BULLETIN

OF

THE AMERICAN MUSEUM OF NATURAL HISTORY

VOLUME LI, 1924-1925



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ERRATA

Page 9, line 21 from top, for time time read same time.

- 23, No. 12816 in ms. incorrect, number not ascertainable.
- " 82, line 19 from bottom, for Parameles read Perameles.
- " 83, line 14 from bottom, for No. 6346 read 6364.
- " 90, Fig. 17, for No. 2702 read 2072.
- " 138, Fig. 4, for Compare with Plate I, Fig. 10, read Compare with Plate I, Fig. 8.
- "138, Fig. 4, for Compare with Plate I, Fig. 11, read Compare with Plate I, Fig. 9.
- " 328, Fig. 4, for teeth read tooth.
- " 391, middle of second line, for maxillary read premaxillary.

BULLETIN

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THE AMERICAN MUSEUM OF NATURAL HISTORY

VOLUME LI, 1924

Article I.—MIOCENE OREODONTS IN THE AMERICAN MUSEUM

By F. B. LOOMIS

As a result of a series of expeditions undertaken annually since 1905, the American Museum has accumulated a large collection of mammals from the various beds of the Miocene, especially in the region of western Nebraska and South Dakota. Parts of this collection have already been described, but the oreodonts have remained almost unknown. This group, by the generosity of Prof. H. F. Osborn and Dr. W. D. Matthew, it has been my privilege to study; and I here thank Dr. Matthew for the many suggestions which have aided me in the study of the group. The collections from the lower and upper Rosebud beds are particularly full, and rich in forms which help toward an understanding of the Oreodontidæ,—a group none too easy to understand, because it contains such a large number of genera and species and, at the same time, displays so little variation in the dentition and foot structure, this in spite of the fact that there were wide ranges of adaptation in the group.

The study of this group involved a comparison of the material with the collections in the Carnegie, National, Princeton, Yale and Amherst Museums, in order to find a better basis, or bases, for the distinctions between genera and species. This led to a review of various parts of the skull in the hope of finding features which could be followed through the various genera and would serve as criteria for distinguishing one from the other and would at the same time register relationships. Two regions have proved of primary value in tracing the relations of the various genera to one another: first, the premolar dentition; and second, the rear of the skull, including the otic region. Whether dealing with such shortheaded types as Merychyus and Leptauchenia or with long-headed genera like Promerycochærus, the dental formula remains the same and

the character of the molars varies but little; but the premolars do vary, and considerably, also purposefully; so that by their aid generic distinctions and relationships may be clearly traced. Not only is this true for the Oreodontidæ; but these premolars are equally important in distinguishing the phyla of artiodactyls and, while I have not carried this study through all the genera of the other phyla of artiodactyls, so far as I have gone it is equally useful in those other phyla outside the Oreodontidæ.

Inasmuch as the premolars of artiodactyls have not been studied systematically and there is no standardization of their changes, it will be necessary to take a little space to discuss premolars in general and to describe certain structures which may be referred to more conveniently in the future, if given names.

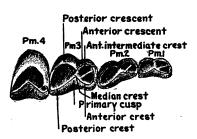


Fig. 1. Upper premolars, left side of *Merycoidodon culbertsoni* Leidy. Natural size.

The upper premolars of *Mery-coidodon culbertsoni* may serve as primitive enough to illustrate early characters and, at the same time, as specialized enough to illustrate the features of the whole group. We may start with premolar 1, the least modified of the series. It consists of a primary cusp (the protocone?) on the outer side of the tooth. From the primary cusp there extends forward a crest which I would designate the

ANTERIOR CREST, and a second crest extends to the rear, the POSTERIOR CREST. From the primary cusp a slight ridge runs to the middle of the inside of the tooth, and I would call this the MEDIAN CREST. These three crests will appear on all the premolars. Those farther to the rear, like premolar 3 or 4, may have other crests, quite generally one running from the primary cusp to the middle of the anterior root of the tooth, and this I would call the ANTERIOR INTERMEDIATE CREST. In like manner, a weaker crest may extend from the primary cusp to, or toward, the middle of the posterior root of the tooth, and this is the POSTERIOR INTERMEDIATE CREST. Lastly, above both the anterior and posterior roots, on the inner side of the tooth, there may be a fold, either low or extending to the full height of the tooth. These I have designated the ANTERIOR and POSTERIOR CRESCENTS. One or both may be either fully developed or entirely lacking. This nomenclature is illustrated in figure 1.

These crests and crescents may all appear on one tooth and are best developed on the third upper premolar. The marked development or

suppression of certain crests, or crescents, is characteristic of phyla and genera. In some cases a further modification is present in the development of a cusp-like pillar at the junction of the median crest and the posterior crescent. The fourth upper premolar appears like a half-molar, and this peculiarity is attained differently in different phyla, making this tooth and its origin of prime importance in studying artio-dactyls. A few cases will illustrate this.

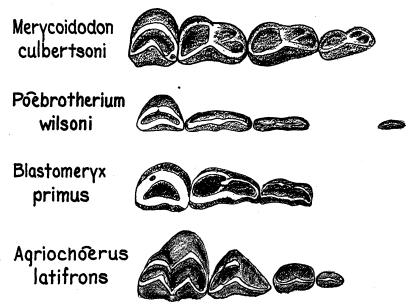


Fig. 2. Upper premolars, left side, of an oreodont, a camel, a deer and an agriocherid, to show differences in character and mode of development.

In the oreodonts, examining the premolars from the first to the fourth, it will be seen that premolar 4 corresponds to the posterior half of premolar 3, the posterior crescent being greatly developed and united to the median crest, and all trace of the anterior part of the tooth has disappeared, except for a tiny pit in the anterior outer corner, which is the vestige of the outer part of the anterior basin seen on premolar 3. In a few very primitive genera, traces of both parts of the anterior basin are retained; and in the more advanced genera, all trace of the anterior half of the tooth is lost. See figure 4.

In contrast with this, the fourth premolar of camels is formed by shortening the whole of premolar 3; its inner crescent is composed of both the anterior and the posterior crescents united, and there is never any pit in the corner. Then the other premolars are characterized by the narrowness and lack of intermediate crests. The fourth premolar of the deer is developed in still another manner. As in camels, both anterior and posterior crescents are developed, together with anterior, median and posterior crests, but the intermediate crests are wanting. Also as in camels, premolar 4 is formed by the shortening of the anterior-posterior diameter of such a tooth as premolar 3; but, in this case, the posterior crescent overlaps the anterior crescent to a greater or less extent. In some cases, between the overlap a pit is preserved, which is located on the inner side and just behind the middle of the tooth. This is more marked in the advanced genera. The Agriochæridæ differ widely from the other artiodactyls, first, in that the anterior portion of each premolar is simple, without either crests or crescents, while the posterior portion has strong crests and a strong crescent. The fourth premolar is unique among artiodactyls, so far as I have seen, in being molariform in character, with two outer cusps and two inner cusps. Then too this double character is attained in an unexpected manner, for the whole tooth is developed from the posterior portion of premolar 3, the outer cusps being formed by dividing the posterior crest, and both inner cusps being already indicated on the rear half of the posterior crescent of premolar 3.

Among the artiodactyls, the lower premolars also have certain fundamental characters in common. As in the upper premolars, there is the primary cusp on the outer side, and from it a crest to the front, the anterior crest, and another to the rear, the posterior crest. A median crest is usually developed, and both anterior and posterior intermediate crests may be present, though one or the other of these last two may be lacking. Anterior and posterior crescents are usually indicated on premolars 1 and 2; and may be more, or less, fully developed on premolars 3 and 4. A cusp-like pillar is likely to develop at the junction of the median crest and the posterior crescent, and in some cases the middle of the posterior crescent is developed to appear almost like a cusp. Premolar 1 is modified into a caniniform tooth in both form and function. Premolar 4 is not modified to molariform character, except in Agriochæridæ, so that the change from premolar to molar teeth is abrupt. Premolars 3 and 4 are the most typical teeth in this series.

Among the oreodonts, the anterior, median and posterior crests are well developed, and the posterior crescent is strong; but the anterior and posterior intermediate crests are usually weak or lacking. Both crescents are likely to be indicated on premolar 2, but usually only the

posterior crescent is well developed on premolars 3 and 4. Camels have the lower premolars markedly compressed, and only one basin, which is a narrow one on the posterior half of premolar 4, between the posterior crest and crescent. Deer have complex lower premolars, on which the anterior, median, posterior intermediate and posterior crests are well developed; but the inner side does not develop the crescents to any large extent, so that basins are not inclosed between the crests. Agriochæridæ are again peculiar in the structure of their lower premolars, especially the

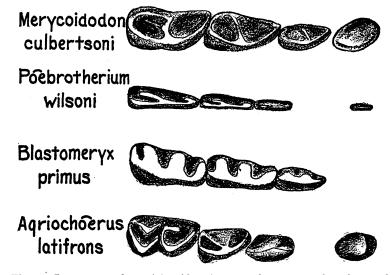


Fig. 3. Lower premolars, right side, of an oreodont, a camel, a deer and an agriocherid, to show differences in character and mode of development.

fourth, on which the posterior portion is more or less independent. The anterior crest is strong, but the anterior crescent is shortened into a pillar-like cusp, unique. The posterior crest also is short and independent, making a cusp, and the posterior crescent also is shortened and tends to become an independent cusp.

Turning to the phylum Oreodontidæ, we may consider the various genera to find generic variations and phyletic relationships, which, in the discussion of the genera, are correlated with the characters of the body and especially with those of the rear of the skull which are shown in figures 9 to 26.

In the Uinta beds there are several selenodont artiodactyls which from time to time have been suggested as related to the higher oreodonts. Studying the premolar dentitions of these, however, such genera as *Eomeryx* and *Protagriochærus* seem to belong to the oreodont phylum but by no means in the ancestral line, in fact far to one side, having developed a dentition which is specialized, though the shape of the skull, especially the orbit's being open behind, is primitive. In like manner, *Protoreodon* is in the oreodont phylum; but in this case, we have a form which is much nearer to the ancestral line, though not directly in it.

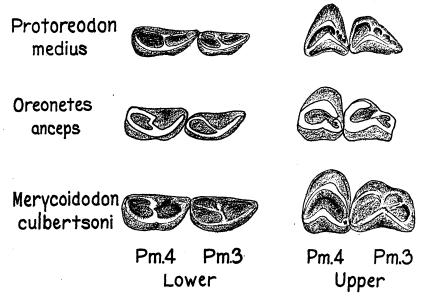


Fig. 4. The third and fourth premolars of oreodonts, uppers from the left side, lowers from the right side, to show the development of the *Merycoidodon* line.

All the above forms have the tiny bulla which is characteristic of *Mery-coidodon* and which separates this group of oreodonts from the much larger group with large bullæ.

Three genera are closely related and make up the series which is characterized by the tiny bulla, *Protoreodon* of the Uinta, *Oreonetes* of the Titanothere beds and *Merycoidodon* of the middle Oligocene. The third and fourth upper and lower premolars are shown in figure 4 for comparison. In *Protoreodon*, upper premolar 3 has, besides the anterior and posterior crests, a weak median crest, no posterior intermediate crest, but on the front portion of the tooth, two weak anterior intermediates. The same features are repeated on the fourth upper premolar, which, in

this case, has progressed toward the half-molar type less than in any other genus. On the lower premolars, the anterior, median and posterior crests are well developed, and both crescents are clearly marked, though low. These characters indicate nearness to the ancestral type, but the anterior crescent on the lower premolars suggests a position to one side of the main line, as does also the rather elongate type of the feet.

Oreonetes¹ has the upper third premolar with a weak median and anterior intermediate crest. In this genus the posterior crescent is well developed. The fourth premolar is formed typically by the reduction of the front half of the tooth, but in this case traces of both parts of the anterior basin are still preserved on this tooth. On the lower premolars the anterior crescent is wanting and the posterior crescent is united to the median crest, making a well bounded and typical posterior basin.

Merycoidodon has rather broad premolars on which the anterior portion of the tooth is less developed than usual. Premolar 3 has the anterior intermediate crescent well developed, dividing the basin into two equal parts. Premolar 4 is formed in the usual way, but in this case, in teeth not too much worn, there is a pit in the anterior external corner representing the outer portion of the anterior basin. On the lower premolars, the anterior intermediate crest is lacking and the posterior intermediate crest, while present, is weak and has a peculiar position, in that it comes off from the median crest instead of the primary cusp.

Turning to the group of oreodonts marked by the presence of very large bullæ, Limnenetes from the Titanothere beds, Eporeodon from the Middle and Upper Oligocene (perhaps into the Miocene) and Mesoreodon of the Lower Miocene form a group which have much in common: in medium length and weight of limbs; in having the back of the skull compressed and drawn out to the rear, and also in the character of their dentition. All tend to have the median cusp weak and at the same time the crescents, especially the posterior crescent, well developed. This is even more true of the later representatives of this phylum.

The type of *Limnenetes* is very old and the pattern of the teeth has to be taken from associated material, on which only the upper premolars have good dentitions. In this form, though the skull has the orbit open behind and is in every way primitive, the upper teeth are enough specialized to cause the genus to be regarded as a little to one side of the main phyletic line. On premolar 3 the anterior crescent is barely indicated and the intermediate crests are wanting. Premolar 4 has the posterior

¹The name is one given to Douglass's *Limnenetes? anceps* in an article to appear in the Annals of the Carnegie Museum.

Limnenetes platyceps



Eporeodon dickinsonensis





Mesoreodon megalodon





Promerycochoerus qrandis





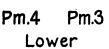
Merycochoerus magnus





Pronomotherium altiramum







Pm.4 Pm.3 Upper

Fig. 5. The third and fourth premolars of oreodonts, uppers from the left side, lowers from the right side, to show the development of the Merycochærus line.

crescent fully united to the median crest and no trace of a pit in the anterior external corner, as might be expected in so early a form. Eporeodon has the third premolar with the anterior portion more nearly equal in size to the posterior portion than is general in this group. The anterior intermediate crest is well developed and both crescents are well marked. Premolar 4 forms in the normal manner by the reduction of the anterior half. In the case illustrated, E. dickinsonensis, an early species, traces of both parts of the anterior basin are preserved, but in the Upper Oligocene and John Day species only one pit is present in this position. The third lower premolar has strong anterior, median and posterior crests, but very weak crescents or none. The posterior basin is divided by a ridge running back from the median crest, which is typical. Premolar 4 has no trace of this ridge, but has the posterior basin completely inclosed between the posterior crescent and the posterior and median crests. It shows also a considerable tendency for the development of a pillar-like cusp at the junction of the posterior crest and the median crest; and this enlargement is prolonged forward noticeably, a feature more developed in some of the later genera.

Mesoreodon was founded on M. chelonyx, which is related to M. megalodon. Both of these have skulls tending to the same form as that characteristic of Promerycochærus, but at the time time they have a skeleton which is about like that of Eporeodon or Merycoidodon; so I take this to represent a group which was transitional between Eporeodon and Promerycochærus, though the known representatives of the genus are contemporaneous with these genera. The other species which have been referred to Mesoreodon, such as M. longiceps and M. laticeps, are far from the type species and close to the form which Douglass called Merycoides; so that I should group them with Merycoides cursor as a separate line. In the true Mesoreodon, the front half of the upper third premolar is shortened, and the anterior intermediate crest, though small, is well developed. The posterior crescent incloses a basin on the rear of the tooth. On the anterior external corner of premolar 4 there is a pit in M. chelonyx, but none in M. megalodon. In like manner, the lower premolars are intermediate. The genus is distinguished in that on premolar 3 only the rear portion of the posterior crescent is developed, and that is united with the posterior intermediate crest. On premolar 4 the intermediate crests are wanting, but the posterior crescent is well developed and confluent with the pillar-like cusp which is developed at the junction of this crescent with the median crest. This pillar-like cusp is not so prolonged forward as that of *Eporeodon*, but is more distinct. Neither is it as isolated as in Promerycocharus.

In the Miocene we find three large oreodonts which have in common very short limbs, heavy bodies and skulls with wide-spreading arches. Promerycochærus of the John Day and Lower Miocene has a prolonged snout and nasal bones, while Merycochærus has the head shortened and the nasals retreating far back on the skull, and Pronomotherium has the shortening of the nasal region in such exaggerated degree that the nasal bones end as far back as the eyes. These forms are successive in time and would seem to be a progressive series, but in each case the one genus abruptly disappears and is replaced by the later genus without intermediate forms. The dentition, however, shows that they are of common stock, but that one genus is not derived directly from its predecessor.

The Promerucochærus upper premolars have both the anterior and posterior crescents well developed, but the median crest is weak, hence there is a suggestion of the union of the anterior and posterior basins. The anterior basin is partly divided by a weak anterior intermediate crest. The fourth premolar has entirely lost the pit in the anterior external corner. The lower premolars are narrow and compressed. The third lower premolar has no anterior crescent and only a weak posterior The posterior intermediate crest is well developed, and it completely divides the posterior basin. Premolar 4 is entirely characteristic, in that the pillar-like cusp at the junction of the posterior crescent and the median crest is greatly enlarged; and not only that, but it remains distinct from both the crescent and the crest until the tooth is worn far Furthermore, there is developed on the posterior crest an enlargement which appears like a smaller cusp. This tooth, therefore, is entirely distinctive, and, because Desmatochyus corresponds entirely with this dentition, I regard it as a small, though not the smallest, Promerycochærus.

Merycochærus has no pit in the anterior external corner of premolar 4. The other upper premolars have the crescents both well developed and the median crest rather weak. The lower premolars are compressed and narrow. Premolar 3 has lost the intermediate crests, its anterior portion being simple and the rear inclosing a simple basin. Premolar 4 is the characteristic tooth, having the posterior crest and crescent inclosing a simple basin, but at the junction of the median crest and the posterior crescent, the pillar-like cusp is not distinct, but is prolonged far forward, into the anterior basin. This, though related to the condition of the corresponding tooth in Promerycochærus, can not be derived from it but seems rather to indicate independent development from common ancestry.

Pronomotherium has a very peculiarly shaped skull, but its dentition is by no means so highly specialized. Upper premolar 3 has so weak a median crest that anterior and posterior basins are confluent, especially as both are bounded by well-developed crescents. There are traces of the intermediate crests, but they are small. The third lower premolar has the anterior portion of the tooth prolonged. The anterior crescent is present,

Merycoides longiceps





Phenacocoelus typus





Ticholeptus petersoni





Metoreodon relictus



Pm.4 Pn Lower Pm.4 Pm.3 Upper

Fig. 6. The third and fourth premolars of oreodonts, uppers from the left side, lowers from the right side, to show the development of the *Ticholeptus* line.

but weak; the median crest is well developed, but there are no intermediate crests. Premolar 4 has a strong median crest, with a cusp-like pillar at the junction of this crest and the posterior crescent, which projects forward as in *Promerycochærus*, but is not isolated as in that genus. Such teeth as these can scarcely be derived from those of *Merycochærus*, and it will be necessary to go back pretty well in the Miocene to find the form which would be the common ancestor of these two genera.

Merycoides, Phenacocælus, Ticholeptus and Metoreodon are a group of genera, all of which have the medium type of limbs, neither long nor short, light nor heavy; skulls which are lightly built, with light arches, and the supra-occipital crests not prolonged behind. In the rear of the skull there are usually pits in the exoccipital bones, and in many species there is a marked tendency to vacuities in the antorbital region. type of the genus Merycoides is M. cursor, and I should associate with this such species as have been known as Mesoreodon longiceps and Mesoreodon laticeps. In all these genera the anterior portion of the upper premolars is shortened, the median crest is weak, and the posterior crescent, though swollen, does not unite with the median crest. In the lower premolars the anterior intermediate crest and the anterior crescent are lacking or weak. The posterior portion of premolar 3 is always inclosed by the median crest, posterior crescent and posterior crest, and into this basin the posterior intermediate crest projects from the rear. Premolar 4 has the rear portion of the tooth inclosed like that of premolar 3, but there is no posterior intermediate crest. There is a marked tendency for the pillar-like cusp to be developed and to project far forward into the anterior basin.

Merycoides does not show specialization in any line and the description just given for the whole group will answer for this genus.

Phenacocælus is a genus in which the skeleton is not specialized, but the skull is highly modified. Its general character is that of Merycoides, but there are excessively deep pits in the rear of the occipital bones, two small vacuities in the frontal bones and large vacuities in the antorbital region. The teeth are those of Merycoides, except that they are less advanced, so that this form belongs to the Ticholeptus line but had already begun to develop its peculiarities before the lower Miocene, when we are first acquainted with it.

Ticholeptus is a large group of Miocene to lowest Pliocene oreodonts which show a tendency to shorten the skull and develop large vacuities in the antorbital region. The teeth are similar in plan to Merycoides, but more advanced, first, in a greater shortening of the anterior portion of premolars 1 to 3 of the upper jaw, so that the anterior basin is in many cases so shallow as to appear almost flat, and, second, in the greater thickening of the posterior crescent of premolar 3. In the lower dentition, premolar 4 has the anterior end of the anterior crescent bifurcated, which serves easily to identify this genus or the following one.

Metoreodon is a Pliocene genus based on lower jaws and is an exaggerated Ticholeptus. It is distinct in that the teeth are hypsodont;

premolar 3 has the anterior crescent developed into an inner boundary of the anterior basin, and the posterior basin is divided completely by the posterior intermediate crest in a peculiar position parallel to the median crest. Premolar 4 is also distinctive in the small size of the posterior region, and the great enlargement of the pillar-like cusp which almost fills the anterior basin.

Merychyus is a genus about which there has been endless confusion. It was based on M. elegans, and to this genus were referred a large number of species which have proved to be of entirely different character. In addition, the genus is extremely conservative, and such a species as M. elegans has been identified as occurring in horizons all the way from Lower

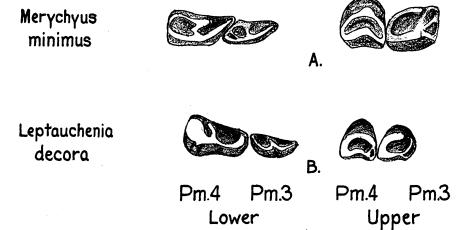


Fig. 7. Third and fourth premolars of oreodonts, uppers from the left side, lowers from the right side, to show the development of *Merychyus* and *Leptauchenia*.

Miocene to Pliocene, to which horizon the type belongs. On page 31 I have listed the species which truly belong to this genus. Merychyus had light slender limbs, a short, rather wide skull, not prolonged behind, and with pits in the exoccipital bones, usually a small antorbital vacuity, but this last is variable. The teeth of the upper jaw are shortened. This is accomplished in the premolar series by the reduction of the anterior portion. The illustration (Fig. 7A) shows about an average amount of shortening of this anterior region. In the lower Rosebud species M. curtus, the anterior is less shortened, and in the Pliocene species M. elegans, it is much greater. The lower premolars remind one of Merycoides, but the posterior crescent is not so much developed. This genus

runs from the lowest Miocene into the Pliocene, with very little change in character, and is represented in the John Day by Oreodontoides oregonensis, which I take to be a Merychyus slightly less advanced than the eastern representatives. Paroreodon is another John Day genus which belongs close to Merychyus, but is different in the greater depth of the skull and in the peculiar pointed, large bullæ.

Leptauchenia and Cyclopidius represent a line of oreodonts which appears suddenly in late Oligocene times and disappears as suddenly at the end of the Deep River epoch. The skeleton is lightly built and slender, somewhat like Merychyus, except that there are five toes on the The skull is excessively shortened; there are enormous bullæ and great vacuities in the antorbital region. This phylum probably unites with the light-limbed Limnenetes of the Lower Titanothere beds, though I doubt if this genus is the actual ancestor. There is much in common between this line and Merychyus, and these two lines probably come together in lower Oligocene times. The upper premolars of Leptauchenia seldom show their pattern, since they are hypsodont and almost always badly worn. When, however, little-worn teeth are studied, it is seen that the upper premolars are shortened by the almost complete suppression of the anterior portion. When such teeth are worn, the median crest appears like the anterior crest, and the tooth seems to stand transversely in the jaw. This peculiar appearance, however, is due to the suppression of the anterior basin. Premolar 3, as seen in figure 7B, has a large posterior crescent which does not unite with the median crest. Premolar 4 in little-worn teeth shows the pit in the anterior external The lower premolars are characterized by the entire lack of crescents and intermediate crests. The fourth premolar is unique in the enormous swelling of the posterior crest, so that this fills the posterior Cyclopidius is Leptauchenia exaggerated, with the incisors reduced to two on either side of each jaw. Chelonocephalus is a Cyclopidius with a markedly depressed skull.

Five lines of Oreodontidæ have been recognized in the foregoing. First, there is the fundamental division based on the tiny or large bulla, and a line ending in *Merycoidodon* represents the tiny bulla. Second, the main line of medium-heavy forms with large bullæ leads into the short-limbed, heavy-bodied *Pronomotherium* and *Promerycochærus* type. Third, there is another group leading from the intermediate stock of the Middle Oligocene to *Ticholeptus* and *Metoreodon*. Fourth, *Merychyus* is a very conservative line of lightly built small forms, the Oligocene representatives of which are unknown. Fifth, the extremely light-limbed and

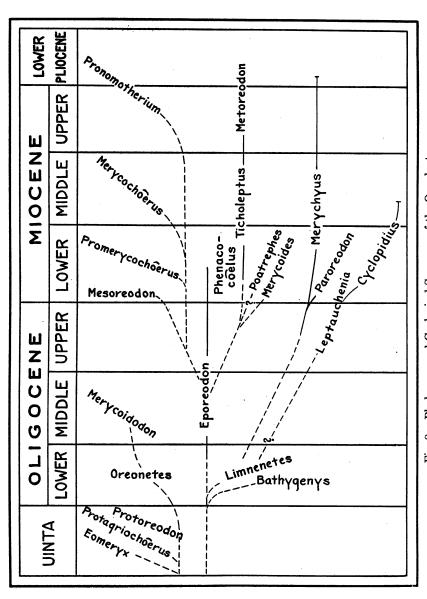


Fig. 8. Phylogeny and Geological Sequence of the Oreodonts.

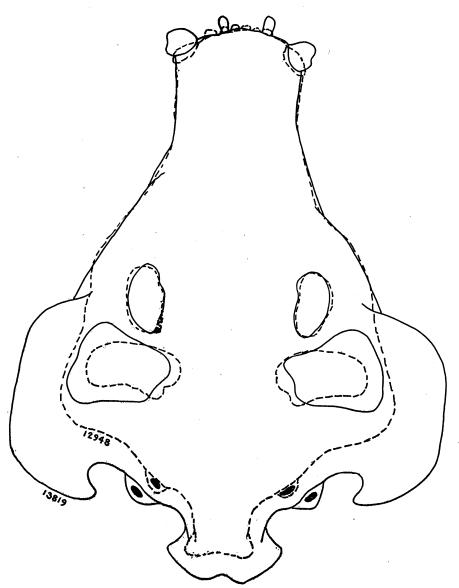


Fig. 9. An outline of a male *Promerycochærus thomsoni* (solid line), superimposed on the outline of a female of the same species (broken line). Two-fifths natural size.

short-headed *Leptauchenia* and *Cyclopidius* represent some special adaptation which it is very difficult to interpret.

Throughout the whole group there is great uniformity in the character of the dentition and the feet. There is none of the progressive adaptation and change characteristic of the grazing types, and I feel that this is probably due to a constancy in the type of food and feeding-ground. I should take the food to be leaves, seeds and fruit; and the feeding-ground the more or less wooded valleys along the streams. One feature characteristic of the group tends to confirm this, and that is the distinctness of the faunas from the different localities. The genera are widely distributed, but the species are local. It would seem that of the various river valleys each had its group of oreodonts, and, when there was a change in climate or other living conditions, the fauna of any given valley was either exterminated or replaced by a new immigration.

The various genera are compared in the chart on the following pages, and their relationships expressed as nearly as I can see them in the phylogenetic tree on page 15.

The following pages describe the new material of the Miocene belonging to the Oreodontidæ and in The American Museum of Natural History.

PROMERYCOCHŒRUS

To this genus has already been assigned a bewildering number of species, from the John Day, Monroe Creek, Lower Harrison, Deep River and certain Montana beds. The American Museum material from the Lower Rosebud formation consists of over twenty skulls, together with considerable skeletal material. On examining this material it at once became clear that either there were five or six species in this one formation or that there was marked sexual dimorphism, as well as considerable individual variation. A careful examination of the two largest types resulted in drawing them superimposed to make figure 9. To me, this indicates that, while No. 13819 and No. 12948 differ in the amount that the incisors protrude, the size of the canines, the width of the zygomatic arch and the length of the posterior projection of the supra-occipital crest, still they are alike in the premolar and molar dentitions, the width of the snout, the position of the orbits and ear openings, the bullæ and the base of the skull. The latter list of characters is of deep-seated features, such as do not change with minor changes of habit, while the first list is entirely of characters which do change where there is sexual dimorphism. I have concluded that in this genus there is wide sexual dimorphism, and

Genera of Oreodonts, their Respective Geologica

	AGE	SKULL	Bullæ	POSTPTERYGOID PROCESS
Protoreodon	Upper Eocene	mesocephalic;	tiny	moderately oval
	(Uinta)	open orbit	1.	, , ,
Oreonetes	Lower Chadron	mesocephalic; open orbit	tiny	small and oval
Mery coid od on	Upper Chadron to Middle Oligocene	mesocephalic; closed orbit	tiny	moderately oval
Limnenetes	Lower Chadron	mesocephalic; open orbit	large	small and oval
Eporeodon	Middle Oligocene to Lower Miocene	mesocephalic; closed orbit	medium large	moderate and ova
Me soreodon	Lower Miocene	dolichocephalic; closed orbit	medium large	small, oval and long
Promerycochærus	Lower to Middle Miocene	dolichocephalic; closed orbit	large	stout, oval and short
Merycoch lpha rus	Upper Harrison to Middle Miocene	brachycephalic; closed orbit	medium large	very wide and flattened
Pronomotherium	Upper Miocene to Pliocene	brachycephalic; closed orbit	small, cylin- drical	wide and flattened
Merycoides	Lower Miocene	dolichocephalic; closed orbit	medium large	moderate and oval
Phenacocælus	Lower Miocene	mesocephalic; closed orbit	large	large and oval
Ticholeptus	Lower Miocene to Pliocene	mesocephalic; closed orbit	large	wide and flattened
Merychyus	Lower Miocene to Pliocene	brachycephalic; closed orbit	large	small and flat- tened
Leptauchenia	Upper Oligocene to Middle Miocene	brachycephalic; closed orbit	enormous	tiny and flattened
Cyclopidius	Lower Miocene to Middle Miocene	brachycephalic; closed orbit	enormous	tiny and flattened

Iorizons and their Diagnostic Skull Characters

ZYGOMATIC ARCH	Exoccipital Bones	NASAL BONES	Antorbital Pit or Vacuity
ight	supraocc. crest prolonged behind	long	neither
ight	supraocc. crest moderate	long	neither
ight	supraocc. crest prolonged behind	long	shallow pit
ight	occiput wide; crest not prolonged	long	pit
ight	supraocc. crest high and prolonged	long	pit
ight	supraocc. crest high and prolonged	long	pit
eavy and wide	supraocc. crest high and prolonged	long	pit
eavy and wide	supraocc. crest none	greatly shortened	pit
nedium and wide	supraocc. crest moderate	greatly shortened	pit
ight	supraocc. crest low, not prolonged pits	long	pit
ight ,	supraocc. crest low, little prolonged pits	long	pit and big vacuity
ight	supraocc. crest moderate, little pro- longed	long	vacuity
ight and fairly wide	supraocc. crest low, not prolonged pits behind	long	pit and small vacuity
ight and very wide	occiput very broad	fused to maxilla	enormous vacuity
neavy and very wide	occiput very broad	fused to maxilla	enormous vacuity

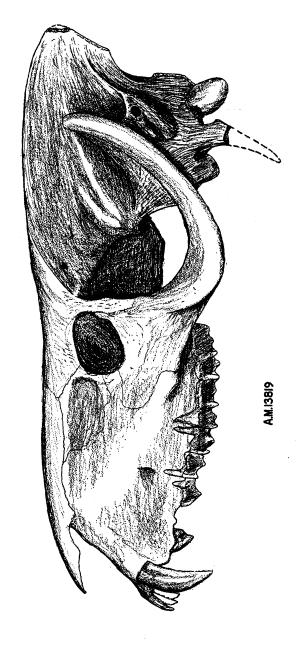




Fig. 10. Promerycochærus thomsomi, male, skull and upper dentition of the type. Two-fifths natural size.

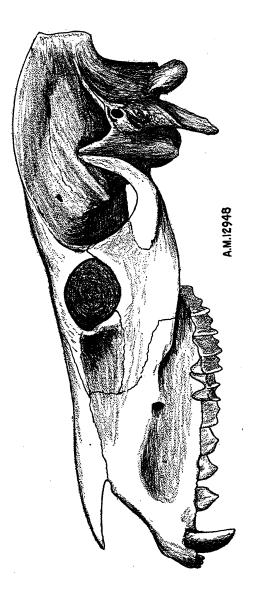




Fig. 11. Promerycocharus thomsoni, female, skull and lower dentition of No. 12948. Two-fifths natural size.

that the width of the arches changes not only with sex, but also with age. I have therefore reduced the number of Lower Rosebud species to three, describing both males and females.

I am convinced that the same applies to the large number of species described from the John Day beds, and I would use the length of the molar and premolar series as a basis of comparison, considering such features as the width of the arches, the size of the canines, or their protrusion as sex or individual variations.

Promerycochærus thomsoni, new species

This is the largest of the Rosebud species, and I have selected No. 13819 of the American Museum as the type, associating No. 12948 with it as the female. The male skull is from Eagle Nest Butte, and the female from Wounded Knee Creek, both of South Dakota and the same bed. The name is in honor of Mr. Albert Thomson, veteran collector in this region and finder of the male skull. Other skulls of the male type are Nos. 13818, 12944 and 12951.

The species is characterized by a broad snout, with large but shallow antorbital fossæ. The brain case is somewhat inflated, with a marked ridge across the inflated parietal region. Upper premolars 3 and 4 and molar 1 all have cingula on the outer side of the teeth. The lower premolars are typically those of the genus (see Fig. 5), except that premolar 3 has the posterior intermediate crest rising from about the middle of the median crest, instead of from the primary cusp.

In the various Lower Miocene beds there are several large Promery-cochæri about the size of this species. P. grandis from the Canyon Ferry beds is of the female type, but is not only larger than P. thomsoni but also has a much narrower skull and arches, and has the snout markedly prolonged, especially the premolar region. P. macrostegus of the Upper John Day is a male type and about the same length as our species, but it has a very small antorbital fossa, where P. thomsoni has a broad one and smaller bullæ, and the whole skull is narrower. P. latidens of the John Day has about the same over-all measurement as the male of P. thomsoni, but its snout is short and the dentition compressed. P. marshi of the John Day is of the female type, but is both larger and longer than the female from the Lower Rosebud. The following table gives the most important measurements for comparison with nearly related species. Other measurements may be taken directly from the drawings.

	P. thom- soni ♂	$P.$ $thom$ - $soni \ \ $	$P.$ grandis \circ	P. macro- stegus	$P.$ latidens $ardsymbol{ardsymbol{ardsymbol{eta}}}$	$P.$ $marshi$ \circ
Length of the skull	388	362	390	∂¹ 380	385	200
Width of the skull	277	$\begin{array}{c} 302 \\ 224 \end{array}$	186	246	383 279	$\frac{380}{344}$
Length of the upper molar	20		••			
series Length of the upper premolar	82	7 8	98	81	79	85
series	66	73	82	71	695	76

Promerycochærus gregoryi, new species

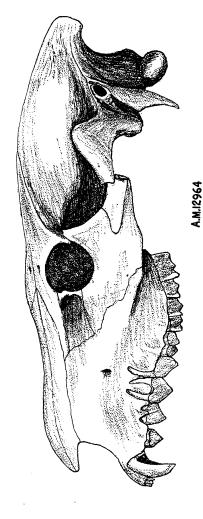
This is the medium-sized form in the Lower Rosebud and the one found in largest numbers. For the type I have chosen No. 12964, a skull and lower jaw, the skull being slightly crushed laterally as shown in the figure. This is a female, a narrow skull with light arches, which are estimated to have had a width of 190 mm. No. 12962 belongs to the same species and is also a female. No. 12816 is slightly longer and with wider, heavier arches, and is the male of this species. The type comes from Porcupine Creek, South Dakota. The name is in honor of Dr. W. K. Gregory, who was a member of the expedition which collected this material.

This species is characterized by its size, rather deep and broad antorbital fossæ, an elongated brain case, moderate-sized bullæ, and the fact that for this genus the premolars, both upper and lower, are quite simple. On lower premolar 3 the posterior intermediate crest runs from the primary cusp, as is normal for the genus.

This species approaches P. hollandi of the Canyon Ferry beds in size, but it has a deeper antorbital fossa, and a shorter snout and dentition. P. chelydra of the Upper John Day is a male of similar size but has a much longer snout and dentition. P. leidyi is another John Day species which approaches our Rosebud form in length of skull, but it too has a longer snout and dentition. I presume P. chelydra and P. leidyi represent the male and female of a Promerycocharus in the John Day, which is perhaps the nearest of any species to P. gregoryi.

The following table gives principal measurements and comparisons with the nearest related species.

	P. greg-	P. greg-	P. hol-	$P.\ chely-$	$P.\ leidyi$
	$oryi$ \circlearrowleft	$oryi$ $\c Q$	$landi \circlearrowleft$	dra artriangle	Q
Length of the skull	344	313	342	342	330
Width of the skull	235	190	234	256	188
Length of the upper molar series	79	70	76	7 8	76
Length of the upper premolar series	60	58	70	$6\dot{3}$	48





type. One-half natural size.





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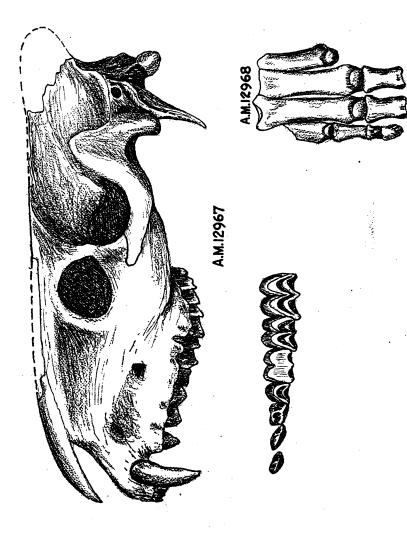


Fig. 13. Promerycochærus pygmyus, female, skull and upper dentition from the type. One-half natural size. Front foot from No. 12968. One-half natural size.

Fig. 14. Merycochærus matthewi, skull from the type. One-half natural size.

Promerycochærus pygmyus, new species

This is a tiny species, the smallest of the true *Promerycochæri*, but it has the characters of the genus not only well developed but in an advanced degree. It is a dwarf species rather than a primitive one. I have chosen No. 12967 as the type of the species, a female found on Porcupine Creek, South Dakota. No. 12968 is a second female of this species, having an imperfect skull, but with good fore feet and some other limb bones. No male has yet been found of this species.

The specific characters are the small size; small bullæ; a wide snout with broad and shallow antorbital fossæ; simple, rather narrow teeth; and an extremely short foot.

There are no other species at all close to this one.

The following measurements of the principal parts will serve to identify the species.

Length of the skull	253 mm. rear estimated, see figure 12.
Width of the skull	179
Length of the upper molar series	59
Length of the upper premolar series	48

MERYCOCHŒRUS

In his description of *Merycochærus proprius*, the type species of this genus, Matthew¹ showed that this was a highly specialized genus in that the cranium was shortened and broadened; the nasals moved far toward the rear; the zygomatic arches heavy and wide, and the limbs short and stocky. So far only one species has been described, but the material in the American Museum furnishes us with two new species. The genus appears abruptly with the Upper Harrison and disappears as abruptly in the Martin Canyon beds.

Merycochærus matthewi, new species

This species is from the Upper Rosebud beds and was found three miles northeast of Porcupine Butte, South Dakota. I have used No. 12970 as the type, a skull and jaws with a good front limb and some other less perfect limb bones. The name is in honor of Dr. W. D. Matthew, who found the Upper Rosebud beds.

The specific characters are: the size; the fact that the sagittal crest extends to the rear of the skull and unites with the lambdoidal crests in making the projection behind, whereas in other species the sagittal crest

¹1898. Mem. Amer. Mus. Nat. Hist., I, p. 401.

does not extend to the lambdoidal crests (compare with M. magnus and M. proprius); the broad upper teeth; and the relatively long limbs and feet. I here introduce a comparison of the three known species.

	Length of	Width of	Length of	Length of	Length of	•
	$_{ m skull}$	\mathbf{skull}	upper	upper	humerus	
			molars	premolars		Horizon
$M.\ matthewi$	299	220	87	65		U. Rosebud
M. proprius	286	244	88	61		Pawnee Cr.
$M.\ magnus$	334	273	95	68	240	U. Harrison

	Length of	Length of	Length of	Length of	Length of	
	radius	metacarpal	femur	tibia	metatarsal	
		IV			IV	Horizon
$M.\ matthewi$	146	71				U. Rosebud
M. proprius	150	63	250	195	68	Pawnee Cr.
$M.\ magnus$	161	66	23 8	195	65	U. Harrison

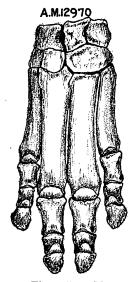


Fig. 15. Merycochærus matthewi, carpus and fore foot from the type. One-half natural size.

From the above it is seen that *M. matthewi*, while small, does not have as short or stocky limbs and feet as do the other two species. The skull also is much less shortened and less broadened than is the case in the other two species. Furthermore, in this species there is not, as yet, a tendency, which is so marked in the other two species, toward dishing in the nasal region. The line of the top of the skull is more or less parallel to that along the top of the premaxillæ, whereas in the other two species the nasals slope down as though to meet the premaxillæ.

Merycochærus magnus, new species

The type for this species is No. 14242, from the Upper Harrison beds, seven miles northeast of Agate, Nebraska. The type is an old individual, but with it are associated both front and hind limbs. It is by no means a rare species in these beds.

This species is nearer to M. proprius, in that the sagittal crest ends some distance in

front of the lambdoidal region. The brain case is greatly shortened and broadened, and the whole rear of the skull is crowded together. The zygomatic arches are heavy and wide, but not as wide proportionally as those of M. proprius. There is a moderate antorbital fossa.

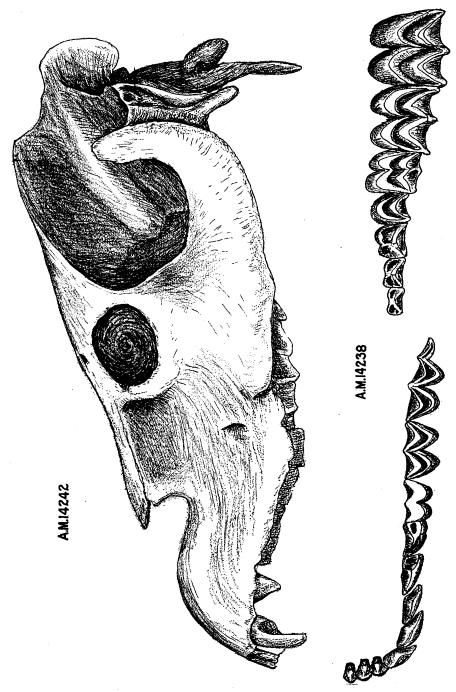


Fig. 16. Merycochærus magnus, skull from the type, upper and lower dentitions from No. 14238. One-half natural size.

The line along the top of the skull pitches down toward the front, so that the nasals approach the much dished premaxillæ. The limb bones have the same character as in M. proprius, being heavy and stocky, with

the feet extremely short and stubby. The phalanges go to the extreme in their shortening.



Fig. 17. Merycochærus magnus, front foot from the type. One-half natural size.

MERYCHYUS

This genus, in which there has been constant confusion, is based on the species *M. elegans* and consists of a series of small light-built oreodonts, ranging from the Lower Rosebud and John Day up into the Pliocene, from which horizon the type species came. I should redefine the genus as follows.

Merychyus is a genus of Oreodontidæ of light build; with slender limbs; having a wide brachyodont skull with light zygomatic arches; large bullæ; and low sagittal and lambdoidal crests, which are not prolonged behind. The back of the skull is broad, with either deep pits or vacuities in the exoccipital bones. There is usually a large antorbital fossa, often with a

small vacuity between the lachrymal, frontal and maxillary bones. The upper premolars are greatly shortened, which is due to the anterior portion of these teeth being reduced, in the later species often to a point where the median crest may be taken for the anterior crest, which makes the tooth seem to stand transversely in the jaw. Peterson¹ has recently figured a complete skeleton of this genus, Merychyus minimus.

The type species of this genus, *M. elegans* Leidy, was found on the Niobrara River in Nebraska, in Hayden's horizon F, which was described as Pliocene. This seems to be the Valentine beds of Lower Pliocene age. A large number of species were referred to this genus, almost always based on teeth alone, and most of them either have already been or must in the future be, referred to other genera, most often to *Ticholeptus*. Below I have listed all the species which really belong to the genus. I include Thorpe's *Oreodontoides oregonensis* from the John Day as a primitive representative. His *Paroreodon marshi* seems to be distinct, though related. Besides there being too many forms referred to this

^{11923.} Annals Carnegie Museum, XV, p. 96, Pl. viii.

genus, there has been some identification of species as M. elegans in more than one horizon, which a study of the premolars serves to straighten out. The following table will serve to show how extremely conservative this genus has been.

viiis gonus into seem.		Length of skull	Length of upper molars	Length of upper premolars
M. (Oreodontoides) oregonensis	Upper John Day	165	33	30
M. curtus	Lower Rosebud	158	37	30
M. siouxensis	Lower Harrison	178	46	35
M. minimus	Upper Harrison	160	39	30
M. leptorhynchus	Laramie Peak	167	43	. 38
M. arenarum	Laramie Peak	191	45	38
M. delicatus	Upper Rosebud	140	36	31
M. parigonus	Deep River		50	
M. paniensis	Pawnee Creek			
M. elegans	Valentine		45	31
		Length of lower molars	Length of lower premolars	
M. (Oreodontoides) oregonensis	Upper Day John	lower	lower	
M. (Oreodontoides) oregonensis M. curtus	Upper Day John Lower Rosebud	lower	lower	
		lower molars	lower premolars	•
M. curtus	Lower Rosebud	lower molars	lower premolars	
M. curtus M. siouxensis	Lower Rosebud Lower Harrison	lower molars 40	lower premolars 33	•
M. curtus M. siouxensis M. minimus	Lower Rosebud Lower Harrison Upper Harrison	lower molars 40 43	lower premolars 33	
M. curtus M. siouxensis M. minimus M. leptorhynchus	Lower Rosebud Lower Harrison Upper Harrison Laramie Peak	lower molars 40 43 46	lower premolars 33 30 32	
M. curtus M. siouxensis M. minimus M. leptorhynchus M. arenarum	Lower Rosebud Lower Harrison Upper Harrison Laramie Peak Laramie Peak Upper Rosebud Deep River	lower molars 40 43 46 46	lower premolars 33 30 32 32 29	
M. curtus M. siouxensis M. minimus M. leptorhynchus M. arenarum M. delicatus	Lower Rosebud Lower Harrison Upper Harrison Laramie Peak Laramie Peak Upper Rosebud	lower molars 40 43 46 46 39	lower premolars 33 30 32 32	

In order to make a basis for the comparison of the different species of this genus, I here figure the premolars of the upper jaw of the paratype of *M. elegans*, the type being too worn to show the character of these teeth. This is from the jaw figured by Leidy, 1869, Jour. Acad. Nat. Sci. Phila., VII, Pl. xI, fig. 3.



Fig. 18. Merychyus elegans, from Leidy's paratype (see text). Natural size.

Merychyus curtus, new species

The type of this species is No. 13817 in the American Museum and was found ten miles east of Kyle, South Dakota, in the Lower Rosebud beds.

While a typical *Merychyus*, it is smaller than most of the species. It has enormous bullæ and a deep antorbital fossa with a small vacuity

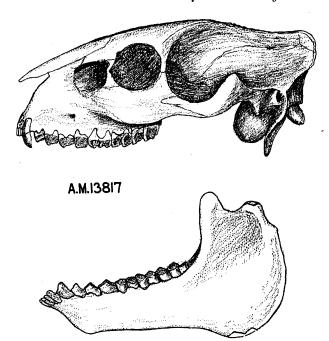


Fig. 19. Merychyus curtus, skull and lower jaw from the type. One-half natural size.

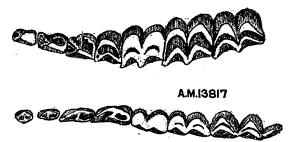


Fig. 20. Merychyus curtus, upper and lower dentitions, from the type. Natural size.

just above it. The whole skull seems foreshortened. The teeth are wide and short from front to back. The upper premolars are characterized by the anterior portion's being abbreviated and having several small striæ running forward from the primary cusp, giving this anterior end a striated appearance. The posterior crescent is well developed but does not unite with the median crest. Premolar 4 has a small pit in the anterior external corner. The lower premolars are those typical of the genus.

As compared with other species, this is about the size of M. minimus, but this species has a large antorbital fossa and a small vacuity, whereas M. minimus has a small fossa and a large vacuity. M. curtus is a little larger than M. delicatus, which is, however, lighter-built throughout and has only a slight antorbital fossa and no vacuity.

Merychyus siouxensis, new species

The type for this species is a fine skull in the American Museum, No. 13774, from the Lower Harrison beds, ten miles west of Agate, Nebraska. It is not far from *M. elegans* in size, which name has been incorrectly applied to some of the material in the Lower Harrison beds, *M. elegans* coming from the Valentine beds.

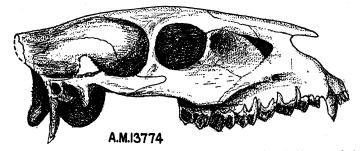


Fig. 21. Merychyus siouxensis, skull from the type. One-half natural size.

The specific characters are a moderately large antorbital fossa and a moderate-sized antorbital vacuity. The premolars are neither crowded in the jaw nor shortened, as are those of M. elegans. This is also about the same size as M. paniensis, which species is lighter-built throughout and has a much narrower dental series. These three species are nearly the same size, but a careful examination of the upper dental series of premolars will readily distinguish them. In M. siouxensis the anterior portion of premolars 2 and 3 is (for this genus) long, and the anterior basin is divided into two parts.

Merychyus delicatus, new species

This species is based on a skull and jaws, numbered 12980 in the American Museum, found on Porcupine Creek, South Dakota. It is the smallest species known and at the same time has the best-marked specific characters.

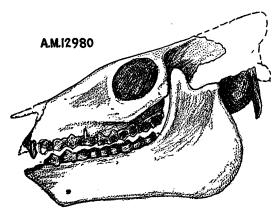


Fig. 22. Merychyus delicatus, skull and jaws from the type. One-half natural size.

The specific characters are: the size; the light build; only a trace of an antorbital fossa, and no vacuity. There is no crowding or special shortening of the premolars. With the measurements in the table on page 31, the species will be readily recognized.

Merychyus paniensis, new species

Merychyus elegans Matthew, 1898, Mem. Amer. Mus. Nat. Hist., I, p. 419.

The material on which this species is based is that which was used by Dr. Matthew in describing the Pawnee Creek fauna. I have chosen No. 9047 of the American Museum as the type for the species, because that is

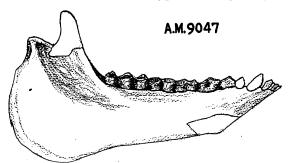


Fig. 23. Merychyus paniensis, lower jaw from the type. One-half natural size.

an adult lower jaw associated with metapodials of both the fore and hind feet and other bones. No. 9442 is an imperfect skull, but it is young; No. 9045 is another lower jaw, with some limb material; No. 9046 has the nearly perfect front foot, illustrated in Fig. 24, and No. 9443 has an equally good hind foot. All show the slender and delicate build of this species.

The species is very similar to M. elegans, but the upper dentition, so far as known, is so largely deciduous that comparisons can not be made on this character. The lower dentitions, however, can be compared. While the length over all of the two premolar series is nearly the same, in M. paniensis the first lower premolar is considerably smaller; premolar 2 is considerably larger; premolar 3 somewhat larger, and premolar 4 of about the same size. The whole dentition of M. paniensis is lighter, both the premolars and the molars being narrower.

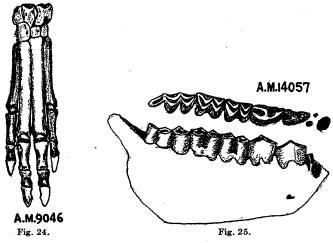


Fig. 24. Merychyus paniensis, front foot from No. 9046. One-half natural size.

Fig. 25. Ticholeptus hypsodus, lower jaw from the type. One-half natural size.

TICHOLEPTUS

This genus was established to include those oreodonts with limbs of intermediate length and with skulls of a mesocephalic or brachycephalic type, on which the supra-orbital crest is high, the exoccipital region broad, the bullæ large, and the antorbital vacuity large. The teeth are shortened from front to back, and the lower fourth premolar is distinguished by having the anterior crest bifurcated at the front end. It ranges from the Lower Harrison beds up into the Snake Creek.

Ticholeptus hypsodus, new species

This is one of the oreodonts from the Snake Creek beds, twenty-three miles south of Agate, Nebraska. I have taken No. 14057, a lower jaw, as the type. The pattern of the teeth is that typical of *Ticholeptus*,

but these are more hypsodont than is usual for the genus. This, however, seems to me simply the expression of the advanced condition of these late forms, and it is not desirable to separate them from their predecessors in the Miocene.

The lower premolars have the anterior crest bifurcated, as is characteristic of the genus, but in this species the fourth premolar is slightly peculiar in that the posterior basin is not completely inclosed until the tooth is much worn. Molars 2 and 3 are characterized by having a cingulum in the gap between the two lobes on the outside of each tooth.

METOREODON

This genus was established by Matthew and $Cook^1$ for several oreodonts in the Snake Creek beds which at the time they associated with Merychyus. The type species of the genus is M. relictus, which represents an exaggeration of the Ticholeptus characters. The teeth are more hypsodont. The cusp-like pillar on lower premolar 4 has grown forward and enlarged so that it almost fills the anterior basin. The furrows on the outer side of the premolars are also distinctive.

 $\it Metoreodon\ profectus$ is a larger specialized form which I should refer to $\it Ticholeptus$.

EPOREODON

This genus, so abundant in the Upper Oligocene and John Day beds, has, so far as known, but one representative in the Miocene of the eastern Rocky Mountain district.

Eporeodon relictus, new species

The type of this species, No. 13813 in the American Museum, was found in the Lower Rosebud, six miles west of American Horse Creek, South Dakota. Other specimens of the same species are No. 13814 and No. 8949, with the latter of which there is a considerable part of the skeleton, but unfortunately the individual is a young one.

The skull is characterized by being nearly straight along the top, with bullæ of medium size, a small and rather deep antorbital fossa, and teeth typical of the genus. There is an unusually wide gap between the postglenoid and paroccipital processes, so that the whole tympanic bone is exposed in the side view.

¹1909. Bull. Amer. Mus. Nat. Hist., XXVI, p. 391.

E. montanus is the only eastern form of similar size, but it is larger and has an arched line along the top of the skull. E. occidentalis of the John Day is similar in size, but this species has a skull of much wider and heavier build.

The front limb is light and slender, even for a member of this genus, but would fall in the class described as medium, that is, about the weight of the skeleton of *Merycoidodon*. The following measurements give the characteristics of the species.

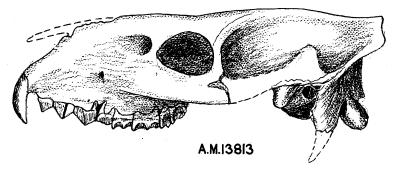




Fig. 26. Eporeodon relictus, skull and upper dentition from the type. One-half natural size.

198	mm.
44	
40	
100	
135	
52	
17	
11	
13	
	44 40 100 135 52 17 11