56.9(1181:78.7)

Article V.— ON THE SKULL OF *APTERNODUS* AND THE SKELETON OF A NEW ARTIODACTYL.

By W. D. Matthew.

Plate VI.

The specimens here described are from a collection made by Mr. W. H. Reed for the University of Wyoming. I am indebted for the opportunity of describing them to the courtesy of Mr. Reed and the good offices of Prof. S. W. Williston. I take pleasure in expressing my cordial thanks to these gentlemen for the privilege.

The locality is in the neighborhood of Bates's Hole, north of the Laramie Plains. Mr. Reed discovered here a very considerable deposit which he has been successfully prospecting for two or more seasons. The fauna is Lower Oligocene, Titanotherium beds, and includes several skeletons and finely preserved skulls of Titanotheres. Among the smaller mammals submitted to me for identification are, besides the two here described, *Cynodictis paterculus* and *Cylindrodon fontis*, both originally described from the Pipestone beds of Montana (Lower Oligocene). It appears therefore that Mr. Reed has discovered a Wyoming locality for the micro-fauna of the Lower Oligocene, similar to those found by Douglass in Montana. The specimens are, so far as I have seen, remarkably well preserved, and a careful study of the whole collection would no doubt yield some interesting results.

Two fossils of special interest are, the complete skull and jaws of an insectivore of the rare and primitive Zalambdodont division of the order, hitherto almost unknown as fossils; and a skeleton of an undescribed genus of Artiodactyla.

Skull of Apternodus.

The insectivore skull and jaws are referable to *Apternodus mediævus*, described by Matthew in 1903 from several fragments of lower jaws from the Lower Oligocene of Montana. The genus was placed in the Zalambdodont division of the Insectivora.

The skull and jaws discovered by Mr. Reed are of remarkable interest. Fossil insectivora of this group are almost unknown, and the living forms are exceedingly rare. The Centetidæ of Madagascar, *Potamogale* of West Africa, *Solenodon* of the West Indies and the Golden Moles of South Africa are the modern types. *Xenotherium* of the North American Oligocene and

Necrolestes of the South American Miocene are the only extinct Zalambdodonts of which the skull is known, and there are six or eight described genera based upon jaws or parts of jaws from the Oligocene and Upper Jurassic of North America. The especial interest of the group is in its extremely primitive skull characters and in the peculiar type of teeth, which according to the Tritubercular theory represent the earliest stage in the development of the mammalian molar.

This specimen is the third and thus far the best preserved Zalambdodont Insectivore from the North American Tertiary.

The generic characters are as follows:

Dentition $I\frac{2}{2}\, C\frac{1}{1}\, P\frac{3}{3}\, M\frac{3}{3}$. Median incisors somewhat enlarged, with oval roots (crowns not preserved); lateral incisors round-cusped with minute heel. Canines two-rooted, crown a stout, recurved cusp with no heel. $P\frac{2}{2}$ small, one-rooted. P^{3-4} three-rooted, triangular, with large high central cusp, and basal cingulum rising into sharp basal cusps at the angles. Upper molars of essentially similar constitution but more extended transversely. The outer marginal cusps are higher than the inner one, and form with the central cusp a trigon which wears against the trigonids of the lower teeth. P_3 is two-rooted, with basal cingulum surrounding a high sharp-conical cusp. In P_4 a high trigonid is formed by the addition of anterior and posterior cusps to the inner side of the high angular principal cusp, and there is a minute heel at its posterior base. M_{1-3} are similarly constructed, the heel becoming successively larger, but even in m_3 it is very small relatively to the trigonid and far below its level.

Skull. The skull has about the size and proportions of *Ericulus.* The basicranial and basifacial axes are parallel. The face is rather short, the postorbital region long and cylindrical, the occipital region broad and short. Orbits imperfectly defined, lachrymal foramen large, marginal, postorbital process of frontal rudimentary, zygomatic arches absent. Sagittal crest prominent, occiput broad and low with moderately strong crest above. The most remarkable feature of the skull is the extraordinary development of the lateral exposure of the mastoid, which with the adjoining parts of the exoccipital and squamosal bones forms a large lateral plane surface of rectangular form continuous with the outer end of the post-glenoid process, and bounded by four prominent heavy crests which project in a vertical plane. The upper crest projects nearly as high as the base of the sagittal crest, the lower crest is considerably below the level of the condyle, the posterior crest projects a little farther back than the occipital condyle, the anterior crest continues upward from the glenoid. The occipital crests end at the posterior upper corner of this plate. The superior and posterior margins of the plate are evidently a development of the lambdoidal crests, and the anterior border is

the remains of the zygomatic process of the squamosal. The inferior crest is evidently composed of the united paroccipital, mastoid and posttympanic processes. I can find no analogue for this extraordinary development.

The occiput is broad, low, concave, bounded by the occipital and posterior lambdoidal crests, consequently composed of the occipital bones only. The foramen magnum is wide but not high, the condyles narrow and wide apart. The basioccipital region is broad and rather short, the petrosal prominences project a little beyond the level of the basioccipital, and between them and the postglenoid process lies a large deep pit, while externally and posteriorly they lie against the base of the mastoid-paroccipital crest. The condylar and jugular foramina are distinct and well separated. The postglenoid process is very broad and heavy, without postglenoid foramen. The glenoid articulation is wide and deep. The pterygoid plates are not very prominent. The palate is of the usual Insectivore type; it is not extended behind the molars and is bounded posteriorly by a rather strong ridge.

The lower jaw has already been described by Matthew (1903). It is short and deep with wide heavy condyle, coronoid process of moderate height, angle prominent and considerably incurved, masseteric fossa deep. The posterior mental foramen lies beneath the anterior part of p_3.

The resemblance to *Ericulus* in the dentition is sufficiently marked — but in none of the Centetidæ do I find any near approximation to the extraordinary characters of the mastoid region of the skull. Setting aside this single specialization the genus may be satisfactorily associated with the Centetidæ, and until additional distinctions in skeleton structure are known, it seems best to regard this specialization as of not more than subfamily value. I place *Apternodus* therefore in a subfamily APTERNODONTINÆ of Centetidæ, distinguished from Ericulinæ by the peculiar development of the mastoid region.

The close resemblance in the construction of the molar-premolar series makes it very probable, that their structural evolution has been uniform. If this be true the following will result as to the molars in Zalambdodonta.

1. The high median cusp is the original cusp, corresponding to the protocone of the premolars.

2. The development of the two outer cusps of the upper, and of the two inner cusps of the lower trigon, proceeds pari-passu.

3. The development of the inner heel of the upper, and the posterior heel of the lower molars is correlated.

4. The method of complication of the premolars is not analogous to that of the ordinary trituberculata. If the premolar analogy argument has any force the same is true of the molars.

5. The order of cusp development indicated is substantially that advocated by Cope and Osborn in their tritubercular theory.

6. Fairly typical Zalambdodont teeth occur in the Jurassic, along with teeth of the normal tritubercular pattern, and at least one other distinct type. There is no reason to believe that these different types are stages in the development of the normal mammalian molar, nor that one is derivable from the other. On the contrary they appear to be independently evolved from the primary reptilian cone, and it is probable that a great number of parallel evolutions took place, some of which have survived, while others have not.

If these conclusions be correct, neither Osborn's derivation of the tritubercular molar from the zalambdodont, nor Gidley's derivation of the zalambdodont from the tritubercular are warranted; the identifications of cusps by Osborn in the tritubercular, and by Gidley in the zalambdodont molar are not warranted, and if the premolar-analogy argument be admitted, are incorrect. Osborn's view is correct for the zalambdodont molar, while for the normal tiitubercular type the evidence adduced by Scott, Woodward, Wortman, and Gidley points to another method of complication.

According to Leche's view, the molars of the Talpidæ and Soricidæ are derivable from the zalambdodont type, while those of Erinaceidæ and other Dilambdodont families are derived from the normal tritubercular type exemplified in the Leptictidæ. This view is not supported by what is known of primitive Talpidæ and Soricidæ, as these show a molar construction much more like that of Leptictidæ and with little if any approach to the zalambdodont molar. Their premolars also show the normal method of complication.

Eotylopus reedi gen. et sp. nov.

Type, a skull, jaws and skeleton from the Lower Oligocene of Wyoming in the Museum of Wyoming University. The specific name is in honor of the discoverer, W. H. Reed, curator of the University museum. Mr. Reed's contributions to science as discoverer of the great fossil fields of the Laramie Plains with their wonderful dinosaur fauna described by the late Professor Marsh, are well known to palæontologists.

Generic characters: Dentition unreduced, teeth continuous without diastemata. Canines slightly larger than adjoining teeth. Anterior premolars simple, compressed, p^3 with inner cusp, p^4 with inner crescent, moderately wide transversely. Molars brachyodont, rather wide transversely, the outer crescents with prominent external ribs and mesostyle, weak para- and metastyles, the anterior inner crescent bifid posteriorly, one crest extending posteriorly, the other externally from the top of the crescent.

Skull of moderate length, no lachrymal vacuity nor fossa, orbits nearly closed behind, bulla of camelid type, folded upon itself and filled with cancellous tissue as in *Poëbrotherium*.

Ulna and radius coössified and distinctly of camelid type, with no channel between the two shafts. Fibula reduced to a distal nodule and presumably a proximal vestigial splint.

Podial bones separate. Toes 4–2, median pair of metacarpals and metatarsals separate, moderately long, not appressed, lateral metacarpals slender, complete, lateral metatarsals reduced to nodules.

Specific characters. In the absence of more than one species the specific characters are included in the general description that follows.

The generic characters as cited place Eotylopus in my opinion as a very primitive and somewhat aberrant ancestral type of the Camelidæ. The molars and premolars are much more like certain Hypertragulidæ, especially *Heteromeryx*, and the peculiar bifid protoselene is paralleled in certain of the Giraffi-

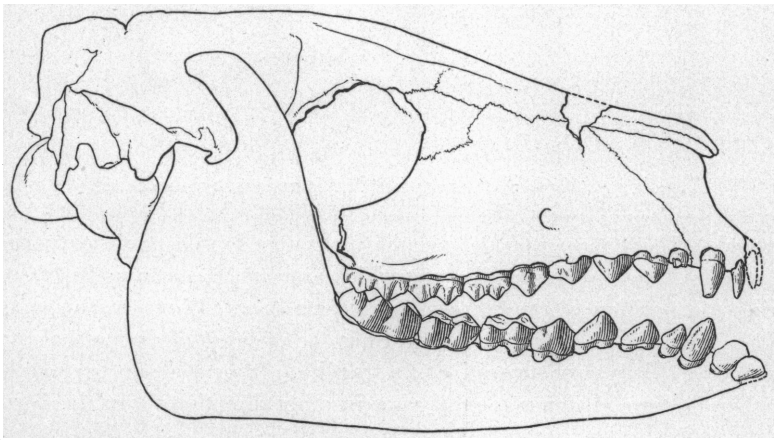

Fig. 1. *Eotylopus reedi*, skull and jaws. Type specimen, two-thirds natural size. Lower Oligocene, Wyoming.

dæ and Bovidæ. The anterior teeth are of rather indifferent type, but the nearest likeness is to *Poëbrotherium eximium*. The peculiar type of bulla is however very strong evidence of camelid relationship, and compares closely with that of *Poëbrotherium*. The absence of lachrymal vacuity and the general form and proportions of the skull support the relationship to *Poëbrotherium*. The consolidation of ulna and radius is likewise of the peculiar camelid pattern, quite different from the consolidation in *Heteromeryx*, *Hypertragulus* or any of the Pecora.

Dentition: The upper incisors are three in number, pointed sub-spatulate, increasing in size from first to third. The upper canine is not complete, but was larger than i^3 and, like it, had a pointed crown. The upper premolars are all two-rooted, the first larger than the second, both with compressed elongate crown and no cingulum, while the third has a strong inner basal

cingulum rising to an irregular double cusp or series of cuspules a little behind the middle of the tooth.

The fourth premolar has the inner crescent complete. It is considerably wider transversely than long anteroposteriorly, and within the posterior wing of the inner crescent lies an accessory cuspule of irregular form.

The molars are quadrate, somewhat broader than long, and very low-

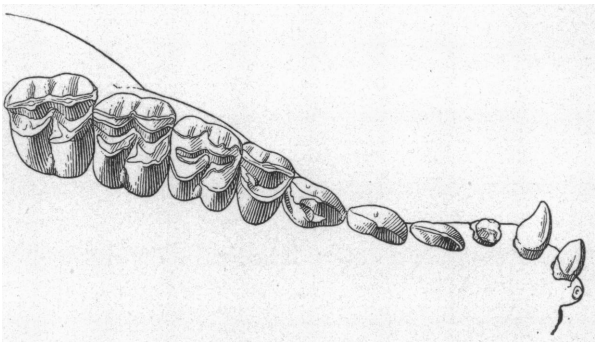

Fig. 2. *Eotylopus reedi*, upper teeth. Natural size, type specimen.

crowned. Their most marked peculiarity is the double posterior wing of the anterior inner crescent; the crest which appears to continue the crescent having the position of the corresponding part in an *Anoplotherium* molar, while a somewhat less prominent crest has the position of the normal ruminant molar. It is very suggestive of a transition from one type to the other, but there is little evidence for this view in other directions. In the Giraffe

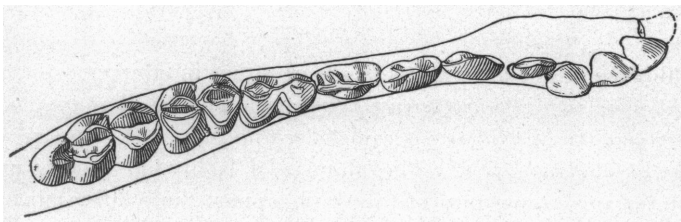

Fig. 3. *Eotylopus reedi*, lower teeth. Natural size, type specimen.

the abnormal wing appears as a weak crest, the normal wing being the principal crest; *Eotylopus* reverses this condition. The size of the molars increases slightly from first to third.

The lower incisors have flattened spatulate crowns, somewhat larger than the corresponding upper teeth. The lower canine is somewhat larger than i_3, with pointed spatulate crown, the first premolar is one-rooted and

relatively small, the others are two-rooted and all have compressed low pointed crowns with posterior internal crests on p_3 and p_4.

Feet: The camelid affinities already observed are strengthened by the characters of the fore and hind feet. These are intermediate between *Protylopus* and *Poëbrotherium*. They have the proportions of the former genus, entirely lacking the long, slender, appressed metapodials of the latter. But they show certain distinctively tylopod features in comparison with corresponding parts of the propecoran and protraguline members of the Hypertragulidæ. In the fore-foot, the lateral digits are complete although slender, the median pair are but slightly appressed. The magnum and trapezoid are separate, the trapezium is not preserved but its presence is indicated by a facet on the trapezoid. The distal keels of the metapodials are confined to the palmar surface; the dorsal surface of the distal facet is slightly convex laterally, less so than in *Protylopus*, more than in *Poëbrotherium*.

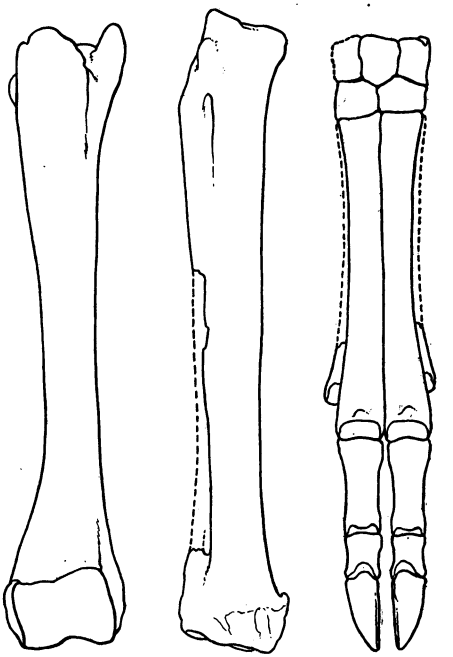

Fig. 4 *Eotylopus reedi*, fore limb. Type, two-thirds natural size.

In the hind foot the lateral digits are reduced to nodular rudiments as in *Poëbrotherium* but larger; the median pair are much shorter and less appressed than in *Poëbrotherium*, more as in *Protylopus*. The median channel characteristic of the Pecora is not indicated here; on the other hand the heads of the metatarsals show the strong plantar processes characteristic of *Poëbrotherium*. The navicular and cuboid are separate, the astragalus is more oblique than in any later Camelidæ, but less so than in Oreodonts. The calcanear fibular facet has the characteristic camelid form, differing from that of Oreodonts in its greater convexity from front to back, from Pecora in its less convexity from side to side. The phalanges are short, intermediate in type between those of *Protylopus* and *Poëbrotherium*, narrower than those of Oreodonts, broader than those of *Leptomeryx*, *Protoceras* and the Pecora.

Eotylopus is evidently a very primitive ancestor of the Camelidæ, aberrant in certain features of the dentition, in other respects intermediate between *Protylopus* and *Poëbrotherium*, but much nearer the former. It is probable that the jaw fragments and teeth which I referred in 1903 to *Leptotragulus* (*L. profectus* Matthew) from the Lower Oligocene of Montana, belong to this genus, although they do not agree well enough for specific identity.

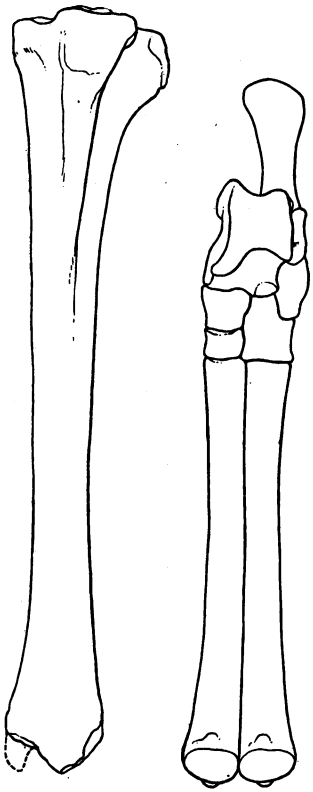

Fig. 5. *Eotylopus reedi*, hind limb. Type, two-thirds natural size.

The neck, judging from Mr. Reed's photograph of the skeleton as mounted in the Wyoming University Museum, was quite short, and this might also be inferred from the shortness of the limbs and feet, and of the head. The proportions of the known parts of the skeleton in *Protylopus* clearly indicate that this genus also had a short neck.

It differs from *Leptotragulus* in the lack of diastema in the lower jaw, from *Protylopus* and others of the better known Uinta genera in the peculiar construction of the upper molars and various other features; but its nearest relationship in skeleton structure is undoubtedly with *Protylopus*. It certainly cannot be regarded as an intermediate stage in the evolution of *Protylopus* into *Poëbrotherium*; on the contrary it throws a great deal of doubt on this alleged direct line of descent, for the following reasons:

1. *Eotylopus* is very much closer to *Protylopus* than to *Poëbrotherium* and might much more readily be derived from it. This is apparent in its brachyodont teeth, construction of molars and of premolars, proportions of skull, length of limbs, length and character of metapodials, etc.

2. *Poëbrotherium* cannot be derived from *Eotylopus* but occurs with it in the Lower Oligocene although much more abundant in the Middle Oligocene. It appears much more probable therefore that *Protylopus* led up into *Eotylopus* than into *Poëbrotherium*.

3. Analysis of the Lower Oligocene fauna shows it to be composed of a few types closely allied to Eocene genera, associated with a much larger

number of more advanced types closely allied to the Middle Oligocene fauna, usually congeneric. *Poëbrotherium* belongs to the latter group.

This is true of most of the phyla which have been supposed to run through from the Eocene into the Oligocene. We may perhaps regard the more primitive types as autochthonic; the others are more probably immigrants from the north and in the Oreodon fauna they had almost wholly displaced the older forms. *Poëbrotherium* is probably derived, not from *Protylopus* of the Uinta, but from some more advanced contemporary genus of more northern habitat.

If, however, we confine ourselves to the broader relations of *Eotylopus*, without making any unprovable assertions as to its direct genetic relations to other known genera and species, but regarding it as one of the successively closer approximations towards the modern Camelidæ which characterize the successive faunal zones of the Tertiary, we find in it a new and interesting stage in the Camelid phylum. While it makes any direct descent of *Poëbrotherium* from *Protylopus* less probable, yet it serves to confirm the position of the latter as an ancestral Camelid. Its close relations to the Eocene genus are obvious, and its position in the Camelid phylum appears to be beyond question. Its family position will depend upon the criteria of classification that we adopt. If we adopt the "linear" system and ignore the more important and obvious structural differences between animals, on the plea that they are merely stages in specialization, if we scatter apart a closely related group of ancestral forms among the widely divergent types to which they have given rise, we involve ourselves in a very doubtful and changeable arrangement, dependent upon hypotheses of relationship instead of facts of structural affinity. The groups will be definable only by certain minor features of structure which have escaped alteration and we wholly lose sight of the near relationship of the ancestral stages of various divergent groups. It is to my mind neither necessary nor wise to attempt this method of classification, and its failure is very well shown in the shifting and uncertain position of so large a part of our early Tertiary faunæ. It is not that opinions have really changed very much, but that a vicious method of classification has made a slight change in relationship responsible for a very wide change in classification.

The genus is by definition a member of the Hypertragulidæ, having four digits with separate metapodials in the fore foot, and but two functional digits in the hind foot, the metapodial keels confined to the palmar surfaces, the dentition primitive, brachyodont and unreduced. The family as thus defined is ancestral to the higher ruminants, and if subdivided into three groups ancestral respectively to the Pecora, Tragulina and Tylopoda we would have the following arrangement:

Leptomerycinæ.

Leptomeryx with affinities to Cervidæ.

Heteromeryx, *Protoceras*, ? *Syndyoceras* } ? giraffine and ?? bovine affinities.

Hypertragulinæ.

Hypertragulus affinities to Tragulidæ.

Leptotragulinæ.

Leptotragulus, *Eotylopus*, *Protylopus* } affinities to Camelidæ.

? *Hypisodus* — affinities to Stenomylinæ.