

PHYLOGENY OF THE MERYCOIDODONTS.

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ABSTRACT.

In spite of the vast amount of merycoidodont material recovered, there are gaps to be filled before a complete phylogeny of this group can be known. The present phylogeny is based mainly upon skulls, for therein lay the major evolutionary changes. It is probable that the ancestral forms were immigrants, but we know no species before the upper Eocene Uinta, and the entire group became extinct by middle Pliocene.

The nearest relatives of the group were the suillines and ruminants. Two upper Eocene genera were related but probably were not in the true stem stock, which was represented in the Oligocene by *Merycoidodon*, from which later *Eporeodon* developed. In the late Oligocene and early Miocene four stocks became differentiated. These were the *Mesoreodon-Pronomotherium*, the *Ticholeptus-Metoreodon*, the *Merychyus*, and the *Leptauchenia-Cyclopidius* stocks, herein briefly characterized diagnostically. Around these the other genera are grouped, either in a phylogenetic series or as related branches. The first two stocks arose from *Eporeodon*. The ancestors of the latter two are unknown, but the *Merychyus* line may well have developed from some form such as *Merycoidodon gracilis*, while the *Leptauchenia-Cyclopidius* stock arose perhaps from *Limnnetes* or an allied genus. A diphyletic evolution is suggested in which certain genera had a parallel development on the West Coast, proceeding along the lines of the more eastern genera. All are confined to North America as now known.

In the past few years a great amount of new merycoidodont material has been collected and much of it described. However, in spite of the vast quantity of remains of these extinct artiodactyls already known, there are still many gaps, and a complete and proper understanding of some of the relationships can come about only through the recovery and intensive study of complete skeletons of many more species and possibly of genera.

During recent years several of the gaps have been filled, and the relationships of various genera are now very much clarified. Of necessity the present phylogeny is based, to a considerable extent, upon the skull characters which, while highly important, are not in themselves all sufficient. In extenuation of this procedure it may be stated as an indisputable fact that the major evolutionary changes in this entire family involved the skull to a much greater extent than they did the skeleton.

No recent finds have extended the known habitat beyond the

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confines of North America, and no further light has been shed upon the ancestry of these mammals.

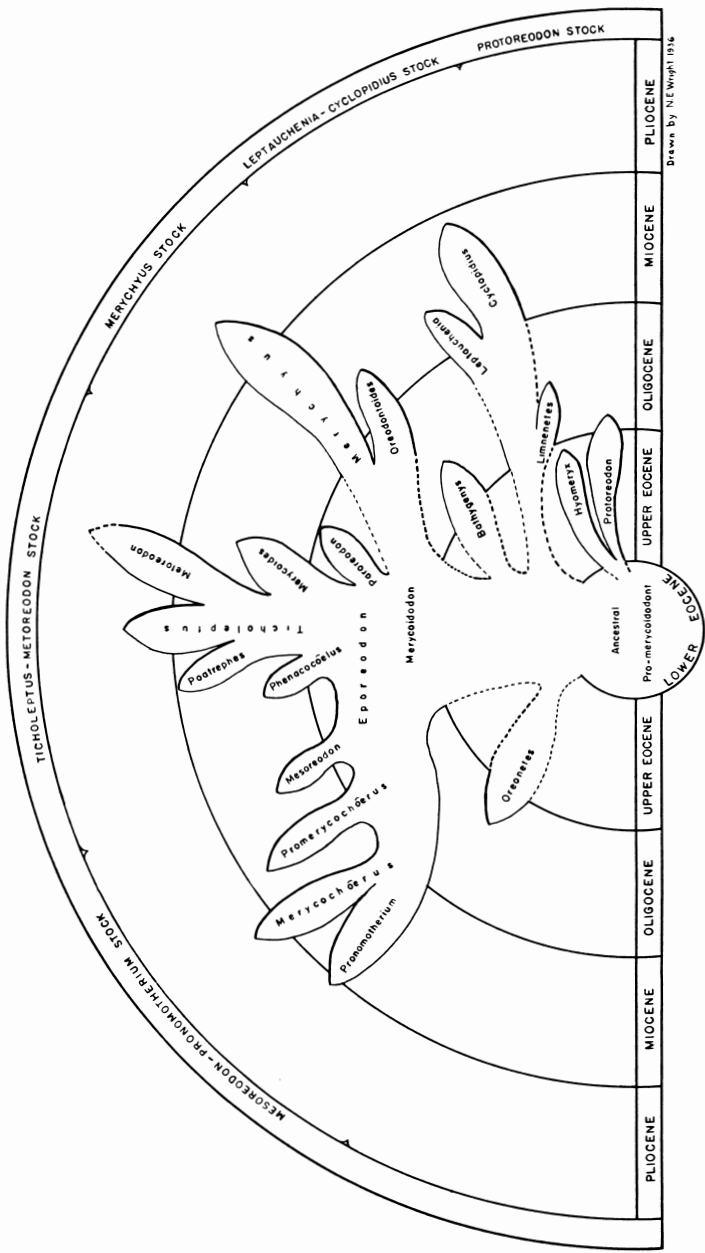
No remains of artiodactyls which seem to be related to the ancestral stem of the merycoidodonts have been found in strata older than the Uinta Eocene, and the evidence apparently indicates that the earliest genera were immigrants, rather than members of the indigenous fauna. On the other hand, it may be argued equally well that this family was evolving in the same or neighboring areas previous to Uinta time and that a change in conditions of preservation brought them thus suddenly into our range of observation.

The nearest relatives of the oreodonts are to be found among the early suillines and ruminants, but it cannot be stated with certainty which of the two groups these extinct forms resemble the more. On the basis of our present knowledge we must assume that the affinities of the early Merycoidodontidæ are with the Anoplotheriidæ, Cænotheriidæ, and Dichobunidæ, in the order Ancodonta of Matthew or the Protoselenodontia of Romer.

The earliest known allied genus, *Protoreodon*, was first collected in the Eocene Uinta Basin in Wyoming. Beginning in the Uinta or earlier, the family spread over nearly all of the area of the western half of the United States and into Saskatchewan, Canada. It is possible that the Canadian area may have been an area of supplementary dispersal. To date no true member of this family has been described from Arizona, Idaho, or Washington. It is possible that their range may have been much greater, especially over the eastern part of the United States, but this must be left to conjecture, as the critical Tertiary sediments are absent over so much of that area.

Protoreodon, with a skull length of between 129 mm. and 173 mm., possessed a fifth cusp, the protoconule, on the very low crowned molars, which have conical lingual cusps and wide, open valleys. The orbit is open, the auditory bullæ are small, there is neither facial fossa nor vacuity, and the pentadactyl manus and tetradactyl pes are unusually long.

By comparison with the Mongolian Eocene Archæomeryx, in which the molars have the pattern of the modern selenodonts, with no indication that these teeth ever had more than four cusps, I believe that the Eocene merycoidodonts, *Protoreodon* and *Hyomeryx*, are side branches, rather than being in the true line of descent. *Emeryx* Marsh and *Agri-*



Drawn by N.E. Wright 1934

Fig. 1. Phylogeny of the Merycooidontidae.

otherium Scott are considered synonymous with *Protoreodon*. *Hyomeryx* is seemingly related to *Protoreodon*, although unfortunately we know very little about this genus.

The Lower Oligocene genera, *Bathygenys*, *Oreonetes*, and *Limnenetes*, are not well known. The material of the first genus is so fragmentary that it warrants no definite conclusions as to its position, but at present it appears to be an aberrant branch, nearest to *Limnenetes*. In *Oreonetes* the orbit is open, as it is also in *Limnenetes*, the teeth are brachyodont, the antorbital fossa is large, and the bullæ are very small. The skeleton is unknown. *Limnenetes* possesses moderately large bullæ and a shallow fossa, and the limbs are long and slender, suggestive of *Merychys*. In all of the succeeding genera the orbit is closed.

Merycoidodon, of Lower and Middle Oligocene age, has a skull length of from 120 mm. to 220 mm., small to medium sized bullæ, shallow to deep fossæ of moderate size, limbs of medium length, a long tail, and the pentadactyl manus.

Protoreodon, *Oreonetes*, and *Merycoidodon culbertsonii* possess very small bullæ. Largely on this character these forms, including all of the species of *Merycoidodon*, were grouped in a separate stock by Douglass and later by Loomis. To this I take exception, for in *M. gracilis*, a true member of this genus, the bulla is proportionally as large as it is in some of the eopreodonts. While it is a fact that large, inflated bullæ are generally present in all of the genera subsequent to the Middle Oligocene, yet in some of the species of these genera the bullæ are proportionally as small in relation to skull size as they are in *M. culbertsonii*.

In *Agriochærus antiquus dakotensis* Thorpe the holotype shows a very small bulla on the right side, about the size of that seen in *Oreonetes* and *M. culbertsonii*, whereas the other side possesses a large, inflated bulla. This condition may indicate either that there has been an unequal development of the auditory capsule or that the inflated one on the right side has been lost. It is well known that in some of the recent mammals the bulla is so loosely attached to the skull that it becomes detached from the basicranial region during maceration. Possibly this may have occurred in *Merycoidodon*, since it is assumed that the inflated bulla is a primitive character. On the other hand, the bulla may have been cartilaginous, a condition found in certain of the living animals.

If this was the case, the chances of its preserval were practically nil.

From *Merycoidodon* I believe that the true *Eporeodon* emerged in the Upper Oligocene and continued into the Lower Miocene. This genus, with a skull length of between 170 mm. and 255 mm., shows an advance in dental structure in that the molars increase gradually in length and the anterior crescents of the superior premolars are reduced. The anterior fossette of P⁴ in *Merycoidodon* has nearly disappeared in *Eporeodon*. The manus has become definitely tetradactyl.

Marsh emphasized the presence of large bullæ as one of the distinguishing generic characters. Some of the species now assigned to *Eporeodon*, which are based on skulls alone and which possess inflated bullæ, perhaps should be referred to *Merycoidodon*. In that event the range of the latter genus would be extended into the Upper Oligocene and possibly into the Lower Miocene. There are several examples in this family of the ancestral stock persisting side by side with the presumed derivatives.

There are some borderline species in the skulls of which the chief and almost the only deciding factor is the presence of large bullæ. If by analogy with *M. gracilis* these actually should be other species of *Merycoidodon*, with bullæ relatively larger than those of *M. culbertsonii*, that genus and *Eporeodon* would be equalized to a much greater extent than they are at present. This would more logically explain the apparent great expansion in this family which seemingly began with a sudden burst of Upper Oligocene and Lower Miocene eporeodonts in California, Oregon, Montana, North and South Dakota, Colorado, Wyoming, and Nebraska. I believe that *Merycoidodon* was much more widespread than we can at present prove. Furthermore, the presence or absence of inflated bullæ alone in *Oreonetes* and *Limnnetes* is, in my opinion, an insufficient basis for the independence of these two genera.

This problem can be settled only by the recovery of skeletons of those species now assigned to *Eporeodon* and by the discovery, if possible, of specimens of *Merycoidodon* which show ossification of larger bullæ. This ossification, especially if incipient, might be hard to detect, and the basicranial area of skulls of that genus should be cleaned with the utmost care.

By late Oligocene time there are four stocks foreshadowed, and by early Miocene these are clearly discerned. They are respectively the *Mesorcodon-Pronomotherium*, the *Ticholeptus*-

Metoreodon, the *Merychys*, and the *Leptauchenia-Cyclopidius* stocks. Around these are grouped certain genera, either in a phylogenetic series or as related branches.

The first two stocks I should derive directly from *Eporeodon*. The ancestors of the latter two must be sought in the Middle or Lower Oligocene and are, I believe, derivatives of a form similar to *M. gracilis* on the one hand and to *Limnenetes platyceps* on the other, perhaps the former for *Merychys* and the latter for *Leptauchenia-Cyclopidius*. For these last two we can do no more than surmise, since there is no connecting series leading to either stock so far discovered in Oligocene strata.

The *Mesoreodon-Pronomotherium* stock, ranging from Upper Oligocene to Lower or perhaps Middle Pliocene, contains the largest members of the family. *Mesoreodon* is not far removed from *Eporeodon*, but its dentition shows incipient hypsodonty. The length of skull varies between 248 mm. and 270 mm. The tail is much shorter than that of *Eporeodon*, and the limbs vary from medium to slender. *Promerycocharus*, with a skull range of from 253 mm. to 411 mm., has species as large as the wild boar. Some of the skulls are nearly as wide as long, while others are very long and narrow. All of the sutures closed apparently early in life, and the posterior palatine foramina are seldom discernible. Occasionally P⁴ contains a small pit in the anteroexternal corner, like that in *Eporeodon* but smaller than that in *Merycoidodon*. The inferior premolars are narrow and compressed, and P₄ has a large, pillar-like cusp at the junction of the median crest and the posterior crescent. The body is long and the tail short, and the limbs are heavy to medium. From some of the wider-skulled species of the last genus it is probable that *Merycocharus* was derived. This genus is characterized by brachycephalic skull, recession of the nasal bones, foreshortened cranial region, hypsodont dentition, short, stocky limbs, medium to long body, and short tail. The skull is from 286 mm. to 334 mm. in length, and the premaxillaries are usually coössified. There is no pit in the anteroexternal corner of P⁴, but there is a marked increase in molar length from first to last. It is highly probable that this genus possessed an incipient proboscis or at least very flexible lips. *Pronomotherium*, whose skull range (250 mm. to 335 mm.) is nearly identical with that of *Merycocharus*, is an exaggerated form of the latter in its general physical characteristics. The skull

is brachycephalic, the dentition is strongly hypsodont, and the recession of the nares is carried to such an extreme that we must assume that a proboscis was present, probably much like that of the modern tapir. The lower premolars are somewhat shortened and crowded, with P_4 similar in construction to that tooth in *Promerycochærus*.

The *Ticholeptus-Metoreodon* stock is characterized in part by vacuities in the skull located chiefly in the facial area, in advance of the orbits. Its geologic age ranges from Upper Oligocene to Middle Pliocene. *Paroreodon* has a sub-brachycephalic skull, large bullæ, and small vacuities; *Merycooides* is mesocephalic in skull shape, and the vacuities are occasionally absent. These two genera, together with *Phenacocælus*, are approximately within the size range of *Merycooidodon culbertsonii* and, like the latter, have brachyodont dentition. *Phenacocælus* has small facial, frontal, and occipital vacuities, a mesocephalic skull, large bullæ, a long body, a short tail, and limbs of medium length and weight. These three genera seem to be aberrant branches from the *Eporeodon-Ticholeptus* stem stock. *Ticholeptus*, with a skull length between 200 mm. and 270 mm. and a skull shape usually mesocephalic, rarely brachycephalic, has large bullæ, hypsodont dentition, small to large facial vacuities, body and limbs of medium length, and a short tail. In the dentition the molars increase in length; the premolars are reduced by the shortening of the anterior part and are somewhat crowded. P_4 has a bifurcation at the forward end of the anterior crest. *Poatrephes* has a brachycephalic skull, slightly longer than the average length of skull in *Eporeodon*, moderately large bullæ, subhypsodont dentition, and large vacuities. This genus, derived from *Ticholeptus*, is an aberrant branch. *Metoreodon*, the skull of which ranges from 220 mm. to 400 mm., has exaggerated many of the characters of *Ticholeptus*. The anterior bifurcation of P^4 has enlarged to a cusp-like pillar and has become an integral part of the three posterior inferior premolars, while the anterior three superior premolars show a corresponding cusp. This genus has a brachycephalic skull, large bullæ, hypsodont dentition, large vacuities, and large, deep fossæ.

The Lower Miocene to Lower Pliocene *Merychyus* stock presents a moderate uniformity of generic characters. *Oreodontoides*, about the size of the smaller species of *Merychyus*, has a mesocephalic skull, as has the latter genus. The former possesses medium-sized bullæ, brachyodont dentition, and deep

fossæ, whereas in *Merychys* the bullæ are large, the dentition changes from subhypsodont in the early forms to hypsodont in the later ones, and the superior premolars have suffered a marked anterior reduction. Vacuities are absent in *Oreodontoides* but are occasionally present in *Merychys*. The skeleton of the latter shows a body of medium length, a short tail, and slender limbs.

The *Leptauchenia-Cyclopidius* stock ranges from Upper Oligocene to Upper Miocene. The skulls are decidedly brachycephalic, the bullæ are very large, the dentition is hypsodont, and the vacuities are very large, being formed by the confluence of frontal and facial vacuities. The zygomatic arch of *Leptauchenia* (skull 85 mm. to 145 mm. long) is light and the fossa large; in *Cyclopidius* (skull 93 mm. to 146 mm. long) the arch is very heavy, and the fossa is small. In *Leptauchenia* the superior premolars appear to slant somewhat backward. *Cyclopidius* has lost one superior incisor and, occasionally, one lower. The premolars often overlap and seem to be set obliquely, due to the reduction of the anterior moiety. In both genera there is a marked increase in size of the molars from first to third. Both possess long bodies, short tails, and slender limbs. Curiously enough, the manus of both forms is pentadactyl (primitive), while the skull has become highly specialized.

At present the writer suggests that certain genera of the Merycoidodontidæ had a parallel development on the West Coast proceeding along the lines of the more eastern genera. In the western area *Eporeodon* is certainly present and back of that, in all probability, *Merycoidodon*, although not positively known. From the western *Eporeodon* I should derive *Promerycocharus* in one line and *Paroreodon*, leading into *Ticholeptus*, in another, while *Oreodontoides* represents the *Merychys* stock and *Cyclopidius* itself, both from sources unknown but probably similar to those in the Great Plains. These are all contemporaneous with their eastern representatives. If we do not assume this major diphyletic development from some common Eocene ancestor, then we must presume that there were several waves of migration during respective geologic times. The former hypothesis is possibly the more logical.

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