor			950e	3	1½
Amebelodon					
fricki			3047e	10e	
paladentatus			1825e	6	
Trilophodon					
macrognathus			3250e	10	8
giganteus	2365	7 ft. 9 in.	2594	8	6
chinjiensis			2500e	8	2⅜
pontileviensis			2300e	7	6½
angustidens			2295e	7	6⅜
gaillardi			2295e	7	6⅜
osborni			2106e	6	10⅞
fricki			2100e	6	10¾
cooperi			2100e	6	10⅝
Megabelodon					
lulli			2600	8	6⅓
phippsi			2600	8	6⅓
Trilophodon (Tatabelodon)					
gregorii			3100e	10	2
riograndensis			2450e	8	½
Tetralophodon					
grandincisivus			2700e	8	10¼
punjabiensis			2475e	8	1⅜
campester			2475e	8	1⅜
falconeri			2440e	8	
Tetralophodon					
elegans			2300e mm.	7 ft.	6½ in.
fricki			2100e	6	10¾
longirostris			2050e	6	8⅝
sinensis			2025e	6	7¾
bumiajuensis			1850e	6	¾
Morrillia					
barbouri			2440e	8	
Cordillerion					
edensis			2200e	7	2½
andium			2200e	7	2½
Rhynchotherium					
tlascalæ			2650e	8	8¼
browni			2450e	8	½
falconeri			2350e	7	8½
edense			2000e	6	6¾
spenceri			1850e	6	¾
Blickotherium					
euhypodon			1727e	5	8
blicki			1600e	5	3
Aybelodon					
hondurensis			2200e	7	2½
Anancus					
arvernensis			2550	8	4⅜
perimensis			2150e	7	⅔
properimensis			2000e	6	6¾
Pentalophodon					
sivalensis			2450e	8 ft.	½
falconeri			2450e	8	½
Synconolophus					
dhokpathanensis			2642e	8	8
corrugatus			2550e	8	4⅓
hasnoti			2400e	7	10½
Cuvieronius					
superbus			3022e	9	11
platensis			2867e	9	4¾
postremus			2200e	7	2½
ayoræ			2050e	6	8¾
Eubelodon					
morrilli	2440		2520	8	5⅛

	Skeletal Height			Height in Flesh		
Stegomastodon						
arizonæ	2520			2648mm.	8 ft.	8¼ in.
aftoniæ				2642e	8	8
mirificus				2550e	8	4¼
texanus				2300e	7	6½
Serridentinus						
proavus				2000e	6	6¾
serridens				1900e	6	2¾
gobiensis				1850e	6	¾
productus	1624	5 ft.	6¾ in.	1727	5	8
subtapiroideus				1700e	5	7
prochinjiensis				1250e	4	1¼
Ocalientinus						
floridanus				2714e	8	10¾
ojocaliensis				2262e	7	5
Platybelodon						
grangeri				2135e ♂	7	
grangeri				1830e ♀	6	
danovi				1650e	5	5
Torynobelodon						
barnumbrowni				1950e	6	4¾
Notiomastodon						
ornatus				2700e	8	10¼
argentinus				2450e	8	½
Serbelodon						
burnhami				2050e	6	8¾
Palæomastodon						
beadnelli				2328e	7	7¾
Miomastodon						
merriami				2250e	7	4
Pliomastodon						
vexillarius				2800e	9	2¼
Mastodon						
americanus (largest recorded, Ohio State University) 2920 mm. or 9 ft. 7 in.				3105	10	2¼
"Warren Mastodon" 2780 mm. or 9 ft. 1½ in.				2956	9	8½
(Average height)				2895	9	6
Turicius						
turicensis				2600e	8	6¼
virgatidens				2400e	7	10½
tapiroides				2100e	6	10¾
Zygolophodon						
borsoni				3000e	9	10
pyrenaicus aurelianensis				2725e	8	11¼
Stegolophodon						
Stegolophodon cautleyi progressus				1400e	4	7
(Restoration in Pl. xix, but without measurements)						
Stegodon						
ganesa				3050e	10	
pinjorensis				2745e	9	
grangeri				2256e	7	5
bombifrons				2148emm.	7 ft.	½ in.
insignis				1925e	6	4⅞
trigonocephalus				1428	4	8¼
airâwana				1176e	3	10⅓
Archidiskodon						
maibeni	3826	12 ft.	6⅝ in.	4068	13	4¼
planifrons (Chagny)				3745e	12	3½
meridionalis (Durfort)	3499	11	5⅔	3721	12	2½
meridionalis nebrascensis	3454			3672	12	½
planifrons (Siwaliks)				1980	6	6
imperator	3482	11	5	3702	12	1¾
proplanifrons				1387e	4	6½
subplanifrons				1387e	4	6½
Parelephas						
trogontherii (Mosbach)				4500e	14	9⅛
trogontherii (Taubach)				4054e	13	3½
floridanus				3721e	12	2½
columbi (Georgia)				3646e	11	11½
jeffersonii (Indiana)	3200	10	6	3402e	11	1⅕
intermedius	3750?	12	3½			
columbi (Amherst)	3430	11	3	3644	11	11½
Mammonteus						
primigenius	2999e	9	10	3189e	10	5¾
primigenius fraasi	3700	12	1⅝	3934	12	10¾
Loxodonta						
africana (adult)	3290	10	9½	3520	11	6½
africana oxyotis ("Jumbo")	3194	10	5¾	3396	11	1¾
africana pumilio				2032	6	8
Hesperoloxodon						
antiquus italicus (Rome)				4068e	13	4⅛
antiquus (Upnor)				3934	12	10⅞
antiquus italicus (Pignataro)	3673	12	⅝	3905	12	9¾
antiquus platyrhynchus (Spain)				3828e	12	6¾
antiquus germanicus				4074e	13	4⅜
Elephas						
indicus (living—Vernay specimen)	2558	8	4¾	2720	8	11
(according to Rowland Ward, 1928)					10	8
"Gunda" (Amer. Mus. 39081)	2660	8	8¾	2828	9	3¼
indicus bengalensis				3200	10	6
Palæoloxodon						
recki	3600e			3828e	12	6¾
namadicus				3736e	12	3
mnaidriensis				1900e	6	2¾
melitensis				1400e	4	7⅛
falconeri				900e	2	11½

CONCLUSION

The proboscideans are geologically long lived,—55,000,000 to 65,000,000 years (Osborn, 1933.901, p. 159), originating (Osborn, 1934.924, p. 177) "exclusively in Africa, probably in Upper Cretaceous or Lower Eocene time." According to Professor Osborn (1934.922, p. 211) they "rank next to man in biological importance, and far surpass the mechanically inferior man in demonstration of all the main principles of biomechanical aristogenesis and alloiometry."

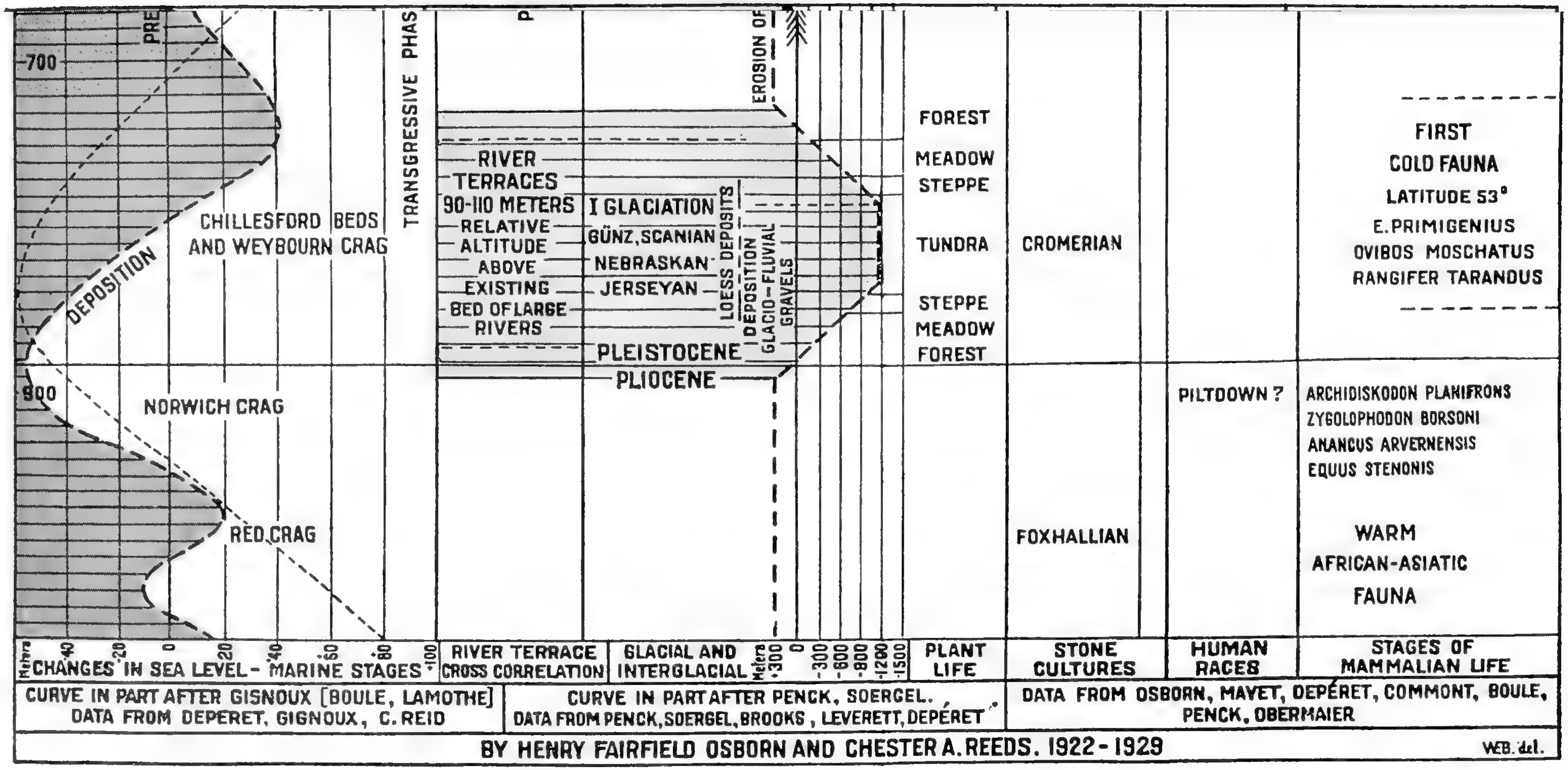


Plate XXIV. The Osborn-Reeds Correlation Table of 1922 and 1929.

Continental subsidences and marine transgressions in dark shading. Alternating glacial advances in light shading. Relative time intervals between the four glacial advances as estimated by Penck-Brückner, 1908–1921.

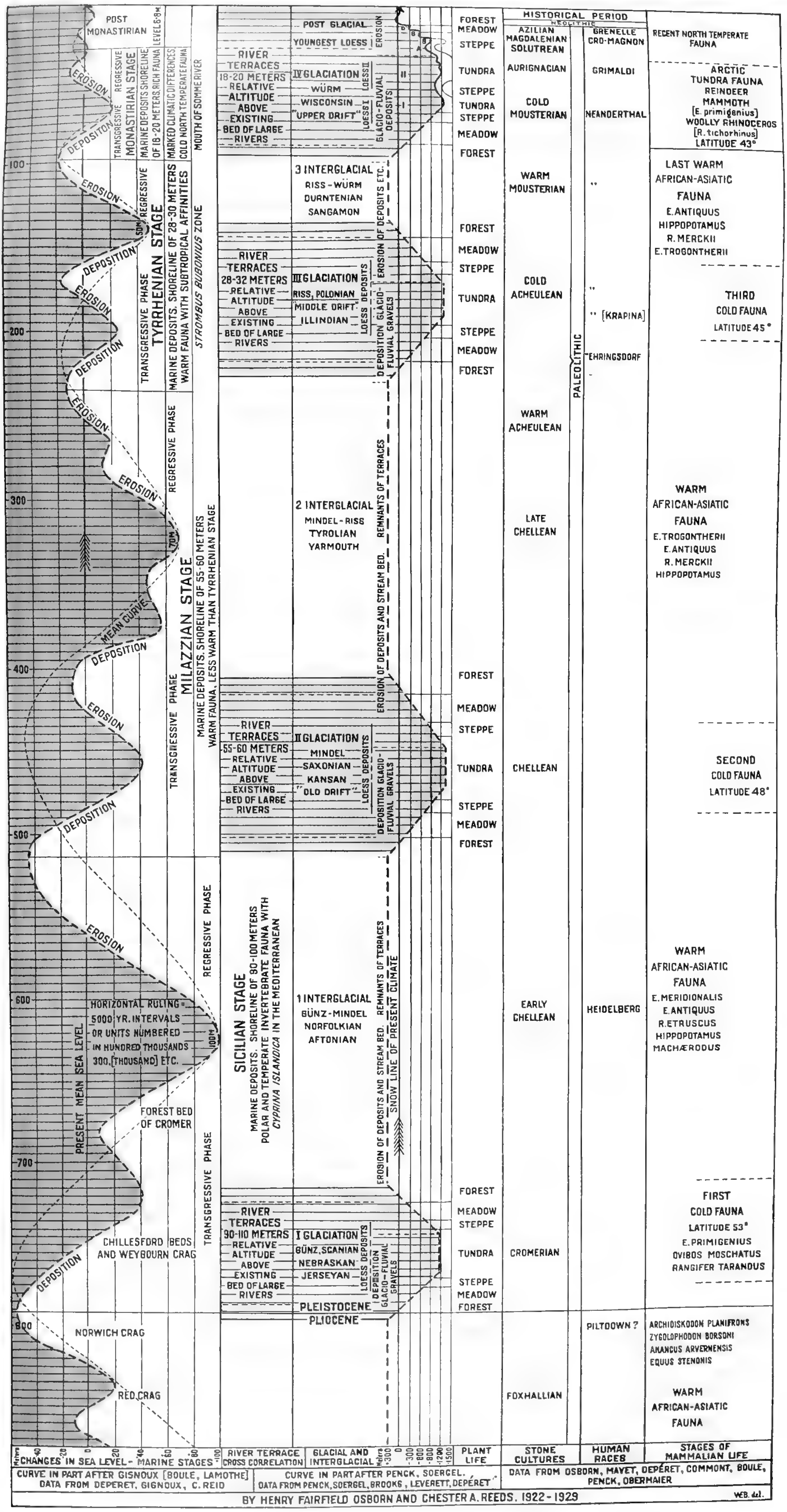
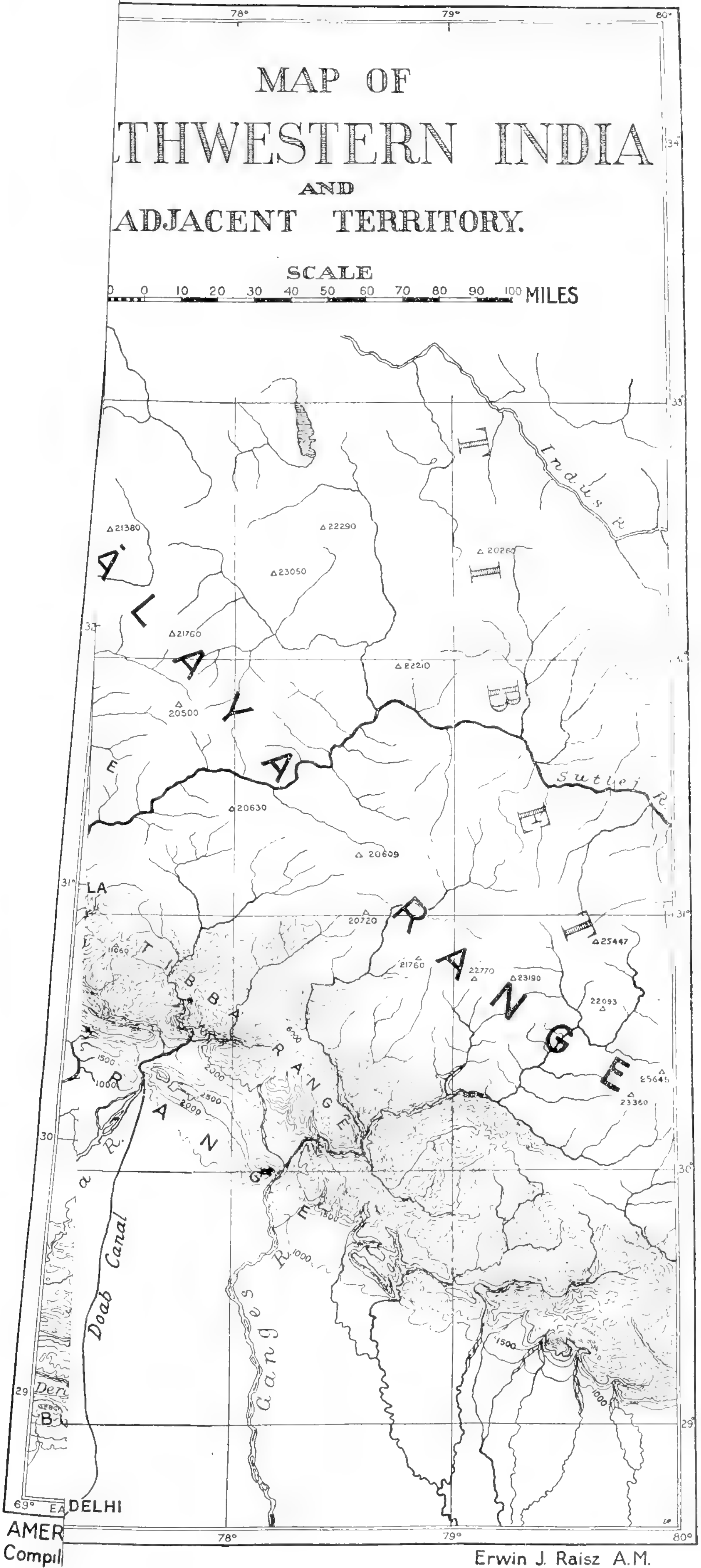


PLATE XXIV THE OSBORN-REEDS CORRELATION TABLE OF 1922 AND 1929.

Continental subsidences and marine transgressions in dark shading. Alternating glacial advances in light shading. Relative time intervals between the four glacial advances as estimated by Penck-Bruckner,1908-1921.



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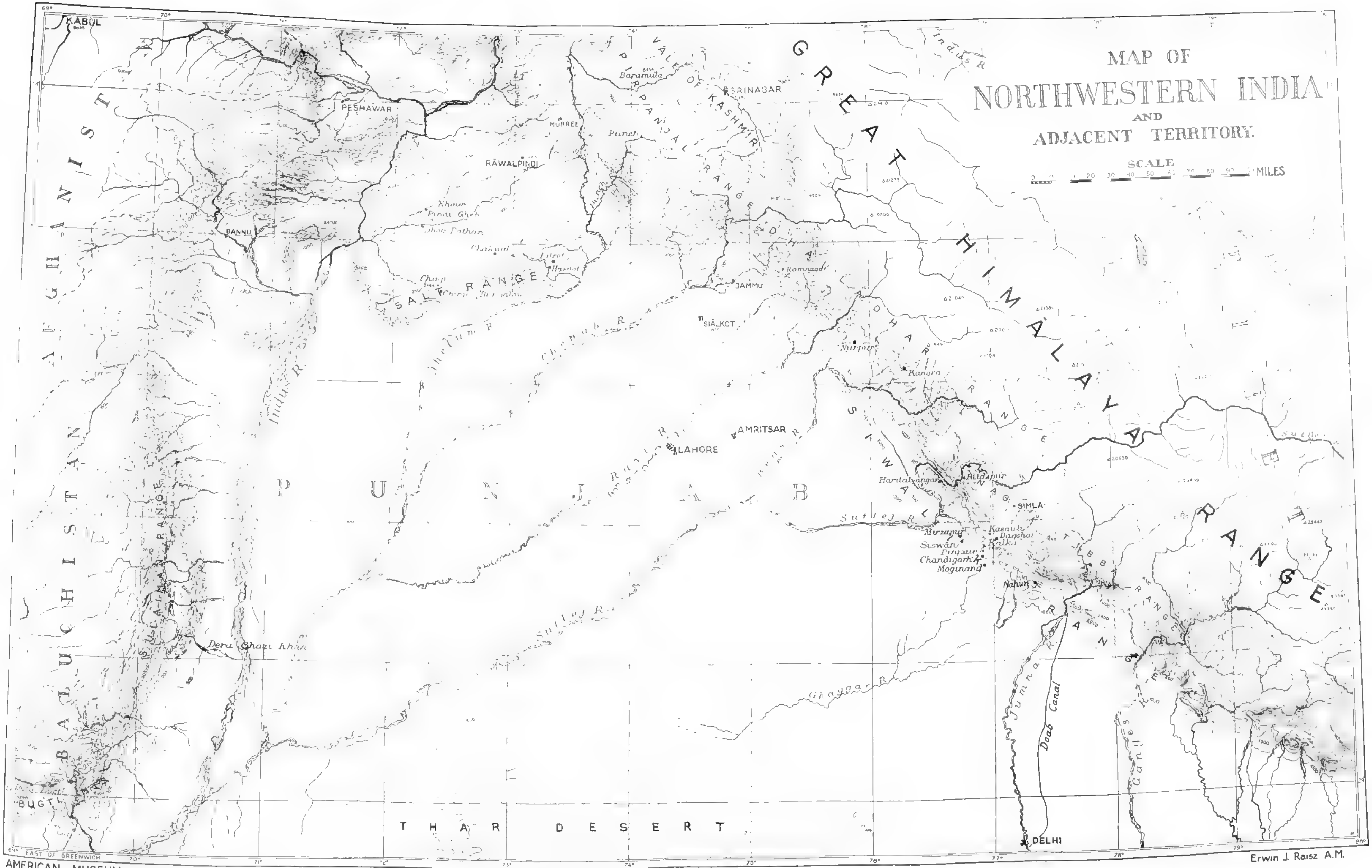

AMERICAN MUSEUM OF NATURAL HISTORY 1927.
Compiled from the Survey of India 1 1000000 sheets Nrs. 38, 39, 43, 44, 52, 53

PLATE XXV. Map of Northwestern India showing the Siwalik Hills and the adjacent Salt Range and the important localities where vertebrate fossils have been recovered by the American Museum.

APPENDIX TO VOLUME II

PROBOSCIDEAN DENTAL HISTOLOGY

By George Gaylord Simpson

It was Professor Osborn's intention to include in this Memoir an appendix devoted to the microscopic structure of proboscidean teeth. For this purpose he had Mr. A. E. Anderson prepare and photograph a number of thin sections of such teeth and write notes on some aspects of their study. It was intended that an eminent dental histologist, the late Dr. J. Leon Williams, should also study these sections and prepare an interpretation of them. Unfortunately no part of this plan was carried far enough for it to be possible now to achieve the results desired without a vast amount of further research impossible to us at this time and going far beyond the editorial intention of publishing the work done under Professor Osborn's direction without substantial change.

Mr. Anderson's notes were intended and are useful rather as a guide for the study of his photographs than as results of such study. Dr. Williams prepared a few additional photographs of the same sections, but had not yet supplied an accompanying manuscript when he died suddenly on February 23, 1932. The sections themselves, and the photographs of them, pertain to only three genera, *Elephas*, *Phiomia*, and *Trilophodon*, and only to the tusks of these except for two sections of a *Trilophodon* molar. Even within this limited sphere, they are inadequate to reveal all the important details. For instance, there are no tangential sections and without them the shapes of the enamel rods cannot be determined.

Despite this very fragmentary character of the data left, it includes photographs and observations that have not been made obsolete by any publication in the meantime and that do give at least a glimpse at a subject the complete omission of which would be a fault in this Memoir. A selection of the most important photographs has therefore been made for publication here, legends for them have been prepared in part from Mr. Anderson's notes and in part from independent observation, and this introductory comment written, all without the benefit of Professor Osborn's direction but making available material that was in his hands.

With a single exception (Pl. xxviii, Fig. 2, by Dr. Williams) these photographs were made by Mr. Anderson. A few were made with ordinary light, but most by means of a petrographic microscope, some in plane polarized light, and some between crossed nicols. The use of crossed nicols is not only valuable for determining the optical properties and mineralogy of the tissues, a matter of secondary interest here, but also to bring out, by the phenomena of birefringence, details of tissue structure and orientation that are not visible, or not so clearly visible, in ordinary or in plane light. This is a technique of considerable importance, the value of which can be seen, for instance, by comparing figures 3 and 4 of Plate xxvii. Although the two are identical in subject, each reveals important structural features not visible in the other.

The histology of a tooth is an important part of its structure. It is impossible really to understand either its gross structure or its functional characters without knowing something of its microstructure and of the distinctive features of the tissues composing it. There is also good reason to believe that histological characters may be of value in the identification of fossils and in the determination of animal affinities. Dental tissues individually and in combination have complex characters, fairly constant within limited taxonomic groups and sometimes radically distinct in different groups. Some of these distinctions seem to be adaptive or habitus characters, but others are probably deep-seated heritage characters and they may prove to be exceptionally reliable helps in tracing animal descent.

The present material gives examples of proboscidean dental tissues that must be more or less typical of that group. This purely descriptive aspect is sufficiently expressed by the photographs and their legends. These data also show that for the three genera in question the microstructure even of a simple transverse section of a tusk is determinative. *Elephas*, *Phiomia*, and *Trilophodon* differ in dental histology and on this basis alone any one of these genera can at once be distinguished from the other two. This fact should stimulate the preparation of the many additional sections necessary to determine to what extent thin sections can be useful in the diagnosis and recognition of taxonomic groups of Proboscidea. The histology of these three genera also shows that they have many characters in common, some of which do not appear to be shared by more distantly related animals. Moreover *Phiomia* and *Trilophodon* resemble each other more than either resembles *Elephas*. These facts warrant and urge further study to see how far such resemblances can be used to determine relationships.

Although inadequate to establish them definitely, these imperfect data also hint at evolutionary trends of considerable interest functionally and in other ways. This is seen, for instance, in the fine structure of the tusk enamel. In *Phiomia* (e. g., Pl. XXVIII, Fig. 2), the rods have a pronounced spiral arrangement which makes for toughness and resistance to injury, suggestive of the very tough enamel of rodent incisors. In *Trilophodon* (e.g., Pl. XXIX, Fig. 3), this arrangement persists, but in appreciably weaker form. In *Elephas* (Pl. XXVI, Fig. 3), it has practically disappeared and the enamel is weak in histologic structure. Thus these three genera, at least, show progressive simplification and weakening of the enamel in microscopic characters as it becomes more reduced macroscopically and less important functionally. The peculiar enamel stringers in *Trilophodon* and the relationships of cement in *Trilophodon* and *Elephas* also suggest potentially fruitful lines of investigation. Another will be found in the evolution of the "engine-turning" effect of the dentine and another in the probable changes in enamel structure in the molars, with changes from the primitive condition to the heavy cones of some later mastodonts or the lamellæ of the elephants. Another of the more interesting of the many points merely glimpsed in these sections is the possible relationship between the dentine cylinders of some mastodonts, such as *Platybelodon*, and the peculiar dentine modification seen in the most juvenile part of a tusk of *Elephas* (Pl. XXVI, Fig. 1).

CATALOGUE NUMBERS OF SPECIMENS MENTIONED IN THE PROBOSCIDEA MEMOIR, VOLUME II

Algiers: School of Sciences
Amherst: Amherst College Museum
Amsterdam: Zoological Gardens

Berlin: Geological-Palæontological Institute of the University
    Museum for Natural History
Bologna: University Museum
Bonn: Museum
Brno: Moravian Government Museum
Brussels: Museum
Bucharest: Laboratory of Geology of the University
    Laboratory of Palæontology of the University
Buenos Aires: Argentinian Museum of Natural Sciences

Calcutta: Asiatic Society of Bengal
    Indian Museum
Canterbury: Museum
Capetown: South African Museum
Chicago: Field Museum of Natural History
College: University of Alaska (formerly Alaska Agricultural College and School of Mines)
Columbus: Ohio State University Museum
Cromer: Savin Collection[1]

Florence: Natural History Museum
Fukuoka: Kyushu Imperial University

Geneva: Museum of Natural History
Göttingen: Zoological Institute of the University
Gotha: Museum

Halle: Museum

Iowa City: University of Iowa
Ipswich: Natural History Museum

Jena: Museum

Kimberley: McGregor Museum
Kobe: Takikawa Middle School
Kyoto: Imperial University

La Plata: Museum
Leiden: Dubois Collection
    Natural History Museum
    Royal Museum of Geology and Mineralogy
Leipzig: Palæontological Collection of the University
    State Ethnographical Museum (Grassi Museum)
Leningrad: Museum of the Institute of Mines, Academy of Sciences of the U.S.S.R.
    Palæozoologic Institute of the Academy of Sciences
    Zoological Museum of the Academy of Sciences
Lincoln: Nebraska State Museum
Lisbon: Zoological Gardens
London: British Museum (Natural History)
    Imperial Institute
    India House
    Museum of the Geological Society
    Royal College of Surgeons
    Zoological Society

Los Angeles: Museum of History, Science and Art
Lyons: Museum of Natural Sciences

Marseilles: Museum of Natural History
Mexico: Engineering School
    Geological Institute
Moscow: University
Munich: State Zoological Museum

New York: American Museum of Natural History
    Zoological Society
Norwich: Norwich Castle Museum and Art Gallery

Oran: Museum
Oxford: Museum

Paris: Museum of Natural History
Pasadena: California Institute of Technology
Philadelphia: Academy of Natural Sciences
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Private Collections: Walter W. Holmes, Florida
    ————Kato, Kokubo, Japan
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    ————Natsume, Minato, Japan
    Duc d'Orleans, Wood Norton, England
    C. V. A. Peel, Oxford, England
    ————Powell-Cotton, Birchington, England
    Lord Rothschild, Tring, England[2]

Quito: Museum of the Central University of Ecuador

Rome: University Museum
Rotterdam: Zoological Gardens

Saint John, New Brunswick: Museum
Sendai: Tohoku Imperial University
Sendai (probably): Second High School
Stockholm: Museum of King Adolph Frederick
Stuttgart: Wurttemburg Natural History Collection

Tallahassee: Florida Geological Survey
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Turin: Museum

Vienna: Natural History Museum

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[1] [The entire collection of vertebrate fossils made by Alfred C. Savin was purchased by the British Museum in 1897.—Editor.]

[2] [Probably at the British Museum.—Editor.]

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[1] [The entire collection of vertebrate fossils made by Alfred C. Savin was purchased by the British Museum in 1897.—Editor.]

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[1] [Not determined by the present author.—Editor.]

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[1] [Not determined by the present author.—Editor.]

[2] [Probably at the British Museum.—Editor.]

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v-4529	*Parelephas floridanus* ref	1115
	Tervueren: Museum of the Belgian Congo	
	Loxodonta africana fransseni type	1193
	Tokyo: Geological Institute of the Imperial University	
	Stegodon auroræ type	893
	Stegodon orientalis shodoënsis ref	893
	Tokyo: Museum of Education at Ochanomizu	
	Palæoloxodon tokunagai type	1298
	Toyko: Uyeno Museum	
2194	*Stegodon orientalis shodoënsis* type	893
2208	(See Museum of Education, Ochanomizu, Tokyo)	
	Turin: Museum	
15	*Mammonteus primigenius astensis* paratype	1154, 1407
	Mammonteus primigenius astensis type	1154, 1407
	Anancus arvernensis ref	1601
	Parelephas trogontherioides lectotype	1054
	Parelephas trogontherioides cotype	1054
	Vienna: Natural History Museum	
	Stegolophodon sublatidens type	846

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1614	*Parelephas columbi* ref	1077
2195	*Parelephas jeffersonii* ref	1086, 1087, 1088, 1089, 1095, 1096, 1097
2216	*Archidiskodon imperator* ref	1002
2217	*Archidiskodon imperator* ref	1002
4162	*Mammonteus primigenius* ref	1145
4761	*Parelephas jeffersonii* ref	1097
6052	*Parelephas jeffersonii* or *P. washingtonii* ref	1088
6662	*Archidiskodon imperator* ref	1003
6663	*Archidiskodon imperator* ref	1003
6666	*Mammonteus primigenius* ref	1145, 1146
6668	*Parelephas jeffersonii* or *P. washingtonii* ref	1088
6669	*Parelephas jeffersonii* or *P. washingtonii* ref	1088
8579	*Mammonteus primigenius* ref	1091, 1145, 1146
8580	*Mammonteus primigenius* ref	922, 939, 1051, 1091, 1143, 1144
10261	*Parelephas jeffersonii* ref	922, 1052, 1084, 1087, 1088, 1090
11620	*Archidiskodon imperator* ref	996, 1005, 1078
11805	*Archidiskodon imperator* ref	996, 1005
11806	*Parelephas floridanus* ref	996, 1077, 1078, 1079, 1108
11808	*Parelephas floridanus* ref	996, 1077, 1078, 1079, 1108
11810	*Parelephas floridanus* ref	996, 1077, 1078, 1079, 1108
11814	*Archidiskodon imperator* ref	996, 1005

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1931.1 Die Bedeutung der Equiden für die Altersstellung des rheinhessischen Dinotheriensandes. Centralb. Min. Geol. Pal., Abt. B, pp. 42–48, 1 text fig. Stuttgart.

1939.1 Das Pleistocän Javas. Quartär (Berlin), II, pp. 28–53, Taf. ix–xi, Abb. 1–6.

Mounted skeleton of *Stegodon trigonocephalus* in the Geological Museum of Bandoeng.

1939.2 The Relationship between the Fossil Mammalian Faunae of Java and China, with Special Reference to Early Man. Peking Nat. Hist. Bull., XIII, Pt. 4, June, pp. 293–298, 1 text fig.

Kraglievich, Lucas

1934.1 La antigüedad pliocena de las faunas de Monte Hermoso y Chapadmalal, deducidas de su comparación con las que le precedieron y sucedieron. 8vo, "El Siglo Ilustrado," Montevideo, 136 pp., fontispiece and 1 text fig.

Designated the Lower Pampean, or Ensenadense, as "Upper Pliocene or Pliopleistocene."

Krejci-Graf, Karl

1932.1 Parallelisierung des südosteuropäischen Pliozäns. Geol. Rundschau, XXIII, pp. 300–339, text fig. 1.

Beds of true Sarmatian age, bearing *Hipparion*.

Lapparent, A. de

1906.1 Traité de Géologie. Fifth edition, 8vo, Masson et Cie., Paris, III, pp. 1289–2015, text figs. 584–883.

Remarks concerning the Œningen fossils.

Leverett, Frank

1902.1 Glacial Formations and Drainage Features of the Erie and Ohio Basins. Monogr. U. S. Geol. Surv., XLI, pp. 1–802, Pls. i–xxvi, text figs. 1–8.

Lewis, G. Edward

1937.1 A New Siwalik Correlation. Amer. Journ. Sci., (5), XXXIII, March, pp. 191–204, text figs. 1, 2.

Tawi, new name for Boulder Conglomerate.

Licent, Emile, and M. Trassaert

1935.1 The Pliocene Lacustrine Series in Central Shansi. Bull. Geol. Soc. China, XIV, pp. 211–219, text fig. 1, 2 maps.

Lugn, Alvin L.

1935.1 The Pleistocene Geology of Nebraska. Neb. Geol. Surv., (2), Bull. 10, pp. 1–223, Pls. i, ii, text figs. 1–38, tables A-D.

1939.1 Classification of the Tertiary System in Nebraska. Bull. Geol. Soc. Amer., L, No. 8, pp. 1245–1275, 1 pl.

Use of the long abandoned name Ogallala for a large stratigraphic group of Pliocene age.

MacCurdy, George Grant

1924.1 Human Origins. A Manual of Prehistory. 8vo, D. Appleton and Company, New York, I, pp. xxxviii+440, frontispiece, text figs. 1–254; II, pp. xvi+516, frontispiece, text figs. 255–410.

Makiyama, Jiro

1929.1 Chikyû-The Globe, XII, No. 5, pp. 364, 365 (in Japanese). Not available to the present author.

New subspecies: *Elephas* (*Palæoloxodon*) *namadicus setoensis*.

1938.1 Japonic Proboscidea. Mem. College Sci. Kyoto Imp. Univ., (B), XIV, No. 1, Art. 1, May, pp. 1–59, text figs. 1–31.

New species: *Bunolophodon yokotii*, pp. 12–14, figs. 5a, 5b. *Stegodon shodoensis akashiensis* (Takai, 1936) = *Parastegodon akashiensis* (p. 21). *Stegodon insignis sugiyamai* (Tokunaga, 1936) = *Parastegon sugiyamai* (p. 27).

Mansuy, H.

1916.1 Sur Quelques Mammifères Fossiles Récemment Découverts en Indochine. Mem. Serv. Geol. Indochine, V, Fasc. II, pp. 1–26, Pls. i-vii, 1 text fig.

Stegodon insignis, *S. Cliftii*, *Elephas* sp. ? aff. *E. namadicus*, *E. namadicus*, and *E. indicus*.

Mather, Cotton

1717.1 An Extract of Several Letters from Cotton Mather, D. D. to John Woodward, M. D. and Richard Waller, Esq.; S. R. Secr. Phil. Trans., XXIX, No. 339, for April, May, and June, 1714, pp. 62–71.

Matsumoto, Hikoshichiro

1939.1 On Some Fossil Elephants from Province of Kazusa, from Province of Shimotsuke, and from other Localities. Dobutugaku Zassi (Zool. Mag., Tokyo), LI, No. 10, October, pp. 701–717, text figs. 1–8.

New species: *Archidiskodon paramammonteus*, pp. 704, and 716 (English)

Matthew, William Diller

1924.1 Third Contribution to the Snake Creek Fauna. Bull. Amer. Mus. Nat. Hist., L, Art. II, July 3, pp. 59–210, text figs. 1–63.

Matthew, William Diller, and Ruben Arthur Stirton

1930.1 Equidae from the Pliocene of Texas. Bull. Dept. Geol. Univ. Calif., XIX, No. 17, November 29, pp. 349–396, Pls. xlv-lviii.

Maxson, John H.

1930.1 A Tertiary Mammalian Fauna from the Mint Canyon Formation of Southern California. Publ. Carnegie Instn. Wash., No. 404, August, pp. 77–112, text figs. 1–18.

Merriam, John Campbell

1919.1 Tertiary Mammalian Faunas of the Mohave Desert. Bull. Dept. Geol. Univ. Calif., XI, No. 5, pp. 437a-e, 438–585, text figs. 1–253.

Fauna of the Barstow formation.

Merriam, John Campbell, Chester Stock, and C. L. Moody

1925.1 The Pliocene Rattlesnake Formation and Fauna of Eastern Oregon, with Notes on the Geology of the Rattlesnake and Mascall Deposits. Publ. Carnegie Instn. Wash., No. 347, October 8, pp. 43–92, text figs. 1–45.

Meyer, Hermann von

1841.1 Fossile Knochen von Wiesbaden. Neues Jahrb. Min., pp. 458–461.

New species: *Dinotherium minutum*, p. 459

Middendorf, Alexander Theodor von

1860.1 Übersicht der Natur Nord- und Ost-Sibiriens. Reise in den Äussersten Norden und Osten Sibiriens wahrend der Jahre 1843 und 1844. . ., IV, Th. I, Lief. 2, pp. 201–332. 4to, St. Petersburg.

Moir, J. Reid, and Arthur Tindell Hopwood

1939.1 Excavations at Brundon, Suffolk (1935–37). Part I. Stratigraphy and Archaeology (Moir). Part II. Fossil Mammals (Hopwood). Proc. Prehist. Soc., (N. S.), V, No. 1, pp. 1–32, Pls. i, ii, text figs. 1–18.

Moody, C. L., John Campbell Merriam, and Chester Stock

1925.1 See Merriam, John Campbell, Chester Stock, and C. L. Moody.

Morris, Frederick K., and Charles P. Berkey

1927.1 See Berkey, Charles P., and Frederick K. Morris.

Osborn, Henry Fairfield

1933.901 Biological Inductions from the Evolution of the Proboscidea. Proc. Nat. Acad. Sci., XIX, No. 1, January, pp. 159–163.

1935.940 The Record Proboscidean Tusk. Nat Hist., XXXV, April, p. 357. (Unsigned article.)

Record tusk of *Archidiskodon imperator* from Texas.

1936.951 L'Age Géologique de l'Homme de Piltdown (Eoanthropus) et de l'Homme de Trinil (Pithecanthropus). Mélanges de Préhistoire et d'Anthropologie offerts au Professeur Henri Bégouen a l'occasion de son 70ᵉ Anniversaire (20 Novembre, 1863–1933) par ses Élèves, ses Collègues et ses Amis, pp. 23–36, text figs. 1–6.

These sheets were received September 28, 1936, with a letter from Comte Bégouen in which he says: ". . . L'impression fut meme un instant arretée et elle vient de recommencer. Je vous envoie, sous pli separé, en justificatif les premières bonnes feuilles. . . ." No other sheets have been received.

1938.952 Eighteen Principles of Adaptation in Alloiometrons and Aristogenes. Palaeobiologica, VI, pp. 273–302, text figs. 1–12.

Paterson, T. T., Hellmut de Terra, and Pierre Teilhard de Chardin

1936.1 See Terra, Hellmut de, Pierre Teilhard de Chardin, and T. T. Paterson.

Peale, Rembrandt

1802.1 Account of the Skeleton of the Mammoth, a Non-Descript Carnivorous Animal of immense Size found in America. Sm. 8vo, London, 46 pp.

1803.1 An Historical Disquisition on the Mammoth, or, Great American Incognitum, an Extinct, Immense, Carnivorous Animal, whose Fossil Remains have been found in North America. 12mo, E. Lawrence, London, pp. viii+91, 1 pl.

Pei, W. C., Davidson Black, Pierre Teilhard de Chardin, and Chung-Chien Young

1933.1 See Black, Davidson, Pierre Teilhard de Chardin, Chung-Chien Young, and W. C. Pei.

Pfizenmayer, F. W.

1937.1 Mammut-Funde in Sibirien. Natur u. Volk, LXVII, June, pp. 279–288, text figs. 6–14.

Sangajurach-Mammuts.

Piette, Édouard

1907.1 L'Art pendant l'Age du Renne. 4to, Masson et Cie., Paris, pp. iv+12, 100 pls., 128 text figs.

Pilgrim, Guy Ellcock

1931.1 Catalogue of the Pontian Carnivora of Europe in the Department of Geology. 4to, British Museum (Natural History), London, pp. vi+174, 2 pls., 30 text figs.

1934.1 Correlation of Ossiferous Sections in the Upper Cenozoic of India. Amer. Mus. Novitates, No. 704, March 15, pp. 1–5.

Pilgrim, Guy Ellcock—Continued

1939.1 The Fossil Bovidae of India. Mem. Geol. Surv. India, Palaeont. Indica, N. S., XXVI, Mem. 1, pp. iii+356, 8 pls., 35 text figs.

1940.1 The Application of the European Time Scale to the Upper Tertiary of North America. Geol. Mag., LXXVII, pp. 1–27.

Pilgrim, Guy Ellcock, and Arthur Tindell Hopwood

1939.1 Are the Equidae Reliable for the Correlation of the Siwaliks with the Coenozoic Stages of North America (Pilgrim). Appendix on the Correlation of Certain Tertiary Deposits of India and Europe (Hopwood). Rec. Geol. Surv. India, LXXIII, Pt. 4, December, 1938, pp. 437–482.

Piveteau, Jean, and Marcellin Boule

1935.1 See Boule, Marcellin, and Jean Piveteau.

Pohlig, Hans

1887.3 [Casts of Elephant Teeth, E. antiquus typus and E. antiquus var. minor.] Verh. natur. Vereins preuss. Rhein., Jahrg. XLIV, p. 115. Bonn.

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Pontier, G.

1930.1 A propos d'Anomalies dentaires observées chez les Proboscidiens. Ann. Soc. géol. du Nord, LV, pp. 2–10, Pls. i, ii.

Roman, F., and J. Viret

1934.1 La Faune de Mammifères du Burdigalien de la Romieu (Gers). Mem. Soc. géol. France, (N. S.),IX, Fasc. 2–3, (Mem. No. 21), pp. 1–67, Pls. i-xix, text figs. 1–25.

Romer, Alfred Sherwood

1933.1 Pleistocene Vertebrates and their Bearing on the Problem of Human Antiquity in North America. In "The American Aborigines, Their Origin and Antiquity," edited by Diamond Jenness. 8vo, University of Toronto Press, pp. 47–83.

Roverto, Cayetano

1914.1 Los Estratos Araucanos y Sus Fosiles. An. Mus. Nac. Hist. Nat. Buenos Aires, XXV, pp. 1–249, Pls. i-xxxi, text figs. 1–92.

Rusconi, Carlos

1937.1 Contribucion al conocimiento de la geologia de la ciudad de Buenos Aires y sus alrededores y referencia de su fauna. Actas Acad. Nac. Cien. Córdoba, X, Nos. 3–4, December 20, pp. 177–384, Pls. i-xix, text figs. 1-58. Buenos Aires.

Russell, R. Dana, and V. L. VanderHoof

1931.1 A Vertebrate Fauna from a New Pliocene Formation in Northern California. Bull. Dept. Geol. Univ. Calif., XX, No. 2, February 5, pp. 11–21, text figs. 1–7.

Tehama formation named and described. Contains *Stegomastodon* cf. *arizonæ.*

Saheki, Shirô

1931.1 On Parelephas protomammonteus (Matsumoto) Recently Found in the Province of Kazusa. Japanese Journ. Geol. and Geog., VIII, No. 3, February, pp. 125–129, Pl. xv, 1 text fig.

New subspecies: *Parelephas protomammonteus* (Matsumoto) *matsumotoi*, p 127.

Schneider, Carlos Oliver

1929.1 La Distribución Geográfica de los Mastodontes en Chile. Actes Soc. Scientifique Chili, XXXVI, pp. 73–83, 1 map. Santiago.

1930.1 Algunos comentarios sobre mastodontes chilenos. Revista Universitaria (Univ. Católica de Chile), No. 8, Ano XV, pp. 886–893. Santiago.

Remarks on the questionable type locality of *Mastodon [Cuvieronius] humboldtii.*

Schroeder, Henry

1928.1 Über Elephas antiquus und trogontherii aus dem Diluvium der Mittelmark. Jahrb. Preuss. Geol. Landesanstalt, Berlin, XLVIII, for the year 1927, pp. 699–723, Pls. xxxiv-xxxvi, text fig. 1.

New subspecies: *Elephas primigenius* Blumenb. var. n. *pachyganalis*, p. 718.

Schultz, Charles Bertrand, and Erwin Hinckley Barbour

1937.1 See Barbour, Erwin Hinckley, and Charles Bertrand Schultz.

Scott, William Berryman

1937.1 A History of Land Mammals in the Western Hemisphere. Revised edition, 8vo, Macmillan Company, New York, pp. xiv+786, frontispiece, 420 text figs.

New family: Stegomastodontidæ. New subfamilies: Trilophodontinæ, Pentalophodontinæ, Cordillerioninæ, Stegomastodontinæ.

Serebryakov, A. H.

1938.1 Elephas mammonteus Cuvier versus E. primigenius Blumenbach. Bull. Acad. Sci. U. S. S. R., Classe des Sci. Math. et Nat., Serie Biol., pp. 1063–1068.

He regards the name *Elephas primigenius* Blumenbach (1799) as an indisputable *nomen nudum*, hence must be rejected, and maintains that *E. mammonteus* Cuvier (1799) must be restored, recognizing as the type the skull described by Messerschmidt in 1721, or Adams' mammoth (Tilesius, 1815).

Shikama, Tokio

1936.1 Note on Parastegodon akashiensis Takai from the Akasi District. Proc. Imp. Acad., Tokyo, XII, No. 1, January, pp. 22–24, text figs. 1–4.

1937.1 Parastegodon infrequens sp. nov. from the Akasi District. Japanese Journ. Geol. and Geog., XIV, Nos. 3–4. October, pp. 127–131, Pl. ix.

1937.2 Nomenclative Notes on Parelephas Protomammonteus (Matsumoto). Japanese Journ. Geol. and Geog., XIV, Nos. 3–4, October, pp. 163–166.

New subspecies: *Parelephas proximus uchataensis.*

Shuler, Ellis W.

1934.1 Collecting Fossil Elephants at Dallas, Texas. Bull. Texas Archaeol. and Palaeont. Soc., VI, September, pp. 75–79, Pl. xii.

Soergel, Wolfgang

1921.3 Die Ursachen der diluvialen Aufschotterung und Erosion. 8vo, Borntraeger, Berlin, pp. iv+74, 1 text fig.

1925.1 Die Säugetierfauna des altdiluvialen Tonlagers von Jockgrim in der Pfalz. Zeits. Deutsch. Geol. Ges., LXXVII, Heft 3, November 20, pp. 405–438, Taf. xvii, 2 tabellen.

Spock, Leslie Erskine

1930.1 New Mesozoic and Cenozoic Formations encountered by the Central Asiatic Expeditions in 1928. Amer. Mus. Novitates, No. 407, March 18, pp. 1–8, text figs. 1–6.

Stamp, L. Dudley

1922.1 An Outline of the Tertiary Geology of Burma. Geol. Mag., LIX, No. 11, November, pp. 481–501, text figs. 1–6.

Stehlin, Hans Georg

1908.1 Notices paléomammalogiques sur quelques dépôts Miocènes des Bassins de la Loire et de l'Allier. Bull. Soc. géol. France, (4), VII, for the year 1907, pp. 525–550, text figs. 1–3.

Stehlin, Hans Georg, and Auguste Dubois

1932.1 and **1933.1** See Dubois, Auguste, and Hans Georg Stehlin.

Sternberg, C. M.

1930.2 Miocene Gravels in Southern Saskatchewan. Trans. Roy. Soc. Canada, (3), XXIV, Sec. 4, pp. 29, 30.

The scanty and fragmentary fauna includes an indeterminate Mastodont.

Stirton, Ruben Arthur

1933.1 A Critical Review of the Mint Canyon Mammalian Fauna and its Correlative Significance. Amer. Journ. Sci., (5), XXVI, December, pp. 569–576.

1936.1 Succession of North American Continental Pliocene Mammalian Faunas. Amer. Journ. Sci., (5), XXXII, pp. 161–206.

1939.1 Methods and Procedure in the Valentine Question. Amer. Journ. Sci., CCXXXVII, pp. 429–433.

Stirton, Ruben Arthur, and William Diller Matthew

1930.1 See Matthew, William Diller, and Ruben Arthur Stirton.

Stock, Chester

1928.1 Canid and Proboscidean Remains from the Ricardo Deposits, Mohave Desert, California. Publ. Carnegie Instn. Wash., No. 393, pp. 39–47, Pls. i-iv, text fig. 1.

Trilophodon sp., consisting of fragmentary skull, incomplete mandibular ramus, humerus, femur, and a calcaneum, found at three distinct localities in the Ricardo deposits.

1936.1 A Pliomastodon Skull from the Thousand Creek Beds, Northwestern Nevada. Publ. Carnegie Instn. Wash., No. 473, July 10, pp. 35–39, Pl. i.

New species: *Pliomastodon nevadanus*, p. 37.

Stock, Chester, John Campbell Merriam, and C. L. Moody

1925.1 See Merriam, John Campbell, Chester Stock, and C. L. Moody.

Stromer, Ernst

1907.1 Geologische Beobachtungen im Fajûm und am unteren Niltale in Ägypten. Abhand. Senckenb. naturf. Ges., XXIX, Heft 2, pp. 133–148, Taf. xxi.

Takai, Fuyuji

1936.1 On a New Fossil Elephant from Okubo-mura, Akashi-gun, Hyogo Prefecture, Japan. Proc. Imp. Acad., Tokyo, XII, No. 1, January, pp. 19–21, text figs. 1, 2.

New species: *Parastegodon akashiensis*, p. 20.

1936.2 Fossil Elephants from Tiba Prefecture, Japan. Japanese Journ. Geol. and Geog., XIII, Nos. 3–4, October, pp. 197–203, Pl. xxiv, text fig. 1.

The author states that from "this district, the following species have thus far been reported:
Stegodon orientalis Owen.
Parelephas protomammonteus typicus Matsumoto.
P. protomammonteus proximus Matsumoto.
P. protomammonteus matsumotoi Saheki.
Palaeoloxodon naumanni (Makiyama)."

Takai, Fuyuji, and Shigeyasu Tokunaga

1936.1 See Tokunaga, Shigeyasu, and Fuyuji Takai.

Teilhard de Chardin, Pierre

1937.1 The Post-Villafranchian Interval in North China. Bull. Geol. Soc. China, XVII, No. 2, June, pp. 169–176, text fig. 1.

Teilhard de Chardin, Pierre, Davidson Black, Chung-Chien Young, and W. C. Pei

1933.1 See Black, Davidson, Pierre Teilhard de Chardin, Chung-Chien Young, and W. C. Pei.

Teilhard de Chardin, Pierre, and Hellmut de Terra

1936.1 See Terra, Hellmut de, and Pierre Teilhard de Chardin.

Teilhard de Chardin, Pierre, Hellmut de Terra, and T. T. Paterson

1936.1 See Terra, Hellmut de, Pierre Teilhard de Chardin, and T. T. Paterson.

Teilhard de Chardin, Pierre, and M. Trassaert

1937.1 The Proboscideans of South-Eastern Shansi. (Yushê basin). Pal. Sinica, (C), XIII, Fasc. 1, March, pp. 1–84 (also 4 pp. in Chinese), Pls. i-xiii, text figs. 1–6.

New species: *Pentalophodon cuneatus*, p. 11; *Mastodon intermedius*, p. 22; *Stegodon licenti*, p. 27.

Teilhard de Chardin, Pierre, and Chung-Chien Young

1936.1 On the Mammalian Remains from the Archæological Site of Anyang. Pal. Sinica, (C), XII, Fasc. 1, pp. iii-61 (also 8 pp. in Chinese), Pls. i-viii, text figs. 1–26.

Terra, Hellmut de

1936.1 Late Cenozoic History in India. Nature, CXXXVII, No. 3469, April 25, pp. 686–688.

Terra, Hellmut de, and G. E. Hutchinson

1936.1 Data on Post-Glacial Climatic Changes in North-West India. Current Science, V, July, pp. 5–10. Bangalore City.

Terra, Hellmut de, and Pierre Teilhard de Chardin

1936.1 Observations on the Upper Siwalik Formation and Later Pleistocene Deposits in India. Proc. Amer. Phil. Soc., LXXVI, pp. 791–822, text figs. 1–14.

Terra, Hellmut de, Pierre Teilhard de Chardin, and T. T. Paterson

1936.1 Joint Geological and Prehistoric Studies of the Late Cenozoic in India. Science, (N. S.), LXXXIII, No. 2149, March 6, pp. 233–236.

Thomas, Oldfield

1895.1 An Analysis of the Mammalian Generic Names given in Dr. C. W. L. Gloger's "Naturgeschichte" (1841). Ann. Mag. Nat. Hist., (6), XV, pp. 189–193.

Tobien, H.

1938.1 Über Hipparion-Reste aus der obermiozänen Süsswassermolasse Südwestdeutschlands. Zeits. Deutsch. Geol. Ges., XC, Heft 4, May 5, pp. 177–192, Taf, vi.

Tokunaga, Shigeyasu

1933.2 A List of the Fossil Land Mammals of Japan and Korea with Descriptions of New Eocene Forms from Korea. Amer. Mus. Novitates, No. 627, May 27, pp. 1–7, text figs. 1, 2.

1934.1 Fossil Elephant teeth found at Yokohama and Kakio, Kanagawa Prefecture. Journ. Geog., XLVI, No. 546, July, pp. 363–371, Pls. viii, ix, 5 text figs. Tokyo.

New species: *Palaeoloxodon yokohamanus*, p. 363, Pl. vii; *Parastegodon? kwantoensis*, p. 365, Pl. ix. Text in Japanese.

1935.1 A New Fossil Elephant found in Shikoku, Japan. Proc. Imp. Acad., Tokyo, XI, No. 10, December, pp. 432–434, text fig. 1.

New species: *Parastegodon sugiyamai*.

Tokunaga, Shigeyasu – Continued

1936.1 Geology of the District of Shichinohe and Fossil Elephant found there. Journ. Geog., XLVIII, No. 564, February, pp. 67–70, Pl. i. Tokyo.

Original description (in Japanese) of *Palaeoloxodon aomoriensis*, p. 70.

Tokunaga, Shigeyasu, and Fuyuji Takai

1936.1 On a Fossil Elephant, Palaeoloxodon aomoriensis, from Shichinohe, Kamikata-gun, Aomori Prefecture, Japan. Journ. Geol. Soc. Japan, XLIII, No. 511, April 20, pp. 254–258, Pls. xiii (iii), xiv (iv).

Type description (in English) of *Palaeoloxodon aomoriensis*.

Trassaert, M., and Emile Licent

1935.1 See Licent, Emile, and M. Trassaert.

Trassaert, M., and Pierre Teilhard de Chardin

1937.1 See Teilhard de Chardin, Pierre, and M. Trassaert.

Troxell, Edward L.

1916.1 An Early Pliocene One-Toed Horse, Pliohippus lullianus, sp. nov. Amer. Journ. Sci., (4), XLII, October, pp. 335–348, text figs. 1–7.

Oak Creek formation named and described, pp. 345–348.

VanderHoof, V. L.

1933.1 Additions to the Fauna of the Tehama Upper Pliocene of Northern California. Amer. Journ. Sci., (5), XXV, pp. 382–384.

VanderHoof, V. L., and R. Dana Russell

1931.1 See Russell, R. Dana, and V. L. VanderHoof.

Van Es, L. J. C.

1931.1 The Age of Pithecanthropus. 8vo, Martinus Nijhoff, The Hague, pp. xii+142, 4 pls., 11 maps.

van Riet Lowe, C.

1929.1 Further Notes on the Archaeology of Sheppard Island. So. Afr. Journ. Sci., XXVI, pp. 665–683, text figs. 1–5.

Excellent table of associated fauna during the Pleistocene, including among the Proboscidea *Mastodon* (*Bunolophodon*) sp. [=*Trilophodon*], *Archidiskodon subplanifrons*, and *A.* [=*Palæoloxodon*] *transvaalensis* and *A.* [=*Palæoloxodon*] *sheppardi* of the early Pleistocene, to *A. broomi* of the late Pleistocene. Stellenbosch industry of the Stone Age.

Viret, J., and F. Roman

1934.1 See Roman, F., and J. Viret.

Ward, Rowland

1922.1 Rowland Ward's Records of Big Game with Their Distribution, Characteristics, Dimensions, Weights, and Horn and Tusk Measurements. Eighth edition edited by J. G. Dollman and J. B. Burlace, 8vo, Rowland Ward, London, pp. xiii+527, illustrated.

1928.1 Rowland Ward's Records of Big Game with Their Distribution, Characteristics, Dimensions, Weights, and Horn and Tusk Measurements. Ninth edition edited by J. G. Dollman and J.B.Burlace, 8vo, Rowland Ward, London, pp. xiii+523, illustrated.

Weber, Max

1896.1 [1897] Vorstudien über das Hirngewicht der Säugethiere. Festschrift z. Siebenzigsten Geburtstage von Carl Gegenbaur, III, pp. 103–123.

Wilmarth, M. Grace

1938.1 Lexicon of Geologic Names of the United States (including Alaska). Bull. U. S. Geol. Surv. 896: Part 1, A-L, pp. 1–1244; Part 2, M-Z, pp. 1245–2396.

Young, Chung-Chien, and Pierre Teilhard de Chardin

1936.1 See Teilhard de Chardin, Pierre, and Chung-Chien Young.

Young, Chung-Chien, Davidson Black, Pierre Teilhard de Chardin, and W. C. Pei

1933.1 See Black, Davidson, Pierre Teilhard de Chardin, Chung-Chien Young, and W. C. Pei.

Zittel, Karl Alfred von

1925.1 Text-book of Palaeontology. III, Mammalia. 8vo, Macmillan and Company, London, pp. viii+316, 374 text figs.

PLATES XXVI—XXX

PLATE XXVI

PLATE XXVI

Fig. 1. *Elephas indicus.* Complete transverse section near tip of unerupted tusk, probably of an immature female. Ordinary light. Seven times natural size.

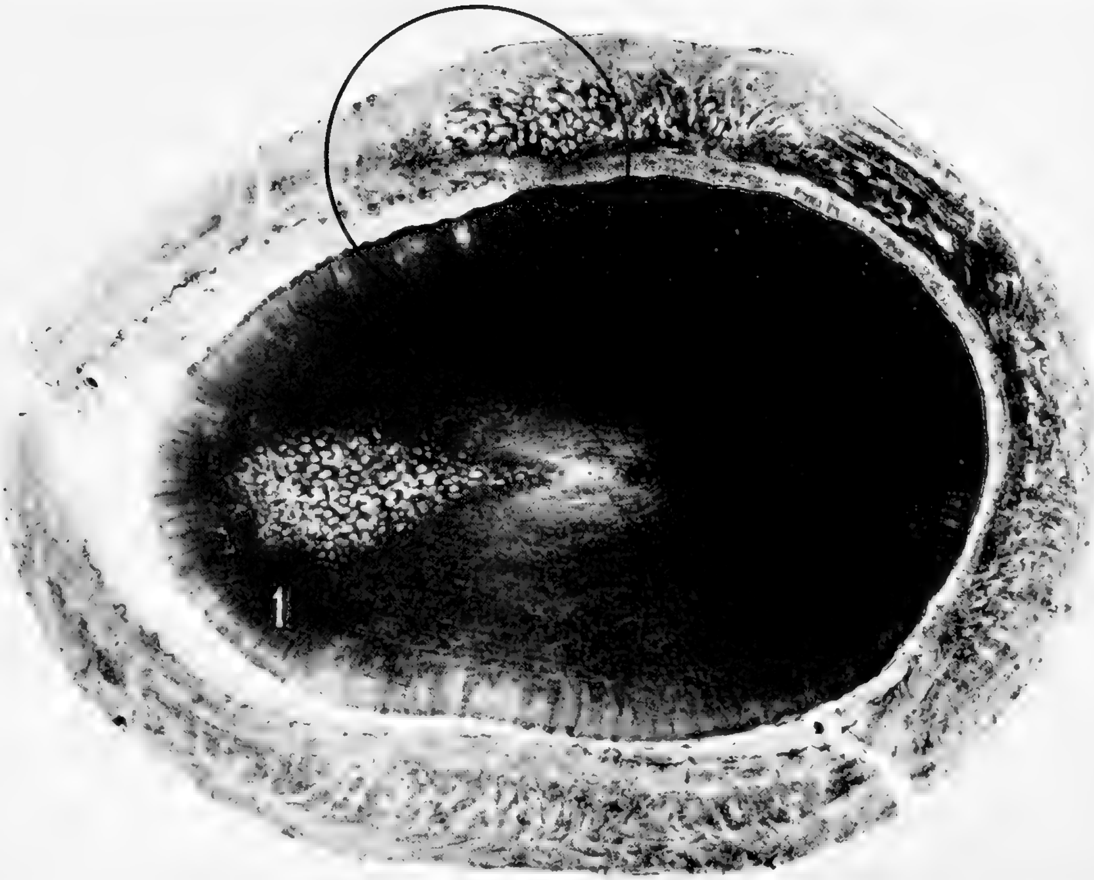
The dark central area is dentine. In it, to the left, is a triangular area of tubular or cylindrical structure, suggestive of the development in *Platybelodon* and its allies, but absent in the later dentine of *Elephas.* The "engine-turning" effect is not visible in this juvenile dentine. An enamel band encircles about two-thirds of the circumference of the dentine, being absent only to the right and upper right in the photograph. Much of it has been lost in making the section to the left, where it is thickest, but elsewhere it is clearly visible as a relatively transparent and homogeneous tissue. The whole tusk is here encased in a thick layer of cement, irregular in structure but in general with relatively dense, laminated internal and external zones and a thicker, non-laminated intermediate zone, with large canals rather like the Haversian canals of bone.

Fig. 2. *Elephas indicus.* Area of thin section within the circle on figure 1. Plane light. Nineteen times natural size.

The dark, lower region is dentine and the irregular, spotty mass forming the greater part of the photograph is cement. Between these, to the left, is the enamel band, ending naturally near the middle of the photograph. It is sharply defined, the dentine border undulating and the cement border rugose. In the cement, the part to the right clearly shows the three layers, inner and outer dense and vaguely laminated, middle spongy, all with innumerable lacunæ.

Fig. 3. *Elephas indicus.* Same as figure 2, photographed between crossed nicols.

The enamel is characterized by high birefringence and relative simplicity and homogeneity of rod arrangement, with a narrow zone of deflection, dark as photographed, parallel to the dentine border. The cement also shows birefringence but is highly irregular with little consistent orientation except in the inner (lower) layer.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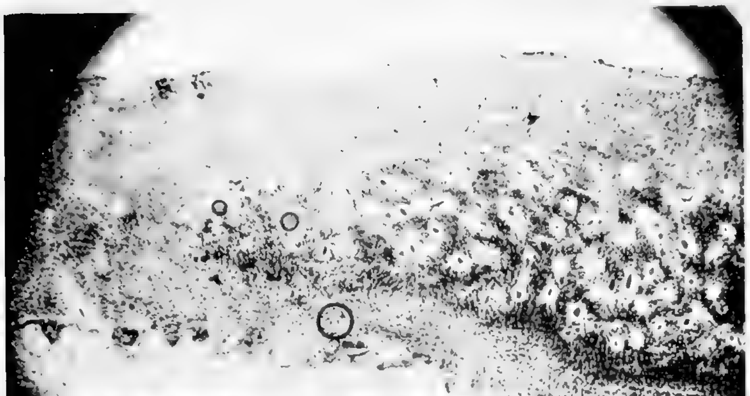
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PLATE XXVII

PLATE XXVII

Fig. 1. *Elephas indicus.* Area within the circle on Pl. XXVI, Fig. 2. Plane light. Three hundred thirty-seven times natural size.

In this innermost area of the cement, just above the enamel, lacunæ are very numerous and have many branching canaliculi. There are also more sparse, small tubules, one of which appears in the upper right in this figure.

Fig. 2. *Elephas indicus.* Transverse section of about half of a small, mature tusk about 14 inches long. Ordinary light. Four times natural size.

The section is taken about 3 inches from the tip of the tusk. Several inches had been worn off, including all the enamel and most of the cement. At this point, there is only a thin band of cement, seen in the figure as a more translucent coating above the dense dentine. The dentine as a whole shows three distinct, superimposed types of structure: (a) radiating tubes, too small to be clearly seen in this figure, directed away from the center of the tusk, (b) well-marked, fine, concentric lamellæ, (c) curving, criss-cross markings of coarser character, visible as dark lines in the thinner parts of this section, that give the "engine-turning" effect. This last effect appears to be the result of regularly recurring undulations in the courses of the dentine tubes and in the orientation of the surrounding calcified mass. (The prominent white lines are scratches on the section.)

Fig. 3. *Elephas indicus.* Part of the section within the circle on figure 2. Plane light. Forty times natural size.

This shows the whole thickness of the cement on this part of the tusk. In ordinary light the cement here appears vaguely laminated, with fairly numerous lacunæ but no trabeculæ or canals. The boundary against the dentine is smooth and very sharp.

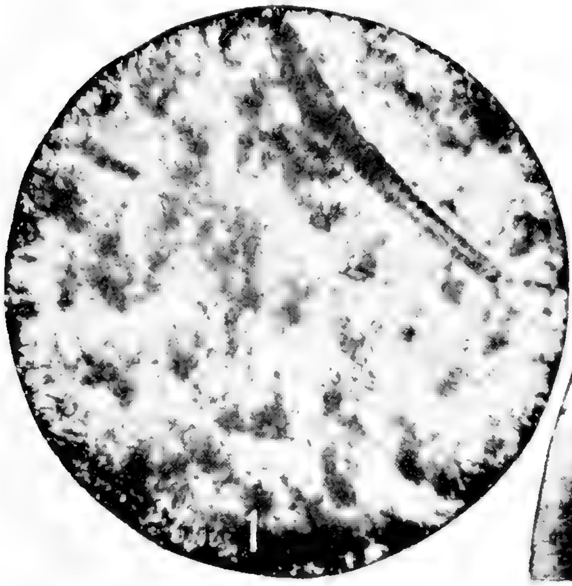
Fig. 4. *Elephas indicus.* Same as figure 3, with crossed nicols. The effect of strong birefringence in the cement is to bring out a wavy, interwoven, fabric-like structure in this tissue.

Fig. 5. *Elephas indicus.* A small area near the outer edge of the cement band of the section shown in figures 2–4. Plane light. Three hundred thirty-seven times natural size.

This shows a fabric-like texture similar to that seen more plainly and on a larger scale in figure 4. The lacunæ have very few and very short canaliculi and most of them appear to be empty (or filled with colorless fluid) in this section of a fresh tooth. Contrast with this figure 1, which shows the abundant canaliculi and opaque appearance typical of younger cement. The inner part of the cement in the present section, near the dentine, is about intermediate between the two conditions.

Fig. 6. *Phiomia wintoni.* Transverse thin section about one-half inch from tip of small, worn tusk. Plane light. Thirty-eight times natural size.

The lower part of the section is dentine and above this is the whole thickness of the enamel, cut at right angles to its surface. The clear bands in the dentine are caused by infiltration of the embedding medium into the cut ends of tubes and these zones, in fact, have tubes like those seen so clearly in the lower part of the picture. For details of enamel and of enamel-dentine junction see Pl. XXVIII, Fig. 2. There is no indication of cement on this tusk.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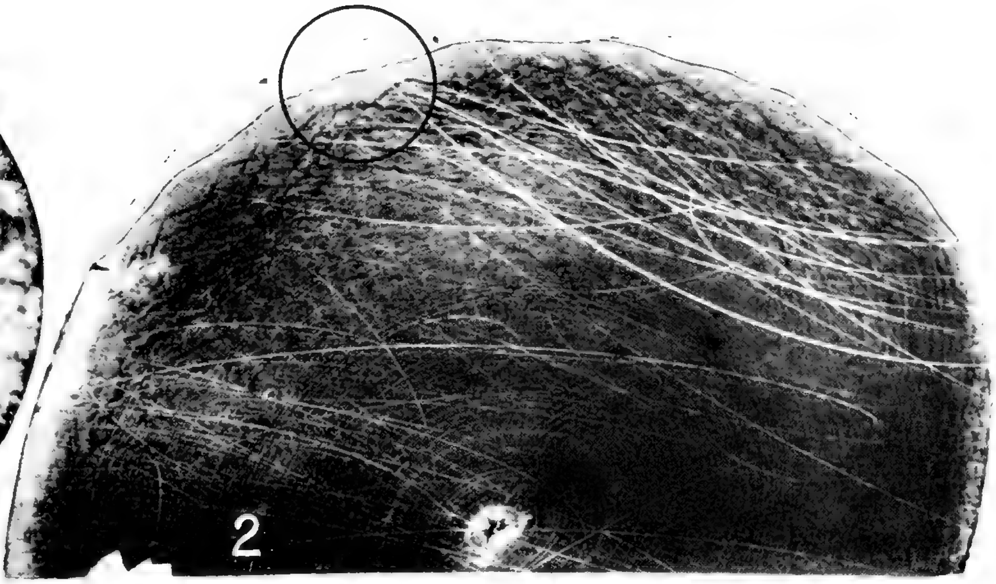
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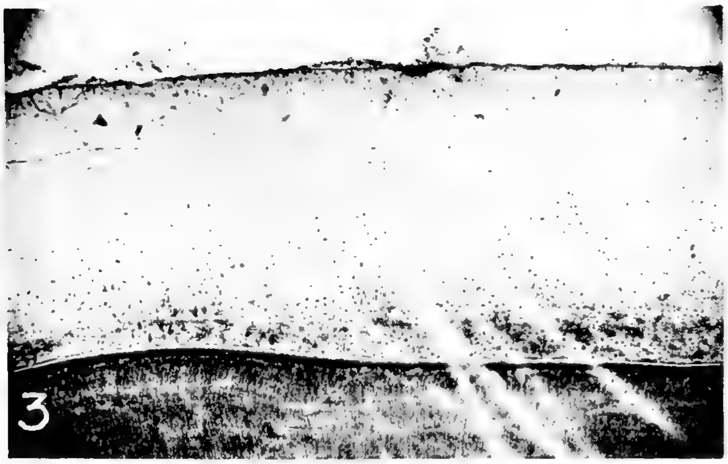
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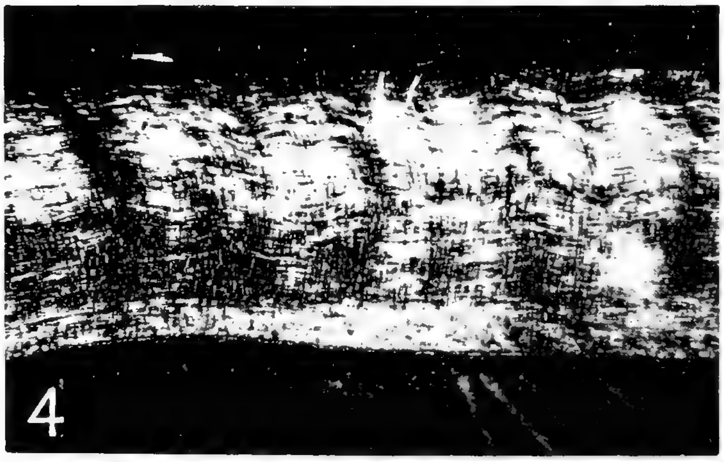
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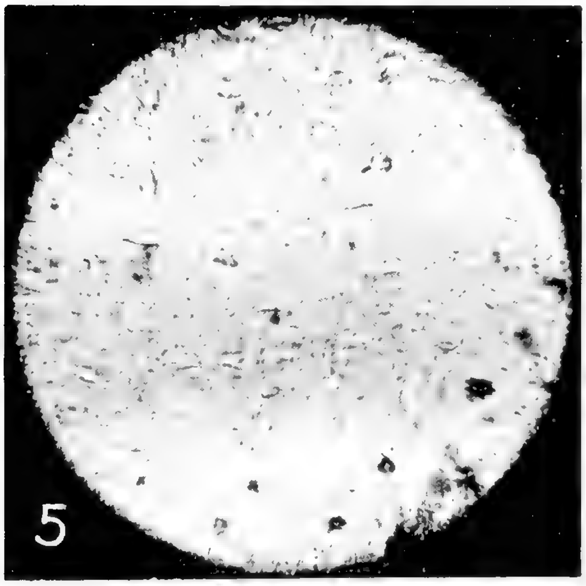
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PLATE XXVIII

PLATE XXVIII

Fig. 1. *Phiomia wintoni.* Same as Pl. XXVII, Fig. 6, with crossed nicols.

The dentine is not birefringent. The enamel is strongly birefringent and variations in extinction angle show the varying orientations of the rods through the greater part of the thickness of the enamel, but near the outer surface (up in the photograph) the illumination is even and shows the rods there to be essentially parallel.

Fig. 2. *Phiomia wintoni.* Area within the circle on Pl. XXVII, Fig. 6. Ordinary light. About three hundred times natural size. Photograph by Dr. J. Leon Williams.

The small bottom area in the photograph shows part of the granular layer of the dentine. Above this is the sharp enamel boundary, and then the full thickness of the enamel. Natural staining and variable refringence clearly brings out the pattern of the enamel rods, which lie in long, open spirals through most of the thickness of the enamel and become approximately straight and perpendicular to the surface only in the outermost zone, which is on the order of .02 mm. in thickness. The enamel as a whole is here about .5 mm. in thickness.

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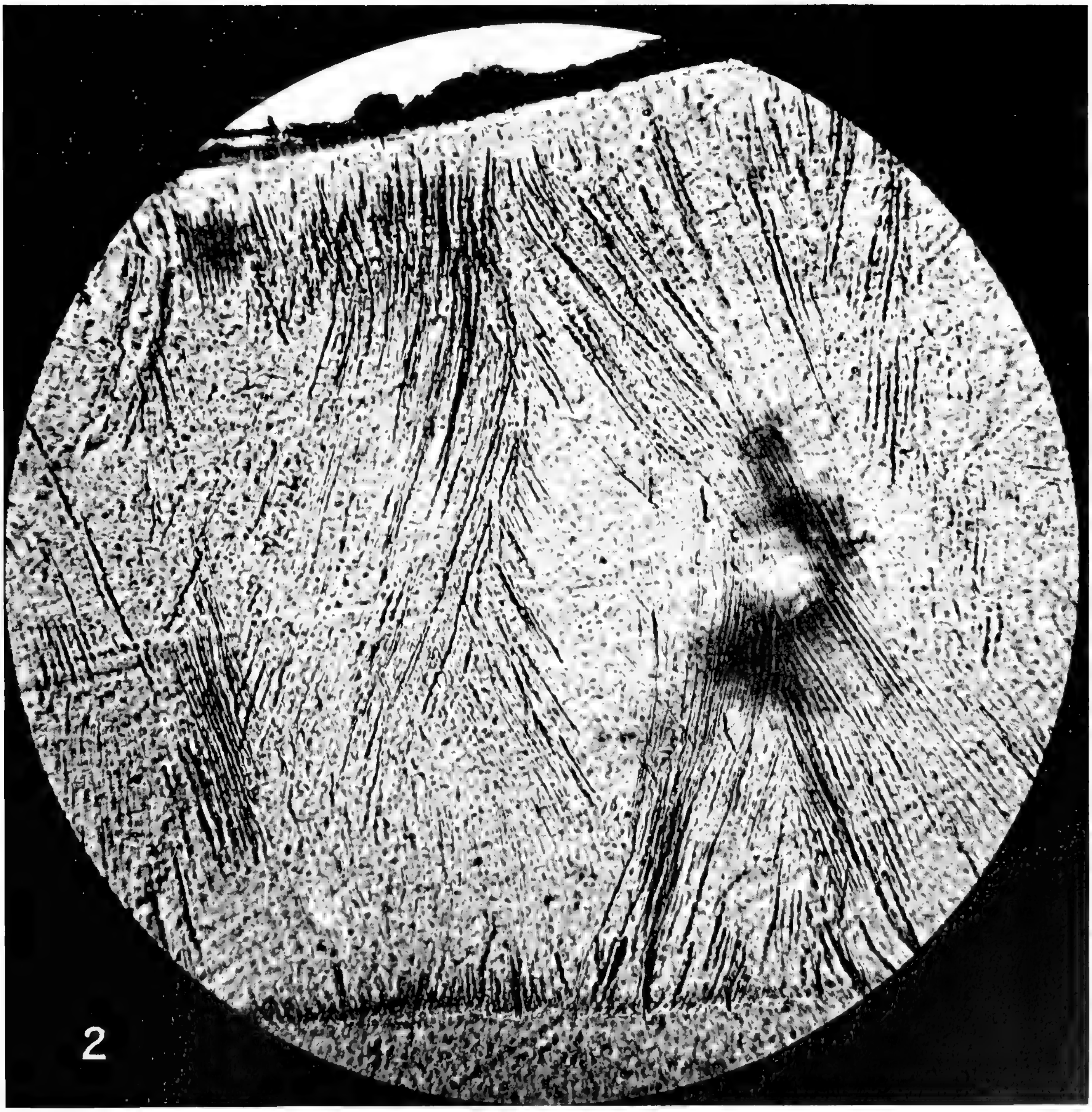

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PLATE XXIX

PLATE XXIX

Fig. 1. *Trilophodon obscurus.* Transverse section of part of tusk. Ordinary light. Four times natural size.

The bulk of the section is in the dentine in which the radial and concentric structures are shown, but not the "engine-turning" effect, which was, nevertheless, present. Above this the whole width of the enamel band is shown. There is no cement on the specimen as preserved, but this probably occurred when the tusk was fresh.

Fig. 2. *Trilophodon obscurus.* Area within circle on figure 1. Crossed nicols. Forty times natural size.

In this region the enamel rods are only very gently and obscurely spiral and tend rather to be parallel to each other in simple curves from the dentine to the outer surface. Toward the edge of the enamel band, to the left, the rods are strongly curved and the enamel overhangs a natural pocket. An isolated stringer of enamel occurred beyond this and its edge is barely visible at the left margin of the photograph. The enamel is also marked throughout by fine striations, not very prominent in the photograph, parallel to the outer surface even when this is strongly curved, as at the left of the photograph, and hence approximately at right angles to the enamel rods throughout. The dentine is very feebly birefringent and shows uneven lamination parallel to the surface.

Fig. 3. *Trilophodon obscurus.* Same tusk as figures 1 and 2, thin section across enamel cut in a plane vertical to the surface and parallel to the longitudinal axis of the tooth. Crossed nicols. Forty times natural size.

Away from the edge of the enamel band, the rods show a slight spiral arrangement much like that of *Phiomia* (Pl. XXVIII) in kind but far less in degree. Striations as seen in figure 2 are somewhat more prominent in this photograph.

Fig. 4. *Trilophodon* (*Megabelodon*) sp. Transverse thin section of tusk near edge of enamel band. Plane light. Eleven and a half times natural size.

The area covered by the lower part of the photograph was occupied by dentine, fragments of which can be seen although most of it has broken away. Above this is the enamel and cement covering. To the left is the edge of the main band of enamel. Beyond this to the right were five long, isolated stringers of enamel. Transverse sections of two of these are seen in the middle and to the right in the photograph and another is cut by the right margin. Between the main enamel band and the stringer in the middle of the photograph is a mass of cement. From thinner films around the stringers and main band and from the character of the enamel surface it appears that the enamel was all embedded in a coating of cement and was wholly exposed only at the wearing edge. The cement also extends in a thicker coating around the dentine beyond the last enamel stringer, outside the area of the photograph.

Fig. 5. *Trilophodon* (*Megabelodon*) sp. A different part of the same thin section as figure 4. Crossed nicols. Nineteen times natural size.

This photograph includes the last two enamel stringers, to the right of the three visible in figure 4. The strong birefringence clearly brings out the peculiar, fan-like divergence of the enamel rods in these stringers, which is equally developed in the other stringers and at the edge of the main enamel band. The stringers are separated and in part surrounded by a mass of cement so feebly birefringent that it can hardly be seen in the photograph.


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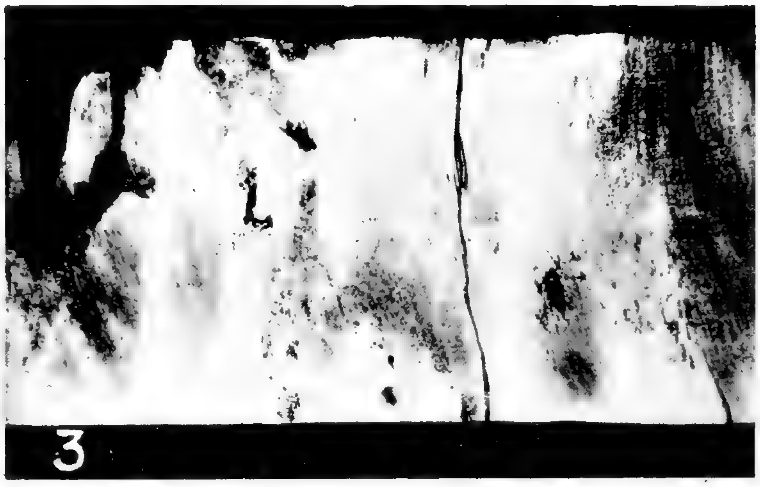
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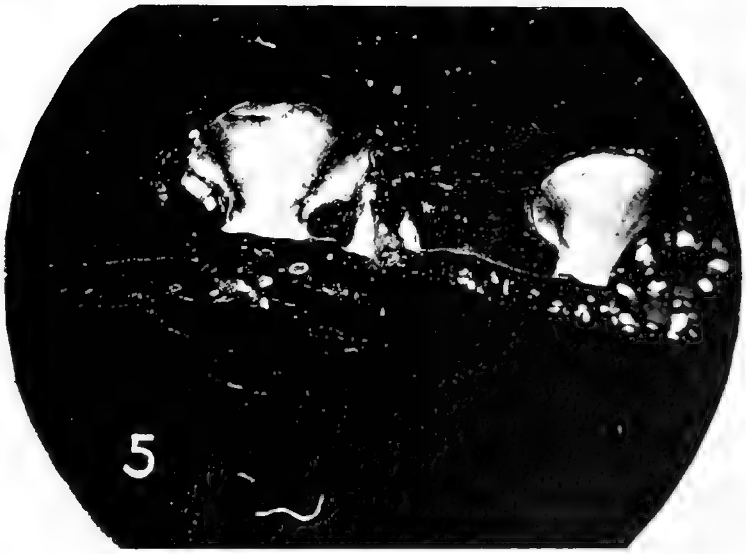
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PLATE XXX

PLATE XXX

Fig. 1. *Trilophodon* (*Megabelodon*) sp. Vertical thin section of broken molar tubercle. Ordinary light. Four times natural size.

The worn apex of the tubercle is at the top, dentine to the left, and enamel to the right. The enamel here reaches a thickness of about 5 mm. Aside from the mineral staining, largely casual but in part emphasizing natural structure, the most striking thing is the presence and orientation of the numerous enamel striations or laminations.

Fig. 2. *Trilophodon* (*Megabelodon*) sp. Part of section in circle on figure 1. Crossed nicols. Twenty times natural size.

To the left may be seen a small part of the dentine, worn into a pit above. The margin of the enamel is also a wear surface. Within the enamel the striations are emphasized by mineral stain as well as by birefringence and are very prominent, especially in the more internal part of the enamel where they are more wavy than externally. The enamel rods are less clearly distinguishable. In a thin inner zone, very obscure in the photograph (but see Fig. 4), they appear to be spiral. In the bulk of the section they are simple, nearly parallel, arranged in a sweeping curve becoming more horizontal as they pass from the inner (left) to outer (right) side of the enamel coating.

Fig. 3. *Trilophodon* (*Megabelodon*) sp. Transverse thin section of a molar cusp, from the same tooth as figures 1 and 2 but a different cusp. Ordinary light. Four times natural size.

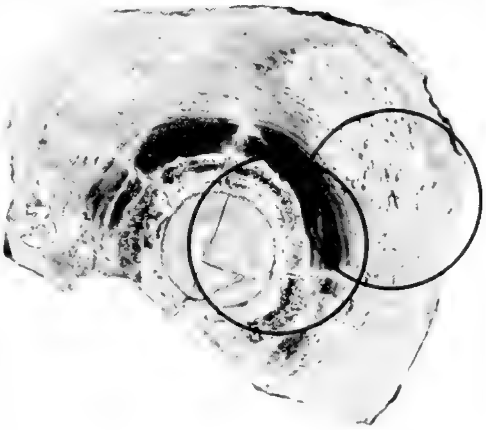
In the center is the circular core of dentine, about 4 mm. in diameter, and surrounding this (except where broken away, lower left) the enamel, 5–7 mm. in thickness. The dentine shows no pronounced structure. The enamel has an inner zone, about 1 mm. in thickness, with vague concentricity but no strong striations, and an outer zone of 4–6 mm. with pronounced concentric striations, which are homologous with those cut in a different plane in figures 1 and 2.

Fig. 4. *Trilophodon* (*Megabelodon*) sp. Part of section in inner circle on figure 3. Plane light. Forty times natural size.

To the left is the dentine with sharply visible tubules and terminating in a granular layer below the enamel. The light band down the middle of the photograph is the thin inner zone of enamel. Mineral staining shows the rods to be oriented in an irregular, highly complex, spiral pattern.

Fig. 5. *Trilophodon* (*Megabelodon*) sp. Part of section in outer circle on figure 3. Plane light. Twenty times natural size.

This shows the outer part of the enamel, with its well-defined concentric striations and with the rods, not very clear in the photograph, generally radial and much simpler in orientation than in the innermost enamel.



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INDEX

Page references in small roman figures refer to Volume I only

ERRATA

Page 4: Middle column, 36th line under heading 4, for Dietrich, Wolfgang O. read Dietrich, Wilhelm O.

Page 14: Left-hand column, 50th line, for Wolfgang O. Dietrich read Wilhelm O. Dietrich.

Page 773: Right-hand column, first line, for Dietrich, Wolfgang O. read Dietrich, Wilhelm O.

Page 841: Caption to Fig. 712, 5th line should read "5; 1884.3, Pl. xvi, fig. 2 (as *M. perimensis*);" etc.

Page 1022: Footnote 2 refers to *Loxodonta africana oxyotis*, the upper-case 2 belonging at the end of the 2nd line of the right-hand column.

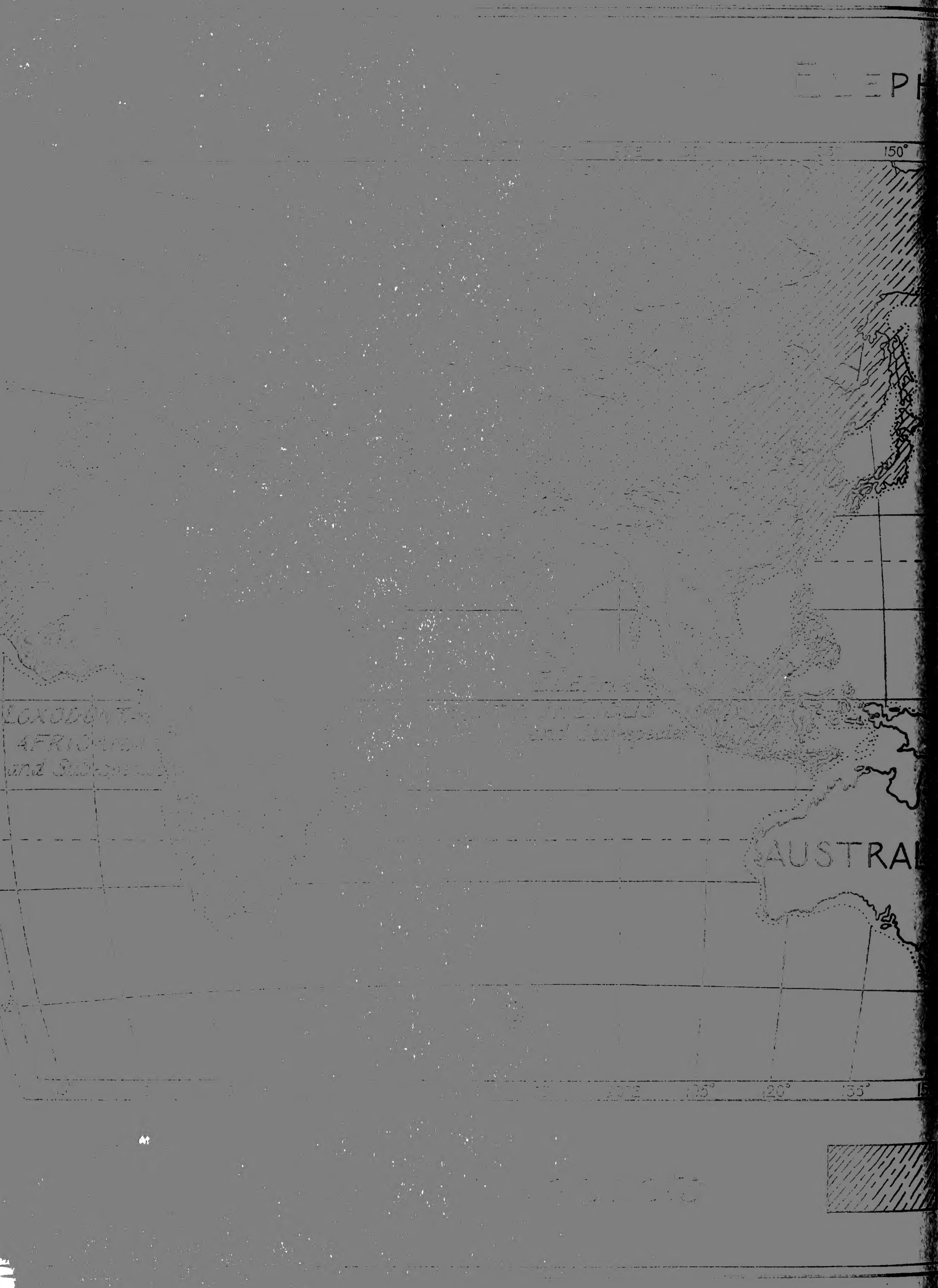
Page 1382: Under the genera *Hypselephas* and *Platelephas*, for 1941 as the date of this volume read 1942.

Page 1393: Right-hand column, 20th line under the heading, for *Anancus arvernensis* read *Anancus arvernensis macroplus*.

Page 1401: Right-hand column, 4th and 5th lines under the heading, for *Loxodonta capensis cyclotis* read *Loxodonta africana cyclotis*.

Page 1514: To the list of Proboscideans on this page add ? *Rhynchotherium francisi*.

Page 1520: 16th line, for *Cordillerion chilensis* read *Cuvieronius chilensis*.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150°
ELEPHAS MAXIMUS and Subspecies
LOXODONTA AFRICANA and Subspecies
AUSTRAL
135°
120°
135°

S: LOXODONTA [illegible]

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