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ON THE EVOLUTION OF THE PROBOSCIDEA.

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IV.—*On the Evolution of the Proboscidea.*

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Communicated by Prof. RAY LANKESTER, F.R.S.

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THE Proboscidea form one of the most isolated groups of the mammalia, for although it is now generally recognised that they belong to the Ungulata, they nevertheless differ widely from all other members of that order. They are further remarkable for the fact that, while in some respects, *e.g.*, in their large size and peculiar dentition, they are among the most specialised of mammals, in others, as, for instance, in the structure of their feet, they are relatively very primitive. The history of such an isolated group is necessarily of exceptional interest, and the peculiarities of the animals themselves render it the more easy to follow the course of their development, because the danger of confusing them with allied types is to a great extent eliminated; furthermore, in scarcely any other group can the phylogenetic history be traced back through so long a series of forms.

Until quite recently the earliest Proboscidea known were from the lowest Miocene beds (Burdigalien) of France, where they are represented by at least two species, viz., *Dinotherium cuvieri* and *Tetrabelodon angustidens*.* In somewhat later deposits these two genera *Dinotherium* and *Tetrabelodon* occur widely distributed in Europe and as far east as India. *Tetrabelodon angustidens* has also been recorded from the northern part of the Libyan Desert and from Morocco. The group seems to have reached North America during the Miocene, and the earliest recorded species is found in the Upper Miocene beds of Montana. This form has been described by COPE under the name *Tetrabelodon brevidens*; it is remarkable for the simplicity of its molars. *Dinotherium* is not found in any American deposits. The Mastodons did not penetrate into South America till the Pliocene. The absence of *Dinotherium* from America and the circumstance that the teeth of *Tetrabelodon brevidens* are at least as simple as those of any European species, suggests the possibility that the Proboscidea may have reached North America not by way of Europe, but along some independent land connection. The absence of the dinotheroid type might also be accounted for by the

* This name is here adopted in preference to the more usual one, *Mastodon angustidens*, because there can be no doubt that this animal is generically distinct from the *Mastodon americanus* for which the genus *Mastodon* was founded by CUVIER, and falls within the genus *Tetrabelodon* as defined by COPE.

fact that these animals were very heavily built and probably semi-aquatic, so that their spread into new areas may have been very slow and perhaps was checked by barriers that would not interfere with the Tetrabelodonts.

The fact that no remains of Proboscideans have been found in any pre-Miocene deposit of Europe, Asia or North America shows clearly that the group cannot have originated in any of those continents, but must have arisen on some adjacent land-area, from which also several other families, appearing for the first time in the European Miocene, may have been derived, and various speculations as to the position of this land-area have been put forward. Among later writers the hypothesis that the Ethiopian region was the centre of distribution of the Proboscidea has been formulated most distinctly by STEHLIN* and OSBORN,† both of whom consider that not only the Proboscidea, but also a number of other groups such as the Hyracoidea, the Orycteropodidæ, the antelopes and the giraffes are of African origin; and to these FORSYTH MAJOR‡ would add the Cercopithecidæ. OSBORN considers that migrations from Africa into the Eurasian continent have occurred on several occasions, notably towards the end of the Eocene, at the beginning of the Miocene and at the beginning of the Pliocene. On this hypothesis it must have been during the early Miocene immigration that the Proboscidea reached the northern region, probably along some land connection established at the commencement of the great earth movements that culminated in the formation of the Alpine mountain system.

The accuracy of the hypothesis of an Ethiopian centre of distribution of the Proboscidea has been fully demonstrated during the last two years by the discovery of a number of primitive members of the sub-order in the Middle and Upper Eocene beds of the Fayum district of Egypt, where they occur associated with remains of other mammals, especially of early Hyracoidea, as well as of some remarkable reptiles. The great interest of this discovery will be recognised when it is considered that in the paper by Professor OSBORN, above referred to, Africa is spoken of as "the dark continent of palæontology, for it has practically no fossil mammal history." The material for at least the beginning of such a history is now available, and it is to be hoped and expected that within the next few years much will be added to it.

The Proboscidea so far collected from Egypt are: (1) From the Middle Eocene, *Meritherium* (three species) and *Barytherium*; (2) from the Upper Eocene, *Palæomastodon* and perhaps *Arsinoitherium*.§ The presence in these beds of so considerable a

* STEHLIN, "Ueber die Geschichte des Suiden-Gebisses," II Theil; 'Abh. d. Schweiz. Palæont. Gesellschaft,' vol. 27 (1900), p. 477, *et seq.*

† OSBORN, "Correlation between Tertiary Mammal Horizons of North of Europe and America," 'Ann. N.Y. Acad. Sci.,' vol. 13, pp. 1-72, 1900.

‡ 'Geological Magazine,' Dec. 4, vol. 3 (1896), p. 436.

§ [July, 1903. Since this was written, remains of a species of *Meritherium* have been found by Mr. BEADNELL and myself in the Upper Eocene beds, where, however, they are very rare. On the other hand, no trace of *Palæomastodon* has been found in the Middle Eocene.]

number of Proboscideans of such diverse forms, points to the conclusion that they were a predominant Eocene type in this region, and that probably many other peculiarly modified members of the group are still to be found. Furthermore, from the presence of a gigantic form like *Barytherium* in the Middle Eocene beds, it seems clear that still earlier types are to be sought in the Lower Eocene.

Of the genera mentioned above, *Palæomastodon* and *Mæriotherium* appear to be on the direct line of the ancestry of the Elephants and Mastodons, and will be described below. *Arsinoitherium*, if indeed it is a Proboscidean at all, is an extraordinarily specialised and aberrant type, and appears to have left no descendants. *Barytherium* shows some similarity to the Dinotheriidae in the structure of its teeth, and may be nearly allied to those animals, though probably not their direct ancestor. *Barytherium* also shows certain likeness to those remarkable South American mammals, the Pyrotheriidae, which have been described by AMEGHINO, who regards them as Proboscideans of Cretaceous age. This writer has lately published a paper* in which he seeks to trace back the Proboscidea through a long series of genera to a group of Jurassic mammals, the Microbiotheriidae, apparently closely allied to the Didelphiidae. While it seems possible that some of the forms described by AMEGHINO are actually Proboscideans, and that there was a land connection between Africa and South America in older Tertiary times, as for various reasons has been considered probable by many writers, nevertheless it is difficult to accept his views as to the age of the beds in which these remains occur, and it seems far more likely that the *Pyrotherium*-beds are Tertiary rather than Cretaceous. AMEGHINO further considers that *Mæriotherium* and *Barytherium* form side branches and are not on the main line of descent of the later elephants. The whole question of these South American forms is at present so obscure that, for the purposes of the present paper, they may be ignored and attention directed to the Old-World genera only.

In following out the course of the evolution that has taken place in a group of mammals we may either begin with the later more specialised forms and then pass backward to the earlier and simpler members of the series, or the reverse. In the present communication it is proposed to adopt the former alternative, since in this case it is particularly interesting to note the persistence with which modification along certain lines has taken place and to show that by following back in time the known Post-Tertiary and Neogene species it would have been almost possible to predict that the earlier terms of the series would present precisely the character which we now find actually existing in the Middle and Upper Eocene genera, *Mæriotherium* and *Palæomastodon*.

It is not now intended to enter into details of the evolution of the group even were this possible, but merely to take four stages, so as to show the general trend of the modification that has taken place. The numerous intermediate stages between

* "Linea Filogenetica de los Proboscideos," 'Anales del Museo Nacional de Buenos Aires,' Tom. VIII (Ser. 3, tom. 1), 1902, p. 19, *et seq.*

the Mastodons and the true Elephants found among the fossil Proboscidea of the Siwalik Hills have been described by several writers (see, for instance, 'Falconer's Palæontological Mémoires') and will therefore be omitted, as also will be many of the species that seem to stand apart from the main line. In some of these latter certain characters seem to have remained almost unchanged, while others have undergone modification along the same lines as in the rest of the group. An example of this is

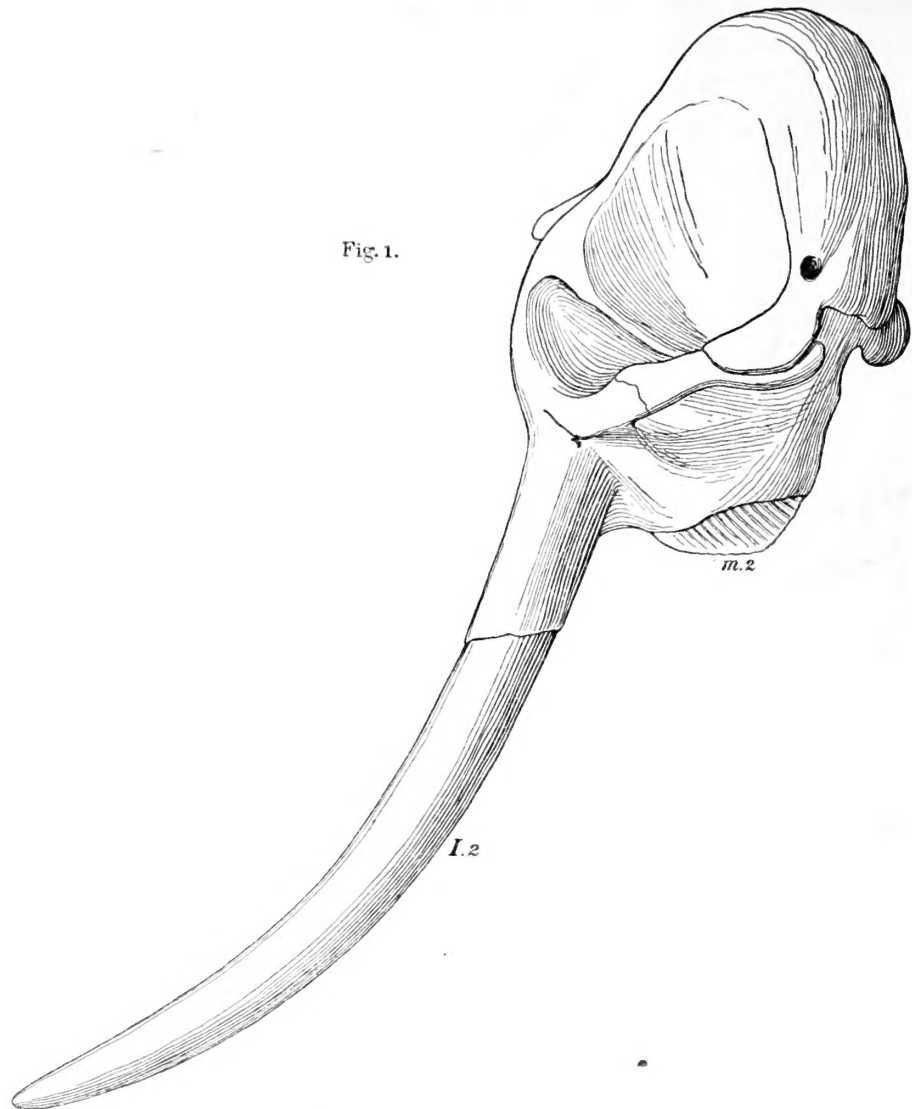


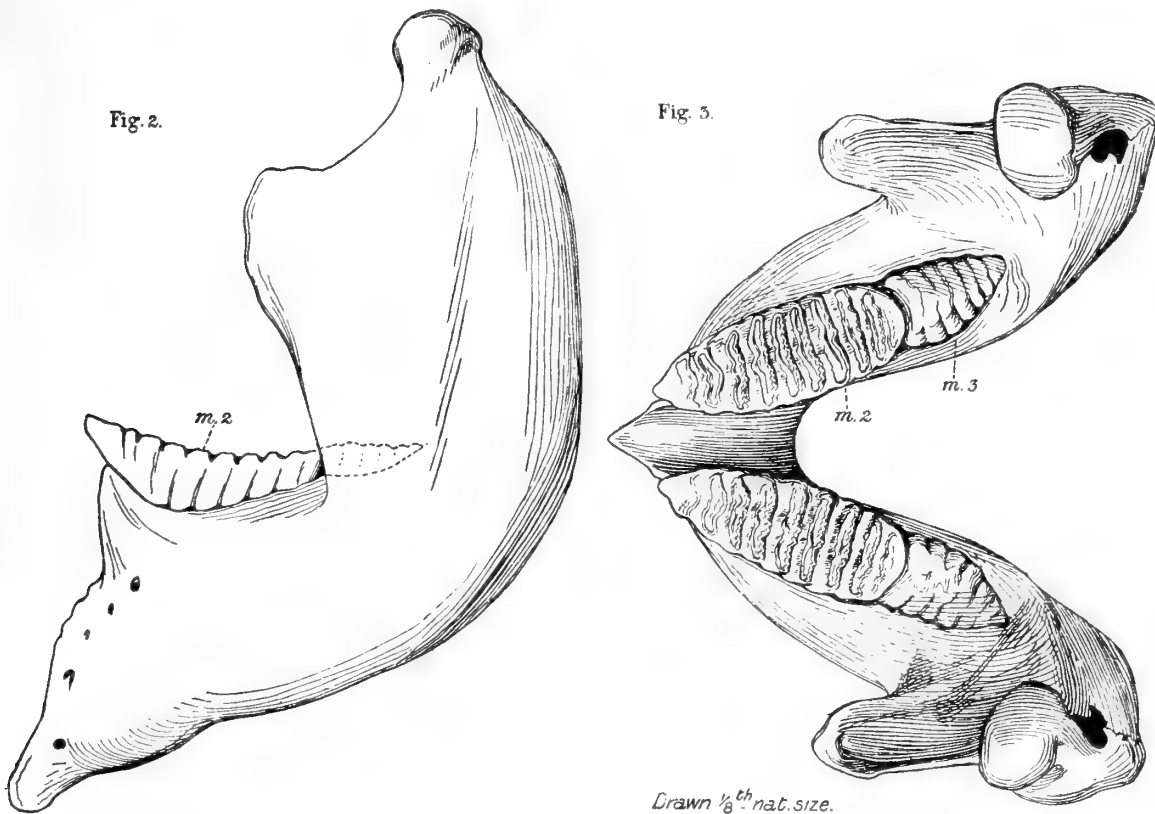
Fig. 1.—Skull of *Elephas maximus*, LINNÆUS. Recent. India.

seen in *Mastodon americanus* which survived till the Pleistocene; in this animal the molar teeth have remained in a condition of simplicity that would not be out of place in a Miocene species, while at the same time the symphysis of the mandible has been shortened to almost the same extent as in the Elephants (figs. 4 and 5).

The representatives of the stages of evolution to which attention is here directed

may be taken as (1) *Elephas maximus*; (2) *Tetrabelodon angustidens*; (3) *Palæomastodon beadnelli*; (4) *Mærittherium lyonsi*. The greatest gap is between the first and second members of this series, but, as already pointed out, this is to a great extent bridged over by a number of species, more especially from the Siwaliks; some of these species have been placed in an intermediate genus, *Stegodon*.

The skull and mandible with the dentition are of course the most important portions of the skeleton for the purpose in view, but some reference is made to one or two other points.



Figs. 2 and 3.—Mandible of *Elephas maximus*, LINNÆUS. Recent. India.

Elephas maximus, LINNÆUS. (*E. indicus*, CUVIER.)

The *Skull* (fig. 1).—The chief peculiarities of the skull of the elephant are due to the great size of the molar teeth and their mode of succession, and also to the weight of the tusks and trunk. The latter factor accounts for the enormous extension of the occipital surface which is brought about by the development of the diploë to an extent unparalleled in other mammals. The bones chiefly affected are the parietals and squamosals, but most of the other bones of the skull present the same peculiarity to a greater or less extent. The consequence is that the region usually occupied by the lambdoidal crest is here expanded into a large mass of bone which forms attachment

for the great muscles necessary to support the heavy head. The reduction of the nasal bones and the posterior position of the external nares is due to the presence of the proboscis, which also accounts for the width and concavity of the premaxillæ between the sockets of the tusks. The depth of the alveolar region of the maxillæ is due to the large size and peculiar mode of succession of the molars.

There is no post-glenoid process, but a broad post-tympanic process of the squamosal meets the hinder border of the glenoid surface and forms the boundary of the external auditory meatus. The jugal is small and forms only the middle of the jugal arch, though it sends back a prolongation beneath the zygomatic process of the squamosal as far as the glenoid surface. There is no condylar foramen.

The *Mandible* (figs. 2 and 3).—The horizontal ramus is very massive owing to the great size of the molar teeth. The symphyseal region is short and spout-like, and is prolonged downwards into a short blunt process, the last remnant of the immensely prolonged symphysis found in the form next to be described. The ascending ramus

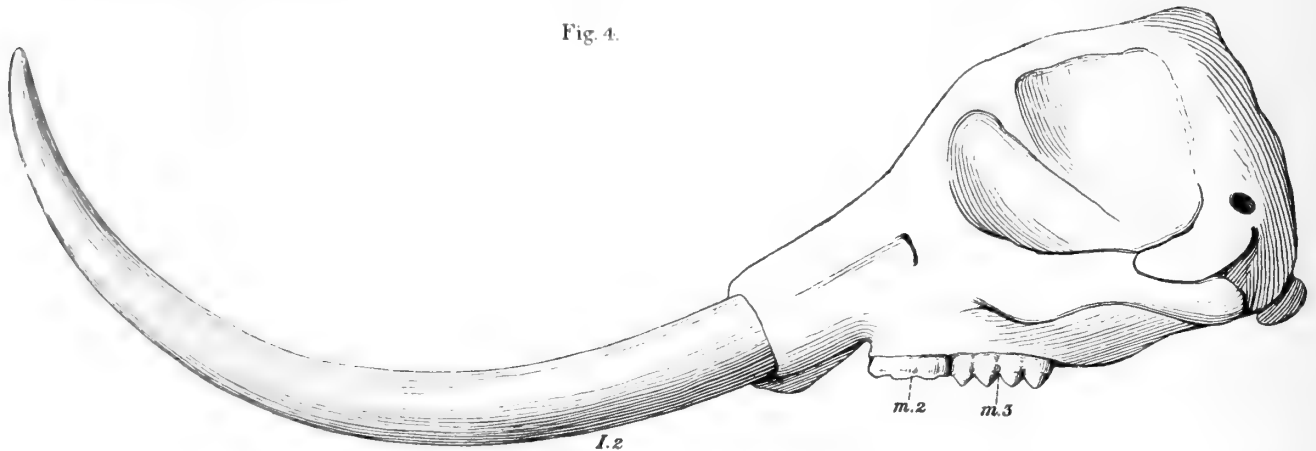


Fig. 4.—Skull of *Mastodon americanus*, CUVIER. Pleistocene. N. America.

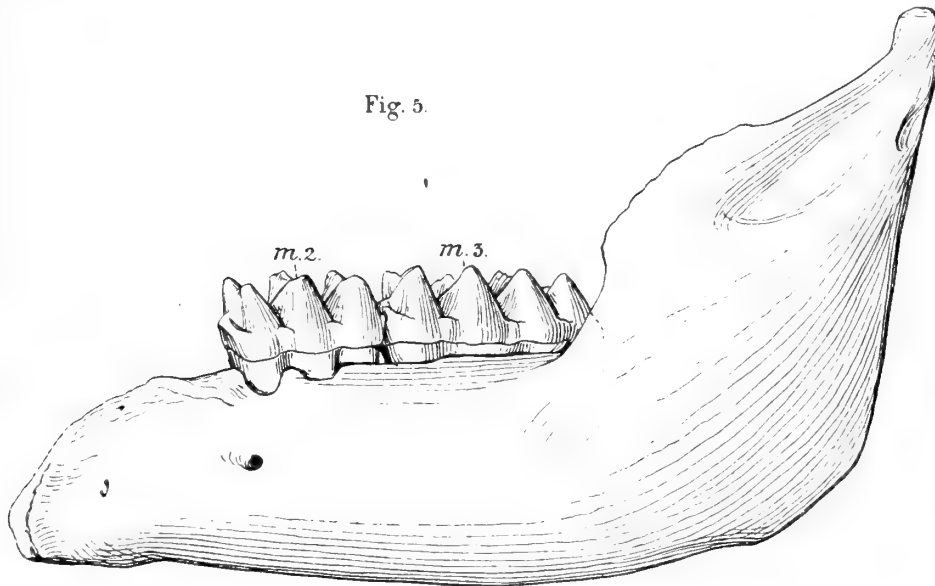
slopes somewhat forwards and terminates in a rounded articulation; the coronoid is short and does not rise as high as the articulation, and its anterior border arises on the outer surface of the jaw in front of the hinder extremity of the molar series. The teeth of *Elephas* are so well known that any detailed description of them is unnecessary, except so far as is needful for comparison with the earlier types.

There is a large pair of tusk-like upper incisors (I. 2) which are homologous with the second pair of the full mammalian dentition; the dentine presents the peculiar "engine-turning" characteristic of elephant ivory; there is a small enamel cap lost through wear at an early age. The permanent incisors are preceded by a pair of milk teeth shed very soon. There are during the animal's whole life six pairs of cheek teeth in the upper jaw, of which the anterior three are milk-molars, never replaced by premolars. The succession of teeth is from behind, the whole series moving slowly forwards and the anterior worn teeth being shed as the hinder ones come into position, and the true molars are so large that never more than portions of two on either side are

in use at the same time, and late in life the posterior molars alone remain. The individual teeth are extremely complex in structure, each consisting of a number of transverse plates united in a common investment of cement; the plates are extremely hypselodont and increase in number from before backwards; thus in the Indian elephant the first milk-molar has four plates, while in the last true molar there may be as many as twenty-four. In the lower jaw the number and character of the teeth and their mode of replacement are the same.

The essential peculiarities of the elephant's dentition, therefore, are :—

- (1) The absence of vertical successors to the milk-molars.
- (2) The gradual forward movement of the series.
- (3) The increase in the size and complexity of the teeth from before backwards.
- (4) The lophodont and hypselodont character of the teeth.



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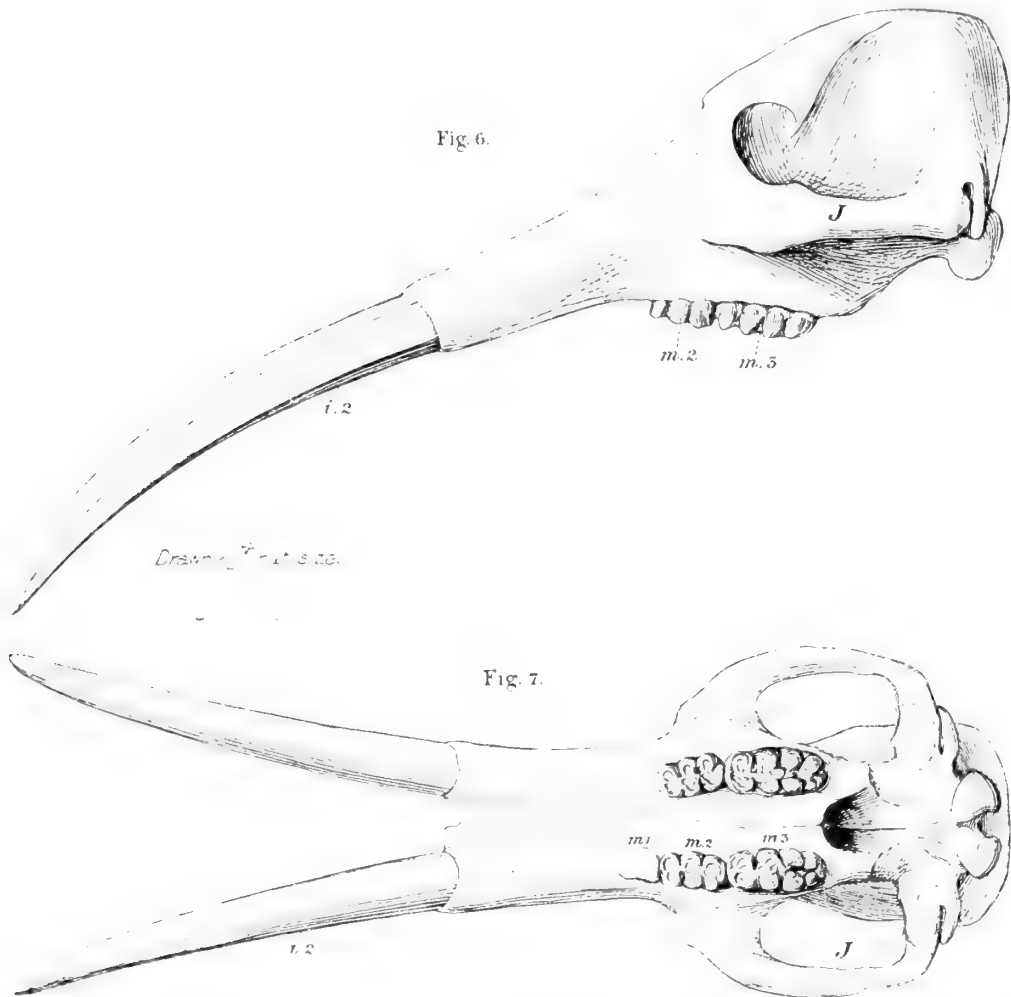
Fig. 5.—Mandible of *Mastodon americanus*, CUVIER. Pleistocene. N. America.

Tetrabelodon angustidens, CUVIER sp.

The *Skull* (figs. 6 and 7).—Unfortunately I have only been able to examine a much crushed skull of this species, but with the assistance of photographs of specimens in the Musée d'Histoire Naturelle at Paris, kindly supplied by Professors GAUDRY and MARCELLIN BOULE, it has been possible to make out the main points.

The occipital region is only a little less elevated and expanded than in *Elephas*; this is what might be expected, since in this animal, in addition to large tusks and the proboscis, there was also the weight of the greatly elongated mandible to be supported. It seems, however, that the development of cells in the cranial bones is somewhat less than in the recent type, and the skull is rather longer in proportion to its height, so

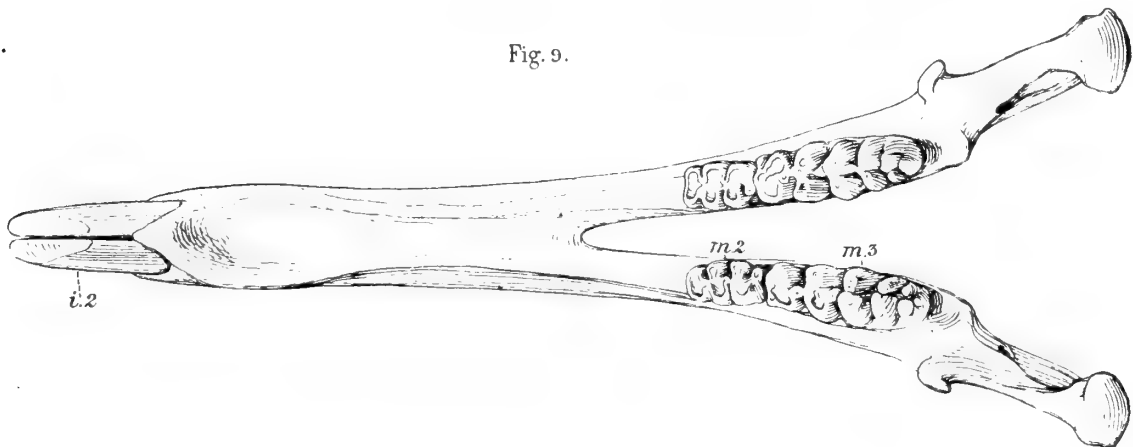
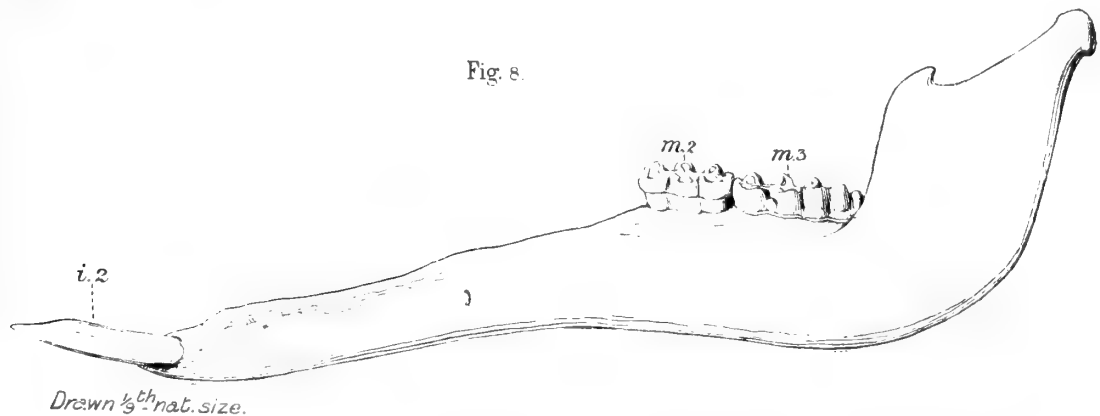
that it differs a little less than that of *Elephas* from the ordinary proportions of the mammalian skull. At the same time the facial region is almost exactly as in *Elephas*. The maxillæ by reason of the more brachydont character of the cheek-teeth are not so deep as in the elephant, but are still very large owing to the great size of the molars and to their mode of replacement from behind; anteriorly the maxillæ send forward processes beneath the premaxillæ, thus helping to support the tusks, of the alveoli of which they may form the hinder edge. In the zygomatic arch the jugal perhaps extends slightly farther forward than in *Elephas*, at least ventrally. In short, the skull of *Tetrabelodon* is essentially similar to that of *Elephas*.



Figs. 6 and 7.—Skull of *Tetrabelodon angustidens*, CUVIER sp. Lower and Middle Miocene. Europe.

The *Mandible* (figs. 8 and 9).—It is in the mandible that the most remarkable divergence from *Elephas* is found. The symphyseal region is enormously elongated and its upper surface deeply concave from side to side, forming a spout-like channel, the sides of which are formed by the edentulous alveolar border. The channel is narrow posteriorly but widens out in front, and its concavity is continued forward

by the upper surface of the pair of procumbent lower incisors which are in close contact with one another, at least through the greater part of their length. The horizontal ramus behind the symphysis is not so deep in proportion to its length as in *Elephas*. The angle is rounded and the hinder border of the ascending ramus slopes backwards and terminates above in a transversely elongated articulation, convex in all directions. The anterior border of the ascending ramus rises on the outer surface of the jaw in front of the hinder end of the alveolar border, so that in a side view the last molar is more or less concealed by it, but owing to the forward movement of the tooth



Figs. 8 and 9.—Mandible of *Tetrabelodon angustidens*, CUVIER sp. Lower and Middle Miocene. Europe.

series the relative position of the teeth and the ascending ramus changes. There is a small coronoid process which does not rise so high as the articulation.

The *Teeth*.—The dental formula is I. $\frac{1}{1}$, Pm. $\frac{2}{2}$, M. $\frac{3}{3}$.

Upper Teeth.—The upper incisors (figs. 6 and 7) form a pair of large tusks differing from those of *Elephas* in the following points:—(1) They are straight and decurved, often to a considerable extent; (2) they are usually more or less oval in section, the long axis of the oval being antero-posterior; (3) there is a band of enamel on their outer face, extending from root to tip.

There are three milk-molars, the hinder two of which are replaced by premolars in the ordinary way, *i.e.*, from beneath.

The first and second milk-molars are bilophodont, each ridge consisting of a pair of tubercles; in the second (m.m. 2) the cingulum forms a ridge at each end of the tooth. The third (m.m. 3) is trilophodont with an anterior and a posterior ridge of the cingulum; this tooth remains in use some time after the first true molar has come into wear, the last two milk-molars are replaced by premolars, the anterior of which consists of a large anterior cusp with a smaller one internal to it, and a talon of two or three small tubercles. The posterior premolar (Pm. 4) is quadritubercular, the cusps forming two crests. Both the premolars seem to be shed very soon, probably because the development of the large posterior molars leads to a forward movement of the series.

The first and second true molars are trilophodont, the cingulum forming a small talon. The last molar consists of three ridges and a large talon consisting of three or four tubercles.

The molars are bunolophodont, each transverse crest consisting of a number of distinct tubercles and being primarily divided into an inner and an outer half by a longitudinal furrow more or less clearly defined. In the upper teeth the outer half is the higher and is composed of two transversely placed tubercles, so closely united that they are often difficult to distinguish, and when worn the division between them may be completely obliterated. The inner half of the crest consist of a main tubercle to the antero-external and postero-internal sides, a pair of accessory tubercles are usually attached so that in wear the inner lobe gives a trefoil or V-shaped surface, the apex of the V being turned to the inner side of the tooth. In the intermediate molars the anterior accessory cusp of the anterior lobe is united with the anterior cingular ridge, while the posterior accessory cusp of the hinder lobe is united with the talon formed by the cingulum; it is from a succession of such talons that in the later forms, the additional transverse crests of the molars seem to have been developed. The talon of the posterior molar consists of several cusps.

Lower Teeth (figs. 8 and 9).—Of the three milk-molars the anterior one is a small blunt single-cusped tooth; the second is bilophodont, each ridge consisting of two tubercles; there is also a small cingular ridge in front and a much larger one posteriorly; the third is trilophodont with a cingulum anteriorly and posteriorly.

The first premolar has a large anterior tubercle and tubercular talon; the second is bilophodont.

The first true molar is trilophodont with a small ridge of the cingulum in front and a much larger talon-like one behind. The last molar has four transverse ridges and a talon.

In the details of their structure the lower molars are like the upper ones reversed, that is to say, the outer side of the lower teeth corresponds to the inner side of the upper.

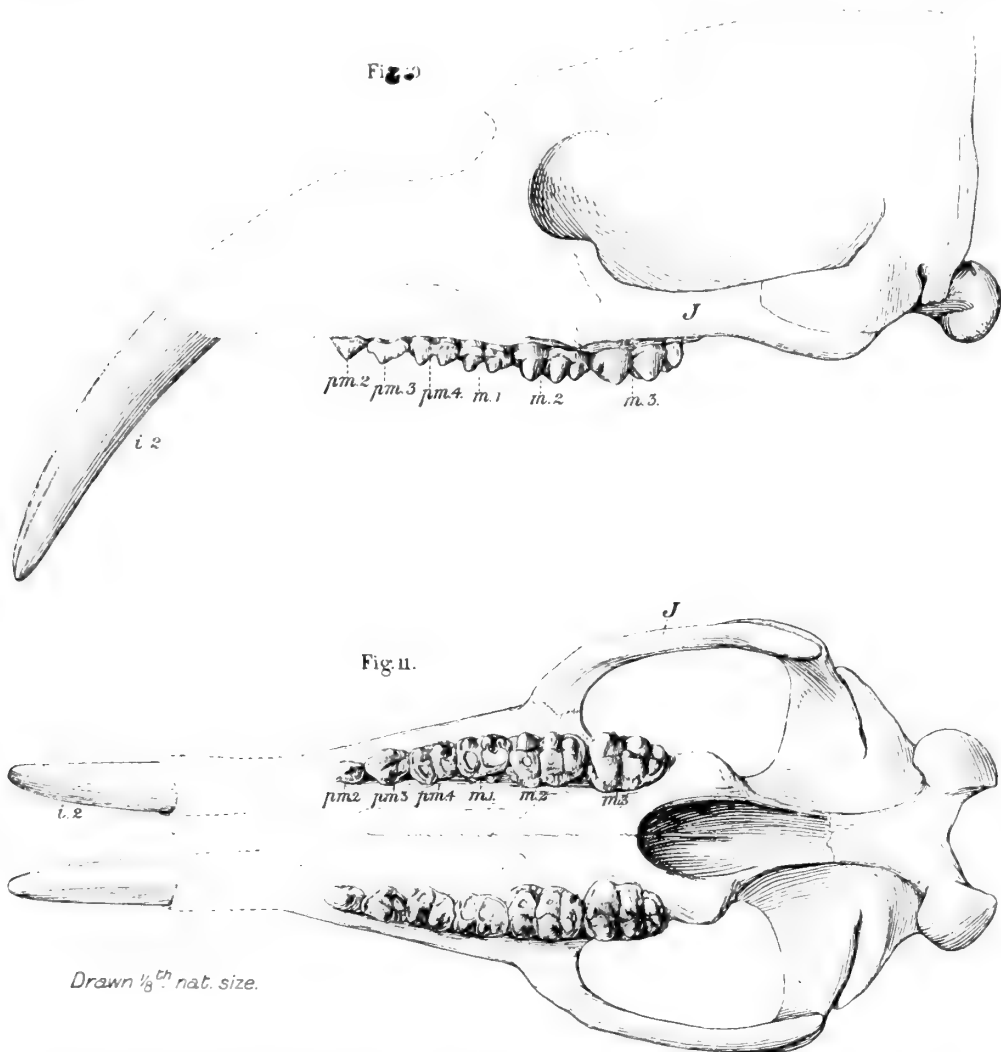
Comparing *Tetrabelodon* with *Elephas* we find that, so far as the skull is concerned

the differences are not great, the same mechanical conditions having existed in both forms. In *Tetrabelodon* the upper tusks are somewhat less unlike ordinary incisors than in *Elephas*, in being curved downwards and in bearing a continuous band of enamel on their outer face. As in *Elephas* they are separated by a considerable interval at their alveolar ends and diverge widely distally.

It is in the mandible that the greatest differences between the two genera are found. In *Elephas* the symphyseal region has undergone reduction to such an extent that it forms merely a very short downwardly directed spout-like projection. In *Tetrabelodon*, on the other hand, the most remarkable condition of things prevails (*see* figs. 8 and 9). The enormously elongated symphyseal region bearing a pair of procumbent incisors, projects far beyond the premaxillæ and between the divergent upper tusks (*see* figs. 6 and 7), with which the lower incisors cannot have been in contact at any time; nevertheless, these lower teeth bear on their extremities flat surfaces of wear, both on their upper and lower sides, a condition that can only be accounted for by supposing that they were employed for digging and rooting in the earth. The great length of the mandible, combined possibly with a somewhat longer neck than is found in *Elephas*, rendered it possible for this animal to reach the ground with its lower incisors. No doubt the portion of the mandible projecting beyond the upper jaw was covered by a sort of proboscis formed by the combined nose and upper lip (compare figs. 7 with 9 and 6 with 8); the extremity of this must have been more or less prehensile and capable of thrusting the food, rendered available by the action of the incisors, into the channel formed by the symphyseal region of the mandible. Subsequently, it must be supposed, that owing to some change in the nature of the food and probably also to the increased efficiency of the end of the proboscis as an organ of prehension, the mandible became shortened so that it was no longer possible for the animal to reach the ground with its lower incisors, and when this happened the elongated symphysis would not only cease to be of any service, but possibly even prove a disadvantage as interfering with the free action of the proboscis, and therefore it was rapidly lost. This may account for the fact that some species of *Mastodon* (*e.g.*, *M. americanus*, *see* fig. 5), but little advanced beyond *Tetrabelodon angustidens* in the structure of their molars, have the symphysis nearly as short as in *Elephas*, the reason apparently being that while in the case of the molars the increase of efficiency was gradual, in the case of the shortening of the symphysis and the projecting incisors there was a sudden transition from utility to uselessness or worse. *Tetrabelodon* seems to represent the stage at which the length of the mandible culminated, for it is an animal of much the size and build of the elephant and yet could reach the ground with its lower incisors. The above explanation of the possible mode of origin of the trunk in the Proboscidea was in part, so far as the main points are concerned, suggested to me by Professor E. R. LANKESTER.

Palaeomastodon beadnelli, ANDREWS.*

The *Skull* (figs. 10 and 11).—Unfortunately no perfect specimen of the skull has yet been found, and the most complete example wants the whole of the cranial, and most of the facial region; from this the following points can be determined. Owing to the very brachydont character of the molars, the maxillæ are low and their zygomatic processes rise a very short distance above the alveolar border, and over the second true molar. The jugal extends forwards and is a much more important factor of the zygomatic arch than in *Elephas* or *Tetrabelodon*: posteriorly its relations to



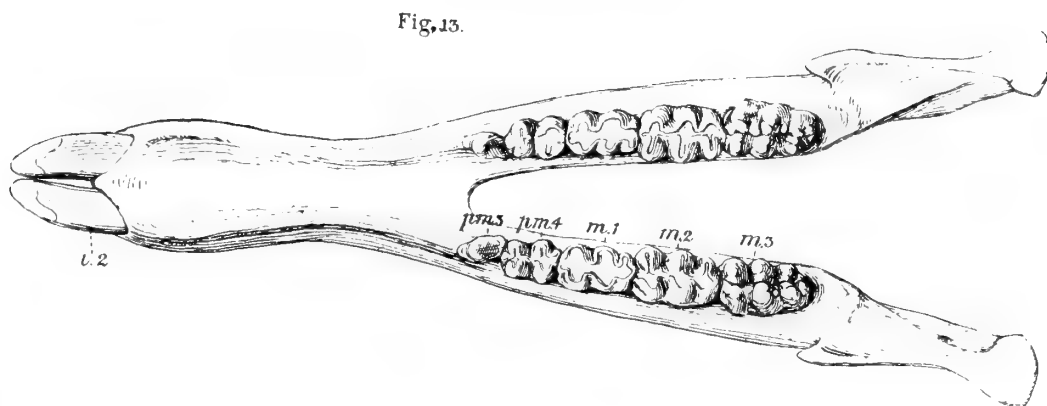
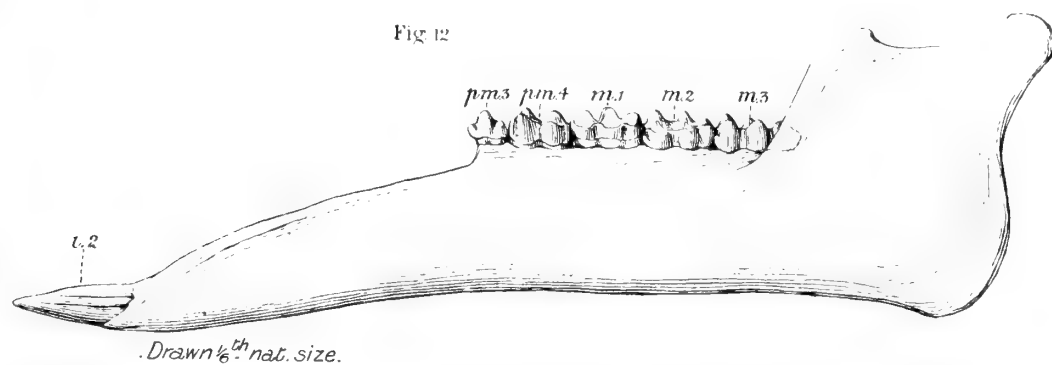
Figs. 10 and 11.—Skull of *Palaeomastodon beadnelli*, ANDREWS. Upper Eocene. Egypt.

the squamosal are the same as in those genera. The glenoid surface is like that of *Elephas*: there is no post-glenoid process, but a post-tympanic flange of the squamosal

* 'Geological Magazine,' dec. IV, vol. 8 (1901), p. 401.

is in contact with the hinder border of the articular surface and helps to enclose the external auditory meatus, just as in the elephants. The axis of the *basis cranii* is parallel with that of the palate; the palatines, pterygoids and alisphenoids are much as in *Elephas*, but the *basis cranii* is more elongated and the occipital condyles are more prominent.

The *Mandible* (figs. 12 and 13).—The symphysis of the mandible is greatly elongated, but still to a less degree than in *Tetrabelodon*. It is somewhat decurved, and its upper surface forms a spout-like channel, which is continued forward by the procumbent and spatulate incisors (figs. 12 and 13). The angle is more prominent and less rounded than in *Tetrabelodon*, and the ascending ramus slopes backwards to a less degree. The coronoid border rises from the outer surface of the jaw opposite the last molar.



Figs. 12 and 13.—Mandible of *Palaeomastodon beadnelli*, ANDREWS. Upper Eocene. Egypt.

The *Teeth*.—The dental formula is I. $\frac{(?)}{1}$ C. $\frac{0}{0}$: Pm. $\frac{3}{2}$: M. $\frac{3}{3}$.

The upper incisors (figs. 10 and 11) were laterally compressed tusks, bearing a broad band of enamel on their outer surface and being downwardly directed. It is not known whether any trace of incisors, other than the tusks, existed. The anterior upper premolar (Pm. 2) is a blunt simple cone with a slightly developed cingulum. The next (Pm. 3) consists of a large outer cone and a smaller inner one arranged

transversely, there is also a small inner cone behind the chief one. The cingulum is fairly well developed and forms a small prominence both in front and behind. The last premolar (Pm. 4) is bilophodont, each ridge consisting of a pair of tubercles. The postero-internal cusp is continued backward into a small talon-like portion of the cingulum.

The first true molar (M. 1) is trilophodont, the inner cusp of each ridge is the larger and most worn, the outer is the higher; the internal cusps tends to unite longitudinally in wear. The second molar (M. 2) is much larger than M. 1, the sudden increase in size being most striking; its structure is similar to that of the tooth in front; the postero-internal cusp is united to the talon-like cingulum. The posterior molar (M. 3) is similar in most respects to M. 2, but the hind lobe is much smaller, so that the tooth is actually simpler than that in front of it.

The *Lower Dentition*.—The single pair of lower incisors are in close contact along their straight inner borders, and their concave upper surface forms an anterior prolongation of the spout-like symphysis. The upper surface of their anterior and antero-external borders is considerably worn.

The anterior premolar (Pm. 3) consists of a strongly compressed main cusp with small accessory cusps in front and behind. The last premolar (Pm. 4) is a narrow bilophodont tooth, each ridge consisting of a pair of cusps. There are also small accessory cusps on the anterior and posterior borders of the tooth. The first molar is a small trilophodont tooth with a small talon. The second molar (M. 2) is much larger, but is likewise trilophodont; there is a small anterior cusp connected with the antero-external main cusp, and also a small posterior talon connected with the postero-external main cusp. The posterior molar is similar but the talon is considerably larger.

Palæomastodon is more primitive than *Tetrabelodon* in the following points. The *basis cranii* and the facial region of the maxilla are longer; the zygomatic arch is larger and the jugal not only takes a greater share in its composition but also extends farther forward. In the mandible the symphysis is not so extremely elongated, and the lower incisors are more normal and less tusk-like. It is in the cheek-teeth, however, that the more generalised character of *Palæomastodon* is most manifest. Thus the molars and premolars are all in wear at the same time and their mode of succession is almost as in ordinary Ungulates, such as the pig. The premolars replace milk predecessors, and the molars come into use one after the other in the usual way, the first molar being always the most worn. As to the structure of the individual teeth, it may be said that they are still more brachydont than in *Tetrabelodon*, the main tubercles of the transverse ridges more distinct from one another and the accessory tubercles less developed.

In both genera the first and second molars are trilophodont, but in *Tetrabelodon* the last molar is much the more complex in both upper and lower jaws (*see* figs. 7 and 9). The sudden increase in the size of the last two molars in *Palæomastodon* seems

to be the first indication of the great relative magnitude they are destined to attain in the later forms. The form of the atlas vertebra in *Palæomastodon* indicates that the neck was longer than in the later forms. The limb bones, as far as known, differ from those of *Elephas* in little except size.

Mæritherium lyonsi, ANDREWS.*

The skull, mandible and dentition of *Mæritherium* are fairly well known and have been briefly described and figured by me. Here, only the points necessary for the purpose in hand need be mentioned.

The *Skull* (figs. 14 and 15).—The occipital surface is very wide and its plane nearly vertical. The *foramen magnum* is large, and the occipital condyles prominent and almost pedunculate. The zygomatic process of the squamosal is very massive and prominent, and the glenoid surface is a broad and ill-defined slightly concave area; there is no post-glenoid process, but a broad post-tympanic flange is closely applied to the hinder edge of the glenoid surface and encloses the large external auditory meatus precisely in the manner characteristic of the later Proboscidea. The parietals form most of the cranial roof, and like the cranial portion of the squamosals are greatly thickened, so that in one species (*Mæritherium gracile*, ANDR. †) there is a distinct inflation of the hinder portion of the sides of the skull, possibly the first indication of the enormous development of diploë found in the later forms. The frontals seem to have been small, and there is no well-defined post-orbital processes. The nasals also were small and the nasal opening very large; the form of this opening, together with the grooving of the upper surface of the large premaxillæ, seem to point to the existence of some kind of small proboscis-like structure. The premaxillæ bear the alveoli of three pairs of incisors. The second pair are greatly enlarged, trihedral and downwardly directed tusks, the roots of which run back into the maxillæ and probably grew from a persistent pulp. The maxillæ bear sockets for a pair of canines and six pairs of cheek-teeth; there is a prominent zygomatic process which is to a great extent overlapped by the anterior portion of the jugal, which here forms a large part of the zygomatic arch and extends back beneath the zygomatic process of the squamosal as far as the articulation for the mandible.

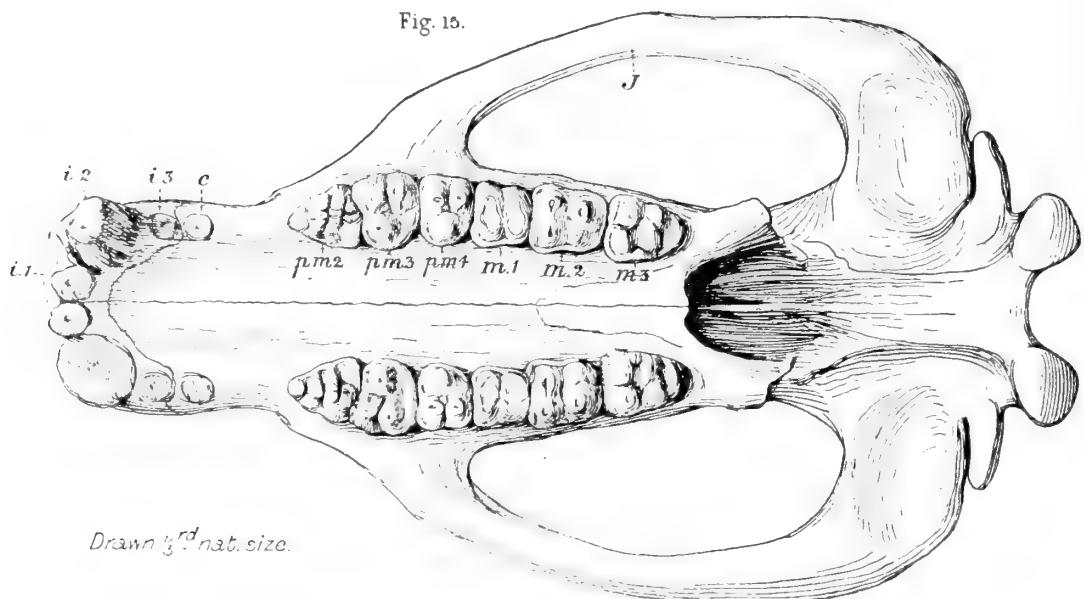
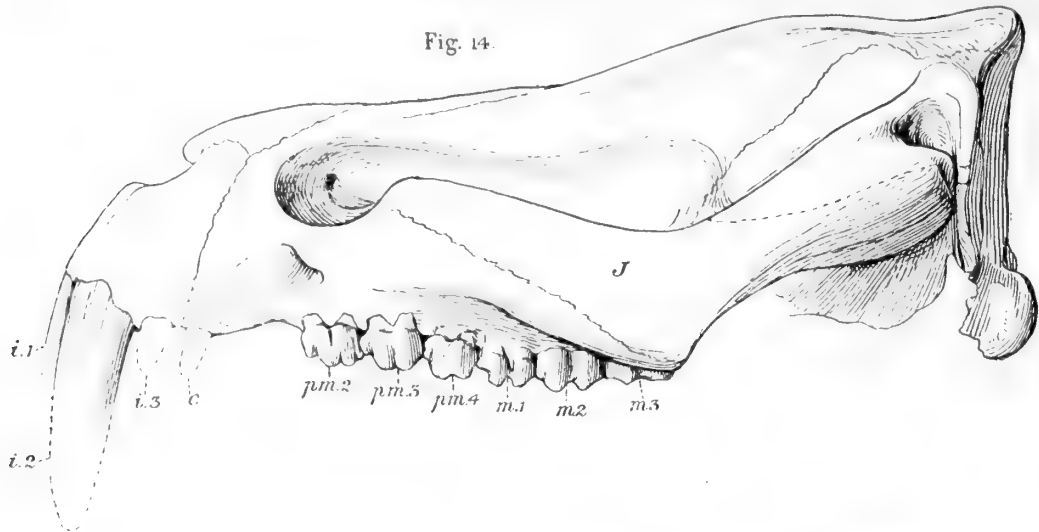
The *Mandible* (figs. 16 and 17).—The horizontal ramus of the mandible is very stout, and its outer surface rounded from above downwards; anteriorly they unite in a massive symphysis, the upper spout-like surface of which is continued forward by the procumbent incisors, of which there are two pairs, the median of which are small and laterally compressed teeth, the outer, large tusks. The ascending ramus is broad and is inclined somewhat forward; its anterior border rises from the outer surface of the horizontal ramus in front of the hinder end of the molar series as in other

* 'Geological Magazine,' dec. IV, vol. 8 (1901), p. 403.

† 'Geological Magazine,' dec. IV, vol. 9 (1902), p. 292.

Proboscidea. The coronoid does not rise above the articulation, which is a transversely elongated condyle. The angle is broad and rounded.

The *Dentition* (figs. 14-17).—There are three pairs of upper incisors; the first are comparatively small teeth in close contact in the middle line; the second are large downwardly directed trihedral tusks which, as previously mentioned, probably grew from persistent pulps; the third pair of incisors and the canines were small teeth represented



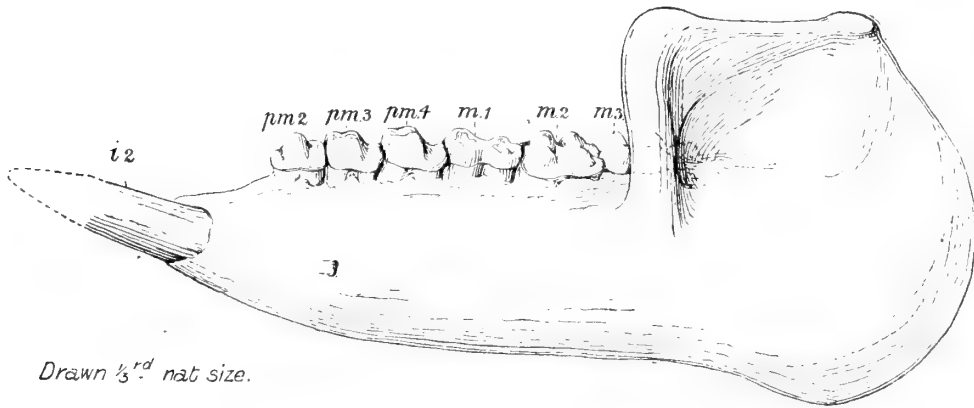
Skull of *Moritherium lyonsi*, ANDREWS. M. Eocene. Egypt.

in all the available specimens by the alveoli only. The first premolar is wanting, the second (Pm. 2) is triangular in outline, the crown consists of an outer row of cusps and a postero-internal shelf-like projection (*see* fig. 15). The next tooth (Pm. 3) consists of a pair of transversely arranged anterior cusps and a postero-internal one, internal to which is a small shelf-like projection. The next premolar (Pm. 4) is

similar. The two anterior molars are bilophodont, each transverse crest being composed of a higher and more pointed outer cusp and a blunter and more worn inner one. The postero-internal cusp is also prolonged backward into a small blunt lobe which, when worn, gives rise to the pattern shown in the figure (fig. 15); the last molar is bilophodont and has a small talon.

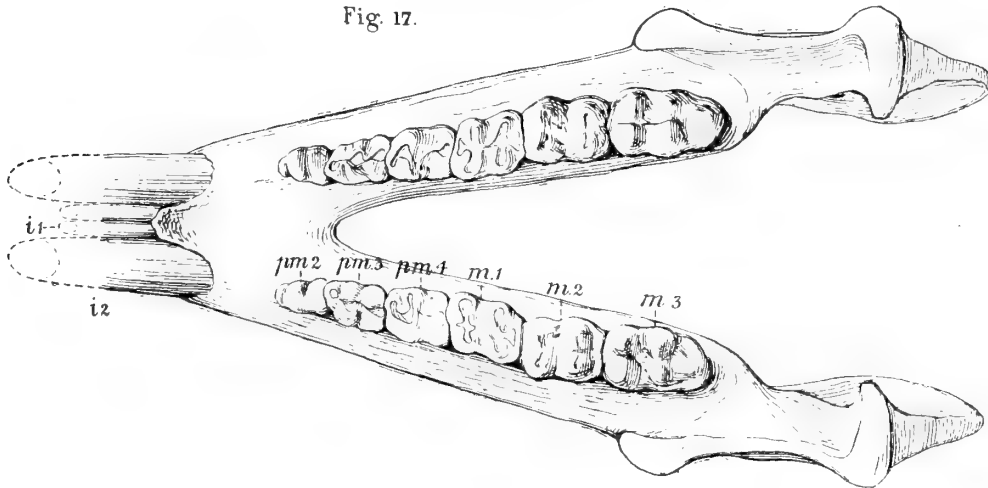
The lower incisors have already been referred to. The cheek teeth are six in number, the first premolar being wanting. The second premolar is a comparatively small tooth, and is compressed from side to side. It consists of a large anterior cusp

Fig. 16.



Drawn $\frac{1}{3}^{rd}$ nat size.

Fig. 17.



Mandible of *Mærittherium lyonsi*, ANDREWS. M. Eocene. Egypt.

behind which is a talon of considerable size. The third premolar is much larger; it consists of a high anterior portion and a posterior talon. The anterior part is composed of three cusps, one of which forms the antero-internal angle of the tooth, while behind this the other two are arranged transversely. The talon has a median ridge which rises posteriorly into a tubercle. The fourth premolar the anterior cusp is less distinct, but those forming the transverse ridge are better developed, especially the inner one. The cusp on the talon is also larger than on the tooth in front. The first true molar is bilophodont, each ridge consisting of two almost distinct tubercles. The cingulum

forms a small shelf-like ridge at the anterior end of the tooth and a larger one behind; in wear this latter becomes connected with the worn surface of the postero-external cusp, and it forms the rudiment of a third ridge. The next molar is similar. The last is likewise bilophodont, but has also a large tuberculate talon.

The relatively primitive character of *Mærittherium* is shown by the fact that the skull presents no very striking peculiarities beyond the forward extension of the maxillæ and the great thickness of the cranial bones. In the mandible the massive symphysis is little elongated. In the upper jaw only one tooth (Pm. 1) of the full Eutherian dentition is wanting; in the mandible three (I. 3, C. and Pm. 1) have been lost. The incisors are becoming specialised, but the premolars and molars are of a simple type, though they already show a tendency to increasing specialisation along the lines subsequently pursued throughout the group.

The discovery of an early and comparatively generalised type like *Mærittherium* naturally raises the question of the relationship of the Proboscidea to the other mammals, and although at present it is not possible to arrive at any definite conclusion as to the origin of the group, the view put forward by BLAINVILLE and others that they may be related to the Sirenia receives some support. It must be said, however, that several writers* have strenuously opposed this opinion.

The relationship between the two groups must necessarily be a remote one since a Sirenian (*Eosiren*), very little less specialised than *Manatus* or at any rate than *Halitherium*, occurs associated with *Mærittherium*, so that a common ancestor of the two groups cannot have existed later than the Lower Eocene. Nevertheless, the following characters are common to the two:—

- (1) Placenta non-deciduate and zonary.
- (2) Pectoral mammæ.
- (3) Abdominal testes.
- (4) Bifid apex of heart.
- (5) Absence of the condylar foramen, always in the elephants and generally in the Sirenia, where, however, it may be bridged over by a thin strand of bone.
- (6) The bilophodont character of the molars with a tendency to the formation of an additional lobe from the posterior part of the cingulum (talon). The molars of some Sirenia are extremely like the anterior molars of *Mærittherium*.
- (7) In both groups the molar series moves forward in the jaws throughout life, the anterior worn teeth being shed while fresh ones come into use behind. In the Sirenia this is effected by the continuous addition of teeth similar to the other molars, while in the Proboscidea no fresh teeth are added but the individual molars become longer and more complex through the addition of further transverse crests to their posterior ends.

* See for instance T. GILL, "On the Affinities of the Sirenians," 'Proc. Acad. Nat. Sci., Philadelphia,' 1873, p. 262.

(8) The humerus of *Mærittherium* is extremely like that of a Sirenian. Many of the above-mentioned characters are by themselves of little import, but the coincidence of so many points of similarity seem to render the existence of a common ancestry for the two groups at least probable.

Summary.

The changes undergone by the skull, mandible and dentition in the Proboscidea in passing from the Eocene to the recent types, may be summarised as follows:—

The *Skull*.—Owing to the increase in the size of the tusks and to the presence of the proboscis the facial region of the skull becomes shortened, and at the same time the premaxillæ become wider. The presence of the proboscis also accounts for the position of the external nares. The demand for a greater surface of attachment for the muscles, supporting a skull rendered heavy by the tusks and trunk, is met by the great development of the diploë in certain of the cranial bones, resulting in the enormous expansion of the forwardly sloping occipital surface. The maxillæ become greatly enlarged *pari passu* with the increase in the size and degree of hypselodonty of the molars. At the same time the zygomatic arch becomes weaker and the jugal takes a smaller share in its composition.

The *Mandible*.—The mandible is at first short and stout with a massive symphysis. Afterwards it becomes more and more elongated as the stature of the animals increases; the elongation is for the most part effected by the lengthening of the symphyseal region, but the rotation backward of the ascending ramus tends to the same end. The prolongation of the mandible beyond the premaxillæ must have been covered by a proboscis-like structure composed of the upper lip and nose, probably more or less prehensile at its extremity. The lengthening of the mandible seems to have reached its maximum degree in the Middle Miocene, after which for some reason or other it again became shortened by the reduction of the symphysis, while the fleshy and now mobile proboscis was left behind as the sole organ of prehension.

The *Dentition*.—In the upper jaw the chief changes are the loss of I. 1 and I. 3, and the great increase in size of I. 2, which finally forms the great tusk characteristic of the later Proboscidea. The canines are soon lost. In the early forms some at least of the milk-molars are replaced by premolars in the usual manner, and these teeth remain in wear simultaneously with the true molars, but in later forms no vertical succession takes place, and as the milk-teeth are worn they are shed, being replaced from behind by the forward movement of the molars. Of these also the anterior may be shed, until at length, in old individuals of the later types, the last molar is alone functional. The gradual increase in the complexity of the Proboscidean molars is one of their most striking characteristics. All stages are to be traced between the simple brachydont bilophodont (quadritubercular) molars of *Mærittherium*,

to the extraordinarily complex type of tooth found in *Elephas*. Thus in *Palæomastodon* the molars are trilophodont, and the same is true of the first and second molars of *Tetrabelodon*, in which, however, the last molar is complicated by the addition of further transverse crests. In the Stegodonts of the Siwalik Hills a further increase in the number and height of the crests takes place, and the whole crown of the tooth is more or less covered with a thick coat of cement. Still later the transverse crests become highly compressed laminae united by cement, and in *Elephas maximus* and *E. primigenius* there may be as many as twenty-seven of them.

In the lower jaw the median and outer pairs of lower incisors (I. 1 and 3) were soon lost, but the second pair (I. 2) remained functional, and being prolonged in the direction of the mandibular symphysis helped to lengthen the animal's reach. After the symphysis became shortened, the lower incisors were in some cases (*e.g.*, *Mastodon americanus*) retained, but the irregularity of their occurrence in known specimens shows that they were probably functionless. In *Elephas* no trace of the lower incisors remains.

The changes undergone by the lower molars are similar to those of the upper molars.

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