ARTICLE VII.

(Plates XVII and XVIII.)

THE OSTEOLOGY OF ELOTHERIUM.

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Elotherium is one of the many genera of fossil mammals concerning which the growth of our knowledge has been exceedingly slow, and only of late has it become practicable to give a complete account of its bony structure. The genus was named in 1847 by Pomel ('47 *a*, *b*) and shortly afterward renamed *Entelodon* by Aymard ('48) from a better specimen, but for several years only the dentition was known and that imperfectly. In 1850, Leidy ('50, p. 90) described the first American species, but, not suspecting its generic identity with the European forms, he at first referred it to a new genus, *Archæotherium*. Leidy's material enabled him to give a fairly complete account of the skull. Kowalevsky, in 1876, described an imperfect skull found in France and he further showed that the feet were didactyl, a very unexpected fact in view of the pig-like character of the dentition. In this country Profs. Marsh and Cope have added materially to our knowledge of this remarkable animal (Marsh, '73, '93, '94; Cope, '79) and the former has published a restoration of one of the species. In spite, however, of this list of workers who have, from time to time, occupied themselves with the study of *Elotherium*, much still remains to be learned regarding its structure, and its phylogenetic relationships are even more obscure.

In the summer of 1894, Mr. H. F. Wells discovered in the White River Bad Lands of South Dakota certain bones, which, with the expenditure of infinite pains and skill, were excavated from the rock by Mr. J. B. Hatcher, and which proved to be a most remarkably complete skeleton of *Elotherium*. This beautiful specimen (Princeton Museum, No. 10885,) formed the subject of a preliminary communication which I made to the third International Zoölogical Congress, at Leyden (Scott, '96), and will be more fully described in the following pages. Except for a single thoracic vertebra (and perhaps a few caudals) and part of the hyoid apparatus, the skeleton is complete; it is represented in Pl. XVII, which will enable the reader to judge of its unusual state of preservation. Additional material, belonging to several species, will also be made use of for purposes of of comparison, but the description will deal almost exclusively with the White River forms.

The Artiodactyla may almost be designated as the despair of the morphologist. So manifold are the forms which this puzzling group has assumed, and so variously are the characteristics of its minor groups combined, that the confusion seems hopeless. The only way in which this tangled skein can be unraveled and its many threads separated and made straight, is by the slow but sure method of tracing the phylogenetic development of each family step by step from its incipient stages. Many years must pass before sufficient palæontological material has been gathered to make this possible, but already some progress has been made in the work. Each successive form in a series, as soon as it is recovered, should be fully described and illustrated for the benefit of other workers, a necessity which must excuse the minuteness of detail into which the following description enters. For the sake of convenience the entire bony structure of the animal will be described, including those parts which are already well known, in order that the reader may be spared the trouble of searching through many scattered papers, written in several languages.

I. The Dentition.

The teeth of *Elotherium* are already familiarly known and require but a brief account here. The dental formula is I $\frac{3}{3}$, C $\frac{1}{1}$, P $\frac{4}{4}$, M $\frac{3}{3}$.

A. *Upper Jaw.*—The incisors, three in number, increase regularly in size from the first to the third, the latter being much the largest of the series; it has a conical or somewhat trihedral crown and resembles a canine in shape and appearance. In some individuals the crown of this tooth is worn in a peculiar manner, a deep groove or notch being formed on its posterior side, in a place where it cannot have been made by the attrition of any of the lower teeth. The other incisors have spatulate crowns, with blunted tips, the attrition of use wearing down the apices as well as the posterior faces of these teeth. This description applies more particularly to the larger White River species, such as *E. ingens* and *E. imperator;* in *E. mortoni* the upper incisors are of more nearly equal size and more conical shape. In all, the median incisors are separated from each other by a considerable notch, and the whole series is much more extended antero-posteriorly than transversely, the external incisor standing behind the second one. I ^{3} is separated by a short diastema from the canine and at this point the premaxillary border is quite deeply notched to receive the lower canine.

The canine is a very large and powerful tusk, with a swollen, gibbous fang; the crown is long, massive, recurved, and bluntly pointed; it is oval in section, and has a prominent posterior ridge.

The premolars are very simple in construction. The first three are well spaced apart and have compressed, but thick, conical crowns, without accessory cusps of any kind, and each is implanted by two fangs. In size, they increase posteriorly and p^{3} has a decidedly higher crown than any other premolar. P^{4} is smaller than p^{3} in every dimension except the transverse, this diameter being increased by the addition of a large internal cusp (the deuterocone) and the crown is carried upon three fangs. In the smaller species of the genus, such as *E. mortoni*, p^{3} and p^{4} are placed close together, while in the larger forms these teeth are separated by a short space, and the diastemata between the other premolars and between p^{1} and the canine are relatively somewhat greater, the enlargement of these teeth hardly keeping pace with the elongation of the muzzle. In the European species, *E. magnum*, the arrangement of the premolars is somewhat different, p^{2}, ^{3} and ^{4} forming a continuous series, while p^{1} and ^{2} are quite widely separated.

The molars are relatively quite small; m^{2} is the largest and m^{3} the smallest of the series. The crowns are low and bunodont, bearing six tubercles arranged in two transverse rows. The hypocone, though functionally important, is decidedly smaller than the protocone, and structurally is still a part of the cingulum. Schlosser is, however, mistaken in supposing that there is any important difference between the American and the European species of *Elotherium* with regard to the position of the protocone. In m^{3}, which has a more oval crown than the other molars, the sexitubercular pattern is obscured by the development of numerous small tubercles upon the hinder half of the tooth. The cingulum of the molars is quite strongly marked, especially upon the anterior and posterior faces.

B. *Lower Jaw.*—The incisors resemble those of the upper jaw, except that they are of more nearly equal size and somewhat more spatulate shape; i_{3} is little enlarged and is much smaller than the corresponding tooth in the upper jaw.

The canine is a very large, recurved tusk, like the upper one in size and shape; it bites between the upper canine and enlarged external incisor, the three teeth together making up a very formidable lacerating apparatus. An interesting hint as to the habits of this animal is given by a peculiar mode of wear of the lower canine which occurs in some well-preserved specimens. In these we find a deep groove on the posterior face of the tooth, beneath the enamel cap and close to the level of the gum. No other tooth can reach this point to cause such a mode of attrition, and the groove is doubtless due to the habit of digging up roots with the lower tusks; the pull of the roots, especially when covered with sand or other gritty material, would naturally wear such a groove.* The

* This ingenious and highly probable explanation of a somewhat puzzling fact was suggested to me by my colleague, Prof. C. F. Brackett.

same explanation applies to the curious notches sometimes worn in the external upper incisor. The numerous specimens examined do not indicate that there was any difference between the males and the females in the size of the canines, the tusks being invariably large and powerful. If, as here suggested, the canines served other purposes than those of weapons, the lack of any such sexual difference would be intelligible enough.

The premolars are very simple and quite like those of the upper series in shape; their crowns are massive, compressed cones, without additional cusps. The cingulum is usually prominent, but varies in the different species. $P_{\overline{3}}$ is much the highest of the series, especially in *E. imperator,* where it rises to the full height of the canine, and gives a very characteristic appearance to the lower dentition. $P_{\overline{4}}$ has its posterior face flattened, forming an incipient fossa with a number of small tubercles in it. $P_{\overline{3}}$ and $_{\overline{4}}$ stand quite close together, and $p_{\overline{1}}$ is separated by a short space from the canine, while $p_{\overline{2}}$ is isolated by considerable diastemata both in front of and behind it.

The lower molars are small in proportion to the size of the jaw and to the space occupied by the premolar series. In size they increase posteriorly, and they have a simple, quadritubercular pattern, the crowns surrounded by a strong cingulum. There is much variation in the development of the fifth or posterior unpaired cusp (hypoconulid); it is frequently absent and represented only by a strong cingulum, though sometimes it is present as a distinct cusp on $m_{\overline{1}}$ or $m_{\overline{2}}$. It is less commonly found on $m_{\overline{3}}$ and only in the very large *E. leidyanum* is it well developed.

The Milk Dentition.—The temporary canines and incisors differ from the permanent ones only in size. It is uncertain whether the first premolar, in either jaw, has a predecessor in the deciduous series, none of the specimens distinctly showing such a predecessor. In one individual, however, the tip of p^{1} is just visible in the centre of a large alveolus, from which a milk-tooth has apparently been shed. If this change does actually occur, it must take place at an early stage, and, on the whole, it seems probable that, at least in the upper jaw, the number of deciduous premolars is four. Dp^{2} has a compressed, elongate, conical crown, without accessory cusps of any kind; it is carried on two widely separated fangs, and is isolated by diastemata both in front of and behind it. Dp^{3} consists of three principal cusps. The antero-external cusp (protocone) is an acutely pointed pyramid, while the postero-external cusp (tritocone) is lower and smaller. The internal cusp (tetartocone) is posterior in position and placed on the same transverse line as the tritocone, while between the two is a small conule. The cingulum is distinct on the front and hind faces, obscure on the outer and absent from the inner face of the crown. Dp^{4} is molariform, but differs somewhat from the molar pattern in the fact that the postero-internal cusp is even more distinctly an elevation of the cingulum and that the posterior conule is double.

The lower milk-premolars are even simpler than the upper; dp $_{\overline{2}}$ and $_{\overline{3}}$ are compressed and conical, without accessory cusps, but with serrate edges and sharply-pointed summit. Each of these teeth is supported upon two fangs. Dp $_{\overline{4}}$ is of the usual artiodactyl type, consisting of three transverse pairs of cusps, of which the median pair is the largest, and the anterior pair the smallest. A small talon is formed by the elevation of the cingulum in the median line, behind the posterior pair of cusps.

This account of the milk dentition applies only to *E. mortoni;* I have not seen these teeth in the larger species.

Measurements.

	No. 11156	No. 10885	No. 11009	No. 11440
Upper dentition, length I 1 to M 3			?0.270	
" molar series, length	.118	.104	.064	.065
" premolar series, length	.238*	.175	.124	.113
" canine, ant.-post. diameter	.048*	.046	.032	
" " transverse diameter	.0385*	.042	.022	
" P 1, length	.030*	.024	.019	
" P 2, "	.038*	.038	.025	.023
" P 3, "	.041*		.028	.028
" P 4, "	.035*	.031	.0195	.018
" M 1, length	.035	.033		.020
" " width		.036		.019
" M 2, length	.042	.035	.025	.023
" " width		.039	.0235	.024
" M 3, length	.037	.034	.021	.021
" " width		.033	.022	.0215
Lower dentition, length I 1 to M 3	.432*			.261
" molar series, length	.121*	.108		.070
" premolar series, length	.211*	.192		.126
" P 1, length	.028*	.026		.017
" " height of crown	.026*			.019
" P 2, length	.031*	.033		.020
" " height	.038*			.023
" P 3, length	.046*	.043		.027
" " height	.061*			.031
" P 4, length	.046*	.037		.025
" " height	.044*			.020
" M 1, length	.037*	.031		.0215
" " width	.029*	.027		.013
" M 2, length	.0395*	.035		.0225
" " width	.036*	.030		.016
" M 3, length	.043*	.039		.0245
" " width	.037*	.028		.016

*No. 11161.

II. The Skull.

The skull of *Elotherium* is one of the most remarkable features of this very curious animal. It is characterized by great length and slenderness, with the supraoccipital and nasal bones lying in the same horizontal plane. The muzzle is exceedingly long and narrow, and tapers somewhat anteriorly, though expanded by the sockets of the great tusks; the orbit has been shifted far back, its anterior border being, in some species, over m $\frac{2}{}$, and in others above m $\frac{3}{}$. The cranium is short and of absurdly small capacity, which, with the great temporal openings, gives an almost reptilian appearance to the skull when viewed from above or below. The sagittal crest is very high and thin, and the zygomatic arches, though rather short, are enormously developed. One of the most peculiar features of the skull is the great, compressed plate which is given off from the ventral surface of the jugal and descends below the level of the lower jaw, and this grotesque appearance is further increased by two pairs of knob-like processes on the ventral borders of the mandible. The occiput (Pl. XVIII, Figs. 1, 2) is high and very broad at the base, but narrowing rapidly to the summit; above the foramen magnum it forms a broad, flat projection of almost uniform breadth, with a very deep fossa on each side of it.

The *basioccipital* is stout and rather short, keeled in the median ventral line and slightly contracted to receive the auditory bullæ; at its junction with the basisphenoid it forms a pair of small, roughened tubercles. The *exoccipitals* are very large bones, especially in the transverse direction along the base of the occiput, dorsally they narrow fast. Above the foramen magnum they form the very broad, prominent and nearly square projection which has already been mentioned; this is thick and is filled with cancellous bone, the fossa for the vermis of the cerebellum making but a slight depression upon its internal face. On each side of the projection is a large and deep triangular fossa, which, however, is not confined to the exoccipital, the periotic and squamosal both being concerned in its formation. The inferior part of the exoccipital extends widely outward, reaching to the line of the glenoid cavity, and ending in the large, prominent and massive, but not elongate paroccipital process. In this region the exoccipital is brought very close to the zygoma, but, ventrally at least, does not quite touch it, a narrow band of the tympanic intervening between them. The foramen magnum is strikingly small and of a transversely oval shape. The occipital condyles are relatively rather small, especially in the vertical dimension, laterally they are well extended, and they are widely separated both above and below. In the very large *E. imperator* the external angles of the condyles are abruptly truncated in a curious way, and bear flat articular surfaces, though in some individuals this truncation is found only on one side; while in the smaller species the condyles are of the usual form. The *supraoccipital* is a large bone, widest at the base (*i. e.*, the suture with the exoccipitals) and narrowing dorsally. Superiorly it is drawn out into two posterior wing-like processes, such as are found in *Oreodon* and other White River ungulates. Between these wings the hinder face of the bone is concave and at the bottom of this concavity are two small, but profound pits. The supraoccipital is continued over upon the roof of the cranium and forms a part of the sagittal crest.

A considerable part of the *periotic* is exposed on the surface of the skull, at the bottom of the lateral occipital fossa, where it is enclosed between the exoccipital and the squamosal; it does not give rise to any distinct mastoid process.

The occiput of the European species, *E. magnum*, as figured by Kowalevsky ('76, Taf. XVII, Fig. 5), is different in many details from that which characterizes the American species. It has more of an hour-glass shape, not so wide at the base, more contracted in the middle and more expanded at the top, but with much less conspicuous wing-like processes, and it has no such projection above the foramen magnum, nor such deep lateral fossæ. The condyles are larger and of an entirely different shape, having their principal diameter vertical, instead of transverse. The paroccipital processes are longer, more compressed and not so widely extended laterally. The foramen magnum is large and of more nearly circular outline.

The *basisphenoid* is narrower than the basioccipital and is not keeled on the ventral surface, but is otherwise like that bone. So much of its course is concealed by the union of the palatines and pterygoids along the median line that its length cannot be determined, while the presphenoid is nowhere exposed to view.

The *tympanic* is very extensively developed (Pl. XVIII, Fig. 1). Part of it is inflated into an oval, somewhat flattened and rather small auditory bulla, which differs from that of *Hippopotamus* and of all existing suillines in being hollow and not filled up with spongy tissue. On the outer side of the bulla the tympanic is extended as a narrow strip, which broadens considerably between the squamosal and the exoccipital, with both of which it articulates suturally, as well as with the alisphenoid in front. The bulla itself terminates anteriorly in a blunt spine.

The *alisphenoid* is small and forms very little of the side of the cranium. It is most elongate antero-posteriorly along the ventral line, but has hardly any distinctly developed pterygoid process. At the line of the sphenoidal fissure, which notches but does not perforate the bone, the alisphenoid is narrowed, to expand again at its suture with the parietal and frontal. The *orbitosphenoid* is relatively rather large, but is low in the vertical dimension, and does not extend upward into the orbit proper. Two sharp ridges on the external face of the bone enclose a V-shaped groove, in which lie the optic foramen and foramen lacerum anterius.

The *parietals* are very large proportionately to the size of the cranium, but quite small as compared with the entire length of the skull; they roof in most of the cerebral chamber, but toward the ventral side they rapidly contract, forming narrow strips between the squamosal and frontal. Throughout their length the parietals unite to form the very high, thin and plate-like sagittal crest, which is one of the most characteristic features of the skull. In the European species, *E. magnum*, this crest has a remarkably straight and horizontal course, but in the known American species it is gently arched from before backward. Large sinuses are developed in the parietals, so that the cerebral chamber is even smaller than it appears to be, when viewed from the outer side. These sinuses extend over the entire roof of the cerebral fossa, even invading the supraoccipital; they appear to be traversed by numerous small trabeculæ, the ends of which are seen, in the sagittal section, embedded in the matrix which fills the sinuses.

The *frontals* are much larger than the parietals. In the postorbital region they are very narrow, in conformity with the very small size of the brain, but at the orbits they expand widely to form the broad, lozenge-shaped forehead, which is convex from side to side, though slightly depressed, or "dished" in the middle; the supraciliary ridges are very inconspicuous. Anteriorly the frontals diverge to receive the nasals between them, sending forward long, pointed nasal processes, which, owing to the great elongation of the muzzle, are widely separated from the premaxillaries. The orbit is large and projects prominently outward; it is completely encircled by bone, the long and massive postorbital process of the frontal uniting suturally with the shorter process of the jugal. The orbits do not rise above the level of the forehead, as they do in *Hippopotamus*, and present more anteriorly, less directly outward, than in that animal. Mention has already been made of a groove on the orbitosphenoid, which terminates below and behind in the foramen lacerum anterius; this groove is continued upward and forward upon the frontal, steadily widening as it advances. The postero-superior ridge bounding the groove is the more prominent; it extends almost to the postorbital process, from which it is separated by a distinct notch, while the antero-inferior ridge dies away within the orbit. In most of the American species the forehead rises very gradually and gently behind to the sagittal crest, but in *E. ingens* the rise is much more sudden and steep. The frontal sinuses are large, giving the convex shape to the forehead which has been described; these sinuses appear to communicate with those formed in the parietals.

Except posteriorly, the *squamosal* forms but little of the side-wall of the cranium, its suture with the parietal curving abruptly downward and forward; its compressed and prominent hinder margin forms nearly the whole of the lambdoidal crest, though a continuation of it extends upward upon the supraoccipital, ending in the wing-like processes of that bone. The zygomatic process is enormously developed; it extends widely outward from the side of the skull as a massive, vertical plate, which is shaped much as in *Hippopotamus*, and is not continued forward as a broad, horizontal shelf, such as is found in *Sus*. The superior border curves upward into a great, hook-shaped process, which resembles that seen in *Merycochœrus*, and gives a highly characteristic appearance to this region of the skull. That portion of the zygomatic process which is directed anteriorly is short and, though massive, is much less so than that which extends out laterally; in front it is received into a notch of the jugal. The glenoid cavity is large, transversely directed and quite deeply concave, though the postglenoid process is not strongly developed and is hardly more conspicuous than the preglenoid ridge. This disposition is unusual among the ungulates, but it occurs also in the Eocene genus *Achænodon* and in the modern *Dicotyles*. The glenoid cavities of the two sides are very widely separated, their *inner* margins lying external to the line of the paroccipital processes. The posttympanic process of the squamosal is small, and is closely applied to the paroccipital process. The shape of the zygomatic arches, together with the extreme narrowness of the cranium proper, causes the temporal openings to be very large and to appear widely open when the skull is viewed from above. These openings are, however, less extended transversely and more antero-posteriorly than in *Hippopotamus*, while in *Sus* they are hardly visible from above.

The *jugal* is a very remarkable bone and constitutes one of the most extraordinary features of the *Elotherium* skull. Posteriorly it is notched to receive the zygoma, and sends out a process along the ventral face of that bone, extending to the preglenoid ridge. The jugal forms the inferior half of the nearly circular orbit, and for this purpose its dorsal border is made deeply concave, giving off a stout postorbital process to meet that of the frontal, while anteriorly it is moderately expanded upon the face in front of the orbit, where it is wedged in between the lachrymal and the maxillary. The most peculiar feature of the jugal, however, is the immensely developed vertical plate, which descends from beneath the orbit downward and outward to below the level of the ventral border of the mandible, recalling the similar, but much less massive processes found in certain edentates, *e. g.*, *Megatherium*. These plates are laterally compressed, but quite thick, and when the skull is viewed from the front, they are seen to diverge quite strongly downward; their shape varies in the different species. In the very large forms from the Protoceras beds, such as *E. imperator*, the process retains its plate-like form throughout, its free end being only moderately thickened. This appears to be true also of *E. mortoni*, though my material is not sufficient to allow me to make this statement positively, but in the large species from the Titanotherium and Oreodon beds (*E. ingens*) it forms a club-like thickening at the tip, which in *E. ingens* is coarsely crenulate on the posterior border (see Pl. XVII). These processes are, so far as is yet known, quite unique among the hoofed mammals, and it is difficult to form even a conjecture as to what their functional significance may have been. Some misunderstanding has arisen as to the species in which these jugal plates are found. Nothing is known concerning their presence or absence in the European representatives of the genus. Leidy's material gave him no reason to suspect their occurrence in the species described by him, and he consequently restored the zygomatic arches without them ('69, Pl. XVI). Marsh first discovered the processes in a skull of the species named by him *E. crassum*, and it has sometimes been assumed that they were more particularly characteristic of that form. As a matter of fact, they have been observed in all of the American species of which well-preserved skulls are known, viz., *E. mortoni*, *E. ingens*, and *E. imperator*, and, in all probability, all the American forms, at least, possessed them.

The *lachrymal* is a rather large bone and forms nearly half of the anterior boundary of the orbit. On the face it is expanded into quite a large plate, which articulates below with the jugal, in front with the maxillary, and above with the frontal, the long anterior process of which prevents any contact between the lachrymal and nasal. In *Hippopotamus* the very short, broad frontal has no anterior process, and so the nasal and lachrymal are connected, as they are also in *Sus*. Within the orbit the lachrymal is but little extended; the foramen is single, very small, and placed inside the orbital margin. The lachrymal spine is very low.

The *nasals* are narrow, slender and very much elongated. Their greatest width is at the anterior end of the nasal processes of the frontal, and here is also their greatest transverse convexity; from this point they narrow and flatten, both in front and behind. Anteriorly they contract very gradually and terminate in sharp points, with their free ends quite deeply notched. In *E. ingens* the nasals appear to be relatively shorter than in the other species. In *Hippopotamus* these bones have much the same shape as in *Elotherium*, but they narrow more abruptly behind the point of greatest width, and their free ends are not notched. In *Sus* the nasals are truncated posteriorly and in front their free tips project far beyond the borders of the premaxillaries.

The *premaxillaries* are very large and heavy bones, the horizontal or alveolar portion especially so. Posteriorly, this portion is constricted, forming a groove for the reception of the lower canine, expanding again in front to carry the large incisors. The palatine processes are not much developed, the very large incisive foramina leaving but little space for them; the spines are long and slender, extending behind the canine alveolus. The ascending ramus of the premaxillary is low and rises gradually behind, and though broad at first, it rapidly becomes very slender, terminating behind in a fine point. Though these bones in *Elotherium* have a very different appearance from the immensely enlarged premaxillaries of *Hippopotamus*, yet both may have been formed by divergent modifications of a common plan.

The *maxillary* is greatly extended antero-posteriorly, in correspondence with the elongation of the whole muzzle; its facial portion is low, gradually diminishing in height forward, where its suture with the premaxillary forms a very gentle, sweeping curve. The longest suture of the maxillary is that with the nasal, the connection with the frontal being very short, owing to the extension of the lachrymal. Posteriorly, this bone projects but little beneath the orbit, which has an imperfectly developed floor, and the projection which it sends out to the jugal is much less massive than in *Hippopotamus.* The face gradually narrows forward, until it reaches the infraorbital foramen, expanding again in front of the foramen and swelling out into the prominent canine alveolus. The palatine processes of the maxillaries are long and narrow, and as the molar-premolar series of the two sides form almost straight and parallel lines, the bony palate is of nearly uniform width, slightly concave transversely, but almost plane antero-posteriorly. In front, these palatine processes are deeply emarginated by the large incisive foramina, and in the median line are still further notched to receive the long premaxillary spines.

The *palatines* make up but very little of the bony palate, forming only a narrow strip in front of the posterior nares, and narrow bands along the sides. The palatal notches are small and shallow. The *pterygoids* are elongate, but quite low; there are no hamular processes or pterygoid fossæ; the two bones meet suturally along the median dorsal line, completely concealing the presphenoid from view. The posterior nares are long, narrow and low, extending forward to the middle of m $\frac{2}{}$; the opening gradually contracts posteriorly, where it becomes very narrow, while the side-walls slope upward and die away upon the alisphenoids. Anteriorly the nares are divided by the very large *vomer,* which is distinctly visible, and which at its hinder termination expands into a transverse plate, articulating with the palatines. The meeting of the two pterygoids forms a small canal, which appears to overlie the whole length of the posterior nares and to open forward into the nasal chamber on each side of the vomer. This is a very exceptional arrangement, and I am unable to suggest what its functional meaning may be (see Pl. XVIII, Fig. 1, *c*).

The *cranial foramina* are, in some respects, quite peculiar. The condylar foramen is large and conspicuous, being placed well in front of the condyle; it is, however, smaller than in the specimen of *E. magnum* which Kowalevsky has figured. The close approximation of the paroccipital and stylomastoid processes, and the outward extension of the tympanic between them, have given a somewhat unusual position to the postglenoid and stylomastoid foramina; they are crowded close together at the postero-external angle of the auditory bulla, and both of them perforate the enlarged tympanic bone. The foramen lacerum posterius forms a long, narrow and curved slit at the postero-internal angle of the bulla, while the foramen lacerum medium and the opening of the eustachian canal occupy their ordinary position at the front end of the bulla. No distinct carotid canal is visible externally.

Kowalevsky inferred from the study of his specimen that the foramen ovale "nicht als selbständiges Foramen existirte, wie z. B. bei den Ruminanten, sondern mit dem For. lac. med. verschmolzen war, wie bei den heutigen Suiden und bei Hippopotamus" ('76, p. 433). This is probably a mistake; at all events, it is not true of the American species, in which the foramen ovale is a long, conspicuous opening, of oval shape, perforating the alisphenoid. As in the ungulates generally, there is no separate foramen rotundum, that opening being fused with the foramen lacerum anterius. The latter is a large and somewhat irregular opening, which notches the anterior border of the alisphenoid, passing between that bone and the orbitosphenoid. The optic foramen is small and well separated from the foramen lacerum anterius, lying in front of and at a slightly higher level than the sphenoidal fissure; it does not open so far forward as in *E. magnum*, and, in consequence, it does not form such a remarkably elongated canal as in the European species (see Kowalevsky, '76, Taf. XVI, Figs. 1 and 3, *dd*), but, on the other hand, it is far from being a simple perforation of the orbitosphenoid, such as occurs in the recent ungulates. This elongation of the optic canal should probably be correlated with the very small size of the brain, which would seem to have been relatively smaller than in the ancestors of the genus. Though the orbits are far behind their primitive position, the backward shifting of the optic tract would seem to have kept pace with the change in the position of the orbits.

The posterior palatine foramina are large and conspicuous openings, placed at the maxillo-palatine suture, and separating the two bones at these points; the palatine plates of the maxillaries are deeply grooved for some distance in front of the foramina. The incisive foramina are likewise large, invading both the maxillaries and the premaxillaries; indeed, their size prevents the development of any considerable palatine processes on the latter bones. These foramina are in very marked contrast to those of *Hippopotamus*, in which the enormously expanded and massive premaxillaries are perforated by two small and widely separated openings; in *Sus* also the incisive foramina are proportionately much smaller than in *Elotherium*. The infraorbital foramen is large and is separated from the orbit by a considerable interval, opening above the anterior border of p $\frac{3}{}$. In front of the foramen a deep groove channels the outer face of the maxillary for a short distance. The canal itself is much elongated, in correspondence with the great length of the jaws, and its posterior orifice, within the orbit, is very large. The lachrymal foramen, which is single, is quite small and is placed inside of the orbit.

The supraorbital foramen is subject to some variation in the different species. In *E. ingens*, from the Titanotherium beds, these openings are of good size, are placed quite near to the median line, and have well-marked vascular channels running forward from them. In specimens of *E. mortoni* from the Oreodon beds, and in the very large species

(*E. imperator*) from the Protoceras beds, the openings have become minute; they are shifted laterally and have no anterior grooves leading from them.

The *mandible* is not the least curious part of this remarkable skull. The horizontal ramus is extremely long and nearly straight, with an almost horizontal inferior border. The depth and thickness of the ramus vary considerably; even in skulls of the same length the mandible is decidedly more slender in some specimens than in others. The materials are, however, not yet sufficient to determine whether this difference is of a specific, sexual, or merely individual character. A remarkable knob-like process is given off from the ventral border of the mandible, beneath $p_{\overline{4}}$, which is subject to much variation in shape and elongation, in accordance with the age and size of the animal. In young individuals still retaining the milk-dentition, the process is a mere rugose elevation, and in the adults of the smaller species it is hardly more than a knob, while in the large forms it becomes greatly elongated and club-shaped. No marked difference in this regard is observable between the species from the upper and those from the lower horizons of the White River formation, the process being relatively quite as long and prominent in *E. ingens* from the Titanotherium beds, as in *E. imperator* from the Protoceras beds, but in the huge John Day species it has become particularly long and heavy.

The symphysis is quite long and very thick and massive; the two rami are indistinguishably fused together and laterally expanded, so as to somewhat resemble the symphysis of *Hippopotamus*, though not attaining any such extreme degree of massiveness as in the modern genus. The chin is abruptly truncated and flattened, and rises very steeply from below; on each side, beneath or a little behind the canine alveolus, there arises from the ventral border a second club-shaped process, similar to, but much heavier and more prominent than the posterior process already described. These two pairs of knobs give to the jaw a highly peculiar and characteristic appearance; they form another of the enigmatical features of the *Elotherium* skull, for it is difficult to imagine what part they can have played in the economy of the animal.

The two inferior dental series pursue a nearly parallel course, diverging backward but little, but behind the molars the two rami turn outward and diverge rapidly, so that posteriorly they are very widely separated, in correspondence with the great interval between the glenoid cavities of the two squamosals. The angle of the mandible is prominent and descends below the ventral border of the horizontal ramus, much as in *Hippopotamus*, though not to the same extent. The ascending ramus is not high, but of considerable antero-posterior extent. The masseteric fossa is quite small, but very deeply impressed, and is situated quite high upon the side of the jaw. The condyle is relatively little raised above the level of the molar teeth, and it is sessile, hence inconspicuous, though it is large, transversely expanded, and strongly convex. The coronoid process is strikingly low and small; it is of triangular shape, erect and not at all recurved, and is separated from the condyle by a very wide sigmoid notch. The mental foramen is small, single, and placed below $p_{\overline{2}}$.

Several of the *hyoid* elements are preserved in connection with the skeleton of *E. ingens* which forms the principal subject of this description. The stylohyal is quite long and slender; its proximal portion is laterally compressed and very thin, but moderately broadened in the fore and aft direction. For the distal two-thirds of its length the bone is thicker and of a compressed oval section, expanding into a club-shaped thickening at the lower end, which is excavated for the connecting cartilage. The ceratohyal is considerably shorter than the stylohyal, but of quite similar shape; its proximal end bears a cup-shaped expansion, beneath which it becomes very thin and much compressed, but broadened antero-posteriorly; the inferior part of the shaft is slender and oval in section, with another cup-shaped expansion at the distal end. The epihyal and basihyal have not been preserved. The thyrohyal is of remarkable length and slenderness, and obviously was not coössified with the basihyal; the bone is of subcylindrical shape, with expansions at the proximal and distal ends.

This hyoid apparatus does not resemble that of any artiodactyl with which I have been able to compare it. The elements of the anterior arch somewhat resemble those of *Hippopotamus*, but are more slender and elongate. In the modern genus, on the other hand, the thyrohyals are very short, and are ankylosed with the basihyal, a totally different arrangement from that which characterizes *Elotherium*.

From the foregoing description and accompanying figures it will be obvious that the skull of *Elotherium* is an extremely peculiar one. Among recent animals that of *Hippopotamus* approximates it most closely, and displays, with many striking differences, several decided and, it may be, significant resemblances. Some of these resemblances, such as the straight cranio-facial axis and the long sagittal crest, are of no particular importance, because they occur so very generally among the primitive ungulates of all groups. Other similarities, again, are not of this nature. The proportions of the cranial and facial regions, the degree of backward shifting of the orbits, the relations of the zygomatic and paroccipital processes, the broadening of the muzzle, and the general plan of skull construction, are all similar in the two genera. On the other hand, each genus has certain peculiarities correlated with its manner of life. Thus, the elevation of the orbits and the backward displacement of the posterior nares in *Hippopotamus* are adaptations to its aquatic habits. Doubtless the extraordinary peculiarities of *Elotherium*, such as the dependent processes of the jugals and the great knobs on the mandible, are of a similar nature, though, in the absence of the soft parts, it is difficult even to conjecture what their use may have been.

Measurements.

	No. 11156.	No. 10885.	No. 11009.	No. 11440.
Skull, extreme length on basal line	0.803	?0.648	?0.460	
" width across zygomatic arches (behind jugal process)	?.500	.443	.297	.264
" width at p $\frac{4}{}$	.133	.140	.089	.082
Cranium, length to anterior border of orbit	.282	.288	.198	.193
Face, length to anterior border of orbit	.518	?.378	.270	
Occiput, breadth of base	.281	.252	.160	.158
" height	.158		.120	
Bony palate, length in median line		?.376	.247	
Zygomatic arch, length	.279	.271	.146	.146
Descending process of jugal, length	.330	.256		.126
Mandible, length	.659*	.608		
" height at coronoid process	.253*	.171		.107
" depth at p $\frac{}{4}$	.133*	.091		.052

* No. 11161.

III. The Brain.

Attention has been repeatedly called, in the foregoing description of the skull, to the extraordinarily small size of the brain-cavity. Even on viewing the skull externally, this smallness of the cranium proper strikes the observer immediately, and, in connection with the long, slender muzzle, gives the skull something of a reptilian aspect. When the cranium is sawn open in longitudinal section, it becomes apparent that the brain is even smaller than would be inferred from the external view alone, much of the space being, so to speak, wasted in the great frontal and parietal sinuses which overlie the whole cerebral chamber. In a large, full-grown skull this chamber will hardly contain an ordinary human fist.

The *olfactory lobes* are very large and are connected with the cerebrum by short thick olfactory tracts. The lobes are not at all overlapped by the hemispheres, but are entirely exposed for their whole length.

The *cerebral hemispheres* are relatively small, though they are, of course, much larger than the other segments of the brain; so short are they that they do not extend over the olfactory lobes in front, or the cerebellum behind. In shape, they are low and wide, narrowing gradually forward, but with blunt anterior termination. The frontal lobe is very small, for the frontals take but little share in the roof of the cerebral chamber. The parietal lobe, on the other hand, is relatively large and forms the greater part of the hemisphere, for there is, properly speaking, no occipital lobe, the occipital bones not taking any part in the formation of the cerebral fossa. The temporo-sphenoidal lobe is also quite large and prominent, but is short antero-posteriorly. The brain-cast shows that the hemispheres were convoluted, but the convolutions are so feebly marked that they are hardly worth description. It is obvious, however, that the gyri were fewer and simpler than in any of the modern ungulates.

The *cerebellum* is rather small, though the cerebellar fossa has a vertical diameter not much less than that of the cerebral fossa. Antero-posteriorly the former is quite short and its transverse breadth is not great. This breadth is still further reduced by the relatively very large size of the periotic bones which extend freely into the fossa.

IV. The Vertebral Column.

The vertebral formula is: C 7, Th ? 13, L 6, S 2, Cd 15 +

The *atlas* (Pl. XVIII, Fig. 3) is very wide transversely, and at the same time it is of considerable antero-posterior extent, a shape which recalls that of *Anoplotherium*, rather than that of the recent ruminants or suillines. The anterior cavities for the occipital condyles are deep and wide, but low and depressed. Dorsally, these cotylcs are widely separated by a broad, but not very deep emargination of the neural arch, nor do they approximate each other very closely on the ventral side, a notch of considerable width intervening between them at this point. The neural arch is thick and heavy, but short from before backward and quite narrow transversely; it is also low, not arching strongly toward the dorsal side, and nearly smooth, being free from any but the most obscurely marked ridges. The foramina perforating the arch for the first pair of spinal nerves are unusually large. The neural spine is rudimentary and forms only an inconspicuous tubercle. The neural canal is low and broad, forming a transversely directed ellipse. The inferior arch is considerably more elongated antero-posteriorly than the neural, and has but little transverse curvature, except laterally, where it rises to form the sides of the neural canal. The hypapophysis is represented by a small, backwardly directed tubercle, which arises from the hinder margin of the ventral arch, and occupies the same position as in the pigs, but is much less strongly developed. The articular surfaces for the axis are low and broad, and have a very oblique position, presenting inward toward the median line, almost as much as backward; they have also a slight dorsal presentation. In shape, they are very slightly concave and are surrounded by prominent borders. The facet for the odontoid is wide, and deeply concave in the transverse direction, but quite short antero-posteriorly. This facet is connected at the sides with those for the centrum of the axis, but distinct ridges are formed along the line of junction.

The transverse processes of the atlas extend out widely from the sides of the arch, attaining their greatest transverse breadth along the posterior line; they are also very long in the fore-and-aft direction, reaching far behind the surfaces for the axis. For most of their course the transverse processes have thin borders, but posteriorly the margin becomes much thicker and more rugose. The vertebrarterial canal, which is notably small, occupies much the same position as in *Sus*, opening posteriorly upon the dorsal side of the hinder border. The anterior extension of the transverse processes has converted into foramina (atlanteo-diapophysial) the notches for the inferior branches of the first pair of spinal nerves. On the ventral face of each process is a large fossa, enclosed between the side of the inferior arch and the greatly thickened posterior border of the process. The resemblance in shape to the atlas of *Anoplotherium*, to which attention has already been called, affects more particularly the form of the transverse processes but they are more extended transversely than in that genus and are not so pointed at the postero-external angles.

The *axis* (Pl. XVIII, Fig. 4) is a short, but very massively constructed bone, which in general shape and appearance resembles that of *Hippopotamus.* The centrum is short, anteriorly very broad and depressed, but thickening posteriorly, and with a nearly circular and slightly concave hinder face. A strong and prominent keel runs along the ventral face of the centrum, enlarging backward, and terminating behind in a trifid hypapophysis. The odontoid process is short, heavy and conical, with no tendency whatever to assume the depressed and flattened shape which occurs in so many White River ungulates. The ventral articular surface of the odontoid seems like something superadded to the process itself, for it is clearly demarcated by a groove running all around it, and projects slightly in front of the body of the process. On the dorsal side of the centrum a broad and well-defined ridge runs backward from the odontoid along the floor of the neural canal. The atlanteal articular surfaces are very broad and low, not rising so as to enclose any part of the neural canal. They are very oblique with reference to the median line of the centrum, with which they form angles of about 45°. These surfaces are slightly convex in both directions, and ventrally they project much below the level of the centrum.

The transverse processes are short, thin and compressed, much less massive and widely extended than in *Hippopotamus;* they are perforated by very large foramina for the vertebral arteries. The pedicels of the neural arch are low and short, but very heavy; they are not pierced for the passage of the second pair of spinal nerves, as they are in *Hippopotamus* and in some of the pigs. The neural canal is decidedly small, especially its anterior opening; behind, it enlarges somewhat, particularly in the dorso-ventral dimension, the posterior opening being high and narrow, while in *Hippopotamus* it is low and broad. The neural spine is a large plate which is very thin in front, but becomes thick and massive behind, ending in a broad rugosity. This spine resembles that of *Hippopotamus,* but is not produced so far backward and does not overhang the third cervical. The postzygapophyses are large, slightly concave, and present obliquely outward, as well as downward; their bases are separated by a broad and deep groove, which is continued upward upon the posterior side of the neural spine.

The *third cervical vertebra* also bears a considerable resemblance to that of *Hippopotamus*, differing only in some points of detail. The centrum is short, heavy and moderately opisthocœlous, depressed, but increasing posteriorly in vertical thickness. It bears a strong ventral keel, which terminates behind, as in the axis, in a trifid hypapophysis. The pedicels of the neural arch are not, as in the pigs, pierced by foramina for the spinal nerves; they are low and short, but very thick, and the neural canal is strikingly small. The dorsal side of the arch is short, broad and nearly flat. The neural spine is remarkably well-developed (when the anterior position of the vertebra is taken into account), rising as high as that of the axis. It is rather thin and compressed, although its base occupies the whole fore-and-aft length of the arch. From the base, however, it rapidly tapers upward and terminates in a small, rough tubercle. In *Hippopotamus* the third cervical has an even better developed neural spine, not higher, but broader and less tapering than in *Elotherium*. The prezygapophyses are large, oblique and somewhat convex; they are placed very low, so that their inferior margins are separated from the centrum only by narrow notches. The posterior zygapophyses are much larger and more prominent than the anterior pair; they are also less oblique in position and are raised higher above the centrum, corresponding to the posterior elevation of the neural arch. The transverse process is a compressed plate, which has no great vertical height, but is well extended from before backward, exceeding the centrum in length; the posterior portion of the process is thickened and recurved, ending in a rugose hook. The absence of any distinctly marked diapophysial element distinguishes this vertebra from the corresponding one of *Hippopotamus* and *Sus*, and in the latter genus the inferior lamella is more slender and rod-like, while the spinal nerves make their exit through foramina in the pedicels of the neural arch.

The *fourth cervical vertebra* is different, in many respects, from the third. The centrum is somewhat shorter and is less distinctly carinate on the ventral side, but is more decidedly opisthocœlous. The neural arch is remarkably short in the antero-posterior dimension, so that the articular faces of the postzygapophyses actually extend forward beneath those of the anterior pair, which gives to the pedicel of the neural arch, when seen from the side, a curiously notched appearance. The neural spine is higher, but more slender and recurved than that of the third cervical. The transverse process is altogether different in shape from that of the latter. It has, in the first place, a very prominent diapophysial element, which projects outward as a heavy, depressed bar, thickened, rugose, and slightly upcurved at the distal end. In the second place, the inferior lamella is much higher vertically, but decidedly shorter from before backward.

In *Hippopotamus* and in *Sus* this vertebra is very similar to that of *Elotherium*, but the neural spine is notably heavier.

The *fifth cervical vertebra* has an even shorter neural arch than the fourth and a much higher neural spine. The spine tapers rapidly from the base upward and becomes very slender, but it is nearly straight and only slightly recurved. The neural canal is somewhat larger than in the fourth vertebra, but, as in all the cervicals, it is strikingly small as compared with the size of the vertebra as a whole. The diapophysis is strong and prominent, but more slender than on the preceding vertebra, while the inferior lamella, though relatively short from before backward, has attained great vertical height and is strongly everted. In *Elotherium* the fifth vertebra is of the same type as the sixth, whereas in *Hippopotamus* it more nearly resembles the fourth.

The *sixth cervical* is very like the fifth, but displays certain obvious differences. Thus, the neural arch is even shorter antero-posteriorly, and the neural spine is higher, heavier and much more strongly recurved. The postzygapophyses are decidedly smaller and are very characteristic in their markedly oblique position, for they rise steeply backward in a way that occurs in none of the other vertebræ. The diapophysis is shorter but heavier than that of the fifth, while the inferior lamella is of similar shape, but larger, higher and with the free margin more thickened. In *Hippopotamus* this vertebra has much the same construction as in *Elotherium*, but the spine is shorter and more massive and the inferior lamella is much larger. In *Sus* the sixth cervical bears considerable resemblance to that of the White River genus.

The *seventh cervical* is characterized by the height and thickness of the spine, which in these respects much exceeds that of the sixth. This spine tapers superiorly, but expands again at the tip into a rough tubercle. The posterior zygapophyses stand at a higher level than the anterior pair and are unusually concave. The peculiarities seen in the postzygapophyses of the sixth and seventh vertebræ are to provide for the curvature of the neck, which changes its direction at this point. From the occiput to the sixth cervical the neck is nearly straight and inclines downward and backward, while the seventh vertebra begins the rise which culminates in the anterior thoracic region. This change in direction requires greater freedom of motion, which is supplied by the modification of the zygapophyses upon the vertebræ mentioned. The transverse process is, as usual, not perforated by the vertebrarterial canal; it is rather short, but heavy and much expanded at the distal end. On the posterior face of the centrum are large facets for the heads of the first pair of ribs. In *Hippopotamus* the neural spine of the seventh cervical is relatively much longer and heavier than in *Elotherium* or in *Sus*.

As a whole, the neck of *Elotherium* is short and massive, with very strongly developed processes for muscular and ligamentous attachments, as are indeed necessitated by the immense weight and length of the head. Among recent artiodactyls *Hippopotamus* has cervical vertebræ most like those of *Elotherium*, though there are many differences in the details of construction. The most apparent of these differences lies in the greater and more uniform height and thickness of the neural spines in the modern genus. Doubtless the even more exaggerated massiveness of the skull in the latter is the occasion of this increased development of the cervical spines. In *Sus* the perforation of the neural arches for the passage of the spinal nerves constitutes an important difference from *Elotherium*.

The *thoracic vertebræ* would appear to have numbered thirteen, though this point cannot, as yet, be determined with entire certainty, and while the thoraco-lumbar vertebræ were, in all probability, nineteen in number, as is well-nigh universal among the artiodactyls, yet there were doubtless variations in the number of ribs, as is very frequently the case among existing animals.

The first thoracic has a rather small centrum, with decidedly convex anterior and nearly flat posterior face; the facets for the rib-heads are very large and deeply concave. The transverse process is rather short, but very large, heavy and rugose, and bears an unusually large, concave facet for the tubercle of the first rib. The prezygapophyses are of the cervical type, but present more obliquely inward than in the vertebræ of the neck, while the postzygapophyses are, as in the other thoracics, placed upon the ventral side of the neural arch. The neural canal is high and narrow and its anterior opening has assumed a cordate outline. The neural spine is inclined strongly backward, much more so than that of the seventh cervical, and though laterally compressed it is extremely high, broad and massive, greatly exceeding in all its dimensions that of the last neck vertebra.

The anterior six thoracic vertebræ (see Pl. XVIII, Fig. 5) are very much alike in appearance. The first three have broader and more depressed centra, which in the others become deeper vertically and more trihedral in section. The transverse processes are very large and prominent and carry large, deeply concave facets for the rib tubercles. The neural spines are very high, thick and heavy, and are strongly inclined backward, with club-shaped thickenings at the tips. At the seventh thoracic begins a rapid reduction in the length and weight of the spines, a process which reaches its culmination on the eleventh vertebra, which has a remarkably short, weak and slender spine. This arrangement results in a great hump at the shoulders, somewhat as in *Titanotherium*, though in a less exaggerated form. In both genera, the length of the anterior thoracic spines should be correlated with the great elongation and weight of the skull which requires immense muscular strength in the neck and shoulders. *Hippopotamus* has no such hump, but this is probably explained by its largely aquatic habits.

A change in the character of the facets for the rib tubercles occurs simultaneously with the shortening of the neural spines; they suddenly become much reduced in size and are plane instead of concave. The transverse processes, however, remain very large and prominent as far back as the eleventh thoracic. In no case are these processes perforated by vertical canals, such as occur in *Sus*. The twelfth thoracic is the anticlinal vertebra and has a nearly erect spine of lumbar type, though somewhat more slender than in the true lumbars. On the thirteenth the spine is quite like that of the lumbars and inclines slightly forward. Transverse processes are absent from the last two thoracic vertebræ, which display the feature, very unusual in an ungulate, of large and conspicuous anapophyses.

As far back as the eleventh vertebra the zygapophyses are of the ordinary thoracic type; they are small, oval facets, the anterior pair on the front of the neural arch and presenting upward, the posterior pair on the hinder part of the arch and presenting downward. On the eleventh thoracic a change takes place; the anterior zygapophyses are as before, but the posterior processes are flat and present obliquely outward, rather than downward, the two together forming a prominent, wedge-shaped mass. The prezygapophyses of the twelfth vertebra are correspondingly modified; they present obliquely inward and together constitute a cavity which receives the wedge-like projection from the eleventh. Prominent metapophyses also make their appearance on the twelfth thoracic. The posterior zygapophyses of the latter and both pairs of the thirteenth are of the cylindrical, interlocking type characteristic of the lumbars. These processes are remarkably complex and in a fashion that does not occur in *Hippopotamus*, but is found in *Sus* and many of the Pecora. The complexity is occasioned by the development of large episphenial processes, which give an additional articular surface above the zygapophyses proper; in section these processes have an S-like outline, and they constitute a joint of great strength.

The *lumbar vertebræ* (Pl. XVIII, Fig. 6), almost certainly six in number, have rather short, but massive centra. In the anterior part of the region the centra are somewhat cylindrical in shape, but they become more and more depressed and flattened as we approach the sacrum. The neural canal is broad and very low, especially in the posterior part of the region. The neural spines are inclined forward and are of moderate height; they are broad antero-posteriorly, but thin and laterally compressed, except at the tips, where they are thickened. The spine of the last lumbar is a little different from the others in being more erect and slender. Episphenial processes are present on the first, second and sixth vertebræ, but not on the third, fourth or fifth. These processes are apt to be somewhat asymmetrical and better developed on one side than on the other, and it is probable that more extensive material would show them to be subject to much individual variation. Metapophyses are prominent only on the first and second lumbars, rudimentary on the third and absent from the others. The transverse processes are very feebly developed in proportion to the size of the vertebræ. On the first lumbar they are short and straight, and gradually increase in length up to the fifth, but in all they are strikingly thin and slender. The last lumbar has transverse processes of unusual length, space for them being obtained by the sudden eversion of the anterior ends of the ilia, but even here they are weak.

The trunk-vertebræ of *Hippopotamus* are much more massively constructed than those of *Elotherium*, the decrease in length of the thoracic spines posteriorly is more gradual, while the neural spines and transverse processes of the lumbars are much longer and in every way heavier. The thoraco-lumbar series of *Sus* bears considerable resemblance to that of *Elotherium*, but in the former the transverse processes of the thoracic vertebræ are perforated by vertical canals, and those of the lumbars are much longer and stouter.

The *sacrum* consists of two vertebræ only. The first has a broad, depressed centrum and very large pleurapophyses, which carry most of the weight of the ilia, though the second sacral has also a limited contact with the pelvis. On the first vertebra the prezygapophyses are very well-developed and have large episphenial processes to receive those of the last lumbar. The two neural spines are coössified into a high but short ridge. The second sacral has a very much smaller and especially a narrower centrum than the first, and retains moderately complete postzygapophyses.

In *Hippopotamus* and in *Sus* the sacrum is relatively much larger than in *Elotherium*, and consists of at least four vertebræ, sometimes even as many as six. Even in aged individuals of the White River genus I have not seen more than two vertebræ in the sacrum.

The *caudal vertebræ* (Pl. XVIII, Figs. 7, 8, 9), of which fifteen are preserved in association with one individual, indicate a tail of only moderate length, and present a number of peculiarities. The first caudal has somewhat the appearance of a miniature lumbar; its centrum is short, broad and depressed, with quite strongly convex faces; the neural canal is relatively large and a distinct, though small, neural spine is present. The zygapophyses, especially the anterior pair, are large and prominent and project much in front of and behind the centrum. The transverse processes are quite long and heavy, and are directed outward and backward. A pair of tubercles on the ventral side of the centrum represent rudimentary hæmapophyses.

The succeeding caudal vertebræ resemble the first in a general way, but passing backward, the centra become more and more slender and elongate, while the neural canal diminishes in size, and the various processes are reduced. The hæmapophyses, on the other hand, increase in size and on the (?) fifth vertebra they curve toward each other, almost meeting and enclosing a canal, which continues as far back as the (?) eighth vertebra, behind which the hæmapophyses are again reduced. The middle portion of the tail is composed of very long, cylindrical vertebræ, which in shape strikingly resemble those of the great cats, and which are proportionately much longer, though apparently less numerous than those of *Anoplotherium.* At the anterior end of each vertebra are six prominent, nodular processes, the zygapophyses, transverse processes and hæmapophyses respectively. Posteriorly the centra become more and more slender, but are not much diminished in length, for what appears to be the penultimate vertebra is nearly as long as those in the middle region. The various processes are, however, reduced to very insignificant proportions. The last vertebra has its anterior portion shaped like that of its predecessor, but it rapidly tapers behind to a smooth, slender, compressed and subcylindrical rod, with a club-shaped thickening at the end. As I have seen but a single specimen of this curious vertebra, I cannot feel quite confident that its shape is a normal one and not due to some injury or morbid process.

The tail of *Hippopotamus* is of about the same relative length as that of *Elotherium,* but the individual vertebræ are very different, being all shorter and heavier, and diminishing in size more gradually to the end. In *Sus* the caudal vertebræ are somewhat more like those of *Elotherium*, but none of them have such slender elongate centra. Little is known concerning the caudals of *Anthracotherium.* Kowalevsky says of them: "Von den Schwanzwirbeln liegt mir nur ein einziges vor. Obwohl seine Erhaltung sehr mangelhaft erscheint, kann man doch aus diesem kleinen Stück den Schluss ziehen, dass der Schwanz bei den Anthracotherien kurz war und somit gar keine Aehnlichkeit mit dem sonderbar langen Schwanze der Anoplotherien hatte" ('73, p. 333; Taf. x, Fig. 36). The vertebra described by Kowalevsky is an anterior caudal and is much smaller and in every way more reduced than the corresponding ones of *Elotherium.* Among existing artiodactyls, it is the giraffe which most resembles the White River genus in the peculiar character of its caudal vertebræ.

Measurements.

Atlas, length	0.160
Atlas, greatest width	.270
Axis, length of centrum	.085
Axis, length of odontoid	.026
Axis, anterior breadth	.109
Axis, posterior breadth	.054
Third cervical, length	.066
Seventh cervical, length	.056
First thoracic, length	.051

Measurements.

Fifth thoracic, height of neural spine.	.291
First lumbar, length	.050
Sixth lumbar, length	.048
Sixth lumbar, breadth across transverse processes	.176
Sacrum, length	.098
First sacral, width of centrum	.068
Second sacral, width of centrum	.025
Anterior caudal, length	.032
Median caudal, length	.063

V. The Ribs and Sternum.

The *ribs* of *Elotherium* are decidedly smaller and lighter and indicate a less capacious thorax than we should expect to find in such a large animal, a fact which adds to the apparent height of the skeleton, because of the long interval between the thorax and the ground.

The first rib is short, subcylindrical proximally, but broadening considerably at the distal end; it has only a slight lateral curvature, appearing nearly straight when viewed from the front, but it arches moderately backward. The head is large and compressed, and is separated by a deep and narrow notch from the very large and conspicuous tubercle, which is also compressed laterally. The ribs increase gradually in length up to the seventh or eighth of the series, and the posterior five, though successively shortening, retain a considerable relative length throughout. The first five or six ribs are laterally compressed and of moderate breadth, but the posterior part of the thorax is composed of very slender and subcylindrical ribs, very different from those which we find in most ungulates, except in the more primitive groups. The tubercle reaches its maximum of size and prominence on the third rib, behind which it gradually diminishes in size and becomes more and more widely separated from the head, and more sessile in position. On the twelfth and thirteenth pairs the tubercles are absent, corresponding to the lack of transverse processes on the twelfth and thirteenth thoracic vertebræ.

In *Hippopotamus* the ribs are relatively very much longer, broader and heavier than those of *Elotherium*, and grow broader toward the hinder end of the thorax, where the great bony slabs are in the sharpest possible contrast to the slender and subcylindrical rods of the extinct genus. In *Sus* the ribs are more like those of *Elotherium*, but they have not such a regular and symmetrical curvature as in the latter.

The *sternum* of *Elotherium* is a very remarkable structure, and although it is of distinctly suilline type, it is, nevertheless, not altogether like the sternum of any known genus, recent or fossil. The presternum, or manubrium, forms a very large, thin, compressed and keel-shaped plate, which is especially remarkable for its great vertical depth, this dimension exceeding the antero-posterior length, and is proportionately much greater than in *Hippopotamus* or the modern suillines. The body of this segment is extremely thin, but the anterior border, and to some extent the ventral border also, is thickened and rugose. The facets for the first pair of sternal ribs form prominences, which are situated near together and close to the postero-superior angles of the segment, so that nearly the entire length of the latter projects in front of the first pair of ribs.

Of the mesosternum four segments and a part of the fifth are preserved. The first segment somewhat resembles the presternum in shape, being short, narrow and very deep; the dorsal border is much thicker and wider than any other part of the segment, and the ventral border is also thickened, though in a less marked degree. Posteriorly, this element becomes somewhat wider and shallower. The second segment of the mesosternum is decidedly broader and shallower than the first, but still retains a very unusual degree of vertical depth. Both the dorsal and ventral surfaces are much broadened, while the body of the bone is a thin, vertical plate, which connects the horizontally directed dorsal and ventral borders, giving a cross-section somewhat like that of an I-beam. In the third segment these progressive changes are carried still farther, and the bone becomes very distinctly broader and lower than the second segment. The dorsal and ventral borders still project much beyond the vertical connecting plate; this plate, however, is much thicker transversely than in the preceding segment. The ventral surface is rendered quite strongly concave by the elevation of its lateral borders. In part, this concavity may be due to the pressure which has somewhat distorted the entire sternum, but the ventral groove is so symmetrical that it can hardly be altogether due to distortion. The fourth and fifth segments exhibit similar changes, each one being broader and lower than the one in front of it; the vertical plate becomes very much thicker and the ventral groove more widely open. Though the specimen is of an animal past maturity, yet the last three segments distinctly show the median suture, along which their lateral halves united.

In *Hippopotamus* the breast-bone is quite like that of *Elotherium*, but the presternum is longer and not of such exaggerated depth, and the rib-facets are placed much nearer to the anterior end, while the mesosternum consists of fewer, broader and shallower segments. In *Sus* the sternum is still more like that of *Elotherium*, but has a decidedly longer and lower presternum.

VI. The Fore Limb.

The fore limb of *Elotherium* is quite elongate and, in connection with the shallow thorax, and very long neural spines of the anterior thoracic vertebræ, it gives to the skeleton a somewhat stilted appearance.

The *scapula* is remarkably high, narrow and slender, at least in the White River species, while in the John Day forms there is reason to believe that its proportions are quite different. The glenoid cavity forms a narrow, elongate oval, with its long axis directed antero-posteriorly, and is not very deeply concave. The coracoid is a large, but not very conspicuous rugosity, which sends off from its inner side a compressed, hook-like process; when the shoulder-blade is seen from the external side, this process is concealed from view. The neck of the scapula is broad and rather thick, and there is no distinct coraco-scapular notch. The coracoid border in its upward course inclines forward but little, and for the upper one-third of its height curves gently backward, to join the suprascapular border, which is exceedingly short. The glenoid border is more oblique, and inclines backward and upward at a moderate angle. The spine is shifted far forward, dividing the blade very unequally, so that the prescapular fossa is very much smaller than the postscapular. Indeed, the distal one-third of the shoulder-blade can hardly be said to have any prescapular fossa at all. The spine itself is rather low, and for much of its course its free border is curved backward and thickened to form a massive metacromion. The acromion is very short and inconspicuous, ending considerably above the level of the glenoid cavity.

The scapula associated with the large species of *Elotherium* from the John Day beds, which Cope has described under the name of *Boöchœrus* ('79, p. 59), is very different in shape from that of *E. ingens* from the White River, to which the description in the preceding paragraph more particularly applies. The blade is very much broader, both fossæ widening rapidly toward the dorsal end; these fossæ are of nearly equal width and the spine is placed almost in the middle of the blade. There can be little doubt that this scapula is properly referred to the incomplete skeleton with which it was found associated. Aside from its similarity in color and texture to the rest of the skeleton, there is no other animal known from the John Day horizon to which so large a scapula could belong.

The shoulder-blade of *Hippopotamus* is much broader, in proportion to its height, than that of *E. ingens;* the coracoid is more prominent and the coraco-scapular notch is distinctly marked; the postscapular fossa is somewhat larger than the prescapular, but the difference is much less extreme than in the White River species, the spine occupying a more median position; the acromion is much the same in the two forms, but the metacromion is larger in the fossil. In *Sus* also the scapula is relatively broader than in *E. ingens*, and, in particular, it has a wider prescapular fossa, but is without any distinct coraco-scapular notch. The spine rises from the suprascapular border very steeply to the high (but much smaller) metacromion, and then descends gradually to the neck, without forming an acromion. In spite of these differences, the resemblance in the character of the scapula between *Sus* and *Elotherium* is unmistakable.

The *humerus* is relatively long, but is, at the same time, a massively constructed bone. The head is large and very strongly convex, especially from above downward, although it is not set upon a very distinct neck, nor does it project far behind the plane of the shaft. The external tuberosity is very large, forming a massive and roughened ridge, which runs across the whole anterior face of the head and rises toward the internal side, where it terminates in a high, thick and recurved hook, overhanging the bicipital groove. The internal tuberosity is very much smaller, but is, nevertheless, quite prominent; it likewise projects over the bicipital groove, which is very broad and deeply incised into the bone. The great transverse breadth of the external tuberosity displaces the groove far toward the internal side of the humerus. The shaft is long and heavy; its proximal portion has a great antero-posterior diameter, and its transverse thickness, though less, is still very considerable. The fore-and-aft diameter gradually diminishes downward, until the shaft assumes an almost cylindrical shape, below which point it begins to expand transversely. The deltoid ridge is rugose and prominent, and runs far down upon the shaft, but forms no deltoid hook. The distal end of the shaft is very heavy, being both broad and thick. The supratrochlear fossa is low, wide and shallow, while the anconeal fossa is very high, narrow and deep, its depth being much increased by the great production of the posterior angles of the distal end. The supinator ridge is rough, heavy and prominent. The trochlea, which is very completely modernized, in correspondence with the advanced differentiation of the ulna and radius, is somewhat obliquely placed with reference to the long axis of the shaft, descending toward the ulnar side. The trochlea differs very markedly from that of such primitive artiodactyls as *Oreodon* and *Anoplotherium;* it is high, full and rounded and is divided into two unequal radial facets, of which the inner one is decidedly the larger. The intercondylar ridge, which, in most primitive artiodactyls, forms a broad and rounded protuberance, is, in *Elotherium*, compressed into a sharp and prominent ridge, and shifted well toward the external side. The internal epicondyle, which is so largely developed in *Oreodon* and other early artiodactyls, has practically disappeared.

The humerus of *Hippopotamus* is relatively much shorter and more massive than that of *Elotherium;* the external tuberosity is not extended so far across the anterior face of the bone and the bicipital groove is, in consequence, not shifted so far toward the inner side; the deltoid ridge is much better developed and gives rise to a prominent deltoid hook. In the existing species of *Hippopotamus* the intercondylar ridge is narrower and less conspicuous, but in a Pliocene species from the Val d'Arno it has quite the same appearance as in *Elotherium* (see de Blainville, Ostéographie, Hippopotamus, Pl. V). The epicondyles are much more prominent than in the latter, and the postero-internal border of the anconeal fossa projects much more than does the external border, while in *Elotherium* this difference is decidedly less marked. In *Sus* the humerus resembles that of the White River genus in form, but is proportionately very much shorter; the deltoid ridge is shorter and less prominent, while the supinator ridge and the epicondyles are more so.

The *radius* and *ulna* (Pl. XVIII, Fig. 10) are firmly coössified in all the known species of *Elotherium*, though the suture between them is clearly marked, even in old animals. The radius is relatively very long, but rather slender; the head is quite thick, but of only moderate breadth, projecting most toward the external side. The humeral surface is composed of three connected facets, of which the internal one is much the largest and bears an elevated ridge for the corresponding depression on the humeral trochlea. The groove for the intercondylar ridge of the latter is quite broad and notches the anterior border of the radius. The shaft is rather narrow transversely, but quite thick and heavy, and arches forward but moderately; the distal portion is broadened and thickened and bears upon its dorsal face a deep tendinal sulcus, bounded by very prominent ridges. The distal face is quite broad, but without much dorso-palmar extension, and carries two well-distinguished carpal facets, which pursue an oblique course, from before backward and inward. The scaphoidal facet, which is the smaller of the two, is concave in front, saddle-shaped behind, and is reflected up upon the posterior face of the bone. The facet for the lunar is much larger than that for the scaphoid, and has a somewhat similar shape, but the anterior concavity is not so deep, and the articular surface is carried much farther up upon the palmar side of the radius. The radius has no contact with the pyramidal.

In *Hippopotamus* the forearm bones are ankylosed, though somewhat less intimately than in *Elotherium*. The radius is very short, broad and thick, and is almost straight. The external facet for the humerus is larger and more concave and the carpal facets are of more nearly equal size, while that for the lunar rises much more steeply toward the ulnar side. In *Sus* the two bones are separate, and the radius is short, very heavy and arched forward; its distal end is much more thickened than in *Elotherium*, the facet for the scaphoid is relatively larger, while that for the lunar is smaller and is extensively reflected upon the palmar face of the radius. In *Dicotyles* the ulna and radius have coalesced even more completely than in *Elotherium*.

The *ulna* has a very long, thick and prominent olecranon, which projects far behind the plane of the shaft. The process is convex on the outer side and concave on the inner, thickened and club-shaped at the free end, which displays a broad, shallow sulcus for the extensor tendons. The sigmoid notch is deep and the coronoid process prominent, as is required by the great depth of the anconeal fossa on the humerus. The articulation of the ulna with the latter is confined to the posterior and superior aspects of the humeral trochlea, no part of the articular surface on the ulna presenting proximally, for the radius occupies the entire distal aspect of the humerus. Only the proximal portion of the facet for the humerus extends across the entire breadth of the ulna; for the rest of its course this facet is confined to the inner side. The shaft of the ulna is somewhat reduced, but is not interrupted at any point and, indeed, it is quite stout for its entire length; its principal diameter is the transverse, the antero-posterior thickness being decidedly diminished. Below the head it narrows and then expands to its maximum breadth, from which point it narrows gradually to the distal end. On its external side the shaft is quite deeply channeled. The distal end is small and bears a saddle-shaped facet for the pyramidal, which is concave transversely and convex in the dorso-palmar direction; its external border is compressed and extends as a sharp edge behind the body of the bone, forming a concavity on the palmar face. The pisiform facet is continuous with that for the pyramidal. The ulna extends distally below the level of the radius and thus arises the very exceptional condition of an articulation between the ulna and the lunar. The facet for this carpal element is small and is entirely confined to the radial side of the ulna, the distal end of the latter not extending at all upon the proximal face of the lunar. In most artiodactyls in which the functional digits have been reduced to two, the radius tends to encroach more or less extensively upon the proximal face of the pyramidal, for which extension the diminution of the ulna makes a way. In *Elotherium* the arrangement is different, the ulna occupying the entire proximal surface of the pyramidal, and by extending below the level of the radius securing a lateral contact with the lunar. Indeed, this arrangement quite precludes the attainment of the more usual radial-pyramidal articulation.

The ulna of *Hippopotamus* is proportionately much shorter and in every way more massive than that of *Elotherium;* it also has a very much larger and more prominent olecranon, as would naturally follow from the immensely greater weight of body which requires support upon the limbs. There appears to be a slight disto-lateral contact between the ulna and the lunar; at all events, the radius does not extend over upon the pyramidal. In *Sus* the ulna is free throughout and its shaft is relatively much shorter and heavier than in *Elotherium;* the ulna and lunar do not come into contact. The ulna of *Dicotyles* is more reduced than that of the White River genus and the connections of the carpals with one another and with the metacarpus are upon quite a different plan.

Measurements.

Scapula, height	0.430
Scapula, greatest width	.245
Scapula, breadth of neck	.065
Scapula, glenoid cavity, ant.-post. diameter	.068

Measurements.

Scapula, glenoid cavity, transverse diameter	.050
Humerus, length	.405
Humerus, width of proximal end	.132
Humerus, thickness of proximal end	.128*
Humerus, width of distal end	.095
Radius, length	.350
Radius, width of proximal end	.074
Radius, width of distal end	.062
Ulna, length	.443
Ulna, length of olecranon fr. coronoid process	.103
Ulna, width of distal end	.037

VII. The Manus (Pl. XVIII, Fig. 11).

The principal facts of the structure of the fore foot have already been determined by Kowalevsky, but the material now at command permits a more complete account to be given. Certain differences also which obtain between the European and American representatives of the genus should not be passed over without mention.

The *carpus* of *Elotherium* is a curious one in many ways, and while modified to suit the didactyl condition of the foot, by the reduction of the lateral and enlargement of the median elements, it has yet retained many of its primitive characteristics.

The *scaphoid* is high and thick in the dorso-palmar direction, but very narrow transversely. The dorsal and internal (*i. e.*, radial) surfaces of the bone are very rugose, and on the palmar border, which is the narrowest part of the scaphoid, is a blunt and massive mammillary process. The articular surface for the radius is of unusual shape. It is divided into two parts, an antero-external and a postero-internal; the latter is much the larger and is saddle-shaped, convex transversely and concave in the dorso-palmar direction, while the former is convex and descends steeply toward the ulnar side. These two parts of the articular surface are continuous, but they meet at nearly a right angle, and their junction forms a ridge, which is the highest point of the scaphoid. On the ulnar side are three facets for the lunar; the largest one is proximal and dorsal, and is continuous with the surface for the radius, which it meets at almost a right angle; this facet is very oblique and presents distally as well as laterally, the scaphoid here forming a projection which extends over the lunar. The second lunar facet is dorsal and distal in position; it is small, nearly plane, and not very distinctly separated from the facet for the magnum. The third lunar facet is distal and palmar, and is placed upon the ulnar side of the mammillary process already mentioned; it is of oval shape and nearly flat. The contact between the scaphoid and the lunar is confined to these three points, and as the

*Somewhat reduced by crushing.

facets on both bones are more or less prominent, they are elsewhere separated by considerable interspaces. The distal side of the scaphoid is much narrower than the proximal and is occupied by facets for the trapezoid and magnum, no articular surface for the trapezium being apparent. The trapezoidal facet is considerably the smaller of the two, and is simply concave. The magnum facet is in two parts, a very slightly concave distal portion, and a somewhat smaller lateral portion on the ulnar face of the scaphoid.

In the European species figured by Kowalevsky ('76, Taf. XXVI) the scaphoid is somewhat broader than in the American forms. In both groups a remarkable resemblance to the scaphoid of *Anthracotherium* is observable, which extends to even the details of structure (see Kowalevsky, '73, Taf. XI, Fig. 38). As *Anthracotherium* is, however, a tetradactyl form, the scaphoid is somewhat broader in proportion to its height than that of *Elotherium*, though hardly so much so as would be expected. In *Hippopotamus* and *Sus* the scaphoid is of quite a different shape from that of the fossils, being distinctly shorter and wider.

The *lunar* is a very large and complex carpal, which exceeds the scaphoid in all of its dimensions, and especially in breadth. The radial facet is in two parts, continuing those which occur on the scaphoid; the anterior or dorsal part extends across the width of the bone and is very convex antero-posteriorly, while the palmar portion is very much larger and is concave in the same direction. The dorsal border rises steeply toward the ulnar side, where the lunar is drawn out into a blunt, projecting, hook-like process, which extends over the pyramidal, as the scaphoid does over the lunar. On the radial side are three facets for the scaphoid, corresponding to those on the latter, which have already been described. The palmar face is greatly extended transversely, and, though lower, is much broader than the dorsal surface. On the ulnar side are two facets for the pyramidal, which constitute an interlocking joint of unusual firmness and strength. One of these facets is proximal and dorsal and overlaps the pyramidal; the second, which is very much larger, is palmar and distal in position, and has a saddle-like shape; it interlocks closely with a similar facet upon the pyramidal. When seen from the front, the contact between the lunar and the magnum appears to be entirely lateral, but as it passes toward the palmar side, the magnum facet broadens, becomes very concave, and assumes a distal position. The unciform facet is also oblique and the beak between the two is not in the median, but shifted far toward the radial side. Dorsally the unciform facet is considerably wider than that for the magnum, but on the palmar side these proportions are reversed.

The lunar of *E. magnum* figured by Kowalevsky resembles that of *E. ingens*, except that its proximal surface does not rise so steeply toward the ulnar side and does not project over the pyramidal. The lunar of *Anthracotherium* (see Kowalevsky, '73, Taf. XI, Fig. 37) is like that of *Elotherium*, but is narrower, especially its palmar face, and much thicker, and the distal beak is more nearly in the median line. In *Hippopotamus* the lunar is broad and rests almost equally upon the magnum and the unciform, as it does also in *Sus*.

The *pyramidal* quite resembles the scaphoid in shape, but is much broader, not so thick antero-posteriorly, and generally of a more rugose and massive appearance. In view of the reduced lateral digits and the coössified radius and ulna, the relatively large size of the pyramidal is somewhat surprising. The proximal end is occupied by the ulnar facet, which is convex transversely and deeply concave antero-posteriorly. On the palmar side is a narrow, plane facet for the pisiform, which is very oblique in position. This facet is carried upon a compressed and slightly recurved, hook-like ridge, which runs for nearly the full vertical height of the bone, though not quite reaching to the distal end. On the radial side are two facets for the lunar, separated by a wide and deep sulcus; the palmo-distal one is larger than the corresponding surface on the lunar, and its curvatures are, of course, in opposite directions to those of the latter, being concave in the vertical, and convex in the dorso-palmar diameter. The distal end of the pyramidal is taken up by a large, but slightly concave facet for the unciform.

In the material described by Kowalevsky the pyramidal of *Elotherium* is not represented, while that of *Anthracotherium* is so badly preserved and of such uncertain reference, that any comparison founded upon it would be valueless. The pyramidal of *Hippopotamus* is broad, square and heavy, as is also that of *Sus*, on a smaller scale.

The *pisiform* is quite small and slender, though of considerable length; it is strongly recurved toward the median side of the carpus, presenting the convexity externally; the distal end is thickened and club-shaped, though but little expanded in the vertical dimension. The pyramidal facet is nearly plane and oblique in position, broadest externally and narrowing to a point on the radial side. The ulnar facet is very much smaller and somewhat concave; the two meet at almost a right angle.

The pisiform of *E. magnum* (Kowalevsky, '76, Taf. XXVI, Fig. 27) is not unlike that of *E. ingens*, but is of a more irregular shape, which looks as though it might be due to disease, that of *Anthracotherium* (Kowalevsky, '73, Taf. XI, Fig. 58) is of quite similar shape, though much larger. In *Sus* the pisiform is of an entirely different shape from that of either of the extinct genera, being much deeper vertically, more compressed and plate-like, and less strongly recurved. That of *Hippopotamus* is more like that of the fossil forms.

The *trapezium* is not associated with any of the specimens which I have seen, nor is any facet for it distinctly visible on either the scaphoid or the trapezoid. If present at all, it must have been in a very reduced and rudimentary condition, having lost all functional importance.

The *trapezoid* is high, narrow and thin; it is closely interlocked with the magnum, lying in a depression on the radial side of that bone. The facet for the scaphoid is simple and strongly convex. Three facets for the magnum occur on the ulnar side, one proximal and two distal; the former is much the largest of the three, but is confined to the dorsal part of the ulnar side. Of the two distal facets, one is dorsal and one palmar; they are separated by a narrow space and are situated in different planes, almost at right angles to each other. On the radial side, near the distal end, is a shallow depression, which may have lodged a rudimentary trapezium, though there is no facet for such a bone. The distal side of the trapezoid bears a small, plane facet, of triangular shape, for the rudimentary second metacarpal.

The trapezoid is not yet known in connection with the European species of *Elotherium*, or with *Anthracotherium*. In *Hippopotamus* it is lower and broader and of more functional importance than in *Elotherium*, as it also is in *Sus*, and in the latter, differing from all of the other genera mentioned, it articulates extensively with the third metacarpal.

The *magnum* is a relatively large and massive bone, the three diameters of which are nearly equal, though the dorso-palmar dimension somewhat exceeds the other two. The dorsal moiety of the bone is the lower, quite a prominent head rising proximally from the palmar portion. The palmar hook is represented by a short, but broad, rough and massive ridge. The proximal end is unequally divided between the facets for the scaphoid and lunar; dorsally the former is much the wider and occupies almost the entire breadth of the bone, but it does not extend so far posteriorly and on the head is confined to the antero-internal aspect of that elevation. The lunar facet is very narrow on the dorsal side, and lateral rather than proximal in position, but posteriorly it widens and covers nearly the entire head. When viewed from the ulnar side, the lunar facet appears to be of a horseshoe-shape, narrow arms extending far down upon the dorsal and palmar borders, and separated below by a very large sulcus. These two arms of the lunar facet are obscurely demarcated from the two small facets for the unciform, in which they may be said to terminate distally. The distal end of the magnum is covered by the large, saddle-shaped surface for the third metacarpal, which is convex transversely and concave antero-posteriorly; and proximal to this, on the radial side, is a small facet for the second metacarpal. On the radial side also is a depression, running almost the full vertical height of the magnum, for the reception of the trapezoid. The depression contains a larger proximal and two smaller distal facets for the trapezoid, corresponding to those already described on the latter.

The magnum figured by Kowalevsky ('76, Taf. XXVI, Figs. 21, 32) is of the same general type as in the American species, but with some differences of detail. Thus, the bone is of relatively greater antero-posterior thickness; the palmar face is narrower and the palmar hook very much more prominent; the sulcus which, on the ulnar side, separates the two arms of the lunar facet is much narrower, and, in consequence, the arms themselves are broader; the head of the magnum rises less abruptly toward the palmar side. The magnum of *Anthracotherium* is not sufficiently well known for comparison. That of *Hippopotamus* is low and broad, and differs from the magnum of *Elotherium* in that the dorsal portion of the lunar facet is proximal in position. In *Sus* also the magnum is low and wide; its lunar facet is relatively larger than in *Hippopotamus*, and it has no articulation with the second metacarpal, from which it is excluded by the contact of the third metacarpal with the trapezoid; the head is low.

The *unciform* is the largest and most massive bone of the carpus; in shape it is low, broad and thick, with its principal diameter directed transversely, and has on the palmar side a hook-shaped process, which is not very prominent, but broad and heavy. The proximal end is occupied by the facets for the lunar and pyramidal, of which the latter is much the wider; the junction of the two forms a prominent ridge which curves across the proximal end, from the dorsal to the palmar side. These two facets are both slightly concave transversely, but very strongly convex antero-posteriorly, being reflected far down upon the palmar face. On the radial side are two vertical articular bands, separated by a wide and deep sulcus. The dorsal band, which is much the wider of the two, is composed of two very obscurely separated facets, a minute proximal one for the magnum and a very large distal one for the unciform process of the third metacarpal. The palmar band is a high and narrow facet for the magnum only, and is much more extended vertically than the corresponding surface on that bone. The distal end carries a large facet for the head of the fourth metacarpal, and on the ulnar side is a minute facet for the rudimentary fifth metacarpal.

The unciform of Kowalevsky's specimen does not differ in any significant way from that of the American species. In *Anthracotherium* this bone is much wider and lower than in *Elotherium* and the facet for the fifth metacarpal is more distal than lateral. In *Hippopotamus* the unciform is exceedingly large, and its dorsal face is of a low, wide, rectangular outline, and its great breadth corresponds to the large size and functional importance of the fifth metacarpal. The proximal end is divided almost equally between the lunar and pyramidal facets, and the absence of a distal beak on the lunar allows a larger contact between the unciform and magnum. In *Sus*, which has much reduced lateral digits, the unciform is narrower than in *Hippopotamus*, but broader than in *Elotherium*, and the facet for the fifth metacarpal is not so completely displaced toward the ulnar side as in the latter.

The *metacarpus* consists of four members, two functional, the third and fourth, and two mere rudimentary nodules, the second and fifth.

Metacarpal II is not preserved in any of the specimens which I have seen, though it is figured by Marsh ('93, Pl. VIII, Fig. 4), but the facets on the neighboring bones show that it was carried by the trapezoid and retained a lateral connection with the magnum, excluding mc. iii from any contact with the trapezoid. The manus of *Elotherium* is thus a typical example of what Kowalevsky has called the "inadaptive mode" of digital reduction.

Metacarpal III is long and massive. The head is heavy, enlarged in both dimensions, and has a stout prominence upon the palmar side; it bears a broad, saddle-shaped surface for the magnum. On the radial side is a depression for mc. ii, at the proximal end of which are two small facets for that bone. The unciform process is very large, prominent and heavy, and projects far over the head of mc. iv, but is, as usual, confined to the dorsal half of the head. On the distal side of this process and on the ulnar side of the shaft is a continuous, concave facet for the head of mc. iv. A second facet for the same metacarpal is borne upon the palmar projection from the head. The shaft of mc. iii is broad, but much compressed and flattened antero-posteriorly; both width and thickness are nearly uniform throughout, but increase slightly toward the distal end. The distal trochlea is broad and rather low, but is reflected well up upon the palmar face; on the dorsal side it is demarcated from the shaft only by an obscure ridge, with no deep depression above it. The carina is very prominent, but is confined entirely to the palmar face. The lateral pit on the ulnar side is large and deep, but that on the radial side is faintly marked.

In Kowalevsky's specimen ('76, Taf. XXVI, Fig. 21) the third metacarpal does not differ in any important way from that of the American species, though the magnum facet is somewhat more concave transversely and the shaft is rather more slender. In *Anthracotherium* (Kowalevsky, '73, Taf. XIII, Fig. 80) mc. iii is very similar to that of *Elotherium*, but is relatively heavier; at the proximal end the tubercle for the insertion of the extensor carpi radialis muscle is more conspicuous, and the palmar projection of the head more prominent.

Metacarpal IV is a little shorter and narrower than mc. iii, with which it articulates by two large facets, separated by a wide and deep groove; of these facets the dorsal one, which is overlapped by the unciform process of mc. iii, is strongly convex, while the palmar facet is flat and borne upon the palmar projection. The ulnar side has a shallow groove, in which lies the nodular mc. v; the articulation with the latter is by means of a single, small, triangular facet. The shaft is somewhat narrower transversely than that of mc. iii, but is otherwise like it, as is also the distal trochlea.

In *E. magnum*, Kowalevsky's figure shows a somewhat differently shaped proximal end ('76, Taf. XXVI, Figs. 21, 24), the head is somewhat more extended transversely, especially toward the ulnar side, while the palmar projection is narrower and less prominent. In *Anthracotherium* the head of mc. iii has no such transverse extension.

Metacarpal V is an almond-shaped nodule, almost exactly like the specimen figured by Kowalevsky (Taf. XXVI, Fig. 25), though of a rather more regular outline. Proximally the nodule has quite a large, subquadrate, and slightly concave facet for the unciform, which presents more laterally than superiorly, and forming a very obtuse angle with this surface, is a smaller, triangular facet for mc. iv.

The metacarpus of *Hippopotamus* has four functional members, though the median pair are longer and stouter than the lateral. Compared with those of *Elotherium* they are relatively shorter and much heavier. In *Sus* there are also four metacarpals, but the laterals are much reduced, while the median pair, which carry most of the weight, are very short and thick, and the distal carina surrounds the entire trochlea, dorsal as well as palmar. The mode of articulation between the carpals and metacarpals is quite different from that found in either *Elotherium* or *Hippopotamus*, the head of mc. iii being much broadened and articulating extensively with the trapezoid, so that mc. ii is cut off from any contact with the magnum. This is what Kowalevsky has called the "adaptive method" of digital reduction, and it is in decided contrast to the inadaptive method exemplified in *Elotherium*.

The *phalanges*, which are quite short, as compared with the length of the metacarpals, are developed only in the median pair of digits. The proximal phalanx of digit iii is relatively elongate, straight, broad and depressed; its proximal end is both wide and thick, and carries a concave facet for the metacarpal trochlea, which is deeply notched on the palmar border for the carina. Toward the distal end the phalanx narrows but little, though diminishing much in the dorso-palmar diameter; the distal trochlea is low, wide, depressed and only slightly notched in the median line. The second phalanx is short, broad and thick, and of quite asymmetrical shape; its proximal trochlea is obscurely divided into two facets, of which that on the radial side is the larger and extends more in the palmar direction, while the median dorsal beak is not prominently developed. The distal trochlea is much thicker than that of the first phalanx, is reflected much farther upon the dorsal face, and is more distinctly notched in the median line. The course of this surface is oblique, so that it faces somewhat to the ulnar side. The ungual phalanx is curiously small and nodular in shape, and is short, but quite broad and thick; the proximal trochlea is imperfectly divided into two slightly concave facets. The palmar surface is nearly plane, except for its rugosities, while the dorsal margin descends abruptly to the blunt distal end.

In *Anthracotherium* (Kowalevsky, '73, Taf. XI, Figs. 53, 54) the phalanges are of the same general type as in *Elotherium*, but are proportionately much shorter and stouter. In *Hippopotamus* they are short, broad and very heavy, while the unguals are reduced and of nodular form. In *Sus* the three phalanges of a digit are together considerably longer than the metacarpal, which is far from being the case in *Elotherium*; they are also of quite a different shape from those of the latter. The proximal phalanx is much thicker in proportion to its length, and its proximal trochlea is deeply grooved across its whole face for the metacarpal carina. The ungual phalanx is longer, broader and more depressed and pointed.

Measurements.

Carpus, height	0.072
Carpus, width	.077
Scaphoid, height	.038
Scaphoid, breadth	.026
Scaphoid, thickness	.047
Lunar, height	.047
Lunar, breadth	.036
Lunar, thickness	.050
Pyramidal, height	.033
Pyramidal, breadth	.027
Pyramidal, thickness	.039
Pisiform, length	.042
Trapezoid, height	.025
Trapezoid, breadth	.012
Trapezoid, thickness	.019
Magnum, height (excl. of head)	.025
Magnum, breadth	.035
Magnum, thickness	.048
Unciform, height	.036
Unciform, breadth	.037
Unciform, thickness	.050
Metacarpal iii, length (in median line)	.167
Metacarpal iii, width proximal end	.044
Metacarpal iii, width distal end	.039
Metacarpal iii, thickness proximal end	.039
Metacarpal iv, length	.161
Metacarpal iv, width proximal end	.038
Metacarpal iv, width distal end	.039
Metacarpal iv, thickness proximal end	.035
Phalanx 1, digit iii, length	.060
Phalanx 1, digit iii, width proximal end	.039
Phalanx 1, digit iii, width distal end	.032
Phalanx 2, digit iii, length	.048
Phalanx 2, digit iii, width proximal end	.031
Phalanx 3, digit iii, length	.028

VIII. The Hind Limb.

The *pelvis* is remarkable in many ways. As a whole, it is curiously long and narrow, except anteriorly, where the sudden and strong eversion of both ilia gives it considerable breadth. The ilium is elongate, and has a long, heavy, trihedral peduncle, which expands quite abruptly into the broad anterior plate. This plate is very strongly everted in its antero-inferior portion, and in shape is not at all like that of *Sus*, or of most existing artiodactyls, but rather resembles that of such ancient perissodactyls as *Palæosyops*. The plate rises high above the sacrum and conceals much of that bone from view, when the pelvis is seen from the side; the gluteal surface is concave and the sacral surface strongly convex; the suprailiac border is quite thin for most of its course, but becomes very thick and rugose at its inferior angle. The iliac surface is relatively wide and may be traced through the whole length of the bone, the pubic border being very distinctly marked throughout. The ischial border is, for the most part, thick and rounded, but becomes sharp and compressed above the acetabulum. The pectineal process is a very prominent and rough tuberosity, and a second rugosity lies above and behind it. The acetabulum is rather small, but deep, and is of almost circular form; its articular surface is but little reduced by the deep and narrow sulcus for the round ligament.

The ischium is likewise elongate, though much shorter than the ilium; above the acetabulum its dorsal border arches upward into a high, thin and roughened crest, the ischial spine, very much like that seen in *Sus*, behind which is a distinct ischiadic notch, a difference from the true pigs, which have no such notch. For most of its length, the ischium is laterally compressed, but expands posteriorly into a large, thick plate, with everted hinder border and very massive tuberosity. The pubis is short, heavy and depressed. The symphysis, in which both the pubes and the ischia take part, is very long, the posterior notch between the two ischia being shallow. Consequently, the obturator foramen is much elongated antero-posteriorly, and of oval shape. This region of the pelvis is entirely different from that of *Sus*, in which the ischia are widely separated behind, the symphysis is short, and the obturator foramen is nearly circular in outline. In *Hippopotamus* the pelvis is more like that of *Elotherium*, but is much larger and more massive in every way; the peduncle of the ilium is not so elongate or so slender, the spine of the ischium is very much less prominent, and the posterior expansion of the ischium is very much larger and heavier. Unfortunately, the pelvis is not sufficiently well known in *Ancodus* or *Anthracotherium* for comparison with that of *Elotherium*.

The *femur* is a long and proportionately rather slender bone. The proximal end is quite widely expanded in the transverse direction; and in shape recalls that seen in the camels and llamas. The head is almost hemispherical in form and has a small, deep pit for the round ligament; it is set upon a very distinct neck, which is connected by a long, narrow bridge of bone with the great trochanter. The latter is very large and massive, especially in the antero-posterior direction, but does not rise above the level of the head, and hence is not very conspicuous, when the femur is seen from the front. The digital fossa is deep and widely open, which is due to the great thickness of the trochanter, but is not much extended in the vertical direction. The second trochanter is also large and very rugose, but not very prominent; it projects almost entirely backward, so that the trochanter is hardly visible, when the bone is viewed from the anterior side. There is no plainly marked intertrochanteric ridge, connecting the great and second trochanters, but from the latter a ridge runs proximally and almost reaches to the head.

The shaft of the femur, which in its proximal portion is much expanded transversely and compressed antero-posteriorly, rapidly narrows downward, and below the second trochanter becomes quite slender and subcylindrical in shape. Toward the distal end the shaft widens considerably, though increasing little in thickness. Above the external condyle is a long, narrow pit, with rugose margins, which serves for the origin of the plantaris muscle. The rotular groove is very broad, but quite shallow; its inner border is much thicker and more prominent than the outer, and ascends higher proximally, where it terminates in a short, overhanging hook, while the external border dies away more gradually. The condyles are relatively small; they present directly backward, though not projecting very strongly behind the plane of the shaft, and are of almost equal size, the external one but slightly exceeding the internal in height and breadth. The intercondylar fossa is broad and deep and has nearly straight borders.

The proportionately small antero-posterior diameter of the distal part of the femur in *Elotherium* is in decided contrast to the thickness of this region in *Ancodus*. The femur of *Anthracotherium* is much like that of *Elotherium*, but it is even more slender in proportion to its length, and the condyles are smaller. *Sus* has a femur of quite a different type; the proximal end is not so wide, the head is more sessile and has a much larger pit for the round ligament; the bridge connecting the head with the great trochanter is shorter and much thicker, and the trochanter itself is more prominent; the shaft is relatively less elongate, the rotular groove has borders of nearly equal height, and the condyles are more prominent. The femur of *Hippopotamus*, though extremely massive, has yet a certain resemblance to that of *Elotherium*, as may be seen in the transverse expansion of the proximal end and in the obliquity and asymmetry of the rotular groove.

The *patella* is large, massive and of rather peculiar shape. It is high, quite broad and thick in the middle portion, but with the distal part quite thin and narrow, and tapering to a blunt point; the proximal portion is also narrow and rises above the articular surface as a compressed, but thick and rugose process. The femoral surface is convex transversely, and only very obscurely divided into external and internal facets by a broad and low median ridge. This patella bears very little resemblance to the very thick knee-cap of *Ancodus* and still less to that of *Sus*. In the latter the patella is a short, rather narrow, but very thick bone, the posterior surface of which is of a regularly oval outline. *Hippopotamus* also has a patella which bears but little resemblance to that of *Elotherium;* it is short, but very broad and extremely thick, and sends off a long, horizontal process from the internal border.

The *tibia* is a massive bone, considerably shorter than the femur, but relatively heavier. The proximal end is very broad and thick; the condyles are of the usual saddle-shaped form and have a rather small antero-posterior extension; the inner condyle is somewhat more extended in this direction, while the outer one is wider transversely, and projects over the external side of the shaft. The fibular facet is small and is confined to the postero-external angle of the outer condyle. The tibial spine is low and bifid. The cnemial process is exceedingly heavy and prominent, and runs far down upon the shaft, extending for nearly half the length of the bone; its proximal portion displays a depression for the long patella, and the sulcus for the tendon of the extensor longus digitorum is deeply incised. The shaft of the tibia is heavy throughout, not diminishing much in diameter distally; it has a decided lateral and a slight anterior curvature. The distal end is quite broad, but not very thick, and has an unusually quadrate outline. The astragalar surface is divided by a low intercondylar ridge into two facets, of which the external one is much the larger and the inner one more deeply impressed. The intercondylar ridge, which pursues a very straight course across the distal end, is remarkable for its bifid termination at the anterior margin. A considerable sulcus is placed upon the intercondylar ridge, invading the articular surface on each side. On the external side of the distal end of the tibia is a broad, rugose depression for the fibula, but with only a very small external facet for the latter; an additional fibular facet forms a narrow band upon the *distal* surface, the tibia extending somewhat over this portion of the fibula. The malleolar process is short and compressed, and has no great antero-posterior extension.

The tibia of *Anthracotherium* (Kowalevsky, '73, Taf. X, Fig. 29) is much like that of *Elotherium*, but is relatively shorter and heavier. *Sus* also has a similar tibia, differing only in minor details. The tibia of *Hippopotamus* is of the same general type, but is extremely short and massive.

The *fibula* is complete and is not coössified with the tibia at any point, but is, nevertheless, very much reduced. The proximal end is laterally compressed and very narrow, but retains considerable antero-posterior extent, and bears a narrow, obliquely placed and slightly convex facet for the tibia. The shaft tapers and becomes exceedingly thin and delicate, though of very irregular shape; distally the shaft thickens much in the fore-and-aft diameter, but remains very narrow. The distal end forms a large external malleolus, but continues to be very narrow. The malleolus projects inward beneath the tibia and has a narrow facet which presents proximally and articulates with the facet, already mentioned, on the distal face of the tibia. The astragalar facet is quite large, extending for almost the whole thickness of the malleolus and curving downward in front; the calcaneal facet, which occupies the entire distal end of the fibula, is narrow, but has a very considerable antero-posterior extension. On the outer side of the malleolus are two deeply incised sulci for the peroneal tendons. In *Sus* the fibula is very much stouter and less reduced than in *Elotherium*, while the distal end is less enlarged and does not extend beneath the tibia. The fibula of *Hippopotamus* is relatively very slender, but it differs from that of the White River genus in having a smaller proximal and very much larger distal end.

Measurements.

Pelvis, length	0.495
Pelvis, antero-inferior breadth	.395
Pelvis, breadth at acetabulum	.191
Ilium, length	.280
Ilium, greatest width	.197
Ischium, length	.215
Obturator foramen, length	.094
Symphysis, length	.190
Femur, length	.405
Femur, breadth proximal end	.115
Femur, breadth distal end	.100
Femur, thickness distal end	.103
Femur, breadth of trochlea	.052
Patella, vertical diameter	.107
Patella, transverse diameter	.056
Tib'a. length	.338
Tibia, breadth proximal end	.092
Tibia, breadth distal end	.063
Tibia, thickness proximal end	.088
Tibia, thickness distal end	.054
Fibula, length	.305
Fibula, breadth proximal end	.012
Fibula, breadth distal end	.016
Fibula, thickness proximal end	.023
Fibula, thickness distal end	.040

IX. The Pes.

The *tarsus* has undergone little specialization, although the hind foot, like the fore foot, is didactyl.

The *astragalus* is elongate, though broad and massive as well. The proximal trochlea is deeply but very broadly grooved and its two parts are unequal, the external condyle rising much more, both proximally and dorsally, than the internal, but not produced so far distally. While the outer condyle is widely separated from the cuboidal facet, the inner one is continued so far distally as to become confluent with the navicular surface. A very large and deep pit occupies a great part of the dorsal surface between the proximal and distal trochleæ. The distal trochlea is broad and is unequally divided into facets for the cuboid and navicular, the latter being much the wider and of a different shape. The surface for the cuboid is strongly convex in the dorso-plantar direction, but nearly plane transversely, while the navicular facet is hour-glass shaped, and on the fibular side of the median line has a distinct, though wide and shallow groove for a corresponding ridge on the proximal side of the navicular. The junction of the two facets forms a sharp but not prominent edge.

The facets for the calcaneum somewhat resemble those which we find in *Ancodus*, but they have not attained to such a degree of specialization as in the American species of that genus. The proximal external facet is divided by a sulcus into two parts, both of which are concave and present distally, as well as laterally. The proximal portion is set on a conspicuous prominence of the fibular side of the astragalus, and is clearly visible when the bone is seen from the dorsal side, while the distal portion is also prominent, but is concealed when looked at from the same point of view. The sustentacular facet is very large and is strongly convex in the proximo-distal direction, but almost plane transversely; its external border projects as a shelf beyond the body of the astragalus, and thus helps to enclose the large and deep sulcus which is found upon the external side of the bone. The distal external facet for the calcaneum is very small. The fibular facet is well extended in the proximo-distal diameter, but is narrow in the dorso-plantar direction.

In Kowalevsky's specimen ('76, Taf. XXVII, Fig. 34) the astragalus, so far as it is preserved, resembles that of the American species, but the external part of the proximal trochlea is too much damaged to show the characteristic external calcaneal facet. In *Anthracotherium* (Kowalevsky, '73, Taf. XI, Fig. 59, de Blainville, Ostéographie, Anthraco., Pl. II) the astragalus is proportionately much broader and lower than in *Elotherium*, the ridge on the distal trochlea, formed by the junction of the two facets, is more prominent and pursues a more oblique course. The sustentacular facet is narrower and shorter and the proximal calcaneal facet projects less. The astragalus of *Sus* is quite like that of *Elotherium*, especially in the proportions of the distal trochlea. In *Hippopotamus* the astragalus is remarkable for its extreme shortness, for the asymmetry of its proximal trochlea, the outer condyle much exceeding the inner in size, and for the almost equal division of its distal trochlea between the navicular and cuboid facets.

The *calcaneum* has a long tuber, which is deeply channeled on the external side and for most of its length is compressed and rather slender, but swells at the free end into a massive, club-shaped expansion, which has a broad, shallow tendinal sulcus on the plantar face. From the free end the dorso-plantar diameter of the calcaneum increases gradually to the fibular facet, where it reaches its maximum, and from which it contracts rapidly toward the distal end. The sustentaculum is very prominent and bears a wide, slightly concave facet for the astragalus. The distal astragalar facet is much more extended in the dorso-plantar direction than is the corresponding surface on the astragalus and indicates an unusual amount of movement between the two bones. The cuboidal facet is narrow transversely, but much extended antero-posteriorly; it is divided, though very obscurely, into dorsal and plantar parts, of which the former is the larger and has something of a saddle-like shape, while the latter is smaller and concave.

Kowalevsky does not describe the calcaneum of *E. magnum* and his description and figures of *Anthracotherium* do not furnish data for comparison. The calcaneum of *Sus* resembles that of *Elotherium*, but is broader and has a tuber of more uniform thickness, not channeled on the outer side. The articular surface for the cuboid is very distinctly divided into two facets, the junction of which forms a sharp ridge. In *Hippopotamus* the calcaneum has an exceedingly long and massive tuber, which is greatly swollen at the free end.

The *navicular* is a large bone, not very broad, but of considerable dorso-plantar diameter. The surface for the astragalus is hour-glass shaped, with two concavities separated by a broad, convex ridge, which on the dorsal side is marked by an elevation of the proximal margin. The concavity on the tibial side is the larger of the two and its plantar border rises much higher than that of the external concavity. There are three facets for the cuboid on the fibular side of the bone, one plantar and two dorsal; the former is very strongly convex, projecting well outward, and is high vertically, but narrow antero-posteriorly. The two dorsal facets are both small and plane, and are placed at the proximal and distal margins of the navicular. The plantar hook is very much reduced, forming hardly more than a roughened ridge. The distal end is occupied principally by the large facet for the ectocuneiform, which extends across the whole dorsal side and much of the tibial side also. Partially separated from this is a minute surface for the mesocuneiform. The facet for the entocuneiform is much larger than the latter; it stands isolated at the postero-internal angle of the distal end and is somewhat saddle-shaped, concave antero-posteriorly and convex transversely. In one species of *Elotherium*, not yet identified, a somewhat different proportion of these cuneiform facets is found; the mesocuneiform facet is larger and that for the entocuneiform smaller and in shape and in position more as in the recent pigs.

Kowalevsky's figures ('76, Taf. XXVII, Figs. 34, 37) do not display any characteristic differences in the structure of the navicular between the American and the European species of *Elotherium*. In *Anthracotherium* (Kowalevsky, '73, Taf. XI, Figs. 48, 59) the navicular has a long, massive and rugose hook, given off from the plantar side; the facet for the ectocuneiform is relatively smaller and that for the mesocuneiform much larger than in *Elotherium*, and the two surfaces are distinctly separated. Much the same description will apply to *Sus*. In *Hippopotamus* the navicular is very low and broad, and its distal facets are well distinguished.

The *entocuneiform* is in shape not unlike the rudimentary, nodular metapodials; it is high, narrow and compressed, thickest proximally and tapering distally to a blunt point. The navicular facet is relatively large, and is saddle-shaped, with curves the converse of those which occur on the corresponding surface of the navicular. Distally, there is a facet on the fibular side for the plantar projection from the head of the third metatarsal.

This element has not yet been found in connection with *Anthracotherium*, or with the European species of *Elotherium*. In *Sus* it is of quite a different form and decidedly smaller, while in *Hippopotamus* it is broader, heavier and shorter than in the fossil form.

The *mesocuneiform* is firmly ankylosed with the ectocuneiform, but its shape is, nevertheless, clearly distinguishable; it does not extend quite so far distally as the latter and is very small, especially transversely, and narrows toward the distal end. Its facet for the second metatarsal is obscurely displayed and it has no contact with the third. In *E. magnum* (Kowalevsky, Taf. XXVII, Figs. 35, 37) the two cuneiforms are even more completely fused than in the American species. In *Anthracotherium* the mesocuneiform is separate and has a large surface for articulation with the second metatarsal, as is also the case in *Hippopotamus*. In *Sus* this element is likewise distinct, but higher and narrower, and articulates with the second metatarsal more extensively than with the third.

The *ectocuneiform* is a large bone, of irregularly quadrate shape; its proximal surface bears a large, plane facet for the navicular, and the distal end is occupied by a still larger surface for the third metatarsal; the latter is abruptly contracted toward the plantar side. On the tibial side and distal to the mesocuneiform is a minute lateral facet for the second metatarsal. The contact with the cuboid is restricted to two facets near the proximal end, one dorsal and the other plantar, of which the latter is the smaller, but the more prominent. In *E. magnum* this bone is very much as in the American species, but the distal facet is of a different shape, not contracting so much toward the plantar side (Kowalevsky, Taf. XXVII, Figs. 35). In *Anthracotherium* (Kowalevsky, '73, Taf. XI, Figs. 48, 59) the ectocuneiform is lower and has a more extended connection with the second metatarsal. The ectocuneiform of *Hippopotamus* is low, but very broad, in keeping with the great size of the third digit. In *Sus* this element is not so wide as in *Elotherium*, and differs from that of all the genera mentioned in having no contact with the second metatarsal, from which it is cut off by the articulation of the mesocuneiform with the third.

The *cuboid* is massive and large in all its dimensions, high, broad and thick. The proximal surface is about equally divided between the facet for the calcaneum and that for the astragalus, though the latter is slightly the wider. This facet, which is simply concave antero-posteriorly, is widest near the dorsal border, and in the middle of its course is deeply emarginated from the tibial side. The calcaneal facet is imperfectly divided into two parts, of which the dorsal portion is much the larger, particularly in width, while the plantar portion curves inward so as to lie, in part, behind the astragalar surface. The cuboid is firmly interlocked with the navicular by means of the deeply concave facet on the tibial side near the plantar margin, which receives the projection from the navicular already described. Dorsally the contact between these bones is limited to two small facets, one of which is proximal, and the other is distal on the navicular, median on the cuboid, where it helps to form the projection between the navicular and the ectocuneiform; this prominence is, however, very short. The facets for the ectocuneiform are also dorsal and plantar, and are just distal to those for the navicular. The distal end of the cuboid is taken up by the large facet for the fourth metatarsal, that for the rudimentary fifth being very small and lateral in position. The plantar hook is not long, but is very broad and massive, and bears on its tibial side a facet for the posterior projection from the head of the fourth metatarsal.

In *Elotherium magnum* (Kowalevsky, '76, Taf. XXVII, Figs. 34–36) the cuboid is not so high in proportion to its breadth as in the American species, and the tendinal sulcus on the fibular side is deeper. The cuboid of *Anthracotherium* is broader and lower and has, of course, a larger and more distal facet for the fifth metatarsal. In *Sus* similar proportions recur, and the division of the calcaneal surface into two parts is complete. In *Hippopotamus* the cuboid is very low and broad, and the astragalar facet is much wider than the calcaneal.

The *metatarsus*, like the metacarpus, consists of two functional (iii and iv) and two rudimentary members (ii and v).

Metatarsal II is a small nodule, which is much compressed laterally and tapers to a point at the distal end; the articulations are proximally with the mesocuneiform and laterally with the ectocuneiform and mt. iii.

Metatarsal III is considerably longer than the corresponding metacarpal and of a different shape, being much narrower transversely and thicker in the dorso-plantar diameter. The head is of moderate width, but the long and massive projection from the plantar side gives it great thickness. On the tibial side of the head is a depression in which lies the nodular mt. ii. The plantar projection bears a rounded, plane facet on each side; that on the tibial side is for the entocuneiform, and that on the fibular side is for mt. iv; a second facet for mt. iv is formed by a shallow depression near the dorsal border. The shaft of mt. iii is long, straight and slender; it is flattened on the plantar and fibular sides, rounded on the others. Toward the distal end the shaft gradually expands both in width and thickness; a very prominent and rough tubercle is developed on the fibular border of the dorsal face, just above the trochlea. The latter is rather low and narrow and has a prominent carina, which is confined altogether to the plantar face.

Metatarsal IV is a counterpart of mt. iii, with which it forms a symmetrical pair, though the plantar projection is even larger and heavier than that of the latter and articulates with the posterior hook of the cuboid. The connection with mt. iii is by means of two facets, the dorsal one a low, rounded prominence which fits into the depression on mt. iii already described, and the plantar one on the tibial side of the posterior projection. The two metatarsals are held very firmly together, externally by the hook of the cuboid and internally by the entocuneiform. A small depression on the fibular side of the head lodges the rudimentary mt. v. The shaft and distal trochlea are like those of mt. iii.

Metatarsal V is even more reduced than mt. ii. It has a thickened club-shaped head, which bears a facet for the cuboid and another for mt. iv, the two meeting at a very open angle. What remains of the shaft is slender and styliform. The mode of digital reduction in the pes, as in the manus, is entirely "inadaptive," the rudimentary mt. ii still clinging to the mesocuneiform and preventing mt. iii from reaching that tarsal, which is much diminished in size, while the ectocuneiform follows the enlargement of mt. iii.

Kowalevsky found no metatarsals associated with *E. magnum*. In *Anthracotherium* (Kowalevsky, '73, Taf. XI, Figs. 45, 55, 59) the lateral metatarsals are still large, functional and provided with phalanges; the median pair are relatively shorter and heavier than those of *Elotherium*, but in other respects resemble them closely. *Hippopotamus* has very short and massive metatarsals, which do not exceed the metacarpals in length and which retain the primitive mode of articulation with the tarsals. The metatarsals of *Sus* differ from those of *Elotherium* in much the same way as do the metacarpals of the two genera. The laterals are still functional, though much reduced, and the medians are short and very heavy, with the carinæ completely encircling the distal trochleæ; mt. iii has acquired an articulation with the mesocuneiform, cutting off mt. ii from the ectocuneiform.

The *phalanges* of the pes differ from those of the manus principally in their greater slenderness. The first phalanx is a little longer than that of the fore-foot, and decidedly more slender; the proximal trochlea is less deeply concave and the groove for the carina narrower and deeper. The second phalanx is of nearly the same length as in the fore-foot, but is much narrower and somewhat less asymmetrical in form. As Kowalevsky points out, the proportions of this phalanx are very exceptional among ungulates. The ungual is smaller in every dimension than that of the manus and, in particular, is narrower. Apparently, *Anthracotherium* (Kowalevsky, '73, Taf. XI, Figs. 52, 53) displays the same difference between the phalanges of the pes and those of the manus as does *Elotherium*. In *Sus* and *Hippopotamus* the phalanges of the two extremities differ very little.

Measurements.

Astragalus, length	0.083
Astragalus, width proximal trochlea	.045
Navicular, height	.024
Navicular, width	.029
Navicular, thickness	.044
Entocuneiform, height	.037
Entocuneiform, width	.014
Mesocuneiform, height	.016
Ectocuneiform, height	.022
Ectocuneiform, width	.025
Cuboid, height	.045
Cuboid, width	.038
Cuboid, thickness	.047
Metatarsal iii, length	.181
Metatarsal iii, width proximal end	.029
Metatarsal iii, width distal end	.032
Metatarsal iii, thickness proximal end	.041
Metatarsal iv, length	.181
Metatarsal iv, width proximal end	.033
Metatarsal iv, width distal end	.031
Metatarsal iv, thickness proximal end	.046
Proximal phalanx, length	.060
Proximal phalanx, width proximal end	.032
Proximal phalanx, width distal end	.027
Second phalanx, length	.042
Second phalanx, width proximal end	.030
Second phalanx, width distal end	.024
Ungual phalanx, length	.032
Ungual phalanx, width proximal end	.022

X. Restoration of Elotherium (Plate XVII).

The skeleton of this genus has a remarkable and even grotesque appearance. As in so many of the White River genera, the skull is disproportionately large, and the immense, dependant projections from the jugals, together with the knob-like protuberances on the mandible, produce a highly characteristic effect. The long, straight face, the prominent and completely enclosed orbits, the short cranium, the high sagittal crest, and the enormously expanded zygomatic arches give a certain suggestion of likeness to the skull of *Hippopotamus*. The neck is short, nearly straight and very massive, with prominently developed processes for muscular attachment. The trunk is short, but heavy; the anterior thoracic spines are very high and heavy, while those of the posterior region are short and quite slender. In consequence of the sudden shortening of the thoracic spines, a conspicuous hump is formed at the shoulders. The thorax is of moderate capacity and the loins are short. The tail appears to be of no great length, though the individual vertebræ are greatly elongated. The limbs are long and rather slender, and the fore and hind legs are of nearly equal height; the humerus and femur are almost the same in length, as are also the radius and tibia, while the pes is somewhat longer than the manus. The scapula is very large, especially in the vertical dimension, which considerably exceeds the length of the humerus, and has a short but prominent acromion; the pelvis, on the other hand, is rather small, the ilium having a long and slender peduncle, and only a moderate anterior expansion. The elongate limbs and slender, didactyl feet are in curious contrast to the huge head and short, massive trunk, and form a combination which would hardly have been expected.

Prof. Marsh has published, with a very brief explanatory text, a restoration of *Elotherium* ('94, Pl. IX) which differs in several details from the skeleton here figured. It is difficult to tell from the data furnished exactly how much of this restoration is conjectural, or to determine how far the discrepancies to be mentioned are the result of the association of parts of many different individuals in a single figure, and how far they are due to actual specific characters. On comparing the two figures, one is struck by the following differences: (1) In Marsh's restoration the skull is somewhat smaller in proportion to the length of the limbs. (2) The neck is more slender and the spines of the cervical vertebræ, notably those of the sixth and seventh, are much less developed. (3) The trunk is decidedly longer and twenty thoraco-lumbar vertebræ are figured. No reason is assigned for this departure from the well-nigh universal formula of the artiodactyls, which is nineteen, and we are therefore ignorant of the evidence by which it is supported. (4) The spines of the thoracic vertebræ are much more slender and decrease more gradually in length posteriorly, so that there is no such decided hump at the withers. These spines are figured as having curious expansions at the tips, which are either absent or much less distinctly shown in the skeleton described in the present paper. (5) The lumbar region is longer and has neural spines which are lower and incline more strongly forward. (6) The conjectural restoration of the presternum is entirely different from the specimen herewith figured. (7) The scapula is relatively shorter and broader, and has a less prominent acromion. (8) The ilium has a shorter neck, expanding more gradually into the anterior plate and with the acetabular border of an entirely different shape. The ischium is much more slender, is more everted and depressed at the posterior end, and has a much less massive and prominent tuberosity.

Materials are yet lacking to determine how wide is the range of variation in the skeleton of the different species of *Elotherium*. So far as I have been able to observe, there are no important differences between the species, save those of size and proportions, the larger forms having more massive as well as longer bones. In particular, the great John Day species have exceedingly heavy limb and foot bones.

XI. The Relationships of Elotherium.

There has been a very general agreement, among those who have made a study of this genus, regarding the systematic position of *Elotherium*. The acute, compressed premolars have, however, led some observers to see affinities with the Carnivora and de Blainville went so far as to include the genus in his carnivorous family Subursi. Almost every other writer has referred these animals to the suillines. Leidy says of it: "*Elotherium* is a remarkable extinct genus of suilline pachyderms. . . . . Its allies among extinct genera are *Chœropotamus*, *Palæochœrus*, *Anthracotherium*, and among recent animals the Hog, Peccary and Hippopotamus" ('69, p. 174). Kowalevsky expresses the same idea in a more definite and specific way: "Schon bei dem ersten Anblick der Bezahnung bleibt kein Zweifel über die Familie zu der diese Form gehört, nämlich den Suiden; sie bildet aber darin wegen des auffallenden Baues der didactylen Extremitäten eine sehr eigenthümliche Gattung. Plötzlich konnte eine derartige Form sich nicht bilden, das Entelodon hatte gewiss Vorahnen, deren Knochenbau einen allmäligen Uebergang von der tetradactylen zu der didactylen Form vermittelten, bis heute aber sind uns solche noch gänzlich unbekannt" ('76, p. 450). Zittel refers the genus to the *Achænodontinæ*, a subfamily of the *Suidæ* ('94, p. 335). Marsh erects a separate family for the genus, and says of it: "The *Elotheridæ* were evidently true suillines, but formed a collateral branch that became extinct in the Miocene. They doubtless branched off in early Eocene time from the main line which still survives in the existing swine of the old and new worlds" ('94, p. 408). Schlosser has expressed a somewhat different opinion and has referred the genus to the bunodont division of the family *Anthracotheriidæ*, which family he derives from an Eocene stock common to the *Anthracotheriidæ*, the *Anoplotheriidæ*, the *Hippopotamidæ* and the *Suidæ* ('87, p. 80).

The complete account of the dental and skeletal structure of *Elotherium* is now before us and yet it is hardly less difficult than before to determine its phylogenetic relationships and systematic position. The genus is so far specialized that it implies a long ancestry, not a member of which is, as yet, certainly known, although there are certain Eocene genera which throw some light upon the problem. In the absence of this ancestral series, we are without any sure criterion by which to distinguish parallelisms from characters of actual affinity, since only by tracing, step by step, all the gradations of a differentiating phylum, can we safely determine the true position of its members. However, some facts seem to bear a clear and definite significance. In the first place, it is plain that Marsh is right in forming a separate family for this genus, as it belongs to a line which diverged very early from the main stem, whatever that was. In the second place, the relationship of this family to the *Suidæ* must be a very remote one. When we compare the skeleton of *Elotherium* with that of the swine and peccaries, point by point, the only notable resemblance between the two groups is found to consist in the bunodont character of the molar teeth, and this resemblance, standing by itself, cannot be regarded as at all decisive. The selenodont molar has been independently acquired by several distinct lines, and so far as the artiodactyls are concerned, the bunodont pattern is almost certainly the primitive one. That two widely separated families should each have retained a common primitive character is too frequent a phenomenon to excite surprise. In all other structures, skull, vertebral column, limbs and feet, no particularly close correspondences between the *Elotheriidæ* and the *Suidæ* can be detected, though that a common early Eocene progenitor should have given rise to both families is altogether likely.

Between *Elotherium* and *Hippopotamus*, on the other hand, are many points of resemblance. The likeness in the dentition is here quite as great or even greater than between either of these genera and the *Suidæ*. In the skull there is much to suggest relationship, though combined with many striking differences, which may perhaps be referable to different habits of life, such as the enormous massiveness of the premaxillary and symphyseal region in the modern genus, the peculiar development of the canines and incisors and the elevated tubular orbits. In the skeleton the two genera are widely separated; *Elotherium* is a long-limbed, long-footed, didactyl creature, with small thorax and slender ribs, evidently of terrestrial habits. *Hippopotamus*, on the contrary, is a short-limbed, short-footed, tetradactyl and isodactyl form, with immense thorax and broad, almost slab-like ribs, which is chiefly aquatic in its habits. Whether the resemblances in skull and dentition indicate any relationship between the two families can be determined only when their history has been worked out. In any event, it is not probable that the relationship can prove to be closer than that both lines were derived from a common stock which separated from the other Artiodactyla at a very early date.

As has already been observed, no direct ancestors of *Elotherium* have yet been recovered, but there are certain Eocene forms which seem to be related to these unknown ancestors in such a way as to suggest the character of the latter. The *Achænodon* (*Elotherium*) *uintense* of Osborn ('95, p. 102) is such a form and differs from the *A. robustum* of the Bridger in the "great elongation of the face and the shortening of the cranium, both of which characters relate it to *Elotherium*" (*l. c.*, p. 103). This species is more specialized in several respects than the White River Elotheres, and like its forerunners of the Bridger, *A. robustum* and *A. insolens*, it has but three premolars in each jaw, and hence is not at all likely to be ancestral to the later genus. In the Wasatch *Achænodon* is represented by *A.* (*Parahyus*) *vagum* Marsh, which likewise has but three premolars, and, so far as it is known, differs from the Bridger species only in its smaller size. There is some reason to think, as Osborn has pointed out, that even *A. uintense* had four functional digits.

While it is very unlikely that *Achænodon* can have been the direct ancestor of *Elotherium*, there are, nevertheless, so many suggestive resemblances between the two genera, and the types of their dentition are so nearly identical, that we can feel little doubt as to their real phylogenetic relationship. In this case, *Achænodon* will represent a somewhat modified side-branch of the stem which culminated in *Elotherium*. A species of *Achænodon*, or of some closely allied genus, with unreduced dentition and unshortened face, may well prove to be the desired ancestral form. If so, the line had already become distinct in the Wasatch and the group thus has no subsequent connection with any existing artiodactyl family, unless possibly with the *Hippopotamidæ*. *Elotherium* would then represent the termination of an ancient and very peculiar line, which attained a remarkable degree of specialization in many parts of its structure and which extended its range over the whole Northern Hemisphere. At the same time, the cerebral development of the genus was very backward and this was doubtless one, at least, of the factors which led to its extinction. After the John Day, the line disappeared, leaving no successors.

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Explanation of the Plates.

Plate XVII.

Skeleton of *Elotherium ingens* Leidy, from the Titanotherium beds of South Dakota, about $\frac{1}{11}$ natural size. Only the eighth thoracic vertebra and the distal ends of certain ribs are conjectural. The tail may well have been considerably longer, as only the vertebræ associated with the skeleton have been drawn.

Plate XVIII.

Fig. 1. *Elotherium mortoni.* Basal view of skull, $\frac{1}{3}$ nat. size. *Ty*, tympanic bone; *c*, canal opening above and behind the posterior nares.

Fig. 2. *Elotherium mortoni.* Occiput from behind, $\frac{1}{3}$ nat. size.

Fig. 3. *Elotherium ingens.* Atlas, ventral side.

Fig. 4. *Elotherium ingens.* Axis, left side.

Fig. 5. *Elotherium ingens.* Fifth thoracic vertebra, from the front.

Fig. 6. *Elotherium ingens.* Last lumbar vertebra, from behind. *es*, episphenial process.

Fig. 7. *Elotherium ingens.* Anterior caudal vertebra, from above.

Fig. 8. *Elotherium ingens.* (?) Fifth caudal vertebra, left side.

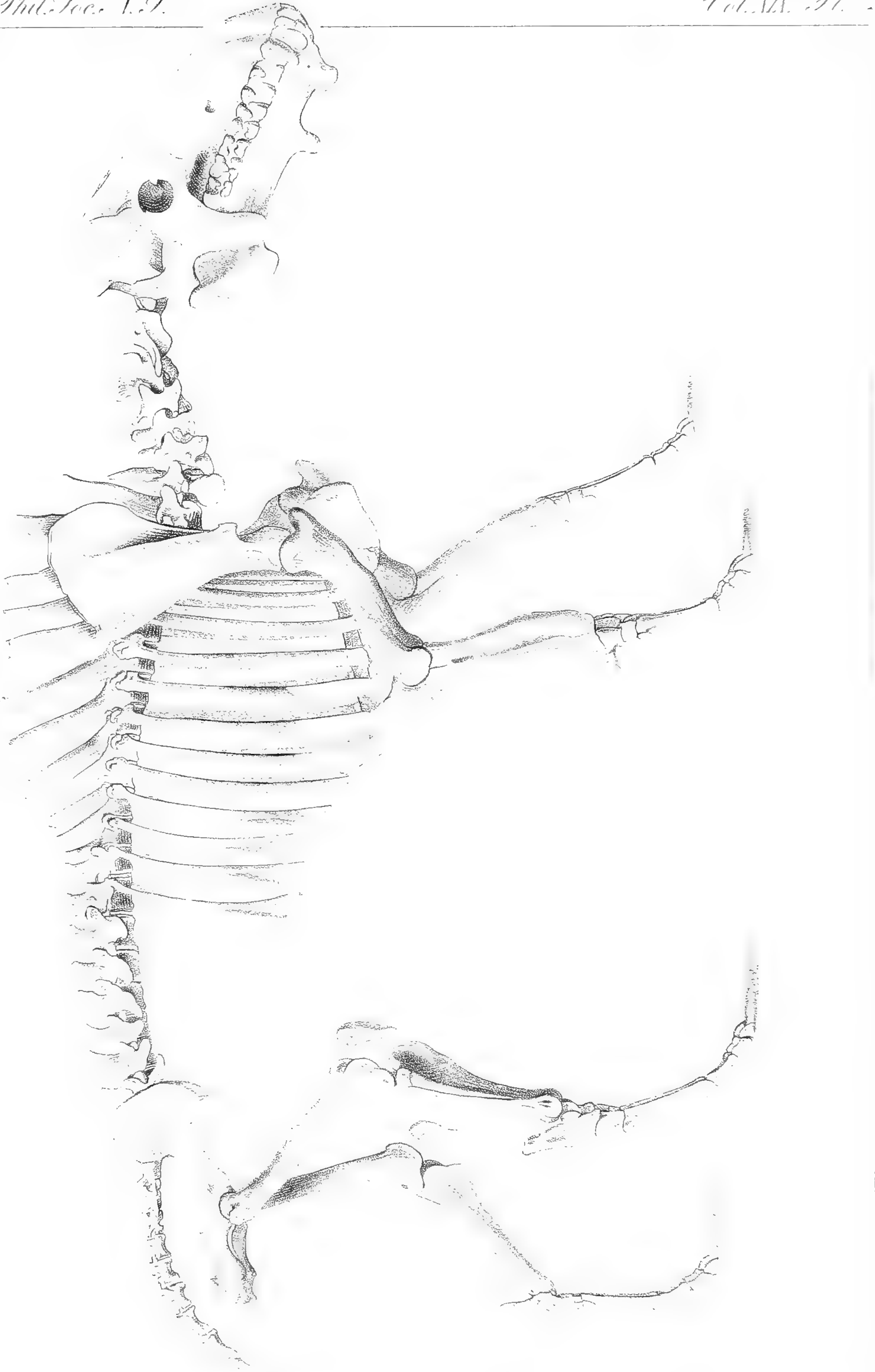
Fig. 9. *Elotherium ingens.* Posterior caudal.

Fig. 10. *Elotherium ingens.* Right ulna and radius.

Fig. 11. *Elotherium ingens.* Right manus. ii, second metacarpal (conjectural); v, fifth metacarpal.

Fig. 12. *Elotherium ingens.* Right pes. ii, v, second and fifth metatarsals.

(*Figs. 3–12 are approximately $\frac{1}{4}$ nat. size and are of bones belonging to the skeleton figured in Plate XVII.*)

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ARTICLE VIII.

NOTES ON THE CANIDÆ OF THE WHITE RIVER OLIGOCENE.

BY W. B. SCOTT.

(INVESTIGATION MADE UNDER A GRANT FROM THE ELIZABETH THOMPSON FUND OF THE A. A. A. S.)

(Plates XIX and XX.)

Read before the American Philosophical Society, February 4, 1898.

The problems concerning the origin and mutual relationships of the various families into which the Carnivora Fissipedia are divided have not yet been satisfactorily solved, principally because of the rarity of well-preserved fossils representing the earlier and more primitive members of the families. Especially obscure are the questions dealing with the derivation and systematic position of the *Felidæ,* a family which by many authorities is regarded as occupying an entirely isolated position, not directly connected with any of the other groups. Hardly less puzzling, however, are many of the facts of canine phylogeny, such as the relations between the two great series of the wolves and the foxes, and the connection between the many divergent genera of successive geological horizons. No satisfactory answer to these questions can be given until many complete phylogenetic series of the Carnivora shall have been discovered, for so long as the numerous wide gaps which now separate the known members of the various series remain unbridged, those series must continue to be largely conjectural. At any time, new discoveries may call for an entire readjustment of our views regarding the lines of descent of the different families.

Recently, there has come into my hands some uncommonly well-preserved material for the phylogenetic history of the *Canidæ* and is the occasion of the present paper. This material was obtained for the museum of Princeton University by Messrs. Gidley and Wells, who in the summer of 1896 made a collecting trip through the Bad Lands of Nebraska and South Dakota. They had the good fortune to discover certain unworked localities where the exposures of the White River Oligocene proved to be richly fossiliferous and, in particular, yielded many unusually complete specimens of primitive dogs. A study of this material has brought to light some very remarkable and unexpected facts, which, to the writer at least, seem to require a revision of some current views upon the phylogeny of the carnivorous families, and to throw some light upon the obscure and difficult problems relating to the origin of the cats. The most valuable of these specimens are referable to the genus *Daphænus* Leidy, which has long been known, though but very imperfectly, and several partially preserved skeletons permit an almost complete account of its osteology to be given.

DAPHÆNUS Leidy.

Proc. Acad. Nat. Sci. Phil., 1853, p. 393. *Amphicyon* Leidy (*non* Pomel), *ibid.* 1854, p. 157 ; *Ext. Mamm. Fauna Dak. and Nebr.*, 1869, pp. 32, 359 ; Cope, *Tertiary Vertebrata*, pp. 894, 896. *Canis* Cope, *Ann. Rep. U. S. Geolog. Surv. Terrs.*, 1873, p. 505.

This genus represents nearly the most primitive type of dogs which has so far been determined from the Tertiary deposits of North America. It was originally described and named by Leidy, who afterward mistakenly referred it to the European genus *Amphicyon*, a reference which was also adopted by Cope. Though more than forty years have thus elapsed since the first discovery of these animals, singularly little has been known about them, for the material obtained has been very scanty and very badly preserved. Fragments of jaws, a few very imperfect skulls and fewer limb-bones have hitherto been the only specimens found, in spite of long and careful search, and beyond the fact that *Daphænus* was apparently a primitive member of the canine phylum, little could be predicated of it.

The new material gathered by Messrs. Gidley and Wells fortunately removes this difficulty and gives us information regarding nearly all parts of the skeleton of these curious animals. These skeletal characters are of a very surprising nature and their interpretation is by no means easy. Especially remarkable are the many points of resemblance which we find between the structure of *Daphænus* and the corresponding parts of such primitive Machairodonts as *Dinictis*. Aside from the dentition and the shape of the mandible, these resemblances in structure between the primitive dogs and the early sabre-tooth cats are ubiquitous, and recur in the structure of the skull, of the vertebræ, of the limbs and of the feet. To bring out the full force of these remarkable characteristics, it will be necessary to enter into a detailed and somewhat tediously minute description of the osteology of *Daphænus*, so that the means of comparison may be completely laid before the reader.

I. The Dentition.

The dental formula of the genus is I $\frac{3}{3}$, C $\frac{1}{1}$, P $\frac{4}{4}$, M $\frac{3}{3}$, the same as that of *Amphicyon*, a resemblance which caused the erroneous identification of the two genera already referred to.

A. Upper Jaw (Pl. XIX, Fig. 2).—The incisors are closely crowded together and form a nearly straight transverse row; they are smaller and occupy less space both transversely and antero-posteriorly than in most recent species of *Canis*. As in that genus, the external incisor is much the largest tooth of the series, and forms with the upper and lower canines a formidable lacerating apparatus. The diastema between the incisors and the canine is somewhat greater than in *Canis*, and the premaxillary is quite deeply constricted at that point, forming a groove for the reception of the lower canine.

The canine is of the usual compressed, oval section, but the compression is less decided than in *Canis*, the longitudinal diameter not so greatly exceeding the transverse. The fang of the canine is long and stout, producing a marked swelling upon the outer face of the maxillary; the crown is of only moderate length, but is both actually and proportionately heavier than in the coyote (*C. latrans*).

The premolars are notably small and simple; they increase in size regularly from the first to the fourth, the sectorial being, of course, much larger than any of the others. The first premolar is implanted by a single fang, and has a small crown of compressed conical shape, with much less conspicuous internal cingulum than in the recent species of the *Canidæ*. The second premolar is decidedly smaller than in most of the modern dogs, and is separated by longer interspaces from both the preceding and the succeeding tooth; it has a low, pointed, simple and much compressed crown, without the small posterior tubercles which are found in nearly all the recent species of the family. The third premolar is much longer and especially has a higher crown than $\mathrm{p}\,\frac{2}{\;}$, but has a similar shape, without posterior basal tubercles, and, like $\mathrm{p}\,\frac{2}{\;}$, is inserted by two fangs. The sectorial ($\mathrm{p}\,\frac{4}{\;}$) is very primitive in character, as compared with that of the typical recent species of *Canis*. Certain modern members of the family, such as *Otocyon* and *Canis corsac*, for example, have, it is true, even smaller and simpler sectorials than *Daphænus*, but as in these forms this is doubtless due to a secondary simplification, they need not be drawn into comparison. The primitive character of the sectorial in the White River genus is shown in the thick, pyramidal shape of the antero-external cusp (*protocone*) which is less compressed and trenchant than in the modern species, in the smaller size of the postero-external cutting ridge (*tritocone*) and in the unreduced internal cusp (*deuterocone*) which is very much larger and more prominent than in *Canis*, and is carried upon a larger fang. The position of this inner cusp with reference to the protocone is the same as in the recent genus. As a whole, the sectorial is small and gives to the dentition a decidedly microdont character.

The premolar series of the two sides diverge quite rapidly posteriorly, each tooth, except p^{1}, being oblique in position, with reference to the long axis of the skull, thus giving the bony palate its greatest width at the hinder edge of the sectorials. The obliquity of the teeth and their divergence posteriorly are even more strongly marked than in most recent dogs.

The upper molars are large and well developed, though the different species vary in this respect, *D. vetus* having larger tubercular molars than *D. hartshornianus*. The first molar is, in general, like that of *Canis*, but differs in certain details. Thus, the two external cusps are more conical in shape, more nearly equal in size, and are not placed so near to the outer edge of the crown, resembling in this respect the upper molars of certain creodonts, such as *Sinopa;* the large inner crescentic cusp is much as in *Canis*, though hardly so prominent, especially in *D. hartshornianus;* in *D. vetus* it is larger. The second molar is much like the first in shape and construction, but smaller and somewhat simplified, the conules being minute or altogether absent. The third molar is very small and has a low, transversely oval crown, in which separate elements are not distinguishable. This tooth is rarely preserved and none of the specimens at my disposal possess it, though the alveolus for it is almost always present; it is well figured by Leidy ('69, Pl. I, Fig. 5).

B. Lower Jaw (Pl. XIX, Figs. 5, 6, 7). In none of the available specimens are the lower incisors sufficiently well preserved to be worth description.

The canine is very much the same as in the recent members of the family. The premolars are somewhat more complex than those of the upper jaw. The first is very small and simple, while p. $\overline{2}$, $\overline{3}$ and $\overline{4}$, increase progressively in size and in the development of the posterior basal cusps. In the more ancient and primitive species *? D. dodgei*, from the Titanotherium beds, the premolars are lower, thicker transversely and less acutely pointed, and have larger posterior basal cusps than in the later species from higher horizons. In all the species these teeth are more widely separated than in the modern genera.

The molars are very characteristic of the genus, but well-marked specific differences may be observed. In *? D. dodgei* the anterior triangle of the lower sectorial is of only moderate height and the heel is but slightly concave, the outer and inner ridges (*hypo-* and *entoconids*) being very little raised. In *D. hartshornianus* the protoconid is high, narrow and pointed, and the talon is more concave than in the first-named species, and has more prominent internal and external cusps. In *D. vetus* the inner cusp of the talon (*entoconid*) is reduced and, as Cope has already pointed out ('84, p. 898), there is a tendency toward the formation of a talon with a single trenchant ridge, a tendency which is fully carried out in the genera *Temnocyon* and *Hypotemnodon* of the succeeding John Day horizon. In all the species of *Daphænus* the inferior sectorial is much more primitive than in the typical modern *Canidæ*, as is clearly shown by the higher and more conical protoconid, the lower and smaller paraconid and much less reduced metaconid. In fact, both the superior and inferior sectorials of *Daphænus* have a close resemblance to those of the creodont family *Miacidæ*, from which this genus could hardly be separated upon the ground of the dentition only.

The tubercular molars are not preserved in the specimens of *? D. dodgei*; in *D. vetus* they are proportionately larger than in *D. hartshornianus*. M_2 is relatively large, especially in the antero-posterior diameter; it resembles the corresponding tooth of *Canis*, except for the presence of the small paraconid, thus giving to the tooth all the elements of a true sectorial, as is also the case in the creodont *Miacidæ*, though in the White River genus all the cusps are lower and more tubercular. $M_{\overline{3}}$ is quite small, though both proportionately and actually larger than in species of *Canis* of similar stature, and is inserted by a single fang; the crown is of oval shape and has an irregularly ridged surface, without distinct cusps.

As a whole, the dentition of *Daphænus* is that of a primitive member of the *Canidæ* and resembles the dentition of the recent members of the family in general plan and structure.

Measurements.

	No. 11421.	No. 11424.	No. 10538.	No. 11423.	No. 11425.	No. 11422.
Upper dental series, length C to M 2	0.069		0.076			
" incisors, transverse width	.014		.015			
" canine, length	.010		.0115			
" " width	.008		.008			
" P 1, length	.005	.005	.006			
" P 2, "	.008	.0085	.0095			
" P 3, "	.009		?.010	.009*		
" P 4, "	?.014	.0145	.015	.015		
" P 4, width	.0085	.009	.0105	.0105		
" M 1, length	.012	.011	.011	.012		
" M 1, width	.015	.015	.015	.016		
" M 2, length	.0065	.007	.007	.007		
" M 2, width	.010	.011	.011	.011		
Lower dental series, length C to M 3	.078			.090*	.090	
" premolar series, length	.036			.041*	.040	.0315
" molar series, length	.026	.0245		.031*	.030	
" canine, length	.011			.011*	.012	.010
" " width	.0085			.009*	.008	.007
" P 1, length	.0045*			.005*	.004	.003
" P 2, "	.0085	.008		.009*	.010	.006
" P 3, "	.0095	.010		.010*	.011	.008
" P 4, "	.012	.012		.012*	.012	.011
" M 1, "	.014	.013		.014*	.017	.014
" M 1, width	.007	.007			.009	.008
" M 2, length	.0085	.008		.0095*	.0095*	
" M 2, width	.006	.0055				
" M 3, length	.003*	.004*		.006*	.004*	
M 3, width	.002*	.003*				

*Alveolus.

II. The Skull (Pl. XIX, Figs. 1–7).

The skull of *Daphænus* is exceedingly primitive in character and plainly shows many traces of the creodont ancestry of the genus. Unfortunately, well-preserved skulls are exceedingly rare and none of the species is represented by an altogether complete specimen. However, several more or less imperfect specimens have been recovered, which together give us information concerning nearly all parts of the skull.

As in the creodonts generally, the cranial region, reckoning from the anterior edge of the orbits backward, is exceedingly elongate, while the face in front of the orbits is very short, slender and tapering. The elongation of the cranium is not due to an enlargement of the cerebral fossa, which on the contrary is short, narrow and of relatively small capacity. The postorbital constriction, which marks the anterior boundary of the cerebral fossa, is notably deep and is removed much farther behind the orbits than in *Canis*. On the other hand, the cerebellar fossa is long, and the postglenoid processes occupy a more anterior position than in the existing species. In consequence of the elongate cranial region, the zygomatic arches are very long, as in the more primitive types of creodonts. The upper contour of the skull is nearly straight, the descent at the forehead being very slight and gradual, which gives to the skull an alopecoid rather than a thooid aspect. This resemblance is, however, entirely superficial, for the frontal sinuses are large and well developed, as in the thooid series of the modern *Canidæ*. The sagittal crest is low, but varies in the different species, being decidedly thicker and more prominent in the larger and heavier *D. vetus* than in the smaller and lighter *D. hartshornianus*.

Turning now to the more detailed study of the elements which make up the skull, we shall find a number of striking and significant differences from the existing representatives of the family, though the general aspect of the whole is distinctively canine.

The *basioccipital* is broad and quite elongate and has a much more decided median keel than *Canis*. All the occipital bones are firmly ankylosed in the specimens at my disposal; hence, in the absence of sutures, it will be necessary to describe the compound bone as a whole, without much reference to the elements of which it is made up. The occiput is of quite a different shape from that found in the existing members of the family, being broader, lower, and with a wide, gently arched dorsal border or crest (see Pl. XIX, Fig. 3); in *Canis* this crest is pointed and somewhat like a Gothic arch in shape. The occipital crest is thin, but much more prominent than in *Canis*, which is due to the larger and deeper depressions of the cranial walls behind the occipital lobes of the cerebral hemispheres, the shape of which is plainly visible externally. The foramen magnum has much the same low and broad outline as in *Canis*. The condyles are low, but well extended transversely, and on the ventral side they are separated by a wider notch than in *Canis*. The depression, or fossa, external to the condyle is very much deeper and more conspicuous than in the modern genus, in consequence of which the condyles project more prominently backward from the occiput than in the modern dogs. The paroccipital processes are short, but quite stout and bluntly pointed; they project much more strongly backward and less downward than in the living forms, and are less compressed laterally. Another difference from the modern genus consists in the fact that, while in the latter the paroccipital process has quite an extensive sutural contact with the tympanic bulla, in *Daphænus* there is no such contact, the minute bulla being widely separated from the process. The direction taken by the paroccipital process in its course is thus evidently not determined by the size of the bulla, for in the John Day genera, *Temnocyon*, *Hypotemnodon* and *Cynodesmus*, in which the tympanic is greatly inflated, the shape and direction of the paroccipital are the same as in *Daphænus*, with its insignificant bulla. A considerable portion of the mastoid is exposed on the surface of the skull, but it is rather lateral than posterior in position, a difference from *Canis*, in which the mastoid is hardly visible when the skull is viewed from the side. The mastoid process is slightly larger than in the existing genus and is channeled on the inner side by a groove leading to the stylo-mastoid foramen.

The limits of the *basisphenoid* are not clearly shown in any of the specimens, but this element appears to have much the same broad and flattened form as in the recent dogs. The presphenoid is long and narrow and, as in the existing species, is almost concealed from view by the close approximation of the palatines and pterygoids along the median line. The ali- and orbito-sphenoids are not well displayed in any of the specimens, but so far as they are preserved, they differ little from those seen in the more modern members of the family.

The auditory bulla of *Daphænus* is very remarkable and differs from that of any other known carnivore. Its principal peculiarities were observed and noted by Leidy, but the material at his command was insufficient to enable him to describe these peculiarities with confidence. The *tympanic* is exceedingly small, and is but slightly inflated into an inconspicuous bulla, the anterior third of which is quite flat and narrows forward to a point. There is no tubular auditory meatus, the external opening into the bulla being a mere hole, but the anterior lip of this opening is drawn out into a short process, somewhat as in existing dogs. Behind the bulla is a large reniform vacuity or fossa, of which Leidy remarks: "At first, it appeared to me as if this fossa had been enclosed with an auditory bulla and what I have described as the latter was a peculiarly modified auditory process" ('69, p. 33). Several specimens representing both the White River and John Day species of *Daphænus* show that the fossa is normal and was either not enclosed in bone, or, what seems less probable, that the bony capsule was so loosely attached that it invariably became separated from the skull on fossilization. At the bottom of the fossa (*i. e.*, when the skull is turned with its ventral surface upward) is seen the exposed periotic, or petrosal, which is only partially overlapped and concealed by the tympanic. Such an arrangement is far more primitive than that which is found in any other known member of the canine series, and is not easy to interpret. A clue to its meaning may, however, be found in the mode of development of the bulla in the recent *Canidæ*. Here, as is well-known, the structure consists of an anterior membranous and posterior cartilaginous portion, which eventually ossify and coalesce into a single bulla. Reasoning from this analogy, we may infer that in *Daphænus* the bulla was also composed of two portions, but that only the anterior chamber was ossified, the posterior one remaining cartilaginous. Communication between the two chambers was provided for by the space which separates the hinder edge of the anterior chamber from the petrosal. If this interpretation be correct, it supplies an interesting confirmation of the results derived from the ontogenetic study of the recent genera. At all events, it seems much more probable that we have to do here with a primitive rather than a degenerate structure.

The *parietals* are large and roof in most of the cerebral fossa; they are much less convex and strongly arched than in *Canis*, in correspondence with the smaller size of the cerebral hemispheres, and posteriorly the depressions behind the hemispheres are much larger and deeper. As already remarked, the sagittal crest varies in the different species, and is much thicker and more prominent in *D. vetus* than in *D. hartshornianus*. The frontals are more or less damaged in all the specimens and in none of those at my disposal is it possible to determine the posterior limits of these bones, though from the position of the postorbital constriction we may confidently infer that they formed a smaller proportion of the cranial roof than in the modern members of the family. The supraciliary ridges are feebly developed, especially in *D. hartshornianus*, and the postorbital processes are likewise much less prominent than in most of the recent dogs; from this process a ridge descends downward and backward to the optic foramen, which, though not prominent, is yet more so than in *Canis*. The frontal sinuses are large and yet in spite of them the forehead is nearly flat, both longitudinally and transversely, with a very shallow depression along the median line. The nasal processes of the frontals are long, narrow and pointed, and are separated by only a short interval from the ascending rami of the premaxillaries.

The *squamosal* is of moderate size and differs only in subordinate details from that of *Canis*. One such difference is the presence of a broad shelf-like projection, the posterior extension of the root of the zygomatic process, which overhangs the auditory meatus and is doubtless to be correlated with the lesser breadth and convexity of the brain. The glenoid cavity is like that of the recent species, but has a much more distinct internal boundary, due to an elevation of the squamosal at that point. The zygomatic process is stout and well-developed, especially in *D. vetus*, which has heavier arches than a large wolf, while in *D. hartshornianus* the zygoma is lighter and more slender, much as in the coyote. The *jugal* is strongly curved upward, as well as outward, and is shaped quite as in *Canis*, forming nearly the whole anterior and inferior boundary of the orbit; the postorbital process is very feebly indicated, being even less prominent than in the modern genus, so that the orbit is more widely open behind. The *lachrymal* is rather larger than in *Canis*, forming more of the anterior orbital border, and has a quite well-developed spine.

The *nasals* have a general resemblance to those of *Canis*, but, in correspondence with the shortness of the whole facial region, they are considerably shorter, and somewhat broader and more convex transversely; their posterior ends are more simply rounded and have a less irregular suture with the frontals, while the anterior, free ends are much less deeply notched.

The *maxillary* is somewhat peculiar in shape, corresponding to the remarkably constricted, narrow muzzle. The facial portion of the bone is relatively higher than in existing representatives of the family, especially in front, its anterior border rising in a steeper and bolder curve. Just in advance of the orbits the maxillaries expand quite suddenly in the transverse direction, much more abruptly than in *Canis*. The infraorbital foramen occupies nearly the same position, with reference to the teeth, as in the latter genus, being above the front edge of the sectorial, but it is very much nearer to the orbit, which occupies a more anterior position. The palatine processes of the maxillaries follow the shape of the muzzle, and are long, narrow for most of their length, but broadening much behind; anteriorly they are emarginated in an unusual degree to receive the long premaxillary spines.

The *premaxillaries*, especially their alveolar portion, are somewhat narrower than in *Canis*, and behind the external incisor the alveolar border is constricted on each side, forming well-marked grooves for the reception of the lower canines. The exposed part of the ascending ramus is much narrower than in the modern genus, forming a mere strip on the side of the narial opening. At the same time, this ascending ramus is relatively longer than in existing dogs and extends almost to the nasal process of the frontal. The anterior narial opening is somewhat larger proportionately than in the recent members of the family, especially in the vertical direction, and its borders are less inclined; the floor, formed by the dorsal surface of the horizontal rami of the premaxillæ, is more simply and deeply concave, and the horizontal rami themselves are less massive. The palatine processes of the premaxillaries are distinctly smaller than in *Canis*, while the spines are relatively longer and more slender. The incisive foramina are large and from them quite deep grooves are continued forward to the alveolar border, while in the modern genus these grooves are very shallow and feebly marked.

The *palatines* are shaped very much as in *Canis*. As a whole, the bony palate differs from that of the latter genus in the greater and more abrupt expansion of its posterior half, beginning at p ^{3}; it is also somewhat more concave transversely and has a more prominent ridge along the median line. The palatine foramina are likewise somewhat different from those of recent dogs; one conspicuous opening on each side occupies the same position as in the latter, opposite the middle of the sectorial, but instead of a single opening opposite m ^{1}, is a group of two or three minute foramina.

The *Cranial Foramina*. Unfortunately, none of the specimens are sufficiently well preserved to permit a complete account of the cranial foramina, though the more important facts concerning these structures may be determined. Leidy states that in *D. vetus* "the anterior condyloid, Eustachian and oval foramina present very nearly the same condition as in the Wolf" ('69, p. 33). The specimen upon which Leidy's description was founded, belonging to the Academy of Natural Sciences of Philadelphia, has been mislaid and is not at present available for comparison, but the description cited above does not altogether apply to the cranium of *D. hartshornianus*, of which an account has been given in the foregoing pages. In this specimen the condylar foramen is widely removed from the condyle, much more so than in *Canis*, and is placed near the edge of the reniform fossa which lies behind the tympanic bulla. The existence of this fossa removes the necessity for a distinct foramen lacerum posterius, which is indicated only by a notch in the hinder margin of the fossa; similarly, the stylomastoid foramen is an open groove, only partially enclosed by bone. The postglenoid foramen is large and conspicuous and is not concealed by the anterior lip of the auditory meatus as is the case in the John Day *Cynodesmus*. The foramen lacerum medium appears to occupy a somewhat more internal position than in *Canis*, though this is not altogether certain, because of the unfavorable condition of the fossil just at this point. The Eustachian canal is more concealed under the long anterior process given off from the tympanic bulla than in the existing genus, and the foramen ovale is separated from the entrance to the canal by a much more prominent bony ridge, so that the foramen presents forward instead of downward.

By a curious coincidence all the crania of *Daphænus* in the Princeton museum are damaged in such a way that none of them displays the alisphenoid canal, the foramen rotundum or the foramen lacerum anterius, though there is no reason to doubt that all of these foramina were present and corresponded in position to those of *Canis*. The optic foramen is overhung by a ridge, already described, which is much more prominent than in the latter, and the lachrymal foramen is decidedly larger and more conspicuous. The parietal is perforated by a venous foramen which opens in the depression behind the cerebral hemispheres; this foramen, the postparietal, is not found in the modern genus.

The *mandible* differs considerably in the various species, though the comparison between them can as yet be but partially made, for the only specimen known to me in which the angle and coronoid process are preserved, is that figured by Leidy (*l. c.*, Pl. I, Fig. 2), which belongs to *D. vetus*. In *? D. dodgei* (Pl. XIX, Figs. 6, 7.) the horizontal portion of the mandible is thick, heavy and relatively short; the inferior border is very far from straight, rising beneath the masseteric fossa almost to the level of the molars and descending forward from this point in a bold, sweeping curve, quite as in the modern *Canis aureus;* the masseteric fossa is very deep and its ventral border forms a prominent ridge, distinct from the lower border of the jaw; the symphysis is short and the chin abruptly rounded and steeply inclined.

In *D. vetus* the horizontal ramus is of an entirely different shape (see Pl. XIX, Fig. 5) being longer, more compressed and slender and with a decidedly straighter ventral border; the symphysis is longer and the chin more gently rounded, rising more gradually from the inferior margin of the ramus. The masseteric fossa is quite deeply impressed, though less so than in *? D. dodgei*, and is very large, extending far up upon the ascending ramus. The angle is a stout hook, which is less elevated above the general level of the horizontal ramus than in modern wolves or foxes. The condyle also has a low position, below the level of the molars, while in recent species the condyle is raised above the molars, and in some species very much so. The ascending ramus has great antero-posterior extent, by which the condyle is removed far back of the last molar. This is a primitive feature which recurs in most creodonts and is evidently correlated with the characteristic elongation of the cranium and zygomatic arches. The coronoid process is high and wide, and has a bluntly rounded end; it inclines much more strongly backward than in *Canis* and has a much more concave posterior border. The condyle resembles that of the recent dogs, but is set upon a more distinct neck, is more extended transversely, and is less cylindrical in shape, tapering more toward the outer end.

In *D. hartshornianus* the mandible, so far as it is preserved in the various specimens, resembles that of *D. vetus*, save that the horizontal ramus is somewhat shallower and more slender.

The *Brain*. Very little can be said concerning the brain, since no complete cast of the cranial cavity is available for study. The general shape and development of the brain are, however, indicated in the specimen of *D. hartshornianus* already described (Pl. XIX, Fig. 1). Its proportions are very different from those found in existing members of the family, a difference which may be briefly stated as largely consisting in the much greater relative size of the cerebral hemispheres and smaller size of the olfactory lobes in the modern species. In *Daphænus* the brain is narrow and tapers rapidly toward the anterior end; the cerebellum and medulla oblongata are long, the hemispheres narrow and short, and the olfactory lobes very large. The partially exposed cast of the cerebral fossa shows that the cerebral convolutions are fewer, simpler and straighter than in any known species of *Canis*, and are even more primitive than those of *Cynodesmus* (see Scott, '94, Pl. I, Fig. 2). The only sulcus visible in the specimen is apparently the suprasylvian, which is short and pursues a nearly straight course, but curving downward slightly at both ends. From the external character of the skull it is clear that the hemispheres overlap the cerebellum but little.

Measurements.

	No. 11421.	No. 11424.	No. 10538.	No. 11423.	No. 11425.	No. 11422.
Skull, length		?0.151				
Cranium, length fr. occ. condyles to preorbital border		.108				
Face, length in front of orbits	.065	?.050	.073			
Zygomatic arch, length		.080				
Palate, length	.076		.092			
" width at p^4	.044*	.047*	.052			
Mandible, length from chin to masseteric fossa	.084			.093	.096	?.079
" depth at $m_{\overline{1}}$	.020	.018		.023	.025	.025
" " " p	.0175	.015		.017	.020	.019
" thickness at m_1	.010	.009		.010	.012	.012

* Approximate.

III. The Vertebral Column.

The vertebral column is remarkable in many ways. All the regions of the column are well represented by several specimens of *D. vetus* and *D. hartshornianus*, but no complete backbone belonging to a single individual has as yet been recovered.

Cervical Vertebræ. The collection contains only a single imperfect specimen of the atlas and this belongs to *D. vetus*. Imperfect as it is, this atlas displays some important differences from that of *Canis* and most of these differences are approximations to the feline and viverrine types of structure. In *Daphænus* the atlas is elongate in the antero-posterior direction, the anterior cotyles are small and only moderately concave, and are somewhat more widely separated on the ventral side than in *Canis*. When viewed from above, the cotyles are seen not to project so far in front of the neural arch as in the cats, but farther than in the dogs. The posterior cotyles for the axis are small, nearly plane, and but slightly oblique in position, with reference to the fore-and-aft median line of the vertebra. These cotyles are more distinctly separated from the articular surface for the odontoid process of the axis than in the modern dogs, in which all three facets are confluent. The neural arch is low and broad, considerably elongated from before backward, and without ridges of any kind, save an inconspicuous tubercle, which represents the neural spine. Near its anterior border the arch is perforated by the usual foramina for the first pair of spinal nerves. The inferior arch is very slender, forming a more curved bar and has a much less antero-posterior extension than in *Canis.*

Wortman ('94, p. 137) has pointed out that the foramina of the atlas display certain characteristic features in the various carnivorous families. "In all of the *Felidæ* which I have had the opportunity of studying, the [vertebrarterial] canal pierces the transverse process at its extreme posterior edge, where it is thickened and joins the body of the bone. The superior edge of this posterior border slightly overhangs the inferior edge. . . . . This character appears to be very constant in the *Felidæ* and so far as we know the structure of the atlas in the more generalized *Nimravidæ* [Machairodonts], it is true of them also. In the *Canidæ,* upon the other hand, the foramen for the vertebral artery is situated well in advance of the posterior border of the process, and instead of having a fore-and-aft direction, as in the cats, pierces the process almost vertically from above. In the *Viverridæ* and *Hyænidæ* the position of the foramen is very much as in the cats. There is, however, an important difference between these two families and the felines where the artery enters the suboccipital foramen in the anterior part of the atlas. The difference consists in the formation of a bony bridge in this situation, which gives to the suboccipital foramen a double opening in the hyænas and civets, whereas it is single in the cats."

In *Daphænus,* it is interesting to observe, the foramina of the atlas are in all respects like those characteristic of the cats and thus depart in a very marked way from the arrangement found in the recent *Canidæ.* The transverse processes are broken away, so that their shape is not determinable, but enough remains to show that the atlanteo-diapophysial notch is not converted into a foramen, thus agreeing with the canines and felines and differing from most of the hyænas and civets.

The *axis* is likewise feline rather than canine in its general character and appearance. The centrum is elongate, narrow and depressed, with a thin and inconspicuous hypapophysial keel, running along the ventral surface, and has a slightly concave posterior face. The articular facets for the atlas are convex and rise higher upon the sides of the neural canal than in *Canis,* and on the ventral side they project below the level of the centrum, so that they are separated by a broad notch, which is not present in the modern dogs, and is not well marked in the cats. The odontoid process is a long, slender, bluntly pointed peg, with a heavy, rounded ridge upon its dorsal surface, which is continued back along the floor of the neural canal. The transverse processes are quite long and relatively very stout; they are shorter and heavier than in *Canis,* and keep more nearly parallel with the centrum, not diverging so much posteriorly. As in the felines, the vertebrarterial canal is longer than in the modern dogs, and its posterior opening is not visible when the vertebra is seen from the side; the anterior opening is larger and is placed farther forward than in the recent *Canidæ*. The neural canal is proportionately larger than in the latter, both vertically and transversely, nor does it contract so much toward the hinder end. The neural spine forms the great, hatchet-shaped plate usual among the Carnivora, and in its details of structure it is feline rather than canine. In the latter group, the spine is not continued back of the postzygapophyses into a distinct process, but its hinder borders curve gently into them. In *Daphænus*, as in nearly all the cats and viverrines, the spine is drawn out into a blunt and thickened process behind the zygapophyses, from which it is separated by a deep notch. The zygapophyses are rather small and do not project so prominently from the sides of the neural arch as they do in *Canis*.

The other cervical vertebræ are more slender and lightly constructed than in the existing *Canidæ* of corresponding stature. The centra are long, narrow, depressed and very feebly keeled in the ventral median line; in most of the species this keel does not terminate in a posterior hypapophysial tubercle, such as is found in the existing dogs. In the largest species, however, *D. felinus*, the keels are more prominent, especially on the third and fourth vertebræ, and there is some indication of the tubercle. The centra are slightly opisthocœlous and the faces are somewhat oblique in position. In very few of the specimens are the transverse processes sufficiently well preserved to require description, and in such cases as they are present (as, for example, on the fifth and seventh cervicals of one individual of *D. hartshornianus*) they display no noteworthy differences from the corresponding processes of *Canis*. The vertebrarterial canal is, however, somewhat longer than in the latter.

The neural arches are very different from those seen in the modern representatives of the family. In them the dorsal surface of the neural arch is very broad and on each side projects outward as an overhanging ledge, which connects the prezygapophysis with the postzygapophysis of the same side; ridges and rugosities for muscular attachment are well marked and in the large species often very prominent; the zygapophyses, and especially the posterior pair, project but little in front of and behind the arches, and those of each pair are separated by notches of only moderate depth. In consequence of this arrangement, there are but small interspaces visible between the successive arches, when the vertebræ are in position. In *Daphænus*, on the other hand, the dorsal surface of the neural arch is relatively narrow, somewhat convex transversely and usually smooth, without ridges or tubercles; the overhanging ledge which gives such an appearance of breadth to the arch in *Canis* is little developed; the zygapophyses project far in advance of and behind the arch, and between each transverse pair is a deep notch which greatly reduces the antero-posterior length of the bony arch in the median line. When the vertebræ are placed in position, the openings between the successive arches, on the dorsal side, are very large and are longer antero-posteriorly than broad transversely. In these peculiarities of the cervical vertebræ of *Daphœnus* we find no approximation to the structure of the cats or the viverrines.

The neural spines are also quite differently developed from those of the recent dogs. The third cervical has no spine, merely a very faintly marked keel, the overhanging spine of the axis leaving no room for the development of one on the third vertebra. The fourth cervical has a very low spine, and on each successive vertebra the spine becomes higher and more pointed; that of the seventh is very high and slender, very much more prominent than in *Canis*, being almost as high, though not nearly so stout, as the spine of the first thoracic vertebra in the modern genus. The length of the spines in the neck constitutes another similarity to the structure of the felines.

Thoracic Vertebræ.—The number of trunk vertebræ characteristic of *Daphœnus* cannot as yet be definitely determined for any of the species, for no specimen has been found with complete backbone. In one specimen of *D. vetus* are preserved twelve thoracic and five lumbar vertebræ and the type of *D. felinus* contains six lumbars. It is altogether probable that the extinct genus agreed with the existing dogs in having thirteen thoracics and seven lumbars. The first thoracic has a broad, very much depressed centrum, with anterior face convex and posterior face deeply concave. The prezygapophyses project forward very strongly and, as in the cervicals, the notch between them is very deeply incised, invading the base of the spine, a very different arrangement from that seen in *Canis;* these processes are relatively larger and more concave in *D. vetus* than in *D. hartshornianus.* The postzygapophyses are much smaller, but project prominently from the hinder end of the neural arch, extending both laterally and posteriorly; the articular faces are somewhat convex transversely and have an oblique position, presenting outward rather more than downward. The neural spine is high and compressed, shaped very much as in *Canis*, but somewhat more slender. The transverse processes are very long, prominent and heavy, especially in the large species, *D. felinus;* at the distal end of the process is a large and deeply concave facet for the tubercle of the first rib.

The second thoracic very much resembles the first, but has a smaller, narrower, lighter, and much less depressed centrum; the prezygapophyses are smaller, less concave and less widely separated, while the postzygapophyses are larger and present downward, instead of obliquely outward, as they do on the first. The transverse processes are much smaller in every dimension than those of the first thoracic, and spring from the neural arch at a higher level, though they are still very prominent and carry large, concave facets for the second pair of ribs. The neural spine is somewhat heavier than on the preceding vertebra, and was probably higher, as well, but in none of the specimens is the spine preserved for its entire length.

The other vertebræ in the anterior part of the thoracic region have rather small centra, and in general character are very much like those of *Canis*. The (?) sixth vertebra has a curiously shaped spine, which exaggerates the condition seen in the modern genus; its proximal portion is inclined very strongly backward, while the distal portion is curved so as to project upward; the other thoracics, as far back as the (?) tenth, have similar spines. One very marked difference from the recent *Canidæ* consists in the deep notch which, in *Daphænus*, separates the two prezygapophyses. The anticlinal vertebra is probably, as in the existing dogs, the tenth, and at this point the thoracic vertebræ undergo an abrupt change of character, assuming more the appearance of lumbars. In *Canis* the spine of the tenth thoracic is exceedingly small and much lower than those of the ninth and eleventh, but in *Daphænus*, on the other hand, the spine is much better developed, both in length and thickness; the postzygapophyses are small, somewhat convex and placed high up upon the neural arch, presenting outward. The (?) eleventh thoracic is not preserved in any of the specimens. The (?) twelfth and thirteenth are much like lumbars, except for the smaller and lower spines, thickened at the distal end, and for the entire absence of transverse processes, which in *Canis* are present, though very short, even on the thirteenth; the anapophyses are remarkably long and stout, being much heavier and more prominent than in the recent dogs, and high, massive metapophyses rise above the prezygapophyses.

The *lumbar vertebræ* (Pl. XIX, Fig. 8) were probably seven in number, though not more than six have been found in connection with any one specimen. These vertebræ are remarkable for their relatively great size and massiveness, and for the length of all their processes, being in these respects feline, rather than canine in character and appearance. Assuming that seven is the full number, the missing one will then be the third, and the following description is made upon that assumption. The centra increase in length posteriorly, reaching a maximum in the fifth and sixth, but the seventh is no longer than the first, though much broader and heavier. Compared with those of *Canis*, these centra are longer, stouter, less depressed and more rounded. The transverse processes are longer and heavier than in *Canis* and less so than in the large species of *Felis*. The neural spines are likewise intermediate in character between those of the recent dogs and of the larger felines; they are much higher, more extended antero-posteriorly, more thickened at the distal end and more steeply inclined forward, than in the former. In *D. felinus* especially, the great height of these spines is very striking and the resemblance of the lumbar vertebræ to those of the contemporary Machairodont *Dinictis* is very great. Another similarity in the structure of the lumbar vertebræ between *Daphænus* and the felines consists in the great height and heaviness of the metapophyses, which are much better developed than in the recent *Canidæ;* on the last lumbar these processes become very much reduced and are, in fact, almost rudimentary. The anapophyses are smaller than on the thoracic vertebræ and diminish in size on each successive vertebra posteriorly; only on the first and second are they very large and prominent. In the existing representatives of the *Canidæ* these processes are rudimentary, except on the first lumbar, where they are small. This constitutes another point of resemblance between *Daphænus* and the cats, and emphasizes the statement already made, that the posterior thoracic and lumbar vertebræ of this Oligocene dog, for as such it must be regarded, are decidedly more feline than canine in appearance, using those terms only with reference to their modern application.

The *sacrum* (Pl. XX, Fig. 14) consists of three vertebræ, and, in correspondence with the great development of the tail, it resembles that of the larger cats in many respects. Only the first sacral vertebra has any contact with the ilium and bears massive pleurapophyses. The centra are much larger and heavier than in the modern dogs and the postzygapophyses much more prominent. The resemblance between the sacrum of *Daphænus* and that of the large cats is not very close, and the following differences may be noted: (1) the neural spines are much lower and weaker; (2) the neural canal is smaller; (3) the transverse processes of the second, and especially of the third vertebra, are decidedly shorter, so that the posterior portion of the sacrum appears much narrower. From the sacrum of the recent dogs that of *Daphænus* differs particularly in its greater proportionate length and massiveness.

Caudal Vertebræ (Pl. XIX, Figs. 9, 10).—In none of the specimens of the collection is the tail completely preserved, the largest number of vertebræ found being thirteen of one individual and eleven of another, but enough remains to satisfactorily demonstrate its character. The tail is remarkably long and stout and is, in fact, almost as well developed as in the leopard or tiger, and, consequently, is much longer and thicker than in any of the existing *Canidæ.*

The first caudal vertebra is quite like that of the lion, but is relatively lighter and more slender in all its parts, and has a short but distinct neural spine; the zygapophyses are very prominent, and even the metapophyses are distinctly shown; the transverse processes are very long, but are not so broad proportionately as in the lion, and are quite strongly recurved. Posteriorly the caudal vertebræ become successively more and more slender and elongate, while all of the processes are gradually reduced in size. The middle region of the tail is made up of extraordinarily elongate vertebræ, which are very much like the corresponding caudals of the long-tailed cats, but are decidedly longer and more slender proportionately. Near the tip of the tail the vertebræ become very small.

The *ribs* are represented only by fragments, which, so far as they are preserved, do not differ materially from those of the modern *Canidæ*. From the character of the posterior thoracic vertebræ, it may be inferred that the eleventh, twelfth and thirteenth pairs of ribs did not possess tubercles.

Of the *sternum* very little is preserved. One segment of the mesosternum is associated with the type specimen of *D. felinus;* it has much the same shape as in modern dogs, but is somewhat thicker transversely and shallower vertically, in proportion to its length. Another segment accompanies a specimen of *D. vetus* (No. 11424) and is much wider and more depressed than in any of the existing fissipedes, except certain hyænas. As the association of this weathered fragment with the skeleton of *Daphænus* may be accidental, no great stress can be laid upon it.

Measurements.

	No. 11421.	No. 11423.	No. 11425.
Atlas, length		0.031	
Axis, length (excl. of odontoid)			.041
" " of odontoid process		.013	.014
" width anterior face		.028	.031
Third cervical vertebra, length		.030	.031
" " " width of anterior face		.014	.016
Fourth " " length		.030	.030
Fifth " " "		.030	
Sixth " " "	.024	.028	.031
" " " width of anterior face	.012	.014	.016
Seventh " " length	.022	.024	.026
First thoracic vertebra, length	.017	.020	.021
Thirteenth thoracic vertebra, length	.021	.024	.024
" " " width anterior face	.017	.021	.021
First lumbar vertebra, length		.028	.028
" " " width anterior face		.020	.020
Sixth " " length		.037	.037
" " " width anterior face		.021	.021
Last lumbar, length		.030	.028
" " width anterior face		.022	.025
Sacrum, length		.058	
" width across pleurapophyses		.051	.051
First caudal vertebra, length		.020	
" " width across transverse processes		.060	
Median caudal, length		.040	

IV. The Fore Limb.

Of the *scapula* no part has yet been recovered.

The *humerus* (Pl. XX, Fig. 15) differs in several important respects from that of the recent *Canidæ*. Unfortunately, in all of the specimens the proximal end of the bone is broken away, so that nothing can be determined with regard to the head, tuberosities, or bicipital groove. The shaft is rather short and stout, and is arched strongly forward, though less so than in *Canis;* the deltoid ridge descends low upon the shaft and is very prominent, much more so than in the existing canines or felines, though it does not attain the exaggerated development seen in the early Machairodonts, such as *Dinictis* and *Hoplophoneus*. The distal end of the humerus is remarkably cat-like in appearance, and does not suggest any relationship with the modern *Canidæ*. The supinator ridge is very prominent and extends far up upon the shaft, while in *Canis* this ridge is almost obsolete. The internal epicondyle is very much larger, more rugose and more prominent than in the modern genus, quite as much so, indeed, as in the cats, and there is a large entepicondylar foramen, bridged over by a stout, straight bar of bone. The anconeal fossa is lower, broader, shallower, and altogether more cat-like than in *Canis*, and does not perforate the shaft to form a supratrochlear foramen. The humeral trochlea is extremely low, its vertical diameter being conspicuously less than in *Canis* and less even than in *Felis*, resembling in this respect the humerus of the sabre-tooth *Hoplophoneus*. The shape of the trochlea is of feline appearance, having a simply convex surface for the capitellum of the radius, and no such distinctly marked intercondylar ridge or convexity as is found in the recent *Canidæ*. The internal border of the trochlea is prolonged downward into a large flange.

The *radius* (Pl. XX, Fig. 16) is also singularly cat-like in structure and in all its parts is much more feline than canine. The proximal end bears an oval and somewhat concave capitellum, for articulation with the humerus; its transverse diameter only slightly exceeds the antero-posterior dimension. The anterior notch of the humeral surface is somewhat more deeply incised than in *Felis*, but not more so than in *Hoplophoneus*, which has an entirely similar capitellum. The articular facet for the ulna surrounds more than half the circumference of the head of the radius, which is in remarkable contrast to the small size of this facet in *Canis*. The shape and mode of articulation of the bones which enter into the formation of the elbow-joint show that *Daphænus* possessed unimpaired powers of pronation and supination of the manus. In the existing members of the *Canidæ*, on the contrary, this power is lost, the head of the radius being so much expanded transversely, as to occupy nearly the whole width of the humeral trochlea, and interlocking with it in such a way as to allow only the movements of flexion and extension.

The shaft of the radius in *Daphænus* is slender and has a similar shape to that which we find in the cats, although it is not so much expanded distally; it is thus very different from the broad, antero-posteriorly compressed and almost uniform radial shaft of the modern dogs. The distal portion of the radius is likewise very feline in appearance, but is rather lighter and narrower in proportion to the length of the bone; it is convex anteriorly and quite deeply concave posteriorly, with well-marked sulci for the extensor tendons upon the dorsal face. The distal facet for the ulna is small and of subcircular shape and forms quite a projection upon the ulnar side; upon the inner side of the distal end is a tubercle, which is even more rugose and prominent than in *Felis*, and more distinctly set off from the carpal surface. This carpal facet has a shape like that seen in the cats, and is more concave transversely and narrower in the dorso-palmar diameter than in the existing forms of *Canidæ*, and its internal border is more prolonged distally into a downward projecting flange.

Had this radius been found isolated, one would hardly have hesitated to refer it to one of the Machairodont genera, so completely does it differ from the radius of the modern dogs. Fortunately, there is no room for scepticism regarding the reference of this bone to *Daphænus*, for several of the specimens, representing different species, have radii of the same type. In this connection, it may be of interest to note that the Eocene creodont genus, *Miacis*, which has a remarkably canine type of dentition, has a very cat-like form of radius.

The *ulna* is hardly less characteristically feline than the radius. In marked contrast to the creodonts, which have a very long olecranon, that of *Daphænus* is rather short; its antero-posterior diameter is proportionately less than in *Felis*, or even than in *Canis*, and its postero-superior angle is thickened and rugose, though somewhat less so than in either of the modern genera mentioned, which gives its proximal border a straighter contour than in them. The tendinal sulcus is wider and deeper than in the recent dogs, less so than in the cats. The sigmoid notch is deeply incised, but describes a parabolic curve rather than a semicircle; the proximal humeral facet is relatively much wider than in *Canis*, and is continuous with the broad distal internal facet, which is likewise broader than in the existing dogs and is shaped much as in the cats, while the external distal facet is nearly or quite obsolete. The radial facet is large, quite deeply concave, and continuous or single, while in *Canis* it is much smaller and is divided by a sulcus into two portions.

The shaft of the ulna is stout and, in the proximal portion, laterally compressed, tapering toward the distal end, where it becomes trihedral in section. In shape this shaft is very much like that of the cats and differs entirely from the ulnar shaft of the recent *Canidæ*, which has become very much more slender, reduced and styliform, a change which is obviously correlated with the increased size of the radius. The distal end of the ulna in *Daphænus* is narrow and carries a continuous convex articular surface, which is not divided into separate facets for the pisiform and pyramidal. The distal radial facet is raised upon a prominent projection, another point of resemblance to the cats and of difference from the existing representatives of the *Canidæ*.

Measurements.

	No. 11424.	No. 11425.
Humerus, width of distal end		0.050
" " " trochlea		.033
Radius, ant.-post. diameter of head		.016
" transverse " " "		.021
" breadth of distal end	.022	
" " " carpal facet	.014	
Ulna, " " distal end	.013	
" " " carpal facet	.008	

V. The Manus.

Of the *carpus* the only element preserved is a single scapho-lunar of *D. vetus*, interesting as showing that the coalescence of these elements had already taken place. This bone differs in a marked way from that of both recent canines and felines, but resembles the scapho-lunar of the White River sabre-tooth, *Hoplophoneus*. It is broad transversely and thick in the dorso-palmar diameter, but very low proximo-distally, even more so than in *Canis;* the tubercle at the postero-internal angle of the bone is well marked, but smaller than in the felines or modern dogs. The radial facet is simply convex in both directions, not having the postero-internal saddle-shaped extension which occurs in the recent dogs. This radial facet is reflected far over upon the dorsal and internal surfaces of the bone, converting the inner side into a thin edge, formed by the junction of the radial and trapezial facets.

On the distal end of the scapho-lunar are three plainly distinguished facets, for the unciform, magnum and trapezoid respectively. The very deeply excavated unciform surface reduces the ulnar side of the scapho-lunar to an edge, not very much thicker than the radial border, and hence there is no well-defined facet for the pyramidal, such as occurs in *Canis*. The shape and proportions of the unciform and magnum surfaces are very much as in the latter genus, but that for the trapezoid is not demarcated from that for the trapezium, though there can be little doubt that the latter element articulated with the scaphoid, as it certainly does both in *Cynodictis* and in *Canis*. The general shape of the scapho-lunar, recalling that which we find among the mustelines, strongly suggests that *Daphænus* had a plantigrade or, at least, a semiplantigrade gait.

The *metacarpus* (Pl. XX, Fig. 17) consists of five members, which bear little resemblance to those of the recent *Canidæ*. Schlosser ('88, p. 24) has pointed out the essential characteristics of the metacarpus among the modern forms, and it will be well to quote his description, in order to make clear how widely *Daphænus* departs from the arrangement which has been attained by the later representatives of the family.

"Die Metapodien haben sich auffallend gestreckt und sind zugleich kantig geworden. Sie zeigen nahezu quadratischen Querschnitt, in Folge ihres gegenseitigen Druckes; sie liegen einander nämlich ungemein dicht an. . . . . Die distalen Gelenkflächen haben das Aussehen von sehr kurzen Walzen und sind beiderseits scharf abgestutzt. Es lässt sich eine freilich sehr entfernte Aehnlichkeit mit dem Fusse von Hufthieren, namentlich vom Schweine—nicht verkennen. . . . . Die Anordnung der Carpalien ist scheinbar primitiver als bei den übrigen Raubthieren, wenigstens als dieselben unter einander und mit den Metacarpalien nur reihenweise artikuliren, statt wechselseitig in einander zu greifen. Auch hat nur das Scapholunare eine etwas beträchtlichere Grösse erreicht, Magnum sowie Trapezoid und Trapezium bleiben sehr kurz und enden sowohl oben als auch unten sämmtlich in einer Ebene. Demzufolge liegen auch die proximalen Facetten der Metacarpalien so ziemlich in einer einzigen Ebene."

This description of the structure of the manus in the recent *Canidæ* does not at all apply to *Daphænus*. In this genus the metacarpals are remarkably short and quite slender; they are not very closely approximated, but diverge somewhat toward the distal end, and hence they have not acquired the quadrate shape which Schlosser mentions as so characteristic of the modern dogs. The general appearance and character of the metacarpals, and their mode of articulation with each other and with the carpals are very much as in the wolverine (*Gulo*).

The *first metacarpal*, even of the large *D. felinus*, is actually not much longer than that of the coyote (*C. latrans*), but is much longer in proportion to the other metacarpals, as well as much stouter and in every way better developed. The proximal end is thickened both transversely and antero-posteriorly, and bears a large facet for the trapezium, which must have been a relatively large bone; this facet is convex in the dorso-palmar direction and is very slightly concave transversely, while in *Canis* it is deeply concave in this direction. In *D. vetus* the articular surface for the trapezium is more oblique and inclined toward the radial side than in *D. felinus*. There is no other well-defined facet for any carpal but the trapezium, nor for mc. ii. The shaft is short, slender, of oval or subcircular section, and arched toward the dorsal side.

The distal end is large and has a well-developed trochlea, which is much more strongly convex than in *Canis* and of a different shape, the modern genus having here a trochlea which is more like that of a phalanx than of a typical metacarpal. In *Daphænus*, but not in *Canis*, there is a well-defined palmar carina, and the lateral processes for ligamentous attachment are more prominent than in the recent type.

The *second metacarpal* is much longer and stouter than the first, though very short with reference to the size of the animal and to the length of the other segments of the fore limb. The proximal end is not much expanded transversely, but has a great dorso-palmar extension, the head projecting much farther behind the plane of the shaft than in *Canis*. The facet for the trapezoid is less concave transversely than in the modern genus and is of more uniform width, narrowing less toward the palmar side; the ulnar border rises more above the head of mc. iii and has a more extensive contact with the magnum. Though larger than in the recent *Canidæ*, this contact with the magnum is much smaller than in existing felines, and is of about the same proportions as in the early sabre-tooth, *Hoplophoneus*. The combined facets for the magnum and for mc. iii form a broad, curved band upon the ulnar side of the head, which is made slightly concave to receive the adjoining metacarpal. No distinctly marked facet for the trapezium is visible upon the radial side. The shaft is short, weak, of transversely oval section, and is arched toward the dorsal side. The distal end is expanded, and made broad by the large, rugose processes for the attachment of the lateral metacarpo-phalangeal ligaments, processes which are much better developed than in *Canis*. The distal trochlea is of a quite different shape from that seen in the modern genus, being narrower, higher and of more nearly spherical outline, and is demarcated from the shaft by a deep depression, such as does not occur in the existing members of the *Canidæ*. The palmar carina is prominent and thins to a narrow edge.

The *third metacarpal* is incomplete in the only manus found in the collection (*D. felinus*, No. 11425, Pl. XX, Fig. 17) as it lacks the distal end. The portion preserved is, however, as long as the whole of mc. ii and the complete bone was evidently considerably longer. The shape of the proximal end is much as in *Canis*, except for the relatively greater dorso-palmar diameter. The magnum facet is narrow, but deep, somewhat concave transversely and strongly convex antero-posteriorly, but less so than in existing dogs. The facet on the radial side for mc. ii is larger, more oblique and more prominent, and is more extensively overlapped by mc. ii than in the latter, and the surface for mc. iv, while not so deeply concave, is larger. When the third and fourth metacarpals are placed together in their natural positions, it is seen that the former rises higher proximally than the latter and has a contact with the radial side of the unciform, which, though narrow, is larger than in *Canis*. The shaft is somewhat more slender than that of mc. ii and is of a more quadrate section, the dorsal and lateral surfaces forming distinct angles.

The *fourth metacarpal* has a narrow, but deep head, which projects prominently behind the plane of the shaft; the facet for the unciform is slightly concave in the transverse and strongly convex in the dorso-palmar direction. Compared with the corresponding bone of *Canis,* the following differences in the shape of the facets for the adjoining metacarpals may be observed. The surface for mc. iii is, as in the recent animals, divided into dorsal and palmar portions, but they are not completely separated; the dorsal moiety is much larger, but not nearly so prominent, and the palmar portion is much smaller. The facet for mc. v is of about the same shape in both genera. The shaft is slender and nearly straight, but slightly arched toward the dorsal side; though relatively short, it considerably exceeds mc. ii in length. The prominence of the lateral ligamentous processes gives great proportionate breadth to the distal end. The trochlea is like that of mc. ii, except for its greater size and presents the same differences from the modern type.

The *fifth metacarpal* has been lost from the specimen.

The *phalanges* are very remarkable, but can be most conveniently described in connection with the pes, with which the most complete specimens are associated.

Measurements.

	No. 11424.	No. 11425.
Scapho-lunar, breadth	0.015	
" " depth (dorso-palmar)	.011	
Metacarpal i, length	.023	.026
" breadth of proximal end	.007	.009
" " distal end	.006	
" " distal trochlea	.0045	
Metacarpal ii, length		.0395
" " breadth of proximal end		.009
" " " distal end		.012
" " " " trochlea		.009
Metacarpal iii, breadth of proximal end		.0105
Metacarpal iv, length		.050
" " breadth of proximal end		.0095
" " " distal end		.012
" " " " trochlea		.010

VI. The Hind Limb.

The *pelvis* is represented by several specimens belonging to *D. vetus*, *D. hartshornianus* and *D. felinus*, all of them incomplete, but so supplementing one another, that the shape of the os innominatum may be determined, with the exception of the anterior border of the ilium, which is unfortunately missing from all the individuals.

So far as it is preserved, the pelvis is rather feline than canine in character, both in its general outlines and in its details of structure. The neck or peduncle of the ilium is wider and shorter than in *Canis*, narrower than in *Felis;* the anterior plate expands to its full width somewhat more abruptly than in the latter, but enough of the broken fossils remains to show that the iliac plate has the narrow form which is found in the cats and does not expand so much at the free end as in the modern dogs. The gluteal surface is not simply concave, as it is in the two recent genera mentioned, but is divided into two unequal fossæ by a prominent longitudinal ridge, such as occurs, though not so prominently developed, in certain viverrines. This feature is repeated in another White River dog, *Cynodictis*, and is almost duplicated in the contemporary sabre-tooth, *Dinictis*, another of the many correspondences between *Daphænus* and the early Machairodonts. The sacral surface is placed much less in advance of the acetabulum than in *Canis*, and occupies about the same relative position as in the cats. The ischial border of the ilium is, for most of its length, nearly straight and parallel to the acetabular border, but descends more abruptly than in either the recent dogs or cats, and follows a course more like that seen in *Viverra*. As in *Canis*, the acetabular border is more distinctly defined than in the true felines, and ends near the acetabulum in a long, roughened prominence, the anterior inferior spine. The pubic border is very short, and hence the iliac surface is not well defined. The acetabulum is of moderate size and has somewhat more elevated borders than in the cats.

The ischium, which in the existing *Canidæ* is much shorter than the ilium, is very elongate, and is proportionately even longer than in the felines. The anterior portion of this element is straight, rather slender, and of obscurely trihedral section; behind the acetabulum the dorsal border is arched upward into a convexity, the spine of the ischium, terminated abruptly behind by the ischiadic notch, which is as conspicuous as in the cats, while in *Canis* it is very faintly marked. The posterior part of the ischium is expanded into a broad and massive plate, which is very rugose upon the external surface. This posterior portion is not so strongly everted and depressed as in the modern dogs, and there is no such stout and prominent tuberosity, which, again, constitutes a resemblance to the cats.

The pubis is L-shaped and its anterior, descending limb is unusually long, broad and thin, much more so than in the felines or modern dogs. The obturator foramen is very large, forming an oval, with its long axis directed antero-posteriorly, in shape and size agreeing much more closely with the condition found in the cats than with that of the recent dogs.

The *femur* (Pl. XX, Fig. 18) is stout, and long in proportion to the length of the fore-limb bones, but not very long as compared with the size of the animal. While not differing in any very marked fashion from the thigh-bone of *Canis*, it yet has some resemblances to that of the felines. The small, hemispherical head is set upon a longer neck than in recent dogs and has a smaller, deeper and more circular pit for the round ligament, than in the latter. As in *Canis*, the head projects more obliquely upward and less directly inward than in *Felis*. The great trochanter is large and has a very rugose surface, but it has no such antero-posterior extension, does not rise so high and is not so pointed as in the existing forms of *Canidæ*. In consequence of this shape of the great trochanter, the digital fossa is smaller and much shallower than in the cats or recent dogs. From the great trochanter a sharp and prominent ridge, the linea aspera externa, descends along the external border of the shaft. Whether a third trochanter was present cannot yet be definitely determined, because in the only two femora preserved in the collection, the outer edge of the shaft is broken away at the point where the third trochanter would be, if present. In all probability, however, *Daphænus* did possess this trochanter, at least, in rudimentary form, as may be inferred from the analogy of the sabre-tooth *Dinictis*, and still more from the little contemporary dog, *Cynodictis*, which in many respects approximates the structure of the modern *Canidæ* more closely than does *Daphænus*. The lesser or second trochanter is larger, more prominent, and of more decidedly conical shape than in the recent species of either *Canis* or *Felis*.

The shaft of the femur is long, slender and nearly straight, though slightly arched toward the dorsal or anterior side; it differs from that of the modern dogs in its lesser curvature, and in broadening and thickening more gradually toward the distal end, and from that of the true cats in being more slender and of more nearly cylindrical shape. The rotular trochlea is rather narrower transversely than in the true cats, or even than in *Dinictis*, but is characterized by the same shallowness, and resembles that of the latter genus in its shortness vertically and lack of prominence. Transversely, the groove is but slightly concave, and it has much less prominent borders than in the existing species of *Canis;* these borders are slightly asymmetrical, the external one rising a little higher and being a trifle more prominent than the internal. A decided difference from both *Canis* and *Felis* consists in the fact that the trochlea hardly projects at all in front of the plane of the shaft, the anterior face of the latter gradually swelling to the level of the groove. In both of the recent genera mentioned, and especially in the canines, the trochlea projects prominently in advance of the shaft.

The femoral condyles are feline rather than canine in shape; they are small and of nearly equal size, though the outer one is slightly the larger of the two, and project much less strongly behind the plane of the shaft than in *Canis.* They are also less widely separated and less expanded transversely than in the latter genus. As in so many features of the limb bones, the whole distal end of the femur is more like that of *Dinictis* than it is like the corresponding part of the modern dogs or cats. In *Dinictis,* however, the rotular groove is shorter proximo-distally and broader, and the condyles are even less prominent.

The *patella* is very different from that of the recent *Canidæ,* in which group this bone is small, narrow and thick, but has more resemblance to that of *Dinictis.* It is quite broad, but very thin in the antero-posterior dimension; the anterior face is more roughened than in the Machairodont genus and the proximal end is more pointed, not so abruptly truncated. The facet for the rotular trochlea of the femur is, in correspondence with the shallowness of that groove, but slightly convex transversely and slightly concave proximo-distally.

The *tibia* (Pl. XX, Figs. 19, 20) is relatively short and slender, and bears considerable resemblance to that of *Dinictis,* more than to that of *Canis.* The proximal facets for the femoral condyles are small and but little concave; the outer facet is somewhat larger than the inner, and projects farther beyond the line of the shaft, both posteriorly and laterally. On the distal side of the overhanging shelf thus formed is a facet for the head of the fibula, which is much larger than in the recent dogs and more rounded in shape than in *Dinictis.* The spine of the tibia is very low and is more distinctly bifid than in the Machairodont genus, though much less so than in *Canis.* As in the former, the cnemial crest is not very strongly developed; it is far less prominent than in the existing *Canidæ* and does not descend so far upon the shaft as in them.

The tibial shaft is slender and nearly straight, not displaying the lateral and antero-posterior curvatures seen in *Canis;* proximally the shaft is of trihedral section, becoming approximately cylindrical below and transversely oval at the distal end. The latter is shaped much as in *Dinictis* and is conspicuously different from that of *Canis;* the astragalar facets are less deeply incised, and the intercondylar ridge is less elevated than in the latter, but the facets are deeper and the ridge higher than in the Machairodont, in correlation with the deeper grooving of the astragalus. The large transverse sulcus, which in the recent dogs invades these astragalar facets, is not shown in *Daphænus.* The internal malleolus is very large and resembles that of *Dinictis,* save that its posterior border is more inclined and the process is thus distally somewhat narrower. The sulcus for the posterior tibial tendon is very distinctly marked, more so than in *Canis.* The distal fibular facet is quite large, being much as in *Dinictis* and consequently much larger than in the recent *Canidæ*.

The *fibula* (Pl. XX, Figs. 19, 20), which is greatly reduced in the modern dogs, is in *Daphænus* much stouter and has heavier ends, both proximal and distal. In *Canis* these ends have the appearance of being reduced and simplified from the condition seen in the White River genus. In the latter the proximal end of the fibula is relatively very large, especially in the fore-and-aft dimension, in which it considerably exceeds that of *Dinictis*, though the excess is principally due to a large tuberosity which projects from the hinder border, and which is present, though much less prominent, in the Machairodont. The facet for the head of the tibia is longer antero-posteriorly and narrower transversely than in the latter, forming a long, narrow, irregular oval. The shaft of the fibula is slender, though very much thicker both actually and proportionately than in *Canis*, and has about the same proportions as in *Dinictis;* it is laterally compressed, the principal diameter being the antero-posterior one, and of oval section, though its size and shape vary from point to point in an irregular fashion.

The distal end of the fibula resembles that of *Dinictis*, though it is somewhat smaller, in proportion to the length of the bone. The enlargement is both antero-posterior and transverse and gives rise to a very stout outer malleolus, at the postero-external angle of which is a deep sulcus for the peroneal tendons. The distal tibial facet is rather larger than that of *Dinictis*, while the surface for the astragalus is somewhat smaller, the two together making a high narrow band.

Measurements.

	No. 11421.	No. 11424.	No. 11423.
Femur, length (fr. head)			0.195
" breadth of proximal end			.044
" " distal end			.038
" " rotular groove			.014
Tibia, length		.149	
" breadth of proximal end		.031	.036
" " distal end	.021	.021	.025
Fibula, ant.-post. diameter prox. end			.019
" " " dist. "	.0145		.017

VII. The Pes (Pl. XX, Figs. 21, 21*a*, 22).

The *pes*, which displays structures of the highest interest, is much better represented in the collection than the manus and may be more adequately described. As a preliminary, it will be useful to cite Schlosser's account of the salient characteristics of the hind foot among the recent *Canidæ.*

"Die Anordnung der Tarsalien und Metatarsalien weicht natürlich weniger ab von jener der übrigen Carnivoren als jene der Carpalien und Metacarpalien, doch finden wir auch hier immerhin einige nicht unwesentliche Modificationen. Es hat sich das Naviculare ziemlich beträchtlich verschmälert, so dass es nicht mehr die Aussenseite der unteren Astragalus-Partie umhüllen kann. Das Metatarsale II, das sonst nur von zwei Punkten mit dem Mt. III in Berührung kommt, legt sich hier seiner ganzen Breite nach an das Oberende desselben. In Folge der Verkürzung des Tarsus ist auch der aufsteigende Fortsatz des Mt. V sehr kurz geworden. Die Phalangen haben gleich den Metapodien nahezu quadratischen Querschnitt, die Krallen sind sehr spitz, aber wenig gebogen, haben jedoch ziemlich bedeutende Länge. Die Hunde sind die ausgesprochensten Zehengänger unter allen Carnivoren" ('88, p. 22).

In *Daphænus* the *astragalus* is decidedly different both from the astragalus of *Dinictis* and from that of *Canis,* but approximates more the latter. The trochlea is low and but moderately grooved, decidedly more than in *Dinictis,* but less than in the modern dogs, and the articular surface does not descend so far upon the neck as in the latter. The trochlea is asymmetrical, the outer condyle considerably exceeding the inner in size. The neck of the astragalus is much longer than in *Hoplophoneus, Dinictis,* or even than in *Canis,* and is directed more strongly toward the tibial side of the foot; the head is depressed, but very convex. The external calcaneal facet is hardly so large or so oblique in position as in *Dinictis,* but it is more like the facet seen in that genus than like the facet of *Canis.* The sustentacular facet is shorter and wider than in the latter, and the sulcus separating it from the external facet is very much shallower. In *Dinictis* the sustentacular facet has a posterior concave prolongation, such as is not found in *Daphænus,* nor does the latter possess the distal accessory facet for the calcaneum which is so distinctly shown in *Canis.* The navicular facet is depressed, but very convex, and there is a small facet for the cuboid.

The *calcaneum* is more like that of *Dinictis* than that of the recent dogs; though the tuber calcis is longer, thinner and more compressed than in either of those groups, and its dorso-plantar diameter is more uniform, increasing less toward the distal end; its free end is less thickened and more deeply grooved by the sulcus for the Achilles tendon. Along the outer edge of the dorsal border is a quite deep and conspicuous groove, which occurs also in *Dinictis,* but not in *Canis.* The external astragalar facet is very like that of the Machairodont, being more angulated and more oblique in position than in the modern dogs, presenting inward as much as dorsally. The sustentaculum also resembles that of *Dinictis* in being less oblique, much more prominent and in having its facet much more widely separated from the external astragalar facet than in *Canis*. In the latter genus occurs a third astragalar facet, which is distal to the sustentaculum, and which is found in neither *Dinictis* nor *Daphænus*. The distal end of the calcaneum is occupied by the large cuboidal facet, which is more regularly oval in outline and much more deeply concave than in the existing forms of *Canidæ*. In these forms we find a facet for the navicular, which adjoins and forms a right angle with the accessory astragalar surface already mentioned, but is not present in either of the White River genera. On the external side of the calcaneum, near the distal end, is a prominent projection for ligamentous attachment. This process is not present in *Canis*, but it recurs in *Dinictis*, less markedly in *Hoplophoneus*, and is found in many of the recent viverrines, mustelines and raccoons.

The *cuboid* is not peculiar in any noteworthy way; it is longer proximo-distally than in *Dinictis* and is proportionately narrower and thinner (*i. e.*, in the dorso-plantar diameter). The long, thick and rugose ridge which on the fibular side of the bone overhangs the sulcus for the peroneal tendons is more prominent, especially on the plantar face, than in the Machairodont, but lacks the great, rugose plantar protuberance, which occurs in the recent *Canidæ*. The facet for the calcaneum is more convex than in *Dinictis*, very much more so than in *Canis*, in which this surface is almost plane. On the tibial face of the cuboid are three facets, a narrow proximal one for the navicular, and a median and minute distal facet for the ectocuneiform. The facet for the head of the fourth metatarsal is very much more concave than in the modern dogs, while that for mt. v is smaller than in the recent forms, and lateral rather than distal in position.

The *navicular*, as compared with that of *Canis*, is short proximo-distally, but broad transversely, not having undergone the reduction in width which Schlosser mentions as characteristic of the recent members of the family. The astragalar facet is not more concave than in the latter, and there is no such stout tubercle on the plantar side of the bone as occurs in them. Two very small facets articulate with the cuboid, one near the dorsal and the other near the plantar border of the fibular side. The distal facets for the three cuneiforms have nearly the same shape and proportionate size as in *Canis*, but they are more in the same transverse line, the surface for the entocuneiform being less displaced toward the plantar side.

The *entocuneiform* is of similar shape, but relatively better developed than in *Canis*, as would naturally be expected from the presence of a complete hallux in *Daphænus*. The bone is long proximo-distally, thick antero-posteriorly, and narrow, though broader than in *Canis*, and its proximal and distal facets, for the navicular and first metatarsal respectively, are relatively larger and more concave. The only other facet is an obscurely marked one on the tibial side for the mesocuneiform.

The *mesocuneiform* is a very small, wedge-shaped bone, broadest dorsally and thinning to an edge on the plantar side. The navicular facet is concave and very different from the curious oblique surface which we find in *Dinictis*. As is well-nigh universal among the Carnivora, the proximo-distal diameter of this bone is much less than that of either of the two adjoining cuneiforms, an arrangement which allows the head of the fourth metatarsal to rise above the level of the first and third.

The *ectocuneiform* is, as usual, much the largest of the three, though it is not so large proportionately as in *Dinictis*. The shape of this element is very much as we find it in *Canis*, but with certain minor differences. Thus, the proximal end is less extended in the dorso-plantar diameter, and the navicular facet is more concave; the plantar tubercle has a more constricted neck and enlarged, rugose head; the facets on the tibial side for the mesocuneiform and second metatarsal, and on the fibular side the inferior facet for the cuboid are more distinctly developed, while the distal facet for mt. iii is more concave and has a shorter plantar prolongation.

As a whole, the character of the tarsus is rather more machairodont, or viverrine, than canine. A conspicuous difference from the tarsus of the modern *Canidæ* is to be seen in the fact, that the articulations which in the latter are nearly plane (*e. g.*, the cubo-calcaneal) in *Daphænus* retain their more primitive concavo-convexity.

The *metatarsus* consists of five members, which are longer and relatively more slender than the metacarpals, though an exact comparison between the two cannot yet be made, because the collection contains no specimens in which both metacarpals and metatarsals are represented by anything more than fragments.

The *first metatarsal* is considerably longer and stouter than the corresponding metacarpal. In this case we can determine the true proportions, for of the species to which the finely preserved hind foot (Pl. XX, Fig. 21) belongs, *D. hartshornianus*, we also possess a pollex, though associated with a different specimen. The almost exactly similar skulls of the two individuals show that the animals were of approximately equal size. The head of mt. i is enlarged in both the transverse and dorso-plantar diameters, and bears a roughened tubercle upon the plantar side. The proximal facet, for the entocuneiform, is large, and strongly convex antero-posteriorly, nearly plane transversely; no other facets are visible on the proximal end. The shaft is slender and arched toward the dorsal side; in section it is transversely oval, expanding somewhat at the distal end, where the breadth is increased by the prominent tubercles for the lateral ligaments. The distal trochlea is small, but well developed, and of irregularly spheroidal shape, with plantar carina. The first metatarsal of *Dinictis* is like that of *Daphænus*, and certain viverrines, such as *Cynogale*, also have a hallux of much the same proportions, but in all the recent *Canidæ*, with the exception of certain domesticated breeds, mt. i is reduced to a nodule.

The *second metatarsal* is much longer and stouter than the first, but it is much shorter and weaker than mt. ii in *Canis*, and rather resembles that of the viverrine genus *Cynogale*, though it does not have the peculiar shape of the proximal end which characterizes that genus. In *Dinictis* mt. ii is somewhat heavier than in *Daphœnus*, but is otherwise similar. In the latter the proximal end of mt. ii rises considerably above the level of mt. i and iii, owing to the shortness, proximo-distally, of the mesocuneiform, and is firmly wedged in between the ento- and ectocuneiforms, an arrangement common to all families of the fissipedes and already general among the creodonts. On the fibular side is a wedge-shaped projection which is received into a corresponding depression on mt. iii, thus making a very firm and close connection between the two bones. Above this projection are two facets for the tibial side of the ectocuneiform, one near the dorsal border and the other on the plantar projection. The shaft is straighter than in *Canis*, but is slightly arched dorsally, the distal end not curving toward the tibial side, as it does in the modern genus. In section the shaft is transversely oval, while in the recent dogs it has become trihedral for most of its length, owing to its close approximation to the shaft of mt. iii. The distal trochlea resembles that of *Dinictis* and differs from that of *Canis* in its more spheroidal and less cylindrical shape, and in its demarcation from the shaft by a deep depression; the lateral ligamentous processes are likewise more symmetrically developed.

The *third metatarsal* is much longer and stouter than the second, the difference between the two being greater than in *Dinictis* or the viverrines, or even than in *Canis*. The proximal end bears a facet for the ectocuneiform, of the usual shape, but the plantar prolongation of this facet is shorter and broader than in the last-named genus, and it resembles that of *Dinictis* in being oblique to the long axis of the bone, inclining decidedly toward the tibial side of the foot. The tibial side of this facet is deeply incised to receive the wedge-shaped prominence of mt. ii, an incision which does not appear in the recent dogs, but occurs, though somewhat less conspicuously, in *Dinictis*. On the fibular side are two facets for mt. iv; one near the dorsal border, which is a deep spherical pit, and the other a small, plane surface placed upon the plantar prolongation of the head. The shaft, when viewed from the front, appears quite straight, but when looked at from the side is seen to have a slight curvature toward the dorsal side. The distal end displays the same differences from *Canis* as do the other metatarsals.

The *fourth metatarsal* forms a symmetrical pair with the third, very much as it does in the recent dogs and cats, though in *Daphœnus* they are relatively shorter and weaker. In *Canis* these two metatarsals are closely pressed together for most of their length, and their shafts have thus acquired a more or less trihedral section, with the approximate surfaces flattened, while the distal ends curve away from each other, somewhat as in

Poebrotherium. In *Daphænus* it is only the proximal portions of the two shafts which are thus closely pressed together; for the greater part of their length they are not in contact, and thus preserve the primitive oval section. As their divergence is due to the relative positions of the tarsal bones, there is no necessity for the lateral curvature of the distal ends. The two metatarsals are very closely interlocked and in much the same fashion as in *Canis.* On the head of mt. iv are two facets for mt. iii, of which the dorsal one is a stout hemispherical prominence, which is received into the pit on the head of mt. iii, already described. The plantar facet is actually upon the plantar rather than on the tibial face of the bone; the prolongation from the head of mt. iii extends around and embraces this facet, and by means of the double articulation a very firm interlocking of the two bones is effected. On the fibular side of mt. iv is a large and deep depression which receives the projection from mt. v. The facet for the head of the latter is large, slightly concave, and continues without interruption from the dorsal to the plantar border, while in *Canis* there are two distinct and quite widely separated facets. The shaft resembles that of mt. iii, but is somewhat more slender. In both of these metatarsals the distal carina is placed symmetrically with reference to the trochlea, but is less compressed and prominent than in *Canis.*

The *fifth metatarsal* is not completely preserved in any of the specimens, the only representative of it being the proximal end, belonging to a large individual of *D. vetus* (No. 11423). As the specimen is incomplete, nothing can be determined respecting its length, but probably this was equivalent to that of mt. ii, the two forming a symmetrical pair, much as in *Dinictis,* though mt. v, so far as it is preserved, seems to be somewhat the stouter of the two. On the fibular side of the head is a very prominent projection, ending in a roughened thickening, and directed obliquely outward and upward, the "ascending process" (aufsteigender Fortsatz) of which Schlosser speaks in the passage already quoted. In the recent dogs this process is very much reduced, while in *Dinictis* it is of quite a different shape. In the Machairodont the process is a long and prominent ridge, extending along the whole dorso-plantar thickness of the head, and projects much more proximally than externally, while in *Daphænus* it is a blunt hook which projects more outward than upward. The Machairodont *Hoplophoneus* has the process developed in very much the same way as in *Daphænus.*

The facet for the cuboid differs from that of *Canis* in being quite concave transversely and in presenting as much toward the tibial side as it does proximally, while in the modern genus the facet is small, plane, subcircular in outline and altogether proximal in position. On the tibial side is a rounded protuberance which fits into the pit on the head of mt. iv; this protuberance is more prominent than in *Canis* and decidedly more so than in *Dinictis.* What little of the shaft is preserved is transversely oval in section, with a sharp ridge running down the fibular side, and is thus quite different from the trihedral section, with flattened tibial side, which is found in *Canis*, and is much more like the corresponding metatarsal of *Dinictis*.

The parallel arrangement of the metatarsals which we observe in the modern *Canidæ* is in *Daphænus* replaced by a radiating arrangement, the bones diverging toward the distal end. This distal divergence is, however, less decided in the pes than in the manus.

The *phalanges* display a very curious and surprising combination of characters. They are long, both actually and proportionately; compared with the tibia as a standard, they have about the same length as in the recent species of *Canis*, but they are decidedly longer than in that genus when compared with the length of the metatarsals.

A *proximal phalanx* of one of the median digits is long and depressed, but quite strongly arched upward or dorsally. The metatarsal facet has quite a different shape from that seen in *Canis*, the transverse diameter being relatively greater and the dorso-plantar less. The facet is also somewhat more oblique to the long axis of the phalanx, presenting rather more dorsally and less entirely proximally; the notch for the metatarsal carina is less deeply incised. Similar differences are observable in the body of the bone; its breadth being proportionately greater and its thickness less. The distal trochlea, which in *Canis* describes a semicircle from the dorsal to the plantar surface, is in *Daphænus* much more restricted, projecting less prominently from the plantar side and not reflected so far upon the dorsal face. On the other hand, this trochlea is more deeply cleft in the median line than in the modern genus and the tubercles for the attachment of the phalangeal ligaments are larger.

In all the differences from the modern *Canidæ* which have been mentioned, we may observe resemblances to the corresponding phalanx of *Dinictis*, in which the bone is somewhat shorter and broader than that of *Daphænus*, and has rather more prominent ligamentous tubercles, but is otherwise very like it.

The proximal phalanges of the lateral digits differ from those of the median pair only in being shorter, more slender and less symmetrical, and in having a lateral curvature which becomes very pronounced in the hallux.

The *second phalanx* is of about the same length, with reference to the first, as in *Canis*, but is broader, more depressed, and more asymmetrical than in that genus. The proximal facet, for the first phalanx, is more distinctly divided into two depressions by a more prominent median ridge, and the beak-like process of the median dorsal border is much more pronounced. The distal trochlea is reflected farther upon the dorsal side and projects more from that side, but extends less upon the plantar face; it is thus more convex in the dorso-plantar direction, but much less concave transversely than in *Canis*.

The asymmetry of this phalanx is quite marked: its tibial side is straight, while the fibular border is quite concave, and the dorsal surface is hollowed, or cut away, near the distal end, *allowing a retraction of the claws, to a limited extent,* as may be readily seen when the second and third phalanges are put together. This asymmetry of the second phalanx is much less conspicuous than in *Dinictis*, not to mention the modern felines, but it is, nevertheless, unmistakable and is certainly one of the most surprising features in the whole structure of *Daphænus.*

That an animal with the skull and dentition of a primitive dog should prove to possess even imperfectly retractile claws is not what our previous knowledge of the early carnivores would have led us to expect. So unlooked for was this character, that at first I was strongly inclined to believe that the association of the hind foot shown in Pl. XX, Fig. 21, with the skull of *D. hartshornianus* was an accidental one, and that the pes must belong to some genus of felines or Machairodonts as yet unknown. Fortunately, however, the collection contains a number of other individuals with more or less well-preserved hind feet, and the agreement among them all is complete. Curiously enough, the characteristic second phalanges are preserved only in connection with the specimen figured, but other specimens have parts of the tarsus, metatarsus, proximal and ungual phalanges, and a comparison of them shows that the reference of this particular hind foot is not open to question. The fact that the pes and the skull were found enclosed in the same block of matrix corroborates this inference, though, of course, such a fact is not of itself entirely conclusive.

The *ungual phalanx* is hardly less peculiar than the second, being short, very much compressed laterally, and bluntly pointed; it is very little decurved and has a plainly marked groove on the plantar face near the distal end. The narrowness, compression and straightness of this claw are in very decided contrast to the heavy and strongly decurved ungual phalanges of the modern *Canidæ*, though among the latter there is considerable variation in these respects. The articular surface for the second phalanx is much more strongly concave than in *Canis*, permitting a greater freedom of motion in this joint, as was necessary in order to provide for the retraction of the claw. The subungual process is not so large as in the modern genus and does not project so prominently upon the plantar face of the bone, but it is produced much farther proximally, extending beneath the distal end of the second phalanx, when the two are in their natural position. The long hood which envelopes the base of the claw is of about the same size and shape as in *Canis*, though the space between this hood and the body of the ungual phalanx is narrower. The ungual phalanx of *Dinictis* is shorter, more compressed, but deeper in the dorso-plantar diameter than in *Daphænus*, and has a decidedly larger subungual process, in correlation with the more complete retractility of the claws. The few specimens of these phalanges which I have seen are without the bony hood around the base of the claw, having much the appearance of the unguals in the viverrine genus *Cynogale*. It is possible that the apparent absence of the hood may be due to the breaking away of that delicate structure, but this does not seem very likely.

Measurements.

	No. 10546.	No. 11421.	No. 11424.	No. 11423.	No. 11425.
Calcaneum, length	0.045	0.044		0.051	0.055
" dorso-plantar diameter	.016	.015		.020	.020
" length of tuber	.031	.029		.036	.040
" extreme distal breadth	.017	.017		.022	.022
Astragalus, length		.027		.031	.031
" proximal breadth		.018		.021	.022
" width of head		.014		.016	.019
Cuboid, height		.015	.016		
" width		.011	.012		
Navicular, width		.017		.019	
Ectocuneiform, width		.010		.010	
Metatarsal i, length		.031			
" breadth prox. end		.009		.010	
" " dist. "		.007			
Metatarsal ii, length		.041			
" breadth prox. end		.006		.007	
" " dist. "		.009			
Metatarsal iii, length		.051			
" breadth prox. end		.009		.011	
" " dist. "		.0105			
Metatarsal iv, length		.056			
" breadth prox. end		.006			
" " dist. "		.010			
Metatarsal v, breadth prox. end				.011	

The species of *Daphænus* hitherto recognized are three in number, two of them, *D. vetus* Leidy and *D. hartshornianus* Cope, from the White River stage, and the third, *D. cuspigerus* Cope, from the John Day. Two additional species are described in the sequel, one of which, however, can be referred only provisionally to the genus, until more complete material has been obtained, though the species in question is evidently very closely allied to *Daphænus*, if not actually referable to it.

DAPHÆNUS VETUS Leidy.

Daphænus vetus Leidy, *Proc. Acad. Nat. Sci. Phila.*, 1853, p. 393. *Amphicyon vetus* Leidy, *ibid.*, 1854, p. 157; 1857, p. 90. *Extinct Mamm. Fauna of Dakota and Nebraska*, pp. 32, 369. Cope, *Tertiary Vertebrata*, p. 896.

This species has a skull about equal to that of the coyote (*Canis latrans*) in size, but the vertebræ are much larger and the tail is longer and stouter. The tubercular molars of both jaws are relatively larger than in the other species. The inferior sectorial has a low anterior blade, and the internal cusp of its talon is reduced in size. The horizontal ramus of the mandible is long and slender and has a nearly straight inferior border. White River.

Daphænus hartshornianus Cope.

Daphænus vetus Leidy, *Amphicyon vetus* Leidy, in part, *loc. cit.* *Canis hartshornianus* Cope, *Synopsis New Vert. from Colorado*, 1873, p. 9. *Ann. Rept. U. S. Geolog. Surv. Terrs.*, 1873, p. 505. *Amphicyon hartshornianus* Cope, *Tertiary Vertebrata*, p. 896.

This species is somewhat smaller, and the tubercular molars of both jaws are proportionately smaller than in the preceding species; the anterior triangle of the lower sectorial is high and acute, and its talon is basin-shaped, with the internal cusp as large as the external. The horizontal ramus of the mandible is straight and slender. Both this species and the preceding one have been found in the middle division (Oreodon beds) of the White River formation, but not as yet, to my knowledge, in the lower (Titanotheriam beds) or the uppermost division (Protoceras beds).

Daphænus cuspigerus Cope.

Canis cuspigerus Cope, *Proc. Amer. Phil. Soc.*, 1878, p. 70. *Amphicyon entoptychi* Cope, *ibid.*, 1879, p. 372. *Amphicyon cuspigerus* Cope, *Bull. U. S. Geolog. Surv. Terrs.*, Vol. VI, p. 178; *Tertiary Vertebrata*, p. 898.

D. cuspigerus is much the smallest known species of the genus. The sagittal crest is very short and inconspicuous; the cranium is fuller and more rounded, the postorbital constriction is shallower and more anterior in position than in the White River species, and the mandibular ramus is nearly straight and very slender. The inferior sectorial is very robust and has a low anterior triangle and basin-shaped heel. John Day stage.

Daphænus felinus, sp. nov.

The inferior dental series of this species slightly exceeds in length that of *D. vetus* and the sectorial is larger. The lower tubercular molars are inserted in the border of the ascending ramus of the mandible, and, judging from the alveoli, were reduced in size. The horizontal ramus is not much longer, but much heavier than in *D. vetus*, and has a more sinuous ventral border, which rises more beneath the masseteric fossa. The limb bones and vertebræ are somewhat larger and heavier than those of *D. vetus*, and the neural spines of the lumbar vertebræ are very high and incline strongly forward. In size *D. felinus* is the largest and most massive species of the genus. The type specimen consists of a fragmentary skeleton (No. 11425) with which are associated both mandibular rami, and which was found by Mr. Gidley in the Oreodon beds of Hat Creek Basin, Neb., in 1896.

? Daphænus Dodgei, sp. nov.

As already intimated, the reference of this species to *Daphænus* cannot yet be definitely made, but the material so far obtained, consisting of lower jaws, affords no sufficient ground for separating it from that genus. The inferior dental series is relatively short; the premolars are much smaller, especially in the antero-posterior dimension, than those of the later species from the Oreodon beds, but, at the same time, they are proportionately thick and heavy. The lower sectorial has a low, massive anterior triangle and a basin-shaped talon, with the inner cusp much smaller than the outer. The horizontal ramus of the mandible is short, but relatively much stouter than in any of the other species, and has a more sinuous ventral border, which rises steeply toward the angle.

This species is dedicated to my friend, Mr. Cleveland H. Dodge, of New York, whose liberality has made possible much of the work undertaken by the Princeton Museum and to whose kindness I am under the greatest obligations.

The type specimen (No. 11422) was found by Mr. Gidley in the Titanotherium beds of the Hat Creek Basin.

Before proceeding to an examination of the next genus of White River *Canidæ*, *Cynodictis*, it will be necessary to introduce a brief description of a species which has been found in the Uinta stage of the upper Eocene (or lower Oligocene) and which apparently represents the forerunner of *Daphænus*, though more perfect specimens will be required before its position in the canine phylum can be definitely determined.

MIACIS Cope.

This form differs from *Daphænus* in the construction of the upper tubercular molars. M [1] has an exceedingly broad external cingulum, forming at the antero-external angle a very large projection; the internal unpaired cusp found in *Daphænus* and in all subsequent genera of the *Canidæ* is absent in both $m^{\underline{1}}$ and $m^{\underline{2}}$. The upper sectorial is of very primitive and undeveloped character in the shortness of the posterior cutting ridge and the great transverse breadth of the crown.

Miacis uintensis Osborn.

Bull. Am. Mus. Nat. Hist. N. Y., Vol. VII, p. 77.

Size rather less than that of *D. hartshornianus*; upper sectorial relatively small and tubercular molars large; premolars short and thick.

Measurements.

	MM.
Length, p^3 to m^2 inclusive	37
P^3 length	7
P^4 length	11
P^4 width	11
M^1 length	11
M^1 width	16
M^2 length	9
M^2 width	7.5

Fig. A.—First upper molar of the left side:
1, of ? *Miacis uintensis*. 2, of *Daphænus hartshornianus*. 3, of *Canis latrans*. *x*, cusp usually regarded as the protocone.

If *Miacis* be rightly regarded as having a place in the canine phylum, then the structure of its upper tubercular molars is of great interest and will require a revision of the current views concerning the homologies of the cusps in the upper molars of the dogs. In *Canis*, according to the usual interpretation, m^1 is composed of two external cusps, the para- and metacones, and at the apex of the triangle of which the para- and metacones form the base, an unpaired internal cusp, the protocone, with the proto- and metaconules on the anterior and posterior sides of the triangle respectively. Internal and somewhat posterior to the protocone is a large crescentic cusp, which is commonly regarded as an enlargement of the cingulum, although in unworn teeth a faint cingulum may be traced all around this crescentic cusp and is continuous with the prominent cingulum which bounds the anterior wall of the crown. If this interpretation of the cusps be correct, and further, if *Miacis* is ancestral to the *Canidæ*, them m^1 in the Uinta genus *is without a protocone* and has only the para- and metacones, minute conules and the large inner crescentic cusp. It seems much more rational to conclude that the latter is really the protocone and that the cusp which has been so named in *Canis* is an additional element subsequently developed. In *Daphænus* this inner crescentic cusp and the conules are relatively smaller than in the modern representatives of the family, which goes to confirm the conclusion that the name protocone should be given to the innermost cusp and that in *Canis* the middle part of the crown has undergone a special increase in complexity.

CYNODICTIS Gervais.

Amphicyon Leidy, Marsh, in part. *Canis* Cope, in part. *Galecynus* Cope, *non* Owen.

It is with much hesitation that I employ the name of this European genus for North American species, for there are certain constant differences which Schlosser ('88,) appears to consider as being of generic value. An actual comparison, however, of the American forms with specimens of *Cynodictis lacustris*, Gervais' type species, and from the typical locality, Débruges, has failed to reveal any important differences between the two, and, therefore, for the present at least, I retain the name of the European genus for the American species, which are very closely allied, if not positively referable to it.

The structure of these small carnivores, especially of the John Day species, is much better known than that of *Daphænus*, though our knowledge of the White River species has hitherto remained very incomplete, and even of the better known John Day forms only Cope's brief descriptions have as yet been published. Despite the fact that *Cynodictis* is one of the commoner White River fossils, well-preserved specimens are comparatively rare and of these the greater part consist only of skulls. The bones of the skeleton are so small and so fragile that it is exceedingly difficult to obtain more than fragments of them. By dint of great care and attention paid to these small forms, Messrs. Hatcher and Gidley have succeeded in gathering some very fine specimens for the Princeton Museum, and others I owe to the kindness of Mr. John Eyerman. Together, these various individuals represent nearly all parts of the skeleton and enable us to reconstruct the animal and to compare it with the better preserved and more abundant species of the succeeding John Day formation.

I. *The Dentition.*

The dental formula of *Cynodictis* is: I $\frac{3}{3}$, C $\frac{1}{1}$, P $\frac{4}{4}$, M $\frac{2}{3}$, differing from that of *Daphænus* only in the absence of the third upper molar.

A. *Upper Jaw.*—The incisors are very small, simple and antero-posteriorly compressed, giving them chisel-shaped crowns; they increase in size from the first to the third, but the latter does not greatly exceed the others; not nearly so much, for example, as in *Canis* or *Daphænus*, and hardly more than in the viverrines. A very short diastema separates the lateral incisor from the canine.

The canine has a stout, gibbous fang, which produces a marked convexity upon the side of the maxillary; its crown is quite elongate and somewhat recurved and much compressed laterally. The tooth is relatively smaller than in the recent dogs and thinner transversely, and has therefore quite different proportions from those seen in *Daphœnus.*

The premolars increase in size posteriorly ; in the unworn condition they have high, compressed, thin and very acute crowns, but in old individuals, without showing much appearance of wear, these teeth have low crowns, elongated in the fore-and-aft direction. The first premolar is very small and simple ; it is inserted by a single fang and follows immediately behind the canine, without a diastema, which is a difference from *Daphœnus.* The second premolar is much larger than p $\frac{1}{}$; it is implanted by two fangs and has a perfectly simple crown, without posterior basal tubercle, though the cingulum is thickened at that point. The third premolar is still larger, especially in the vertical height of the crown, and is distinguished by the presence of a posterior tubercle in addition to the thickening of the cingulum already found in p $\frac{2}{}$. The fourth premolar is a very effectively constructed, though small, sectorial blade, being much more compressed and trenchant than in *Daphœnus.* The anterior cusp of the shearing blade (protocone) is relatively higher and thinner and has a sharper point and edge than in the latter genus, and the posterior cutting ridge (tritocone) is better developed and more efficient. On the other hand, the internal cusp (deuterocone) is very much smaller (hardly larger proportionately than in *Canis*) and occupies a more posterior position. In the European species of *Cynodictis* the deuterocone is not so much reduced and is placed as far forward as in *Daphœnus.*

The first molar is large, particularly in the transverse dimension, and is of subquadrâte outline. The outer cusps are high and quite acutely pointed, and the central cusp (usually called the protocone) is lower and of crescentic shape, and the internal cusp is a broad, crescentic shelf, which occupies about the same position as in *Canis.* The conules are very small, but of nearly equal size, a difference from the modern genus, in which the metaconule is large, while the protoconule is rudimentary or absent, and even in *Daphœnus* the posterior conule is much the larger of the two. The cingulum is very prominently developed upon the outer side of the tooth and forms a large projection at the antero-external angle, as in *Daphœnus,* though not in *Canis,* a reminiscence of creodont ancestry.

In the John Day species, *C. geismarianus* and *C. lemur* and still more in *C. latidens,* the first upper molar has a much more distinctly quadrate crown, due to the enlargement of the metaconule, which has become as large as the central cusp, and to the more symmetrical development of the internal cusp (? protocone). In the typical European species, *C. lacustris,* on the contrary, the crown of this tooth retains a more trigonodont character.

The second molar is very small, being relatively much more reduced than in *Daphœ-*

nus. It is composed of the same elements as m $\frac{1}{}$, but has a different shape, owing to the greater proportionate length, antero-posteriorly, of the inner portion of the crown. In appearance this tooth is a miniature copy of that of *Canis.*

B. *Lower Jaw.*—The incisors are very small and closely crowded together, so that the fang of i $\overline{2}$ is pushed back out of line with the other two.

The canine, which is even more compressed laterally than the upper one, is long and recurved; it is separated from p $\overline{1}$ by a very short diastema.

The first premolar is a very small, simple cone, inserted by a single fang. The second is much larger and is supported by two roots; it has an anterior basal cusp, which is formed by the cingulum and is subject to considerable variation, being much larger in some individuals than in others. The third premolar has a high, compressed and sharp-pointed crown and bears three accessory cusps, anterior and posterior basal cusps formed by the cingulum, and a third developed upon the posterior edge of the protoconid, very much as in *Canis.* The fourth premolar is slightly larger than p $\overline{3}$ and has more distinctly developed accessory cusps, but on both p $\overline{3}$ and p $\overline{4}$ these cusps are subject to much variation and in some specimens they are feebly marked or even absent.

The European *C. intermedius* has very similar premolars to those of *C. gregarius,* and in both species the anterior basal cusps (which are not present in *Daphænus*) give a somewhat viverrine character to the dentition.

The first molar has a quite elevated anterior triangle, with a high, pointed protoconid and a well-developed paraconid, both of which are more compressed and trenchant than in *Daphænus.* The metaconid is smaller than in the latter and is placed lower down and more posteriorly, so that it is visible from the outer side, much as in the modern dogs. The heel is basin-shaped and is composed of a large, crescentic external cusp and a smaller internal cusp. In the European species may be observed certain differences in the structure of the lower sectorial from the White River form, though these differences are not great. In the Old World species the anterior triangle is higher and the protoconid less compressed, while the metaconid is larger and occupies a more elevated and anterior position; in other words, the anterior triangle resembles that of *Daphænus.* Another difference from the American forms consists in the presence of a second internal cusp in the heel of the sectorial, which may be observed in most of the individuals figured by Schlosser and Filhol. However, in a specimen of *C. lacustris* from Débruges, which the Princeton Museum owes to the courtesy of Prof. Gaudry, this second cusp is not visible. In perfectly unworn teeth of *Daphænus hartshornianus* a feeble indication of this second cusp may be seen.

The second molar is tubercular and of a narrow and elongate oval shape; in constitution it entirely resembles that of *Canis;* the paraconid has disappeared, while in

Daphænus it is still distinctly visible, though very small. The proto- and metaconids are of equal size and placed on nearly the same transverse line; these cusps are higher, more sharply pointed and more slender than in the recent *Canidæ*. The talon, which is somewhat lower than the anterior half of the tooth, retains a distinctly basin-like form. In the European species we find a more primitive character of m $\overline{2}$ in the retention of the paraconid. The third molar is very small; it has an oval, roughened crown and is carried upon a single fang. As Cope has pointed out, this tooth is usually missing in the fossils, and occasionally a specimen is found which has not even an alveolus for it.

The dentition of *Cynodictis gregarius* is, on the whole, a little more modernized and advanced than that of the European representatives of the genus. This advance is shown in the reduction of the inner cusp of the upper sectorial; in the somewhat more quadrate outline of m $\frac{1}{}$; in the less elevated shearing blade and more posterior position of the metaconid on the lower sectorial, and, finally, in the more complete reduction of the paraconid of m $\overline{2}$. In the John Day species, especially in *C. geismarianus* and *C. latidens*, the departure from the European type is even more marked.

Measurements.

	No. 10493.	No. 10513.	No. 10939.	No. 11012.	No. 11382.	No. 11432.
Upper dentition, length I 1 to M 2			0.014	0.044	0.0435	0.0435
Upper canine, ant.-post. diameter			.005	.005	.005	.0045
" " transverse "			.0035	.003		.003
" premolar series, length			.025		.023	.025
" molar series, length	010	.010	.011	.010	.010	.010
" P 1, length			.0035	.003	.003	.003
" P 2, "	.005		.0045	?.004	.0045	.003
" P 3, "	.0055		.005			.0055
" P 4, "	.010	.009	.009	.0095	.0085	.009
" P 4, breadth	.006		?.004	.0055	.005	
" M 1, length	.0065	.007	.006	.006	.006	.006
" M 1, breadth	.009		.008	.008		
" M 2, length	.0035	.003	.004	.004	.003	.003
" M 2, breadth	.006		.006	.0055	.004	.005
Lower premolar series, length				.021	.019	
" molar series, length	.017	.016		.017	.015	
" P 1, length				.003	.003	
" P 2, "			.005	.005	.004	
" P 3, "	.0055		.005	.006	.005	
" P 4, "	.0065	.007	.006	.0065	.006	
" M 1, "	.010	.0095	.0095	.010	.009	
" M 2, "	.005	.005	.005	.005	.0045	
" M 2, breadth	.003		.003	.0035		

II. The Skull (Pl. XIX, Figs. 11, 12).

The skull of *Cynodictis* is decidedly primitive and in general appearance resembles that of such viverrine genera as *Paradoxurus*, rather than that of the modern *Canidæ*. Among the latter the alopecoid series have skulls more resembling the type of *Cynodictis* than do the thooids, though the Brazilian bush-dog (*Icticyon*) is, on the whole, most like the fossil in the proportions of its skull.

In *Cynodictis*, as in *Daphænus*, the facial or preorbital region of the skull is very short and the cranial portion very long. The occiput is low and the upper contour of the skull rises steeply from the inion to about the middle of the parietals, whence it descends in an almost straight line to the anterior nares, the only departure from straightness being a hardly noticeable concavity or "dishing" of the nasals about midway in their length. In *Vulpes* the profile is quite similar, but the posterior rise from the occiput is much shorter and less steep, and the dishing of the nasals is more conspicuous. The sagittal crest is low and weak, and in the John Day *C. lemur*, the smallest species of the genus, the crest is replaced by a lyrate sagittal area. The cranium, though slender, elongate and contracting anteriorly, is relatively fuller and more capacious than in *Daphænus*, and the postorbital constriction, though much deeper, is as near the orbit as in the modern foxes, and is, therefore, much farther forward than in *Daphænus*. The John Day specimens, which Cope has referred to *C. gregarius* ('85, Pl. LXVIII, Fig. 6), have an even fuller cranium and shallower postorbital constriction, which should, perhaps, be a reason for separating these animals specifically from the White River forms. The muzzle in *Cynodictis* is very slender, but tapers gradually and is not so abruptly constricted at the line of the infraorbital foramina as in *Daphænus*. In the European representatives of the genus the skull is much like that of the American species, but is somewhat more primitive and like that of *Daphænus*. Thus, the muzzle is more abruptly constricted, and the postorbital constriction is deeper and occupies a more posterior position.

A more detailed examination of the skull brings out the following facts:

The *occiput* is low, very broad at the base and narrowing toward the summit less than in the large wolves, but more than in *Vulpes* or *Urocyon*; a well-marked median convexity is produced by the vermis of the cerebellum. The crest of the inion is low and weak, much less prominent than in *Daphænus*. The foramen magnum differs somewhat in shape in the different individuals, being in some low and broad, and in others of subcircular outline, a difference which may, in part, be due to a slight crushing. The dorsal margin of the foramen projects much more prominently than in the recent *Canidæ*.

The *basioccipital* is long, broad and of nearly uniform width throughout; it is slightly concave transversely, but has a low median convexity, with very feebly developed keel, the convexity being much less prominent than in *Daphænus.*

The *exoccipitals* are low and wide and so convex in the median line that this portion projects much behind the sides. The condyles are low and depressed and are separated on the ventral side by a narrower, deeper and more V-shaped notch than in the modern wolves or foxes. The paroccipital processes are very small and project almost directly backward, as if to avoid the auditory bulla, with which they are not in contact at any point.

The *supraoccipital* is a large bone, both high and broad; dorsally it is reflected over upon the cranial roof, and in this region is thickened and diploëtic.

The *mastoid* is exposed quite extensively upon the occipital surface, somewhat more so than in the modern representatives of the family, and as the distance between the paroccipital process and the posttympanic process of the squamosal is greater than in the latter, the mastoid occupies a rather more lateral position. The mastoid process is very small, almost obsolete.

The *sphenoid* bones cannot be described, as none of the specimens allow the limits of these elements to be determined.

The *tympanic* differs in very important ways from that of *Daphænus.* In the first place it is inflated into a very much larger auditory bulla, filling out the entire fossa and leaving no part of the periotic exposed; and in the second place, the posterior chamber of the bulla is ossified and fused with the anterior chamber. The line of junction between the two elements which compose the bulla is very plainly marked by a groove upon the external surface, and shows the posterior chamber to be considerably the smaller of the two. I have not been able to detect any, even partial, septum between the two chambers, but such a septum as that of *Canis* may well have been present. The bulla is relatively as elongate as that of *Canis*, but is much narrower and more compressed, and therefore has a less inflated appearance. The external auditory meatus is a very large, oval aperture, without any tubular prolongation, the borders being flat, except the anterior one, which forms a more prominent lip than in *Canis* and partially conceals the postglenoid foramen. The auditory bulla of *Cynodictis* is thus thoroughly cynoid in development and displays no resemblance to the characteristic viverrine type.

The *parietals* are proportionately very large bones and make up the greater part of the sides and roof of the cranium. Throughout their length they unite to form a very low and weak sagittal crest, which becomes moderately prominent only at the concavity of the cranium formed between the occipital crest and the hinder wall of the cerebral fossa. Owing to the larger size and backward extension of the cerebral hemispheres, as well as to the lowness of the occipital crest, this concavity is shorter and much shallower than in *Daphænus*. In some specimens, even aged ones, the anterior half of the parietals carries a very narrow sagittal area, rather than a crest, but only in the little *C. lemur* from the John Day does this area assume the lyrate form. This fact is of importance in determining the primitive or secondary nature of the sagittal crest, concerning which there has been some dispute.

The *frontals* form relatively as much of the cranial roof as in *Canis* and have, when viewed from above, an hour-glass shape, which is due to the deep postorbital constriction, though the depth of this depression varies considerably in different individuals. The postorbital processes are very small and owe their prominence entirely to the constriction. The forehead is slightly convex, both transversely and longitudinally, though in some specimens it has a narrow and shallow depression along the median line, such as is found, though much more distinctly, in modern species of both *Canis* and *Vulpes*. The forehead is bounded by the obscurely marked supraciliary ridges converging posteriorly to the sagittal crest, which is entirely upon the parietals, none of it being formed by the frontals. Anteriorly the frontals are emarginated to receive the narrow nasals, and send forward slender nasal processes, which are separated by short interspaces from the ascending rami of the premaxillaries. A noteworthy difference from *Daphænus* consists in the *absence of frontal sinuses*, in which respect *Cynodictis* agrees with the alopecoid series of the modern *Canidæ*, as *Daphænus* does with the thooid series. The significance of this fact will be discussed in a subsequent chapter.

The *squamosal* has a relatively small extension upon the side of the cranium, and this portion of it has a different shape from that seen in the modern dogs, the parietal suture descending very steeply forward from the occipital crest, while in the modern genera this suture pursues a nearly horizontal course. From the base of the zygomatic process to the posttympanic process of the squamosal runs a projecting shelf, which overhangs the auditory meatus and is much wider than in *Canis* or *Vulpes*, though not so broad as in *Cynodesmus*, *Hypotemnodon* or *Daphænus*. The posttympanic process is not larger than in *Canis*, but is made more conspicuous by the absence of any tubular meatus auditorius. The zygomatic process is relatively somewhat heavier than in *Vulpes*, and in shape and proportions much like that of the wolves, though not so strongly arched upward; anteriorly it extends to the postorbital process of the jugal. The glenoid cavity is broad and the postglenoid process is proportionately heavier, more extended transversely and its distal end is more curved forward than in *Canis*. There is no preglenoid ridge.

The *jugal* also resembles that of *Canis*, though it displays some differences. Thus, it is not quite so long as in the modern genus and does not extend so near to the glenoid cavity; it has a less decided upward curvature, and the postorbital angle (it can hardly be called a process) is even less conspicuous; the masseteric surface is broader, more lateral and less inferior in position, and is bounded above by a distinct crest; the antero-inferior, or maxillary, process is shorter, and the ascending, or frontal, process is narrower, but extends farther upward along the margin of the orbit. As a whole, the zygomatic arch is of nearly the same proportionate length as in *Canis latrans*, but has a straighter fore-and-aft course, being much less strongly arched upward, though curving outward quite as decidedly from the side of the skull. This comparative shortness of the arch, in association with the very elongate cranium, is due to the anterior position of the zygomatic process of the squamosal, which is placed much farther in advance of the occipital condyle than in the recent members of the family.

The *lachrymal* forms but a very small portion of the anterior rim of the orbit and carries a rudimentary spine. Within the orbit the bone is relatively more extended and occupies a more elevated position than in the modern dogs, while the ascending or frontal process is much shorter; the lachrymal foramen is large and is farther removed from the frontal suture.

The *nasals* are short, narrow and slender, splint-like bones, which are convex transversely and very slightly concave antero-posteriorly; their general shape is much the same as in *Vulpes*, except for the much less distinct fore-and-aft concavity and their lesser elongation.

The *premaxillaries* are small; the alveolar portion is weak, in correspondence with the smallness of the incisors, and is not produced anteriorly in the spout-like form which characterizes *Daphænus;* the groove for the reception of the inferior canine is much less deeply incised than in the latter. The ascending ramus is long and slender, but forms a wider strip upon the side of the muzzle than in the last-named genus. The anterior narial opening is small, oval in shape and more oblique in position than in either *Canis* or *Vulpes.* The palatine processes of the premaxillaries are short and very narrow, and the incisive foramina are small. This portion of the palate has an entirely different appearance from that found in *Daphænus;* the premaxillaries are not nearly so much extended in front of the canines, the incisive foramina are shorter and have no such grooves extending forward from them; the spines are very slender and much shorter, reaching only to the canines and not to the line of p $\frac{1}{}$, as they do in the larger genus. In most of these respects *Daphænus* is nearer to *Canis* and *Vulpes* than is *Cynodictis.*

The *maxillaries* are relatively very short, much shorter than in the existing genera, a statement which especially applies to the facial or preorbital portion. At the same time the vertical height is proportionately great. Except for the swelling produced by the root of the canine, the facial surface of the maxillary is simply convex, there being no distinctly marked fovea maxillaris. Owing to the shortness and height of the facial portion, its superior and anterior margin, formed by the sutures with the frontal, nasal and premaxillary, is more strongly curved and descends much more steeply in front than in *Canis*. As in *Daphænus*, the infraorbital foramen is placed very near to the orbit, while in the modern genera it is much in advance of the orbit. The arrangement seen in *Cynodictis* is due chiefly to the anterior position of the orbit and in much less degree to the backward shifting of the foramen itself. The palatine processes of the maxillaries are short and narrow, corresponding to the shortness and slenderness of the muzzle, and they resemble those of *Daphænus* in being slightly concave transversely, with a faintly marked median ridge along the line of suture.

The *palatines* have nearly the same shape and proportions as in *Canis latrans* (though they are relatively somewhat narrower) and extend forward to the anterior edge of p $\frac{4}{}$; the palatine notch is more deeply incised than in either *Canis* or *Vulpes* and is nearly as deep as in *Urocyon*. Only a single posterior palatine foramen is visible on each side. As a whole, the bony palate resembles that of *Canis* more than that of *Daphænus* in its much less abrupt narrowing at the level of the sectorials. The posterior nares have about the same shape and position as in *Vulpes* and have a similar median spine-like process on the anterior border.

The *pterygoids* terminate in longer, more distinct and more thickened hamular processes than in the recent genera, some of which, like *Urocyon*, have no vestige of such processes. From the descending process of the alisphenoid is given off a prominent lateral spine, which, in *Canis* and *Vulpes*, is represented only by a low ridge.

The *mandible* has a slender and compressed horizontal ramus, which tapers rapidly toward the anterior end; it forms a long symphysis with its fellow of the opposite side and curves very gently upward at the chin. The ventral border describes a somewhat sinuous course, curving downward beneath the sectorial, from which point it rises very gradually and regularly to the symphysis, while beneath the masseteric fossa it is concave. There is no trace whatever of the lobation which is found in so many of the existing *Canidæ*, both alopecoids and thooids. The ascending ramus, which forms an obtuse angle with the horizontal, has a proportionately smaller antero-posterior width than in *Daphænus*, though a greater one than in the modern genera; the coronoid process, in particular, is much narrower than in the former, and the sigmoid notch is wider than in the living forms. The masseteric fossa is very deeply impressed, but it has no such definitely marked upper boundary and it does not extend forward so far beneath the molars as in *Canis*, features of resemblance to the alopecoids. The angle is formed by a short, slender and blunt, hook-like process. The condyle, which is not in any way peculiar, is elevated much more above the level of the molar teeth than in *Daphænus*.

The *cranial foramina* are very minute and hence are often difficult to detect, save in exceptionally well-preserved specimens, a very slight degree of crushing being often sufficient to obliterate them. In general, they may be described as characteristically cynoid. The condylar foramen is an opening, hardly larger than a pin-hole, which perforates the ridge running mesially from the paroccipital process; its position is just as in *Canis*. The foramen lacerum posterius is rather smaller than in existing representatives of the family, which is due to the greater proportionate elongation of the auditory bulla, and for the same reason the stylomastoid foramen is less conspicuously displayed. An important difference from *Canis* and *Vulpes* consists in the presence of a well-defined external opening of the carotid canal, which grooves the inner side of the auditory bulla somewhat behind the middle of its course; it is much better shown in some specimens than in others. In the modern *Canidæ*, "the carotid canal is complete and of tolerable dimensions; but its external opening is not visible on the surface of the bulla, being deep in the foramen lacerum posticum" (Flower, '69, p. 24). The other carnivorous families, however, have the carotid canal with visible opening, but varying in position in the different groups.

The foramen lacerum medium and the Eustachian foramen are very much as in *Canis*, but the glenoid foramen is somewhat concealed by the prolonged anterior lip of the auditory meatus. The foramen ovale is a narrow slit which may be readily overlooked, and is closed by even a slight distortion of the skull. An alisphenoid canal is present, and the other openings, the optic, anterior lacerated and round foramina, are as in the recent cynoids. The whole structure of the cranial basis and its foramina are thus canine in character, with only a single difference, the distinctness of the carotid canal. There is nothing to suggest relationship with the viverrines.

Measurements.

	No. 10493.	No. 10513.	No. 10939.	No. 11012.	No. 11381.	No. 11382.	No. 11432.
Skull, length (fr. occ. condyles)			0.092	0.092		0.086	0.089
Cranium, length (occ. condyles to preorbital border)	.062	?.062	.064	.064		.059	.063
Face, preorbital length			.032	.030		.030	.028
Occiput, breadth across mastoid processes	.033	.034	.034	.038	.035	.032	.033
Brain case, greatest breadth	.031	.032	.032	.035	.033	.033	.033
Skull, width across zygomas	.052					.055	
Zygomatic arch, length	.042	.043	.043	.043		.042	.014
Face, width at p^{4}	.026	.026	.026			.030	.025
" " " canine			.016	.017		.018	.015
Mandible, length (fr. condyle)			.063			.060	
" depth at $m_{\overline{1}}$	.009	.011	.011	.011		.010	
" " " $p_{\overline{2}}$			.010	.008		.007	
" thickness at $m_{\overline{1}}$	.0045	.0055	.0055	.005		.005	
" height of coronoid process (from ventral border)	.027	.029	?.027			.029	
" height of condyle fr. angle	.014					.013	

III. The Brain (Pl. XIX, Fig. 12).

The brain of *Cynodictis* has already been described by Bruce ('83, p. 41), but as I wish to consider it from a different standpoint, some account of it will be necessary. In this genus the brain is relatively smaller than in any of the recent *Canidæ*. The olfactory lobes are large and are left exposed by the hemispheres, with which they are connected by short and thick olfactory tracts. The cerebral hemispheres are pear-shaped, broad behind, but tapering rapidly forward, where they decrease in vertical as much as in transverse diameter. The frontal lobe is short, narrow and of small vertical depth, while the parietal lobe much surpasses it in every dimension; a transverse depression marks the boundary between the two. The temporo-sphenoidal lobe is also quite well developed and adds materially to the dorso-ventral diameter of the brain in this region. Posteriorly the hemispheres slightly overlap the lateral lobes of the cerebellum (which appears not to be the case in *Daphænus*), but leave the vermis entirely uncovered. The shape of the cerebrum is thus alopecoid rather than thooid in character. In the former series the hemispheres are wide behind and taper anteriorly, with slight incurvations at the sylvian and presylvian fissures, while in the thooids the cerebrum is narrower behind and at the presylvian fissure the sides are abruptly incurved almost at a right angle; the frontal lobes are much larger relatively than in the foxes (see Huxley, '80, pp. 245–247). The hemispheres of *Cynodictis* agree well in shape with those of the alopecoids, and when compared with the brain of the later and more advanced genus *Cynodesmus* from the John Day, the greater width of their posterior region is distinctly to be seen. The whole character of the skull makes it evident that *Cynodesmus* is a thooid, while both brain and skull structure approximate *Cynodictis* more to the alopecoids.

The hemispheres are very simply convoluted and the sulci are few, simple and short, though it should not be forgotten that the brain-cast very probably fails to reproduce all of the fissures. In the recent *Canidæ* the convolutions are numerous and complex, and the sulci pursue a remarkably curved course, giving to the convolutions, when seen from the side, the appearance of a succession of U-shaped, concentric coils, grouped around the sylvian fissure as a centre. In *Cynodictis*, on the other hand, the visible sulci are few, shallow, short and nearly straight. On the dorsal surface of the hemisphere only two fissures are to be observed, the lateral and the suprasylvian, the former of which is short and almost straight, dying away before it reaches the hinder part of the parietal lobe. If the coronal sulcus is present at all, it is in the same fore-and-aft line as the lateral, and has not the outward sweep around the crucial fissure which is so characteristic of *Canis*. No trace of the crucial fissure is preserved in the brain-cast, and if it was present in the brain, it must have been short, as is indicated by the straight course of the lateral sulcus. The suprasylvian sulcus is likewise very short and but little curved, and is not divisible into anterior and posterior portions. The sylvian fissure itself is but feebly marked upon the cast, but the rhinal sulcus, on the contrary, is very distinctly shown and extends for nearly the whole length of the hemisphere. Making all due allowance for the fact that a cast of the brain-case can but imperfectly reproduce the features of the brain itself, yet it is clear that the cerebrum of *Cynodictis* was convoluted in a much simpler way than in any of the existing *Canidæ*, and that it retains characteristics which among the modern dogs are embryonic and transitory.

The *cerebellum* is rather large and is less overlapped by the hemispheres than is the case among the recent members of the family. The vermis is narrow, but prominent, and is quite clearly divisible into three lobes, corresponding apparently to the lobus centralis, lobus monticuli and declivus of *Canis*. The vermis is less regularly curved in the antero-posterior direction than in the modern genus, the posterior surface forming nearly a right angle with the dorsal. The lateral lobes of the cerebellum have quite a different appearance from those of the recent *Canidæ*. Thus, the lobus quadrangularis is less extended transversely and narrows less toward the external side, while the lobus lunatus inferior is very imperfectly developed, and the lobi semilunares appear not to be represented at all, or, if present, they must be exceedingly small. This latter point is difficult to decide definitely, because a small fragment of the skull, which cannot be removed without danger to the specimen, covers the place where the semilunar would be if present. A small additional lobe, not represented in *Canis*, lies upon the dorsal surface of the lobus quadratus and near to the vermis. Complex as it looks, the cerebellum of *Cynodictis* is simpler than in the recent dogs.

Measurements.

	No. 10513.
Brain, length fr. cerebellum to olfactory lobe (incl.)	0.045
Olfactory lobe, fore and aft diameter	.005
" " vertical diameter	.011
Cerebrum, length in median line	.030
" height at temporo-sphenoidal lobe	.025
" width " " " "	.030
Cerebellum, length in median line	.013
" width	.024
" vertical height	.018
Medulla oblongata, width	.012

IV. The Vertebral Column.

The backbone is not preserved entire in any of the specimens, but by the aid of the more complete individuals from the John Day, the numbers of the various categories of vertebræ may be inferred.

The *atlas* (Pl. XIX, Fig. 13) is somewhat more canine in character than that of *Daphœnus,* having a short and broad body and moderately developed transverse processes. The anterior cotyles are shallower and more depressed than in *Canis;* the neural arch is well extended in the antero-posterior direction and is quite smooth, without ridges or tubercles of any kind; it is very strongly convex, giving to the neural canal an almost circular shape. The inferior arch is very slender and has but a rudimentary hypapophysial tubercle. The posterior cotyles for the axis are somewhat more concave than in *Canis* and present more obliquely toward the median line. The transverse processes are rather small and are much less extended antero-posteriorly than in *Canis,* not reaching so far behind the surfaces for the axis, nor so far forward upon the neural arch; in consequence of this, the atlanteo-diapophysial notch is less deeply incised. The posterior opening of the vertebrarterial canal presents backward, as it does in *Daphœnus,* but has shifted a little more toward the dorsal side of the transverse process, thus showing a tendency to assume the position which is characteristic of the recent *Canidæ.*

The *axis* is not especially canine in appearance, but rather resembles that of *Viverra.* The centrum is long, narrow and very much depressed anteriorly, becoming somewhat deeper vertically toward the hinder end, which has a transversely oval and nearly flat face for the third vertebra; the ventral keel is relatively better developed than in *Daphœnus.* The articular surfaces for the atlas are low and wide, but project much less outside of the pedicels of the neural arch than they do in *Canis,* and are more convex than in that genus. The odontoid process is slender and elongate, more so than in *Viverra,* and the articular surface on its ventral side is not, as in *Canis,* continuous with the lateral facets for the atlas, but is separated from them by a feebly marked ridge. The transverse processes, which are very thin and compressed, are of no great length; they are perforated by the vertebrarterial canal, which is relatively longer than in the recent dogs. The pedicels of the neural arch are short from before backward, but are quite high, and the neural canal is proportionately much larger in both dimensions than in the existing dogs. The neural spine, at least in the White River species, resembles that of *Daphœnus* much less than it does that of *Canis.* It is long, not very high, and in front extends far in advance of the pedicels, but posteriorly it does not project behind the zygapophyses, as it does so conspicuously in *Daphœnus;* as in the modern genus, the dorsal border of the spine is continued into the hinder margins of the neural arch. The zygapophyses are rather small and do not extend out so prominently from the sides of the neural arch as in *Canis.*

The axis of the John Day species, *C. geismarianus,* as figured by Cope ('85, Pl. LXX*a*, Fig. 12), differs from that of *C. gregarius* in having a much higher neural spine, which is continued posteriorly into a pointed projection, similar to but shorter than that seen in *Daphœnus.*

The *third cervical vertebra* is markedly different from that of *Daphœnus* and quite like the corresponding vertebra of *Canis*. The centrum is moderately elongate (though shorter with reference to the axis than in most of the modern dogs), quite depressed and slightly opisthocœlous, and has a stout, prominent ventral keel, which is better developed than in *Daphœnus*, or even than in *Canis*, and ends behind in a tubercle. The anterior face is broad, depressed, quite convex and very oblique in position with reference to the fore-and-aft axis of the centrum, while the posterior face is more nearly circular in outline. The transverse process is, in general character, quite like that of *Canis*, but has a relatively smaller extension from before backward, and is less obviously divided into anterior and posterior projections, the ventral margin of the process being nearly straight. The vertebrarterial canal is proportionately much longer than in *Canis*, being nearly as long as the entire centrum. The neural canal is relatively larger and especially wider than in the modern genus, while the neural arch is long and broad and but slightly convex on the dorsal surface. One noteworthy difference from *Canis* consists in the fact that the arch does not project over the sides, or pedicels, as an overhanging shelf, or does so but slightly. The neural spine is represented only by an inconspicuous ridge.

The zygapophyses are small and extend but little in front of and behind the neural arch, which constitutes a very marked difference from *Daphœnus*. In the latter, it will be remembered, the neural arches are deeply emarginated between each transverse pair of zygapophyses, so that when the vertebræ are placed in their natural position, large vacuities occur between the successive neural arches. In *Cynodictis*, as in *Canis*, these interspaces are very narrow and in certain parts of the neck they are hardly at all visible.

The *fourth vertebra* is somewhat shorter than the third, but is otherwise very much like it and also like the corresponding vertebra of *Canis*. The transverse process is somewhat larger and heavier than on the preceding vertebra, and the greater antero-posterior extension of its outer portion makes the vertebrarterial canal relatively longer than in *Canis*; the inferior lamella is very thin and light. The neural spine is short and slender, but is relatively better developed than in most of the modern representatives of the family.

On the *fifth cervical* the neural spine is higher but more slender than on the fourth.

The *sixth* is not preserved in connection with any of the specimens.

The *seventh cervical* is almost a miniature copy of the same vertebra in *Canis*; the neural spine is relatively higher, more slender and more pointed than in most species of the existing genus, and the transverse processes are proportionately longer and thinner, but otherwise the resemblance is very close and detailed.

The number of *thoracic vertebræ* cannot, as yet, be definitely stated, because in none of the specimens is the series preserved entire. Probably, however, these vertebræ numbered thirteen, as is commonly the case among the recent representatives of the family. The specimen of *C. geismarianus* figured by Cope ('85, Pl. LXX*a*) has the posterior ten thoracics in place, and there must have been at least three additional ones. The anterior vertebræ of this region have very small, contracted centra, but long and prominent transverse processes and neural spines which are relatively higher and more slender than in *Canis*, and are also inclined more strongly backward than in the latter. Posteriorly the centra become longer, broader and more depressed, and are quite distinctly keeled in the median ventral line. In addition to this median keel are two shorter and less prominent lateral ridges, which, however, terminate behind in distinct tubercles and thus give a very characteristic appearance to these vertebræ. The transverse processes become more and more shortened and the neural spines lower, less strongly inclined, but more compressed and broadened at the base (antero-posteriorly). The antepenultimate thoracic (presumably the eleventh) is the anticlinal vertebra, of which the neural spine is low, broad, compressed and erect. The penultimate (? twelfth) and last (? thirteenth) thoracics are very much like lumbars in appearance and structure, but have no transverse processes, while in *Canis* these processes, though small, are quite distinct on the twelfth and thirteenth thoracics. Large, heavy and prominent anapophyses and metapophyses are present on the last two thoracics.

Of *lumbar vertebræ* this genus probably possessed seven, that many being preserved in position and in connection both with the thoracics and with the sacrum in Cope's specimen of *C. geismarianus*. In the White River material at my command not more than five lumbars have been found in association with any one individual, but the series is obviously incomplete, and there is no reason to suppose that *C. gregarius* differed in this respect from the John Day species. The lumbar region is proportionately long and stout and the individual vertebræ are quite massively constructed (*i. e.* for so small an animal), indicating a powerful musculature in this region. The centra increase in length up to that of the penultimate vertebra, while the first and the last are the shortest of the series. These centra are broad and depressed, and bear distinct median ventral keels, while the lateral ridges and tubercles are present on the first two vertebræ, but not on the last three. The faces are kidney-shaped, slightly convex in front and concave behind, and are placed obliquely with reference to the long axis of the centra. This obliquity is to provide for the curvature of the loins, which rise to the pelvis, the rump standing considerably higher than the shoulders. The transverse processes, which are quite short on the anterior lumbars, increase steadily in length up to the sixth, where they become very long; they are slender, depressed, pointed and curved forward. The neural spines are low, compressed and thin, broad at the base, narrow and pointed at the tip, and are inclined forward rather more decidedly than in *Canis.* Anapophyses are quite prominent on the anterior lumbars, but diminish posteriorly, becoming rudimentary on the fifth, while the metapophyses are conspicuous in all. The zygapophyses are but moderately concave and convex respectively. The general aspect of the lumbar region is not canine in character, but rather resembles that of the civets and mustelines.

The *sacrum* is quite short and consists of three vertebræ, only the first of which has a contact with the ilium. The first sacral has a broad and much depressed centrum and large, expanded pleurapophyses, which give considerable width to the vertebra. The neural spine is a mere feebly marked ridge, while the spines of the second and third are higher and separate. The transverse processes of all the sacrals are fused into a continuous lateral ridge, but that of the third vertebra extends outward much farther than the others and ends in a point, an arrangement which gives to this sacrum an appearance quite different from that of *Canis.* The prezygapophyses of the first vertebra are large and conspicuous, but all the other zygapophyses of the sacrum are small. The neural foramina are remarkably small. The centrum of the last vertebra is almost as large as that of the first and the widely extended transverse processes make the sacrum nearly as broad behind as it is in front.

The *caudal vertebræ* are not preserved entire in any of the specimens, nor, indeed, can all of them be recovered from all the individuals combined, so that the number of tail vertebræ is, as yet, conjectural. However, enough remains to show the character of the tail and of the various elements which compose it. The tail was evidently very well developed, being relatively longer and stouter than in any of the recent *Canidæ,* and much like that of some of the long-tailed viverrines, such as *Herpestes.* The anterior caudal vertebræ have short, but heavy centra and very long, broad and depressed transverse processes, which extend out nearly at right angles with the line of the centrum. The breadth of the first caudal across the transverse processes about equals that of the last sacral. The zygapophyses of the anterior caudals are large and prominent. The anterior caudals are succeeded by a number of vertebræ with very elongate centra, which resemble in miniature the corresponding vertebræ of *Daphænus,* having distinct remnants of the various processes. Toward the tip of the tail the vertebræ become very slender and of a cylindrical shape, the centra being slightly contracted in the middle and expanded at the ends.

The *ribs,* so far as they are preserved in the various specimens, are remarkable chiefly for their length and slenderness and for their subcylindrical shape. Tubercles appear to be absent from the twelfth and thirteenth pair. The sternum is of the usual carnivorous character, without being especially like that either of the dogs or of the civets. The manubrium is long, more so than in *Canis*, as well as narrower and more compressed. The first pair of ribs is attached to a pair of wing-like processes, which are unusually far from the second pair. In front of these processes the bone is compressed and very narrow. For much of its length the manubrium possesses a ventral keel. The segments of the mesosternum, so far as they are preserved in the various specimens, are more elongate, more slender and depressed and more contracted in the middle than in the recent *Canidæ*.

Measurements.

	No. 10493.	No. 11012.	No. 11381.	No. 11382.	No. 11432.
Atlas, length	0.016				
" breadth	.034				
Axis, length (excl. of odontoid)	.019		.020		
" " of odontoid process	.005				
" breadth of anterior face	.013		.0135		
Third cervical, length	.011	.013	.012		.013
Fourth " "					.014
Fifth " "					.013
Sixth " "			.013		.012
Seventh " "			.011		.010
Anterior thoracic, length		.008	.009		.0085
Last thoracic, length	.012	.012	.013		
First lumbar, "			.015	.013	
Second " "			.017	.0145	
Fifth " "		.016	.018	.016	
" " width post. face		.010	.011	.009	
Sixth " length		.015	.017	.014	
Seventh " "			.013	.013	.012
Sacrum, length		.024	.026		
First sacral, width across pleurap.		.024	.024		
Third " " " transv. pr		.021			
First caudal, length		.007	.008	?.010	
" " width across transv. pr		.021	.026		
Median caudal, length					
" " width ant. face		.005			

V. The Fore Limb.

The *scapula* is quite remarkable and is in character rather viverrine or raccoon-like than canine. The shoulder blade is rather low and broad and is divided by the spine into pre- and postscapular fossæ of nearly equal breadth, while in the modern dogs the scapula is high, narrow and of subquadrate shape, and has the spine so placed as to make the postscapular fossa much the larger of the two. The glenoid cavity is moderately concave, and is elongate antero-posteriorly, but narrow transversely. The coracoid process is unusually large, forming an incurved hook, which, however, does not appear prominently when the scapula is viewed from the external side; in the recent *Canidæ* the coracoid is reduced to much smaller proportions. A resemblance to the shoulder-blade of *Canis* is to be found in the broad neck of the scapula and in the absence of any well-defined coraco-scapular notch. The coracoid border is slightly concave at the neck, but then curves forward and upward, giving great width to the prescapular fossa; the glenoid border is, as usual, straight and is steeply inclined, so that the postscapular fossa, which is very narrow distally, becomes very broad proximally. The spine is high and ends in a very long and prominent acromion, which descends below the level of the glenoid cavity, which suggests that in this genus the clavicles were much better developed than in the existing dogs. A very large metacromial process is also present. The metacromion may be observed in most of the existing families of Carnivora, but it is seldom so large and so prominent as in *Cynodictis;* perhaps, the nearest approach to it among modern genera is in *Arctictis.*

The *humerus* is much more suggestive of viverrine than of canine affinities. As compared with the bones of the forearm, or even with the femur, the humerus is elongate, but it is short in proportion to the length of the back or loins. The head is strongly convex and projects farther behind the plane of the shaft than in the modern dogs; the external tuberosity is a heavy, but low ridge, which barely conceals the head when the bone is viewed from the front; a large, irregularly circular area near the hinder end of this ridge plainly indicates the insertion of the infraspinatus muscle. The external tuberosity is both lower and shorter than in the modern dogs, but the internal one is rather more prominent, and the bicipital groove is more widely open, more internal in position and more of it is visible from the anterior side. The shaft is rather long, and, when seen from the side, exhibits a sigmoid curvature, which is somewhat better marked than in *Canis.* For most of its length, the shaft is laterally compressed and has but a very short cylindrical portion before expanding laterally at the distal end. Most of the ridges and prominences for muscular attachment are well developed, more so than would be expected in so small an animal. The deltoid ridge is much more prominent than in the recent dogs, and is more like that of the cats and viverrines; the supinator ridge is likewise very much more prominent than in *Canis,* in correlation with the power of rotation of the radius, which *Cynodictis* appears to have retained in almost undiminished degree. On the other hand, the rough ridge, which runs down from the head upon the outer side of the shaft (spina humeri) and serves for the attachment of the teres minor, anconæus externus and brachialis internus muscles, is much fainter than in *Canis* and the linea tuberculi minoris is very feebly marked. The supratrochlear fossa is very shallow and the anconeal fossa is much smaller and shallower than in the modern representatives of the family, there being no perforation of the shaft at this point. The internal epicondyle is much more prominent and more massive than in *Canis,* and a conspicuous epicondylar foramen is present, in the form of a long, narrow slit. The external epicondyle, on the contrary, is rather smaller than in the recent genus.

The humeral *trochlea* has a much smaller proximo-distal diameter than in the existing *Canidæ,* in which respect it preserves a primitive character and resembles the trochlea of such viverrine genera as *Cynogale* and *Viverra.* The radial surface is small and simply convex, while the ulnar facet is much larger than in the recent dogs; the inner flange of the ulnar facet is also more produced distally and forms a sharper edge than in the latter.

The *radius* is not at all suggestive of canine affinities, but rather resembles the corresponding bone of the cats and viverrines. The capitellum is small and of subdiscoidal shape; while it is somewhat more extended transversely than in *Felis,* it is much less so than in *Canis;* its articular surface is moderately concave and is slightly notched on the anterior border. The proximal facet for the ulna is a simple, convex band, separated from the humeral surface by a distinct angle and entirely resembling that of *Daphænus.* The character of the articulation at the elbow-joint and the large development of the supinator ridge on the humerus would seem to imply that in *Cynodictis* a considerable degree of freedom in the rotation of the manus had been preserved, though probably less than in the cats and in many viverrines. The bicipital tubercle is prominent, but occupies a more posterior position than in either the cats or the recent dogs, and is not visible when the radius is looked at from the front.

The shaft of the radius is relatively short, slender and rounded, very different from the broad, oval and antero-posteriorly compressed shaft seen in *Canis;* it has a slight double curvature, arching anteriorly and externally, and is of almost uniform thickness throughout its length, except at the distal end, where it broadens considerably. A very striking difference from *Canis* consists in the very great size and prominence of the styloid process, which forms a relatively enormous tuberosity; it is even much larger proportionately than in the cats or civets and is as large as in *Mellivora,* though of a different shape. In *Daphænus,* as we have already learned, the styloid process is very prominent and of a generally feline appearance, but it is proportionately smaller than in *Cynodictis.* The radius figured by Schlosser ('89, Taf. VII, Fig. 8) and by him attributed to one of the European species of the latter genus has a styloid process in the form of an enormous, recurved hook, much longer and much more slender than in the American species and of an entirely different appearance. The distal tendinal sulci are not very well marked, though that for the abductor and extensor muscles of the pollex is a deep groove. The distal facet for the ulna is smaller and less deeply impressed than in *Canis.* The carpal facet is small and slightly concave, narrowing toward the internal side; it does not extend over upon the styloid process, from which it is separated by a broad and deep notch.

The *ulna* is, in its way, as peculiar as the radius. The olecranon is quite typically fissipede in character and differs from that of the creodonts in its comparative shortness and breadth; though proportionately somewhat longer than in *Canis*, it is hardly so long as in *Daphænus*, and the sulcus for the tendons of the anconeal muscles is more distinct than in the former. The sigmoid notch is hardly so deep as in *Canis*, and, in particular, the internal facet for the humerus projects less in front of the plane of the shaft, and the external process is very feebly developed. The radial facet is narrower and less deeply concave than in the modern *Canidæ*, but has a somewhat greater vertical diameter.

The shaft of the ulna is decidedly less reduced than in the recent representatives of the family, and for most of its length is little or not at all more slender than that of the radius. In its proximal portion the shaft is much more compressed laterally and thicker antero-posteriorly than in *Canis*, in which genus this portion of the shaft is trihedral. The middle and distal portions are of triangular section, none of it having the subcylindrical shape which characterizes the distal one-third of the shaft in the recent genus. The distal end has quite a different shape from that seen in *Daphænus*, a difference which is due to the much greater prominence of the radial facet in the latter. In *Cynodictis* this facet is almost sessile and projects but little more than it does in *Canis*. The carpal facet is very small and quite simply convex.

Measurements.

	No. 10493.	No. 11012.	No. 11381.	No. 11382.	No. 11432.
Scapula, length		0.054			
" greatest width		?.049			
" width of neck			.013		
" ant. post.-diameter of glenoid cavity			.012	.0095	.0095
" transverse " " "			.008	.007	.007
Humerus, length		.075		.070	.070
" ant. post. diam. prox. end	.012	.015	.019	.015	.015
" transv. " " "		.014	.016	.013	.0125
" breadth of distal end		.016	.020	.015	
" " " trochlea		.012	.0145	.011	
Radius, length	.057	.061			
" ant post. diam. prox. end	.005	.006	.007	.005	.005
" transv. " " "	.007	.007	.009	.007	.007
" breadth of distal end	.012	.013	.013		.009
" " " carpal facet	.0055	.006	.007		.0055
Ulna, length		.072			
" " of olecranon		.007	.010	.0095	.009
" thickness of olecranon			.010	.008	.008

VI. The Manus (Pl. XX, Fig. 23).

By a fortunate discovery of Mr. Hatcher's, I am enabled to give an account of an almost complete carpus belonging to *Cynodictis,* which has hitherto been entirely unknown.

A *scapho-lunar* is present, formed by the coalescence of the scaphoid, lunar and central, which distinguishes *Cynodictis* from the creodonts. This bone resembles that of *Canis* in general character, but displays quite a number of differences in points of detail, and these differences are, at the same time, approximations to the structure found in *Daphænus.* The scapho-lunar has a very small vertical (proximo-distal) diameter, especially on the radial side, where it thins away to a mere edge, the facets for the radius and the trapezium almost meeting. As compared with the corresponding carpal of *Canis,* this bone has a somewhat greater transverse and smaller dorso-palmar diameter. The radial facet is simply convex both transversely and antero-posteriorly, and has not the saddle-shaped extension at the interno-palmar angle which is found in the recent dogs. This facet descends quite low upon the dorsal side of the bone, as is also the case in the modern plantigrade and semiplantigrade carnivores. The hook-like process which arises from the postero-internal angle of the scapho-lunar is much shorter and less massive in every dimension than that of *Canis.* Another difference from the modern genus consists in the absence of any distinct articular surface for the pyramidal, the facet for the radius and that for the unciform almost coming into contact along the ulnar side of the bone.

On the distal side of the scapho-lunar are four facets, for all the carpal elements of the distal row. That for the unciform is relatively smaller than in *Canis,* and is confined to a narrow strip near the ulnar border; the magnum facet is much the same as in the modern genus, but is somewhat more oblique in position. The surface for the trapezoid is fairly large and keeps more nearly parallel with that for the magnum than in the recent dogs, while the trapezium facet is small and of almost circular shape.

The *pyramidal* is a very different-looking bone from that of the modern dogs, being broad, depressed and scale-like in shape; its vertical (or proximo-distal) diameter is very small and relatively much less than in *Canis,* and there is no such process from the ulnar side of the bone as in the latter, in which the pyramidal articulates with the head of the fifth metacarpal by a much more extensive facet than in *Cynodictis.* The recent viverrines have the pyramidal shaped very much as in the White River genus. The proximal surface is divided into two narrow and somewhat concave facets for the ulna and pisiform respectively, of which the latter is slightly the larger. On the distal side is a single large and concave facet for the unciform, and posterior to this a very narrow surface which appears to be destined for articulation with the head of the fifth metacarpal.

The *pisiform* differs very decidedly in shape from that of *Canis*. This carpal is small and light; its proximal (*i. e.*, articular) end is greatly depressed, but much extended transversely (in the existing genus the principal diameter of the proximal end is the vertical one) and the facets for the pyramidal and ulna are correspondingly broadened transversely and narrowed vertically. The pyramidal facet is the larger of the two and is quite deeply concave, while that for the ulna is small and nearly plane; the two facets together form an acute angle and are separated only by an inconspicuous ridge. The distal end of the pisiform is moderately expanded, but in the vertical dimension, so that the proximal and distal expansions are almost at right angles with each other. Between the two expansions the body of the bone is much contracted and very slender, which is in marked contrast to the shape seen in *Canis.*

A so-called "*radial sesamoid*" appears to have been present; at least, there occurs in the same block of matrix through which the carpals of one individual were scattered, a small, irregularly wedge-shaped bone, to which I can give no other interpretation. Assuming that this reference is correct, we find in the relative size and shape of this bone another resemblance to such viverrine genera as *Herpestes*, *Cynogale* and *Paradoxurus*, etc. The radial sesamoid also occurs in *Canis*, at least in certain species, but is very minute.

The *trapezium* is very small and differently shaped from that of *Canis;* its principal dimension is the dorso-palmar, while the transverse diameter is the least. The surface for the scaphoid, which in *Canis* is a very oblique, convex facet, is in *Cynodictis* entirely proximal in position and nearly plane, and there is no such large concave facet for the trapezoid on the ulnar side as in the modern genus; the distal facet for the head of the first metacarpal is less distinctively saddle-shaped than in the latter. In view of the well-developed pollex, the small size of the trapezium is somewhat surprising.

The *trapezoid* is shaped very much as in the existing dogs, but with certain minor differences, especially noticeable in the very small vertical diameter and in the thinning of the bone to an edge on the ulnar side. The proximal end bears a simply convex facet for the scapho-lunar, while the distal facet, for the second metacarpal, is very slightly saddle-shaped; on the palmar side the trapezoid contracts to a point.

The *magnum* is small and that portion of it which is visible from the dorsal side, when all the carpal elements are in their natural positions, is minute, especially in its proximo-distal dimension. In shape the magnum does not differ materially from that of the recent dogs, but the proximal surface is narrower and rises more abruptly to the "head," and on the palmar side the bone broadens out in a fashion not repeated in *Canis.*

The unciform facet is large and plane and does not rise so high upon the head as in the modern genus. On the radial side we find no distinct facet for the trapezoid, which, as already mentioned, thins to a mere edge toward the magnum, but there is a well-defined facet for the projection from the head of the second metacarpal, which is proportionately larger than in *Canis*. On the distal end of the magnum is a narrow facet for the third metacarpal, a facet which is less concave in the dorso-palmar direction than in the case of the last-named genus.

The *unciform* is viverrine rather than canine in character, being much narrower in proportion to its vertical height than in the recent dogs. The facet for the scapholunar, which in *Canis* has an almost entirely proximal position, is in *Cynodictis* much more nearly lateral. The pyramidal facet is also decidedly more steeply inclined than in the existing genus, the two articular surfaces meeting at a very acute angle and making the proximal end of the unciform narrow and wedge-shaped. On the radial side is a large facet for the magnum and a small one, confluent with it, for the extension from the head of the third metacarpal. The distal facets, for the fourth and fifth metacarpals respectively, are narrower than in *Canis*, contracting especially toward the palmar side.

The *metacarpals*, five in number, are remarkably short, slender and weak and have but little resemblance to those of the recent dogs.

The *first metacarpal* is very small, but is, nevertheless, proportionately much less reduced than in *Canis*, taking the length of mc iii in each genus as a standard of comparison. The head is thicker and relatively heavier than in *Canis* and on the radial side, internal to the trapezium facet, is a tubercle for the attachment of the lateral ligament. The facet itself is much less deeply concave transversely than in *Canis*, but more convex in the dorso-palmar direction. The shaft is short, slender, arched toward the dorsal side, antero-posteriorly compressed and of oval section, tapering considerably toward the distal end. The distal trochlea is very small, but formed entirely like those of the other metacarpals; it is strongly convex, almost hemispherical and bears a distinct carina upon the palmar face, just as in *Daphænus*. In *Canis*, on the other hand, this structure is of an entirely different character, forming an asymmetrical hemicylinder, with a broad shallow groove placed somewhat internal to the median line, and thus resembles the trochlea of a phalanx rather than that of the other metacarpals.

The *second metacarpal* is represented in the collection only by a single imperfect specimen, consisting of the proximal end. This shows a much stouter shaft than mc i, being of about the same diameter as the corresponding portion of mc iv, and more slender than that of mc iii. The head is narrow and bears a saddle-shaped facet for the trapezoid, but sends out a projection which rises more above the head of mc iii than in *Canis* and articulates with the magnum by a larger facet than in that genus.

The *third metacarpal*, though short and slender, is somewhat the longest and heaviest of the series. The proximal articular surface for the magnum is shaped very much as in *Canis*, but is slightly broader in proportion and rather more concave transversely; on the radial side of the head is a large facet for mc ii, which has a more oblique position than in the modern genus. On the ulnar side is a small projection which abuts against the unciform and is relatively larger than in *Canis*. The shaft, and indeed the whole metacarpal, has a viverrine rather than a canine appearance; it has not acquired the prismatic, quadrate shape which is so characteristic of the modern dogs, but is of oval section and is of almost uniform width throughout, but broadens slightly at the distal end. The distal trochlea, though much lower in the vertical diameter, is yet of decidedly more canine character than is that of *Daphænus*, being broad and hemi-cylindrical in shape instead of subspherical. The pit above the trochlea, which is absent in *Daphænus*, is distinctly marked and the lateral processes for ligamentous attachment are much less prominent. All of these conditions are approximations to the conditions seen in *Canis*.

The *fourth metacarpal* is not completely preserved in any of the specimens, but it appears to have been of about the same length as mc iii and to have formed with it a symmetrical pair, although the two metacarpals are not so closely appressed as in *Canis*, but diverge slightly toward the distal end. The head has a simply convex facet for the unciform and is somewhat narrower proportionately than in the existing members of the *Canidæ*, owing to the overlapping of the head by mc iii, in order to reach the unciform. So far as it is preserved, the shaft is rather more slender than that of mc iii and of a more cylindrical, less compressed shape.

The *fifth metacarpal* is remarkably short, much more so in proportion to the length of mc iii than is that of *Canis*. The head is less broadened and thickened than in the latter genus, and carries a simple, convex facet for the unciform. In the modern genus there is likewise a large facet for the pyramidal, which extends down over the unciform and comes into contact with mc v. In *Cynodictis* there appears to be a facet of a similar kind, but if so, it is very small and obscurely marked and may be regarded as in only an incipient stage of development. The shaft is slender proximally and broadens distally, the reverse of the proportions which obtain in *Canis*, and the distal trochlea is small and is of somewhat more spherical, less cylindrical, shape than in the existing members of the family.

The *phalanges*. It is unfortunate that in all of the specimens in the collection the phalanges are in such a fragmentary state that only an incomplete account of them can be given, and some important questions must be left unanswered for the present. The proximal phalanx of one of the median digits is short, slender and straight, and is relatively broader but more depressed than in *Canis*. As in *Daphænus*, the proximal articular surface is somewhat more deeply concave and presents more obliquely toward the dorsal side than in the recent genus. The distal trochlea likewise resembles that of *Daphænus* in having a deeper median groove and in being more confined to the palmar aspect of the bone than in *Canis*, which has the distal trochlea reflected well over upon the dorsal side of the phalanx.

Of the second phalanx only the proximal half is preserved in any of the specimens, and I have so far failed to find even a fragment of the distal end. So far as can be judged from the material at hand, *Cynodictis* would appear to have differed from *Daphænus* in the very important respect that the claws were not at all or only very imperfectly retractile. In *Daphænus* the asymmetry of the second phalanx is clearly displayed even in its proximal portion, while in *Cynodictis* the proximal end is quite symmetrical and does not possess any depression or excavation upon the ulnar side. However, a certain resemblance to *Daphænus* and difference from *Canis* may be observed in the greater concavity and more marked separation of the two pits into which the proximal facet is divided, as well as in the greater prominence of the beak-like process which rises from the dorsal margin and fits into the median distal groove of the first phalanx. In the absence of the distal end of the second phalanx, it cannot be positively stated that *Cynodictis* had lost (or had never possessed) all trace of the retractility of the claws, but it does not seem unlikely that such was the case.

Measurements.

	No. 10193.	No. 11012.
Carpus, height in median line		0.006
" breadth		.011
Metacarpal i, length		.012
" " width of proximal end	.0035	.004
" " " " distal end		.003
Metacarpal ii, width of proximal end		.0035
Metacarpal iii, length	.022	.0215
" " width of proximal end	.004	.0035
" " " " distal end	.005	.0045
Metacarpal iv, width of proximal end	.004	.0035
Metacarpal v, length	.017	.016
" " width of proximal end	.004	.004
" " " " distal end	.004	.0045

The ungual phalanx differs in several not unimportant details both from that of *Daphænus* and that of *Canis*, and is, on the whole, intermediate in character between the phalanges of the two genera. As compared with the ungual of *Daphænus*, it has a somewhat less concave proximal trochlea, a smaller subungual process, and a much less extensive bony hood reflected over the base of the claw. Indeed, this hood is rudimentary and can hardly be said to exist at all. The phalanx is also slightly thicker and has more convex faces. Comparing this ungual with that of *Canis*, we find it to be decidedly sharper, narrower and more compressed and to have a more deeply concave trochlea. In the modern genus the bony hood is almost as well developed as in *Daphænus.*

VII. The Hind Limb.

The *pelvis* approximates more nearly to the modern canine type than does that of *Daphænus*, though still retaining a number of primitive characters. A conspicuous difference from the recent members of the family consists in the elongation of the post-acetabular portion of the pelvis, which in *Canis* is short, and in the consequent change of shape of the obturator foramina. The ilium is fairly elongate and in shape is rather more viverrine than canine; the peduncle is short and laterally compressed, but of considerable dorso-ventral breadth. The anterior expansion of the ilium is less extensive than in *Canis*, in which genus the ilium widens gradually to the free end, or crista, while in *Cynodictis* it attains nearly its full width immediately in front of the peduncle, and from this point forward the dorsal and ventral (or ischial and acetabular) borders pursue an almost parallel course. The widening is almost confined to the ischial border, being very feebly marked on the acetabular border, and owing to this the shape of the ilium is much as in the modern *Herpestes.* The gluteal surface does not display the wide and simple concavity which is seen in *Canis*, but, as in *Daphænus* and *Dinictis*, there is a narrow dorsal depression and beneath this a convex ridge, but this ridge is not so prominent as in the other White River genera which have been mentioned. The iliac surface is short and narrow, and the sacral surface is small and placed far back, so that the ilium projects well in front of the sacrum. When viewed from above, the two ilia are seen to curve outward less, and to diverge less anteriorly than in the modern dogs. The acetabular border ends in a well-marked tubercle and the ilio-pectineal process is also quite prominent.

The ischium is relatively long and its anterior portion is slender, but posteriorly it expands into a broad plate. This posterior portion is much less decidedly everted and depressed and occupies a more vertical position than in *Canis*, and the ischial tuberosity, just as in *Daphænus*, is much more feebly developed than in the existing *Canidæ.* On the other hand, the spine of the ischium and the ischiadic notch are much more distinctly shown and are placed farther behind the acetabulum than in the latter, though not so far back as in *Herpestes.* The obturator foramen is narrower and more elongate than in

Canis, and its anterior border is notched by the obturator sulcus. The acetabulum is small, deep and nearly circular.

The anterior or descending ramus of the pubis is long and slender and encloses with its fellow a broad anterior pelvic opening. The horizontal ramus is proportionately longer and stouter and the symphysis is longer than in the recent dogs, almost as long as in the cats. The horizontal ramus is less flattened and depressed than in the former, forming a prominent ridge along the ventral side of the symphysis.

The *os penis* may be conveniently described in connection with the pelvis. In none of the White River specimens that have fallen under my observation is this bone preserved, but in the beautiful specimen of *C. geismarianus* figured by Cope ('85, Pl. LXX) it is present and in nearly its natural position, though Cope has omitted any mention of it in his description. Flower ('69) has pointed out the characteristics of this bone in the three sections into which he divides the fissipede carnivores. The Arctoidea "all have a large penis with a very considerable bone, which is usually more or less curved, somewhat compressed, not grooved, dilated posteriorly and often bifurcated or rather bilobed in front" (p. 14). The cats and viverrines "all have a comparatively small penis, with a more or less conical termination, and of which the bone is small, irregular in shape, or not unfrequently altogether wanting" (p. 22). To this statement *Cryptoprocta* forms an exception, having a bone relatively long, "slender, compressed, slightly curved, not grooved or divided anteriorly, rounded and slightly dilated at each end, but thickest posteriorly" (p. 23). In the hyænas the bone is wanting. The dogs resemble the raccoons, weasels, etc., in having a large os penis, "though the os is of a different form, being straight, wide, depressed and grooved" (p. 26). In *Cynodictis* this bone is entirely different from that of the modern *Canidæ*; it is long, slender, compressed laterally and strongly curved and is slightly grooved upon the sides, but not on the dorsal border; the anterior end is so broken that the presence or absence of a bilobation cannot be determined. The resemblance in the character of the os penis between *Cynodictis*, on the one hand, and *Cryptoprocta* and the mustelines, on the other, is an important fact, the significance of which will be discussed later.

The bones of the hind limb proper considerably exceed in length those of the fore limb, more so than in *Canis*, though the difference is rather between the proportions of the radius and tibia than between those of the humerus and femur.

The *femur* is slender and quite elongate and in essentials differs but little from that of *Canis*. The head is small, of hemispherical shape, and is set upon a somewhat longer and more distinct neck than in the modern genus, projecting more directly inward and less upward; the pit for the round ligament is deeply impressed but very small. The great trochanter is lower than in *Canis* and is separated from the head by a narrower, shallower notch, while the digital fossa is relatively much smaller. The second trochanter occupies nearly the same position as in the modern genus, though somewhat more posterior, so that it is almost or entirely concealed when the femur is viewed from the front; it is of about the same prominence as in the existing dogs, but rather more slender and pointed. The intertrochanteric ridge, which connects the greater and the second trochanters, is rather better developed than in *Canis*, especially in the larger and longer-limbed individuals. What may fairly be regarded as a remnant of the third trochanter is present in the form of a low, short, thickened and rugose ridge, which is placed a short distance below the great trochanter. The third trochanter is all but universal among the Creodonta, and in rudimentary form it persists in many of the earlier and more primitive carnivores, such as *Dinictis*, but it is somewhat surprising to find it retained in so advanced a genus as *Cynodictis*. It is true that in certain muscular and powerful domestic breeds of dogs the third trochanter recurs, though it is not distinctly shown in the existing wild species of *Canidæ*.

The shaft of the femur is long, slender, arched strongly forward and slightly toward the internal or medial side. As would naturally be expected in so small an animal, the ridges for muscular attachment are not so prominent as in the modern species. On the anterior face no ridge for the vastus externus muscle is distinguishable and on the posterior face the linea aspera is neither so long nor so prominent as in *Canis*. The distal end of the femur has quite a different appearance from that seen in the existing members of the family; a difference which is principally due to the smaller size and less prominent projection of the condyles and rotular trochlea. The trochlea resembles that of the viverrines in being shallow and in having the two borders of nearly equal height and length, and also in the absence of any distinctly marked suprapatellar fossa. On the other hand, this trochlea is relatively narrower and extends farther up the shaft than in the civets. The condyles are small, of nearly equal size and prominence, and are separated by an intercondylar space which is relatively narrower than in *Canis;* small sesamoid bones were evidently, as in the existing species, attached to the proximal faces of the condyles.

The *patella* is viverrine, or more accurately herpestine, rather than canine in character. It is a short, rather wide, thin and scale-like bone, of subquadrate more than ovate shape. The articular surface for the femur, in correlation with the shallowness of the rotular groove, is but slightly concave proximo-distally, and even less convex transversely.

The *tibia*, as in *Canis*, is of about the same length as the femur. Compared with the radius, the tibia seems to be very long, but that this is due rather to the shortness of the radius than to the elongation of the tibia, appears from a comparison with the vertebral column, whence it becomes evident that all the limb bones of *Cynodictis* are proportionately shorter than those of *Canis*, and that the bones of the forearm are especially short. The tibia of *Cynodictis* differs from that of the modern canines in several particulars. The proximal condyles are of nearly equal size, but the external one projects much farther behind the plane of the shaft than in *Canis*, and on the distal face of the overhanging shelf thus formed is a facet for the head of the fibula, which is much larger and more distinct than in the recent genus. The tibial spine is bifid and very low, but the two parts are closely approximated, the condyles being less widely separated than in *Canis*. The cnemial crest, though stout and prominent, is much less so than in the modern forms, and the sulcus for the extensor longus digitorum is much less deeply incised. In its proximal portion the shaft is stout and trihedral, but for most of its length it is slender and subcylindrical, expanding moderately at the distal end; it has a double curvature, arching forward and outward. The various ridges which serve for the attachment of muscles are much the same as in *Canis* and are, consequently, better developed than those of the femur. The distal articular surfaces of the tibia are intermediate in character between those of *Daphœnus* and those of *Canis*. The grooves for the astragalar condyles are deeper and the intercondylar ridge higher than in the former, less so than in the latter, and the sulcus which in *Canis* invades the articular surface has not yet been developed. The internal malleolus is somewhat smaller than in *Daphœnus*, but, as in that genus, it forms a heavy, prominent ridge, which extends across the whole dorso-plantar diameter of the bone, while in *Canis* the process has not half this extension. The groove for the tendon of the long flexor muscle is very distinctly marked and has more elevated borders than in the modern dogs. The distal fibular facet is somewhat larger than that of *Canis* and differs from it in having its principal diameter transverse instead of longitudinal. The resemblance in the structure of the distal end of the tibia between *Cynodictis* and *Daphœnus*, on the one hand, and the primitive sabretooth *Dinictis*, on the other, is very marked and very suggestive, though *Cynodictis* has already begun to change in the direction of the modern *Canidæ*. Among living forms the tibia of *Herpestes* offers a close analogy to that of the White River genera which have been mentioned.

The *fibula* is relatively much less reduced than in the existing *Canidæ*, and both the shaft and the terminations are larger. The proximal end of the fibula is much larger and heavier proportionately than in *Canis*, and though smaller than in *Dinictis*, it has a very similar shape; its principal diameter is the antero-posterior one, while transversely it is narrow and compressed; the thickening of the anterior and posterior border is present, as in *Dinictis*, but much less conspicuous. The facet for the head of the tibia is large, subcircular in shape and proximo-lateral in position. The shaft, though slender and delicate, is relatively very much less so than in *Canis,* in which genus the fibula has undergone a more extensive reduction than in *Cynodictis.* Another difference from the recent forms is to be found in the fact that the fibula is not so closely applied to the tibia, the two bones coming into contact only at their proximal and distal extremities. The distal end is expanded and thickened to form a stout external malleolus, which is somewhat smaller than in *Daphænus* or *Dinictis,* but of much the same shape, and has on its outer side a deep sulcus for the peroneus tertius tendon. The distal tibial facet is a narrow band, with its long diameter directed antero-posteriorly; obscurely separated from it is the larger, subcircular facet for the astragalus.

Measurements.

	No. 10493.	No. 11012.	No. 11381.	No. 11382.	No. 11432.
Pelvis, length		?0.064			
" breadth at acetabulum		.036	.037		
Ilium, length fr. acetabulum		?.033	.037		
" breadth of peduncle		.011	.010	.009	
" " " ant. plate				.013	
Ischium, length fr. acetabulum		.027		.026	
Acetabulum, fore-and-aft diameter		.008	.011		
Femur, length			.096	.085	.086
" breadth of prox. end		.017	.020	.015	.016
" " " distal end		.016	.017	.014	.014
Tibia, length		.089	.099		
" breadth of prox. end		.015	.018	.014	.014
" thickness of prox. end		.013	.016	.012	.012
" breadth of distal end	.009	.011	.012	.009	.009
Fibula, thickness of prox. end		.007			
" " " distal end	.0065		.009		

VIII. The Pes (Pl. XX, Fig. 24).

The general appearance of the hind foot recalls that of the viverrines. The *astragalus* is quite like that of *Daphænus,* but with some differences which tend in the direction of the modern *Canidæ,* this bone in *Cynodictis* standing intermediate in structure between the two extremes, though somewhat nearer to *Daphænus.* The proximal or tibial trochlea is but little more deeply grooved than in the latter genus, and is therefore much shallower than in *Canis,* but its borders have the same clean-cut angularity as in the modern forms, instead of curving gradually into the facets for the tibial and fibular malleoli. In *Canis* the tibial trochlea is extended over upon the dorsal side of the neck, but this is not the case in either of the White River canines. The neck of the astragalus is relatively longer than in *Canis* or even than in *Daphænus*, resembling that of such viverrine genera as *Paradoxurus*, but is not directed so strongly toward the tibial side of the foot as in *Daphænus*. The head with its convex navicular facet is shaped much as in *Canis*, except that it is more depressed in the dorso-plantar dimension. In *Daphænus* there is a distinct facet for the cuboid, which meets the navicular facet nearly at right angles; in *Cynodictis* this cuboidal facet is very much smaller and sometimes it is altogether wanting, while in *Canis* the astragalus and cuboid are not in contact. As in *Daphænus*, the external calcaneal facet is more oblique in position and more simply concave than in *Canis*, but the sustentacular facet is different from that of both the genera mentioned; it agrees with that of *Daphænus* in being shorter and wider than in the modern forms, but while in the former this facet is separate from that for the navicular, in *Cynodictis*, as in *Canis*, it is confluent with it, but at a different point; *i. e.*, more toward the tibial side. The interarticular sulcus is somewhat deeper than in *Daphænus*, but shallower than in *Canis*. In the latter we find a third calcaneal facet which forms a narrow band upon the fibulo-plantar side of the head and is connected at one end with the sustentacular facet. This accessory calcaneal facet does not occur in either of the White River genera.

The *calcaneum*, like the astragalus, is more viverrine than canine in general appearance and quite closely resembles that of *Paradoxurus*, but the resemblance to *Daphænus* is even more marked. The tuber is slender, compressed and proportionately much shorter than in *Canis;* in the latter the tuber makes up more than two-thirds of the total length of the calcaneum, while in *Cynodictis* it is about two-fifths of this length. The free end of the tuber is moderately thickened and club-shaped and is deeply grooved by the sulcus for the plantaris tendon. As in *Daphænus*, the dorsal and plantar borders of the tuber are nearly parallel and its dorso-plantar diameter is thus almost uniform throughout, not increasing toward the distal end as it does in *Canis*. Near the distal end of the calcaneum and on the fibular side is a very prominent process for the attachment of the lateral ligaments. This process is not present in the recent *Canidæ*, but is very conspicuous in the primitive carnivores, such as *Dinictis* and *Daphænus*, and it recurs among modern plantigrade and semiplantigrade forms, such as *Procyon*, *Gulo*, *Paradoxurus*, etc. Usually, however, it is smaller and less prominent in the fossil than in the recent genera. The facets for the astragalus are somewhat different from those of both *Daphænus* and *Canis*. In the latter the external astragalar facet is in two parts, one of which presents distally and the other dorsally, the two meeting at an angle which does not much exceed 90°; in the former the whole facet forms one continuously curved convexity, not divided by an angulation. In *Cynodictis* the two parts are distinguishable as in *Canis*, but they meet at a much more open angle. The sustentaculum is of moderate

prominence and, as in *Daphænus*, it carries a subcircular facet for the astragalus; in the modern genus this surface is narrower and more elongate. The sustentaculum also agrees with that of *Daphænus* in not being so obliquely placed, with reference to the long axis of the calcaneum, as in the existing members of the family. On the plantar side, between the sustentaculum and the body of the bone, is a groove, the sulcus flexoris hallucis, which is better marked in *Canis* than in either of the White River genera. This is curious, in view of the fact that the latter possess a well-developed and functional hallux, while in the former this digit is reduced to the merest rudiment. In *Canis* we find a third facet for the astragalus, a small plane surface distal to the sustentaculum, from which it is separated by a narrow sulcus; continuous with this accessory facet, but at right angles to it, is a small facet for the navicular. Neither of these articular surfaces is to be found in *Cynodictis*. The facet for the cuboid, which in the recent dogs is almost plane and semicircular in shape, is quite deeply concave and of nearly circular outline.

The *cuboid* is relatively high and narrow, differing from that of *Canis* principally in the smallness of its transverse and dorso-plantar diameters. The proximal surface is occupied by a large facet for the calcaneum, which, as in *Daphænus*, is much more convex than in the existing dogs. The hook-like projection from the plantar side, which in *Daphænus* is very large and prominent and in *Canis* is even more massive, in the present genus is quite inconspicuous and is continuous with the projection from the fibular side which overhangs the deep tendinal sulcus. The astragalar facet is small and is confined to the dorsal side of the cuboid, being much less extensive than in *Daphænus*. The facet for the navicular is not so prominent as in *Canis* or even as in *Daphænus*, and is continuous with that for the ectocuneiform. The distal end of the cuboid resembles that of *Daphænus* in having quite a concave facet for the head of the fourth metatarsal, while that for the fifth is lateral in position. In *Canis*, on the other hand, the surface for mt. iv is almost plane and that for mt. v occupies an entirely distal position; the plantar portion of the facet for mt. iv is much narrower than in the two White River genera, and has thus quite a different shape and appearance.

The *navicular* is almost a miniature copy of that of *Daphænus* and presents the same differences from that of *Canis*. Seen from the proximal end, it is of more regularly oval shape and is less contracted on the plantar side than in the modern genus. The position of the navicular in the tarsus is likewise different. In *Canis* this bone has been somewhat rotated, so that its principal diameter is the dorso-plantar one, and on the plantar border it has been brought into contact with the calcaneum, for which it has acquired a special facet. It is of interest to observe that a similar but more extensive rotation of the tarsal elements has been carried out in the horses, as Rütimeyer has shown. In the White River genera, on the other hand, the principal diameter of the navicular is transverse, and owing to the elongation of the neck of the astragalus, it is carried so far distally that it can have no contact with the calcaneum, the astragalus articulating with the cuboid. The astragalar surface is concave, but somewhat less so than in *Canis*, and the facet for the cuboid is small and confined to the dorsal moiety of the fibular side. The distal end displays the usual facets for the three cuneiforms, which do not require any particular description.

The *entocuneiform* has much the same shape as in *Canis*, elongate in the proximo-distal diameter, but very narrow and much compressed. The navicular facet is relatively smaller than in the modern genus and there is no such distinct facet for the mesocuneiform. The distal surface, for the head of the first metatarsal, is no wider but much more deeply concave than in *Canis*.

The *mesocuneiform* is a minute bone and, as in the fissipede Carnivora generally, its vertical or proximo-distal diameter is much less than that of the adjoining ento- and ectocuneiforms, forming a depression or recess in the distal row of the tarsus, into which the head of the second metatarsal is tightly wedged. The only articular surfaces visible on the mesocuneiform are the proximal and distal, for the navicular and the second metatarsal respectively.

The *ectocuneiform* is much the largest of the three. Compared with that of *Canis*, it is narrower in proportion to its height and is also less extended in the dorso-plantar dimension, but the projecting process from the plantar surface is even more prominent, and is more thickened and club-shaped at the free end. On the tibial side is a minute facet (not double as in *Canis*) for the side of mt. ii. The facet for the cuboid is much smaller than in the modern dogs and is confined to the dorsal border, while at the infero-external angle of the bone is a minute facet for the head of mt. iv, which is not represented in *Canis*. The distal end of the ectocuneiform is taken up by a facet for mt. iii, which is less concave and has a shorter plantar prolongation than in the modern genus.

The *metatarsus* consists of five well-developed members. Unfortunately, there is not a single complete metatarsal preserved in connection with any of the specimens, but enough remains to show that these bones were much longer and stouter than the metacarpals, and that the disproportion in size and length between the fore and hind feet was much greater than in the recent dogs and quite as great as in many viverrines, such as *Herpestes* and *Paradoxurus* or as in *Daphænus*.

The *first metatarsal* is sufficiently well preserved to indicate that the hallux was well developed and functional, though somewhat more reduced than in *Daphænus*, or in such recent viverrines as *Cynogale* or *Paradoxurus*. The head bears a narrow, convex facet for the entocuneiform and upon its tibial side is a large, rugose prominence for the attachment of the lateral ligament. The shaft is very slender and is arched slightly toward the fibular side of the foot, making the tibial border somewhat concave. The length of the bone, as already intimated, is not determinable, but the portion preserved in one specimen is nearly as long as the entire fifth metacarpal of the same individual.

The *second metatarsal* is much stouter than the first and more slender than the third. The head is very narrow, being slightly excavated on the tibial side. Owing to the shortness of the mesocuneiform, the head of mt. ii rises above the level of mt. i and iii and is firmly held between the ento- and ectocuneiforms, though there are no such distinct lateral facets for these tarsals as we find in *Canis;* a stout prominence occupies the plantar side of the head. The shaft is slender and of oval section, not having acquired the trihedral shape characteristic of the recent dogs.

The *third metatarsal* is the stoutest of the series; the head is broad dorsally but very narrow on the plantar side, where there is a large, projecting process, more prominent than in *Canis.* The facet for the ectocuneiform is convex (in the recent dogs it is slightly concave) and oblique in position, inclining downward toward the tibial side. Deep sulci invade the head on both sides; on the tibial side the sulcus is narrow, but that on the fibular side is broad. A deep pit on the fibular side of the head receives a corresponding prominence from mt. iv, and an additional facet for the same metatarsal is found on the plantar projection, so that the two median metatarsals are very firmly interlocked. The shaft, for most of its length, is of transversely oval section, very different from the squared, prismatic shape seen in *Canis,* though an approximation to this shape occurs in the proximal portion of the shaft, where mt. iii and iv are closely appressed. The distal end is broadened and antero-posteriorly compressed; the trochlea resembles that of the corresponding metacarpal, save that it is larger and relatively somewhat lower.

The *fourth metatarsal* is of nearly the same thickness as mt. iii, though a trifle more slender. The head is narrow and the facet for the cuboid is slightly convex in both directions; the plantar extension is neither so broad nor so prominent as in *Canis.* On the tibial side is a rounded protuberance, which is received into the depression already mentioned, in the head of mt. iii, while on the fibular side is an excavation for a prominence on mt. v, and proximal to this excavation is a narrow but well-defined facet for the same metatarsal. Very little of the shaft is preserved, and this proximal portion has much the same tetrahedral shape as in the recent dogs. Doubtless, however, the distal part of the shaft assumes a transversely oval section, as does that of mt. iii, though the digits of the pes evidently diverge less distally than do those of the manus.

The *fifth metatarsal* is entirely missing from all of the specimens, so that the interesting question regarding the reduction of the external ascending process cannot be answered.

The *phalanges* of the pes do not differ from those of the fore foot, except in their considerably greater size.

Measurements.

	No. 10493.	No. 11012.	No. 11381.
Tarsus, height (excl. calcaneum)	.021		
Calcaneum, length	.0195	.020	
" length of tuber	.012	.012	
" dorso-plant. diam.	.007	.008	
Astragalus, length	.013	.013	.014
" width of trochlea	.005	.0055	.006
" length of neck	.006	.006	.006
" width of head	.007	.007	.008
Navicular, height	.003		
" width	.006		
Ectocuneiform, height	.0045		
" width dist. end	.0045		
Metatarsal i, width prox. end	.0045		
" ii, " " "	.003	.003	
" iii, " " "	.005	.005	
" iii, width dist. end		.005	
" iv, width prox. end	.0035		

IX. Restoration.

The general appearance of the *Cynodictis* skeleton has little about it to suggest canine affinities, but has some resemblance to the civets and especially to the herpestine section of that family. This resemblance is not merely a general one of outline and proportions, but may also be traced in many of the details of structure. The small head, with its elongate and narrow cranium and short, tapering muzzle, is of strikingly viverrine character. So is also the neck, which is relatively long and stout, the vertebræ having heavy centra and well-developed processes. The resemblance to the civets continues into the thoracic region, where the vertebræ are small, especially in the anterior portion, and have short, slender neural spines. The thorax itself, with its slender and moderately curved ribs, is narrow and compressed, as in the Carnivora generally, while the prominent and compressed manubrium has a somewhat viverrine appearance. The lumbar region is long and is strongly curved upward; the vertebræ are much elongated, with stout depressed centra, very long, slender and anteriorly directed neural spines, which are not like those of modern dogs or civets and most resemble the spines of *Lynx*. The transverse processes are likewise peculiar in their length and slenderness. The tail is unlike that of the modern dogs, being much longer, stouter and in every way better developed; it was not, perhaps, quite so long proportionately as in *Herpestes*, but nearly so. This, however, is a primitive feature, which is common to the greater part of the earlier carnivores and ungulates, and is even more conspicuous in *Daphænus* than in *Cynodictis*, while the White River Machairodonts, *Dinictis* and *Hoplophoneus*, have very long and massive tails.

The limbs, though not so long proportionately as in the recent dogs, are much more so than in the John Day species, *C. geismarianus*, the hind legs being especially elongate. The scapula is not at all canine in character, being relatively very large and having the broad blade and irregularly curved coracoid border of the viverrines; the great length of the acromion and the unusual size of the metacromion are peculiar. The humerus is short but quite heavy, and with its low trochlea, prominent deltoid and supinator ridges, and large epicondyle and epicondylar foramen, has an exceedingly viverrine appearance. The ulna and radius are relatively short and slender, and the discoidal head of the latter shows that the power of rotating the manus had been but little diminished; the great styloid process of the radius is very characteristic. The carpus is low and the metacarpals are exceedingly short and weak, resembling in their proportions those of *Paradoxurus*. The phalanges are elongate and the claws sharp and compressed.

The pelvis has a viverrine appearance in its shape and in the elongation of its posterior portion, while the os penis resembles that of the mustelines in size and curvature. The femur is long and the tibia is somewhat longer than the femur, bearing much the same relation to that bone as in *Canis*, while the fibula is much stouter than in the modern genus. The pes is far larger in all its dimensions than the manus, the difference in size between the two being much greater than in *Canis*. It is often exceedingly difficult to determine from the bones alone whether a given animal was plantigrade or digitigrade in gait, but from the resemblance of the limb and foot bones of *Cynodictis* to those of the civets, it seems very probable that the former had a similar semiplantigrade gait.

The John Day species, *C. geismarianus*, is considerably larger than the White River forms, but resembled the latter in proportions. Cope says of it: "Although the skull and pelvis of this species have about the size of those of the fisher, the vertebræ and humerus are more slender and the anterior foot is decidedly smaller. It is probable that the *Galecynus* [*i. e.*, *Cynodictis*] *geismarianus* resembled a large *Herpestes* in general proportions rather than a *Canis*. It stood lower on the legs than a fox and had as slender a body as the most 'vermiform' of the weasels, the elongation being most marked in the region posterior to the thorax. The tail was evidently as long as in the Ichneumons. Its carnivorous propensities were as well developed as in any of the species mentioned, although, like all other *Canidæ* of the Lower Miocene period, the carnassial teeth are relatively smaller than in the recent types" ('85, p. 929).

The White River species of this genus are probably two in number.

Cynodictis gregarius Cope.

Syn. *Amphicyon gracilis* Leidy (*non* Pomel), *Proc. Acad. Nat. Sci. Phila.*, 1856, p. 90; 1857, p. 90; *Ext. Mamm. Fauna Dak. and Nebr.*, p. 36. *Amphicyon angustidens* Marsh, *Amer. Journ. Sci. and Arts*, 3d Ser., Vol. II, p. 124. *Canis gregarius* Cope, *Ann. Rept. U. S. Geolog. Surv. Terrs.*, 1873, p. 506. *Galecynus gregarius* Cope, *Tertiary Vertebrata*, p. 916.

This is the species which has been described so minutely in the foregoing pages. It is one of the commonest White River animals and is very much more frequently met with than any of the contemporary carnivores. Despite this abundance of individuals, well-preserved specimens are rare and even these consist mostly of skulls only. As will be seen from the tables of measurements, the different specimens vary little in size or in the proportions of the various parts of the skeleton. One apparent exception to this statement may be found in the case of No. 11381, which is remarkable for the length of its hind limb, but this probably belongs to the following species:

Cynodictis lippincottianus Cope.

Canis lippincottianus Cope, *Synopsis of Vertebrata Collected in Colorado; Miscell. Publ. U. S. Geolog. Surv. Terrs.*, 1873, p. 9; *Ann. Rept. U. S. Geolog. Surv. Terrs.*, 1873, p. 506. *Galecynus lippincottianus* Cope, *Tert. Vert.*, p. 919.

The status of this species is still a matter of some uncertainty; Cope, who established it upon mandibular rami, describes it as having "dimensions half as large again as in *C. gregarius*," and adds: "Unfortunately there is not enough material in my hands to render it clear whether the specimens represent a distinct species or a large variety of the *C. gregarius*" ('85, p. 920).

Among the specimens described in the foregoing pages is one (No. 11381) in which the limb bones decidedly exceed in length and thickness those of the other individuals, while the cranium is but little larger. Probably this specimen should be referred to *C. lippincottianus*, but in the absence of teeth the reference can be only provisional.

In the John Day formation *Cynodictis* is represented by more numerous and more varied species than in the White River beds; from the former horizon Cope has determined *C. gregarius*, *C. lemur*, *C. latidens* and *C. geismarianus*.

Still another species should be mentioned in this connection. In the American Museum of Natural History, New York, are the remains of a small cynoid animal from the Uinta beds, which may belong to *Cynodictis*, or if not, should be referred to some closely allied genus. It is important to observe that in the Uinta stage (uppermost Eocene or lowest Oligocene) we find that the two canine series, represented in White River times by *Daphœnus* and *Cynodictis*, had already been established.

The Phylogeny of the Canidæ.

It seems probable that the fossil genera of this family already known are sufficient to indicate to us the main outlines of its phylogenetic history. The problem of reconstructing the series is, however, obscured by two circumstances; first, the variety and multiplicity of nearly allied genera, the mutual relationships of which are very complex and difficult to disentangle; and in the second place, by the fact that only rarely do we obtain satisfactory material of any of the genera. Most of the forms are known only from the skull and teeth, and the skeleton has, so far, been found in but few of the species. *Cynodictis, Daphœnus, Temnocyon* and *Ælurodon* are now known from more or less complete skeletons, but we shall need to learn far more than we know at present concerning the structure of the other genera before we can reach a solution of the many problems of canine phylogeny.

Before taking up the discussion of these phylogenetic problems, it will be convenient to establish the order of geological succession in which the various genera make their appearance. We have seen that in the Uinta there appear to be two distinctly separated canine series, one of which is represented by *? Miacis* and the other by a genus which is very closely allied to, if not identical with *Cynodictis*. The former series would seem to be continued into the White River by *Daphœnus* and the latter, of course, by *Cynodictis*. The latter genus may well prove to be of Old World origin, for in the European Oligocene it attains such a variety and fullness of development as it never reached in America, although, on the other hand, the American creodont genus *Miacis*, from which *Cynodictis* probably took its origin, has not yet been found in Europe. In the John Day stage the canine phylum underwent an extraordinary expansion. *Daphœnus* persisted, but is represented only by a single small species, *D. cuspigerus*, while the series branched out into several distinct and more or less specialized genera, such as *Temnocyon, Hypotemnodon, Cynodesmus, Enhydrocyon*, and perhaps even the little known *Hyænocyon*. No new genera of the *Cynodictis* series have yet been detected, but that genus itself became differentiated into many more species than occur in the White River, and some of these may, on better knowledge, prove to be generically distinct. On the other hand, *Oligobunis* probably represents, as Schlosser has suggested, an immigrant from the Old World, belonging to the series which leads from the Oligocene *Cephalogale* to the Pliocene *Simocyon*. The dogs of the Loup Fork, with the exception of the aberrant *Ælurodon*, are very imperfectly known and the remains of them which have been found are not, according to present knowledge, generically separable from *Canis*, though it hardly seems probable that the modern genus had actually been differentiated so early as the upper Miocene, and we may regard it as extremely likely that these supposed representatives of *Canis* will eventually prove to belong to more primitive genera. None of the forms which have hitherto been found in the Loup Fork beds can be referred to the *Cynodictis* line.

The mutual relationships between the two canine series, which are already so well distinguished in the Uinta, are quite obscure and puzzling, although there is nothing to forbid the assumption that both series converge to a common ancestor in the Bridger, perhaps the genus *Miacis*. The *Cynodictis* series, when we first meet with it, is decidedly more advanced than the other phylum, as is shown in the development of the skull, the reduction of the dentition, the character of the limbs and feet and the digitigrade gait. Continuing through the White River age and, so far as North America is concerned, attaining its maximum of development in the abundance and variety of its species in the John Day, the line apparently disappears and can be traced no farther. Whether the series actually died out at the end of the John Day, or whether it continued farther and possesses representatives even at the present time, are questions which cannot yet be definitively answered. Schlosser ('88, p. 247) has suggested that some of the species of *Cynodictis* may, perhaps, be of phylogenetic significance in the canine stem, but if so, they can hardly be placed in the thooid series, which apparently has no place for them. M. Boule ('89, p. 321), in an article upon the Pliocene *Canis megamastoides* Pomel, comes to the conclusion that the modern *Canidæ* are diphyletic, and have arisen by a process of convergence, the thooids and the bears being divergent groups derived from *Amphicyon*, while the alopecoids and viverrines are descended from *Cynodictis*. In discussing the affinities of the Pliocene form Boule says:

"La description précédente nous montre que le fossile de Perrier se rattache de plus près aux Renards qu' aux autres représentants actuels de la famille des Canidés. Par son crâne, le *Canis megamastoides* ressemble beaucoup le Renard de nos pays. Par la forme de sa mandibule, il se place au contraire près des Renards américains (*Canis cancrivorus*, *C. azaræ*, *C. cinereoargentatus*) et près de l' *Otocyon megalotis* de l'Afrique australe. Ces espèces, notamment la dernière, sont regardées par tous les auteurs comme des formes primitives.

"Tout en ratifiant ce premier rapprochement, la dentition presente des caractères particuliers que nous retrouvons en grande partie dans les *Cynodictis* et *Cephalogale* du Miocène (p. 327).

"Les belles récherches de M. Filhol nous ont révélé la richesse en espèces de ces genres si curieux, placés aux confins de plusieurs familles de Carnassiers. Les *Cynodictis* et les *Cephalogale* avaient la formule dentaire des Chiens actuels, mais leurs dents presentaient un aspect particulier qui a valu à ces animaux fossiles le nom de *Chiens viverriens.* Or en étudiant les pièces originales de la collection du Muséum et les livres de M. Filhol sur les Phosporites du Quercy, j'ai été frappé de retrouver, comme parsemés dans diverses espèces de *Cynodictis* beaucoup des charactères présentés par le *Canis megamastoides*" (p. 328).

"Il semble donc que les Renards actuels représentent une branche emanée du buisson touffer des *Cynodictis,* duquel se serait également detachée la branche des Viverridés. Je suppose que lorsqu' on connaîtra suffisament les membres des diverses espéces de *Cynodictis,* on trouvera des formes de passage allant d'un côté aux membres des Viverridés et d'un autre côté aux membres des Renards.

"Si ces considerations sont exactes, les Chiens ont une origine differente des Renards. Les *Amphicyons* représentent les ancêtres communs des Ours et des Chiens, comme les *Cynodictis* représentent les ancêtres communs des Civettes et des Renards" (p. 329).

M. Boule's argument as to the derivation of the foxes from *Cynodictis* is not a very convincing one and is open to several obvious objections. In the first place, M. Boule does not define the sense in which he uses the term *fox;* it is evidently not the same as Huxley's alopecoid, for *C. cancrivorus* and *C. azaræ* are called foxes, while Huxley regarded them as typical though primitive thooids. M. Boule does not say whether *C. megamastoides* possessed a frontal sinus, but from the statement that "le frontal est saillant, à surface arrondie" (pp. 324, 325), one would infer the presence of a sinus, and if so, *C. megamastoides* is not an alopecoid, but a thooid. The presence or absence of frontal sinuses and the shape of the cerebral fossa are the only diagnostic characters which Huxley could find definitely distinguishing the two canine series from each other. In the second place, the resemblances in tooth structure between *Cynodictis* and *Canis megamastoides,* upon which M. Boule places such emphasis, are in themselves of no great value, because the resemblance of the latter species to *Cephalogale* is even greater, and *Cephalogale,* as Schlosser has shown, probably belongs in a totally different line, which has no existing representatives. In any event, the gap between the Pliocene and Oligocene forms is still so wide that no determination of the taxonomic value of their resemblances and differences can yet be made.

Again, it is highly improbable that the viverrines can be descended from *Cynodictis,* for the latter, though having certain marked resemblances to the civets, is in all essentials of structure distinctly a member of the *Canidæ,* and is no more ancient than certain unmistakable viverrines. Indeed, the genus *Viverra* itself is reported from the upper Eocene of Europe, occurring in the same horizons as those in which *Cynodictis* first appears. For similar reasons, it is very difficult to believe that *Amphicyon* can be the ancestor of the thooids, for that genus has already begun to become differentiated in the direction of the bears and is contemporary with or even younger than certain American genera, such as *Temnocyon* and *Cynodesmus*, which are undeniable thooids.

M. Boule's hypothesis involves some rather startling consequences ; if true, we shall be forced to conclude that the two series of modern *Canidæ* have been separated ever since the close of Eocene times and that they had no common ancestor nearer than the middle Eocene or Bridger stage. This conclusion would imply such an extreme and remarkable degree of parallelism or convergence as has hardly been believed possible, an exact parallelism in all parts of the dentition, skeleton and soft parts, terminating in almost complete identity of structure. Indeed, many systematists regard most of the modern foxes and wolves as belonging to the single genus *Canis*, and Huxley speaks of the differences between them as being so slight, that a generic separation can be justified only on the grounds of convenience. Is it conceivable that two series of mammals which were already separated in the Eocene should have converged into what is practically a single genus?

Unlikely as it may appear, I am inclined to believe M. Boule's hypothesis concerning the relationship of *Cynodictis* to the alopecoids is not to be summarily dismissed, but that it may eventually prove to be well founded. It is certainly a suggestive fact that *Cynodictis*, like the foxes, is devoid of any frontal sinus, while all of the other American genera, from *Daphænus* onward, have well-marked sinuses, as in the wolves. Furthermore, whatever conclusion we may reach with regard to the single or dual origin of the *Canidæ*, there is much reason to believe that such extreme cases of parallelism and convergence have occurred among mammalian phyla and that they may be more frequent than is commonly supposed. One very striking example is that of the true cats (*Felinæ*) and the sabre-tooth series (*Machairodontinæ*) originally pointed out by Cope and elaborated in much detail by Adams ('96).

Unfortunately, complete demonstration is lacking in this very extraordinary case of parallel development, because the early stages in the phylogeny of the true cats have not yet been recovered, but the successive genera of the Machairodonts are fairly well known, and they form a connected series. None of these machairodont genera, not even the earliest and most primitive of them, can be regarded as ancestral to the true cats, for without exception they all display the characteristic and unmistakable features which place them in the sabre-tooth series. The more primitive genera, such as *Dinictis*, possess a dentition which is but slightly modified in the direction of the cats, and cranial foramina resembling those of the early dogs in the presence of an alisphenoid canal, the separation of the condylar foramen from the foramen lacerum posterius, etc.; the femur has a third trochanter and the humerus an extremely prominent deltoid ridge; the feet are plantigrade and pentadactyl and, like those of many of the viverrines, they are supplied with partially retractile and very incompletely hooded claws. In all probability these structural characters also occurred in the ancestral *Felinæ*, but what distinguishes even the earliest Machairodonts is the elongation and compression of the upper canines, the reduction in size of the inferior ones and the development of bony flanges from the ventral border of the mandible for the protection of the superior tusks. From such beginnings the sabre-tooth series may be traced, with various divagations and side branches, to the Pleistocene *Smilodon,* which in all parts of its structure is extraordinarily like *Felis,* the only important differences consisting in the dentition (which is of similar type) and in the modifications of the skull, which are necessarily correlated with the enormous enlargement of the upper canine tusks.

Seeing, therefore, that the machairodont series is well-nigh complete and that none of its known members is at all likely to prove ancestral to the true cats, there can be little reasonable doubt that the remarkably close resemblance which we observe between *Felis* and *Smilodon* is not directly due to their relationship, but has been independently acquired in the two series and is the outcome of a parallel course of development, continued from the Oligocene to the Pleistocene. If this be true, there can be no *à priori* ground for denying that the same phenomena may have been repeated in the dogs and that Boule's suggestion concerning the derivation of the alopecoids from *Cynodictis* may possibly prove to be correct. In this case, however, the final identity of the two series is even more striking than in the cats and Machairodonts; to verify the suggestion, it will be necessary to recover the missing links of the alopecoid phylogeny and to show that it has followed a course parallel to but independent of that of the thooids.

Another alternative possibility is that the foxes became separated from the principal canine phylum at a comparatively late date, and that, consequently, *Cynodictis* and its allies represent but an abortive side-branch from the main stem. That the separation is of considerable antiquity is shown by the parallel arrangement of the two series to which Huxley has called attention. In both wolves and foxes we find species with microdont and macrodont dentition, with sagittal crests and lyrate sagittal areas, with lobate and non-lobate mandibles. So far, at least, we are almost certainly dealing with independently acquired characters. From the standpoint of present actual knowledge it is more probable that the separation did not take place before the end of the Miocene than that it had already been accomplished in the Eocene, though this conclusion involves the admission that *Cynodictis* had anticipated the foxes in quite a remarkable way. While very far from denying the possibility of such convergence as is implied in Boule's hypothesis, I think it should not be assumed in a given case except upon the clearest evidence. Whichever of these alternatives be true, it is, in any event, probable that the alopecoids are not of American origin.

Still a third possible solution of the problem concerning the mutual relationships of the wolves and foxes is that *Cynodictis*, or some similar form, is the common ancestor of both lines, and that the supposed early thooids, such as *Daphænus* and *Cynodesmus*, are devoid of permanent phylogenetic significance. This is decidedly the least probable of the three alternatives, for the thooids of the American Oligocene and Miocene seem to form a truly connected series, in which *Cynodictis* has no place. Further, this view involves the assumption that the supposed thooids have independently run a course parallel to that of the true thooids and thus encounters the very difficulty which it was intended to avoid. The conclusion which we reach is, therefore, that the thooids are probably of American origin and that the alopecoids are a branch which the wolf stem gave off after certain of its representatives had established themselves in the Old World.

The thooid genealogy itself is by no means free from difficulties. In a former paper ('94), I suggested that the line begins in *Daphænus* of the White River, and is continued by the John Day *Cynodesmus*, but now that we have learned the remarkable characters of the skeleton, especially of the limbs and feet, of the former genus, this view no longer appears so simple and natural, and its acceptance carries with it some far-reaching and unexpected consequences. In particular, it might be objected to this view that the peculiar differentiation of the feet in *Daphænus* would exclude that form from any place in the direct canine phylum, for it seems *à priori* unlikely that the dogs should first have acquired the power of retracting the claws and should then have subsequently lost it. Indeed, many morphologists are inclined to deny altogether the possibility of this method of evolution. In the present state of knowledge, however, such a denial is at least premature, and there is a considerable body of evidence which goes to show that it does not properly apply in the case of the canine phylum.

In the first place, the John Day genus *Temnocyon*, the osteology of which has been very fully described by Eyerman ('96), appears to be a direct descendant of *Daphnusæ*, with which it agrees in the essentials of structure, though, at the same time, it displays many marked changes and advances. One of the most striking of these changes in the later form is in the great elongation of the limbs and the assumption of a digitigrade gait, both limbs and feet quite closely approximating those of the modern *Canidæ*. Yet even in *Temnocyon* a reminiscence, as it were, of the partially retractile claws of *Daphænus* may be observed in a certain asymmetry of the second phalanges of both manus and pes, which are slightly excavated on the ulnar and fibular sides respectively. While *Daphænus* was a short-limbed, plantigrade or semi-plantigrade form, which, in all probability, was not cursorial in habits, *Temnocyon*, on the other hand, was undoubtedly cursorial and probably essentially resembled the modern wolves in appearance and habits. In this change to a digitigrade gait and cursorial habit, it seems quite reasonable to suppose that the mode of using the claws should have been changed likewise, the feet being used almost exclusively for purposes of locomotion and the claws losing their importance as weapons and grasping organs. Under these circumstances the power of retraction would become superfluous and tend to disappear, although, as we have seen, *Temnocyon* retains recognizable traces of the structure which permits retraction of the claws. It is true that *Temnocyon* itself is not in the direct line which leads up to the modern *Canidæ*, for the heel of the lower sectorial and the whole of m $\overline{2}$ have become trenchant through the loss of the internal cusps, a curious specialization; but, on the other hand, there is no reason to suppose that it differed in any other important respect from its contemporary *Cynodesmus*, which appears to be a member of the direct phylum.

In the second place, a similar loss of the power of retracting the claws has almost certainly occurred among the *Felidæ*. The hunting leopard or cheetah (*Cynælurus*) has acquired something of the proportions and appearance of the wolves, having very elongate limbs and feet and a running gait which is described as quite different from that of the ordinary cats. Comparing the phalanges of *Cynælurus* with those of *Felis*, some marked differences are at once apparent; in the lateral digits the second phalanx is quite symmetrical and is not excavated on the ulnar (or fibular) side; the excavation is distinctly shown only in the third digit and is much less marked in the fourth. The bony hood of the ungual phalanx is much reduced, leaving more than half the length of the phalanx exposed, and the subungual process is much smaller than in *Felis*. The tarsus, in fact the skeleton of the entire pes, has a canine aspect, and the retractility of the claws is very partial and imperfect. Now, there can be little doubt that *Cynælurus* is not the remnant of a very ancient group, given off from the feline stem at a time when the power of retracting the claws had been but partially attained, but that it was derived from ancestors which differed little from *Felis*. If such a transformation could take place among the cats, there would seem to be no good reason for denying that it might also occur in the dogs.

Unfortunately, the phylogenetic history of the dogs is not made clearer and more intelligible by reason of the new material of *Daphænus*, which has been described in the foregoing pages, and which raises more problems than it solves. I am inclined to believe, however, that *Daphænus* should still be given a place in the canine phylum, for the differentiation of its limbs and feet is hardly of that radical kind which would prevent a subsequent change in the trend of development, and its many resemblances to the early Machairodonts are, at least in part, survivals of primitive conditions, several of which, like the shape of the radius, recur in *Cynodictis.* Tending to the same conclusion is the fact that what little is known of the structure of the creodont *Miacis* is of similar composite canine-feline character and it is to that creodont family to which most of the lines of fissipede Carnivora appear to lead back. It may be hoped that the problem will receive its definite solution when we shall have recovered the as yet missing or very imperfectly known dogs from the Uinta, uppermost White River and lowest John Day formations, and are thus enabled to trace the successive changes step by step.

Assuming, then, as probable that *Daphænus* should have a place in the direct canine phylum, the larger question at once arises: What was the relation between the early members of the *Canidæ* and *Felidæ*, and of both of these groups to the other fissipede families? It seems to be a comparatively rare phenomenon among the mammals that parallelism or convergence of development should be manifested in all parts of the structure of two independent lines, though that this may happen is shown by the case of the Machairodonts and felines, to which reference has already been made. Usually, however, parallelism is displayed in a few structures only, such as the dentition, or the feet, or the vertebræ, and the more widely separated any two phyla are at their point of origin, the less likely are they to develop along similar lines. It will be sufficiently clear from the foregoing descriptions that the resemblances between *Daphænus* and the more primitive Machairodonts, such as *Dinictis*, are not only exceedingly close, but that they recur in all parts of the skeleton. The skull, the vertebral column, the limbs and the feet are all so much alike in the two series that, in the absence of teeth, it is often very difficult to decide to which of the two a given specimen should be referred. Such close and general resemblance is *prima facie* evidence of relationship, even though it should have been independently acquired, because parallelism is much more frequent between nearly allied than between distantly related groups. In the present instance, however, there is no reason to infer that the resemblances were separately attained; on the contrary, the evidence now available seems to favor the conclusion that the dogs and cats are derivatives of the same Eocene stock. It cannot be pretended that this conclusion is, as yet, a well-established one, nor can it be so established until we recover the missing links of the canine and feline genealogies. *Daphænus* may eventually prove to be merely an abortive side-branch without phylogenetic significance, though this seems unlikely in view of its relationship to the John Day dogs. On the other hand, when we have learned more of the Uinta dogs, it may appear that all the many resemblances of *Daphænus* to the Machairodonts have been separately attained; but existing evidence does not favor this suggestion either. It seems exceedingly likely that the dogs and cats are more closely related than has hitherto been believed and that they were derived from a common middle or late Eocene progenitor.

On the assumption that the dogs and cats are thus quite closely connected, what can be said concerning the relations of the other fissipede families with these groups and with one another? Of the derivation of the *Procyonidæ* nothing is yet known; the family may be traced back into the Loup Fork without finding essential changes, but beyond that period we lose track of it altogether. The position of the bears and hyænas is reasonably clear, the latter being late derivatives of the viverrines and the former of the dogs, neither family making its appearance until long after the other fissipede groups had become clearly differentiated. The *Viverridæ* have a great many characters in common with both the early dogs and the early Machairodonts; almost all the structural features which are found in both *Daphænus* and *Dinictis* recur also in the viverrines, and the latter again have many points of similarity to *Cynodictis*, as has often been remarked. That the viverrine features of *Cynodictis* are more numerous and apparent than those of *Daphænus* is largely due to the small size of the former, which agrees much better with the stature usual in the recent viverrines. The viverrines thus seem to be derivatives of the same Eocene stock as that which gave rise to both the dogs and the cats, though, perhaps, they are more nearly allied to the latter than to the former, and apparently they have departed less from that primeval fissipede stem than has either of the other families. Aside from the peculiar character of the auditory bulla and the reduced number of the molar teeth, such a genus as *Viverra* would seem to differ but little from the hypothetical Eocene ancestor of all the fissipede families. The *Mustelidæ* represent a quite specialized branch of the fissipedes, but between its earlier and more primitive members and the corresponding representatives of the viverrines are so many structural resemblances that Schlosser does not hesitate to derive them from a common stem. An interesting and significant example of this community of characters among the early representatives of the different fissipede families is given by the *os penis* of *Cynodictis*, which resembles that of the mustelines much more closely than that of the modern dogs. This probably indicates that all of the earlier fissipedes had this bone shaped very much as in the existing mustelines, which have thus retained the primitive form, while in the other families it has become much modified in shape and size. This would explain the apparent anomaly of the very large *os penis* of *Cryptoprocta* which is so different from that of the other viverrines. According to this way of looking at the subject, there was a middle Eocene group of flesh-eaters, perhaps the creodont family *Miacidæ*, which rapidly diverged into four principal branches, the cats, dogs, viverrines and mustelines, all of which families were established in the late Eocene or early Oligocene, and to these should perhaps be added a fifth family, the *Procyonidæ*, though of this we know nothing definite. The Fissipedia are thus probably a monophyletic rather than a polyphyletic group, which was derived from a single creodont family.

It is exceedingly difficult to unravel all this complicated mesh-work of similarities and definitely to distinguish those characters which are due to genetic relationship from those which are merely phenomena of parallelism or convergence. But the important fact remains that in the late Eocene and early Oligocene all of the families of fissipede Carnivora which had then come into existence were very much alike and in all parts of their structure resembled one another much more closely than do their modern representatives. They are obviously converging back to a common term, and the only question is what that common term was and whether we are to look for it in the middle or the lower Eocene. It must be reiterated, however, that natural and probable as this conclusion appears to be, it is only tentative and cannot be demonstrated until the successive phylogenetic stages of each family are much better known than they are at present.

Summary.

1. *Daphænus*, so named in 1853 by Leidy and afterwards referred to *Amphicyon*, is very different from the latter and an entirely distinct genus.

2. The dental formula is: I $\frac{3}{3}$, C $\frac{1}{1}$, P $\frac{4}{4}$, M $\frac{3}{3}$; the premolars are small and simple and are set well apart in the jaws; the sectorials are small and primitive, especially in ? *D. Dodgei*, and the molars relatively large, most so in *D. vetus*. The dentition is more like that of the creodont family *Miacidæ* than of the typical modern dogs.

3. The skull is of a very primitive character, with short face, very elongate cranium and high sagittal crest; the cranial cavity is of small capacity and the postorbital constriction is placed far back of the eyes. Large frontal sinuses are present.

4. The occiput is low and broad, with very prominent crest; the paroccipital processes are short and blunt and are widely separated from the tympanic bullæ.

5. The auditory bulla is minute and does not fill up the fossa, exposing the periotic; it probably represents only the anterior chamber, the posterior chamber was either not ossified or was very loosely attached, so that it is lost in all the known specimens.

6. The cranial foramina differ very little from those of *Canis*.

7. The mandible has a short horizontal ramus, varying in its proportions in the different species; the ascending ramus is low and very broad.

8. The brain is remarkable for the small size and simple convolutions of the cerebral hemispheres and the large size of the cerebellum and olfactory lobes.

9. The foramina of the atlas differ from those of the recent dogs and resemble those of the cats.

10. The axis is also of feline character, especially in the shape of the neural spine.

11. The other cervical vertebræ have more prominent zygapophyses, narrower neural arches and higher neural spines than in *Canis*.

12. The thoracic vertebræ probably numbered thirteen; they resemble those of the modern dogs, except for their longer neural spines, and for the much more prominent anapophyses on the last three vertebræ.

13. The lumbars, probably seven in number, are remarkably large and massive and all their processes are very long; the appearance of these vertebræ is feline rather than canine.

14. The sacrum is composed of three vertebræ and resembles that of the larger cats in its size and weight.

15. The tail is very long and stout, resembling in its proportions and in the development of the individual vertebræ that of the leopard.

16. The humerus is in most respects like that of the Machairodonts, *Dinictis* and *Hoplophoneus*, having very prominent deltoid and supinator ridges, very low trochlea, large epicondyles and an entepicondylar foramen.

17. The radius is very feline in character, as is seen in the discoidal head, the slender curved shaft and expanded distal end.

18. The ulna is much less reduced than in the modern dogs, and its shape, especially that of the distal end, is much more feline than canine.

19. The only carpal element preserved is the scapho-lunar which is very like that of the Machairodont *Hoplophoneus*.

20. There are five metacarpals which are not at all like those of modern dogs, the pollex being far longer and all of the metacarpals having short, slender, rounded shafts, spheroidal distal trochleæ, and a divergent instead of a parallel arrangement. The contact of mc. ii with the magnum and of mc. iv with the unciform is much less than in the true felines and about as in the Machairodonts.

21. The pelvis is machairodont rather than canine, the ilium being relatively short and narrow, the ischium long, with inconspicuous tuberosity, and the obturator foramen large; the pubic symphysis is elongate.

22. The femur is not very long in proportion to the size of the animal; its trochlea is very low and shallow; a third trochanter appears to have been present.

23. The patella is like that of *Dinictis*, being broad, thin and almond-shaped.

24. The tibia is short and slender and bears considerable resemblance to that of *Dinictis;* its distal end bears a very large internal malleolus and feebly grooved astragalar trochlea.

25. The fibula is much stouter than in *Canis* and has more thickened ends.

26. The tarsus is, on the whole, of machairodont or viverrine character, but with not a few canine features.

27. The metatarsus has five members, a well-developed hallux being present; the

character of these is intermediate between those of the dogs and those of the Machairodonts.

28. The phalanges are long and depressed; the second one is excavated on the fibular side, showing that *the claws were partially retractile,* though much less completely so than in the cats; the unguals are straight, compressed and bluntly pointed, and with bony hoods much as in *Canis.*

29. The known species of *Daphænus* are: *D. vetus* Leidy, *D. hartshornianus* Cope, *D. felinus,* sp. nov., ? *D. Dodgei* sp. nov., all from the White River beds, and *D. cuspigerus* Cope, from the John Day.

30. The cynoid from the Uinta beds, *Miacis uintensis,* is regarded as the forerunner of *Daphænus.*

31. The small American cynoids of the White River and John Day, and, perhaps, of the Uinta, should be referred to the European genus, *Cynodictis.*

32. The dental formula of *Cynodictis* is: I $\frac{3}{3}$, C $\frac{1}{1}$, P $\frac{4}{4}$, M $\frac{2}{3}$; the premolars are small, the sectorials microdont and quite viverrine in appearance, but more trenchant than those of *Daphænus,* and the tubercular molars are small.

33. The skull has a very viverrine look; the face is short, the cranium long, though shorter and fuller than in *Daphænus,* and the postorbital constriction is near the orbit; the sagittal crest is low and weak, and in the small *C. lemur* is replaced by a lyrate area.

34. There are no frontal sinuses.

35. The occiput is low and broad, the crest inconspicuous and the paroccipital processes are small and not in contact with the bullæ.

36. The auditory bulla is very large and the posterior chamber fully ossified.

37. The cranial foramina are like those of *Canis,* save for the visible carotid canal.

38. The mandible has a short, slender horizontal ramus and the ascending ramus is much narrower than in *Daphænus.*

39. While the cerebral hemispheres are larger and better convoluted than those of *Daphænus,* they are smaller and have fewer, straighter sulci than in the modern *Canidæ;* the olfactory lobes are large and the cerebellum complex.

40. The atlas has short transverse processes and its foramina are feline in character.

41. The axis is much like that of *Viverra.*

42. The other cervicals are of canine type.

43. The thoracic vertebræ are small and have high, slender spines; on the last two are prominent anapophyses.

44. The lumbar region is long, heavy and arched upward; it is composed of seven vertebræ, which have very long transverse processes and low, slender spines. Anapophyses are large anteriorly, but disappear on the sixth.

45. The tail was very much as in such viverrines as *Herpestes*.

46. The sternum is of a generalized fissipede character, without special resemblance to either dogs or viverrines.

47. The scapula has little resemblance to that of *Canis*, being low and broad, with spine placed nearly in the middle of the blade; the metacromion is very large and the acromion exceedingly long and prominent, from which it may be inferred that the clavicles were less reduced than in the modern dogs; the coracoid is very large.

48. The humerus is much more viverrine than canine in appearance, having, like *Daphœnus*, very prominent deltoid and supinator ridges, a low trochlea and entepicondylar foramen, but no supratrochlear perforation.

49. The radius is like that of *Daphœnus*, except for the immense styloid process.

50. The ulna is much stouter than in the recent dogs and differs from that of *Daphœnus* in having the distal radial facet sessile.

51. The carpus contains a scapho-lunar which is quite like that of *Canis*; the pyramidal is viverrine and the pisiform quite peculiar in shape; a radial sesamoid appears to have been present; the trapezoid and magnum are canine, while the unciform is viverrine.

52. The metacarpus has five elements, which are very short and slender like those of the civets.

53. The pelvis is, in general, canine, but primitive in the elongation of the postacetabular portion.

54. The os penis is very large and shaped like that of *Cryptoprocta* and the mustelines.

55. The femur is elongate and differs little from that of the recent dogs, except in the presence of a small third trochanter and in the narrow, shallow rotular trochlea.

56. The patella is wide, thin and scale-like, herpestine in shape.

57. The tibia is of nearly the same length as the femur, and its distal end is like that of *Daphœnus* and *Dinictis*, but more deeply grooved.

58. The fibula is relatively stout.

59. The general appearance of the pes is viverrine and has many resemblances to that of *Daphœnus* and some to that of *Canis*.

60. A well-developed hallux is present and the metatarsals exceed the metacarpals in length much more than they do in *Canis*.

61. The phalanges differ materially from those of *Daphœnus* in that the claws are little or not at all retractile; the unguals have but rudimentary hoods.

62. The skeleton of *C. geismarianus* was very herpestine in proportions, while that of *C. gregarius* was more like that of a very small fox in which the hind leg much exceeded the fore leg in length.

63. The known American species of the genus are: *C. gregarius* Cope and *C. lippincottianus* Cope (the latter doubtful) from the White River, and *C. gregarius* Cope, *C. geismarianus* Cope, *C. latidens* Cope and *C. lemur* Cope, from the John Day.

64. The dogs are represented in the Uinta by two lines, ? *Cynodictis* and *Miacis*, the former continued through the White River and John Day and the latter apparently passing into *Daphænus* of the White River, and through this into *Temnocyon*, *Hypotemnodon*, *Cynodesmus* and *Enhydrocyon* of the John Day, *Oligobunis* of this formation being probably an immigrant from the Old World.

65. M. Boule's hypothesis that the alopecoids are derived from *Cynodictis* and the thooids from *Amphicyon* implies an improbable degree of convergent development, but it is not to be rejected as impossible. According to present evidence the alopecoids arose relatively late from the thooid stem.

66. The thooid line appears to be *Miacis—Daphænus—Cynodesmus—Canis*, the retractile claws of *Daphænus* having been changed when the digitigrade gait and cursorial habit were assumed.

67. The very many resemblances between *Daphænus*, *Cynodictis* and *Dinictis* were probably not independently acquired, but point to a common Eocene ancestor.

68. The early members of the canines, felines, mustelines and viverrines all have a great many more structural features in common than do their existing representatives and would seem to converge to a single Eocene type, which may prove to be the creodont family *Miacidæ*. The hyænas and bears belong to a later cycle of development and were derived, the former from the viverrines and the latter from the dogs.

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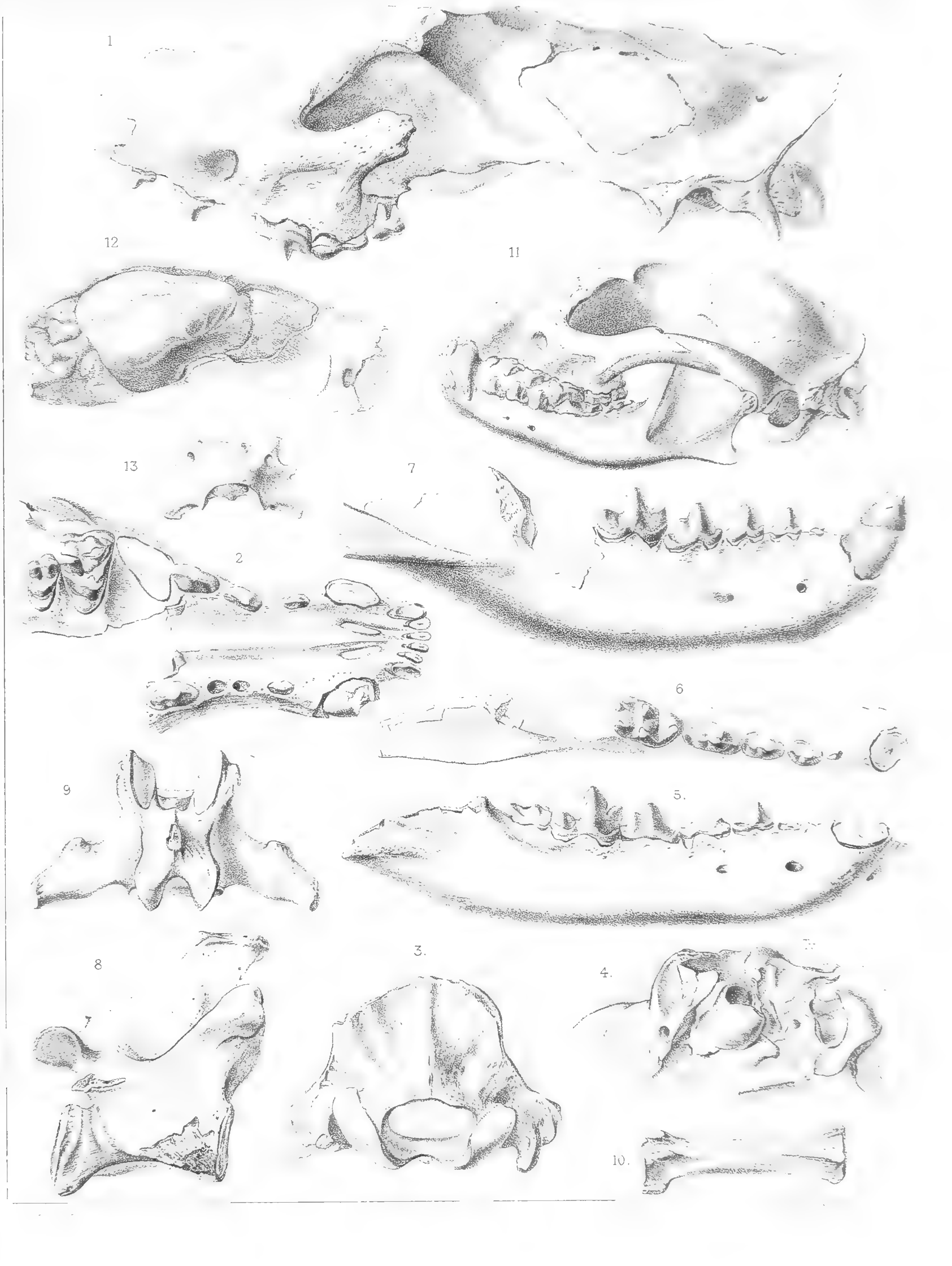
Explanation of the Plates.

Plate XIX.

Fig. 1. *Daphænus hartshornianus* Cope. Side view of skull.
Fig. 2. " " " Palate and teeth of a second specimen.
Fig. 3. " " " Occiput; same specimen as Fig. 1.
Fig. 4. " " " Basis cranii of same individual: *ty.*, tympanic; *f.*, fossa behind bulla; *c. f.*, condylar foramen.
Fig. 5. *Daphænus hartshornianus* Cope. Right lower jaw.
Fig. 6. *Daphænus Dodgei*, sp. nov. Lower teeth, crown view.
Fig. 7. " " " " Side view of right lower jaw.
Fig. 8. *Daphænus vetus* Leidy. Lumbar vertebra, from the side.
Fig. 9. " " " Anterior caudal vertebra from above; same individual.
Fig. 10. " " " Posterior caudal vertebra from the side; same individual.
Fig. 11. *Cynodictis gregarius* Cope. Side view of skull (lower canine broken away).
Fig. 12. " " " Brain cast from the right side: *olf.*, olfactory lobe; *rh.*, rhinal sulcus; *f.*, frontal bone, showing the absence of sinus.
Fig. 13. *Cynodictis gregarius* Cope. Atlas from above.
(*All figures natural size.*)

Plate XX.

Fig. 14. *Daphænus vetus* Leidy. Sacrum from above; same specimen as Figs. 8, 9, 10.
Fig. 15. *Daphænus felinus*, sp. nov. Lower end of humerus, front view.
Fig. 16. " " " " Proximal end of radius; same individual.
Fig. 17. " " " " Metacarpals i–iv of left manus; same specimen.
Fig. 18. *Daphænus vetus* Leidy. Right femur, front view; same specimen as Fig. 14.
Fig. 19. *Daphænus hartshornianus* Cope. Lower half of right tibia and fibula.
Fig. 20. " " " Distal ends of same.
Fig. 21. " " " Right pes; same individual.
Fig. 21*a*. " " " iii digit, from tibial side; same individual.
Fig. 22. *Daphænus vetus* Leidy. Left calcaneum and astragalus; same specimen as Fig. 14.
Fig. 23. *Cynodictis gregarius* Cope. Left manus, front view.
Fig. 24. " " " Left pes, front view. (Specimens seen since this plate was drawn show that the metatarsals should have been made considerably longer.)
(*All figures natural size.*)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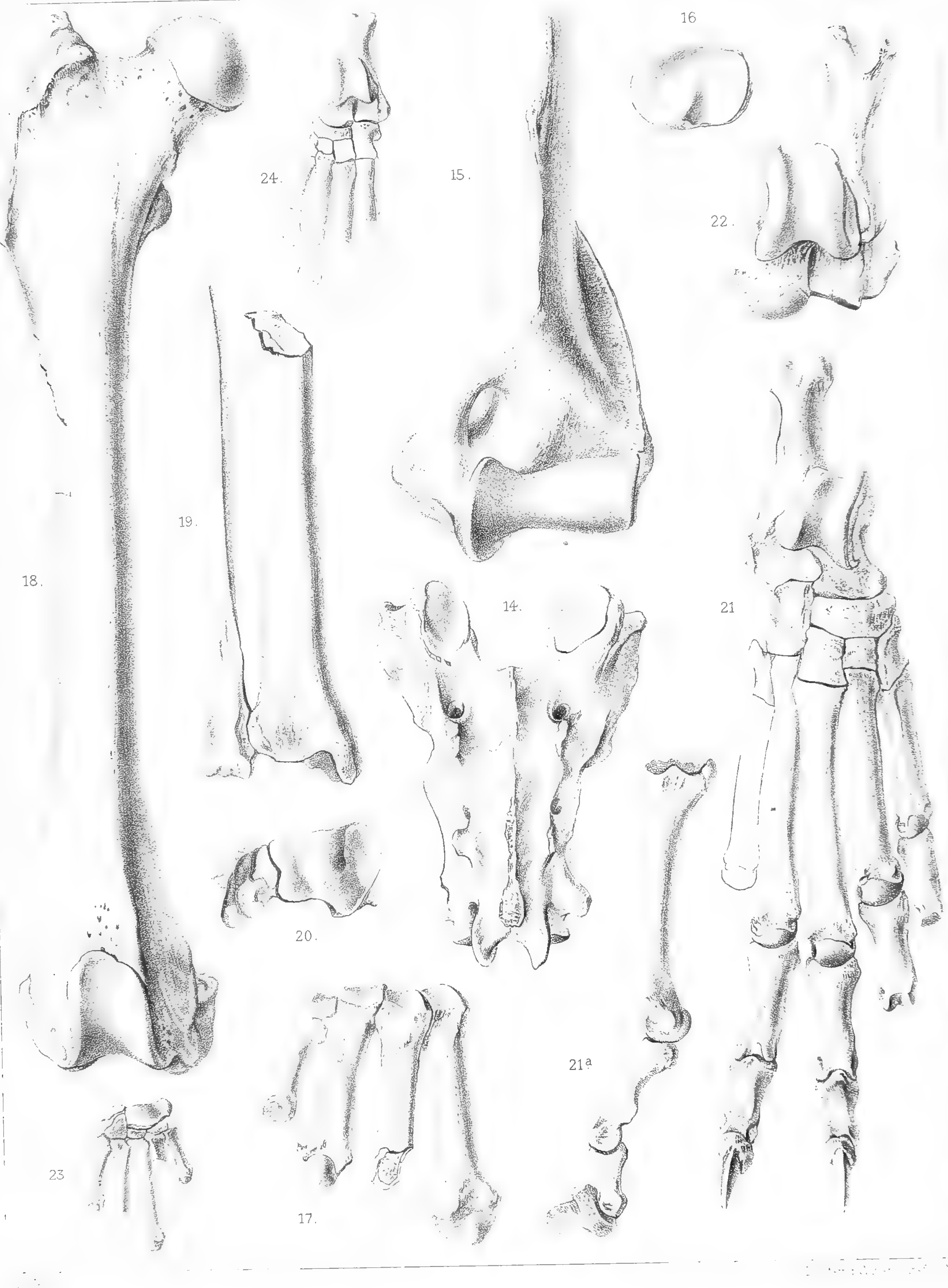
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ARTICLE IX.

CONTRIBUTIONS TO A REVISION OF THE NORTH AMERICAN BEAVERS, OTTERS AND FISHERS.

(Plates XXI–XXV.)

BY SAMUEL N. RHOADS.

Read before the American Philosophical Society, May 6, 1898.

An unusually fine series of the skins and skulls, with reliable data and measurements, of the beavers, otters and fishers of the United States and Canada having lately come into the custody of the writer, it is thought advisable to publish the results of a study of the various nominal forms of these mammals and briefly discuss the nomenclature involved. Owing to a lack of specimens from some regions whose faunal conditions are known to produce in many other mammals well-recognized geographic variations, this paper must be considered rather as a contribution to the subject, and in no sense a complete synopsis. The area covered by this study comprises solely that part of North America north of Mexico, no attempt being made to discuss the relationships of the tropical species.

To Mr. Outram Bangs the author acknowledges his gratitude for a most valuable loan of skins and skulls of nearly every species and race recorded in these pages. To the kindness of Mr. F. W. True, of the National Museum, is due the loan of a series of skulls of the Alaskan otter.

The North Carolina Department of Agriculture has courteously loaned two skins and four skulls of beavers recently killed in Stokes county of that State through the kind offices of Mr. H. H. Brimley, the Curator of the State Museum.

Aid has likewise been generously given by Dr. J. A. Allen, Dr. C. Hart Merriam, Dr. T. S. Palmer, Mr. Gerrit S. Miller, Jr., Dr. M. W. Raub and Mr. C. S. Brimley.

THE BEAVERS OF NORTH AMERICA.

Contrary to evidence which must eventually be accepted by all zoölogists, the American beaver, *Castor canadensis* Kuhl, is still considered by many eminent authorities as specifically the same as the *Castor fiber* Linnæus of Europe. In 1897, Dr. E. A. Mearns described* a subspecies of the typical Canadian animal, naming it *Castor canadensis frondator* and assigning its habitat to the "southern interior area of North America, ranging north from Mexico to Wyoming and Montana." This appears to be the first attempt in literature to formally subdivide the American beaver, a species whose constancy of characters over the vast and varied habitat which it frequents had hitherto been unquestioned. There can be no doubt as to the tenability of Dr. Mearns' "Broad-tailed Beaver" as distinguished from the Hudson bay animal, whose habitat Kuhl designated as "*ad fretum Hudsoni*" in his original description of *canadensis.*

It is probable that the beavers inhabiting the Carolinas, Georgia, Alabama, Mississippi and Tennessee are equally entitled to subspecific rank. So rare has the beaver become in these States, however, it would probably be impossible to verify such a prediction with specimens now in our museums.†

From what we know of the relationships of the representatives of our eastern species inhabiting the Pacific slope, we are led to expect that the beaver of that region would also prove separable from *canadensis.* A very complete series of skulls, with three adult and three young skins from the Cascades of Washington and Oregon, shows this to be the case.

Fortunately the synonymy of the American beaver is not involved and requires no elucidation in this connection, as is shown by reference to Dr. J. A. Allen's *Monograph of the North American Rodentia.* A synopsis of the American forms is herewith presented.

CANADIAN BEAVER. *Castor canadensis* Kuhl.

Plate XXI; Fig. 3. Plate XXII; Fig. 3.

Castor canadensis Kuhl, *Beitr. Zool.*, 1820, p. 64.

?"*Castor americanus* F. Cuvier, *Hist. des Mam. du Mus.*, 1825" (*fide* Brandt in *Kennt. Säugt. Russl.*, 1855, p. 64).

Castor fiber americanus Richardson, *Faun. Bor. Amer.*, I, 1829, p. 105.

Castor fiber var. canadensis J. A. Allen, *Monog. N. Amer. Rod.*, 1877, p. 444.

Type Locality.—Hudson bay ("*ad fretum Hudsoni*" Kuhl).

Geographic Distribution.—Northeastern North America, from the northern limit of trees south to the United States and west to the Cascade mountains; intergrading east of the Mississippi river into subspecies *carolinensis*, south-centrally into subspecies *frondator* and westwardly into subspecies *pacificus.*

* *Proc. Nat. Mus*, Vol. XX (adv. sheet, March 5, 1897).

† As will be seen later, such specimens have since come to hand and are described as *Castor canadensis carolinensis.*

*Color.**—Winter pelage, above, including sides, dark bay or blackish brown, tipped with chestnut or russet, becoming pure chestnut on top and sides of head and on chin, jaws and sides of neck. Rump and thighs purer chestnut. Ears black. Hair of feet, legs and under parts seal brown.

Anatomical Characters.—Size, smallest of the American forms. Scaly portion of tail more than twice as long as wide; hind foot with claw about 175 mm. Skull wide for its length; maximum size of skull 136 by 99 mm. in a New Brunswick example, No. 31, collection of E. A. and O. Bangs. Rostrum and nasals relatively short and wide, the nasal bones averaging more than half as wide as long and extending but little behind the premaxillaries. Upper molar dentition wide and heavy, the crowns oblique, triangular and very wide anteriorly.

Measurements.—Of a large, typical, adult male specimen from Quebec, No. 3825, collection of E. A. and O. Bangs (measurements made by collector from newly killed specimen). Total length, 1130 mm.; tail vertebræ, 410 mm.; scaly portion of tail (dry meas. from skin), 263 by 122 mm.; hind foot, 176 mm.; length of skull, 132 mm.; breadth of skull, 93 mm.; length of nasal bones, 46 mm.; breadth of nasals, 21.4 mm.†

Remarks.—The above diagnosis is taken mainly from the Quebec specimen, because of the authentic measurements and superior condition of the skin and pelt. The average beaver from the Hudson bay regions, however, is somewhat lighter colored than this specimen, which, in its darkness and richness of shade, rivals the best examples of *pacificus*. In size, and ratio of length to width, the skull of the Quebec specimen is typical, but the nasals are too narrow to serve as a standard for *canadensis*, whose nasals average wider than *pacificus* and narrower than *frondator*. In general terms, *canadensis* differs from *frondator* in smaller size, narrower tail, much darker coloration and narrower nasals. It differs from *carolinensis* in smaller size, narrower, longer nasals and somewhat darker coloration. From *pacificus* it differs in smaller size, lighter coloration, wider nasals and broader skull. Subspecies *pacificus* differs from *frondator* in larger size, greatly narrowed and lengthened tail-paddle, rostrum and nasals, and in its dark coloration. In color *frondator* is decisively and uniformly lighter than eastern *canadensis* and *carolinensis* and western *pacificus*, but darkened *canadensis* (not melanistic) are nearly as dark as *pacificus*. In size, *pacificus* is much the longest of the three, with very long hind foot and tail. Its skeleton is slenderer and weaker in every part as compared with the massive frame of *canadensis* and *frondator* of same age. *Carolinensis* is nearly of the color of

* Ridgway's *Nomenclature of Colors* is the standard used throughout this paper.

† The narrow nasals of this specimen are an exception, the average of several east Canadian specimens showing the ratio of length to breadth as less than two to one.

lighter hued *canadensis*, but agrees with all the other characters of *frondator*, to which it seems most nearly allied in cranial and caudal characters.

Specimens Examined.—New Brunswick, 1 skull; Quebec, 1 skin with skull; Canada (?), 3 skulls, 1 skeleton, 2 mounted skins; Ft. Simpson, N. W. T., 1 mounted skin; Idaho, 1 skin with skull.

CAROLINIAN BEAVER. *Castor canadensis carolinensis*, subsp. nov.

Plate XXIII; Figs. 1 and 2.

Type Locality.—Dan river, near Danbury, Stokes county, North Carolina. Type No. z.607, old ad. ♂, in the collection of the North Carolina State Museum, Raleigh, N.C. Collected by a trapper in flesh for the Museum, April, 1897.

Geographic Distribution.—Carolinian fauna, south into the Austroriparian.

Color.—Of type and topotype: Overhair of upper head, neck, back and sides, bright hazel. Underfur of same parts, seal brown. Hinder back and rump lightening from hazel to cinnamon rufous and then to tawny olive near base of tail. Vent and under base of tail, dark, rich burnt umber. Ears pale blackish. Sides of head below eyes light hair brown, shaded with pale cinnamon rufous. Feet bistre. Below, from throat to vent, dark broccoli brown with wood-brown tips to overhair.

Anatomical Characters.—Size large, larger than *canadensis*, with relatively much broader tail, as in *frondator*.

Skull large and broad, with very short, broad nasals. In the type the base of nasals does not reach back to the line connecting the anterior walls of the orbits. Rostrum very short and broad. Audital bullæ remarkably contracted laterally, with a strongly developed osseous column on the outer wall and the transverse diameter less than the longitudinal. Incisors weak, narrowed; molars large, with triangular crowns. Pelage short and harsh as compared with *canadensis*.

Measurements.—Of the type, from carcass: Total length, 1130 mm.; scaly portion of tail, 279 by 158 mm.; hind foot, 184 mm.; ear, from crown, 21 mm.; length of skull, 148 mm.; breadth of skull, 107 mm.; length of nasals, 43.5 mm.; breadth of nasals, 29 mm. Of the topotype (ad. ♂): Total length, 1080 mm.; scaly portion of tail, 260 by 146 mm.; hind foot, 174 mm.; ear from crown, 23 mm.

Remarks.—The two skins and four skulls upon which the above diagnosis of *carolinensis* is based were secured, just before the completion of this paper, from the authorities of the State Museum of North Carolina. They are intended to form a group exhibit in the State Museum, and have been carefully measured by the curator, Mr. H. H. Brimley, while yet in the flesh. The old male which forms the type had lost one of its fore feet, apparently in a trap, some years previous to its final capture, but its evident health and great size show that it had suffered little inconvenience from the loss of the member.

The strong cranial and caudal affinities which this beaver shows to *frondator* as distinguished from *canadensis* indicate that it is more closely related to the western form. In color, however, it shows a nearer approach to *canadensis*, as, in fact, do many other animals of similar distribution and racial differences. The Mississippi and Louisiana beavers are undoubtedly, from what I can hear from the furriers, the darkest and thinnest pelted of our American beavers, but their separability from what I have named *carolinensis* is not probable. They may be considered as belonging to *carolinensis* rather than to *frondator*.

Specimens Examined.—Stokes county, North Carolina, 4.

SONORAN BEAVER. *Castor canadensis frondator* Mearns.

Plate XXI; Fig. 2. Plate XXII; Fig. 2.

Castor canadensis frondator Mearns, *Proc. U. S. Nat. Mus.*, XX, adv. sheet, Mar. 5, 1897.

Type Locality.—San Pedro river, Sonora, Mexico, near monument No. 98, of the Mexican boundary line.

Geographic Distribution.—Southern interior of North America from Mexico to Wyoming and Montana, intergrading northwardly into *canadensis*, southeastwardly into the trans-Mississippian *carolinensis* and westwardly into *pacificus*.

Color.—Much paler than *canadensis* or *carolinensis*. "Above russet, changing to chocolate on the caudal peduncle above and to burnt sienna on the feet; toes reddish chocolate. Below grayish cinnamon, brightening to ferruginous on the under side of caudal peduncle. Sides wood brown enlivened by the tawny-olive color of the overhair."* A specimen from Red Lodge, Montana (No. 32, collection of E. A. and O. Bangs), taken in November, is wood brown above and below, the longer overhair of upper pelage washed with pale rusty.

Anatomical Characters.—Size large, exceeding average of Hudson bay beaver, with a longer foot and broad tail. Scaly portion of tail less than twice as long as wide, hind foot with claw about 185 mm. Skull massive, large, with short rostrum and very wide, short, tumid nasal bones, the average skull probably exceeding *canadensis* in size, certainly exceeding it in relative width to length and in the relative breadth of the nasals. Upper molar dentition as in *canadensis*.

Measurements.—Of the type: Total length, 1070 mm.; tail vertebræ from anus, 360 mm.; scaly portion of tail, 290 by 125 mm.; hind foot, 185 mm.; length of skull, 133

* Quoted from Dr. Mearns' original description (*l. c.*) of type.

mm.; breadth of skull, 99 mm. Maximum length of old males, measured by Dr. Mearns, 1130 mm.; of the tail paddle, 285 by 155 mm.

Remarks.—Dr. Mearns' comparisons of *frondator* with *canadensis* were evidently not made with the largest specimens of the latter, as I have examined some whose cranial and body measurements are about equal to the maximum recorded by him for *frondator*. Nevertheless, there is little doubt that the larger size of average *frondator* is well established. Its long hind foot, broad tail and light coloration distinguish it immediately from *canadensis*. Its approach to *pacificus* is solely along the line of great size as indicated by the length of body and hind foot, but in cranial characters, as also in color, it is farthest removed from that race. The close anatomical relation of *frondator* to *carolinensis* has been mentioned.

Specimens Examined.—Montana, 1 skin with skull; Wyoming, 1 skull.

PACIFIC BEAVER. *Castor canadensis pacificus*, subsp. nov.

Plate XXI; Fig. 1. Plate XXII; Fig. 1.

Type Locality.—Lake Kichelos, Kittitass county, Washington; altitude about 8000 feet. Type, No. 1077, ad. ♀, in the collection of S. N. Rhoads; collected in April, 1893, by Allan Rupert.

Geographic Distribution.—Pacific slope, of America, from Alaska to California.

Color.—Above with very uniform, dark and glossy reddish chestnut overhair, almost concealing along dorsum the seal-brown underfur. Top of head like back; sides of head, throat, rump, thighs and vent not decidedly lighter than back and belly as in the other forms, these parts paling to walnut brown. Overhair of sides and under parts, between seal brown and broccoli brown; under fur of belly drab gray at the roots; hind feet dark seal brown; fore feet and limbs, dark wood brown. Ears black.

Anatomical Characters.—Size, largest of the *canadensis* group, but of more slender build, the skeleton throughout being of much greater longitudinal and lesser lateral dimensions than in the other forms. Tail and hind foot relatively long. Skull large, relatively narrow, with long, narrow rostrum and nasals, the latter with outer margins nearly parallel and reaching basally decidedly beyond the premaxillaries. Upper molar dentition weak, the crowns of molar teeth rectangular.

Measurements.—Of the type from carcass: Total length, 1143 mm.; tail vertebræ, 330 mm.; (from relaxed skin) scaly portion of tail, 295 mm. by 122 mm.; hind foot, 185 mm.; length of skull, 142 mm.; breadth of skull, 101 mm.; length of nasals, 53.6 mm.; breadth of nasals, 24 mm.; average length and breadth of five skulls from Tacoma and Lake Kichelos, Washington, 144 mm. by 99 mm.; average nasal length and breadth of same, 54 mm. by 23 mm.

Remarks.—Reliable measurements of only one adult skin specimen (the type) of *pacificus* were accessible. An adult mounted specimen from Josephine county, Oregon, in the Wagner Institute, Philadelphia, confirms the color and measurements of the type so far as the latter can be ascertained from the stuffed animal.

Pacificus, like its associates, *Mustela americana caurina* and *M. canadensis pacifica* of the Pacific slope regions, is distinguishable by its rich and deep coloration from its darkest trans-Cascadian representatives. No specimens have come to hand from Alaska, but undoubtedly, from what we know of other species found there as well as from the accounts of trappers and furriers, the Alaskan coast beaver represents the maximum of size* and the greatest richness and depth of fur coloration seen in American beavers.

Specimens Examined.—Washington, Tacoma, 1 skeleton, 1 skull; Lake Kichelos, 1 adult skin with skull, 3 young skins with skulls, 1 skeleton, 12 separate skulls; Oregon, Josephine county, 2 mounted specimens; British Columbia, (?) Sumas, 1 skull; † Victoria, 1 skull.

THE OTTERS OF NORTH AMERICA.

As Mr. Oldfield Thomas has shown in his "Preliminary Notes on the Species of Otter," published in 1889 in the *Proceedings of the London Zoölogical Society*, the characters and nomenclature of the North American species are in great need of study. Dr. Elliot Coues has elucidated with sufficient clearness, in his *Monograph of the Mustelidæ*, the habits and characters, and, to some extent, the synonymy of the typical Canadian otter, *Lutra hudsonica* Lacépède. Its relations, however, to other nominal species, especially to the otters of the Pacific slope of America from California northward, demand investigation.

As in the case of the American beaver, just treated, this paper has to do solely with one central Canadian type and its subspecies found in America north of Mexican territory.

Avoiding a general preliminary discussion of the rather perplexing questions of nomenclature and geographic variations and distribution, I will present these in order in the more formal and detailed synopses which follow.

* Dr. Allen's measurements of Alaskan skulls, page 447 of the *Monograph of N. A. Rodentia*, do not indicate unusual size, but as we have no precise locality given they may not have come from the coast region, and, therefore, do not represent *pacificus*.

† This skull (No. 5545, ♂, coll. of E. A. and O. Bangs) is the largest of which I find any record, measuring 154 by 108 mm. The next in size is No. 2146, U. S. Nat. Mus., from Nebraska, recorded by Baird. Its size was 147 by 105.5 mm. Unlike all my *pacificus* specimens, No. 5545 has very wide convex nasals.

HUDSONIAN OTTER. *Lutra hudsonica* ("Lacépède," Desmarest).

Plate XXIV; Figs. 1 and 2.

Mustela lutra Linn., *canadensis* Schreber, *Säugt.*, III, Pl. CXXVI, B. (dated 1778 on title-page, but, according to Sherborn, the text of Vol. III was published in 1777 and this plate in 1776).

Mustela (*lutra*) *canadensis* Kerr, *Linn. An. Kingd.*, I, 1792, p. 173 (see Thomas, *Proc. Zoöl. Soc. Lond.*, 1889, p. 197, and Allen, *Bull. Amer. Mus. N. Hist.*, VII, 1895, p. 188).

"*Mustela hudsonica* Lacép.[ède]," Desmarest, *Nouv. Dict. d'Hist. Nat.*, XIII, 1803, p. 384; (*Nouv. Ed.*) 1817, p. 219.

Lutra canadensis J. Sabine, *App. Frankl. Jour.*, 1823, p. 653, and of nearly all subsequent authors (not *L. canadensis* F. Cuvier, *Dict. Sci. Nat.*, 1823, p. 242; see O. Thomas, *l. c.*, p. 197).

Lutra hudsonica F. Cuvier, *Suppl. Buff.*, I, 1831, p. 194; Merriam, *N. Amer. Fauna*, No. 5, 1891, p. 82.

Lataxina mollis Gray, *List Mamm. Brit. Mus.*, 1843, p. 70.

Lutra destructor Barnston, *Canad. Nat. and Geolog.*, VIII, 1863, p. 147, Figs. 1 to 6.

Type Locality.—"Ou la trouve au Canada sur les bords de la mer."

Geographic Distribution.—Northern North America from the Arctic ocean southward into the United States and from the Atlantic ocean to the Cascade mountains; intergrading southeastwardly into subspecies *lataxina* F. Cuvier and *vaga* Bangs, south-centrally into subspecies *sonoræ* Rhoads, and westwardly into subspecies *pacifica* Rhoads.*

Color (taken from two specimens in the Bangs collection, No. 5638, yg. ad. ♂, Annapolis, Nova Scotia, November 23, 1896, and No. 4190, ad. ♀, Upton, Me., October 25, 1895).—Above, dark seal brown from nose to tip of tail, darkest posteriorly, below from breast to tail between broccoli and vandyke brown in the Nova Scotia specimen and between seal and vandyke brown in the Maine specimen. Head and neck below a line running from nose to lower base of ear and base of foreleg light Isabella color anteriorly darkening on lower neck to wood brown in the Nova Scotia animal. In the Maine specimen the neck is Prout's brown. Feet, legs and tail corresponding to darker shades of upper and lower body. A summer specimen from New Brunswick is dark, vandyke brown, but little paler below than on back, and darker than winter specimens of *lataxina* from Maryland.

* The otters of Louisiana and Mississippi are stated by furriers to be very dark and light-pelted, resembling South Florida and Gulf-coast skins. No specimens having been examined, they are referred to *vaga*.

*Anatomical Characters.**—Size, medium (exceeded by *vaga*, *sonora* and *pacifica*). Tail relatively short. Inferior webs of feet and interspace between posterior and anterior callosities of manus, densely haired. Hind foot with claw about 125 mm. in old adults; but so variable as to have little diagnostic value. Total length rarely exceeding 1100 mm. Skull—size, medium (greatly exceeded by *vaga* and *pacifica*). Teeth large, crowded longitudinally upon each other and obliquely overlapping. Postorbital neck of frontals relatively short and wide, its superior ridge on a plane with nasals and occipital crest. Mastoid width much less than zygomatic width. Postorbital processes short and stout. Audital bullæ large, tumid, rising abruptly from the sides of basioccipital.

Measurements.—See tables.

Remarks.—Variations in the size of adult otters from apparently the same region seem remarkable at first sight, but I find that these are not always to be attributed to sex (for the female otter sometimes reaches near to the average size of the males), but to environment. The otters of the Alleghany mountain streams are uniformly smaller than those of the tide-water creeks and rivers of the Atlantic seaboard. This rule applies from Labrador to Florida and is undoubtedly the result of the relative difficulty of obtaining food and securing shelter from enemies in the two kinds of habitat. On the other hand, this difference lies wholly within the limitations of individual variation and in no sense affects the well-defined cranial and other characters which distinguish the races and species hereafter defined. It has to do solely with size, not with proportions. In a letter from Mr. C. S. Brimley, of Raleigh, North Carolina, the same feature is alluded to where he states: "A trapper of our acquaintance says that otters from the saltmarshes of eastern North Carolina average considerably larger than the otters of the small streams of the central part of the State."

There is rarely to be found a case in mammalian nomenclature more puzzling than that of the first tenable name of the Hudsonian otter. Its synonymy involves that of the mink and the fisher as well as the questions of priority of publication of Erxleben's and Schreber's great works on the Mammalia, and the tenability of plate names. I have consulted Drs. C. H. Merriam and T. S. Palmer at length on these questions and have accepted their ruling as to the first tenable name of the Hudsonian otter being *Lutra hudsonica* Lacépède and that of the northeastern mink to be *Putorius vison* Schreber. In regard to the name of the fisher, however, I prefer to abide by Canon XLIII of the Code of the American Ornithologists' Union, which accepts, under certain conditions, the names of species originally published on plates, which Drs. Merriam and Palmer and Mr. Sherborn do not accept. Returning now to the abstract of synonymy as given above for the Hudsonian otter, the case may be concisely stated thus: *Mustela lutra*

* The diagnostic value of the nose pad has no significance in this study of the relationships of a monotypic group.

canadensis Schreber is a plate name published (*fide* Sherborn) in 1776, and is the earliest applied to this otter. It would stand (A. O. U., Canon XLIII) were it not unquestionably applied and intended by Schreber merely as a geographic name without reference to its specific relations to "*Mustela lutra* Linn." For this reason alone it should be discarded. Furthermore, the name *Mustela canadensis* was used by Schreber on a previous plate in the same volume (Pl. No. 126) in the specific sense for the fisher. This plate was also (*fide* Sherborn) published in 1776, one year before the text, which was published in 1777, and the bound volume of text and plates were dated 1778. In 1777, Erxleben published a description of the fisher and named it *Mustela pennantii*, by which name it has been since designated by authors generally. As this name is antedated by the tenable plate-name *Mustela canadensis* of Schreber by one year, I adopt it as the name of the fisher of Pennant from the northeastern United States. Erxleben published in the same work a description of an animal which he named *Mustela canadensis*, and which Baird and Coues have considered applicable to the mink, and the acceptance of the dates on the title-pages of Schreber's (1778) and Erxleben's (1777) works would give priority to Erxleben's name and displace *Mustela vison* of Schreber. But Sherborn's emendation of these dates makes *M. canadensis* of Erxleben for the mink untenable, it being preoccupied by Schreber's plate-name *M. canadensis* for the fisher, as stated above. Besides this fact, Dr. Merriam considers that Erxleben's description of *M. canadensis* also applies to the fisher and the marten in such a way as to make it untenable for any species.

Returning to the search for a first name for the otter, we find Kerr's name, *M. canadensis* of 1792, to be unavailable because he placed it under the old genus *Mustela*. Next in order appears to be the name *hudsonica*, which is accredited to Lacépède, in an article on the Canadian otter in the first edition of the *Nouvelle Dictionaire d'Histoire Naturelles*, which is signed "Desm." I have not examined this reference personally, but am indebted to Dr. J. A. Allen for a transcript of these facts from the only known copy of the work in America which appears to be available, belonging to the library of the American Museum of Natural History. In agreement with my previous rendering of manuscript names, and on the supposition that Desmarest was the real author and publisher of this name and description of *hudsonica*, I cite it as *Lutra hudsonica* ("Lacépède," Desmarest). I agree with Dr. Merriam that this name should stand for the otter of eastern Canada. Frederick Cuvier seems to have been the first to place this animal in the genus *Lutra* under the Lacépède-Desmarest name *hudsonica* in 1831.

The *Lataxina mollis* of Gray and the *Lutra destructor* of Barnston are no doubt synonyms of *hudsonica*.

Specimens Examined.—Labrador, Okak, 1 skull ; Grand river, 1 skull ; New

Brunswick, Restigouche river, 1 skin; Nova Scotia, Annapolis, 1 skin with skull; Maine, Upton, 1 skin with skull; Bucksport, 1 skull; Massachusetts, Kingston, 1 skin with skull; Westford, 1 skull; Canton, 1 skull; Missouri, 1 skull; British Columbia, Vernon, 1 skull; Alaska, Tanana river, 1 skull.

Carolinian Otter. *Lutra hudsonica lataxina* (F. Cuvier).

Plate XXIV; Fig. 4.

Lutra lataxina F. Cuvier, *Dict. des Sci. Nat.*, 1823, p. 242.

Type Locality.—South Carolina.

Geographic Distribution.—Carolinian faunal region, intergrading through the Transition region northward with *hudsonica* and southward through the Austrariparian into *vaga* of southern Florida.

Color.—Much lighter than *hudsonica*. Above (from a specimen taken at Liberty Hill, Conn., No. 4252, ad. ♂, Nov. 19, 1895, collection of E. A. and O. Bangs*), dark vandyke brown, tipped on upper head, neck and shoulders with wood brown, darkening posteriorly. Upper feet and limbs dark bistre. Below, from lower breast to end of tail, between Prout's brown and broccoli brown. Head, neck and breast, including ears, below a line connecting nose, upper eyelid, upper ear and upper base of fore leg, grayish wood brown, lightest on head, darkening posteriorly to color (*l. c.*) of breast. The average Carolinian winter specimens from Maryland southward are somewhat lighter and some are Prout's brown above, the wood brown of lower head and neck becoming a pale grayish buff.

Anatomical Characters.—Size, smallest of the *hudsonica* subspecies. Inferior webs of feet and interspace between callosities of manus, sparsely haired. Hind foot with claw about 120 mm. Total length rarely exceeding 1100 mm. Skull relatively small, with very large teeth, and weak postorbital processes. In other respects like the *hudsonica* type.

Measurements.—See tables.

Remarks.—The relations of this subspecies to northern *hudsonica* on the one hand and to the southern *vaga* on the other are rather peculiar. It is without question a nearer ally to *hudsonica* than *vaga* in the territory between Connecticut and South Carolina, but, as Mr. Bangs has implied in his remarks on *vaga*, there is a tendency in the Georgia (and we may infer in the South Carolina) otter to the large size and peculiar

* This specimen comes from the northern edge of the Carolinian region. No equally good skins from more southern localities being available, it is used as typical of the Carolinian race. It corresponds closely to two fine 1897–8 winter pelts of Maryland otters, examined through the courtesy of Mr. S. E. Shoyer, of Philadelphia.

skull and color characters of the south Florida animal. There is so much evidence of the intergradation of *lataxina* both north and south that the specific separation of *vaga* from it is not permissible. On the other hand it is impossible to ignore the decided racial differences of the Carolinian otter from the Hudsonian type.

Cuvier's original description of *lataxina* gives "Caroline du Sud" as the locality where the type was taken; it is, therefore, permissible to restrict this name to the Carolinian form as typified in the otters found in the Carolinian lowlands of the eastern United States from south of the "Transition Zone" of Dr. C. Hart Merriam, as far as middle South Carolina, Alabama and Mississippi, where it merges into *vaga* of the Gulf or southern "Austroriparian Realm" of Dr. J. A. Allen.

I know of no restricted synonyms of *lataxina*. Dr. Coues quotes in his *Fur-bearing Animals* a "*Latax lataxina* Gray, *Ann. Mag. N. H.*, I, 1837, p. 119." The work referred to contains no such name. Cuvier's description of *lataxina* gives its color as "dark blackish brown, a little paler beneath. Cheeks, temples, lips, chin and throat pale brownish gray, and under side of tail grayish brown, the hair tips reddish." He compares the skull of *lataxina* with his *Lutra enudris*, "Loutre de Guianæ" of the preceding page and remarks on the "straight line, even concave or depressed," joining the nasals and occiput. This is significant, as one of the peculiarities separating *vaga* from *lataxina* and *hudsonica* is the *convexity* of the frontal plane in the former.

Specimens Examined.—Connecticut, Liberty Hill, 1 skin with skull; Pennsylvania, Clinton county, 2 mounted specimens; Monroe county, 3 skulls; New Jersey, Tuckerton, 1 skull; Mickleton, 2 disarticulated skeletons; Maryland, 2 fresh cased winter furs; North Carolina, Raleigh, 2 skulls.

Florida Otter. *Lutra hudsonica vaga* Bangs.

Plate XXV; Fig. 2.

Lutra hudsonica vaga Bangs, *Proc. Bos. Soc. Nat. Hist.*, XXVIII, 1898, p. 224.

Type Locality.—Micco, Brevard county, Florida.

Geographic Distribution.—Florida, southeastern Georgia and the Gulf regions of Alabama, Mississippi and Louisiana, intergrading (?) northwardly into *lataxina*.

Color.—Dark; less black than *hudsonica*, darker and redder than *lataxina*. Breast and belly nearly unicolor with back. Paler area of head and neck, scarcely reaching breast. Above and below, dark, rich chestnut, scarcely paler on belly. Lower head and anterior throat below line from nose to and behind ears, strongly tipped anteriorly with tawny Isabella color darkening to raw umber on throat, the underfur darker than overfur, instead of lighter as in *lataxina*.

Anatomical Characters.—Size, large. Tail relatively long (*fide* Bangs). Inferior webs of feet and interspace of palms nearly naked. Hind foot with claw reaching maximum (No. 4998 Bangs Coll., yg. ad. ♂, Citronelle, Florida) of 130 mm. Total length (maximum of No. 4998, *l. c.*, 1285 mm.) exceeding 1200 mm. Skull large, teeth relatively small, not crowded longitudinally. Postorbital neck of frontals long and narrow, suddenly constricted at base. Frontal plane strongly upraised above a line connecting occipital crest with base of nasals and above the level of postorbital processes. Mastoid width nearly equaling the zygomatic width in very old specimens, in young adult skulls the mastoid width is the greater. Wings of mastoid processes strongly developed and flattened laterally. Audital bullæ as in *hudsonica* and *lataxina;* well developed, tumid at basioccipital margins. Postorbital processes relatively weak and slender. Underfur short, sparse.

Measurements.—See tables.

Remarks.—This subspecies just described by Mr. Bangs in his most valuable paper on Florida and Georgia mammals is, as already noticed, quite different from *lataxina*, its nearest geographic ally. In color it comes nearer *hudsonica* intermediates from New England. In size and color and lack of hair on the webs and palms it shows approach to the remote *pacifica*, but its peculiar long-waisted and broad-based skull distinguishes it from all other American forms except, perhaps, those of the northern Central American and South American otters which I have examined. The yellowish and reddish shades of south Florida *vaga* suggest affinity with what we find published of the characters of the otters of the Caribbean coasts. In essential respects Mr. Bangs' diagnosis of this animal is very good. He, however, used the skull of a young adult male for cranial comparisons, and while it is true that the ratio of the mastoid to the zygomatic width is much greater in *vaga* than *hudsonica* it is not as great as would appear by Mr. Bangs' figure. In crania of old adult *vaga* in my collection the mastoid and zygomatic widths are about equal, the latter slightly wider. In *hudsonica*, however, the excess of zygomatic width and slight development of the mastoid wings is marked.

Specimens Examined.—Florida, Tarpon Springs, 1 adult pelt, 3 young skins with skulls and 2 extra skulls; Salt Run, St. John's river, 1 skull.

Pacific Otter. *Lutra hudsonica pacifica*, subsp. nov.

Plate XXIV; Fig. 3. Plate XXV; Figs. 1 and 3.

Lutra paranensis and *aterrima* Thomas, *P. Z. S.*, *l. c.*, p. 199; Trouessart, *Catal. Mamm.*, 1897, pp. 286, 287 (not of Pallas, *Zoogr. Ross. Asiat.*, 1811, p. 81).

Lutra californica Baird, *Mamm. N. Amer.*, 1857, p. 187 (not of Gray, *Mag. Nat. Hist.*, I, 1835, p. 580, which is *L. felina;* see Thomas, *l. c.*, p. 198).

Type Locality.—Lake Kichelos, Kittitass county, Washington; altitude about 8000 feet. Type No. 616, yg. ad. ♂, in the collection of S. N. Rhoads; collected in fall or winter* of 1892–'93, by Allan Rupert.

Geographic Distribution.—Pacific slope of North America, from Alaska to California.

Color.—Of type: Lighter than *hudsonica*, with a browner cast, approaching nearly to *lataxina*. Average of coast specimens from Puget Sound northward, ruddy seal brown, sometimes very dark in Alaskan coast specimens. Lower parts from breast to end of tail much lighter (Mars-brown) than back. Ventral region conspicuously lighter. Lower head, neck and breast very pale wood brown, almost dirty gray.

Anatomical Characters.—Size, very large.† Tail normal. Inferior webs of feet and palmar interspaces nearly naked. Hind foot not recorded in type, the calcaneum missing; no measurements of other specimens available. Skull largest of the North American otters (reaching a maximum of 119 mm. in occipito-nasal length and 83 mm. in zygomatic expanse in an Alaskan coast example); teeth relatively weak, less crowded longitudinally than in *hudsonica*. Interorbital width relatively very great, nearly 1½ times postorbital constriction; postorbital processes long and stout. Mastoid and zygomatic proportions as in *hudsonica*. Audital bullæ remarkably flattened.

Measurements.—See tables.

Remarks.—The type specimen, though taken in the mountains and not fully mature, is large and has a skull which would have, perhaps, eventually equaled the maximum size recorded above for an Alaskan specimen of much greater age. A very old female skull from the vicinity of Puget Sound confirms fully the diagnostic characters of *pacifica* as given.

In treating of the otters of the Pacific slope of America we are confronted with two nominal species to which they have been doubtfully referred by authors. In point of time the first to be considered is the *Viverra aterrima* of Pallas,‡ described from a hunter's skin, lacking skull and feet, taken in northeast Siberia, "between the Uth and Amur rivers." Schrenck and Middendorff listed this animal in their works on Siberian Zoölogy with the remark that they were unable to verify its existence or clear up the mystery of its strange characters as given by Pallas. Mr. Thomas (*P. Z. S.*, *l. c.*, p. 199) queries, on the basis of a mistaken suggestion of Dr. Coues, whether it may

* The season of capture was not recorded, but the pelt indicates that it was taken in full winter fur.

† I have no measurements of Alaskan otters, but judging by the great size of the skulls from there they must greatly exceed any known species of *Lutra*. On the basis of the skull they must attain a maximum length of over 1400 millimeters.

‡ *Zoog. Rosso. Asiat.*, *l. c.*

not prove to be the same as the so-called *Lutra paranensis* Rengg. which he assumed might occur throughout the whole Pacific coast regions of America. The close relationship of our Pacific coast otters to *hudsonica* will effectually remove them from any complication with *paranensis,* but as regards *aterrima* we must devote sufficient space to show the impossibility of referring the Alaskan land otter to that animal, as Trouessart has lately done.*

A careful study of Pallas' original description, together with the fact that no later author or explorer has been able to explain or rediscover the animal, convinces me that it is either unidentifiable or will prove not to belong to the *Lutrinæ* but to the *Mustelinæ.* Pallas states it to be intermediate in size between the European otter and the European mink. He states the length of the skin to be 19 inches, 3 lines, and of the tail 5 inches with a *brush of* 1½ *inches!* The color of the animal is said to be very black and shining, except the sides of the head between the eyes and ears, which change from black to "subrufescent." The absurdity of applying such a description to the animal which I have named *pacifica,* or, indeed, to any member of the genus *Lutra,* is certainly evident. So far as any animal now known to zoölogists is concerned, the *Viverra aterrima* of Pallas should be consigned to oblivion.

Another name which has given trouble to those who had to deal with the Pacific coast otter is the *Lutra californica* of Gray. Fortunately, Mr. Thomas has effectually exposed the history and at the same time the inapplicability of that name to a North American animal of the *hudsonica* type. He has shown in his paper in the *Proceedings of the Zoölogical Society* (*l. c.*, p. 198) that Gray's type of *californica* did not come from California, but most likely from Patagonia, in which case he makes it a synonym of *Lutra felina* Molina.

Specimens Examined.—Washington, near Tacoma, 3 skulls; Lake Kichelos, 1 skin with skull, 1 skull; Oregon, 1 skull; British Columbia, Sumas, 1 skull; Alaska (coast?), 3 skulls; Kodiak Island, 2 skulls; Mission, 1 skull; Queraquina† Island, 1 skull.

SONORAN OTTER. *Lutra hudsonica sonora,* subsp. nov.

Lutra canadensis Mearns, *Bull. Am. Mus. Nat. Hist.*, III, 1891, pp. 253–256.

Type Locality.—Montezuma Well, Beaver creek, Yavapai county, Arizona. Type, ad. ♀, No. $\frac{3712}{309}$ in the collection of the American Museum of Natural History. Collected December 26, 1886, by Dr. Edgar A. Mearns.

* *Catalogus Mammalium, l. c.*

† It is conjectured that this skull came from the North Pacific. It has Capt. T. J. Turner's name on it. I cannot find an island of this name on the maps.

Geographic Distribution.—Arid southern interior of North America, from Mexico, probably to Wyoming.

Color.—Of type, *fide* Mearns, *l. c.:* "Above dark brown, without reddish tinge; this color changing gradually to a light grayish brown below, being palest (almost whitish) upon the sides of the head below the level of the eyes and upon the under side of the head and neck as far back as the fore limbs. . . . . The long hairs of the lighter portions of the body are pointed with yellowish gray and upon the upper surface of the head and neck the tips of the hairs are yellowish brown, giving a paler cast to that part of the dorsum."

Anatomical Characters.—Size, large, with a very long hind foot, the body length measurements exceeding those of any other specimen of North American otter examined or recorded.* Webs of feet not densely haired beneath. Hind foot, 145 mm. Total length reaching 1300 mm. Skull—size, large, nearly as great as in largest Alaskan *pacifica,* but small for the great relative length of body, "less massive, broader, with more evenly rounded zygomatic arches and with the brain case more convex or bulging in its outlines." "Arizona skulls differ from all others in the slender, attenuated postorbital processes and in the greater height of the lower jaw from angle to condyle, or to summit of coronoid process. From its geographically near neighbor, *L. felina* of Central America, it presents many cranial and dental differences; in fact, skulls of the latter are so very distinct [in their inferior concavity, frontal depression, short muzzle, narrow postorbital constriction and absence of the heel in front of the antero-internal cusp of the last upper molar] from any known specimens from North America, north of Mexico, as to be distinguishable from them at a glance."

Measurements.—Of type: "Total length, 1300 mm.; head and body (measured from tip of nose to anus), 815 mm.; tail measured from anus to end of vertebræ, 472 mm. . . . . ear, height above crown, 15 mm." No skull measurements given.

Remarks.—I have accepted Dr. Mearns' very full and satisfactory diagnosis of the Arizona otter, given in the *Bulletin of the American Museum of Natural History,* as conclusive evidence of the existence of a recognizable race in arid interior America, south of Montana. Its great size and light color together form a combination not found in any other known or named otter.

It has been thought unnecessary to examine the type, as, owing to the author's removal from Philadelphia during the completion of this paper, such an examination would have caused a greater risk to the type specimens than the facts warranted.

* The great size of the type, as compared with an adult male also recorded by Dr. Mearns from Arizona, indicates that the sex of the type may have been wrongly determined. If correct, the size to be expected of a full-grown male *sonora* would be extraordinary.

Newfoundland Otter. *Lutra degener* Bangs.

Plate XXIV; Fig. 5.

Lutra degener Bangs, *Proc. Biol. Soc. Wash.*, XII, 1898, p. 35.

Type Locality.—Bay St. George, Newfoundland.

Geographic Distribution.—Confined to Newfoundland (?).

Color.—Of type, ad. ♂, taken April 22, 1897: Above, black with seal brown reflections. Ears, seal brown. Lower head and neck areas grayish wood brown, becoming seal brown on breast; the remainder of lower parts nearly as dark as back. Tail unicolor. Feet seal brown and densely haired on under side of webs and palmar interspaces.

Anatomical Characters.—Size, much smaller than any of the *hudsonica* group. Hind foot small, with claw averaging about 112 mm.* long in the two specimens examined. Total length about 1000 mm. Tail relatively short. Skull very small, narrowed, weak and fragile; the brain case wide anteriorly; the frontal and interorbital widths narrow and the postorbital processes weak and slender, strongly grooved on their superior face. Sagittal crest not developed even in old specimens. Interorbital constriction about equal to postorbital constriction. Teeth weak, with normal cuspidation. Audital bullæ normal.

Measurements.—See tables.

Remarks.—The type specimens of *degener*, so generously loaned to me by Mr. Bangs, when compared with the large series used in the preparation of this paper, convince me that this depauperate insular form has no intercourse with the larger typical *hudsonica* of Labrador and New Brunswick. A skull from Grand river, Labrador, shows no approach to the *degener* type, and another from Okak, Labrador, agrees in the same differences. A young adult skull and skin of *hudsonica* from Nova Scotia, and an adult summer skin from New Brunswick, show that the maritime otter of the mainland sometimes attains a size nearly one-third larger than the largest known specimens of old, adult *degener*.

Specimens Examined.—Newfoundland, Bay St. George, 2 skins with skulls, 1 extra skull.

THE FISHERS OF NORTH AMERICA.

Apology must be made for the inferior series of skins and skulls which form the basis of the subjoined remarks on the Pekan. They serve, however, to elucidate some

* The collector's measurement of the hind foot of type is given on label as "126 mm." This is certainly incorrect, as the length determinable by feeling the calcaneum in the dry skin could not have exceeded 115 mm. This accords with the small size of the hind foot and the length of other specimens of *degener*.

questions sure to be soon brought up in the active advance of monographic work in American mammalogy.

The synonymy of Pennant's Fisher has already been discussed under *Lutra hudsonica,* and I have there given reasons for my adoption of the plate-name *canadensis* of Schreber as having priority over the long-accepted name *pennanti* of Erxleben for this animal.

PENNANT'S FISHER. *Mustela canadensis* Schreber.

Mustela canadensis Schreber, *Saugt.*, III, p. 492, Pl. CXXIV. Text published in 1777, plate in 1776 (*fide* Sherborn).
Mustela pennantii Erxleben, *Syst. An.*, 1777, p. 470.
Mustela melanorhyncha Boddaert, *Elench. An.*, 1784, p. 88.
Viverra piscator Shaw, *Gen. Zoöl.*, I, 1800, p. 414.
Mustela nigra Turton, *ed. Linn. Syst. Nat.*, I, 1802, p. 60.
Mustela godmani Fischer, *Syn. Mamm.*, 1829, p. 217.

Type Locality.—"New York and Pennsylvania," Pennant.

Geographic Distribution.—Northern North America, east of the Cascade mountains, from the northern limit of trees to Colorado and North Carolina in the mountains. Intergrading on the Pacific slope into subspecies *pacifica*, and probably in the southern Rocky mountain region into a paler race. Probably represented in the Hudsonian faunal region by a subspecies.*

Color.—From an adult, male, winter specimen taken near Lancaster, Pa., March 11, 1896, and in the possession of Dr. M. W. Raub, of that city, who furnished the description: "Head and one-half of the length of body, gray and black mixed, gray predominating; throat darkest, with snout from tip to line of eyes dark brown. The hinder half of body gradually darkens into a deep chocolate color until it reaches the tail, which is almost black with a tip entirely black. Hind legs and tail, viewed at a distance of six feet, look very dark, almost pure black. The fore legs are black but not so deep. Tips of ears, darkest."

Two specimens from the Bangs collection, one from Moosehead lake, Maine, the other from Idaho county, Idaho, seem to answer closely the above description. The light upper and forward portions of body are a grizzled grayish brown, the long hairs black tipped. The basal half of hairs of anterior back are hair brown. I can discover no color characters to separate the Idaho specimen from the one from Maine, nor do the skulls indicate any reliable differences. The Maine skin (of an animal two-thirds grown)

* Typical *canadensis* must be restricted to the Alleghenian form.

has white patches on lower fore leg, breast and vent, and an immature specimen of *pacifica* has white spots on throat, arm-pits and vent. The four adult specimens examined are not thus pied. Dr. Coues, in his *Fur-bearing Animals*, says that the fisher is an exception to the marten, mink and weasel in not having these patches. They may disappear with age in the fisher, but they do not in the other species.

Anatomical Characters.—Size, smaller than subspecies *pacifica*. Skull small; nasals relatively short, less elongate at basal apex. Posterior upper molar relatively small, its inner lobe not greatly developed longitudinally so as to only slightly exceed the breadth of outer lobe; neck of crown of same tooth but slightly constricted.

Measurements.—Of Dr. Raub's Pennsylvania specimen, old ad. ♂, *l. c.:* Total length, from end of nose to end of tail hairs, 965 mm.; tail vertebræ, 318 mm.; hind foot, 115 mm.; ear from crown, 27 mm. A mounted specimen, No. 507, Academy Natural Sciences, adult ♂, from "Pennsylvania," has a total length of 1000 mm., with tail (minus brush), 390 mm., and hind foot, 112 mm., taken from the dry mount. The Idaho specimen, No. 6964, young adult ♂, coll. of E. A. and O. Bangs, is 978 mm. long, with tail, 369 mm., and hind foot, 117 mm. Skull of No. 7437, yg. ad. ♂, Greenville, Me., total length, 117 mm.; zygomatic width, 63 mm.; mastoid width, 54 mm.; mesial nasal length, 22 mm.

Remarks.—The characters of the Pennsylvania fishers above enumerated, so far as they are based on reliable measurements and color diagnoses, may be considered as representing typical *canadensis*, based on Pennant's original notice of the animal. Whether a series of Alleghenian fishers will show the Hudsonian animal to be separable is an interesting question probably to be decided in the affirmative. The Idaho and Maine specimens examined, though not contrasted by me with Dr. Raub's specimen, must be very close to it. No skulls of Pennsylvania fishers have been examined, but the close resemblance of the Idaho skull to those from Maine, as indeed to *pacifica* also, strongly indicates that no cranial differences exist between the east American fishers of the north and south. The "saturated" color characters of *pacifica* are alone sufficient to distinguish it from all fishers found east of the Cascades.

Specimens Examined.—Pennsylvania, 1 mounted specimen (*fide* Dr. Raub, 1 mounted specimen); Maine, Mooseland lake, 1 skin with skull; Greenville, 2 skulls; Lincoln, 1 skull; Idaho, Idaho county, 1 skin with skull. Other specimens from eastern North America, 1 mounted, 2 old ad. skulls.

Pacific Fisher. *Mustela canadensis pacifica*, subsp. nov.

Type Locality.—Lake Kichelos, Kittitass county, Washington; altitude about 8000 feet. Type, No. 1074, old ad. ♀, in the collection of S. N. Rhoads; collected in the fall or winter of 1892–'93, by Allan Rupert.*

Geographic Distribution.—Pacific slope of America, from Alaska to California.

Color.—Above, from between eyes to middle back, grizzled, grayish ochraceous heavily lined with black, becoming hazel black on hind back and dark black on rump, thighs and tail. Whole head, behind eyes clove brown basally, strongly grizzled with dirty white. Snout to eyes blackish seal brown. Chin, throat, breast and belly between dark chestnut and hazel, obscured with black. Legs and feet black, the fore legs showing the vandyke brown bases of hairs. Basal half of hairs of anterior back are Prout's brown as contrasted with the hair brown of *canadensis.*

Anatomical Characters.—Size, large, skull very large, with relatively long nasals. Posterior upper molar large, with spreading inner lobe much wider longitudinally than outer section of same tooth; the crown suddenly constricted at the middle.

Measurements.—Of type from relaxed skin: Total length, 1090 mm.; tail, 350 mm. without brush; hind foot not determinable, as the bones are missing. Measurements of a specimen two-thirds grown, No. 295, coll. S. N. Rhoads, from near Tacoma, Wash.: Total length (relaxed skin), 970 mm.; tail, 400 mm.; hind foot, 112 mm.; ear from crown, 21 mm. Skull of type: Total length from hinder end of sagittal crest to front end of premaxillæ, 125 mm.; zygomatic expansion, 73 mm.; mastoid expansion, 54 mm.; interorbital constriction, 28.5 mm.; postorbital constriction, 20 mm.; mesial length of nasals, 27 mm.

Remarks.—The dimensions of the type skull, when we consider it was from a female, show that the fishers of the Cascade mountains attain a much greater size than those of the Appalachian chain. Young adult skulls of the same age from western Washington and Maine show the same distinctions. The younger specimen from Tacoma, while approaching nearer to Idaho and Maine specimens in grayer color, is very much darker than they, the difference in shade between the anterior and posterior dorsal areas of the former being slight, while in the latter it is striking. The tawny suffusion so deeply marked in the type of *pacifica* and which separates it at a glance from *canadensis* is also noticeable in the Tacoma specimen.

Specimens Examined.—Washington, Lake Kichelos, 1 skin with skull, 2 skulls; near Tacoma, 1 skin, 1 skull; British Columbia, Sumas, 1 skull.

* Mr. Rupert, whose business is hunting and trapping, first sent me the fresh skull of a very old ♀ fisher, which was entered in my catalogue as No. 621. I wrote him immediately that I would like to have the pelt belonging thereto, and in a later shipment the skin, which forms the type of *pacifica*, was sent on without label. As it is also from a female and a very old animal, I consider the skin and skull as belonging to the same individual.

Skull Measurements of North American Otters (in millimeters)

Collection.	Catalogue Number.	Sex.	Locality.	Species.	Length from posterior apex of occiput to anterior end of premaxilla.	Zygomatic expansion.	Mastoid expansion.	Interorbital constriction.	Postorbital constriction.	Expanse of postorbital processes.	Length of postorbital frontal neck.	Remarks.
E. A. and O. Bangs	5638	yg. ad. ♂	Nova Scotia, Annapolis	L. hudsonica ("Lacép.," Desm.)	113.5	72	68	27.7	23	35	15	Large, coast form.
do.	7431	old ad.	Labrador, Okak	do.		74.5	67	23	19	35	13.5	Coast form.
Acad. N. Sci. Phila.	3150	old ad.	Labrador, Grand River	do.	105	72.5	65	20.8	20	29	10.5	Inland form.
Smithsonian Inst.	21483	old ad.	Alaska, Tanana River	do.	102	72	63.5	24	18	32	12.5	Inland form.
E. A. and O. Bangs	4238	old ad. ♂	Maine, Bucksport	do.	109	73.5	66	25.5	21.5	37	14	Coast form.
do.	4188	old ad. ♂	Massachusetts, Canton	do.	112	76	69	26	22	38	15.	Intermediate.
Acad. N. Sci. Phila.	3569	old ad.	Pennsylvania, Monroe Co.	L. h. lataxina (F. Cuv.)	100	69.5	65	22.8	20	31	13	Inland interm., prob. ♀.
S. N. Rhoads	1840	yg. ad.	do.	do.	104.5	68	61	21.5	19	28.6	12	Probably ♂.
do.	1565	yg. ad.	New Jersey, Tuckerton	do.	104	70	63.5	24.5	23	33.5	11	
do.	3896	yg. ad.	New Jersey, Mickleton	do.	107	70	63	23			12	
E. A. and O. Bangs	3537	old ad. ♂	North Carolina, Raleigh	do.	104	71	62	22	22	33	13.5	
do.	3538	yg. ad. ♀	do.	do.	103	65.5	61	21.5	21	30.5	11	
do.	5749	yg. ad. ♂	Florida, Micco	L. h. vaga Bangs	108	71	71.2	24	18.6	35	16	Type (*fide* Bangs).
do.	4995	ad. ♀ .	Florida, Roseland	do.	[101]	70.3	67	21.8	17.8	30		(*fide* Bangs.)
WagnerInst., Phila	——	ad.	Florida, St. John's Riv., Volusia Co.	do.	105	72	67	24	22	34	18.2	
S. N. Rhoads	1580	old ad. ♂	Florida, Tarpon Springs	do.	116	79	76.5	27	20.5	39.5	20	
do.	616	yg. ad. ♂	Washington, L. Kichelos	L. h. pacifica Rhoads	115.5	72.5	69	25	20	36.5	12	Type.
do.	303	old ad. ♀	Washington, near Tacoma	do.	110.5	77	70	29	21 5	43	16	
Smithsonian Inst.	8686	old ad.	Alaska (coast ?)	do.	115.5	74.5	70.4	27.3	24	41	16	Col. by Dr. T. T. Minor.
do.	8687	old ad.	do.	do.	119	83	76	34	25	49	14	do.
do.	8688	old ad.	do.	do.	110	78	73	27	18	41.5	15	do.
E. A. and O. Bangs	6965	yg.? ad. ♂	Newfoundland, Bay St. George	L. degener Bangs	101	66	60	22	19.5	32.5	11.5	Type.
do.	6966	old ad. ♀	do.	do.	[98]	70	63	22.8	19 4	33.6		Topotype (*fide* Bangs).
do.	3755	yg. ad. ♀	do.	do.	93	64	56	19	18.8	25.8	10	Topotype.

Body Measurements of North American Otters (in millimeters).

Collection.	Catalogue Number.	Sex.	Locality.	Species.	Total Length.	Tail Vertebræ.	Hind Foot.	Remarks.
E. A. and O. Bangs	5638	yg. ad. ♂	Nova Scotia, Annapolis	L. hudsonica ("Lacép.," Desm.)	1090	415	[123]	Large, coast form.
do.	46	?	New Brunswick, Restigouche Riv.	do.	1190	393	115	Meas. taken from stuffed skin.
do.	4189	ad. ♂	Massachusetts, Kingston	do.	1168	457	124	Intermediate.
do.	4190	ad. ♀	Maine, Upton (L. Umbagog)	do.	1065	406	114	Inland type.
Acad. N. Sci. Phila.	3360	im. ♂	Pennsylvania, Clinton Co.	L. h. lataxina (F. Cuv.)	1016	360	115	Inland type, mounted spec'n.
E. A. and O. Bangs	4252	yg. ad. ♂	Connecticut, Liberty Hill	do.	1093	410	127	Intermediate.
H. H. and C. S. Brimley	451	ad. ♀	North Carolina, Raleigh	do.	1066	368		Weight, 15 lbs.
do.	453	ad. ♂	do.	do.	1144	445		Weight, 17 lbs.
do.	——	ad. ♂	do.	do.	1130			Weight, 16 lbs.
E. A. and O. Bangs	4995	ad. ♀	Florida, Roseland	L. h. vaga Bangs	1100	400	110	
do.	4998	yg. ad. ♂	Florida, Citronelle	do.	1285	487	130	
S. N. Rhoads	616	yg. ad. ♂	Washington, Lake Kichelos	L. h. pacifica Rhoads	1117	419	128?	Type.
do.	302	yg. ad. ♂	Washington, near Tacoma	do.	1092	368	120	Meas. from ligamentous skeleton.
Amer. Mus. Nat. Hist.	3712/309	ad. ♀	Beaver Creek, Yavapai Co., Arizona	L. h. sonora Rhoads	1300	472	146	Type. Weight, $19\frac{7}{16}$ lbs.
E. A. and O. Bangs	6965	ad. ♂	Newfoundland, B. St. George	L. degener Bangs	998	358	[115]	Type.
do.	6966	ad. ♀	do.	do.	990	352	109	Topotype.

Explanation of Plates.

Plates XXI and XXII.

(Scale slightly less than two-thirds natural size.)

Figs. 1 and 1. *Castor canadensis pacificus* Rhoads. Topotype; No. 1865, col. of S. N. Rhoads; old adult ♂, from Lake Kichelos, Kittitass county, Wash. Superior and inferior, vertical aspects of same skull.

Figs. 2 and 2. *Castor canadensis frondator* Mearns. No. 32, col. of E. A. and O. Bangs; young adult ♀, from Red Lodge, Mont. Superior and inferior, vertical aspects of same skull.

Figs. 3 and 3. *Castor canadensis* Kuhl. No. 31, col. of E. A. and O. Bangs; old adult (probably ♂), from New Brunswick. Superior and inferior, vertical aspects of same skull.

Plate XXIII.

(Scale four-fifths natural size.)

Figs. 1 and 2. *Castor canadensis carolinensis* Rhoads. Type; No. Z. 609, col. of State Museum of N. Carolina; old adult ♂, from Dan river near Danbury, Stokes county, N. Carolina. Superior and inferior, vertical aspects of same skull.

Plate XXIV.

(Scale six-sevenths natural size.)

Fig. 1. *Lutra hudsonica* ("Lacépède," Desmarest). No. 4188, col. of E. A. and O. Bangs; old adult ♂, from Canton, Mass. Superior, vertical aspect of skull.

Fig. 2. *Lutra hudsonica* ("Lacépède," Desmarest). No. 1201, col. of E. A. and O. Bangs, old adult ♂, from Westford, Mass. Inferior aspect of skull.

Fig. 3. *Lutra hudsonica pacifica* Rhoads. No. 8686, col. of Smithsonian Institution; old adult, from (the coast of?) Alaska. Inferior aspect of skull.

Fig. 4. *Lutra hudsonica lataxina* (F. Cuvier). No. 3537, col. of E. A. and O. Bangs; old adult ♂, from Raleigh, N. Carolina. Superior, vertical aspect of skull.

Fig. 5. *Lutra degener* Bangs. Type; No. 6965, col. of E. A. and O. Bangs; adult ♂, from Bay St. George, Newfoundland. Superior, vertical aspect of skull.

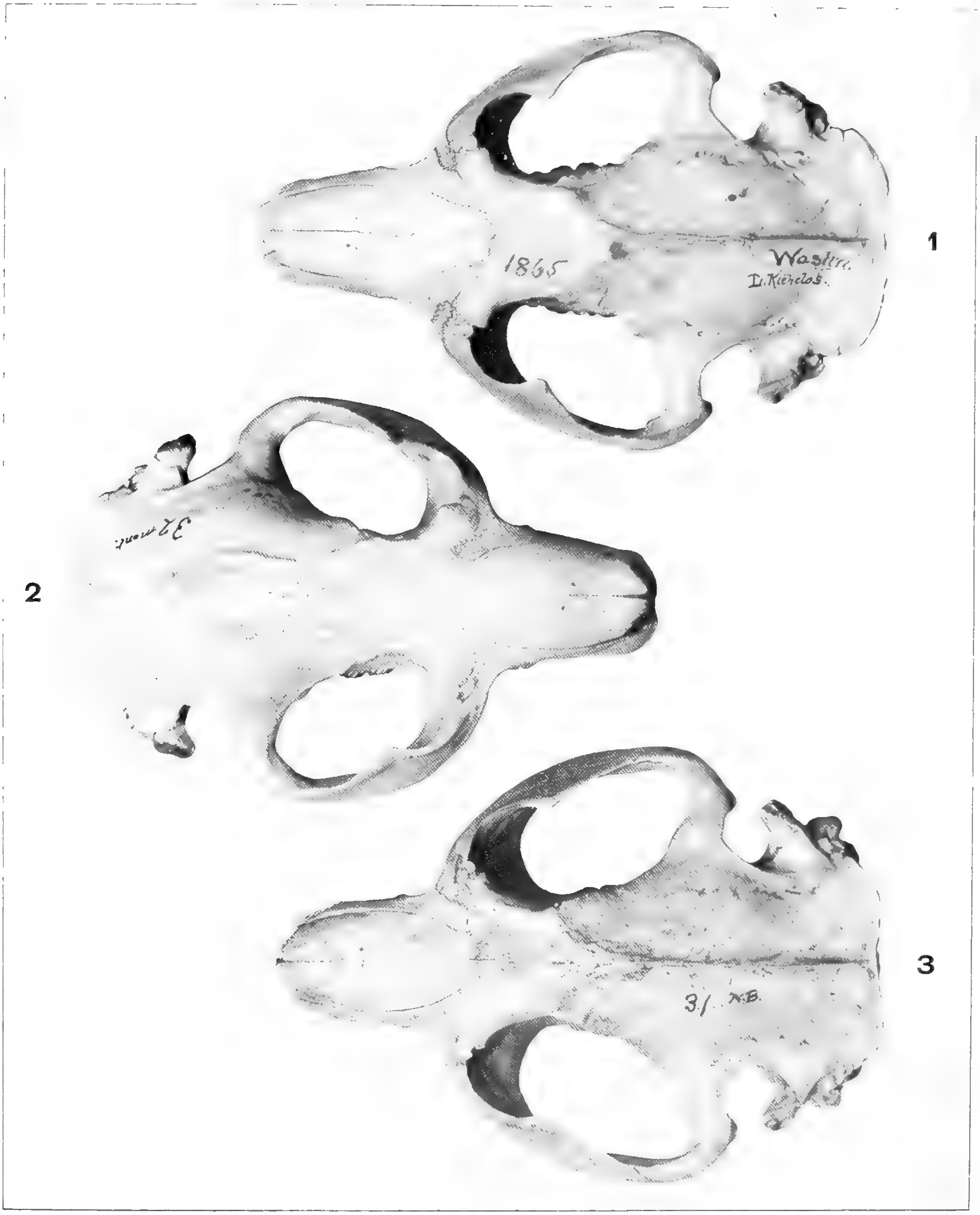
Plate XXV.

(Scale slightly less than five-sixths natural size.)

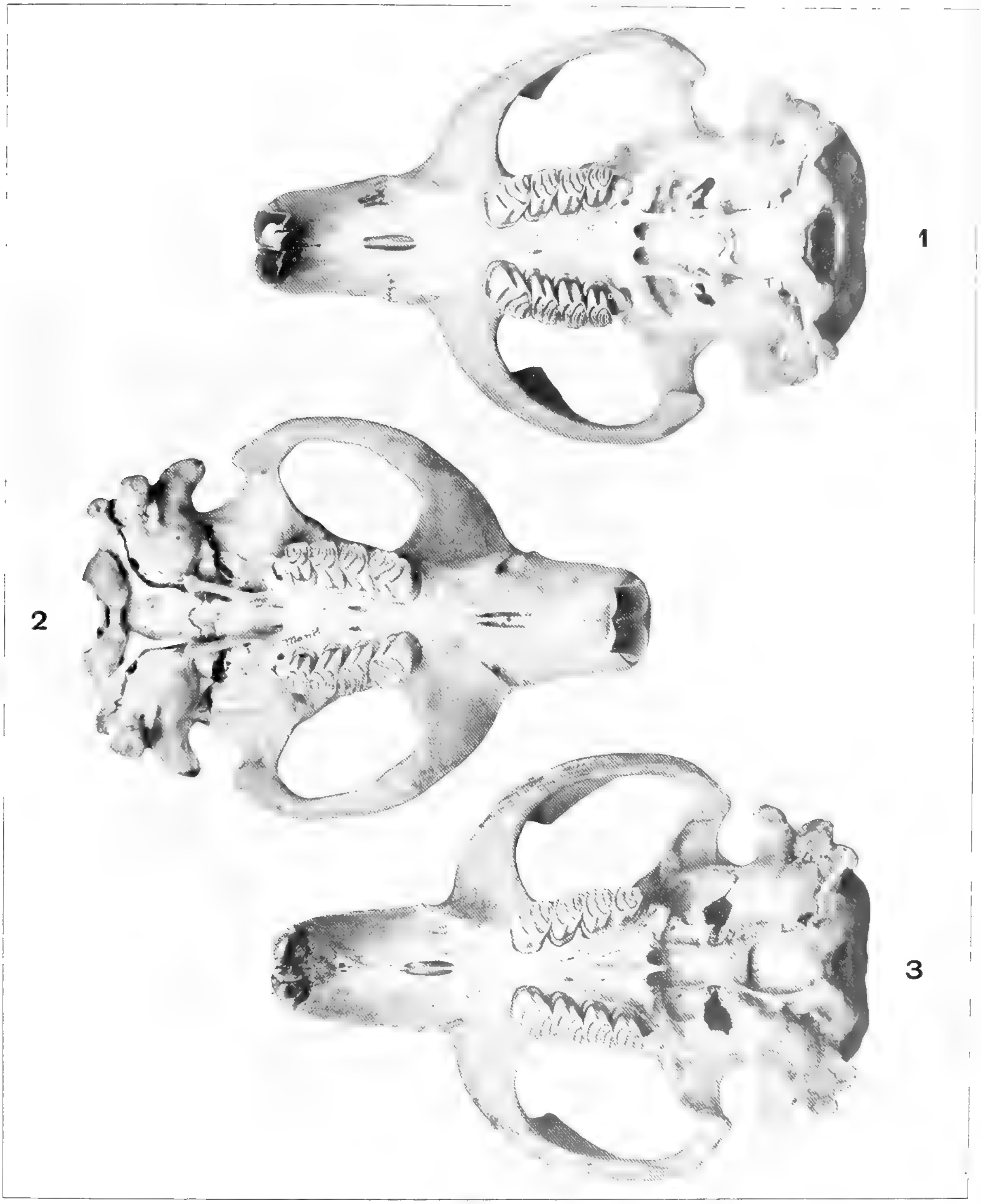
Fig. 1. *Lutra hudsonica pacifica* Rhoads. No. 8687, col. of Smithsonian Institution; old adult (probably ♂), from (the coast of?) Alaska. Superior, vertical aspect of skull.

Fig. 2. *Lutra hudsonica vaga* Bangs. No. 1580, col. of S. N. Rhoads; old adult ♂, from Tarpon Springs, Fla. Superior, vertical aspect of skull.

Fig. 3 *Lutra hudsonica pacifica* Rhoads. No. 303, col. of S. N. Rhoads; old adult ♀, from Tacoma, Wash. Superior, vertical aspect of skull.

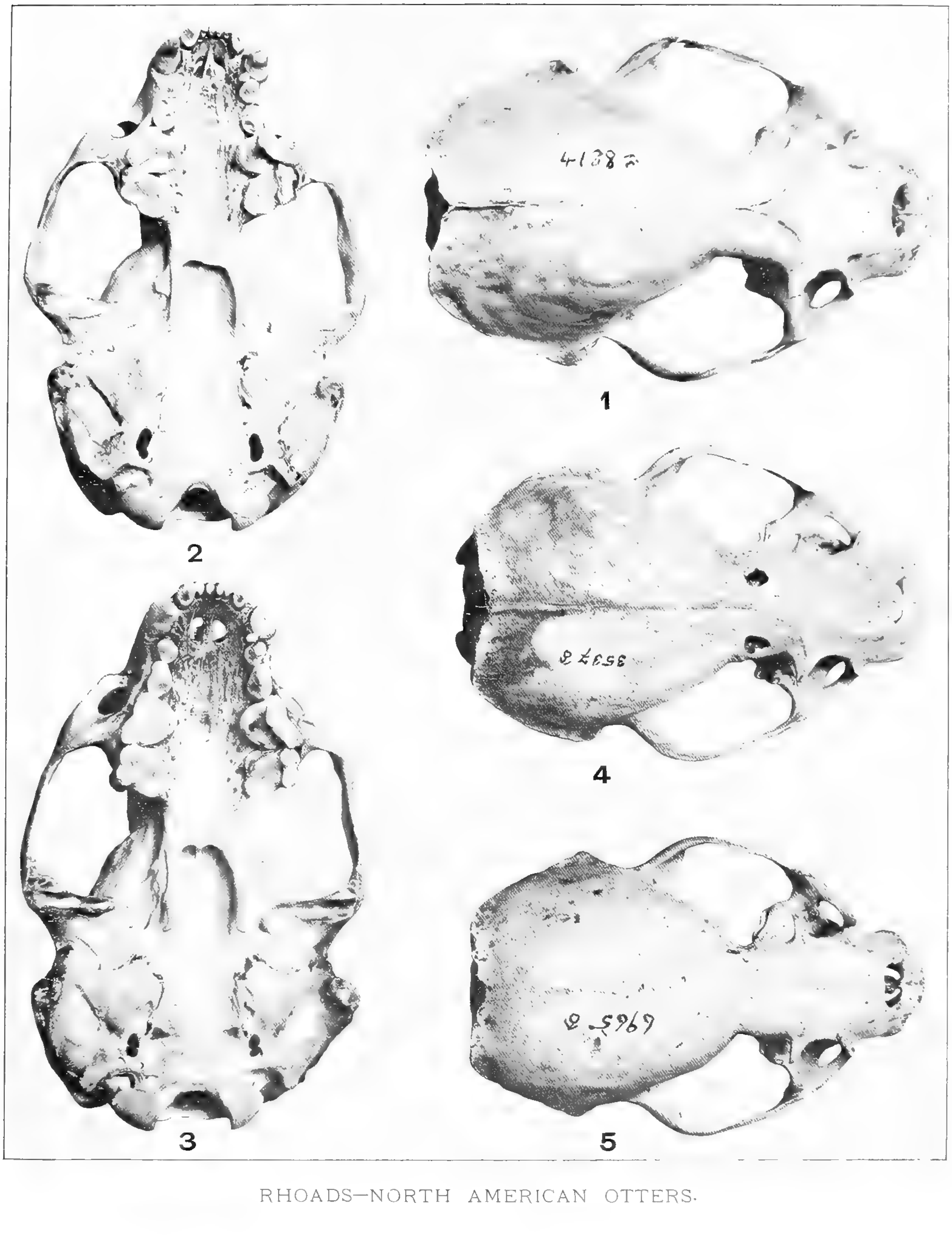


RHOADS—NORTH AMERICAN BEAVERS.

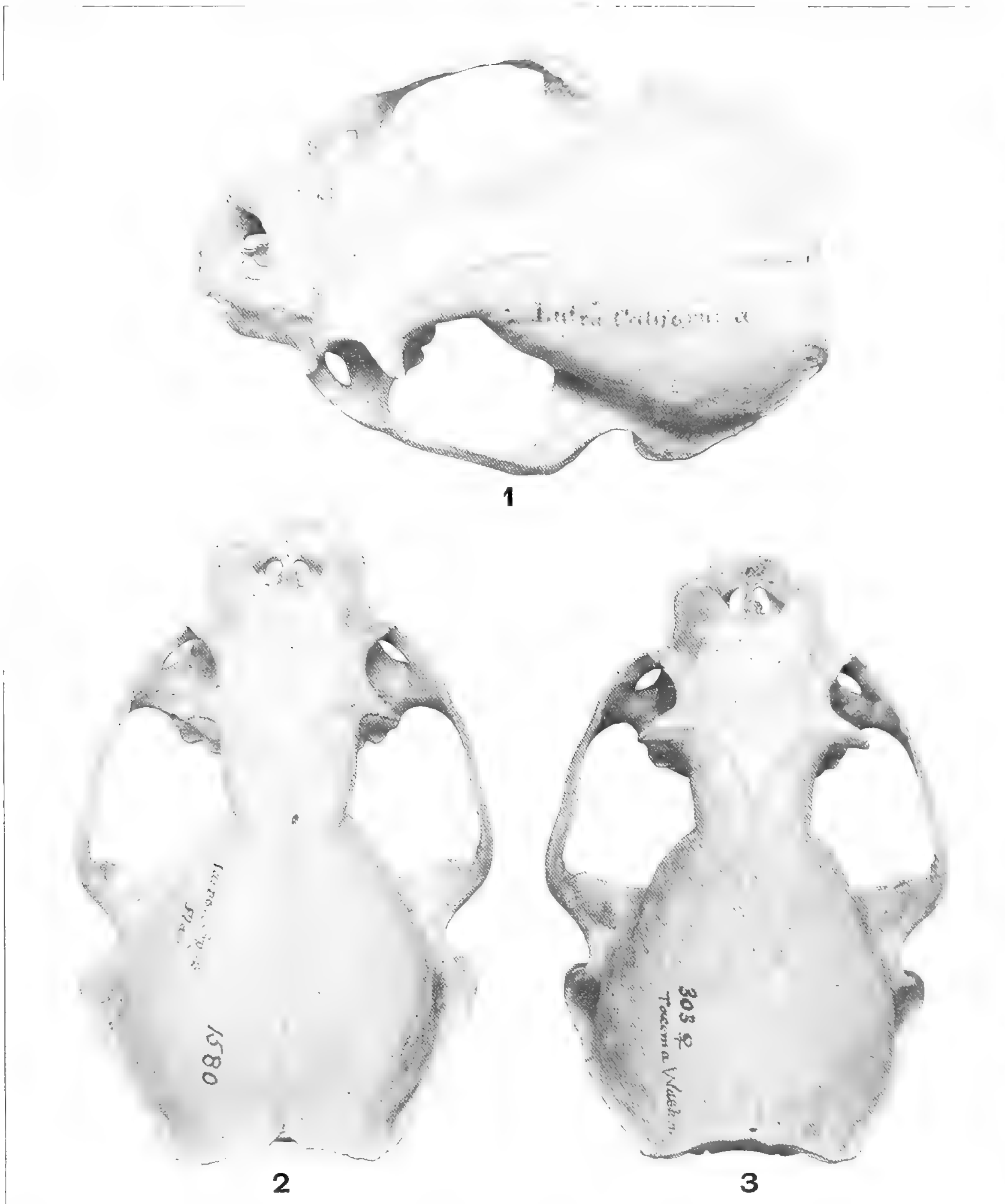


RHOADS—NORTH AMERICAN BEAVERS.

RHOADS—NORTH AMERICAN BEAVERS.



RHOADS—NORTH AMERICAN OTTERS.



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