

ART. XX.—*On Ticholeptus Rusticus and the Genera of Oreodontidæ*; by F. B. LOOMIS.

In 1858 Leidy established the genus *Merycochærus*, with *M. proprius* as the type species for Miocene oreodonts. Since that time the genus has been the one to which every Miocene oreodont with inadequate data has been referred, until the number of referred species became over a dozen. It is not entirely unnatural to do this; for the dentition of oreodonts remains strikingly uniform, while the shape of the skull and the character of the limbs change remarkably. By 1901 it had become obvious that more than one type of animal was included in the genus; and Douglass, using *M. superbus* as the type, gathered together a group of forms characterized by having heavy, elongated skulls, with long nasals, wide heavy zygomatic arches, a long heavy body and short stocky limbs, and established the genus *Promerycochærus* with a half dozen species to start with, to which have since been added as many more. Very shortly after that Matthew published a description of the skull and most of the skeleton of *Merycochærus proprius*, showing this to be a form with shortened nasals, a wide skull, and short limbs. This then established the character of the forms which could be referred to this genus and only one other was left in the group, namely *M. rusticus*.

It was the good fortune of the Amherst Expedition of 1919 to find in the Pawnee Creek Beds of N. E. Colorado a very perfect skull of *M. rusticus* together with considerable quantities of skeletal material. These beds carry only this one species of oreodont so there is very little difficulty in using all the skeletal material, though there was associated with the skull considerable of the skeleton, making the study of numerous other finds very easy. A glance at the complete skull shows that it is not to be associated with *M. proprius* generically; but rather that it is associated with forms described by Douglass under the names *Ticholeptus brachemelis* and *T. breviceps*, though at the same time specifically different.

The type species of this genus is *Ticholeptus zygomaticus* Cope, which was figured by Scott in 1894 and by him referred to the genus *Merychyus*. The specimen lacks the nasal region and the feet, both parts much to be de-

sired in determining the position of an oreodont. This skull of Cope's is less like the one I have than are the two of Douglass's descriptions, but the four (and perhaps *T. bannockensis*) make a very uniform group completely separated from the other oreodonts by having hypsodont dentition, medium length limbs, skulls with light zygomatic arches, and antorbital fenestra of considerable size.

As oreodonts are classified with reference to the whole skeleton perhaps more than any other great group it is essential that as rapidly as possible we should have more figures of the whole skull or better of the whole skeleton. This material is generally abundant in the various museums and it is desirable that for every species a complete skeleton should be described. The following is an outline of all that I can get in regard to *Ticholeptus rusticus*.

*Ticholeptus rusticus* Leidy.

*Merycochærus rusticus* Leidy, 1870, Proc. Acad. Nat. Sci., Philad., p. 109.

*Merycochærus rusticus* Leidy, 1873, Rep. U. S. Geol. Surv. Territories, p. 199, fig. 1-5, Pl. 17.

*Merycochærus rusticus* Matthew, 1901, Mém. Amer. Museum Nat. Hist., vol. 1, p. 412 and figs.

In this species the skull is lightly built throughout, and moderately elongate, more so than in either *T. brachymelis* or *T. breviceps*. The orbit is set well back, its posterior margin being a little behind the back of the last molar, while in *T. brachymelis* it is over the back of this tooth, and in *T. breviceps* it is still further forward. The whole brain case is longer in this species than the others mentioned. The nasal bones are considerably shortened, ending just over premolar 3, while those of *T. brachymelis* and *T. breviceps* end over premolar 1. In all these this is an unusually short nasal, but not of the character of *M. proprius* so that it does not suggest the development of a proboscis as in that genus, but I would take it rather as indicating a snout more like that of modern pigs. Correlated with the shortening of the nasals is the position of the infraorbital foramen which in this species is just over the contact of premolar 4 and molar 1, while in the other two species it is further forward by the width of the fourth premolar. There is a large prelacrymal fenester situated rather far forward on account of the extension

of the lacrymal bone on the front of the orbit. The zygomatic arch is decidedly light more so than in any of the closely related forms, and has no tendency to thicken along the rear margin, but continues as a thin plate into the lambdoidal crest. The sagittal crest is also light and low.

The tympanic bullæ are small and not inflated. The auditory meatus is inclosed in a bony tube of moderate length and opens obliquely upward, but not nearly as high up as in either *Merycochærus* or *Promerycochærus*. The mastoid plate is but moderately expanded. The premaxillæ are small and fused in the median line.

The dentition is not very distinctive, the teeth being

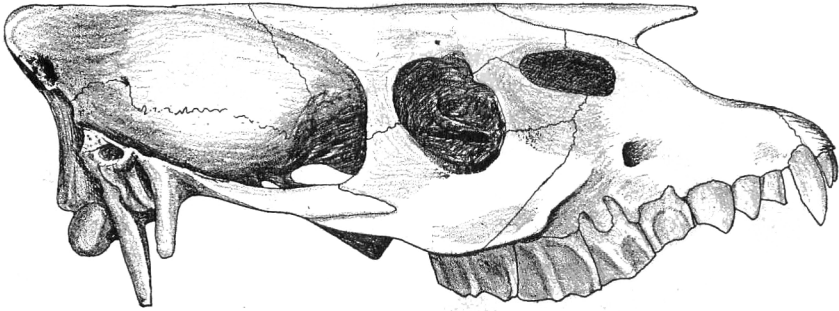


FIG. 1. Skull of *Ticholeptus rusticus* from the side, 2/5 nat. size.

moderately hypsodont, the molars increasing in size from front to back. The premolars are crowded so that in the upper jaw the first three stand obliquely in the maxilla bone. The canines are small and the only gap in the dental series of either jaw is the small interval between the canine and first premolar.

Most of the characters of the skeleton appear in the restoration, for which I had the skull, pelvis and scattered vertebræ and most of the fore limb as one associated specimen. The other parts are drawn from some twenty other finds two of which represented considerable portions of the skeleton associated. There was no complete back bone but vertebræ from every portion of it including the sacrum. The upper part of the femur was preserved in none of my material and is restored. Otherwise all the bones are drawn life size from one or another specimen and the whole photographed down. The pelvis is the only

portion in which I feel any doubt but it was associated with the skull. To me it seems too long, especially the ilium but the animal is slenderly built. Without going into details, the features I would call attention to are that the feet are of the medium type, with metapodials comparable with those of *Oreodon*; the phalanges are short and stocky, especially the unguals, which are flattened from top to bottom in strong contrast to the same bones in *Merychyus*; the radius is of moderate length and has a considerable curvature; the tibia is rather stocky, and both radius and ulna and the tibia and fibula are entirely separate.

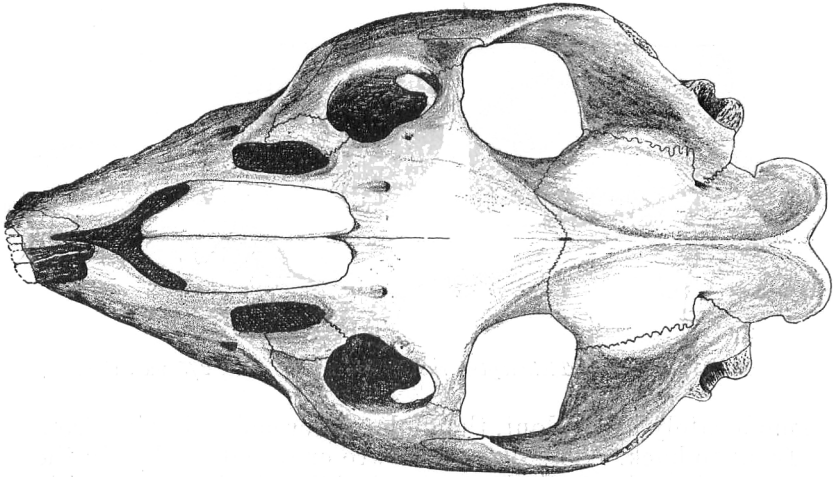


FIG. 2. Skull of *Ticholeptus rusticus* from above; 2/5 nat. size.

The following measurements will indicate the size of the animal, but it is to be remembered that there is considerable range in the figures for any one part of the skeleton, for we find both male and female, and younger and older individuals. I have taken for measurement those of the larger size, though there is less than 10% variation between the largest individuals and the smaller ones.

	mm.
Skull, length from incisors to occipital condyles.....	254
length of dental series .....	138
length of premolars .....	53
length of molar series .....	81

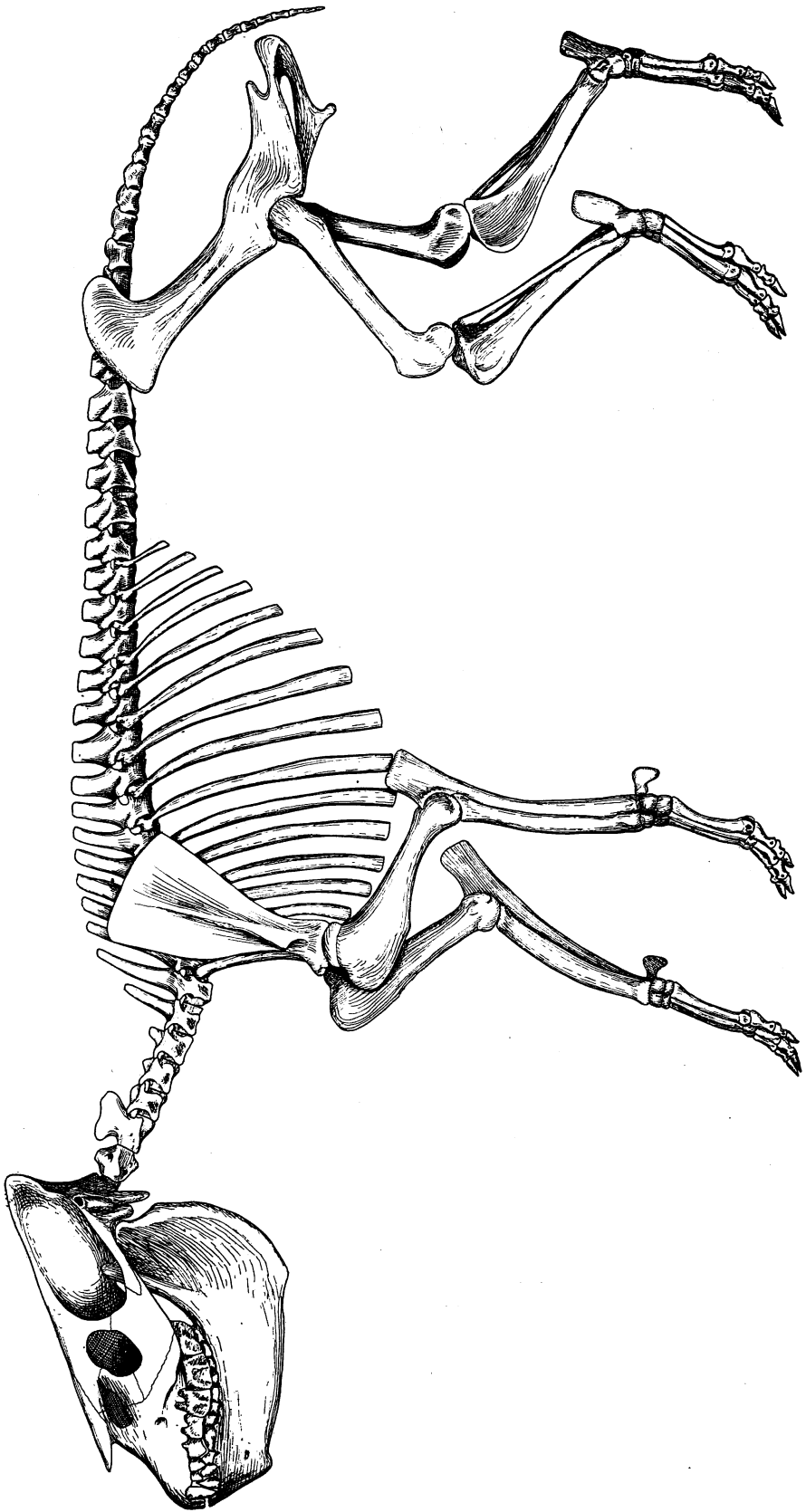


FIG. 3. Skeleton of *Ticholeptus rusticus*; 1/5 nat. size.

Lower jaw, length of dental series .....	132
length of premolars .....	48
length of molar series .....	74
Fourth cervical vertebra, length .....	22
Fourth dorsal-vertebra, length .....	24
Second lumbar vertebra, length .....	30
Humerus, length .....	153
Radius, length .....	124
Metacarpal III, length .....	63
Tibia, length .....	151
Metatarsal III, length .....	64

In order to place this skull it was necessary to make a comparative study of most of the genera of this family and as no such comparisons have been made for a long time, especially since the knowledge of many of the best known forms, I should like to offer the following notes and suggestions for the distinctions of various of the genera and for the relationships of different members of the family. In the case of many species which are founded on fragmentary jaws especially it is not possible to place them definitely.

#### *Oreodontinae.*

Selendont artiodactyls, with the dentition typically  $\frac{3}{3}$ ,  $\frac{1}{1}$ ,  $\frac{4}{4}$ ,  $\frac{3}{3}$  and the teeth in closed series, the lower canine incisiform and the first premolar functioning as a canine; the feet with four functional toes.

- A. Toes clawed, external crescents of molars strongly concave, teeth brachydont, orbit open behind—*Agriochæridæ*.  
 I—Upper premolar 4 not molariform, protoconule present—*Protagriochærus*.  
 II—Upper premolar 4 molariform, protoconule absent—*Agriochærus*.
- B. Toes hoofed, external crescents of molars little concave, premolar 4 never molariform—*Oreodontidæ*.  
 I—orbit open behind, incisors  $\frac{3}{3}$ —*Protoreodon*.  
     incisors lacking in upper jaw—*Hyomeryx*.  
 II—Orbit closed behind;  
     1—limbs of moderate length;  
         a—digit 1 in manus present as vestige, bulla small—*Oreodon*.  
         b—(digit 1 unknown) bulla large—*Eucrotaphus*.  
         c—digit 1 lacking, bulla large, teeth brachydont—*Eporeodon*.

- \* teeth moderately hypsodont—Mesoroedon.
- \*\* teeth strongly hypsodont, antorbital fenester—Ticholeptus.
- \*\*\* teeth strongly hypsodont, no antorbital fenester, but groove on outside of premolars—Metoreodon.
- 2—limbs short and stocky.
  - a—skull elongate and heavy, teeth brachodont—Promerychochærus.
  - b—skull short, nasals shortened, teeth hypsodont—Merychochærus.
  - c—skull short, nasals very short, teeth hypsodont—Pronomotherium.
- 3—limbs long and slender, small antorbital fenester—Merychys.
- 4—Limbs moderate length, both frontal and antorbital fenestra;
  - a—frontal fenestra small—Phenacocœlus.
  - b—frontal and antorbital fenestra confluent—Leptauchenia.
  - c—as above, but incisors  $\frac{0}{1}$ —Pithecistes.
  - d—as above but incisors  $\frac{0}{1}$ —Cyclopidius.

From their origin in the Upper Eocene the Oreodontiæ have stood out clearly from among the other selenodont artiodactyls, and though they survived to the latter part of the Pliocene were less adaptive than other artiodactyls, at the same time retaining through their history many of the primitive artiodactyl characters. The Uinta forms show that the group came off from that division of artiodactyls which retained the anterior intermediate cusp (protoconule), but to just which one of the later groups it is most nearly related is not and can not be determined definitely until more complete material from the Eocene is available. The group is peculiar in that its history is purely American, none of the forms participating in any of the migrations by which American types found their way to other continents.

The Uinta genera *Protoreodon* and *Protagriochærus* are very close to each other and would hardly be separated were it not that some of the species of that period clearly are more closely related to the Oligocene genus *Oreodon*, others to *Agriochærus*. These genera then represent the beginning of the divergence of the two closely related families. Both genera have the anterior intermediate cusp on the upper molars, both have the orbit open

behind, in both the premolars are more crowded than in *Agriochærus* and less crowded than in *Oreodon*. *Protoreodon* has the more closely set premolars and the outer crescents of the molars less concave, and the unguals are neither laterally compressed as for claws, nor broadly depressed as in some of the later oreodonts. In *Protagriochærus* the teeth are less closely set, the molars have the crescents more concave, and the unguals are unknown. *Hyomeryx* represents a side line in which there is a tendency to lose the incisors of the upper set.

In the Oligocene, *Agriochærus* is clearly set off as an independently developing family, by the feet developing claws, by a wide gap behind the canine before the premolars begin, by the fourth premolar above becoming molari-form, and by the great concavity of the outer crescents of the upper molars. The genus is abundant and continues clear though the Oligocene running into a dozen larger and smaller species. *Oreodon* is a very abundant genus though with rather few species, *O. culbertsoni* and *O. gracilis* being the most abundant. The manus retains digit 1 as a vestigial toe, certainly in *O. culbertsoni* and *O. gracilis*, and this is the basis for the separation of *Oreodon* and *Eporeodon*. Two types of skulls very like each other are found but in *O. culbertsoni* the bulla is small; while the other form, otherwise very like this, has a large and inflated bulla. This inflated bulla is the basis of the genus *Eucrotaphus* with *E. jacksoni* as the type. Whether this is sufficient basis for a genus is doubtful but I should let it stand for the present until a study of the skeleton of *Eucrotaphus jacksoni* is made. That may show other characters justifying the genus and there must be material for the study though I have not found it. Whether *E. jacksoni* had the first digit of the manus retained or not is not known. In the development of the bulla it is more like *Eporeodon* than is *Oreodon*. These two genera as known today run through the Lower and Upper Oligocene. From the dwarf fauna found at Pipe Stone Springs, Montana, Douglass described two other genera of Lower Oligocene oreodonts, *Limnenetes* based on a skull which shows the orbit open behind; and so far as known this may well represent *Protoreodon* continuing on into the Oligocene; and *Bathygenus* based on a fragment of a lower jaw. This latter genus needs much more complete material in order to establish its independence and position. In the

Upper Oligocene the oreodonts lack the first digit of the manus and are termed Eporeodon which otherwise resembles especially *Eucrotaphus* having a large bulla. It still retains the brachyodont dentition, though the forms have increased in size and it is to this genus that all the John Day forms are assigned.

The Lower Miocene produced a wealth of oreodonts, both as to numbers and as to variety of adaptations. The least modified genus is *Mesoreodon* which is distinguished from *Eporeodon* by the teeth having begun to show an increase in height, moderate hypsodonty and medium type of limbs being the distinguishing features of this genus. I can find no characters to distinguish the genus *Merycoides* (Douglass) from *Mesoreodon*, the dentition being perhaps less hypsodont, but however, already showing a beginning of the elongation of the teeth. The genus *Mesoreodon* then is typically a Lower Miocene one, only one species, *M. longiceps*, being found in the Middle Miocene, and this species might equally well be placed in the genus *Ticholeptus* for it has a small antorbital fenester, and seems to represent the transition from *Mesoreodon* to *Ticholeptus*. The line of less specialized oreodonts is continued into the Middle Miocene by the genus *Ticholeptus* represented by at least four species. This genus is distinguished by the increased hypsodonty of the molar teeth and by the large fenester in front of the orbit. It may turn out that the type species, *T. zygomaticus*, should be placed among the species of *Merychyus* as it has a slender narrow skull, but the point can not be settled until the feet are found. At any rate there is a group of four or five Middle Miocene oreodonts with the medium type of feet, medium type of elongation of the teeth and large fenestra in front of the orbits and this term is needed to designate a very distinct stage in the evolution of the group.

The genus *Metoreodon* so far as is known, that is the skull and jaws, seems also to belong to this group and extends the line into the Pliocene, but it is not a direct descendant of *Ticholeptus* for it has no antorbital fenester. For the same reason and because it is of more massive build I am confident it was not derived from *Merychyus*. It has the most advanced dentition of the oreodonts being strongly hypsodont and is distinct in that the premolars have an infolding of the enamel on the external side. To me the genus seems to be derived from *Mesore-*

odon through some as yet unknown intermediate types. Metoreodon is the last survivor of the great family and continued until the middle of the Pliocene at least.

Merycochærus, originally described by Leidy and based on jaws, has been the "catch all" for Miocene oreodonts. In 1901 Douglass separated Promerycochærus and Pronomotherium from the mass of species described under this generic name. Then Matthew described in detail the type species *M. proprius* showing it to be a peculiar type with short limbs and a shortened wide skull, in which the nasals were very much reduced and the whole snout modified apparently by the development of a proboscis. So far I have seen no other species which could be associated with this one in this genus. Pronomotherium is the logical descendant of Merycochærus with the snout still more modified and the nasals so far reduced and moved backward as to be actually behind the front of the orbits. The tremendously deepened lower jaw and hypsodont teeth make this type entirely distinct, and with it, this aberrant line died out at the end of the Miocene.

Another aberrant group which came off from Eporeodon and which was long associated with Merycochærus but which probably had less in common with Merycochærus than with other genera is Promerycochærus, large animals with very short limbs, a heavy elongated body and a very heavy long skull, on which the zygomatic arches are especially wide and thickened. Of this fully described and illustrated genus no less than a dozen species are known ranging from the upper part of the Upper Oligocene through the Lower Miocene. One form, *P. montanus*, has indeed been described from the Middle Miocene but it is desirable to have more complete material of this species before being sure it belongs to this line.

Merychys is another genus to which many fragmentary species have been referred. Its type species is *M. elegans* and with it belong several species, like *M. arenarum*, *M. minimus*, *M. harrissonensis*, *M. leptorhyncus*, all small, light built types, with long slender limbs and tiny hoofs so compressed laterally as to suggest the unguals of deer and a very perfect digitigrade mode of locomotion. Such species as *M. medius* and *M. major* are much heavier built and when better known will, I am sure, be assigned to other genera. In the case of *M. medius* some of my material shows it clearly had stocky limbs, a moderately heavy skull without an antorbital fenester, the whole

being very like Mesoreodon. As known today Merychys ranges from the Lower to the Upper Miocene.

In Phenacocœlus, Leptauchenia, Cyclopidius, and Pitheciestes we have a group of highly specialized oreodonts in which the skull has a pair of frontal fenestra as well as the antorbital fenestra. Unfortunately except for Phenacocœlus the limbs have been very scantily described but where known they seem to be of moderate length and not stocky. The group is a progressive one, being more specialized in the order named above and very peculiar in that the nasals become fused to the premaxillæ bones. Phenacocœlus is the least specialized and has the frontal and antorbital fenestra separate, also moderately long and slender limbs. In Leptauchenia the skull is short and wide and the frontal and antorbital fenestra have become confluent, but the dentition is retained in full. Cyclopidius has the same general characters, but the incisors are reduced to  $\frac{0}{5}$ ; while the little known Pitheciestes has gone a step further and has but one incisor (the third) still remaining in the lower jaw.

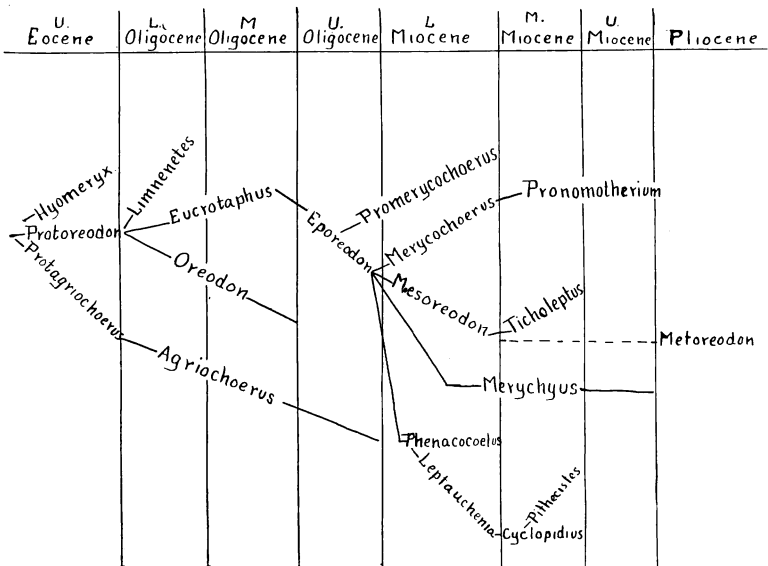


FIG. 4.—Diagram of the Evolution of the Oreodon.

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