

Article XXXII.—NEW MERYCOIDODONTS FROM THE MIOCENE OF MONTANA.

BY EARL DOUGLASS.

The collections which were made in Montana in 1902, by the party from the American Museum of Natural History under Dr. W. D. Matthew, contain some Merycoidodonts which are of much interest in connection with the study of this subfamily of Artiodactyls. Through the kindness and courtesy of Prof. H. F. Osborn and Dr. W. D. Matthew, the best of this material has been sent to me for study. Two of the specimens, which I have named *Mesoreodon longiceps* and *Ticholeptus brachymelis*, are represented by almost complete skulls with large portions of the skeletons. They were found in beds from which no fossils had previously been obtained. Another specimen which came from the Upper Miocene beds of the Lower Madison Valley, is the skull of *Pronomotherium altiramus* (Douglass). The type of this species is a right ramus of a mandible containing the molar and premolar teeth. It was originally assigned by Douglass to the genus *Merycochærus*.

The two first specimens above mentioned were found in beds of fine buff-colored sands, which may contain some clay, on the east side of the North Boulder River about six miles above where it empties into the Jefferson River. The beds are quite definitely stratified or banded. They dip to the westward toward the river and away from the ridge of Palæozoic limestone which forms the eastern boundary of the valley and the western face of the low mountain ridge which separates this valley from the larger one near the head of the Missouri River. A small area, apparently of White River strata (a remnant left by erosion) intervenes horizontally between the Miocene deposits and the Palæozoic limestone. In outcrops of the Miocene a little farther south part of a mandible of a *Cosoryx* was found. On the west side of the river, in deposits similar in appearance, Mr. Douglass obtained portions of a skull and mandible of a small Camel. In another locality but in a nodular stratum many fragments of teeth and bones of small and large Camels were obtained, some of which belonged to a large species of *Procamelus*. Associated with these were remains of turtles, one nearly complete shell of which Dr. O. P. Hay referred to the species *Tes- tudo hollandi* Hay.¹ The type of this species was found by O. A. Peterson

¹ No. 1570 Carnegie Museum Catalogue of Vertebrate Fossils. See Annals of the Carnegie Museum, Vol. IV., No. 1, p. 19.

in the Loup Fork beds near the Running Water River in Nebraska. In another place to the westward and more distant from the river, part of the skull of a *Neohipparion*, very much like *N. isonesum*, was found. Still farther to the westward and at a higher level are beds that contain coarser sand and are more evidently of stream origin. They are much like the later Miocene deposits of the Lower Madison Valley. From these the mandible of *Neohipparion* was obtained. The above named specimens are in the Carnegie Museum. It is impossible to say how nearly of the same age are the beds on the opposite sides of the river, for the various deposits of Oligocene and Miocene times, in western Montana, are so mixed on account of the carving out and refilling of the valleys, good exposures are so isolated, and the lithological characters occasionally so deceptive, that one cannot always be sure as to the horizon without obtaining characteristic fossils. In some places, too, the fossils are nearly all Agriochœrids and of different species from those found elsewhere; while in other places no specimens of this family are obtained. I assign these beds provisionally to the Middle Miocene.

Detailed descriptions and records of variations are of little interest unless they give some evidence as to the vital economy of the animal, and its relations to its surroundings or to kindred forms. I give below some of the portions of the osteological anatomy of the Merycoidodonts which have been found to be especially subject to variations, show how some of these appear to be correlated, and give some conjecture as to their meaning.

Some of the parts subject to variations are the following: (1) The posterior basal portion of the skull, (*a*) tympanic and mastoid portions of the temporal, (*b*) exoccipitals; (2) the skull as a whole — varying proportions of length, height, and width; (3) upper antero-posterior contour of skull — nearly straight or arched; (4) the mandible, (*a*) horizontal ramus relatively short, low or high (none have slender mandibles), (*b*) angle medium or large; (5) sagittal crest low, or absent, light, or heavy; (6) malar (always quite heavy) deep, or relatively shallow.

Some of the following modifications might be considered progressive in their nature as they occur in nearly all the later forms, while other characteristics are possessed by only a portion of the members of the family: (1) Increase in size; (2) teeth, especially molars, becoming more hypsodont; (3) teeth increasing in length and height backward so that the molar is longer than the premolar series; (4) zygomatic portions of the squamosals enlarged or otherwise changed; (5) premaxillaries coössified; (6) limbs and feet shortened or lengthened, becoming heavier or more slender; (7) some slight shifting of the bones of the manus; (8) nasals shortened; (9) angle between basifacial and basicranial axis increased; (10) upper portion of

ascending ramus of the mandible changed; (11) palatines produced posteriorly; (12) modifications of the skull, especially the anterior portion, which in some cases was undoubtedly accompanied by lengthening and other changes in the upper lip and nose.

It is important to endeavor to ascertain how these different modifications are correlated. (1) Most of the specimens which have a heavy malar have a large angle to the mandible. This implies a great development of the superficial portion of the masseter muscle; (2) there is some evidence, perhaps, but not so much, of a similar relation between the portions of the skull and of the mandible to which the temporal muscle is attached; (3) shortening of the skull is usually accompanied by deepening of the mandible, lengthening of the molar as compared with the premolar series, and by heightening of the teeth. It is sometimes accompanied by shortening of the nasals and broadening of the skull; (4) the lengthening of the skull is not necessarily correlated with the lengthening of the limbs.

It is difficult to see of what use was the development of extremely large zygomatic arches like those in some species of *Promerycochærus* unless they were used for defense or had weapons of defense attached to them.

The peculiarities in the structure of the Agriochæridæ which makes it appear probable that they usually inhabited woods, streams, marshes, and thickets, and that they subsisted principally on coarse foods such as leaves, twigs, rushes, coarse grasses, etc., are: (a) attachments for strong masticatory muscles; (b) long and probably large bodies for the accommodation of large viscera; (c) short legs and feet not adapted to life in the open country; (d) phalangigrade gait with spreading toes enabling them to walk on soft ground and probably to swim with facility in the water; (e) no apparent correlation between long heads and long necks or limbs, as is usually the case with animals that subsist on short grasses; (f) a long upper lip or proboscis, in some species, which would undoubtedly be useful in procuring leaves and coarse grasses.

Mesoreodon longiceps sp. nov.

Type No. 9732, American Museum of Natural History. A nearly complete skull with the mandible, the cervical, lumbar, and sacral vertebræ, portions of most of the dorsal vertebræ, a scapula, a pelvis, a femur, a tibia, a fibula, a nearly complete hind limb including the foot, several other foot-bones, and many fragments. From Middle or Upper Miocene deposits on the east side of the North Boulder Valley near Cold Spring post-office in Jefferson County, Montana. Collected by Albert Thomson of the American Museum party under Dr. W. D. Matthew in July, 1902.

The characters which distinguish this species from the type of *Mesoreodon* are numerous, and in some respects considerable in degree. The following are some of the distinguishing peculiarities:

Skull long, especially the posterior portion; brain-case large and full; nasals and frontals arching; sagittal crest sessile, represented by a small low ridge; median pillar of occiput broad; space between paroccipital and postglenoid processes unusually large; palate produced considerably posterior to last molar; teeth but slightly hypsodont.

As the skull is more or less peculiar in most of its details it merits a quite full description. It is long in proportion to its height. This lengthening is principally posterior to the face, especially posterior to the glenoid articular surfaces. The length of the skull is almost twice the width. The upper contour is not quite straight as there is an arching of the anterior portion of the nasals, a depression of the posterior portion, an arching of the posterior portion of the frontals and the anterior portion of the parietal, while posterior to this convexity, the lowness of the sagittal crest forms a depression.

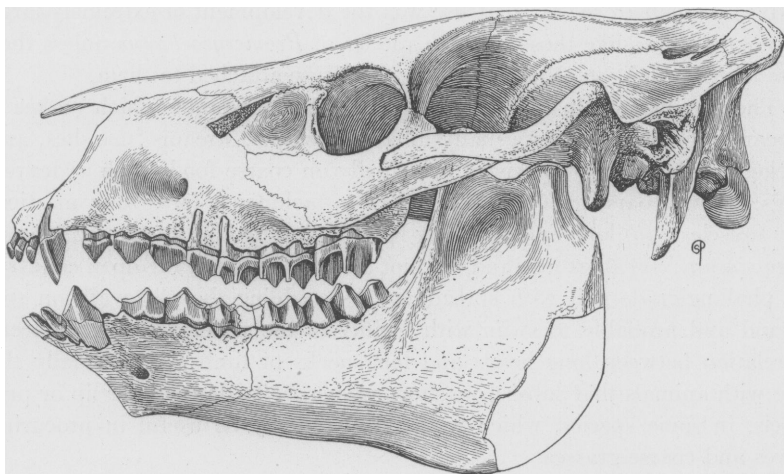


Fig. 1. *Mesoreodon longiceps*, side view of skull and jaws, $\times \frac{1}{2}$. Type specimen, Amer. Mus. No. 9732.

The premaxillaries are only slightly, if at all, coössified. The nasals do not extend as far forward as do the premaxillaries. They have slightly truncate or rounded tips, are convex antero-posteriorly and transversely at their broadest portions which are just posterior to the opening of the anterior nares, and their posterior ends are rounded. The frontals are mostly convex, though there is a depression just behind the nasals. The fronto-parietal suture is a considerable distance anterior to where the supratemporal ridges unite. The sagittal crest is represented by a low sessile narrow ridge which becomes a little higher just anterior to the occipital crest. Its backward extension continues as a very low ridge over the upper Y-shaped surface of the occipital crest, and in the median line beneath the posterior overhanging

portion of this crest between its lateral wings forms a high sharp rugose ridge. The pillar of the occiput is broad, slightly concave above and broadly convex below. It is bounded laterally by small ridges which extend downward from the lambdoid crest. External to the broad pillar are large deep concavities, or openings into the

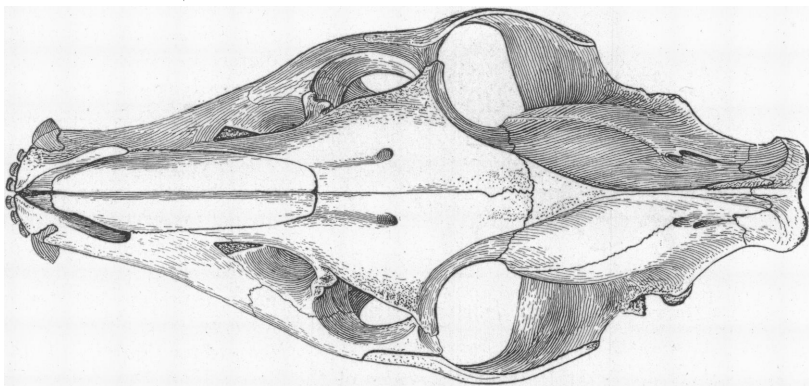


Fig. 2. *Mesoreodon longiceps*, superior view of skull, $\times \frac{1}{2}$. Type specimen, No. 9732.

brain case. Above and external to these are the high, thin, overhanging ridges or plates of the temporal bone. These ridges branch off from the lambdoid crests at the same places as the ridges previously described which are internal to the cavities. They are deflected downward on the outer portions of the mastoid processes which project considerably external to the exoccipitals. The occipital condyles

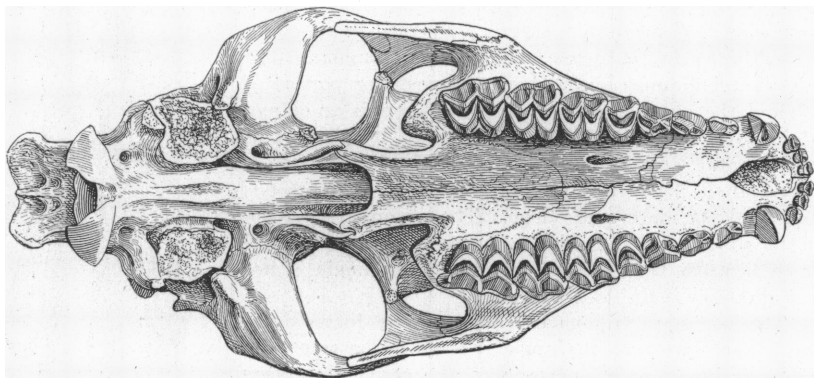


Fig. 3. *Mesoreodon longiceps*, inferior view of skull, $\times \frac{1}{2}$. Type specimen, No. 9732.

and foramen magnum are broad. The lower surface of the basioccipital is quite broad just anterior to the foramen magnum, but between the tympanic bullæ it suddenly contracts. Immediately in front of this on the median basal portion of the skull are two parallel longitudinal ridges instead of one. Anterior to these ridges

the basisphenoid is directed upward forming an angle with the basioccipital. The paroccipital processes are prismatic and are placed behind the tympanic bullæ, the

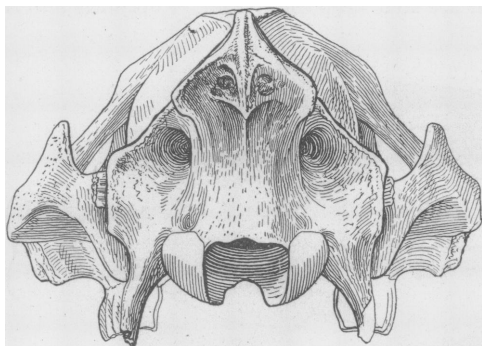


Fig. 4. *Mesoreodon longiceps*, occipital view of skull, $\times \frac{1}{2}$. Type specimen, No. 9732.

lateral expansion of their bases being behind the external auditory meatus and the mastoid process. Their antero-posterior and transverse diameters behind the bullæ are nearly equal. Below this they are laterally compressed and slightly bent inward. The tympanic bullæ were large but the lower portions are not preserved. The opening of the external auditory meatus is just anterior to the mastoid process, but it sends a heavy wing forward to the base of the postglenoid process as in some species, at least, of *Eporeodon* of the Lower John Day beds. The postglenoid processes are unusually slender being narrow transversely. They are concave posteriorly on account of the broad channels which extend downward from the large post-glenoid foramen. The pterygoids are thickened below, thin above, concave on the outside, and convex on the inside. The pterygoid plates of the palatine, to which the pterygoids are attached on the inner surfaces, are concave postero-internally while the pterygoids are concave postero-externally so that the two form an oblong trough-like depression. The palatines extend backward in a trough-shaped extension 2.5 cm. behind the last molar. The infraorbital foramen opens above the posterior portion of p^3 and the anterior portion of p^4 . There is an oblong triangular vacuity on the face surrounded by the maxillary, frontal, and lachrymal bones. The latter bone is large and the lachrymal pit is rather deep. The orbit is small and the malar quite deep. The zygomatic portion of the squamosal is slender in front, it reaches forward much beneath the orbit and the posterior angle is not high or heavy.

The horizontal ramus of the mandible increases in depth backward and the angle is large. The ascending ramus is broad antero-posteriorly, the coronoid process thin, and the masseteric fossa shallow.

The teeth are brachy-hypsodont or brachyodont with a tendency to become hypsodont. The incisors are not large. The canines have a vertical groove on the inner side. Premolars one to three in both jaws increase regularly in size backward and in the development of the ridges and depressions. The

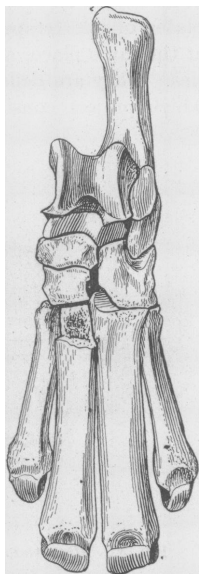


Fig. 5. *Mesoreodon longiceps*, hind foot, $\times \frac{1}{2}$. Type specimen, No. 9732.

molars also increase regularly in length and width. The molar series is slightly longer than the premolar series.

Judging from Scott's description of *Mesoreodon chelonys* some of the bones of the present species show small differences in some of the details, but a comparison of the bones themselves is necessary to ascertain the exact amount of this difference. Judging by Scott's figure of the hind foot the metacarpals, especially the lateral ones (II and V), are more slender in *Mesoreodon chelonys*.

Measurements.

	mm.
Length of skull, total	260
Length of skull, basal	247
Length of upper dental series	124
Length of skull posterior to dental series	124
Length of skull from posterior of m ² to anterior of post-glenoid process	64
Length of skull behind anterior portion of post-glenoid process	60
Width of skull, greatest	129
Width of posterior pillar of occiput	28
Height of skull above posterior base of m ²	72
Length of upper premolar series	45
Length of upper molar series	56
Length of lower premolar series	49
Length of lower molar series	59
Depth of mandible under middle of m ²	41
Length of metatarsal IV	73
Width of shaft of metatarsal IV, middle	12
Proportion of height of skull to length = $72 : 260 = 27.7 : 100$.	
Proportion of width to length = $129 : 260 = 45.7 : 100$.	
Length of upper premolar to molar series = $80 : 100 = \frac{4}{5}$ nearly.	
Length of lower premolar to molar series = $83 : 100$.	
Proportion of width of metatarsal IV to length = $12 : 73 = 16.4 : 100$.	

Ticholeptus brachymelis sp. nov.

Type: No. 9731 American Museum of Natural History. A nearly complete skull with the mandible, the cervical and lumbar vertebræ, nine or ten dorsal vertebræ part of which are incomplete, and the greater portions of the fore limbs. Found in the same beds as *Mesoreodon longiceps*, on the east side of the North Boulder Valley opposite Cold Spring post-office. Collected by Albert Thomson of the American Museum party under Dr. W. D. Matthew in 1902.

Skull high in proportion to length. Greatest height to greatest length, 157 mm.: 257 mm. = $61 : 100$ or approximately $\frac{3}{5}$. Forehead only moderately broad; upper antero-posterior contour of skull nearly straight; sagittal crest short and not high;

orbit small; zygomatic arches deep under the orbit, ascending posteriorly; squamosal portion of arch not heavy; nasals shortened; horizontal ramus of mandible moderately deep, uniform in height from $p_{\frac{3}{3}}$ to $m_{\frac{3}{3}}$; premolar teeth not long or high; molars moderately hypsodont; proportion of length of upper premolar to molar series = 48 mm.: 60 mm. = 80 : 100 = $\frac{4}{5}$; lower molar to premolar series = 49 mm.: 64 mm. = 76.5 : 100; limbs and feet short.

The premaxillaries are coössified for a distance of 12 cm. The upper portion of the anterior narial opening is large and broadly rounded, the borders only moderately steep. The nariums are abbreviated. The infraorbital foramen opens above the anterior portion of $p_{\frac{4}{4}}$. The malomaxillary ridge is heavy and the lachrymal pit deep. The malar is deep beneath the orbits and ascends backward. The squamosal portion of the zygomatic arch is heavy. The forehead is not extremely broad, neither is the occiput. The exoccipitals and the paroccipital processes are moderately expanded laterally. The internal portions of the latter, behind the tympanic

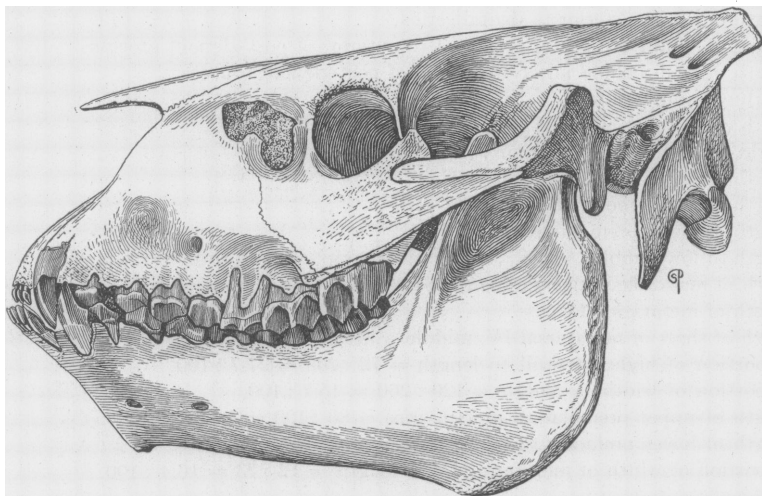


Fig. 6. *Ticholeptus brachymelis*, side view of skull and jaws, $\times \frac{1}{2}$. Type specimen Amer. Mus. No. 9731.

bullæ, are thickened antero-posteriorly. The bullæ are quite large. The external auditory meatus is a long, straight tube directed upward more than outward or backward. The angle of the mandible is large but does not extend very much below the lower border of the horizontal ramus. The masseteric fossa is deep.

From the type of the genus, *Ticholeptus zygomaticus* Cope, this species differs in the greater length of the skull in proportion to the height, in the more nearly straight upper contour of the skull, in the less thickened and rugose squamosal portion of the zygomatic arch, and in the less hypsodont teeth.

From *Ticholeptus breviceps* Douglass, from Divide Creek, Montana,

skull of this remarkable animal, and to compare it with the fine skull of its nearest known relative, *Pronomotherium laticeps*, in the Carnegie Museum.

When the mandible which was used as the type was first described it was lying in a bed of plaster, the removal of which and the more accurate fitting of the fragments, has somewhat changed the contour of the border of the horizontal ramus from that represented in figure 1 in the original description, making it more nearly like the mandible of *Pronomotherium laticeps*.

The skull, which represents a young individual, is longer than that of *Pronomotherium laticeps* and is broad posteriorly. It is more or less distorted, and probably the posterior and upper portions are pushed slightly backward. The length of the dental series is greater than the length of the skull posterior to it. The palate is long and not so broad as in *Pronomotherium laticeps*. It is produced backward of the molars and has a peculiar form. It is concave between the last molars and a little posterior to them, and the borders are thick and rounded. In the middle of this concavity is a low median longitudinal ridge. Posterior to this concave area is an area that is convex antero-posteriorly and concave transversely, being bounded laterally by two antero-posteriorly flattened processes. I cannot



Fig. 8. *Pronomotherium altiramum*, superior view of lower jaw, $\times 2$. Type specimen, Carnegie Mus. No. 759.

say how much of this portion of the skull belongs to the pterygoids and how much to the palatines. Behind the produced palate the pterygoid fossa is deep. The basi-occipito-sphenoid axis is very steep. The glenoid articular surfaces are large, slightly concave transversely, and decidedly convex antero-posteriorly. The postglenoid processes are broad transversely, thin antero-posteriorly, and quite high. The paroccipital processes are directed transversely. They are convex behind and flattened or slightly concave in front. The occipital condyles are broad transversely and narrow antero-posteriorly. The exoccipitals above the paroccipital processes are broad.

The malo-maxillary ridge extends to above m^1 . Above this the floor of the large facial concavity is nearly horizontal as in *Pronomotherium laticeps* but the posterior portion is probably somewhat crushed vertically. The malar beneath the orbit is moderately deep. The zygomatic portion of the squamosal is not deep, neither is its posterior angle high or heavy.

The forehead is flat and on its postero-external borders the temporal ridges are heavy, standing up like a wall.

The mandible is very deep. The chin is steep but it does not appear to have been so concave as in *P. laticeps*. Beneath m_2 the horizontal ramus of the mandible becomes deeper and beneath m_3 it descends still more abruptly.

Dentition.—The teeth are strongly hypsodont, increasingly so from the second premolar backward. Their antero-posterior diameters increase

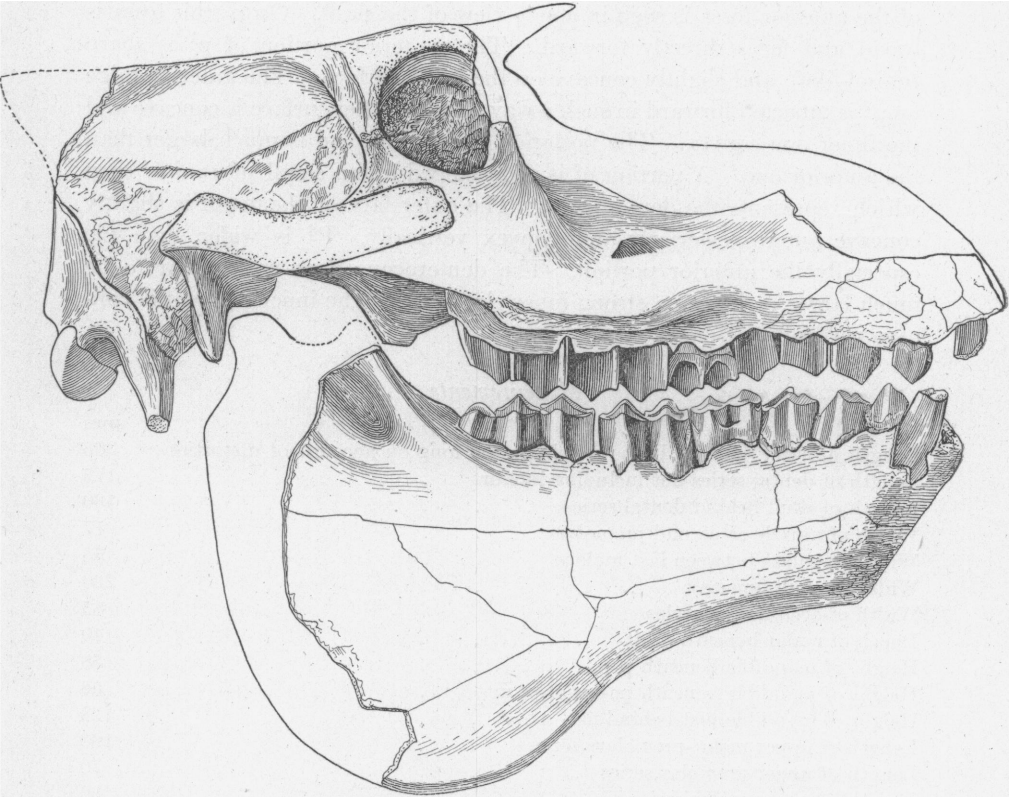


Fig. 9. *Pronomotherium altiramus*, side view of skull and jaws, $\times 3$. The lower jaw, Carnegie Mus. No. 759, is the original type of the species. The skull, American Mus. No. 9740, probably belongs to the same individual.

in the same order. The mandible and its dentition have been described in the paper cited at the beginning of this description.

Although the teeth are on the same general plan as those of other Merycoidodonts, the upper, even more than the lower ones, have some plainly distinguishing peculiarities.

The canine is not heavy. Its outer angle is sharp having an almost

knife-like edge, and on the inner surface there is a sharp and prominent slightly crescent-shaped ridge extending up and down on the tooth. The posterior surface of the tooth is flat, the antero-external one nearly so and the antero-inner one strongly convex. P^1 is much smaller than the other premolars a is not dnset obliquely in the jaw. The antero-inner ridge, which usually separates the anterior and the antero-inner facets in Merycoidodons, in p^1 and p^2 of this specimen projects far forward so that part of the anterior fossa is seen in a side view of the skull. On p^2 this fossa is broad and faces directly forward. The posterior portion of p^1 is sharp (chisel-like), and slightly concave on the inner surface. The anterior ridge on p^2 is inflected forward in such a way that the outer surface is concave and the inner one convex. The posterior cingular festoon is much larger than the anterior one. A portion of it is developed into a small subconical cusp which represents the deuterocone. The outer face of the tooth is slightly concave antero-posteriorly and convex vertically. P^3 is wider than p^2 , especially the anterior portion. The deuterocone does not appear to be much larger. P^4 has a strong inner cingulum. The inner crescent is concave vertically.

Measurements.

	mm
Length of skull, basal. Perhaps a little too long on account of distortion	305
Length of dental series not including incisors	175
Length of skull behind dental series	130
Width of muzzle at second premolars	77
Width of palate between last molars	55
Width of skull, greatest	220
Width of occipital condyles	85
Depth of malar beneath orbit	40
Height of mandible beneath $p \frac{1}{4}$	58
Height of mandible beneath posterior of $m \frac{1}{2}$	66
Height of mandible just behind $m \frac{1}{3}$	128
Length of upper molar-premolar series	160
Length of upper premolar series	70
Length of upper molar series	90
Length of lower molar-premolar series	159
Length of lower premolar series	63
Length of lower molar series	96

Proportion of width to length of skull = 220 mm. : 305 mm. = 72 + : 100.

Upper premolar series to upper molar series = 77.7 : 100.

Lower premolar series to lower molar series = 65.6 : 100.

Length of upper pm. series = $m \frac{1}{1} + m \frac{2}{2} +$ nearly $\frac{1}{2} m \frac{3}{3} =$ a little more than $m \frac{2}{2} + m \frac{3}{3} =$ a little less than $m \frac{1}{1} + m \frac{3}{3}$.

Length of lower pm. series = $m \frac{1}{1} + m \frac{2}{2} + \frac{1}{2}$ anterior crescent of $m \frac{3}{3} =$ less than $m \frac{1}{1}$ and $m \frac{3}{3}$.

Comparison of the skull of Pronomotherium altiramum with that of Pronomotherium laticeps.— The former is larger and but little broader; the palate is actually narrower; there is not so prominent an angle on the maxillary above and external to m^2 at the origin of the zygomatic arch; and the skull does not expand so abruptly here, there being more of a gradual widening posterior to the premolars. The specimen is a younger individual and the teeth not so much worn as in the type of the genus, yet it is evident that they were narrower, more hypsodont, and had sharper cusps and ridges.

A list of Agriochærids from Montana is given below, arranged as nearly as can be done at present in their order of succession, though there is much doubt concerning the proper chronological arrangement of those listed as Middle and Lower Miocene. The list is a long one but nearly all are, so far as I have been able to examine and compare them, well characterized species, with one or two possible exceptions. It may be that *Merycoidodon macrorhinus* may turn out to be a very robust variety or individual of *Merycoidodon culbertsoni* and *Eucrotaphus helenæ* may be *Eucrotaphus bullatus* (Leidy). I have not seen the type of the latter, neither am I aware that it has been figured. I have also doubts as to the specific identity with the type of skulls that have been figured and described under that name. A number of other species — possibly a dozen — in the Carnegie Museum are represented by teeth, jaws, feet, and other parts of skeletons but they have not been named on account of the absence of good skulls.

UPPER MIOCENE.

<i>Pronomotherium altiramum</i>	}	Lower Madison Valley.
<i>Pronomotherium madisonius</i>		
<i>Merycochærus? compressidens</i>		
<i>Pronomotherium laticeps</i>	}	Flint Creek near New Chicago.
<i>Ticholeptus smithi</i>		
<i>Poatrephes paludicola</i>		
<i>Ticholeptus zygomaticus</i>	}	Deep River Beds.
<i>Cyclopidius simus</i>		
<i>Cyclopidius emydinus</i>		
<i>Cyclopidius incisivus</i>		
<i>Promerycochærus montanus</i>		
<i>Ticholeptus breviceps</i> , Divide Creek north of Melrose.		

PERHAPS MIDDLE MIOCENE.

Ticholeptus bannackensis, Grasshopper Creek near Bannack.

Promerycochærus? *sp.*

Ticholeptus brachymelis

Mesoreodon longiceps

} North Boulder River.

Merycoides cursor

Cyclopidius sp.

Promerycochærus hatcheri

Promerycochærus hollandi

Promerycochærus grandis

} Canon Ferry east of Helena on the Missouri River.

LOWER MIOCENE OR UPPER OLIGOCENE.

Promerycochærus minor, Hell Gate River near Drummond.

Eucrotaphus montanus, Stubbs Ferry northeast of Helena.

MIDDLE OLIGOCENE.

Eucrotaphus helenæ

Merycoidodon macrorhinus

Merycoidodon culbertsoni?

} Missouri Valley near Toston.

Eucrotaphus helenæ, Canon Ferry.

LOWER OLIGOCENE.

Bathygenys alpha

Agriochærus? *maximus*

} Pipestone Creek.

Limnenetes anceps

Agriochærus near antiquus

} McCarty's Mountain.

Limnenetes anceps

Limnenetes platyceps

Agriochærus minimus

Trigenicus socialis

} Thompson's Creek near Three Forks.