

# Article XVI.—A REVISION OF THE LOWER EOCENE WASATCH AND WIND RIVER FAUNAS

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## PART V.—INSECTIVORA (CONTINUED), GLIRES, EDENTATA

BY W. D. MATTHEW

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### INSECTIVORA (CONTINUED)

#### AFFINITIES OF EOCENE GROUPS REFERRED TO THE INSECTIVORA

In a preceding section<sup>1</sup> of this revision were reviewed the true primates of the Lower Eocene, genera whose reference to the order appeared either conclusively shown or open to no objections, and also three families which, although referred provisionally to the Insectivora, may also be primates and have been so considered by some authorities. They have been so regarded

<sup>1</sup> 1915. Bull. Amer. Mus. Nat. Hist., XXXIV, pp. 429–483.

tentatively by my colleague Dr. Gregory. Since the publication of that section there has appeared the primate section of Stehlin's great monograph of the Eocene Mammalia of Switzerland<sup>1</sup> — in its scope an authoritative revision of the primates of the Eocene of Europe. Here for the first time an American student can obtain an adequate concept of the Eocene primate fauna of Europe, including, besides full and critical descriptions and admirable illustrations of the described fauna, a great number and variety of new forms. Stehlin points out (*loc. cit.*, p. 1507) that the group of American genera described under the family Apatemyidae are related to the European Plesiadapidae, and I believe that there can be no question that they should be included under this family. He regards the Mixodectidae and Microsyopidae (p. 1503) as more distantly related and of more doubtful affinities. But he is disposed to regard all three families as primates, although careful to disclaim any positive reference of the American genera until they are more completely known.

Stehlin's main reason for this reference is the indubitable fact that the cheek teeth in all these genera are very different from those of any modern Insectivora and much more like those of Eocene lemuroids in their construction. That this summary is far from doing justice to his able and well considered discussion of the evidence I am well aware, but I think it represents fairly the salient point of his argument and I state it in order to indicate why it does not appear to me convincing. Stehlin does not at all overstate the resemblance. It is very close, especially in certain genera, e. g. *Trogolemur*. We have, in fact, found much difficulty in distinguishing fragmentary jaws of *Trogolemur* from those of *Tetonius*, an unquestioned primate. But this is mainly because the Eocene lemuroids and the three groups under discussion have retained the primitive pattern of molar and premolar teeth without much change. There is a very near resemblance in the teeth among the older Eocene and Paleocene mammals of several different orders and, in consequence, there is hardly one of these primitive genera that has not been referred to two or three different orders so long as it was known solely by the cheek teeth. One would hardly suspect the artiodactyl affinities of *Diacodexis* ("*Trigonolestes*," "*Pantolestes*") from its teeth.<sup>2</sup> They are much like those of Eocene primates, and they are quite

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<sup>1</sup> Stehlin, H. G., 1916. Die Säugethiere des schweizerischen Eocäns. Critischer Catalog der Materialien. 7<sup>er</sup> Teil, zweite Hälfte. Abh. schweiz. paläont. Ges., XLI, pp. 1299-1552, Pls. XXI-XXII and 82 fig. in text. August, 1916. This second half of section seven deals with the primates excepting *Adapis*, which was already considered in the first half of the section.

<sup>2</sup> Winge, 1906, Jordfundne og nulevende Hovdyr (Ungulata), E Museo Lundii, III, 1, p. 216, does not admit that "*Pantolestes*" is an artiodactyl. He points out that the teeth do not conform to his theories of cusp evolution and concludes that the artiodactyl characters of the feet are due to parallelism and afford no proof of relationship.

unlike those of any modern Artiodactyla. The same may be said of *Miocænus* and *Hyopsodus*, whose affinities with the Condylarthra are indicated by skull and skeleton; of *Tricentes* and other genera of Oxyclænidae, which have been called lemuroid primates but appear to be primitive creodonts; of *Pantolestes*, whose skull and skeleton indicate affinities to the Insectivora although there is little or nothing in the teeth to suggest it; and of various other genera whose true affinities are still provisional. The difficulty is not that these orders were not well separated in the Eocene, but that many of their members retained the primitive dental type with but little change.

All modern Insectivora have departed widely from this type in different lines of specialization, yet with a certain parallelism due to similar adaptive requirements. There is indeed a certain insectivorous type of cheek teeth; but a moment's consideration will show that it is shared by the Insectivora with other insectivorous mammals—most bats for instance, and some marsupials (setting aside the dental formula). But in the Eocene Insectivora, although some have assumed this type, it is not as well developed, and others do not show it at all. The Paleocene Leptictidae are not far removed from the primitive tritubercular type; the Paleocene zalambdodonts are nearer to it than any modern zalambdodont; the Eocene Pantolestidae have teeth like those of primitive creodonts, not at all of the "insectivore type."<sup>1</sup> Even the imperfectly known types which are provisionally referred to Tupaiidae, Talpidae and Leptictidae have teeth much nearer to the primitive tritubercular type than their supposed modern relatives, while *Apheliscus* and other questionable forms are all primitive in cheek teeth.

It is true, however, that the three families under discussion have certain specialized characters found in certain lemuroid primates. A tendency to develop a pair of front teeth either as pincers or gnawing teeth, together with a short deep jaw, progressive reduction of the premolars, etc., is seen in them as also in *Chiromys*, in *Tetonius*, and to a minor degree in *Omomys*, *Hemiacodon* and *Necrolemur*. But this is a very common type of specialization, the "diprotodonty" of Osborn, and is more or less characteristic of most modern insectivores, assumed at an early date by all rodents, evolved in the tæniodonts, tillodonts, diprotodont and pseudo-diprotodont marsupials. Early stages of it are seen in other primates besides *Chiromys*, but it is not as characteristic of the order as it is of the Insectivora. The shortening and depth of the jaw, the progressive reduction of the remaining front teeth and of the premolars, the tendency to convert the condyle from

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<sup>1</sup> The characters of the skeleton, especially of the limb and foot-bones, are the principal evidence for referring the Leptictidae and Pantolestidae to the Insectivora.

the transverse to the orthal type and the molars into crushing and grinding teeth are associated characters shown in varying degree in all diprotodont specializations and therefore not to be regarded as independent evidence of affinity. I am disposed to believe that the posterior position of the mental foramen is in some instances likewise an associated character of this specialization, although not so uniformly coordinated with the degree of diprotodonty exhibited. (It is very marked in the Pantolestidæ, which do not show any notable diprotodonty; among the soricoids it is most marked in the primitive-toothed genera *Talpa* and *Myogale*, etc.)

In sum, my viewpoint is as follows.

The Plesiadapidæ, Mixodectidæ, and Microsyopidæ are three groups, all of which are characterized by diprotodont specializations of the front teeth and have primitive molars. They do not appear to be especially closely related to each other, nor does the supposed relationship of the first group to *Chiromys* appear to me to rest on any resemblances that may not quite as reasonably be ascribed to parallelism. On the other hand they suggest one or another insectivore group in the front teeth, but the evidence for any real affinity is equally unconvincing. Against any especial affinity with *Chiromys* lies the anatomical evidence of skull, brain, and skeleton characters of the latter, which point to a near affinity to the Indrididæ in spite of its extreme diprotodonty, and indicate that its divergence from the other Malagasy lemurs is not of very ancient date, not at all probably farther back than the Eocene. It would seem therefore that *Chiromys* must be a parallel but much later specialization from the lemuroid stock than these Eocene "chiromyoids" even if they are lemuroids. Against the insectivore affinities lies the fact that the molars in all three groups are somewhat nearer in construction to certain Eocene genera which are demonstrably primates than they are to any Eocene genera which are demonstrably Insectivora. In each family there are certain inconclusive but independent points of evidence in favor of insectivore affinity. The strongest is in *Mixodectes*, which has an astragalus distinctly of insectivore, and not of primate, type. *Microsyops* has a two-rooted canine, a character of some Insectivora, unknown among primates. *Plesiadapis* has an enlarged upper incisor, curiously suggestive of the soricoids in its construction. But none of this evidence has much weight, save the astragalus, and the Mixodectidæ is the only family that I am disposed to refer to the Insectivora with any degree of confidence. The others are retained there merely on the ground that it is better to place primitive groups of doubtful affinities in a generalized and broadly inclusive order, such as I consider the Insectivora to be, rather than in a more compact specialized order such as the primates.

We have recently secured considerable skeleton material of *Nothodectes*

which adds largely to the evidence for its affinities. A preliminary comparison shows that it is more or less on the border-line between undoubted primates and undoubted Insectivora. It has many suggestions of primate affinity, yet it is certainly not a specialized lemuroid. Until the material is completely prepared and thoroughly studied, it seems better to defer an opinion as to its exact position.

#### SUPPLEMENTARY OBSERVATIONS UPON THE PLESIADAPIDÆ (APATEMYIDÆ)

##### **Plesiadapidæ** Trouessart, 1897

Synonym: APATEMYIDÆ Matthew, 1909

Dr. Stehlin, in his work upon the Eocene primates, gives carefully finished enlarged figures of upper and lower teeth of *Plesiadapis*. These admirable illustrations show that the teeth approach so nearly in construction to those of our Apatomyidæ that no family distinction can at present be maintained. The additional material of *Nothodectes* and of *Phenacolemur* obtained in 1916 confirms this relationship.

##### **PHENACOLEMUR** MATTHEW, 1915

Additional specimens of the upper teeth of this genus show the premolars to be two, the fourth being submolariform. The construction of the upper teeth is fundamentally like that in *Nothodectes*, but more progressive. The molars are quadrate, owing to expansion of the postero-internal shelf; the fourth premolar is subquadrate, with a large postero-internal shelf; the metacone (trittocone) is not so widely separated from the paracone ("protocone") as in the molars and is noticeably smaller. The third premolar has no internal shelf or cusp; the main cusp is high, robust, simple, recurved, with small posterior heel, and corresponds very closely to the lower premolar ( $p_4$ ).

Four specimens were found in the Lower Gray Bull beds on South Elk Creek by Wm. Stein. All belong to the smaller species, *P. citatus*.

An isolated upper incisor from the same locality and horizon as the above specimens is provisionally referred to *P. citatus*. It is much like the large upper incisor of *Nothodectes* (*infra*).

##### **NOTHODECTES** MATTHEW, 1915

Additional and more complete specimens of this genus were obtained by Mr. Granger in southern Colorado during the season of 1916. The horizon is the Tiffany beds near Ignacio on the northern boundary of the San Juan

basin, equivalent or nearly so to the Clark Fork beds in the Bighorn basin of Wyoming. A number of upper and lower jaws, some fairly complete, the front of a skull showing the upper molars and premolars, and various skeleton bones have been extracted from the matrix. Preliminary description of the dentition appears in a preceding article in this Bulletin.

The dental formula is  $\frac{2.1.3.3}{1.0.2-3.3}$ , assuming that the enlarged lower teeth are incisors.

The molar pattern of *Phenacolemur* and *Nothodectes* differs notably from that of *Pelycodus* and its allies in the relations to the protocone of the postero-internal crest or cusp. The "hypocone" is not evolved as a cusp budded off from the protocone, as in the Notharctidæ, nor does it originate from a wholly independent basal cingulum, as Stehlin states is the origin of this cusp in the Adapidæ and as it appears to be in the Tarsiidæ and *Microsyops*. The postero-internal cingulum in *Phenacolemur* and *Nothodectes* makes a broad sweeping curve and joins the tip of the protocone somewhat on its inner face, but the hypocone is apparently developed from the heavy middle portion of the cingulum and is clearly not budded off from the tip of the protocone. *Plesiadapis*, judging from Stehlin's figure, presents conditions intermediate between this and *Pelycodus*.

It appears to the writer that the origin of the hypocone in these various tritubercular types presents a great number of variations. Stehlin has pointed out the distinct origin, in some groups by budding from the protocone, in others arising from the cingulum, and has insisted upon its importance in judging of the affinities of the groups. It would appear at first that these two methods of forming a postero-internal cusp were fundamentally distinct, as indeed Stehlin regards them, and that all "hypocones" must belong to the one type or the other. But the present genus, considered along with *Plesiadapis*, shows conditions that may be regarded as intermediate. In *Plesiadapis* the hypocone is obviously, as Stehlin shows, nearer to the budded type of Notharctidæ, the rudimentary cusp appearing on the line of the peculiarly placed crest that rises to the crest of the protocone, while the true postero-internal cingulum sweeps around the inner and hinder base of the tooth. In *Nothodectes* the crest above mentioned supplies functionally the place of the basal cingulum which is absent, or else may be regarded as itself the true basal cingulum rising internally to the tip of the protocone instead of sweeping around its base. It would not be difficult to cite a series of intermediate stages among tritubercular teeth to support either one of the above interpretations.

**Leptictidæ** Gill, 1872

The position of the typical group of this family is unquestionably in the Insectivora, with affinities nearest to the Erinaceidæ. *Ictops*, *Leptictis*, *Mesodectes*, *Diacodon*, and *Parictops* pertain to this group, the first three Oligocene, the last two Lower Eocene. It is not known from the Bridger or Uinta. I have provisionally referred to the family a number of genera of uncertain relations. *Didelphodus*, *Phenacops*, and other genera are of very doubtful affinities but can not easily be placed in any other family. They may prove to be creodonts; the skeleton is unknown.

## Key to Genera of Leptictidæ

- I. *Leptictinæ*: Upper molars with *pa* and *me* external, hypocone strong;  $p_4^4$  molariform; lower molars with vestigial  $pa^d$  or none;  $p_1$  one-rooted.
- A. Two upper incisors; no sagittal crest but paired lateral crests.
1.  $P^3$  with internal, anteroexternal, and posteroexternal cusps. . . . . *Ictops*
  2.  $P^3$  with internal and posteroexternal cusps. . . . . *Mesodectes*
  3.  $P^3$  simple, high, compressed. . . . . *Leptictis*
- B. Three upper incisors; a low sagittal crest but no paired lateral crests.
4.  $P^3$  as in *Ictops*; anterior lower premolars simple. Canines small.  
*Diacodon*
  5. Canine larger; incisors minute. . . . . (subgenus) *Palæolestes*
  6. Anterior lower premolars broad-bladed with accessory cusps. Canines small. . . . . *Parictops*
- II. *Didelphodontinæ*: Upper molars with *pa* and *me* submedian, broad external shelf, hypocone rudimentary;  $p_4^4$  simple or submolariform; lower molars with strong paraconid.
- A. Canines moderately large; incisors small;  $p_1$  two-rooted;  $p_4$  with accessory cusps.
7. Three upper premolars. . . . . *Didelphodus*
- B. Canines large; incisors small;  $p_1$  one-rooted;  $p_4$  unknown.
8. Premolars short, high, crowded. . . . . *Phenacops*

**DIACODON** COPE, 1875

*Type*.— *D. alticuspis* Cope from the Wasatch of New Mexico.

*Synonym*.— *Palæictops* Matthew, 1899, type *Ictops bicuspsis* Cope.

*Generic characters*.— Dentition,  $\begin{smallmatrix} 3.1.4.3 \\ 2.1.4.3 \end{smallmatrix}$ .  $P^4$  molariform with strong parastyle;  $p^3$  with strong metacone and protocone;  $p^2$  with small metacone. Upper molars and  $p^4$  with well separated, externally placed paracone and metacone; strong hypocone; compressed crescentic protocone.  $P_4$  with large paraconid, otherwise like the molars. Lower molars with high, well

separated, angulate protoconid and metaconid of equal height, heel basined, entoconid smaller than hypoconid, paraconid vestigial; hypoconulid minute except upon  $m_3$ .  $P_3$  with posterior accessory cusp and small heel;  $p_2$  with minute heel,  $p_1$  one-rooted, simple. Canines rather small, the upper oval, of moderate length, one-rooted. Skull with low sagittal crest but no lateral crests.

*Diacodon alticuspis* certainly belongs to the Leptictidæ, to which Cope referred it in 1885, and is apparently congeneric with *Palæictops*, although based upon a species distinct from *P. (Ictops) bicuspis* of the Wind River. The second species referred by Cope to the genus, *D. celatus*, is of quite different affinities and is provisionally referred to *Nyctitherium*. The generic characters stated above are drawn from *D. bicuspis* and from the referred specimen of *D. alticuspis*.

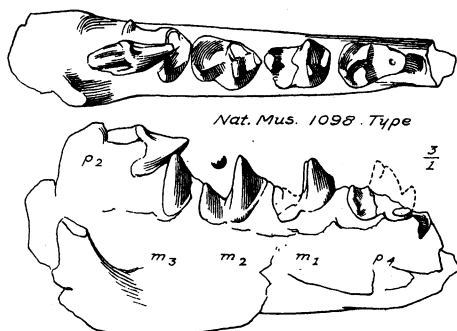


Fig. 1. *Diacodon alticuspis*. Type, U. S. National Museum, from the New Mexican Wasatch. The specimen consists of a part of the right ramus of the lower jaw with  $p_4$ - $m_3$ ; more or less damaged and  $p_2$  displaced. External and superior views, three times natural size.

### *Diacodon alticuspis* Cope

Figs. 1 and 2

*Diacodon alticuspis* COPE, 1875, Syst. Cat. Vert. Eoc. New Mex., p. 12; 1877, Ext. Vert. New Mex., p. 132, Pl. XLV, fig. 19; 1885, Tert. Vert., p. 260.

*Type*.—U. S. Nat. Mus. No. 1098, lower jaw with  $p_4$ - $m_3$  and displaced  $p_2$ , most of the teeth badly mutilated and partly buried in matrix. Figure 1.

*Specific characters*.— $M_{1-3}$  = 9.5 mm.;  $m_1$  smaller than  $m_2$ ; depth of jaw beneath  $m_3$  = 4.7 mm.

Only one additional specimen (Fig. 2) in the American Museum collections can be certainly referred to this species. This consists of a part of the

skull and jaws of an insectivore, No. 12831, collected in the Wind River Basin in 1904 for the Amherst Museum and presented in exchange to the American Museum through courtesy of Dr. F. B. Loomis. The upper and lower teeth from  $p\frac{4}{4}$  to  $m\frac{3}{3}$  are fairly well preserved, although they have been somewhat damaged by weathering and hasty preparation. Parts of the preceding premolars are also shown on the specimen, but the jaws are so locked together and buried in a difficult matrix that I have only partly cleared them, but sufficiently to show that they agree in size and characters with *Diacodon alticuspis* so far as comparisons can be made with the damaged

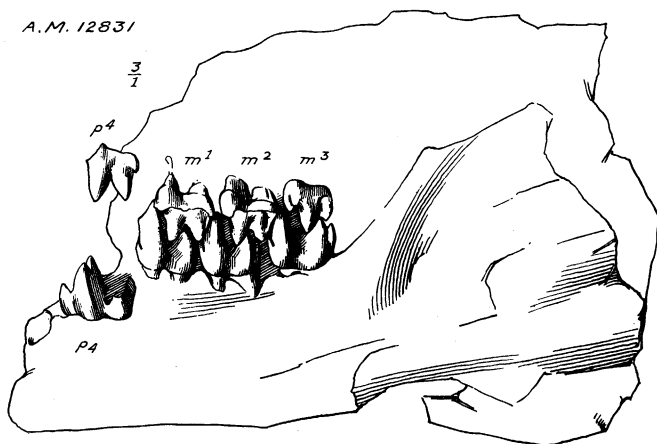


Fig. 2. *Diacodon alticuspis*. Upper and lower jaws from Lysite horizon in Wind River basin, Wyoming; Amer. Mus. No. 12831. Left side view, three times natural size, showing unworn molars and molariform premolar.

lower jaw which is the type of that species. They differ from those of *D. bicuspis* only in the smaller size, less transverse diameter of the upper molars, greater reduction of metacone on  $m^3$  and of heel of  $m_3$ , and other minor characters. The specimen is from the Bridger Creek (Cottonwood Draw) locality in the Wind River Basin, was found by Mr. (Professor) T. C. Brown, and bore the Amherst Museum number 408. It is from the Lysite horizon. The teeth are unworn, the premolars not yet completely erupted from the jaw; the last molar is fully in place. In this genus, as in *Ictops*, therefore, the permanent dentition is very late, replacing the temporary teeth after the skull is fully adult.

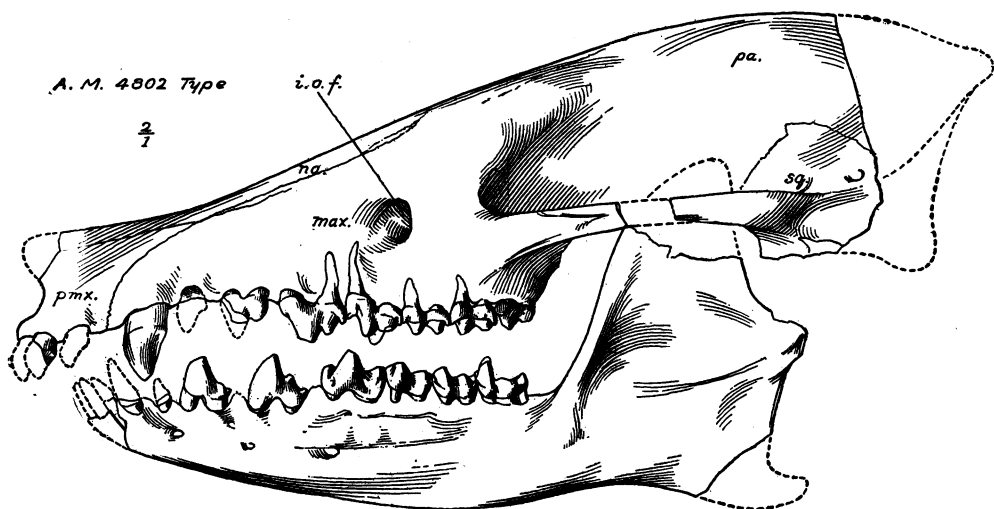


Fig. 3. *Diacodon bicuspis*. Skull and jaws, type specimen, from Lost Cabin horizon in Wind River basin. The original, figured by Cope in *Tertiary Vertebrata*, is considerably crushed, and has been re-set by the artist. Twice natural size. *I. o. f.*, infraorbital foramen; *max.*, maxillary; *na.*, nasal; *pa.*, parietal; *pmx.*, premaxillary; and *sq.*, squamosal bones.

### *Diacodon bicuspis* (Cope)

Figs. 3-5

*Stypolophus bicuspis* COPE, 1880, *Amer. Nat.*, XIV, p. 746; (*Ictops*), 1881, *Bull. U. S. Geol. Survey Terrs.*, VI, p. 192; 1885, *Tert. Vert.*, p. 266, Pl. xxixa, figs. 2 and 3. (*Palæictops*), MATTHEW, 1899, *Bull. Amer. Mus. Nat. Hist.*, XII, p. 31.

*Type*.—*Amer. Mus. No. 4802*; skull and jaws from Lost Cabin beds of Wind River Basin, Wyoming. The original is considerably crushed,

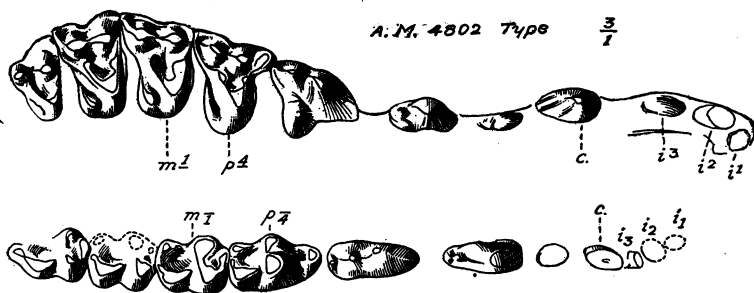


Fig. 4. *Diacodon bicuspis*. Upper and lower teeth. Crown views, three times natural size. From the type skull, Figs. 3-5.

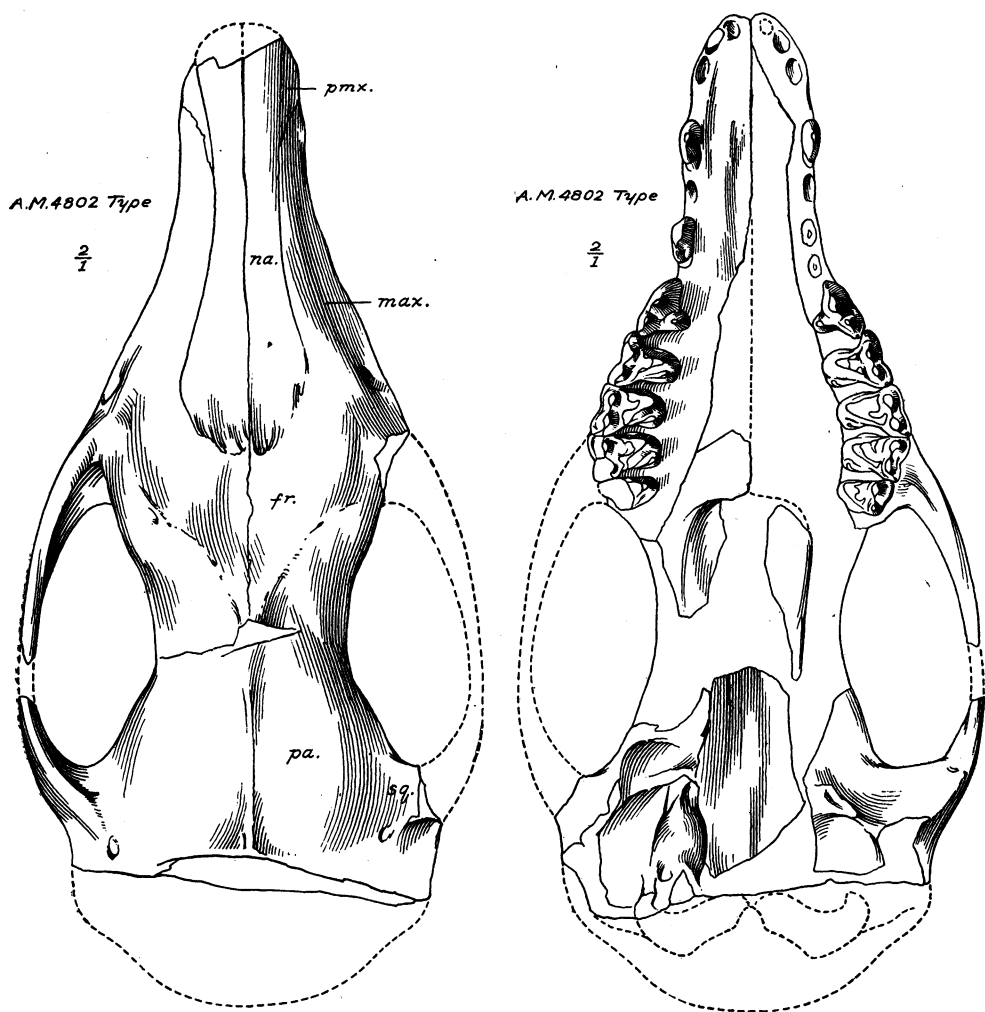


Fig. 5. *Diacodon bicuspis*. Type skull. Top and palatal views, twice natural size. Abbreviations as in Fig. 3.

as is represented in Cope's illustration in 'Tertiary Vertebrata.' In the drawings here published the distortion has been corrected, using skulls of Oligocene Leptictidæ as a guide in reconstruction, with allowance for the very considerable differences in the form and proportions of the cranium.

*Specific characters*.— $M_{1-3} = 9.5$  mm.;  $m_1$  slightly larger than  $m_2$ ; depth of jaw beneath  $m_3 = 6$  mm.

No. 16236, a lower jaw fragment from the Wasatch of New Mexico (? lower beds), and a lower jaw fragment from Willow Creek in the Bighorn Basin (upper Gray Bull level) are referable to this species more nearly than to *D. alticuspis*.

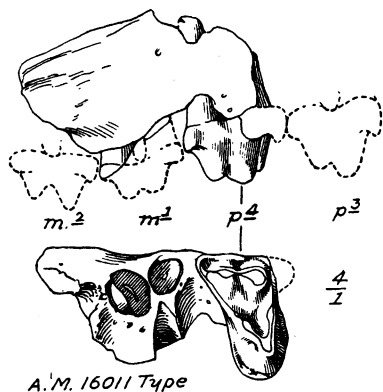
***Diacodon (Palæolestes) puericensis*, new subgenus and species**

Figs. 6-9

*Type*.—Amer. Mus. No. 16011; fragmentary skeleton from Torrejon of New Mexico.

*Paratype*.—Amer. Mus. No. 16748; skeleton from the same locality (not yet prepared).

This species is clearly distinct from any described genus of the Puerco and appears to be a near relative of the Wasatch *Diacodon*. The type specimen (Figs. 6-8) includes the lower jaw and fragments of the upper, but the teeth are all broken off except for  $p^4$ ,  $p_3$  and  $m_3$ , which are preserved although not complete. Most of the humerus, femora, and tibiae, with parts of other limb bones, several foot bones including astragali and calcaneum, parts of pelvis, verte-



A.M. 16011 Type

Fig. 6. *Diacodon (Palæolestes) puericensis*. Upper jaw of type specimen, external and crown views, four times natural size. Upper Paleocene, Torrejon formation, New Mexico.

brae, etc., are present and enable the affinities of the species to be determined. The paratype shows a very perfect upper and lower dentition (Fig. 9).

The teeth agree nearly with those of *Diacodon bicuspis*, except for the large canine and reduced incisors. The upper premolar  $p^4$  is more extended transversely, more compressed anteroposteriorly, the cusps higher and sharper; the metacone, as in *Diacodon* proper, is well separated from the paracone but distinctly smaller. The lower canine root is large, obliquely set, and close to the symphysis; incisors, if present, must have been small and set between the canines as in creodonts, rather than in advance of them as in Insectivora (including *Diacodon bicuspis*).  $P_1$  is small, one-rooted, slightly spaced;  $p_2$  and  $p_3$  are two-rooted, rather short, and high crowned;  $p_4$  is a much longer tooth, considerably longer than any of the molars. The three molars were of nearly equal size;  $m_3$  shows a high but short trigonid,

broken off but evidently with paraconid weak or absent, a long, compressed basined heel, with prominent hypoconulid, hypoconid and two inner marginal cusps. This tooth is quite like that of *Diacodon*, and so are  $p_4-m_2$ . The anterior part of the jaw is somewhat differently proportioned, the premolars shorter, canine larger, and incisors reduced, as compared with *Diacodon* proper. The relationship must, nevertheless, be a very close one, involving a correspondingly close relation in the skeleton of the two genera. As the skeleton of *Diacodon* is unknown, the following description of its Paleocene relative, which will doubtless apply equally to the characters of the Wasatch genus, is given in some detail. The humerus has a small major tuberosity, broad and thick deltoid crest extending nearly half way down the shaft and ending abruptly (but not high and compressed as in *Miacinæ*). The ulna has a long olecranon, sigmoid fossa rather shallow and

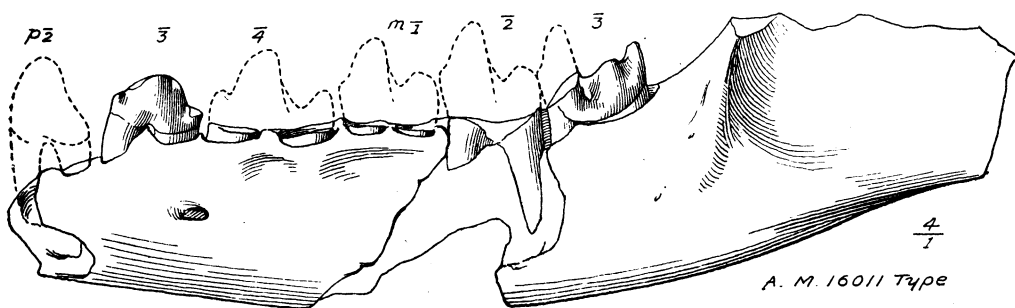


Fig. 7. *Diacodon* (*Palæolestes*) *puercensis*. Lower jaw of type specimen. External view, four times natural size.

very oblique, radial facet flat and indistinctly marked. The femur is very like that of *Ictops*, rather long, the great trochanter expanded posteriorly instead of laterally, trochanteric fossa deep, lesser trochanter posterior, third trochanter an extended marginal rugosity, not prominent. The shaft is of moderate length, the trochlea narrow and elongate, condyles small, not deep. The tibia is as long as the femur or longer, the cnemial crest long, not high, obsolete except at a point about two-fifths down the shaft. The upper part of the shaft is considerably bowed, the lower part straight. The fibula is united to the tibia only at the distal end, the shaft being wholly free, whereas in *Ictops* it is united nearly half-way up. The fibula is broken off and lost from both tibiae; the internal malleolus is not very heavy; the astragalar trochlear grooves are deep and little oblique. The astragalus has a broad trochlea with prominent equal crests and no astragalar foramen, agreeing with *Ictops* and *Insectivora* generally; the head is broken off but

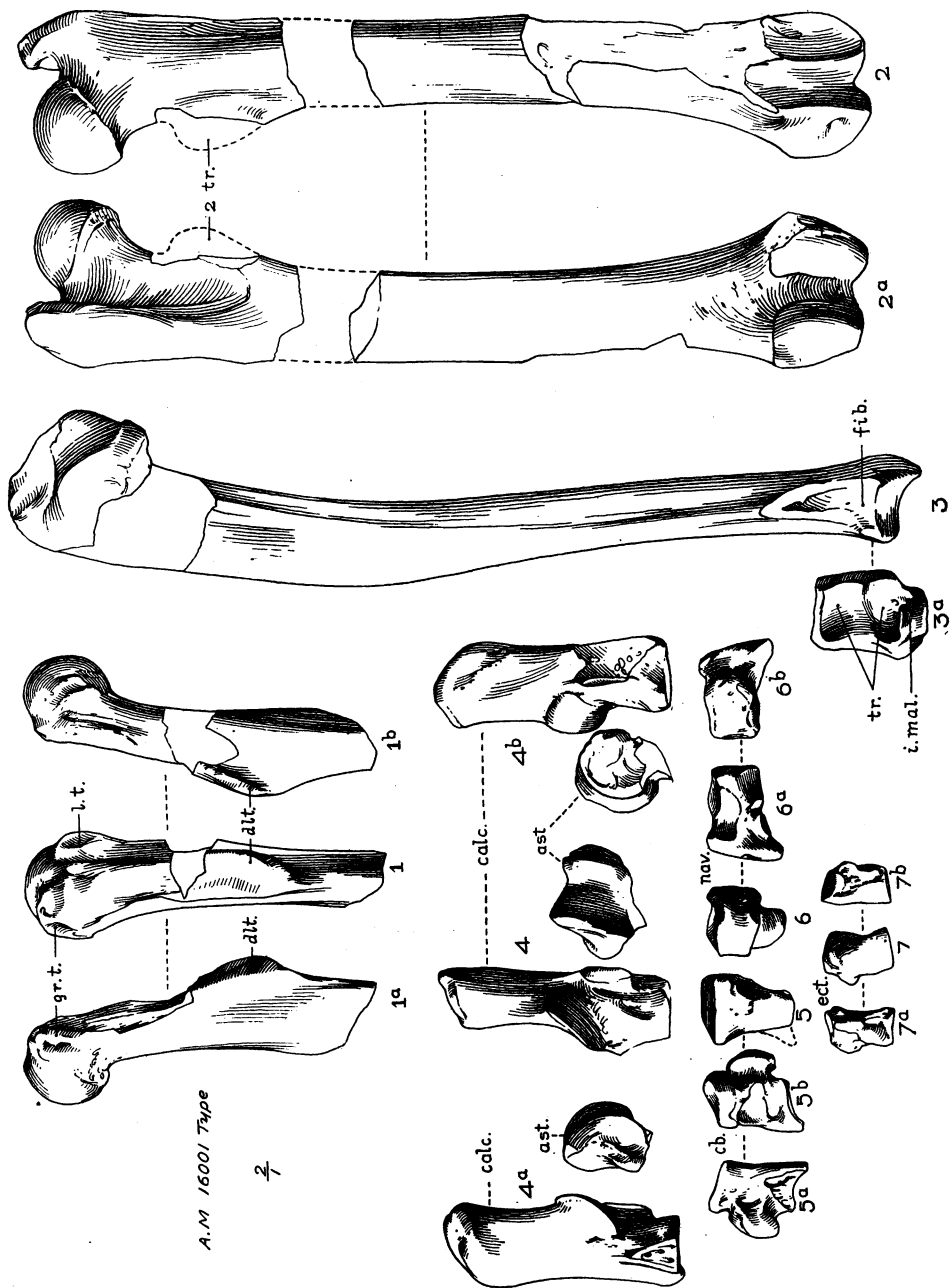


Fig. 8.

the neck is wide and apparently short. The calcaneum has a tuber of moderate length, not compressed; the astragalo-calcaneal facet is smaller and chiefly transverse. There is no fibular facet on the calcaneum. The navicular is rather short, deep, with round-concave facet for the astragalus; deep and strongly concave facet for cuboid; two subequal, flat, triangular distal facets for ecto- and meso-cuneiform; and a strongly convex facet for the entocuneiform, about the same size as the others but facing nearly mesial. The navicular hook is moderately developed. The cuboid has a rather narrow astragalar and broad calcaneal facet, and is of moderate length. No metapodials are preserved, and only one phalanx of the proximal series, short, deep proximally, flattened distally, with the distal facet but slightly convex and facing as much inferiorly as distally. The tarsus agrees in most particulars with that of *Ictops*, but the distal parts of astragalus and calcaneum were considerably shorter and the first digit less reduced.

This species may very well stand as an ancestral type of the leptictine phylum.

#### PARICTOPS GRANGER

*Type*.—*P. multicuspis* Granger, 1910, from the Lost Cabin beds of the Wind River Basin.

*Distinctive characters*.—The lower jaws are like those of *Diacodon* in the molars, but the second and third premolars are peculiarly flattened and trenchant blades with distinct anterior and posterior accessory cusps.

The type of the species is a pair of lower jaws, No. 14741, with  $p_2$ - $m_3$  well preserved and roots or alveoli of the front teeth. No additional specimens of this genus have been found.

#### DIDELPHODUS COPE, 1882

*Type*.—*Deltatherium absarokæ* from the Lower Eocene.

*Generic characters*.—Dentition,  $\frac{7.1.3.3}{3.1.4.3}$ . Upper molars compressed, triangular; paracone and metacone well separated, with a broad shelf external to them, extended at the external angles except the posteroexternal

Fig. 8. *Diacodon (Palæolestes) puercensis*. Parts of skeleton of type specimen. All twice natural size. 1) proximal half of right humerus, anterior view; 1a, external, 1b, internal views; *dlt*, deltoid crest, *gr.t.*, *l.t.*, greater and lesser tuberosities. 2) left femur, anterior view; 2a, posterior view; *tr.*, second trochanter. 3) left tibia, external view; 3a, distal end; *tr.*, trochlea, *i.mal.*, internal malleolus. 4) astragalus and calcaneum, superior view; 4a, external, 4b, internal views. 5) 5a, and 5b, corresponding views of cuboid; 6) 6a, 6b, of navicular; 7) 7a, 7b, of ectocuneiform.

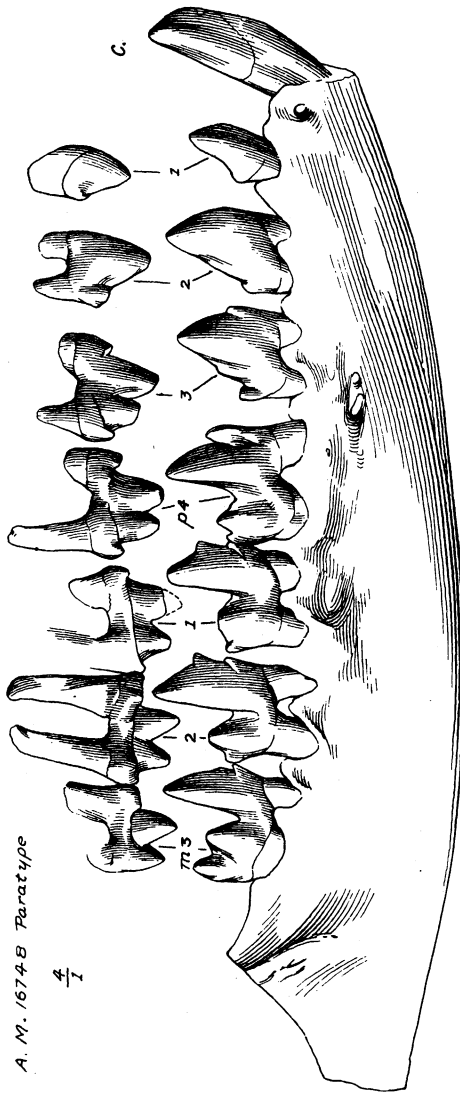


Fig. 9. *Diacodon (Palaeolestes) puericensis*. Upper and lower teeth of paratype, No. 16748, external view of right side. Upper Palaeocene, Torrejon formation of New Mexico.

angle of  $m^3$ . Protocones crescentic, compressed; paracones higher than metacones; conules minute. Premolars simple, the third and fourth with small internal cusps. Lower molars subequal, with moderately high trigonid and basined heel; hypoconulid present on all, in addition to the entoconid and hypoconid. Lower premolars simple, two-rooted, sharp and compressed,  $p_4$  lower than the two preceding and with small internal

anterior and posterior basal cusps. Canines large, incisors quite small, as in Creodonta.

The submedian position of *pa* and *me* in the upper molars, and simple and high premolars easily distinguish this genus. The lower molars have been confused with *Palæosinopa* and *Diacodon*. From the former they are distinguished by narrower heel, higher trigonid with *pr<sup>d</sup>* overtopping *pa<sup>d</sup>* and *me<sup>d</sup>*; from the latter by greater breadth of trigonid, lower *me<sup>d</sup>* and higher *pa<sup>d</sup>*.

The position of this genus is very doubtful. Cope<sup>1</sup> referred it to the Creodonta, and to the family Leptictidæ in the vicinity of *Deltatherium*, to which genus he had at first referred it. The molars differ considerably in construction from *Deltatherium*, and the premolars hardly less so. The broad outer shelves of the upper molars, transverse *m<sup>3</sup>*, and shearing trigonids of the lower molars are suggestive of *Sinopa*. On the other hand,

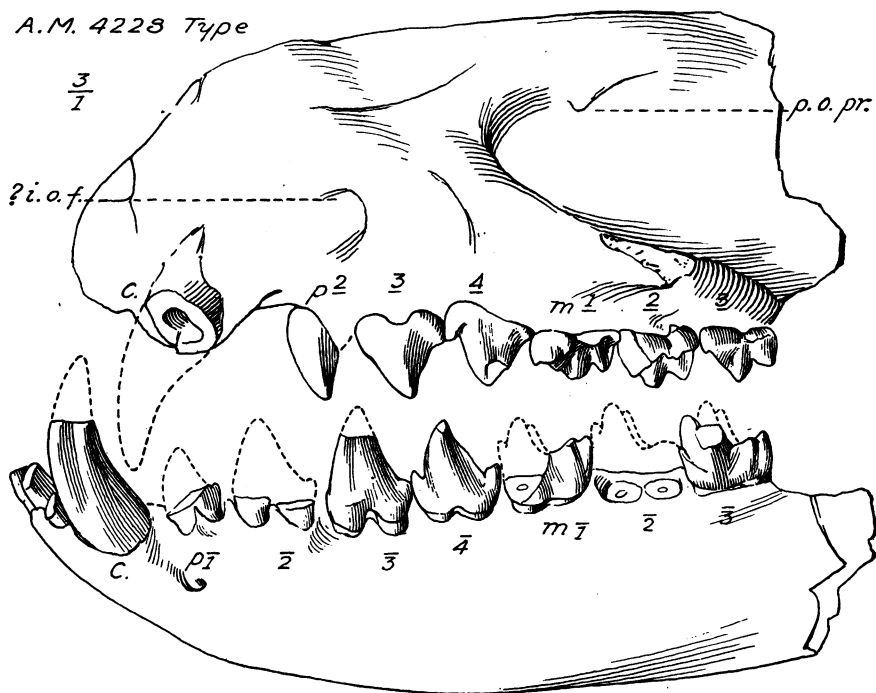


Fig. 10. *Didelphodus absarokæ*. Front of skull and lower jaw, type specimen, side view, three times natural size. Lower Eocene, Wasatch, Bighorn basin, Wyoming. Probably from the lower part of the formation, Gray Bull or Sand Coulee horizon. Cope Coll., Amer. Mus. No. 4228, collected by J. L. Wortman in 1881. *I. o. f.*, infraorbital foramen; *p. o. pr.*, postorbital process.

<sup>1</sup> Cope, 1885, Tertiary Vertebrata, Rep. U. S. Geol. Surv. Terrs. (Hayden), III, p. 283.

the teeth are in many respects not unlike those of the Leptictidæ, except that in the typical leptictids  $p_4$  are more complex, submolariform, the broad outer shelf of the upper molars and other shearing specializations are lacking. The basicranial region of the skull and the skeleton would probably afford diagnostic characters, but these are unknown or at least have not been correlated with the teeth.

The problematic Bridger genus *Phenacops* appears to be an ally of *Didelphodus*, and for the present both may be referred provisionally to the Leptictidæ, although not nearly related to the typical members of that family.

Except for a superficial resemblance in the molars to certain Didelphidæ there is nothing in the teeth, skull or jaws to suggest marsupial affinities.

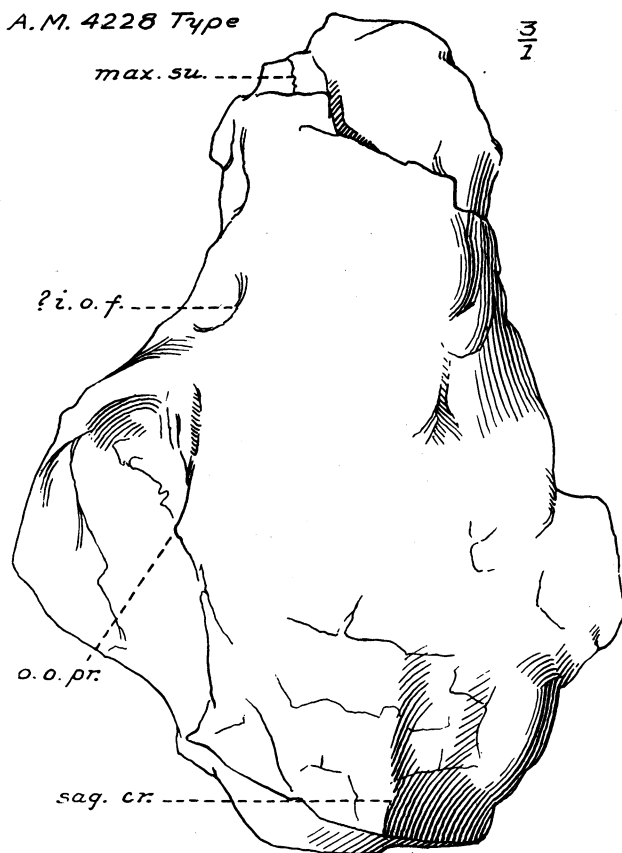


Fig. 11. *Didelphodus absarokæ*. Superior view of type skull, three times natural size. *I. o. f.*, infraorbital foramen; *max. su.*, suture between maxilla and premaxilla; *sag. cr.*, anterior end of sagittal crest.

*A.M. 4228 Type*

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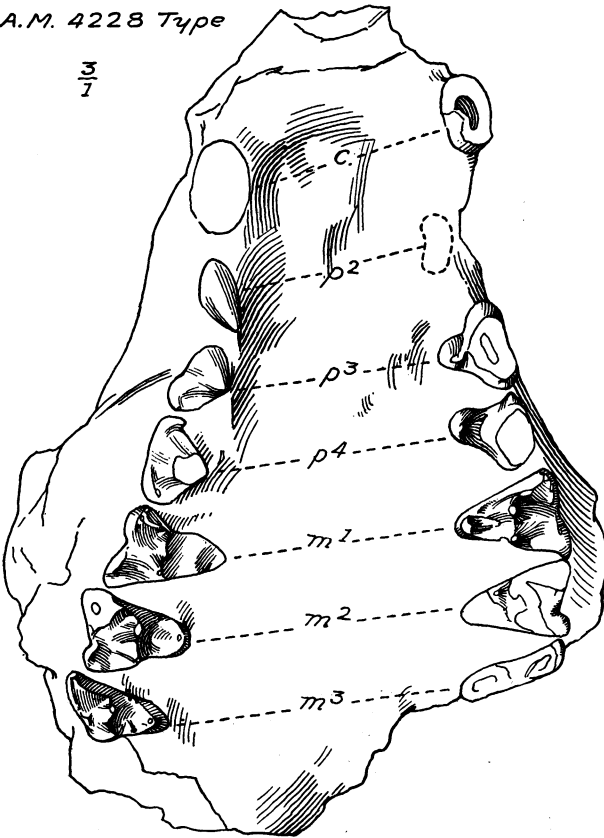


Fig. 12.

*A.M. 4228 Type*

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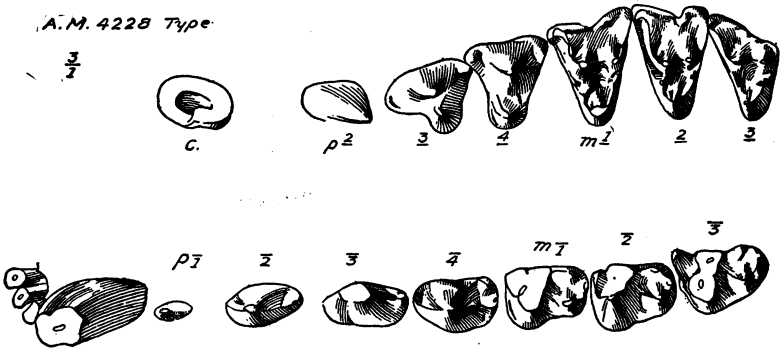


Fig. 13.

Fig. 12. *Didelphodus absarokæ*. Palatal view of type skull, three times natural size.

Fig. 13. *Didelphodus absarokæ*. Crown views of upper and lower teeth, three times natural size. From the type, supplemented by Nos. 15770, 16238.

**Didelphodus absarokæ** (Cope, 1881)

Figs. 10-13

*Specific characters.*— $I_1^1-m_3 = 32$  mm.;  $m_{1-3} = 11$ ;  $p_{1-4} = 15.3$ . First lower premolar set obliquely. There is but one species at present known so that the specific and generic characters are not separable.

The *type*, Amer. Mus. No. 4228, consists of the anterior half of a skull and the lower jaws, partly buried in hard matrix and with the teeth much damaged. No. 4229, part of a lower jaw with three well preserved molars. No. 15700, part of upper jaw with  $m^{1-3}$ ; No. 15101, lower jaw,  $m_{1-2r}$ ; and No. 15102, part of lower jaw with  $m_{1-3}$ , all from the Bighorn Wasatch. No. 16238, lower jaws, from the New Mexican Wasatch (lower beds) agrees with the type except in the reduction of  $m^3$ , but I have some doubts about its reference to the same species.

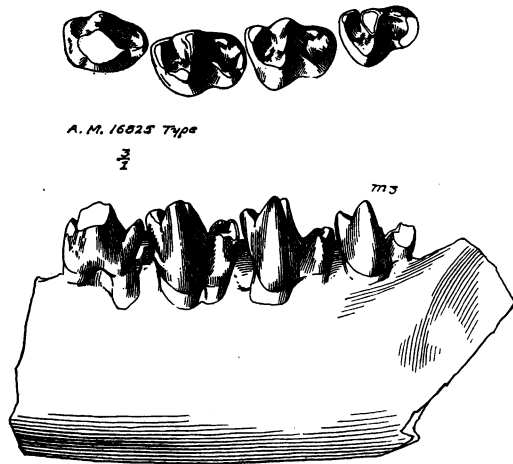


Fig. 14. *Didelphodus absarokæ secundus*. Type specimen, lower jaw, external view, with crown view of teeth, three times natural size. Upper Gray Bull beds of Wasatch formation, Bighorn basin, Wyoming.

**Didelphodus absarokæ secundus**, new mutation

Fig. 14

*Type.*—Amer. Mus. No. 16825; part of lower jaw with  $p_4-m_3$ ; from upper level of Gray Bull beds, at head of Ten-mile Creek in the Bighorn Basin.

*Distinctive characters.*— $P_4$  more robust than in *D. absarokæ*, the anterior basal and internal cusps stronger.  $M_3$  more reduced.

***Didelphodus absarokæ ventanus*, new mutation**

Fig. 15

*Type*.— Amer. Mus. No. 14747; right ramus of jaws with  $p_3$  and heels of  $m_{2-3}$  and roots of remaining postcanine teeth. Lost Cabin beds of Alkali Creek, Wind River Basin.

*Distinctive characters*.—Teeth somewhat smaller and narrower;  $p_3$  with anterior basal cusp and heel and rudimentary inner cusp;  $m_3$  smaller in proportion than in the preceding types.

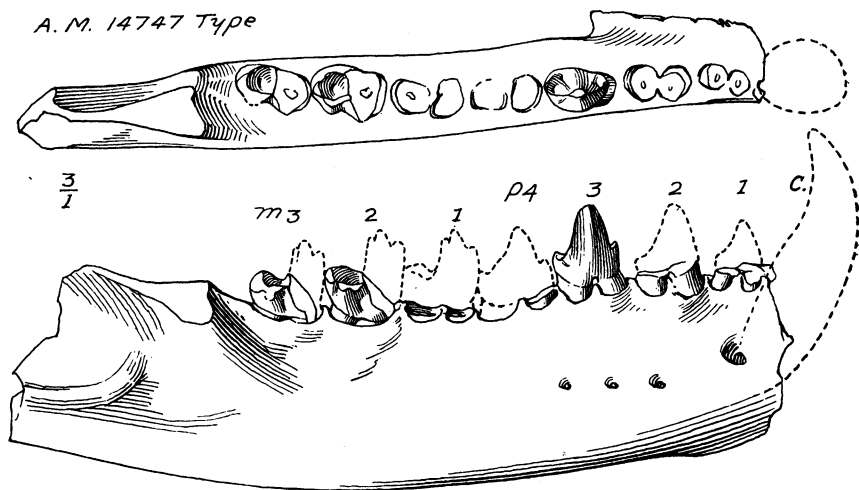


Fig. 15. *Didelphodus absarokæ ventanus*. Type specimen, lower jaw, from the Wind River basin, Lost Cabin beds. The missing teeth are restored in dotted outlines from *D. absarokæ* and *secundus*. Three times natural size.

These three stages afford a clue to the progressive evolution of the *Didelphodus* phylum. The premolars were apparently becoming more complex, the last molar reducing in size. The typical *D. absarokæ* specimens are all from low down in the Gray Bull; *secundus*, from the top of the Gray Bull, probably represents approximately the Lysite stage; while *ventanus* represents the Lost Cabin stage. The New Mexican specimen retains the primitive type of premolar, while its  $m_3$  is reduced. It is probably of somewhat later age than the typical *absarokæ*.

The limited amount and fragmentary character of the material for comparison make it advisable to regard these forms for the present as mutants rather than distinct species.

**Pantolestidæ** Cope, 1884

Although the teeth are creodont in type, the skull and skeleton of *Pantolestes* described by Matthew in 1909 seem to leave no doubt as to the insectivore affinities of this family. Its Lower Eocene representative, *Palæosinopa*, is nearly allied to *Pantolestes* in dentition, but the upper teeth are more like those of the Leptictidæ (compare especially *Palæictops puercensis* and *Didelphodus absarokæ*) and it retains the paraconid on the lower molars. The characteristic position of the posterior mental foramen beneath  $m_1$  readily distinguishes it from creodonts with similar dentition.

**PALÆOSINOPA** MATTHEW, 1901

This genus was at first supposed to be a creodont, but the discovery in 1903 of well preserved skeleton material of *Pantolestes* of the Bridger showed that the two genera were nearly related, were widely different from the Creodonta in skull and especially in limbs and feet, and were referable to the Insectivora, although not closely allied to any living families.

More complete material of *Palæosinopa* confirms this arrangement. The limb bones are widely different from those of the Creodonta and agree substantially with those of *Pantolestes*. These distinctions of limb and foot bones, together with the peculiar position of the mental foramen, constitute ordinal distinctions from the Creodonta. In the teeth the resemblance to the Oxyclenidæ, and especially to certain genera of that family, *Oxyclenus*, *Chriacus* and *Deltatherium*, is so close that it is difficult to believe that they can be otherwise than closely allied. But in *Oxyclenus*, *Chriacus*, and *Deltatherium* such parts of the skeleton as are known are of unmistakable creodont type; and, while this may not be accepted by everyone as conclusive against insectivore affinity, it is certainly strong evidence against it, and, in my opinion, decisive. While, therefore, the oxyclenid dentition of *Palæosinopa* and its known insectivore affinity are obviously suggestive of a similar relationship for all the oxyclenid genera, the fact that none of these possesses the peculiarity of a large mental foramen under  $m_1$  and some are certainly creodont-like in limb and foot bones shows that they are not so closely related as the resemblance in teeth would indicate. It does not afford sufficient evidence for removal of any of the Oxyclenidæ to the Insectivora, as suggested by Wortman, although at first thought very suggestive of the change. Nor does it seem to me tenable to place the Pantolestidæ in the same order with the Creodonta.

If the Tupaiidæ and Macroscelididæ (with the Plesiadapidæ, ?Aphelisidæ, etc.) be removed from the Insectivora to a distinct order, Meno-

typhla, as is advocated by some of the highest taxonomic authorities, it would seem necessary also to regard the Pantolestidae as ordinarily distinct. They might perhaps for convenience be associated with some of the other "Eocene Insectivora" of doubtful position, reviving Cope's name BUNOTHERIA, although not wholly in its original sense. But they do not seem to me to form a natural assemblage.

Three or more species of *Palæosinopa* are represented in the Wasatch collections from the Systemodon zone, chiefly by jaws or parts of jaws, with two very badly preserved and imperfect skulls. A few limb bones are associated with one of the skulls, and a femur with a pair of lower jaws. The femur and tibia agree, so far as preserved, with *Pantolestes*, but the articular ends of both bones are lacking; fragments of the pelvis, axis, lumbar vertebræ, and radius also agree with this genus, but these latter afford no very characteristic distinctions from Creodonta.

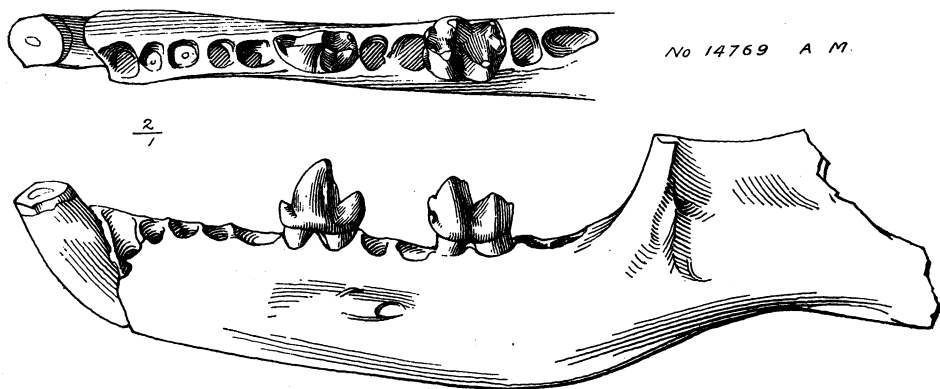


Fig. 16. *Palæosinopa didelphoides*. Lower jaw from the Wind River basin, Lost Cabin horizon; No. 14769. Twice natural size.

The upper dentition has been known hitherto only from the much worn teeth of the type of *P. veterrima*. The unworn teeth are somewhat like those of the Paleocene *Oxyclenus*. At the same time, the construction of the upper teeth is much more suggestive of leptictid affinities than in the more specialized genus *Pantolestes*. They are tritubercular, with a strong postero-internal cingular ledge; the protocone high and crescentic; paracone and metacone round conic, sharp, somewhat inset from the outer border, with a considerable cingular shelf external to them, and a crest curving forward and outward from paracone apex to postero-external angle. There is a narrow cingulum along the anterior side. The third molar is transverse, the metacone vestigial. The premolars are simple with strong

deuterocone on  $p^4$  and small one on  $p^3$ ; the antero-external and postero-external basal cusps of  $p^4$  are small in one species, vestigial in another.

The species are distinguished as follows:

*P. veterrima* Matthew. Larger; lower molars more robust; paraconid strong.

*P. didelphoides* Cope. Lower molars narrower than the preceding; paraconid vestigial.

*P. lutreola*, new species. Dimensions about two-thirds those of the preceding; posterior mental foramen further back, under posterior end of  $m_1$ .

***Palæosinopa didelphoides* Cope**

Fig. 16

The type is a fragment of the lower jaw from the Wind River (Eotitanops zone). A badly preserved skull, No. 15092, associated with several skeletal fragments from the Bighorn Basin, is referred to this species

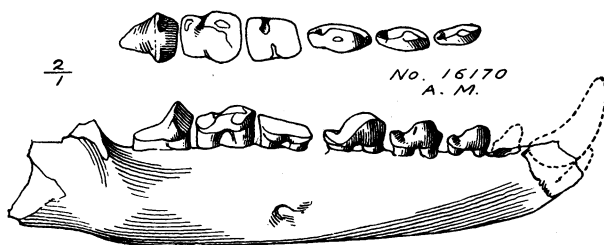


Fig. 17.

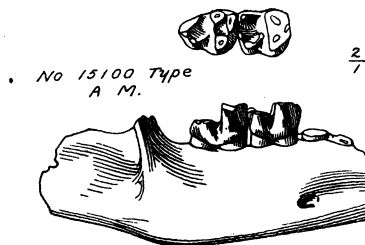


Fig. 18.

Fig. 17. *Palæosinopa lutreola*. Paratype, lower jaw, No. 16170, from the Gray Bull horizon in Clark Fork basin. Twice natural size.

Fig. 18. *Palæosinopa lutreola*. Type specimen, No. 15100. Twice natural size.

provisionally — also No. 15701, lower jaws and femur, No. 15098, part of lower jaw, and other unnumbered jaw fragments all from the *Systemodon* zone. Two other jaws from the Wind River, one of which is here figured, are more certainly referable to *P. didelphoides*.

***Palæosinopa lutreola*, new species**

Figs. 17, 18

*Type*.— Amer. Mus. No. 15100, part of a lower jaw with  $m_{2-3}$ , from Elk Creek in the Bighorn Basin, upper Gray Bull zone of the Wasatch group.

*Paratype*.— Amer. Mus. No. 16170, lower jaws with teeth much worn, from the lower Gray Bull beds in Clark Fork Basin.

The much smaller size sufficiently distinguishes this species; the posterior position of the mental foramen confirms its generic position. The lower premolar and molar teeth are diminutive copies, both in form and in method of wear, of the larger species.

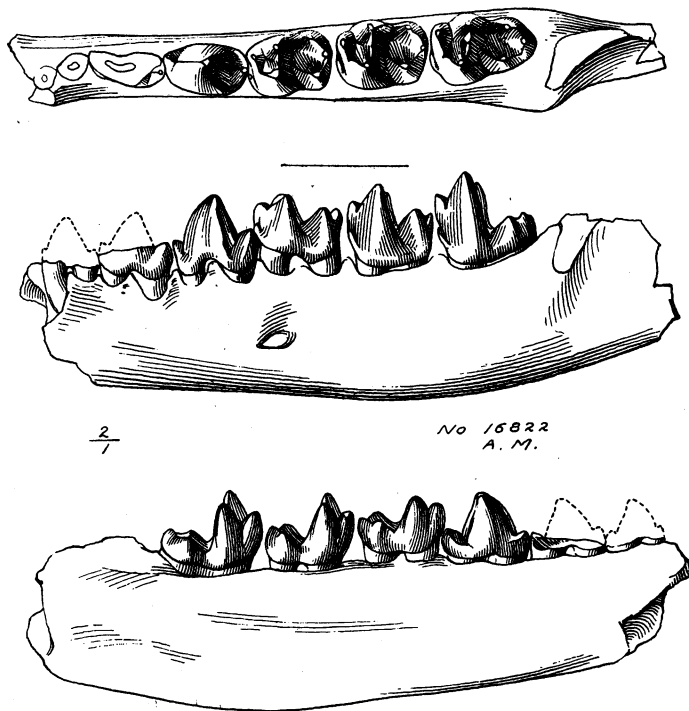


Fig. 19. *Palæosinopa veterrima*. Lower jaw with unworn teeth. Twice natural size.

## Measurements

	<i>P. veterrima</i>	<i>P. didelphoides</i>	<i>P. lutreola</i>
Upper teeth, $p^2$ - $m^3$ length	23.6	23.6	
Upper molars, $m^1$ - $3$ length	13.7	15.0	
$M^2$ diameters, ant. post. $\times$ trans.	$5.0 \times 7.2$	$5.5 \times 7.8$	
$M^1$ " " "	$5.0 \times 7.0$	$5.0 \times 7.0$	
Lower teeth, $c$ - $m_3$ length		37.4	28.0
Lower molars, $m_{1-3}$	17.5	15.5	10.4
$M_2$ diameters, ant. post. $\times$ trans.	$5.5 \times 3.8$	$5.0 \times 3.6$	$3.0 \times 2.6$
Depth of jaw beneath $m$	10.0	9.5	6.0

***Palæosinopa veterrima* Matthew**

Fig. 19

This appears to be the common species of the genus in the Wasatch, and it is not improbable that the Wasatch specimens above referred to *P. didelphoides* are merely variants of this species. Nos. 15091, 15093-7, 15099, 15733, upper and lower jaws and jaw fragments, agree fairly well with the type, but indicate much individual variability. The greater width of the lower molars, especially  $m_{1-2}$ , well developed cusps at the external angles of  $p^4$ , greater transverse width and more triangular form are the distinguishing characters used to separate it.

Dr. Schlosser's opinions in regard to the Pantolestidæ are expressed in the following citation from his memoir upon the Fayûm fauna:

Besides the genus *Sinopa* and its near relative *Cynohyænodon* there might come into consideration as ancestors of *Ptolemaia* also the genus *Palæosinopa* Matthew from the Wasatch beds of Wyoming, which this author now refers to the Pantolestidæ and therewith to the Insectivora. It cannot be denied that it is in fact similar to the genus *Ptolemaia* in the shortness and height of the trigonid and in the size of the talonid of the lower molar, in the triangular form of the upper molar, on which the metastyle appears to be wholly lacking, as well as in the form of the premolars. Matthew is disposed to refer them to the Insectivora, among other reasons, on account of the position of the mental foramen not under the premolars but near to  $m_1$ . So far as this indication is decisive, the lower jaw lying before me can belong to no Insectivore, for the foramen is found here between  $p_3$  and  $i$ . On Osborn's original it is not shown.

Reference to the Bridger memoir which Doctor Schlosser cites shows that I devoted several pages to description of the skeleton of *Pantolestes*, and that it was chiefly upon the skeleton characters that the reference of the Pantolestidæ to the Insectivora was based. I pointed out also several Insectivore features in the skull and noted the position of the posterior

mental foramen beneath  $m_1$  (not "near to" it as Schlosser says) as paralleled in many modern Insectivora but not in all: I cited the Insectivores in which it does and those in which it does not occur. At another page of the same memoir I gave a special discussion of the astragalus in various orders of mammals and showed that all Insectivora (including *Pantolestes*) except *Hyopsodus* show certain common fundamental features about the astragalus, all Creodonta and Condylarthra approach another distinct fundamental type, all primates a third, amblypods a fourth, perissodactyls a fifth, artiodactyls a sixth, and so on. I hesitated on this account to accept the reference of *Hyopsodus* to the order by Wortman and Loomis, and have since obtained definite evidence for its removal to the Condylarthra.

My reference of *Palæosinopa* to the Insectivora was not "motiviert" by the position of the mental foramen; in fact, when I first described the genus from the upper and lower jaws I supposed it to be a member of the Hyænodontidæ, where Schlosser is evidently still disposed to refer it. But there can be no question of its near relationship to *Pantolestes*, and the characters of skull and skeleton in that genus absolutely forbid any near relationship to the hyænodonts, particularly to the contemporary primitive hyænodonts of the Wasatch. The teeth of the Pantolestidæ, as I have repeatedly stated, are quite unlike those of any living Insectivora and resemble those of the most primitive creodonts in a very marked degree. But the skull and skeleton are fundamentally unlike the type common to the most primitive members of the creodont-condylarth group, and they do resemble the Leptictidæ and other Insectivora in various criteria which I have cited in the memoir.

A careful study of the dentition in *Palæosinopa* will show that it is not so fundamentally different from *Palæictops* and that the characters of the skull and skeleton in the two conform fairly well.

As for the position of *Ptolemaia*, it seems very probable that the specimen referred to Osborn's genus by Schlosser is an aberrant hyænodont, but after comparing Dr. Schlosser's figures with Osborn's original I cannot believe that they belong to the same or nearly related species. We had of course made careful comparisons of Osborn's type specimen with all the known hyænodonts, and, if it had seemed reasonable to refer it to this family, it would have been so referred. But the molars, although heavily worn, appear to be of a distinct type from any hyænodonts or any other creodont genera; in some degree they suggest Tillodontia, in some degree Pantolestidæ, but not enough to warrant any suggestion of affinities. It seems better to leave it *incertæ sedis*.

**Apheliscidæ**, new family

*Diagnosis*.—Jaws slender, lower molars tetracuspid with low trigonid and basin heel, the four cusps submarginal in opposite pairs, equal in height, rounded,  $m_3$  without heel. Premolars simple. Upper molars tritubercular, conules united to wings of protocone,  $m^3$  without metacone. Skull of moderate length, occiput wide, crests low, postorbital process rudimentary, zygomata complete, not heavy. Fore limbs long and slender.

The above cited characters afford a tentative diagnosis. They may not all be of family value; but they will serve to indicate the evidence as to the affinities of this very puzzling animal. It is clearly not closely related to any known genus, living or extinct, and it does not seem practicable to refer it to any known family. Its ordinal relations are very questionable; it is referred to the Insectivora but it may be condylarthran, primate or creodont—in any case a very aberrant type. I hardly think it possible that it could be referred to any other order. There is some suggestion in the teeth of affinity to *Rhynchocyon*, but whether that is wholly due to parallelism or partly conditioned by a somewhat distant relationship is undecided. In any event, the position of the family, if it be insectivore, is more probably among the Menotyphla than any other known groups.

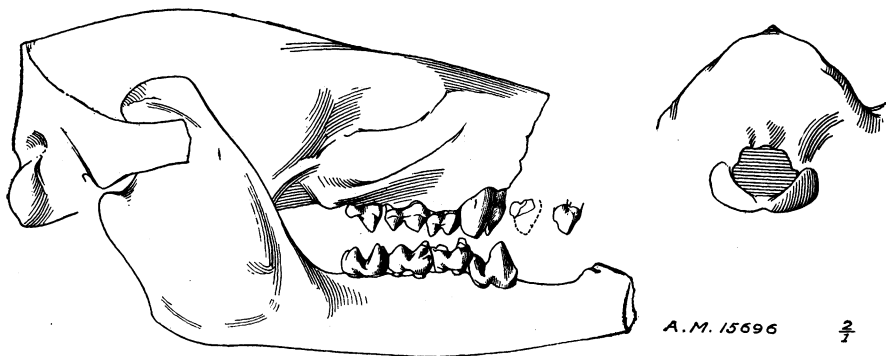


Fig. 20. *Apheliscus insidiosus*. Skull and lower jaw, No. 15696. Right side view, with occipital view of skull, twice natural size.

**APHELISCUS** COPE, 1875

*Type*.—*Prototomus insidiosus* Cope, 1874, from Wasatch of New Mexico.

This genus has hitherto been known only from Cope's description and figure of the type specimen, a lower jaw with  $p_4$ - $m_3$ . The type belongs in

the National Museum collections, but is missing; the figure is very unsatisfactory and the description adds little to it.

A specimen found in the Gray Bull level of the Bighorn Wasatch by the expedition of 1911 agrees with Cope's type, so far as can be judged from the figure and description, and shares with it certain characteristic features that distinguish it from any other Eocene mammal. The trigonid is low, composed of two equal cusps, nearly opposite, rounded, well separated, and barely higher than the heel cusps; the heel basin-shaped, with strong marginal *hy*<sup>d</sup> and entoconid, and on *m*<sub>1</sub> and *m*<sub>3</sub> a small hypoconulid; the last molar has no third lobe and the *p*<sub>4</sub> has a large, simple, rather high, somewhat recurved, main cusp and a high heel cusp flattened externally and with a strong transverse ridge from its posteroexternal point, but no basin. These features accord with Cope's figure and description.

The specimen (Figs. 21-24) consists of a crushed skull, lower jaws, and a few bones of the skeleton. It was buried in a hard concretionary mass from which it has been with great difficulty extracted by Mr. Anderson.

The jaw is rather long and slender; the angle of the jaw is not inflected, and appears to be broad and flat. There are four premolars, *p*<sub>3</sub> smaller than *p*<sub>4</sub>, *p*<sub>2</sub> much smaller, with rudimentary heel; the front teeth are not very large. In the upper jaw *p*<sup>4</sup> has two high round-conical cusps, the

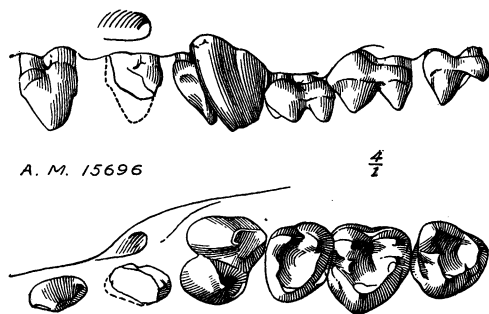


Fig. 21. *Apheliscus insidiosus*. Upper teeth of left side from the skull shown in Fig. 21. External and crown views, four times natural size.

larger external, no heels or basal cingula; *p*<sup>2-3</sup> are small, simple-crowned with two external roots, the internal cusps and roots absent. The upper molars are of peculiar type. The first two are tritubercular, their transverse width small, conules distinct, protocone large, subcrescentic, the wings of the crescent uniting the conules to the protocone, external cingulum strong, paracone and metacone of equal size, round-conical, wide apart. On the third molar there is no trace of metacone; the paracone and

protocone are high rounded cusps, and behind them is a broad cingular shelf or basin, but no metacone.

There are no indications of marsupial affinities in the above. The genus was referred to the Mesodonta by Cope and where listed is placed under the Notharctidæ (Limnotheriidæ). Its affinities with any genera of known ordinal position are certainly not close, and its characters suggest about equally the tupaoid insectivores, Condylarthra, tritubercular Artiodactyla and several of the Eocene groups of Insectivora.

#### *Description of Skull, Jaws, etc.*

*Skull*.—The front of the skull is broken off obliquely, the fracture passing in front of  $p^4r$  and  $p^2l$ . The sutures cannot be certainly distinguished. The orbit is of moderate size, its anterior border above the anterior end of the molar series. The postorbital constriction is wide and short, wholly lacking the narrow elongate proportions characteristic of most typical Insectivora. There is no distinct postorbital process. The post-orbital crests are low, obscure, fading out laterally, uniting posteriorly into a narrow, obscure sagittal crest, which becomes distinct but still low and narrow in its posterior third, uniting with the more distinct occipital crest. This crest is not very high and does not overhang the occiput, but extends laterally into the lambdoidal crests, which pass in turn into the upper border of the zygomatic arch. The occiput is broad, flat, not excavated, slopes moderately forward. The basicranial region is so badly preserved that little can be certainly determined; apparently the condyles are rather widely separated, of moderate size and the usual form, the paroccipital process stout and short, the postglenoid process rather weak, the zygomatic arches of moderate depth and not heavy posteriorly.

The *lower jaw* is rather long and shallow; the symphysis is not preserved, so that it must have been wholly in advance of  $p_2$ . The depth of the jaw is greater beneath  $p_4$  than beneath the molars or the anterior premolars. The condyle is low, only a little above the line of the premolar-molar teeth, transversely oval, not wide as in Carnivora and Creodonta; the coronoid process is high, wide, directed more backward than upward, and moderately recurved. The angular process is not well preserved; it is wide, flat and thin, moderately prominent but not extending backward as far as condyle or coronoid, nor downward much beyond the curve of the inferior mandibular border.

Two *cervicals* are preserved, with rather short centra, remarkably small zygapophyses and rather small and weak transverse processes.

The *humerus* is long, slender, the deltoid crest prominent but extending

only a short distance down on the shaft, the distal end wide transversely, with rather large entepicondylar foramen, supinator crest only moderately developed, the distal trochlea rather shallow, the olecranon fossa not deeply excavated.

The *ulna* has a long shaft; the olecranon, although the tip is broken off, was evidently short, weak, and not backwardly directed, the digital fossa is not deep and the radial facet is flat and obscure. The distal epiphysis is gone. It is clear, however, from the proportions that although elongate the ulna was not reduced, the relative proportion to the radius being more as in *Condylarthra* and other primitive types than as in *Creodonta*.

A part of the *ilium* is preserved, but affords few indications of construction other than that the pelvis was elongate, the acetabulum small, weak,

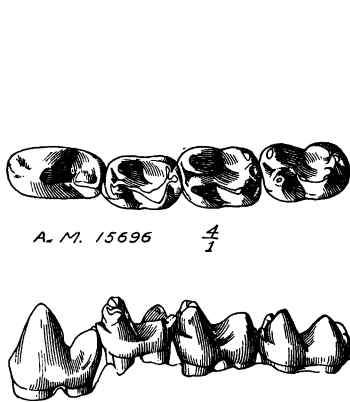


Fig. 22.

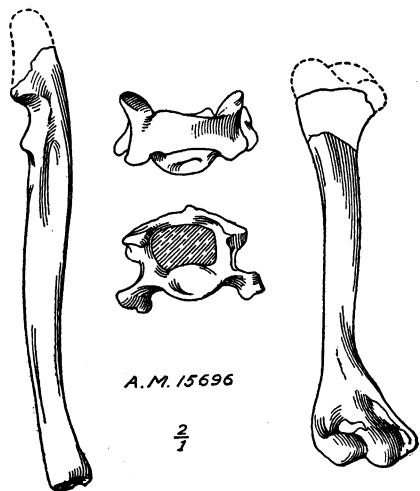


Fig. 23.

Fig. 22. *Aphiliscus insidiosus*. Lower teeth of left side from the skull shown in Fig. 20. External and crown views, four times natural size.

Fig. 23. *Aphiliscus insidiosus*. Bones associated with skull shown in Fig. 20: cervical vertebra, superior and posterior views; right humerus, anterior view; left ulna, anteroexternal view. All twice natural size.

and rather open. There are several other fragments preserved, but so incomplete, broken or distorted by pressure that I cannot obtain from them any data worthy of record.

The above indications point to a long-limbed, weak-jointed skeleton, suggestive rather of *lemuroids* than of most *Insectivora*, and quite unlike *Creodonta* in its proportions. There is nothing in the skull that points to

the typical Insectivora; the resemblances to that order, such as they are, suggest affinity only to such types as the Tupaiidæ. There is nothing to exclude affinity to the primates, but the long slender jaws, the peculiar type of teeth, the small low brain-case do not favor it. There is nothing except the low-crowned teeth to suggest condylarthran or taligrade affinities, and the construction of these teeth is very remote from any known member of these orders, suggestive rather of the Apatemyidæ in the molars, but in no other particulars.

***Apheliscus insidiosus* (Cope, 1874)**

Figs. 20-24

The skull and jaws, No. 15696, agree in all respects with Cope's type, as far as comparisons are practicable. It thus adds one more to the number of species common to the New Mexican and Wyoming Wasatch. It is from the Upper Gray Bull level. Nos. 34, 44, 4201, lower jaw fragments, are probably from the Gray Bull beds; No. 16925, lower jaw with  $m_{1-2}$  from the Sand Coulee beds, and No. 15849, upper jaw fragment with  $p^4-m^1$  from the Clark Fork horizon, are referable to *Apheliscus*. The two latter may represent primitive mutants.

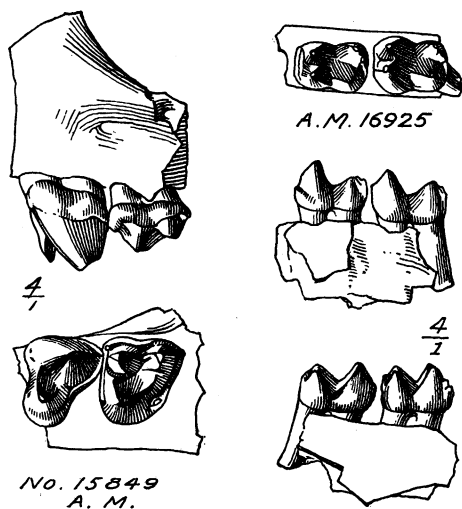


Fig. 24. *Apheliscus insidiosus*?. Upper and lower jaw fragments from Clark Fork and Sand Coulee horizons respectively. These are from a lower geological level than the skull, and may represent primitive mutants. Four times natural size.

? *Tupaiidæ***ENTOMOLESTES MATTHEW, 1909**

*Type*.—*E. grangeri* of the Bridger formation, Middle Eocene.

The resemblance to *Tupaia* in the lower jaw and teeth of this genus has been noted by Matthew and Gregory, but until more is known of the animal the reference must remain provisional, as the teeth are of very primitive, unspecialized character, not affording sure grounds of relationship.

***Entomolestes nitens*, new species**

Figs. 25, 26

*Type*.—Amer. Mus. No. 15697, a jaw fragment with  $p_4$ - $m_2$  perfectly preserved, from the upper levels of the Gray Bull beds near Fenton in the Bighorn Basin.

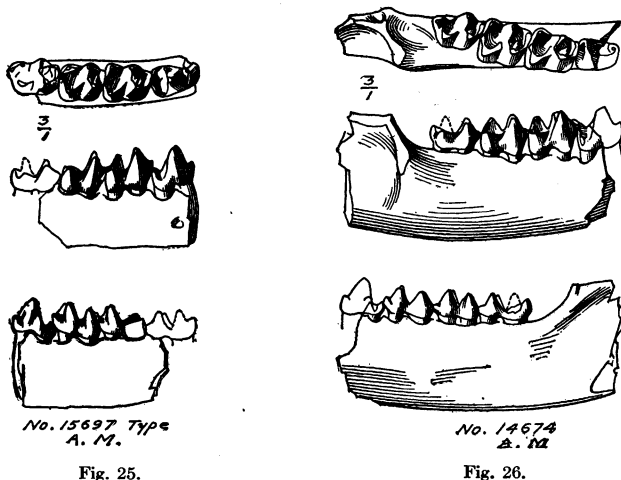


Fig. 25.

Fig. 26.

Fig. 25. *Entomolestes nitens*. Lower jaw fragment, type specimen. Last molar restored in outline from No. 14674. Bighorn basin, upper Gray Bull horizon. Three times natural size.

Fig. 26. *Entomolestes nitens*. Lower jaw from the Wind River basin, Lysite horizon. The fourth premolar is restored in outline from the type. Three times natural size.

*Distinctive characters*.—One-half larger than *E. grangeri*,  $p_4$ - $m_2$  = 6 mm.; teeth apparently similar in proportions and construction.

A second specimen, No. 14674, from the Lysite horizon of the Wind River Basin, contains the molar teeth and heel of  $p_4$ . It agrees with the type in all but the larger size of  $m_2$ , which may be of individual or mutative

value.  $M_{1-3}$  measures 6.4 mm., the last molar being somewhat reduced. The trigonid is low, with two subequal well separated cusps and a strong paraconid crest; talonid slightly wider than trigonid, with hypoconid and entoconid strong; no hypoconulid except on  $m_3$ , where it is small but distinct.  $P_4$  with small but distinct paraconid and metaconid, and broad, low crested heel.

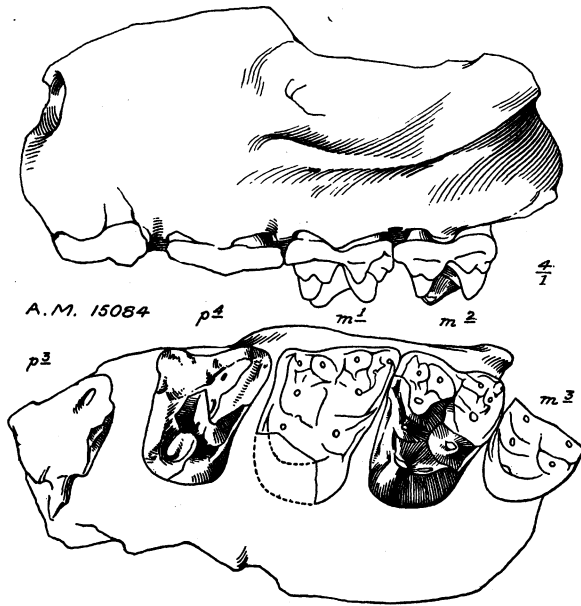


Fig. 27. *Plagiomene multicuspis*. Left maxilla of type specimen, No. 15084, teeth restored in outline from right maxilla and from No. 16166. Gray Bull horizon, Bighorn basin. Four times natural size.

### **Plagiomenidæ, new family**

This family is based upon a genus whose teeth are of very peculiar type, resembling to some extent those of the living genus *Galeopithecus*, inhabiting parts of the East Indies. The new genus is known only from the upper and lower jaws. These show in the molars and posterior premolars certain peculiarities of pattern characteristic of the modern genus. Of the anterior teeth we have only the roots; they are unreduced in number but whether or not they display the peculiar comb-pattern of *Galeopithecus* is unknown.

Some doubt will naturally be felt as to the meaning of this resemblance; the pattern of the cheek teeth is so peculiar and the correspondence so close in the Eocene and the modern genus that I regard it as sufficient evidence

for a provisional phyletic affinity, although not for a positive ordinal reference. Convergence often produces a superficial similarity of form and proportions in the teeth, but I do not know of any instance among mammals where an identical *pattern* in a series of upper and lower teeth of complex construction results from convergence in wholly unrelated types. There is also a certain amount of resemblance in molar pattern to *Myogale*, but it is by no means so close as to *Galeopithecus*.

The anterior teeth, whatever the pattern of the crowns, are entirely primitive in number and proportions, so far as can be judged from the roots and alveoli. These accord in number and proportions with the Eocene Insectivora and related types. There are three small slender incisors, a canine one-rooted and of moderate size, a small one-rooted first premolar, and three succeeding premolars two-rooted, progressively increasing in size, the fourth completely molariform. This is in contrast with the reduced and specialized anterior teeth of *Galeopithecus*. If the modern genus be directly descended, the specialization of the front teeth must have been acquired during the Tertiary, while the peculiarities of the cheek teeth are of more ancient origin. This would be in accord with the relationships

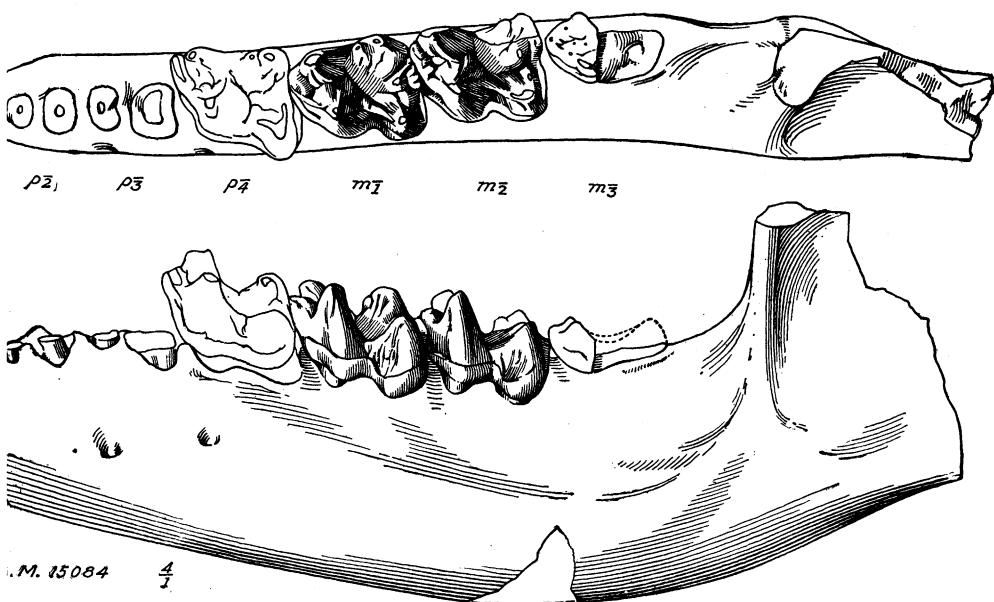


Fig. 28. *Plagiomene multicuspis*. Left lower jaw of type, the fourth premolar restored in outline from No. 15085. Four times natural size.

between Eocene and modern lemuroids. While the pattern of  $p_4^1-m_3^2$  is fundamentally the same, it is not identical in detail.

An undescribed genus from the Paskapoo beds of Alberta affords a curious and suggestive resemblance to the new Wasatch genus, and may possibly represent an early stage in the differentiation of its dentition. There is also a certain degree of suggestion, among some of the Lance tribituberculate teeth, of affinity to this phylum, but not enough to warrant placing them in it. In the Paleocene no relatives have been recognized.

The more distant resemblance to *Myogale* is perhaps also significant of a real though remote affinity. *Myogale*, while distinctly talpid in its affinities, is considered as in most features a very ancient survival, and *Galeopithecus* is regarded as a peculiar specialization from primitive insectivore stock. This Lower Eocene genus is partly intermediate, helping to bridge the gap.

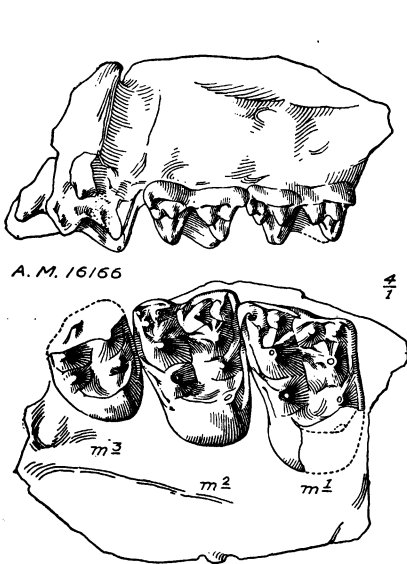


Fig. 29.

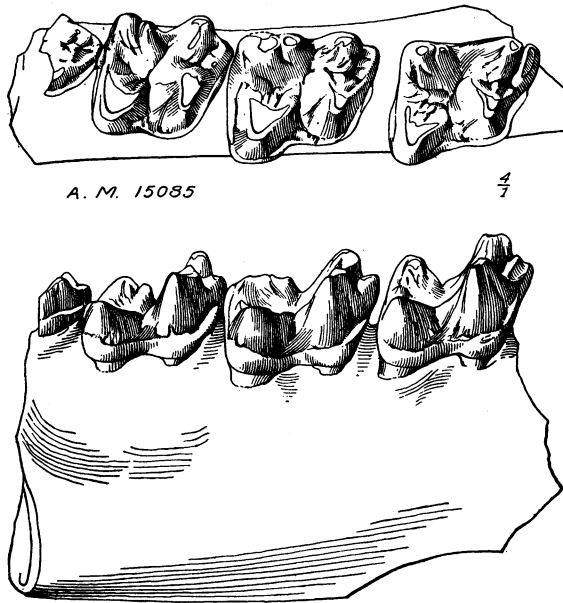


Fig. 30.

Fig. 29. *Plagiomene multicuspis*. Part of right maxilla, No. 16166, with true molars,  $m^1-3$ . Four times natural size.

Fig. 30. *Plagiomene multicuspis*. Part of right lower jaw with  $p_1-m_1$  and part of  $m_1$ , No. 15085. Four times natural size.

**PLAGIOMENE, NEW GENUS**

*Type*.— *P. multicuspis* from the Gray Bull horizon of the Bighorn Basin.

*Generic characters*.— Dentition  $\frac{??.?.?.3}{3.1.4.3}$ . Last molar reduced;  $p_4^4$  molari-form; lower molars with four principal cusps and a partly connate paraconid, the outer cusps subcrescentic, lower and somewhat posterior to the inner cusps so that the anterior and posterior pair set obliquely and connected by imperfect crests. Upper molars with large crescentic protocone, no hypocone, strong conules, paracone and metacone subcrescentic, a pair of distinct cusps exterior to paracone and a second pair exterior to metacone; a deep valley extending from the outer border of the tooth between the anterior and posterior cusps to the protocone. Three small incisors, canine small,  $p_3^3$  submolariform.

The construction of these teeth is peculiar, unlike any placental molars known to me except those of *Galeopithecus*. The anterior teeth are unreduced and unspecialized so far as the roots indicate.

***Plagiomene multicuspis*, new species**

Figs. 27-32

*Type*.— Amer. Mus. No. 15084, upper and lower jaws with the teeth mostly broken off.

*Paratypes*.— No. 16166, upper jaw with  $m^{1-3}$ , No. 15085, lower jaw with  $p_4-m_2$  and part of  $m_3$ , No. 15087, lower jaws with  $p_3-m_3$  and roots of front teeth, and part of maxilla with teeth badly preserved. All from the Gray Bull beds of Bighorn Basin.

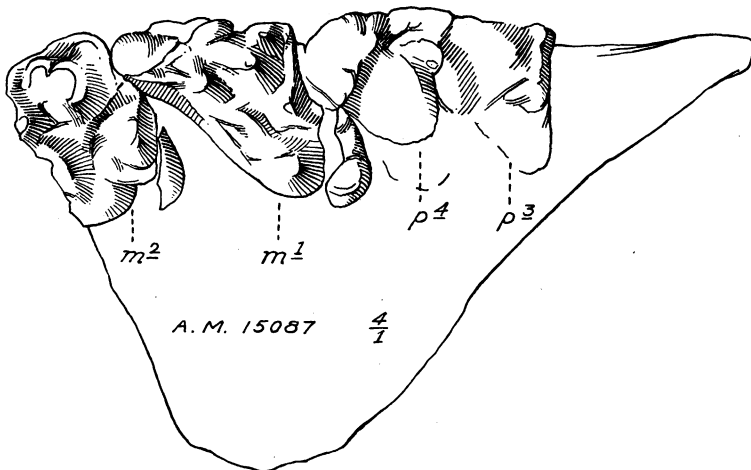


Fig. 31. *Plagiomene multicuspis*. Part of right maxilla with  $p^3-m^2$  badly preserved, No. 15087. Four times natural size.

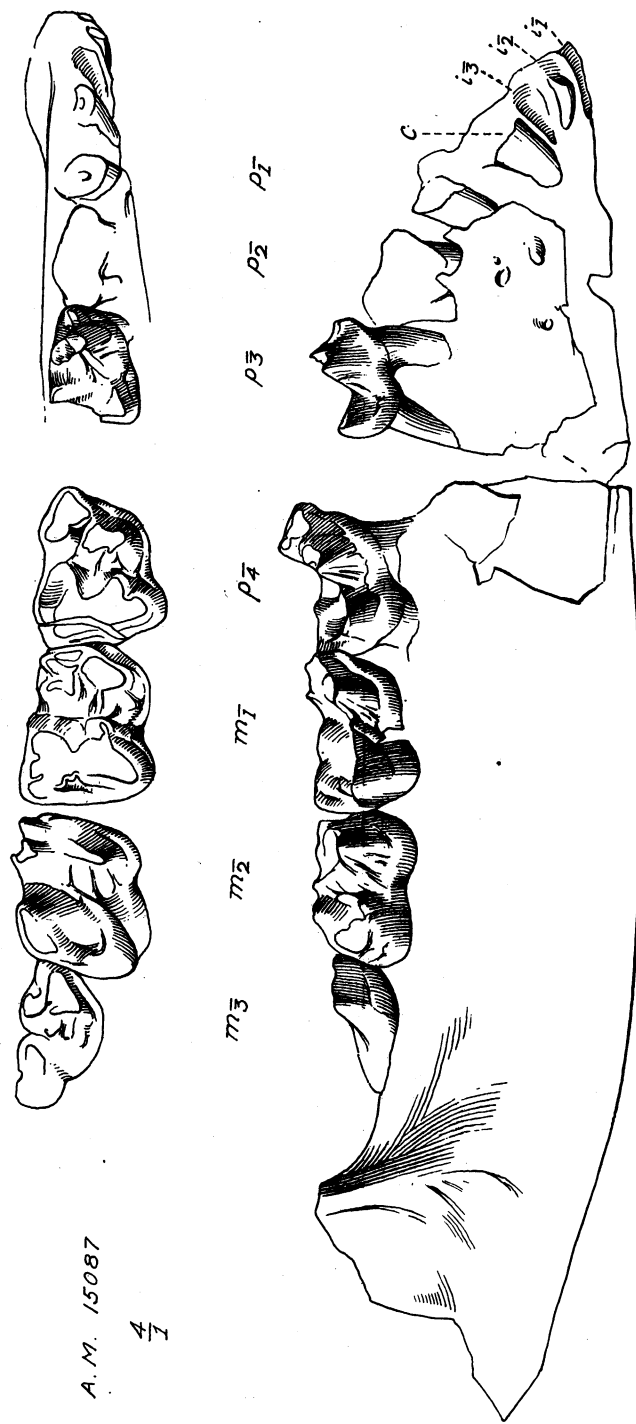


Fig. 32. *Plagionene multicuspis*. Lower jaw of the same individual as Fig. 32, showing  $p_4$ - $m_1$  of the right side and roots of the anterior teeth. The characters of the teeth are supplemented from the left ramus mandibuli of the same specimen. Four times natural size.

## AFFINITIES DOUBTFUL (?SORICOIDEA OR CHIROPTERA)

**NYCTITHERIUM MARSH, 1872**

In 1909 I grouped under this genus a number of minute species with molar teeth of the primitive insectivorous pattern common to several groups of insect-eating mammals of diverse affinities. The reasons for referring them provisionally to the Talpidæ were detailed in the memoir on Bridger Insectivora.

A specimen (Figs. 34-35) referred to *Nyctitherium celatum* (*Diacodon celatus* Cope) affords some additional evidence on the affinities of this species. It consists of portions of upper and lower jaws with which are associated three long slender bones, suitable in size and proportions for the shafts of chiropteran fore limb bones, and a few other small fragments not recognizable. Both the jaw parts and associated bones belong to an immature individual, the upper and lower premolars being in a corresponding stage of emergence, and all the remains were found within a few centimetres of each other, in the original matrix. No remains of any other animals were associated with them. The upper and lower jaws almost certainly belong to the same individual. It is highly probable, therefore, that the supposed limb bones likewise pertain to it. Although the supposed limb bones are too incomplete for positive identification, the ends absent or unrecognizable, yet they show clearly an extremely slender, nearly straight shaft, unlike any bone of any terrestrial mammal with which I have compared them. If this identification is correct, as appears reasonably probable, it indicates that this species is a chiropteran; but whether the genus should be referred to that order is still doubtful, in view of the form of the anterior portion of the jaw in some Bridger species (apparently also in this one) the absence of molar cingula, and the conditions of deposition of the Wasatch formation, these conditions making the preservation of an insectivore in its strata far more probable than of a chiropteran. Practically all the positively identified chiropteran fossils have come from cave or fissure formations; the Wasatch is a river-valley formation. For these reasons I have preferred not to transfer *Nyctitherium* to the Chiroptera, although its known remains are very suggestive of affinity to the bats.

**Nyctitherium celatum** (Cope, 1875)

Figs. 33-34

*Diacodon celatus*, COPE, 1875, Syst. Cat. Eoc. Vert. New Mex., p. 12; 1877, Ext. Vert. New Mex., p. 133, Pl. XLV, fig. 20.

?*Synonym*.—*Anaptomorphus minimus* LOOMIS, 1906.

*Type*.—U. S. Nat. Mus. No. 1126, lower jaw with  $m_{1-3}$ , from the Wasatch of New Mexico.

Although referred by Cope to *Diacodon*, this species apparently does not belong in the Leptictidæ but to the group of minute species which I have assembled under *Nyctitherium*.

No. 15103, lower jaws and upper molars associated with parts of limb bones, is referable to Cope's species. It is from the middle Gray Bull beds

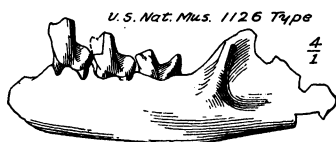


Fig. 33. *Nyctitherium celatum*. Lower jaw, type specimen, U. S. National Museum, No. 1126. Wasatch of New Mexico. Four times natural size.

of the Bighorn Basin and shows the last milk molar and first two true molars of upper and lower dentition.

The molar teeth are much like those of *Vespertilio* in proportions and construction, but have no external cingula. Trigonid wide and short, protoconid and metaconid subequal, opposite, paraconid small, low-set, not projecting far forward; heel as wide as trigonid, short, hypoconid and entoconid wide apart, equal in height, their points at about the same level as paraconid; no hypoconulid; cusps sharp, angulate, basins deep.

The milk molar is a smaller, narrower tooth than  $m_1$ , similar in construction.

The upper molars are sharp-cusped, triangular in form, with subequal paracone, metacone, and protocone, external angles extended into sharp stylar cusps, and a well-developed hypocone at a lower level. The paraconule and metaconule are sharp, although low-set, the mesostyle distinct but small. The three principal cusps with the parastyle and metastyle outline a sharp oblique triangle.

The anterior portion of the lower jaw is broken off in front of  $dp_2$ . A part of this tooth is preserved and apparently projected strongly forward.

The posterior end of the symphysis is more doubtfully indicated; it appears to be of the long loose type characteristic of many Insectivora, quite unlike anything in the Chiroptera.

If this species be really chiropteran it had the long slender symphysis which Schlosser ascribed to *Vespertiliavus*.

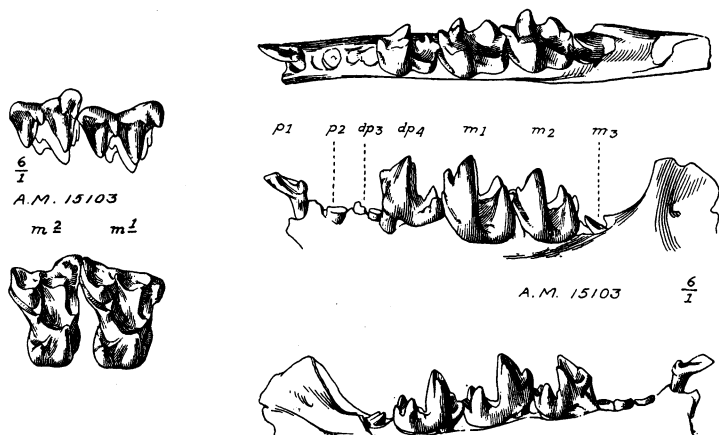


Fig. 34. *Nyctitherium celatum*. Upper teeth,  $m_1$ - $m_3$  of the right side, external and crown views, and lower jaw of the same individual crown, external, and internal views of the left ramus, six times natural size. No. 15103, from the Bighorn basin, Wyoming. With this are associated certain supposed chiropteran limb bones.

#### WINGE ON AMERICAN EOCENE INSECTIVORA

Winge has recently published a review of the mutual affinities of the Insectivora<sup>1</sup> in which he discusses the position of various American Tertiary genera. His conclusions differ — in some cases differ widely — from those of most palæontologists and, although very positively expressed, are in some instances quite untenable.

The following translation expresses his views:

Near to the Galeopithecidae, originating from a family of very primitive forms, stands a little group of mutually near-standing North American families, all extinct in the Tertiary period: Leptictidae, Tillotheriidae, Peripitychidae and Stylinodontidae.

<sup>1</sup> Winge, 1917. Udsigt over Insektædernes indbyrdes Slægtskab. Vidensk., Medd. fra Dansk naturh. Foren., LXVIII, pp. 83-203.

The peculiarity that unites these American families with the Galeopithecidae and places them at a lower stage in specialization than all other members of the Insectivore order, is that they have normally proportioned nasal cartilages; the nasals were not or scarcely at all tubular, to judge from the form of the facial bones, and the nasal muscles have not impressed their attachments upon the cheek arches or in other ways moulded their environment. A peculiarity that is common to the named American families and sets them upon a higher stage [of development] than the Galeopithecidae, is that the intermediate, second, of the three outermost cusps [i. e. mesostyle] upon the upper molariform teeth has disappeared, and that the 4th and 5th cusps [parastyle and metastyle] have lost more or less of the V-shape and become conical.

Lowest among the named American families stands the Leptictididae [Leptictidae] with the genera *Ictidops* [*Ictops*] and *Leptictis*, both genera with assuredly mouse-like body form.

*Ictidops* [*Ictops*] with *Palæictidops* [*Palæictops*] <sup>1</sup>, which is known from the anterior part of the skull, with lower jaws, is in some respects the most primitive of the genera: all three upper incisors are present; upper P<sup>3</sup> has intermediate form with inner heel; the temporal crests unite in a sagittal crest. It appears otherwise to be very close to the better known *Leptictis*. Upon the upper molariform teeth the 7th cusp [hypocone] may be proportionately of considerable size and the intermediate cusps [conules] can be found upon the anterior and posterior borders [wings] of the 6th cusp [protocone]. In the lower jaw, p<sub>4</sub> is molariform, with the primitive five cusps; upon the remaining molariform teeth, the 1st cusp [paraconid] appears to be much reduced or wanting. The lower jaw has a rather primitive form, elongate and slender with strong coronoid process and quite small angular process; its condyle lies at a level scarcely higher than the cheek teeth.

The following comments may be made upon the above. *Ictops* is an Oligocene genus, *Palæictops* a Lower Eocene and Paleocene genus. *Ictops* is known from many complete skulls and most of the skeleton; the skull of *Palæictops* (*Diacodon*) is figured in this article. *Ictops* has, like *Leptictis*, two upper incisors and separate temporal crests; *Palæictops* (= *Diacodon*) has three upper incisors and a single sagittal crest. The cheek teeth in the two genera are practically identical. (All these data are to be found in previously published articles by Cope, Leidy, Scott, Douglass and myself.) Whether the construction of the molars is a derivative of that of *Galeopithecus* or vice versa appears to the present writer to be purely speculative. Both types are present in the Lower Eocene (*Diacodon*, *Plagiomene*), and if the leptictid type is recorded from the Paleocene while the other is not,

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<sup>1</sup> Dr. Winge appears to be somewhat hypercritical in these emendations. He has himself proposed the name *Amphictidae* and finds no difficulty in accepting *Icticyon*, *Ictitherium*, etc. His emendation of *Leptictidae* is technically correct; the emendations of *Ictops* and *Palæictops* are not warranted, since in these instances the names are compounds presumably with the first syllable of *Ictis*, not with the whole word. *Ictidops* was proposed by Broom for a genus of Permian reptiles, but on this understanding is not preoccupied by *Ictops*.

it is probably a mere matter of accident, for a type of dentition which approaches the galeopithecoid is found in the still older Lance. The zalambodont and soricoid types of teeth appear to be equally ancient, and we know too little about the Mesozoic mammals for their phyletic relations to the early Tertiary types to be any better than conjectural.

Winge's arrangement of the Insectivora appears to be solely upon the basis of his theories of cusp evolution, and it is for this reason alone, as far as one can judge, that he places the highly specialized and peculiar *Galeopithecus* at the base of his phyletic tree. Undoubtedly there is a great deal of truth in Winge's insistence upon the antiquity of the outer cusps or styles in some at least of the mammalian races. But I have never believed that any one order of cusp evolution applies to all mammalian phyla, and the absurd results to which an uncritical dependence upon any theory of this kind will lead, are very well illustrated in the paper cited.

So far as the Leptictidæ are concerned, they are undoubtedly related in the structures of skull, teeth, and skeleton to the Erinaceidæ, share some of the specialized characters diagnostic of that family, and are not remote in dentition from such primitive genera as *Proterix*, *Gymnura* and *Hylomys*. *Ictops*, however, at least, has a true ossified tympanic bulla, delicate and loosely united to the skull so that it is only occasionally preserved; none of the genera have any false (alisphenoid) bulla.

Much may be said likewise in favor of including the Tillodontia among the Insectivora, so long as one considers only the teeth. The skulls and skeletons of *Esthonyx* and *Tillotherium*, so far as I have examined them, afford no diagnostic insectivore characters. They share indeed a great many primitive characters with some or all of the Insectivora. But the same may be said of all Paleocene and most Lower Eocene mammals. If they are not allowed a separate order, their most convenient place is doubtless with the Insectivora.

The inclusion of the Peripitychidæ (including the Miocænidæ but exclusive of *Ectoconus* which Winge refers to the Condylarthra) and of the Tæniodonta in the Insectivora, and the characterization of them as forming with the leptictids and tillodonts "a little group of closely related families," are, however, quite impossible, and deserve almost to be ranked with the taxonomic eccentricities of Steinmann and Jaekel. It is difficult to find in Winge's discussion of them any real reasons for associating any of these families with the Insectivora, except a recognition that the teeth are all more or less of the "tritubercular" type or clearly derivatives from it. But this is true of all early Tertiary mammals, a fact upon which American palæontologists have been insisting for many years. The earliest creodonts, condylarths, perissodactyls, artiodactyls, primates, amblypods, etc. show

this derivation quite as clearly. On the other hand, there are marked differences in skull and skeleton structure, especially in the characteristic construction of manus and pes, among types which are often difficult to distinguish by their cheek teeth; and, for this reason, the teeth alone are not a safe guide to affinities. Winge apparently attaches little weight to these features; and he wholly ignores another important part of the evidence, the relative geological age of the various genera. All of them in his view are from the "American Tertiary." In other words, his derivations are purely structural, not genetic, and he makes no use at all of the direct or approximate genetic phyla which have been studied so extensively in this country and elsewhere, and which should serve to test and check his theories of structural derivation.

The results of such checking of theories by facts would be somewhat unfortunate for certain of his views upheld in this paper and elsewhere. He regards the outer styles of the upper molars as original elements, and ranks those genera which have them strongly developed as more primitive than those in which they are weak or absent. Now many instances can be cited among phyletic series which are *known* to be true series by the succession in time and gradual modification in *all parts of teeth, skull and skeleton* from the first to the last member, in which the styles are progressively developed — none in which they progressively disappear. He regards the molariform fourth premolar as primitive and the simple fourth premolar as a derivative of it. Many true genetic series can be cited which show the fourth premolar becoming progressively molariform — none in which it is at first molariform and becomes progressively simple.<sup>1</sup>

With regard to the Periptychidæ and Mioclænidæ, the facts are as follows: *Ectoconus*, which Winge says is known only from parts of the jaws, is in fact known from a complete skeleton not yet described, but some characteristic bones of the skeleton were described many years ago. *Periptychus*, which he says is known only from pieces of upper and lower jaws and a few isolated parts of the skeleton, is, in fact, known from the greater part of

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<sup>1</sup> It might be objected indeed that the succession of genera forming these phyla were arranged in it upon the theory that the fourth premolar, at first simple, has become molariform; that if arranged upon the opposite theory, an entirely different collation of genera would result; that the validity of the phyla depends therefore upon the validity of the theory of cusp sequence. But in every instance where the skulls and skeletons are completely known, the validity of the accepted arrangement is confirmed by the coordinate gradual modification of all other parts of skull, vertebrae, limbs and feet, so that it is amply proven to be correct.

Winge's theories have their place among other speculative hypotheses as to the origin of the several types of dentition that we find at the beginning of the Tertiary. But as a guide to the affinities of Tertiary and modern orders they are wholly misleading. It is noteworthy that Winge, Ameghino, and other authorities who have maintained various peculiar views as to the evolution of the mammalian molars, have either disregarded the evidence of the geologic succession or have been compelled to distort it in order to maintain their theories.

the skull, complete lower jaws, and the hind limb and foot and other parts associated<sup>1</sup> in every instance with the characteristic jaws and teeth. Both genera show throughout the skull and skeleton, and especially in the very characteristic construction of tarsus and phalanges, an unmistakable affinity to *Pantolambda*, also known from the complete skeleton, and through *Pantolambda*, are connected with the Amblypoda. The specific points of resemblance were stated by Osborn in 1898; much confirmatory evidence is afforded by the more complete specimens obtained in the last few years. They are not unguiculates but ungulates; the construction of the tarsus, while much less specialized than in *Coryphodon*, is very clearly advanced in that direction as compared with any generalized forms ancient or modern.

As to the smaller Periptychidæ, they are known chiefly from the jaws and poorly preserved skulls. The few diagnostic fragments of the skeleton show that they differed considerably from *Periptychus* in spite of the resemblance in teeth, but there is no evidence sufficient to disprove their reference to the same family.

*Miocænus* and its relatives are also known chiefly from the jaws and poorly preserved skulls; a few characteristic fragments of the skeleton show that the tarsus was more like that of the condylarths and early creodonts than that of Periptychidæ. The teeth do not resemble the Periptychidæ in any of the features of construction special to that group. Herein they differ from the smaller periptychid genera. The premolars indeed are more or less enlarged and inflated, and it appears to be upon this single feature, not peculiar to the Periptychidæ, that Winge bases his union of the Miocænidæ with that family. But in details of molar and premolar construction the Miocænidæ are much closer to the earliest phenacodonts, the hyposodonts and the creodont oxyclænids.

All of these Paleocene groups differ widely in skull and skeleton structure as well as in teeth from the contemporary Leptictidæ, also known from the complete skeleton, in which tibia and fibula are coössified distally, the astragalus of the characteristic insectivore type with broad shallow short trochlea defined internally by a sharp crest, no astragalar foramen, etc.

The position of the Tæniodonta is not so clear. Dr. Winge regards them as all representing one phylum and does not hesitate to derive the Puerco "*Hemiganus*" (= *Wortmania*) from the Torrejon *Conoryctes*. In fact they represent two distinct phyla diversely specializing; *Conoryctes* is decidedly more specialized in most characters than the older *Hemiganus*, but in a

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<sup>1</sup> I. e., positively known to belong to the same individual.

different direction. The oldest stages of each phylum, *Onychodectes* and *Wortmania*, both have very primitive teeth, but little different from the Creodonts; but the astragalus of *Onychodectes* and the metapodials of *Wortmania* differ much more from the creodont type and approach the primitive edentate type as exemplified in the armadillos. This may, however, be a matter of parallelism; the evidence is not sufficient to decide. The further specialization of the stylinodont phylum, superficially resembling the ground-sloths, is unquestionably a matter of parallelism. It is unfortunate that all the arguments presented by Scott, Winge and Ameghino against the edentate affinities of the Tæniodonta have been directed against the quite untenable position that the stylinodonts were the direct ancestors of the ground-sloths. It is a simple matter to show that this could not have been the case; no palæontologist save Wortman has maintained that they were so. But this does not at all disprove the view that they were a side branch from primitive armadilloid edentates, from near the base of the ordinal phylum, the stylinodonts paralleling the ground-sloths, the conoryctids paralleling the armadillos. This is the view tentatively held by Dr. Wortman's colleagues, whom Winge cites as accepting Wortman's own conclusions. The arguments pro and con will be presented in describing the more complete tæniodont material recently secured by the American Museum expeditions. It is sufficient for the present to observe that none of the arguments presented by the three writers above mentioned are in any degree valid against it. It might seem that Winge, who admits *Manis* and even *Orycteropus* to the Edentata, is quite unduly critical in excluding the tæniodonts and even *Metacheiromyidæ* from the order; but an examination of his argument shows that his acquaintance with them is rather slight and not altogether accurate.

It must be observed, however, that the reference of the *Metacheiromyidæ* and tæniodonts to the Edentata, *sensu lato*, which I have advocated, does not exclude affinity to the Insectivora. I regard the two orders as derived from a common Cretaceous ancestry and their representatives in the Paleocene as rather nearly related — more nearly, perhaps, than to the condylarth-creodont group or the taligrade-amblypod group or the primate group. Dr. Winge is by no means so far wrong in referring the tæniodonts to the Insectivora as he is in referring the peripitychids to this order.

## ORDER AND AFFINITIES UNCERTAIN

**CREOTARSUS**,<sup>1</sup> NEW GENUS

*Type*.—*C. lepidus*, *infra*.

*Generic characters*.—Dentition  $\overline{??.4.3}$ .  $P_1$  one-rooted;  $p_{2-4}$  two-rooted, subequal, spaced,  $p_4$  with strong well separated metaconid (deuteroconid), small paraconid and broad short heel. Molars with protoconid and metaconid of equal height, widely separate, paraconid small, low, internal in position on  $m_1$ , doubtfully present on  $m_{2-3}$ . The trigonid is rather high and wide; talonid basined, equal in width to trigonid; hypoconid strong, set well out; entoconid marginal, small; hypoconulid rudimentary.  $M_1$  and  $m_2$  similar in size and construction;  $m_3$  longer, with (?narrow) heel. Canine probably small; incisors unknown. Jaw slender, elongate, with broad angle not incurved. Posterior mental foramen beneath anterior part of  $p_3$ . Tarsus of creodont type in some particulars; the astragalus with oblique, moderately grooved trochlea, distinct astragalar foramen, calcaneum with well-marked fibular facet, cuboid with astragalar facet of moderate width, shaped as in Artiodactyla. Metatarsal IV of moderate length, its facets and those of the cuboid indicating a well developed (unreduced) Mt. V.

The ordinal position of this genus is very doubtful. The peculiar astragalo-cuboid articulation approximates the characteristic type of the Artiodactyla; but the astragalus exhibits very slight approach, if any, to the artiodactyl form. The calcaneo-fibular facet has not the peculiar form and relations seen in that order; it is much more like the corresponding facet in *Limnocyon* and other creodonts. The long slender jaw, spaced and rather long premolars, and the construction and proportions of the molars are suggestive of *Diacodexis*; but the peculiar double-cusped  $p_4$  is quite unlike any of the genera positively known to be dichobunids,<sup>2</sup> while suggesting Insectivora or Condylarthra. While it is not impossible that it has some affinities to the Artiodactyla, this appears unlikely.

Comparison with the Condylarthra is equally unsatisfactory. There are no very decisive characters in the teeth and jaw to exclude it from this order, but there is certainly nothing characteristically condylarth about them; in the tarsus, the astragalus agrees fairly well, but the peculiar cuboid and the broad fibular articulation are unlike the known groups of this order.

<sup>1</sup> Creo-donta, *ταρσος*, foot, in reference to the creodont type of tarsal bones.

<sup>2</sup> But compare *Sarcolemur*.

From the Creodonta the genus is distinguished by the general type of molars and  $p_4$ , and the small canine (inferred from the slenderness of the jaw under  $p_1$ ); the tarsus is of creodont type; the peculiar naviculo-cuboid facet is of somewhat the same type as in the Mesonychidæ; but there is no near approach to any one of the creodont families in the tarsal construction.

Primate affinities are excluded by the long slender jaw, and the radically different type of tarsus.

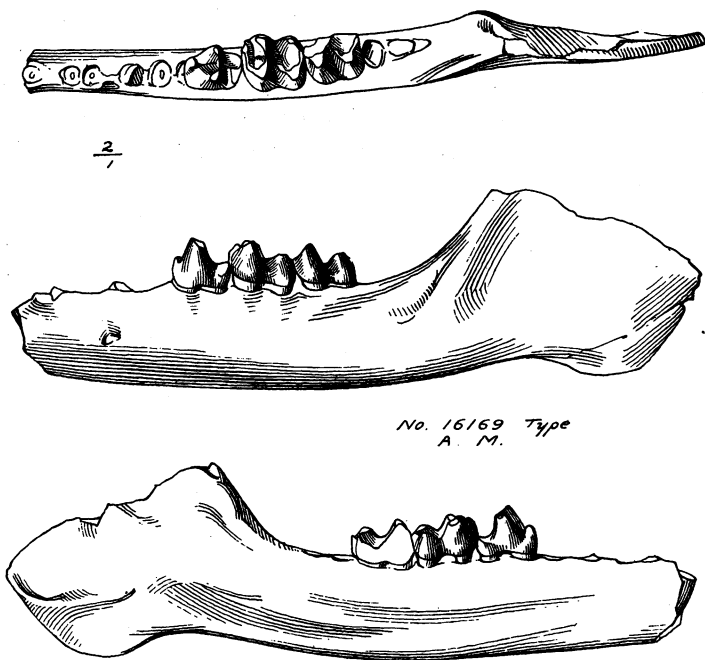


Fig. 35. *Creotarsus lepidus*. Lower jaw of type specimen, crown, outer and inner views, twice natural size. Lower Wasatch, Gray Bull horizon, Bighorn basin, Wyoming.

The lower jaw is perhaps nearer to the insectivore type, especially to the Leptictidæ, than any other, and it is chiefly the peculiar tarsus that makes the ordinal reference of the genus difficult. It is not far outside the range of construction of the tarsus in different groups of Insectivora; but it is not of the characteristic insectivore type, and on this account I am compelled to regard the reference of *Creotarsus* to this order as untenable.

Whatever its ordinal position may be, its affinities with any known mammals appear to be rather distant. It is on this account that it is so

difficult to place. *Apheliscus* has some degree of resemblance, but probably this is rather superficial. Relationships to the Leptictidæ, suggested by the teeth, are not at all confirmed by the tarsal characters.

***Creotarsus lepidus*, new species**

Fig. 35-36

*Type*.— Amer. Mus. No. 16169, lower jaw, tarsal bones, and other fragments from the lower Gray Bull beds in the Bighorn Basin.

*Specific characters*.—  $P_1-m_3 = 27$  mm.; other characters included in generic description.

Besides the lower jaw the specimen includes calcaneum, astragalus,

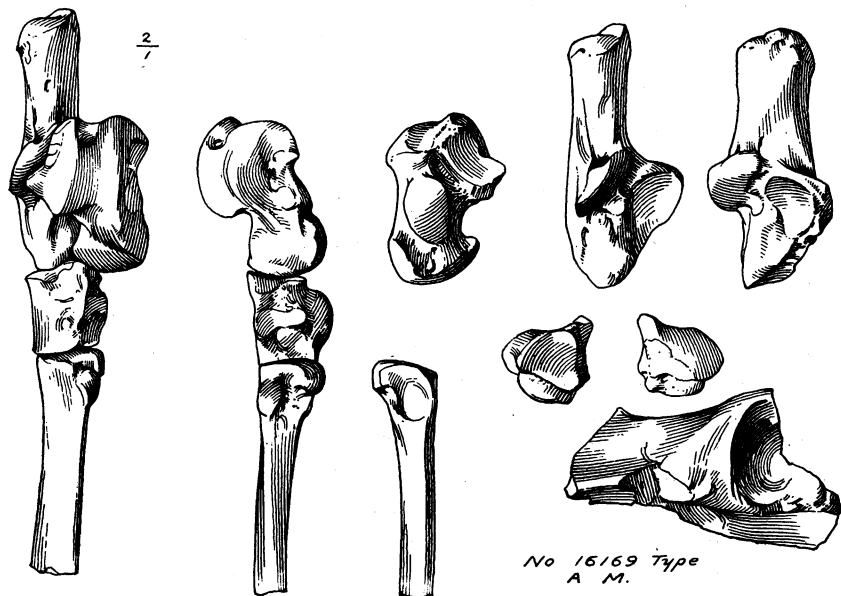


Fig. 36. *Creotarsus lepidus*. Parts of the hind foot and fragment of pelvis. Type specimen, same as Fig. 35, twice natural size. From left to right the figures are (1) dorsal view of astragalus, calcaneum, cuboid, and fourth metatarsal; (2) inner view of astragalus, cuboid and mt.iv; (3) palmar view of astragalus and outer view of mt.iv; (4) dorsal and inner views of calcaneum above, distal and proximal views of cuboid in center, and fragment of pelvis below.

cuboid, most of the fourth metatarsal, two fragments of the proximal end of the femur, and part of pelvis with acetabulum, all found together without association of any other remains, so that there is no reasonable doubt of their pertaining to one individual.

## GLIRES (RODENTIA)

**Ischyromyidae** Alston, 1876

This order, so numerous and diversified in the later Tertiary faunæ, is represented in the Middle and Lower Eocene by three or more nearly allied genera of a single family. Of these, *Paramys* is the best known. It is also the earliest to appear, and probably represents the primitive type of the Ischyromyidae. Rodents are unknown in the Paleocene, first appearing in the Sand Coulée level of the Wasatch along with Artiodactyla, Perisodactyla and primates, but are not found in great abundance in the Wasatch faunas. They are all small species of *Paramys*, except for one minute and rare form from the Lost Cabin beds which I have referred to *Mysops*.

The Lower Eocene rodents, so far as known, do not come any nearer to the primitive tritubercular type of dentition than do their successors in the Middle Eocene. The differentiation of the order is evidently of much earlier date than its first appearance in our Tertiary succession.

**PARAMYS** LEIDY, 1871

*Type*.— *P. delicatus* Leidy from the Middle Eocene (Bridger) of Wyoming.

*Generic characters*.— Dentition  $\frac{1.0.2.3.}{1.0.1.3.}$ . Superior molars tritubercular, hypocone absent or small; lower molars with broad and shallow basin heels, entoconid a distinct cusp,  $pa^d$  vestigial or closely connate with metaconid. Incisors typically of moderate width.

The skull and skeleton characters of this genus were fully described in a former article in this Bulletin.<sup>1</sup> The Lower Eocene species are mostly of small size, with low-crowned teeth and marginal cusps. They were revised by Loomis in 1907,<sup>2</sup> but the true correlation of the horizons was not correctly understood at that time, and the additional material somewhat alters the scope and validity of the species as distinguished by Dr. Loomis.

**Paramys major quadratus** Loomis

*Type*.— Amherst Mus. No. 226a, lower jaw from ?Lost Cabin beds of Buffalo Basin, Wyoming.

*Specific characters*.—  $P_4-m_3 = 18$  mm. Otherwise as in *P. major*.

<sup>1</sup> Matthew, 1910. Osteology of *Paramys* and affinities of the Ischyromyidae. Bull. Amer. Mus. Nat. Hist., XXVIII, pp. 43-71.

<sup>2</sup> Loomis, 1907. Wasatch and Wind River Rodents. Amer. Jour. Sci., XXIII, pp. 123-130.

The locality as given by the describer indicates that the type is from the upper Wasatch of the Bighorn Valley, probably from the Lost Cabin level, although it may be Lysite. The only specimens in our collections that agree in size are from the Lost Cabin, No. 14718, and Lysite, No. 14722, of the Wind River Basin, both lower jaws; a fragmentary skeleton, No. 15605, from the Lost Cabin of Buffalo Basin appears to be a little smaller, agreeing approximately with Loomis's *P. major* in size. There do not seem to be any constant characters except size to distinguish this species from *P. major*, of which it is very probably merely an advanced mutant.

### ***Paramys major* Loomis**

*Paramys major* LOOMIS, 1907, Amer. Jour. Sci., XXIII, p. 128, fig. 5; *Plesiarctomys delicatior* COPE, 1881, Bull. U. S. Geol. Geog. Sur. Terrs., VI, p. 184; 1885, Tert. Vert., p. 182, Pl. xxiva, figs. 11-13. Not *P. delicatior* of Leidy.

*Type*.—Amherst Mus. No. 327a, a lower jaw from Lysite beds of Wind River Basin.

*Specific characters*.— $P_4-m_3 = 16.5$  mm. Molars robust, cusps marginal, basins broad and shallow.

Thirteen specimens from the Lost Cabin beds and three from the Lysite of the Wind River Basin, twelve from the Lysite of the Bighorn Basin, and two from the upper beds of the New Mexican Wasatch are referable to this species. It is the common species of the Lysite and Lost Cabin. In the Gray Bull horizon it is relatively scarce, although some specimens agree with it so far as comparisons are practicable. It is more robust than *P. copei* and the skeleton parts are uniformly larger; but the construction of the teeth shows no constant distinctions.

### ***Paramys copei* Loomis**

*Paramys copei* LOOMIS, 1907, Amer. Jour. Sci., XXIII, p. 128; *Plesiarctomys delicatissimus* COPE, 1885, Tert. Vert., p. 179, Pl. xxiva, figs. 1-10. Not *P. delicatissimus* Leidy (*auct. Loomis*).

*Synonym*.—*P. primævus* Loomis, *bicuspis* Loomis, *loc. cit.*

*Type*.—Amer. Mus. No. 4755, skull, jaws, and parts of skeleton from Lost Cabin beds of Wind River Basin.

The characters which Dr. Loomis has used to distinguish *P. primævus*, *bicuspis* and *copei* do not appear to be very constant and are so easily obscured by the wear of the teeth that they do not afford any satisfactory separation. There is little but size and robustness of teeth to distinguish *P. major* from this species, and these characters are not wholly constant.

From *P. delicatior* they are distinguished by inferior size, shallower basins, more marginal and smaller cusps, and the surface of the unworn teeth less rugose. *P. delicatissimus* has decidedly larger cusps, deeper and more contracted basins, smaller  $m_3$ ,  $p_4$  with anterior cusp narrow and simple.

It is doubtful whether this species is more than a smaller variety or subspecies of *P. major*.

In synonymizing the three species described by Loomis in his paper of 1907, I have given preference to *P. copei* as it rests upon a much more complete type specimen, disregarding page priority for this reason.

To *P. copei* are referred four specimens from the Lost Cabin and two from the Lysite beds of Wyoming, and two from the lower (Almagre) beds of the New Mexican Wasatch. No. 14716 from the Lost Cabin beds consists of teeth and fragmentary skeleton; No. 16299 is a skull and jaws; the others are mostly lower jaws. Twelve jaws from the Gray Bull horizon of the Wasatch are referable to it, but it has not been found in the lowest level.

#### ***Paramys excavatus* Loomis**

*Paramys excavatus* LOOMIS, 1907, Amer. Jour. Sci., XXIII, p. 129, fig. 6.

*Type*.—Amherst Mus. No. 327, a lower jaw from the Lysite beds of the Wind River Basin.

*Specific characters*.— $P_4-m_3 = 12$  mm. Cusps small, marginal, basin broad, shallow and smooth.

A lower jaw with probably  $dp_4$  and  $m_{1-2}$  from the Lost Cabin beds near Wolton on Alkali Creek in the Wind River Basin is doubtfully referable to this species. No. 15636 and two unnumbered jaws from the Lysite of Fifteen Mile Creek in the Buffalo Basin are more nearly in accord with the type.

Four fragmentary specimens from the Systemodon zone of the Gray Bull and two from the Sand Coulée beds may be provisionally referred to this species, but the reference is based chiefly on size.

#### ***Paramys atwateri* Loomis**

*Type*.—Amherst Mus. No. 180, a lower jaw with  $m_{1-2}$  from the ?Gray Bull beds in the Bighorn Basin.

*Specific characters*.— $P_4-m_3 = 12.5$  mm., cusps large, basin contracted, metastylid comparatively large.

No. 14724, a lower jaw from the Lost Cabin beds at Davis' ranch on Alkali Creek, Wind River Basin, is provisionally referred to this species.

It is considerably smaller, the teeth measuring only 10 mm. ( $p_4-m_3$ ), but agrees with *P. atwateri* in the other characters specified by Dr. Loomis. Some of the specimens referred to *P. excavatus* may perhaps pertain to this species.

***Paramys buccatus* Cope**

*Plesiartomys buccatus* COPE, 1877, Ext. Vert. New Mex., p. 171, Pl. XLIV, fig. 8; 1885, Tert. Vert., p. 179; (*?Sciuravus*) LOOMIS, 1907, Amer. Jour. Sci., XXIII, p. 130; (*Paramys*) MATTHEW, 1910, Bull. Amer. Mus. Nat. Hist., XXVIII, p. 51.

*Type*.—U. S. Nat. Mus. No. 1129, upper jaw with  $p^4-m^2$  from Wasatch of New Mexico.

*Specific characters*.— $P_4-m_3$  (calculated from the upper teeth of type) = 10 mm.  $P^4$  as large as  $m^1$ .

No topotypes have been found; a jaw from the Lysite with  $p_4$  and alveoli of  $m_{1-3}$ , and a jaw from the Sand Coulee beds with  $p_4-m_3$ , agree in size with the type, but are referred only provisionally. The species appears to be scarce. An upper jaw, No. 15710, from the Systemodon zone is of about this size, but does not agree closely with the type. All the above specimens are from the Bighorn and Clark Fork Basins.

***Paramys murinus*, new species**

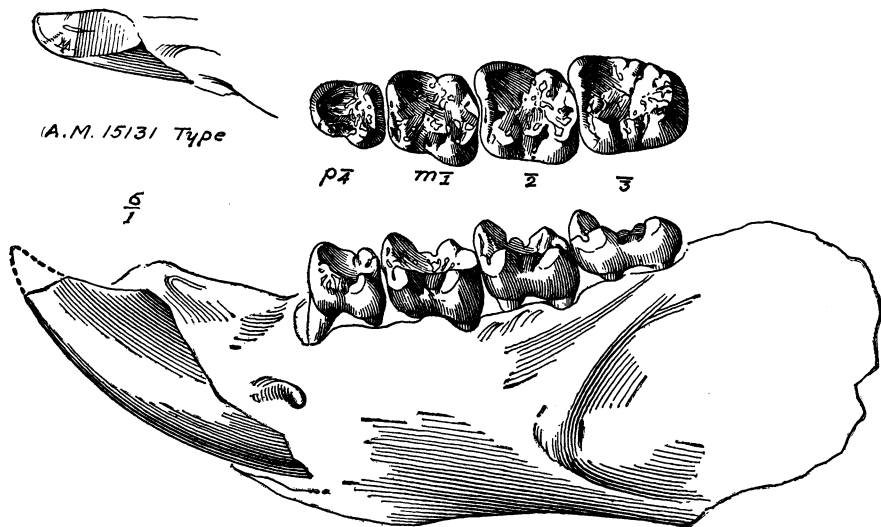


Fig. 37. *Paramys murinus*. Lower jaw of type, external view, and crown view of teeth, left ramus, characters supplemented from the right ramus. Six times natural size. Gray Bull horizon of the Bighorn Wasatch.

*Type*.—Amer. Mus. No. 15131, lower jaws and part of maxilla from Gray Bull beds of the Wasatch formation, Bighorn Basin, Wyoming.

*Specific characters*.— $P_4-m_3 = 8.5$  mm. Premolars relatively small,  $p^3$  minute,  $p^4$  much smaller than  $m^1$ ; hypocone of  $m^1$  distinct but much smaller than protocone; protoconid of  $p_4$  small, closely connate on flank of metaconid.<sup>1</sup> Molars longer than wide, heel of  $m_3$  somewhat narrowed. Incisors narrow.

This species differs from *P. buccatus* in its smaller size and reduction of premolars. It is much smaller than any other described species of *Paramys* and agrees with *Sciuravus* in size and in the narrow incisors, but the pattern of the cheek teeth is very different and typically *Paramys*. It probably belongs to the *P. buccatus* group.

#### **MYSOPS** LEIDY

*Type*.—*M. minimus* Leidy, 1873, from the Bridger formation (Middle Eocene) of Wyoming.

*Generic characters*.—"A smaller animal than *Sciuravus*, with narrower teeth, the upper molars less quadrate, the inner cusps less distinctly separate, the center of the crown more basined. Lower molars narrower, the anterior pair of cusps higher and more crested, the entoconid more central in position. Construction of antorbital region as in *Sciuravus* and *Paramys*."<sup>2</sup>

The above characterization is based upon referred material of the typical species. I refer provisionally to this genus a species from the Lost Cabin beds which may be structurally ancestral and can hardly be placed in *Paramys*.

#### **Mysops kalicola**, new species

Fig. 38

*Type*.—Amer. Mus. No. 14731, lower jaw with  $p_4-m_2$  from the Lost Cabin beds near Wolton, Alkali Creek, Wind River Basin, Wyoming.

*Paratypes*.—Nos. 14729, 14730, lower jaws from the same horizon and locality.

*Specific characters*.— $P_4-m_3 = 6.3$  mm. Lower molars quadrate, with anterior and posterior transverse crests, extero-median cusp, prominent anterior and distinct posterior cingula as in the type species, but the crests lower and less perfected, the crown more flattened than in the type species.

<sup>1</sup> The metaconid or deutoconid is the principal cusp of  $p^4$  in rodents. See Wortman, 1903, Amer. Jour. Sci., XVI, p. 367.

<sup>2</sup> Matthew, 1910, Bull. Amer. Mus. Nat. Hist., XXVIII, p. 60.

This species resembles the earlier species of *Paramys* in the low and imperfectly crested cusps and the tendency to form a broad, shallow basin crown with moderate wear.

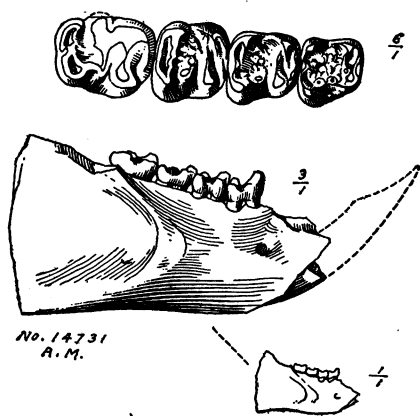


Fig. 38. *Mysops kalicola*. Lower jaw, type specimen, three times natural size; with crown view of molars, six times natural size. The third molar is supplied from the paratype, No. 14729, and is more worn by use than the teeth of the type. From the Lost Cabin zone on Alkali Creek in Wind River basin.

Geological Distribution of *Paramys*, *Mysops* and *Sciuravus* and of the Lower Eocene Species, as Shown by American Museum Specimens

	Sand Coulee	Gray Bull	New Mexican Wasatch	Lysite	Lost Cabin	Bridger	Uinta
<i>Mysops</i>					×	×	
<i>M. kalicola</i>					3		
<i>M. minimus</i>							
<i>Paramys</i>	×	×	×	×	×	×	×
<i>P. quadratus</i>				1	1		
<i>P. major</i>			2	15	13		
<i>P. copei</i>		12	2	2	4		
<i>P. excavatus</i>		?4		3	?		
<i>P. buccatus</i>	?1	?1	×	?1	?		
<i>P. atwateri</i>		?			?		
<i>P. murinus</i>		1					
<i>Sciuravus</i>						×	×

## EDENTATA

**PALÆANODONTA**, NEW SUBORDER

Ancestral edentates with nomarthrous vertebræ, no ischio-caudal symphysis, canine teeth present and enamel-bearing, no calcified dermal shield, otherwise as in Loricata but less specialized than the Miocene and later members of that group.

Osborn in 1904<sup>1</sup> placed *Metacheiromys* under the Loricata. Its edentate affinities are questioned by Ameghino,<sup>2</sup> Scott,<sup>3</sup> and Winge,<sup>4</sup> and it apparently represents an aberrant side branch not directly ancestral to the South American Tertiary loricates. It is convenient to rank it for the present in a distinct suborder, whose relations to the Loricata are, I suspect, much like those of the creodonts to the fissipede Carnivora. The only family at present known is the Metacheiromyidæ, which, like the hyænodonts, oxyænids or mesonychids among the Creodonta, is an aberrant side branch, although primitive in most features, and affords important clues as to the derivation and affinities of the Xenarthra and Pholidota.

The Tæniodonta are also, in my opinion, probably an aberrant side branch of the primitive Edentata, and it may be possible in the future to unite the palæanodonts with this group. But at present I see no good evidence for such a step, and, pending a re-examination of the tæniodonts, the present arrangement is less open to objection. The edentate affinities of the Metacheiromyidæ are much clearer than those of the tæniodonts, and they approach nearest to the armadillos, which are regarded by all authorities as the oldest and most primitive group of the undoubted Xenarthra. The tæniodonts were referred by Wortman to the edentates chiefly upon the evidence of resemblances between the stylinodonts and the ground sloths which I think must be explained in large part as convergent, since the sloth group appears to be a derivative of the armadillo group, and there

<sup>1</sup> Osborn, H. F., 1904. An Armadillo from the Middle Eocene (Bridger) of North America. Bull. Amer. Mus. Nat. Hist., XX, pp. 163-165.

<sup>2</sup> Ameghino, F., 1905. An. Mus. Nac. Buenos Aires, XIII, p. 234. Dr. Ameghino reserves judgment as to its affinities until illustrations are published, regards the presence of large compressed enamelled canines as a "conformation tout-à-fait extraordinaire pour un Edenté primitif," but suggests that it may be related to *Galliatatus* of the European early Tertiary — which he considers a loricata. This was a rather shrewd guess, not so far from the conclusions reached in this discussion.

<sup>3</sup> Scott, W. B., 1913. History of the land mammals of the Western Hemisphere, p. 617. "While these curious animals may very possibly have been referable to the Edentata and at all events had several features suggestive of relationship to that order, it can hardly be maintained that they were unequivocal members of it."

<sup>4</sup> Winge, Herluf, 1915. Jordfundne og nulevende Gumlere fra Lagoa Santa, p. 307. Dr. Winge concludes that *Metacheiromys* has probably nothing to do with the edentates.

are comparatively few points of affinity between stylinodonts and this more ancient group of the undoubted Xenarthra. The most earnest defender of Wortman's view must admit that there is a good deal of overstatement in his argument, and allow some justice in Winge's recent criticism. But it appears to the present writer that Wortman's critics have gone to the opposite extreme in their views.<sup>1</sup>

### **Metacheiromyidae** Wortman, 1903

Upper and lower canines sharp, compressed, laniary, post-canine teeth reduced or absent, a horny plate probably replacing them. No incisors. Fore and hind feet armadilloid in type, with four or five digits on manus and pes, the lateral digits reduced, the inner possibly vestigial.

The reference of this family to the Edentata was made by Osborn in 1904, upon the basis of two well preserved skeletons of *Metacheiromys*. Owing to the fact that only the preliminary diagnoses of these skeletons have been published, and those without illustrations, the propriety of this reference has been denied. I believe, however, that the publication of the full description and figures will place it beyond reasonable doubt.

In the Gray Bull and Clark Fork horizons of the Wasatch are found species of a more primitive genus of this family. The upper teeth, in *Metacheiromys*, are reduced to one or two vestigial stumps with the exception of the sharp angulate canines. In the new genus they form a series of certainly four, probably six or more, post-canine teeth, represented in our specimens only by alveoli, but of considerable size. The skeleton parts, including the highly characteristic metapodials, are very like the Bridger genus, but less specialized.

### **PALÆANODON**,<sup>2</sup> NEW GENUS

*Type*.—*P. ignavus*, new species, from Lower Eocene Gray Bull beds of the Bighorn Basin, Wyoming.

*Distinctive characters*.—Cheek teeth small, one-rooted, but less reduced than in *Metacheiromys*.

<sup>1</sup> See Wortman, J. L., 1897, Bull. Amer. Mus. Nat. Hist., IX, pp. 59–110, text figs. 1–36.

Ameghino, F., 1905, An. Mus. Nac. Buenos Aires, XIII, pp. 230–234.

Scott, W. B., 1904, Rep. Princ. Exped. Patagonia, V, p. 361.

Gregory, W. K., 1910, Bull. Amer. Mus. Nat. Hist., XXVII, p. 340.

Scott, W. B., 1913, History of the Land Mammals of the Western Hemisphere.

Winge, Herluf, 1915, Jordfundne og nulevende Gumlere fra Lagoa Santa, p. 300.

The affinities of the Tæniodonta can best be determined after the new material from the Paleocene horizons has been described in a revision of the Puerco and Torrejon faunas, shortly to be undertaken by the present writers. Until then, detailed critical consideration of Ameghino's, Scott's and Winge's arguments is postponed.

<sup>2</sup> Gr. παλαιος, ancient; ἄ, without; ὀδόν tooth; i. e., ancient edentate.

**Palæanodon ignavus**, new species

Figs. 39-56, 61-62, 65-68

*Type*.—Amer. Mus. No. 15086, skull, vertebræ, foot bones, and other fragments of skeleton, from the Systemodon zone of the Wasatch in the Bighorn Basin, Wyoming.

*Paratypes*.—No. 15698, part of lower jaw; No. 15699, part of lower jaw, ulna, and fragments of humerus and femur; No. 16831, part of lower jaw with several limb and foot bones; No. 15137, fragmentary skeleton, including most of the vertebræ and limb bones and parts of the feet, but no skull parts; No. 15088, limb bones and parts of foot bones; No. 16832, parts of limb and foot bones.

*Skull* (Figs. 39, 40).—The front and top of the skull are broken and weathered and all parts of the type are partly buried in a hard sandy matrix. The front teeth are not preserved, but on one side of the skull the palate is complete as far forward as the anterior part of the premolar region. Four alveoli are shown, two anterior to the infraorbital foramen, the others behind it. There is no indication of the alveolus of the large caniniform tooth which is so prominent in *Metacheiromys*; if present, this tooth must have been considerably in advance of the four whose alveoli appear. The anterior end of the maxillary-palatine suture is just back of the posterior end of the tooth row. The outer part of the palate is a raised and flattened surface, rugose with irregular longitudinal ridges and grooves, apparently indicating a horny plate; the grooves are more prominent posterior to the tooth row and fade out opposite it, indicating that the plate was thicker posteriorly.

The infraorbital region of the skull is elongate, the cranial region short and wide. The natural brain cast indicates a smooth brain; the inter-orbital constriction is little marked; the occiput is broad and low, the occipital crest sharply defined.

The posterior part of the lower jaw shows a short condyle, somewhat expanded transversely, a small coronoid process and a wide flat angle, not incurved, but ending posteriorly in a prominent spine. The form of the angle is rather more like that of creodonts and primitive insectivores than armadillos. The dentigerous portion of the lower jaw (Fig. 41A) has the same peculiar form as in *Metacheiromys*, a heavy buttress extending along the inner side as far back as the base of the coronoid process, presumably for the support of a horny plate; but the alveoli of the cheek teeth are much larger than in the Bridger genus.

The condyles of the skull are large and wide, the basioccipital broad and flat, but narrowing sharply towards the basisphenoid suture, and the basi-

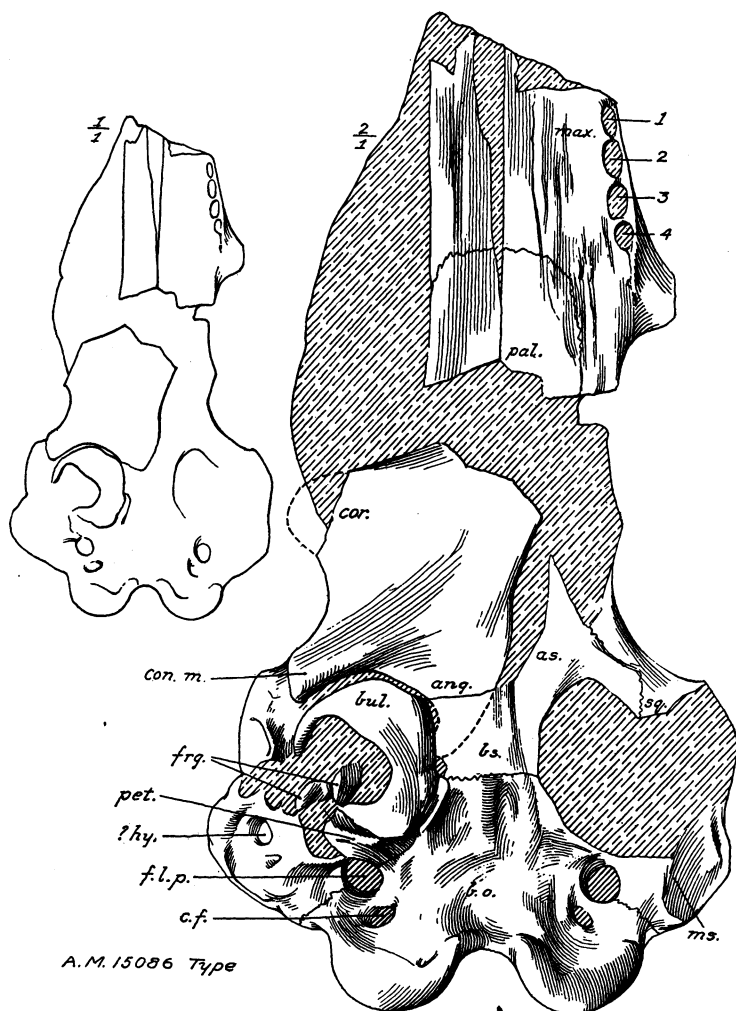


Fig. 39. *Palearodon ignavus*. Skull of type specimen, twice natural size. Lower Eocene, Big-horn basin, Wyoming. Palatal view, with posterior part of the lower jaw overlying the pterygoid region. 1, 2, 3, 4, alveoli of cheek teeth; *ang.*, angular process of lower jaw (the tip was lost during preparation but had about the form shown in dotted outline); *as.*, alisphenoid bone; *b.o.*, basioccipital; *bs.*, basisphenoid; *bul.*, tympanic bulla (probably composed chiefly of the os bullæ); *c.f.*, condylar foramen; *con. m.*, mandibular condyle; *cor.*, coronoid process of lower jaw; *f.l.p.*, posterior lacerate foramen; *frg.*, fragments possibly of tympanic ring; *hy?*, socket of hyoid arch; *max.*, maxilla; *ms.*, mastoid; *pal.*, palatine; *pet.*, petrosal crest; *sq.*, squamosal.

sphenoid is comparatively narrow. The space between the condyles and the otic region is considerably greater than in modern armadillos; the mastoid exposure is extensive on the side and base of the skull; it presents large posterior and inferior faces separated by a sharp crest. The condylar

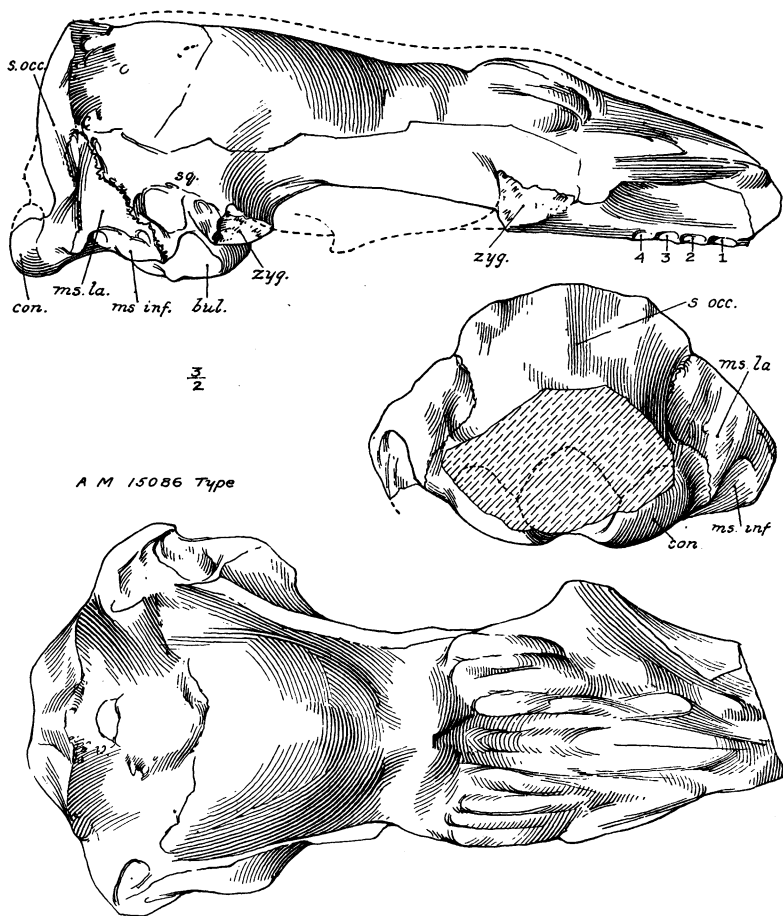


Fig. 40. *Palæanodon ignavus*. Skull of type specimen. Lateral, occipital, and superior views, three halves natural size. 1, 2, 3, 4, sockets of cheek teeth; *bul.*, tympanic bulla; *con.*, occipital condyle; *ms.inf.*, inferior exposure of mastoid; *ms.la.*, lateral exposure of mastoid; *s.occ.*, supraoccipital; *zyg.*, roots of zygomatic arch.

foramen is small and well in advance of the condyles; the posterior lacerate foramen is a little antero-external to it, circular in form as in most primitive placentals, not slit-like as in armadillos or in *Manis*. The tympanic

is expanded into an incomplete bulla supported apparently on the posterior and internal side by ossifications arising from the petrosal, but without any ossified meatus. In the condition of the tympanic region *Palæanodon* appears to be nearest to *Cabassous* among modern forms, but the anterior portion of the tympanic is more expanded, the mastoid exposure much more extensive.

*Tatusia* has a very narrow mastoid exposure and lacks the supporting plates for the tympanic; *Dasyppus* has a completely ossified bulla and bony meatus; so also has the larger species of *Metacheiromys*. *Manis* has a posterior crest on the petrosal that is not a little like *Palæanodon* but the lateral crests of the basioccipital in *Manis* are not present in *Palæanodon*. I cannot be certain whether the sphenoidal wings that extend the posterior nareal channel backwards to the basioccipital in *Manis* are present in *Palæanodon*; there are some doubtful indications of them, but the specimen is somewhat damaged and the hard matrix cannot be safely removed. The well defined occipital crest in *Palæanodon* is a very obvious difference from *Manis*, but there would seem to be a considerable amount of structural correspondence underlying the differences in the cranium.

In several respects the basicranial region of *Palæanodon* approaches the primitive type seen in creodonts and Insectivora. The form and relations of the condylar and posterior lacerate foramina, the extensive exposure of the mastoid and various details of sculpture of the adjacent parts are suggestive of Oxyænidæ, Leptictidæ and Pantolestidæ. They are presumably due to the comparative nearness of all these early Eocene placentals to a common ancestral stock. Modern armadillos have diverged widely both from each other and from *Palæanodon*; the Santa Cruz genera are less diverse, but Scott's figures and descriptions are not very satisfactory for exact comparisons, the specimens being presumably imperfect, so that I have found it better to compare with the modern genera.

If the skull of *Palæanodon* alone were known, one might hesitate to say whether the genus stood nearer fundamentally to the armadillos or to the pangolin, although superficially it is nearer to the former. The skeleton, as will be seen, approaches decidedly nearer to the armadillo type in the structure of the limb bones and of the manus and pes. The vertebræ retain, however, many important characters, for the most part obviously primitive, which are also retained in *Manis*. The characters regarded as primitive are those in which *Palæanodon* resembles the early Tertiary mammals in general, and in particular the Eocene and Paleocene Insectivora and Creodonta. They are not arbitrarily selected in accord with any particular theories of derivation, but are the characters which *Palæanodon* shares with all or most of these primitive placentals, as shown in various well preserved skulls and skeletons which I have studied.

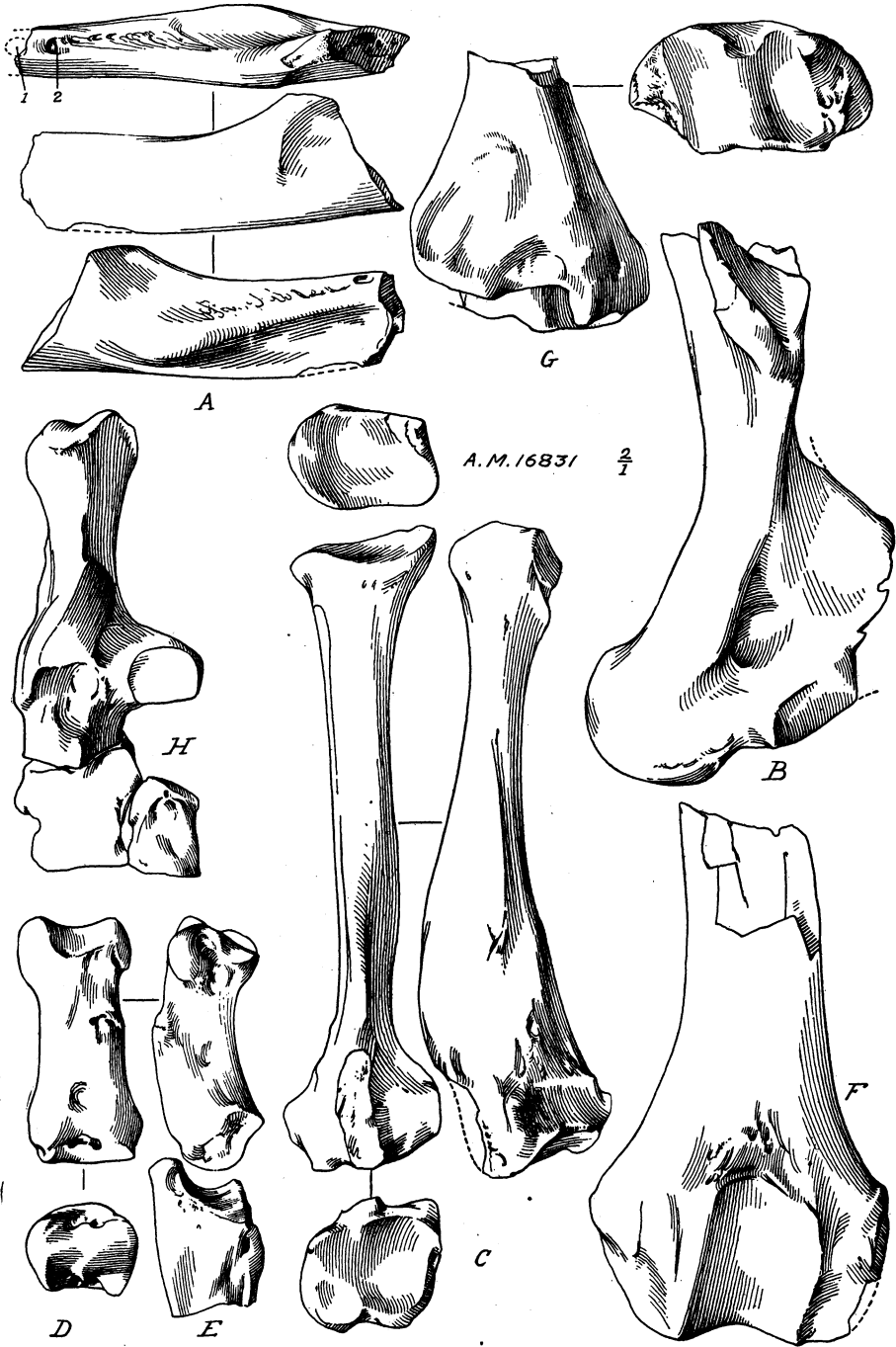


Fig. 41.

*Cervical vertebræ* (Fig. 42).—The cervicals are preserved in articulation with the skull in the type specimen, but part of the neural arches is weathered away and the remainder buried in such extremely hard matrix that it has not been practicable to clear them up. They are proportioned much as in *Tatusia* or *Manis*, much less shortened than in *Dasypus*. The cervicals are all free, instead of  $C_{2-4}$  being united as in the armadillos.

The centra are separate, short and wide and considerably flattened. The vertebrarterial foramen is present except upon the seventh cervical; but the spinal nerves make their exit through a notch in the posterior border of the arch, as in *Manis*, not through separate closed foramina for the upper and lower nerves, as in the modern armadillos. *Palæanodon* and *Manis* retain the primitive condition in this respect, so do the sloths.

The *atlas* is insufficiently exposed to show any very characteristic distinctions.

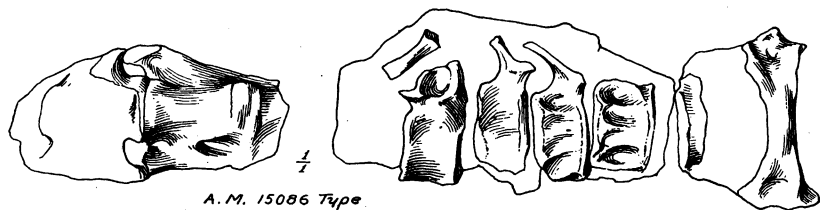


Fig. 42. *Palæanodon ignavus*. Cervical vertebræ and fragment of sacrum, type specimen. Inferior view, natural size.

The *axis* has the anterior part of the spine removed by weathering, but the posterior portion projects strongly backward, overhanging the third cervical, a primitive character retained in *Tatusia*, partly lost in *Manis*, wholly altered in *Dasypus*.

The remaining cervicals have rather slender transverse processes, those of the fourth and fifth strongly projecting backward; the sixth has the usual dependent plate and laterally projecting process; the seventh, a rather slender long process projecting slightly forward. So far as can be judged from the half-buried processes of these vertebræ, they are decidedly more

Fig. 41. *Palæanodon ignavus*. Lower jaw and fragments of skeleton, No. 16831, Lower Eocene, Gray Bull horizon of Wasatch, Bighorn basin. A, part of left lower jaw, superior, external and internal views with alveoli of molar teeth; B, part of humerus, front view, showing deltoid crest and entepicondyle; C, radius, anterior view to left, internal to right, above and below proximal and distal ends; D, third metacarpal, dorsal, inner and distal views; E, ungual phalanx of manus, side view; F, distal end of femur, front view; G, distal end of right tibia, anterior and distal views; H, calcaneum, cuboid, and ectocuneiform, dorsal views. All twice natural size.

like the normal primitive placental type in details than the simplified flattened plates of *Manis* or the short knobby processes of *Dasypus*. Both modern genera have departed far, in diverse directions, from the primitive type which is still largely retained in *Palæanodon*.

*Dorsal vertebræ* (Fig. 43).—The postcervical vertebræ are not preserved in the type except for a badly weathered portion of the sacrum. In No. 15137 a large number of vertebræ are preserved, sixteen presacral and twenty-seven postsacral, together with the sacrum, pelvis, hind limbs, fragments of the fore limbs, etc. The specimen includes, however, some fragments of a second individual of the same species (besides a few bones of a much smaller mammal and of a lizard) and is therefore unreliable as to the number of vertebræ present in different regions. The anterior dorsals are somewhat smaller than the cervicals; the centra slightly longer but of less

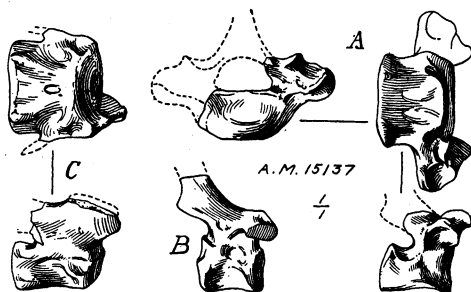


Fig. 43. *Palæanodon ignavus*. Dorsal vertebræ from No. 15137; A, first dorsal, inferior and right side views; B, second dorsal, anterior and right side views; C, posterior dorsal, inferior and right side views. All natural size.

width, much more convex inferiorly. The neural spines are preserved in only one of them, and portions of the arches in others. The first dorsal has the anterior zygapophyses of the usual wide-set cervical type, their articular facets oval and comparatively small but not so small as in *Dasypus*. The tubercular facet is notably large, strongly concave anteroposteriorly and faces downward. The spinal nerve issues through a deep notch, bordered by a sharp rising edge of the centrum behind it. The capitular facet is not concave or sharply defined. Another anterior vertebra, probably the second or third, has part of the neural spine preserved, enough to show that it was of the usual primitive backwardly directed type, trihedral in cross section, much like that of *Dasypus* but less depressed. The zygapophyses also compare with those of *Dasypus*; the centrum has the primitive semi-cylindrical form partly lost in *Manis* by flattening of the under surface, in

*Dasypus* by excavation of the upper surface. The spinal nerve issues through a notch as in *Manis* but more contracted and more sharply bordered by bony crests.

The posterior dorsals are of larger size, with somewhat broader and more flattened centra, small transverse processes apparently much like those of *Manis*, a deep constricted notch for the spinal nerve; no zygapophyseal facets are preserved on the vertebræ, but they were probably simple and nearly flat, as no other type is indicated among the fragments.

*Lumbar vertebræ* (Fig. 44).—The centra of four lumbar are preserved, and one with the arch nearly complete. The centra are somewhat longer than in *Manis*, more excavated on the under side and with the median inferior crest much more distinct. The transverse processes are slender, flattened, rise from the anterior end of the centrum, and are directed strongly forward as well as outward. The zygapophyses have large, nearly flat facets, in contrast with the strongly convex facets in *Manis*; the neural spine is apparently short, small, not expanded; the spinal nerves issue through a deep notch with margins more clearly defined than in *Manis*. There is no recognizable foreshadowing of the peculiar “xenarthral” articulations, the spinous zygapophysial process or the reduced transverse process seen in *Dasypus*, the two latter also present in the larger species of *Metacheiromys*; the vertebra differs from that of *Manis* chiefly in retaining primitive characters.

*Sacrum* (Fig. 48).—There are four sacral vertebræ, the two anterior being the true sacrals. The centrum of the anterior vertebra is like those of the lumbar, those of the two posterior vertebræ are like the caudal centra in type. The neural spines of all four are united into a single crest; the transverse processes of the two anterior are massive, united except for the usual foramina at the base for exit of the nerves, and expanded distally for sutural union with the ilium. The two posterior sacrals have their transverse processes united into a thin, flat, broad plate, perforated at the base for exit of the spinal nerves, its lateral margin approaching the superior border of the ilium but not united to it at the anterior end as it is in *Dasypus* and *Manis*. The anterior zygapophyseal facets are large, wide apart, face upward, and are but slightly concave.

*Caudal vertebræ* (Fig. 45).—The caudals are of large size and numerous,

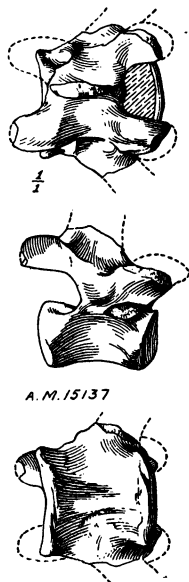


Fig. 44. *Palæanodon ignavus*. Lumbar vertebra from No. 15137. Superior right side, and inferior views, natural size.

and the tail was evidently long and heavy, comparing more nearly with *Manis* in relative size, and with *Dasypus*, less closely with *Tatusia*, in the structure of arches and transverse processes; the chevrons, however, are like those of *Tatusia* or of *Manis* but very unlike those of *Dasypus*. The anterior caudals have moderately long centra, comparable with the coössified caudals that constitute the posterior part of the sacrum of *Dasypus*, but with transverse processes of less width — wider than those of the first free caudals in *Dasypus* — and not united to the ischium nor, so far as known, to each other. Their zygapophyses are of moderate size, further apart than in *Dasypus*, not so far as in *Manis*, with slight curvature of the facets. In the anterior median caudals the zygapophyses are much reduced, and both these and the transverse processes appear to be much like the anterior free caudals of *Dasypus* except for the greater length of the centra

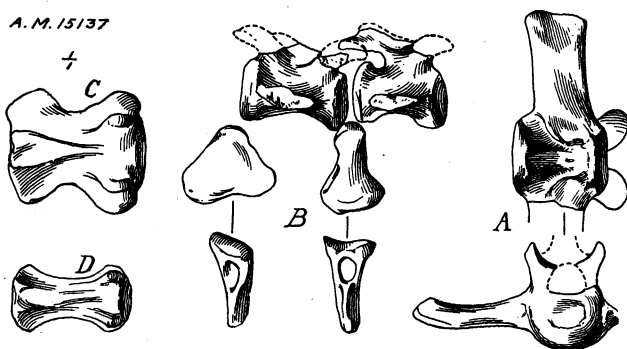


Fig. 45. *Palæanodon ignavus*. Caudal vertebræ from No. 15137; A, proximal caudal, inferior and anterior views; B, anterior caudals, right side views with chevrons in position, and anterior views of chevrons; C, median caudal; D, distal caudal, superior views. All natural size.

and the widely different type of chevron, which is very like that of *Tatusia*, differing from *Manis* chiefly in that the hæmal canal is (as in *Dasypus*) very much smaller. In *Dasypus* the inferior ends of the chevron bones are divergent and expanded for support of the tail-sheath.

The posterior median caudals have the zygapophyses and neural arch progressively reduced, the transverse processes changed in type, reduced in length and expanded anteroposteriorly to a horizontal plate, much as in the corresponding region of the tail in *Dasypus*; the vertebræ are of larger size throughout.

The distal caudals maintain their length but decrease in size, and the transverse plates and neural arches are progressively reduced, much after

the fashion of *Dasypus* save as to size. But, so far as can be judged, the tail must have been nearly as long and robust as in *Manis*; the caudals of *Manis*, however, maintain almost to the tip of the tail the same type of transverse process as in the anterior portion. In *Tatusia* the tail is perhaps somewhat longer than in *Dasypus*, but the ends of all the caudal transverse processes are expanded and modified for support of the tail-sheath.

*The fore limb.*—In the type specimen, No. 15086, the distal half of one radius, the distal end of the other, a ?cuneiform, one complete and one incomplete metacarpal represent the fore limb. In Nos. 15137 and 16831 some parts of the fore limb bones are preserved; but they are best shown in No. 15088, a partial skeleton, chiefly fore and hind limb bones.

*Humerus* (Figs. 41B, 61B).—The right and left humeri are preserved in No. 15088 but both, unfortunately, lack the proximal end. No. 16832 includes a humerus with the proximal end complete. The bone is nearly as large as in *Dasypus*, and like it in most features; the deltoid crest is prominent, broad and flattened, ending abruptly distally, but it is directed anteriorly instead of anteroexternally, and the external margin is continued proximally as a prominent crest instead of fading out toward the head as in *Dasypus*. The construction and proportions of the trochlea and entepicondylar foramen are very much alike in the two genera; the supinator crest is more prominent in *Palæanodon*, the inner epitrochlean process less massive. In *Manis* the deltoid process is reduced to a single crest, which is less prominent but continues down nearly to the entepicondylar bridge; the supinator crest is much reduced, the trochlea is of less width and greater depth.

*The ulna and radius* (Figs. 41C, 46, 62) are somewhat longer in the shaft than in *Dasypus*, and less massively proportioned. The olecranon lacks the peculiar inward twist of *Dasypus* but is like that of *Tatusia*; it is fully as long, extends directly in line with the shaft, and is transversely expanded toward the tip by inner and outer crests. The humeral articulation is less expanded than in *Dasypus*, but

its margins are damaged so that its complete form is not seen. The upper part of the ulnar shaft is as wide and as deep as in *Dasypus*; distally it contracts in width instead of expanding, and the cuneiform articulation is much smaller than in the modern form and strongly oblique, facing more internad than distad. The radius has, like the ulna, a smaller humeral

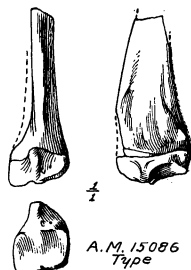


Fig. 46. *Palæanodon ignavus*, type specimen, distal half of radius, anterior, external and distal views, natural size.

articulation than in *Dasypus*, being less extended transversely; the proximal portion of its shaft has about the same proportions, but distally it is more enlarged, the characteristic anterior crest being more prominent and continuous than in the modern armadillos, and the distal facets for scaphoid and lunar much larger, facing more distally, and distinct from each other. The prominent styloid and anterior processes at the distal end of the radius of *Dasypus* are lacking in *Palæanodon*.

In *Manis* the olecranon is much shorter, the ulnar shaft is not so broad, the head of the radius is larger but less expanded transversely, the anterior crest of the distal part of the radius is less prominent; the distal articulations of radius and ulna are very much the same as in *Palæanodon* and *Metacheiromys*.

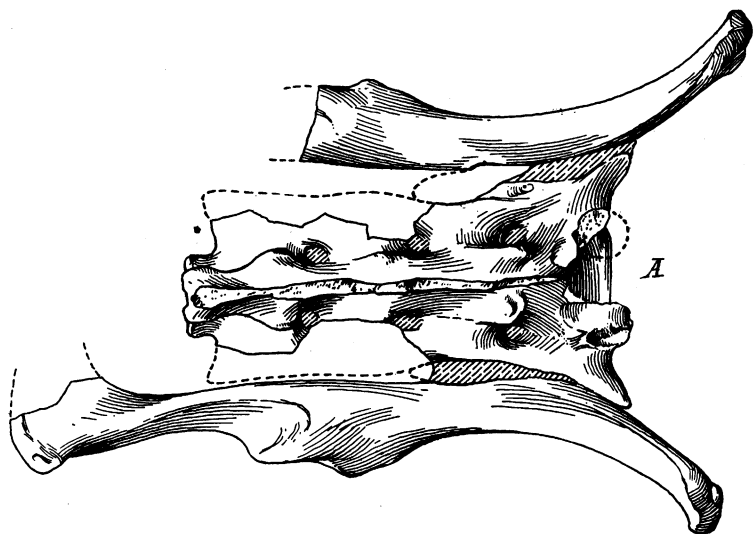
The fore limb bones are very near to those of *Metacheiromys* in all details of construction. In the humerus the deltoid crest does not extend so far down and the supinator crest appears to be less expanded; in both these features *Palæanodon* is nearer to *Dasypus* than is *Metacheiromys*. The radius differs from that of the Bridger genus in the distal articulation, the facets for scaphoid and lunar being indistinguishable in *Metacheiromys*. The shaft of the ulna is broader and flatter in *Palæanodon*, which, in this respect also, comes nearer to the modern armadillos. The olecranon of *Metacheiromys dasypus* is quite different from that of *Palæanodon* and like that of the modern *Dasypus*; in the small *M. tatusia* it is like *Palæanodon* and the modern *Tatusia*.



Fig. 47. *Palæanodon ignavus*. Third metacarpal of type specimen. Anterior and distal views, natural size.

*Manus* (Figs. 41 D and E, 47; compare also figs. 57-60, 64).—Of the carpus no recognizable bones are preserved except the cuneiform in the type, which, so far as can be seen, is very much like that of *Manis*. One complete metacarpal, the third of the right side, and another damaged mc. II? are preserved in the type. Mc. III is a rather short stout bone, but longer and less specialized than in *Metacheiromys*. The diaclasts are much less developed than in *Dasypus*, and the distal articulation, while evidently on the way to assume the peculiar form characteristic of *Metacheiromys* and of the armadillos, has retained a good deal more of the primitive normal type. The dorsal process at the internal side of the middle of the shaft is distinct, but less prominent than in *Metacheiromys*. In *Dasypus* it is nearer to the proximal end of the shaft.

The supposed mc. II is considerably shorter than mc. III and appears to be somewhat smaller in the shaft; its distal end is weathered and it is incased in very hard matrix so that it cannot be fully examined.



A. M. 15137  $\frac{1}{7}$

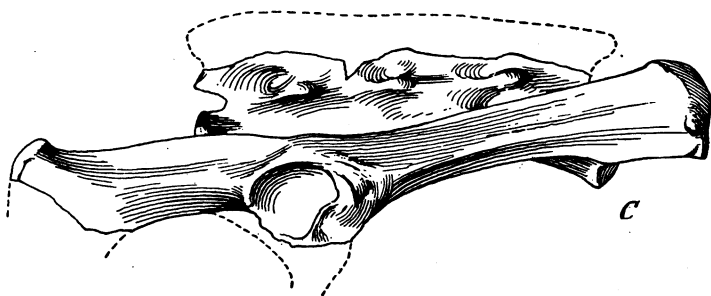
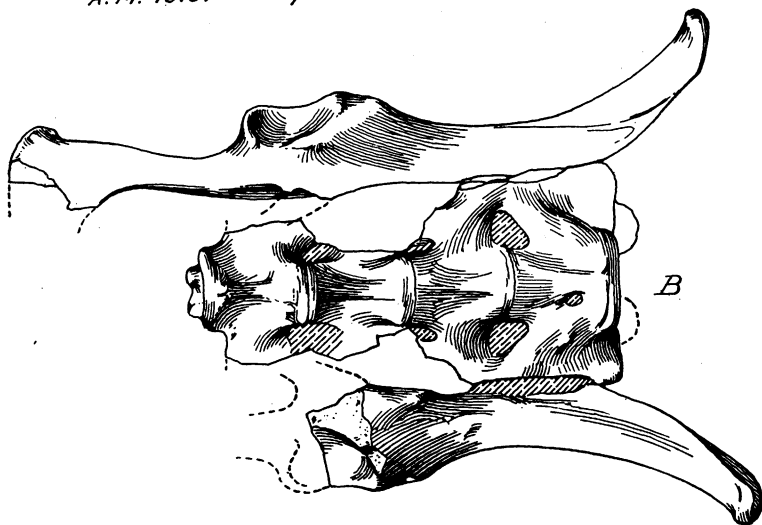


Fig. 48. *Palaeonodon ignavus*, No. 15137. Pelvis and sacrum, superior, inferior, and right lateral views, natural size.

*Manis* has metacarpals of a different type; short and stout, with very prominent high median keels at the distal end, very like those of the sloths, especially the Miocene sloths, but quite unlike those of the armadillos. *Palæanodon* and *Metacheiromys* are decidedly nearer to the armadillos in this respect, although more primitive; but it should be observed that the peculiar articulations of *Manis* may well be considered as derived from the metacheiromyid type, just as the similar sloth articulation is a derivative of the primitive armadillo type.

The phalanges of the first and second row in the manus are broader and longer than in *Metacheiromys*, otherwise very similar. They are much

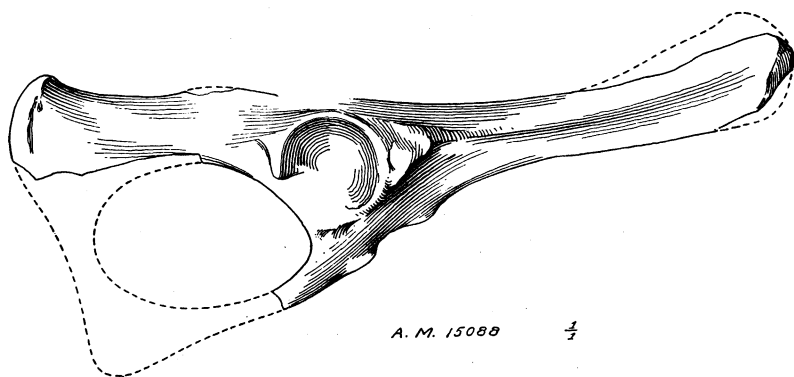


Fig. 49. *Palæanodon ignavus*, No. 15088. Pelvis, right side view, natural size.

less shortened and specialized than in *Dasyurus*, but quite similar to those of *Tatusia*. The ungual phalanges are large, compressed, unfissured, quite similar to those of *Metacheiromys*. They are higher and more compressed than the unguals of the armadillos, very like those of *Hapalops* and other primitive ground-sloths, except for the smaller size. They are quite unlike the long and very deeply fissured, but not compressed, unguals of *Manis*.

*Pelvis and Hind Limb.*—The pelvis (Figs. 48–49) is preserved in No. 15137, No. 15088, and a part of the ilium in the type specimen No. 15086. Fragments of the pelvis are also included in other fragmentary specimens, but the characters are drawn from the two first mentioned individuals.

The ilium is a long trihedral rod, considerably but not abruptly everted, flattened towards the tip into a thick vertical plate, but not notably expanded. The sacral articulation occupies the entire width of the middle third of the ilium; the external crest is obscure and not at all sharp, in

contrast to *Dasypus* or *Tatusia*; the eversion of the tip is intermediate between these two genera.

The ischium is a long straight rod continuing backward in a direct line with the ilium; it is more flattened and only two-thirds as long. The superior crest, which in the armadillos unites with the transverse processes of the posterior sacro-caudal vertebræ, is in *Palæanodon* quite rudimentary, and limited to the middle portion of the shaft. In *Metacheiromys* it is more advanced. The distal end of the ischium is broadened and twisted so as to throw the upper point outward.

The pubis has the characteristic edentate type of a long slender rod, arising from below the anterior part of the acetabulum and extending almost as much downward as backward, so as to inclose an exceptionally large obturator foramen. This is the xenarthral type; the pelvis of *Manis* is quite different, the pubis being shorter, flatter, arising from beneath the posterior side of the acetabulum, the obturator foramen small, the pelvis considerably shorter, with only a ligamentous union between ischium and caudals. In *Metacheiromys* the ischium is shorter and the crest along its superior border is more developed; otherwise there is little difference from *Palæanodon*.

The femur (Figs. 41 F, 50-52, 65) is of moderate length, not unlike that of *Dasypus*, but longer and heavier and somewhat less flattened distally. The head is not so sessile, the great trochanter is wider and farther apart from the head, but of less depth; the lesser trochanter does not extend up so close to the head; the digital fossa is broad and deep; the third trochanter is somewhat less prominent and stands relatively further up on the shaft than in *Dasypus*. The patellar trochlea is a little narrower and longer, is set nearly median instead of being nearer the external side, and directs rather towards the head of the femur than towards the great trochanter as it does in *Dasypus*. In *Tatusia* the femur is larger, with high massive greater trochanter; the lesser trochanter has more the form of *Palæanodon*; the third trochanter is lower down on the shaft and more prominent; the distal end of the *Tatusia* femur is somewhat deeper antero-posteriorly than in *Palæanodon*, but the direction and position of the patellar groove is much as in *Dasypus*. The marked ridge of the front of the femoral shaft in *Tatusia* is quite rudimentary in *Palæanodon*.

The tibia (Figs. 41 G, 53-54, 66 B; compare also fig. 57) is about as heavy as in *Dasypus* but a fifth longer, suturally united with the fibula at the lower end, but with a circular, flat, distally facing fibular facet at the upper end. The cnemial crest is hardly as heavy and continuous as it is in *Dasypus* and *Tatusia*, but of similar type. The distal end is also of similar general type to that of *Dasypus*, but not so wide, of slightly greater antero-

posterior depth, with somewhat heavier internal malleolus and the fibular articulation for the astragalus definitely confined to the external side of its outer trochlean crest. *Tatusia* has a larger tibia-fibula, the consolidation more advanced; further stages in this union are seen in the glyptodonts.

The hind limb bones compare rather closely throughout with those of *Metacheiromys* in details of construction. The femur of the Bridger genus is nearer to that of *Dasyops* in the more flattened shaft and broader distal end, the broader and shorter trochlea, somewhat

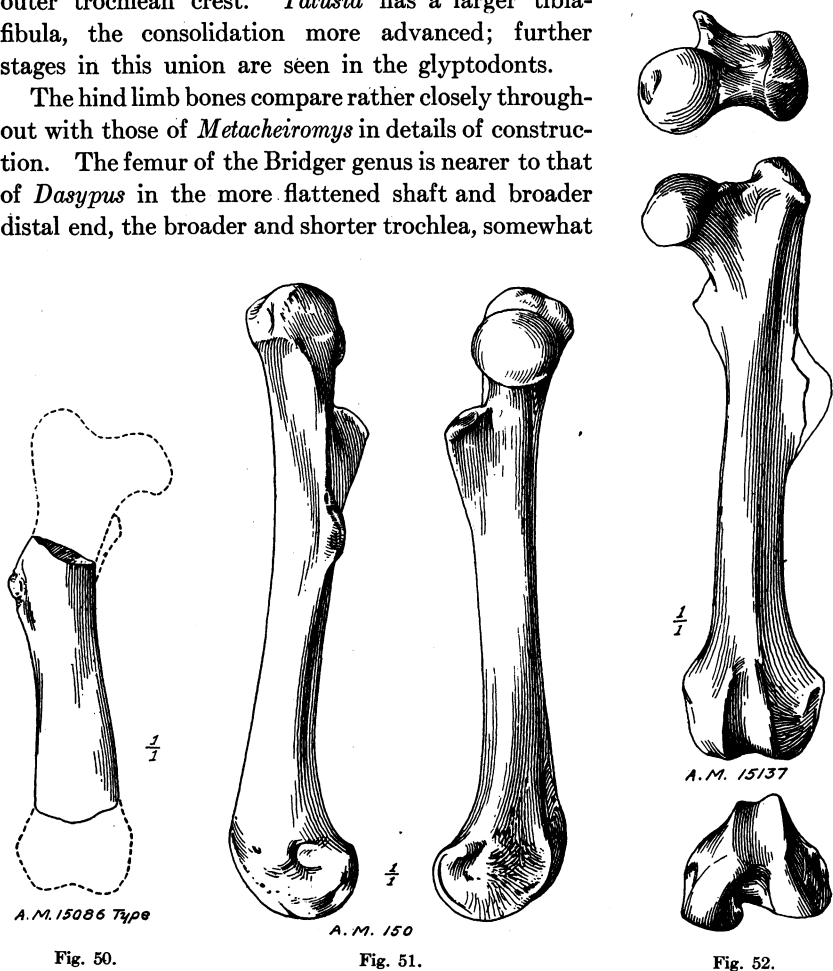


Fig. 50. *Palaeonodon ignavus*, type specimen. Part of femur, the ends restored in dotted outline from No. 15088. Front view, natural size.

Fig. 51. *Palaeonodon ignavus*. Femur of No. 15088. (No. 150 in error on figure). Internal and external views, natural size.

Fig. 52. *Palaeonodon ignavus*. Femur of No. 15137. Proximal, anterior, and distal views, natural size.

higher position of the third trochanter, etc.; the tibia also is somewhat more like that of *Dasyops*.

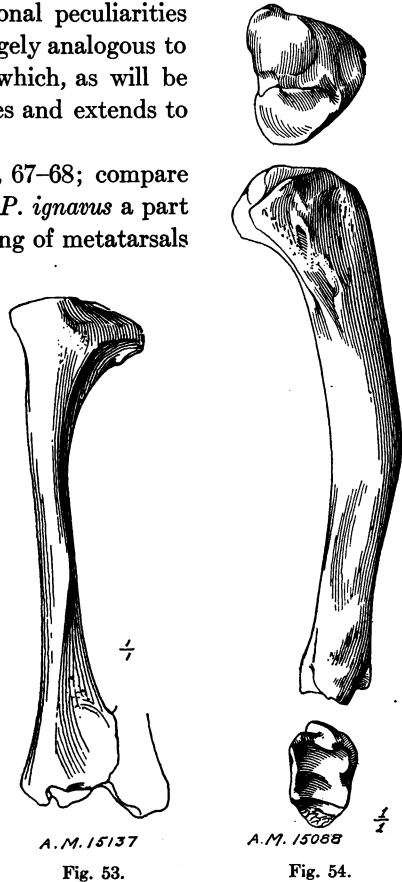
*Manis* differs rather widely in the structure of the hind limb bones.

The great trochanter of the femur is reduced so that the head considerably overtops it, the digital fossa has disappeared, the lesser trochanter is a rounded knob instead of a flattened prominent crest, the third trochanter has wholly disappeared; the patellar trochlea is very wide, short and flat. The tibia has wholly lost its cnemial crest and is separate from the fibula at either end. The constructional peculiarities of the hind limb bones in *Manis* are largely analogous to those of the *Gravigrada*, an analogy which, as will be seen, is more marked in the foot bones and extends to other parts of the skeleton as well.

*The Hind Foot* (Figs. 41 H, 55-56, 67-68; compare also figs. 57 and 60).—In the type of *P. ignavus* a part of the hind foot is preserved, consisting of metatarsals II-V, more or less imperfect but nearly in articulation and with some of the phalanges attached. In No. 15088 the astragalus, lacking the head, and a few phalanges and parts of metapodials are present; in No. 15137 the principal tarsal bones, parts of metatarsals, and a few phalanges; and various other specimens include complete hind foot bones mostly unassociated.

The astragalus has a moderately wide body with trochlea about as deep as in the armadillos but not nearly so short anteroposteriorly. The trochlea is bounded by two symmetric keels, and the fibular facet is more vertical than in *Dasypus*. There is no astragalar foramen. The head is of flattened oval form, not unlike *Dasypus* except that it is hardly as sessile. The sustentacular facet is circular and distinct, the astragalo-calcaneal facet rather broad and shallow, widest behind, both being much as in *Dasypus*.

The calcaneum has a shorter body than in *Dasypus*, the tubercalcis is slightly longer and deeper but not so wide toward its outer end, the peroneal tubercle is somewhat less prominent.



A. M. 15137

Fig. 53.

A. M. 15088

Fig. 54.

Fig. 53. *Palaeonodon ignavus*. Tibia of No. 15137. Anterior view, natural size.

Fig. 54. *Palaeonodon ignavus*. Tibia of No. 15088. Proximal internal and distal views, natural size.

The navicular has a heavy inferior hook, but not so large as in *Dasyopus*. The facet for the ectocuneiform is wider but not so deep; the mesocuneiform facet is convex rather than concave, somewhat wider than in *Dasyopus* but not nearly so deep dorso-palmar, and the entocuneiform facet is quite small, strongly convex, and faces ento-distad, instead of being flat and facing internally as it does in *Dasyopus*. This conforms with the greater reduction of the internal digit in the Metacheiromyidæ.

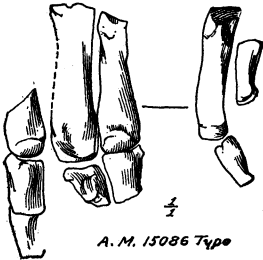


Fig. 55. *Palæanodon ignavus*, type specimen. Part of hind foot, dorsal and internal views, natural size.

Of the four metatarsals in the type, only the distal end of mt. IV is preserved. It is about as robust as in *Dasyopus*. The entire length of the others is preserved. The second and third are about four-fifths as long as in *Dasyopus*, the second considerably slenderer and less expanded proximally. The first metatarsal is greatly reduced, as in *Dasyopus*, but is about three-fourths as long with a considerably heavier shaft. The distal ends of all these metatarsals are more primitive than in *Dasyopus*, although they show the armadilloid type of specialization in a rather rudimentary stage; but their precise form in the type has been largely obliterated by weathering or unskillful preparation. In other specimens the metatarsal facets retain part of their primitive convexity from side to side on the dorsal portion; the median keel on the palmar side of the facet is limited and similar in type to that of *Dasyopus*,

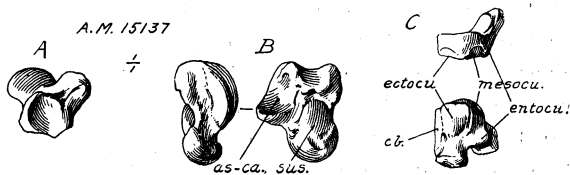


Fig. 56. *Palæanodon ignavus*. Tarsal bones of No. 15137; A, distal view of calcaneum; B, internal and inferior views of astragalus; C, superior and distal views of navicular. All natural size.

but the lateral ledges are less sharp or prominent. There is nevertheless a distinct tendency to excavation of these facets in the palmar face on each side of the median keel, a character much more marked in the metacarpals and very characteristic of the Loricata.

The phalanges of the pes in *Palæanodon* are somewhat shorter than in *Dasyopus*, and somewhat flatter. The distal facets of the first series are not reflected over the dorsal surface of the bone as they are in *Dasyopus*, but

face only distad and palmad. The proximal facets of the phalanges of the second row are correspondingly limited. This is a primitive character found in many Paleocene and early Eocene mammals. The ungual phalanges attributed to the pes are much like the corresponding bones of *Dasyopus*, and differ from those of the manus in their small size and uncompressed subtriangular form.

The pes of *Tatusia*, as compared with *Dasyopus*, has some nominal points of resemblance to that of *Palæanodon* but none that appear to me significant. The tuber calcis is deep and narrow, but of peculiar type; the metapodials, especially the lateral pair, are short and massive and the phalanges very short in comparison with those of *Dasyopus*, but there is nothing that adds to the evidence as to the relationships of *Palæanodon*.

The pes of *Manis* is widely different from that of the armadillos, and parallels the ground-sloths in some significant features of construction. The astragalar trochlea is somewhat oblique, not so short anteroposteriorly, and the head has developed a concave facet for the navicular, just as in the *Gravigrada*. The fourth digit is much enlarged at the expense of the others; and the distal ends of the metatarsals, like the metacarpals, have developed strong median keels, much resembling the Miocene ground-sloth type.

### Measurements

	No. 15086	No. 15137	No. 15088	No. 16831
Skull, length of portion preserved	65.5			
“ width at interorbital region	18.5			
“ “ “ mastoid region	34.8			
“ height, condyles to occiput	23.2			
Cervical vertebræ, length of 7 in series	57.			
Humerus, length				
Radius, length				44.
Ulna, length				
Metacarpal III, length	15.			16.
Femur, length		80.	85.	
Tibia, length		67.5		
Metatarsal, length	19.5			
Pelvis, length		94.3	106.	
Sacrum, length		55.5		
Astragalus, length		13.		
“ width of trochlea		8.3	8.1	
Calcaneum, length				23.

***Palaeanodon parvulus*, new species**

Fig. 57

*Type*.—Amer. Mus. No. 15859, fragments of skeleton including limb and foot bones from Clark Fork beds of Wyoming.

*Specific distinctions*.—Size one-fourth less than *P. ignavus*, and considerably more slender throughout.

The portions of the skeleton preserved include the entire tibia, the radius

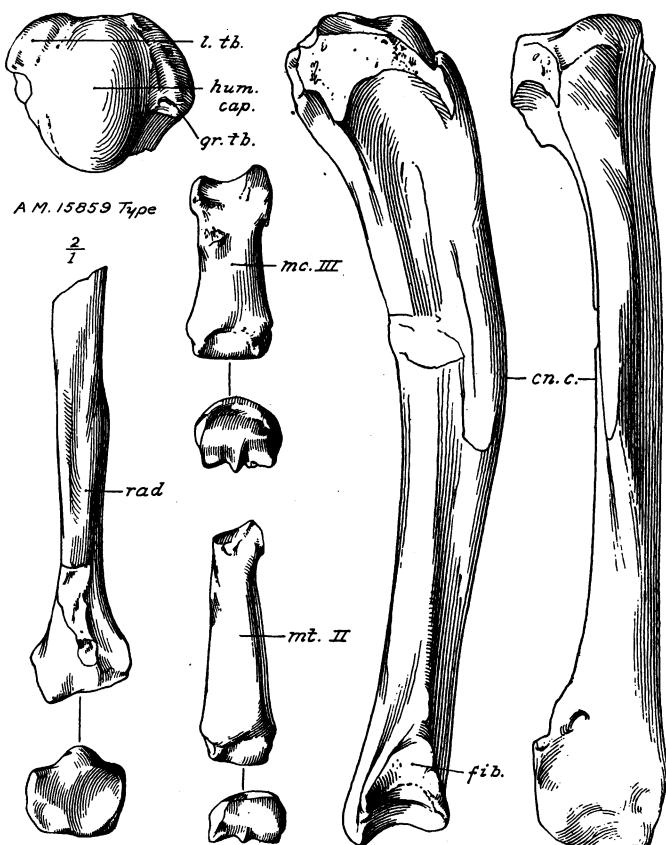


Fig. 57. *Palaeanodon parvulus*. Type specimen, No. 15859. Clark Fork horizon, uppermost Paleocene from Clark Fork basin of Wyoming. Twice natural size.

lacking the proximal end, parts of both humeri, mc. III entire, one metatarsal and both ends of another, parts of scapula and caudal vertebræ. The chief interest of the specimen is that it indicates the occurrence of a

smaller and probably more primitive species of this group in the top of the Paleocene. It is too fragmentary to show any important primitive characters, such as might be expected in a species from an older horizon than that of *P. ignavus*, except the small size and slender proportions above indicated.

Geological Range of the Metacheiromyidæ	PALEOCENE			EOCENE					
	Puerco	Torrejon	Clark's Fork	LOWER			MIDDLE		UPPER
				Gray Bull	Lysite	Lost Cabin	L'r Bridger	Up'r Bridger	Up'r Uinta
<i>Metacheiromys</i> sp. indesc.								×	
" <i>dasyopus</i>							×		
" <i>marshi</i>							×		
" <i>tatusia</i>							×		
? <i>Palæanodon</i> sp. indet.						×			
" <i>ignavus</i>				×	?				
" <i>parvulus</i>			×						

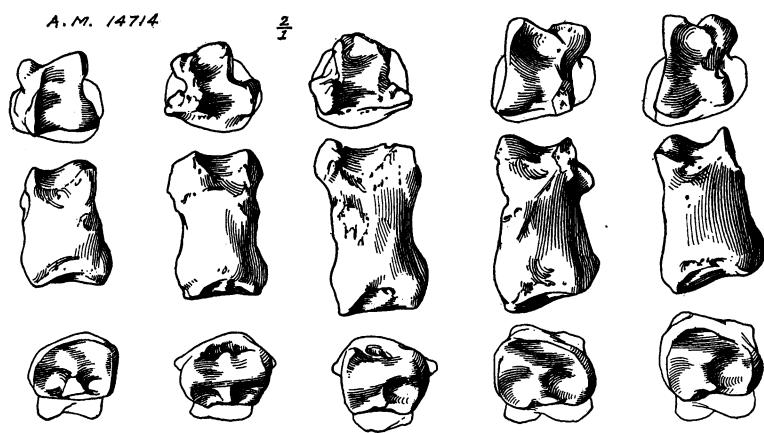


Fig. 58. Palæanodont metacarpals from the Lost Cabin horizon in Wind River basin. No. 14714. Twice natural size.

The principal specimens referred to *P. ignavus* are from the Gray Bull horizon, but there are two specimens from the upper Gray Bull or Lysite, their exact level not being known. In the Lost Cabin three associated lots

of foot bones, Nos. 14732, 14733, and 14734, (Figs. 58-60) and a number of isolated limb and foot bones are recognizable as *Metacheiromyidae*, and intermediate between *Palæanodon* and *Metacheiromys* in specialization. They represent two or more species, one about as large as *Palæanodon ignavus*, the other about one-fourth smaller. In the smaller species the distal end of the radius has the scaphoid and lunar facets indistinguishable, but the form of the combined facet is subquadrate as in *Palæanodon*, instead of oval as in *Metacheiromys*. The mc. III is shorter than in *P. ignavus*, its proximal facet somewhat more saddle-shaped, but not so deeply warped as in *M. dasypus*; its distal facet is more nearly like that of *P. ignavus*, retaining more of the primitive hinge joint than does *dasypus*. The first and second phalanges of digit III of the manus are of nearly equal length; in *Metacheiromys* the first is shorter. The second metacarpal exhibits a similar intermediate stage of evolution. The astragalus of a larger species has a wider trochlea, shorter anteroposteriorly, and the head has less dorso-

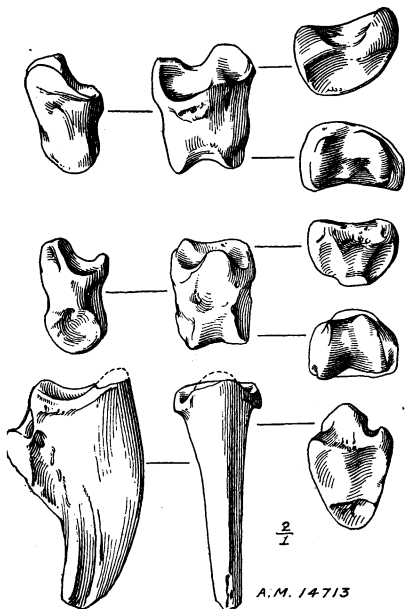


Fig. 59.

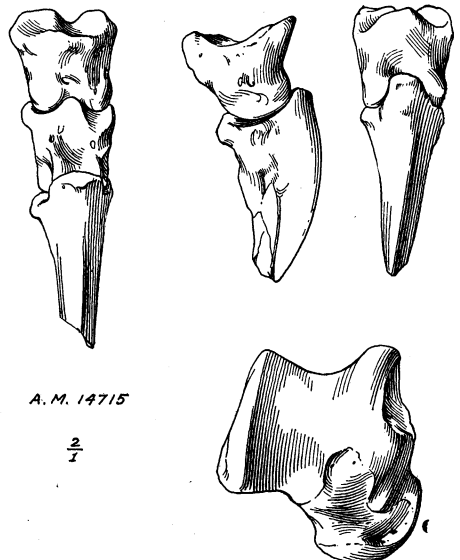


Fig. 60.

Fig. 59. *Palæanodont* phalanges of manus, No. 14713, (associated) from Lost Cabin beds, Wind River basin. Twice natural size.

Fig. 60. *Palæanodont* phalanges of manus, and right astragalus, No. 14715, from Lost Cabin beds, Wind River basin. Twice natural size.

plantar depth. In the absence of skull parts it seems inadvisable to give specific names to any of this material. It serves to show transitional characters to *Metacheiromys* from *Palæanodon*, and thus confirms the derivation of the one from the other.

#### Affinities of *Palæanodon*

Any consideration of the relationships of this very interesting Lower Eocene genus turns primarily upon the position of *Metacheiromys*, its successor in the Middle Eocene (Bridger formation). Unfortunately, *Metacheiromys* has never been figured or adequately described. The brief diagnosis published by Osborn and Granger in 1904<sup>1</sup> is sufficient indeed, if carefully read and the significance of the stated characters weighed and fairly evaluated, to show that it was a relative of the armadillos. But the diagnosis, unsupported by figures and lengthy detailed descriptions, has failed to carry conviction, and has indeed been apparently disregarded by critics save in the features in which the genus is stated to differ from the armadillos. The two species described in 1904 were based upon admirably preserved specimens, the skull, jaws, and anterior half of the skeleton of a larger species (*M. dasypus*) and the skeleton of a smaller one (*M. tatusia*), less perfectly preserved but sufficiently complete to mount without an undue amount of restoration. There are, in addition, a number of minor specimens from the Bridger formation, which add nothing of importance to its osteology.

There is no question that *Palæanodon* is a near relative of *Metacheiromys*, differing only in various minor characters, some of which have been cited in the foregoing description. Its more general affinities can best be considered after summarizing the principal osteological characters of skull and skeleton.

It appears probable that certain fragmentary specimens from the Oligocene and Miocene of France and Germany, which have been referred to the Edentata by Filhol, Schlosser and Ameghino, may have an important bearing upon the problems here involved. Filhol in 1893<sup>2</sup> described and figured a number of isolated bones from the Phosphorites which he referred to the Edentata under the names of *Necrodasyus*, *Leptomanis* and *Palæorycterus*. Schlosser in 1904<sup>3</sup> referred to the same order a number of limb and foot bones, some of them associated parts of a single individual, which had

<sup>1</sup> Osborn, H. F. and Granger, W., 1904, Bull. Amer. Mus. Nat. Hist., XX, Art. 12, pp. 163-165.

<sup>2</sup> Filhol, H., 1893, Ann. Sci. Nat. Zool. et Paléont., (7) XVI, Nos. 1-3, pp. 134-139.

<sup>3</sup> Schlosser, M., 1904. Notizen über einige Säugethierfaunen aus dem Miocän von Württemberg und Bayern. Neues Jahrb. Beil., XIX, p. 499, Pl. xxvi.

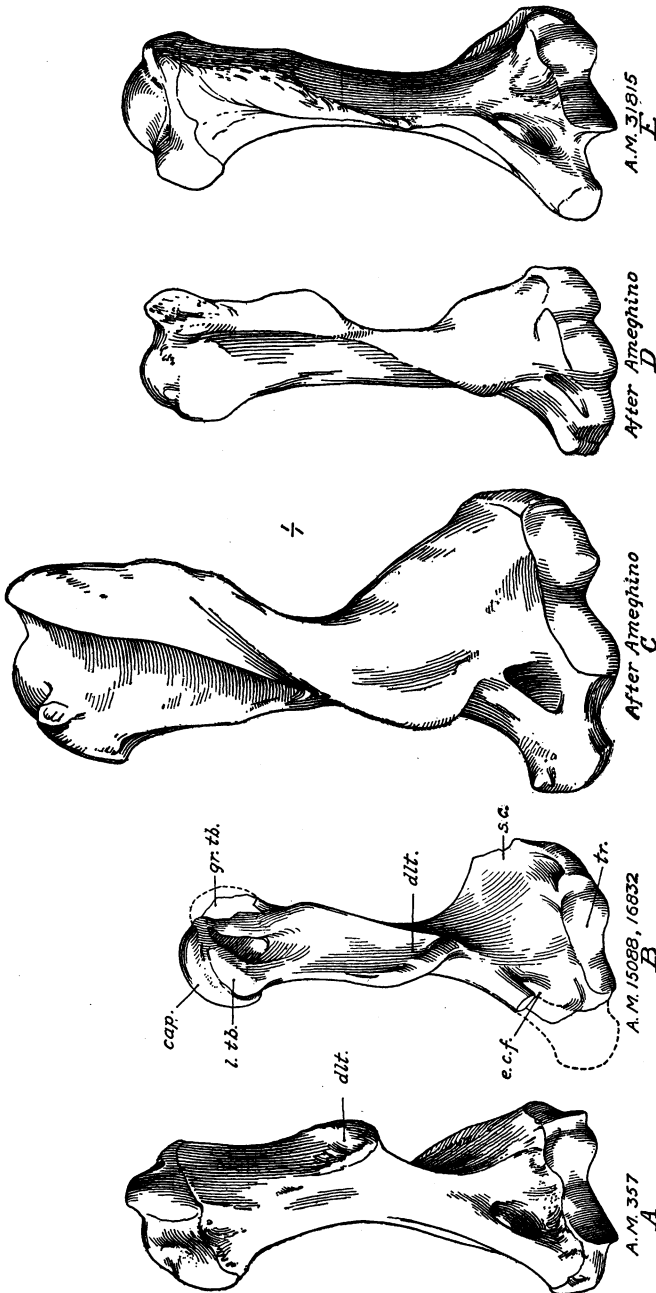


Fig. 61. Comparative anterior views of humeri, natural size, in A, *Dasyus*, B, *Palaeonodon*, C, '*Gallietatus*,' D, *Neoromaris*, E, *Manis*. The head of the humerus in *Palaeonodon* is taken from No. 16832, the remainder from No. 15088. The *Dasyus* and *Manis* humeri are from skeletons in the American Museum; the two European fossils are copied from Ameghino's brochure.

been described some years before by Quenstedt<sup>1</sup> under the name of *Lutra franconica*. Ameghino in 1905<sup>2</sup> discussed the affinities of these remains, along with some additional fragmentary and non-associated bones from the Miocene of Mont Ceindre near Lyons, France. Some of them he regarded as true armadillos (*Necrodasypus*, *Galliatatus*), others as related to *Manis* (*Leptomanis*, *Teutomanis*) and to *Orycteropus* (*Palæorycteropus*). In a later paper,<sup>3</sup> he strongly contested Schlosser's criticism<sup>4</sup> that the remains referred to *Galliatatus* and *Teutomanis* belonged in large part to the same individual skeleton.

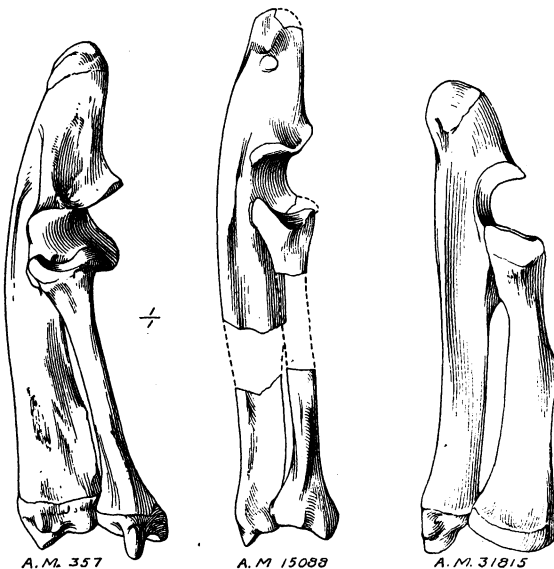


Fig. 62. Radius and ulna in *Dasypus*, *Palæanodon* and *Manis*, anterior views, natural size. From American Museum specimens.

While Ameghino refers the foot bones of "*Lutra franconica*" to the armadillos under the name of *Galliatatus schlosseri*, he regards the limb bones as pertaining to the Pholidota and proposes for them the name of *Teutomanis*. Schlosser, however, (*loc. cit.*) states positively that the foot bones and limb bones pertain to the same individual skeleton, and that the foot bones are metacarpals, and not, as Ameghino holds them to be, metatarsals.

Winge in his recent volume upon the fossil edentates of Lagoa Santa, Brazil, in reviewing the affinities of the various extinct genera, refers briefly

<sup>1</sup> Quenstedt, Fr. Aug., *Handbuch der Petrefaktenkunde*.

<sup>2</sup> Ameghino, F., 1905. *Les Edentés Fossiles de France et d'Allemagne*. An. Mus. Nac. Buenos Aires, XIII, p. 176.

<sup>3</sup> Ameghino, F., 1908, An. Mus. Nac. Buenos Aires, XVII, pp. 104-106.

<sup>4</sup> Schlosser, M., 1907, *Neues Jahrb.*, I, pp. 462-466.

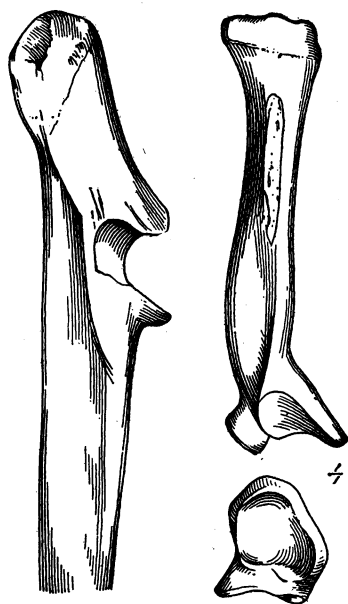
to these European Tertiary remains,<sup>1</sup> and while admitting the armadilloid characters of the foot bones of "*Galliatatus*," concludes that the characters of the limb bones show that it was nevertheless related to *Manis* and not to the armadillos.

Although regarding the Xenarthra as exclusively American, Winge still ranks both *Manis* and *Orycteropus* with them in the order Edentata, as does Schlosser in his revision of Zittel's 'Grundzüge der Palaöntologie,' 1911.

Most of the recent authorities, however, place them in distinct orders, Pholidota and Tubulidentata, and question or deny any especial affinities between these and the Xenarthra.<sup>2</sup>

Oldfield Thomas in 1887 advocated raising the New World edentates to the rank of a sub-class Paratheria, coordinate with the remaining Placentalia and the Metatheria, and this arrangement is adopted by Scott (1904, *loc. cit.*, p. 3). Thomas' stated reasons for this classification are confined to certain rather speculative theories concerning the evolution of the milk and permanent dentition in mammals<sup>3</sup>; Scott presumably accepts the classification upon quite other grounds, as he adopts<sup>4</sup> the generally accepted theory regarding the origin of the milk dentition.

A careful consideration of the characters and affinities of *Palæanodon* and *Metacheiromys*, in comparison with the armadillos and other Xenarthra, with



After Ameghino

Fig. 63. Ulna of '*Galliatatus*' and radius of '*Teutomanis*,' after Ameghino. Natural size. The views do not correspond with those in the preceding figure.

<sup>1</sup> Winge, Herluf, 1915. Jordfundne og nulevende Gumlere fra Lagoa Santa, Brasilien. E. Museo Lundii, III, Part 2, p. 306.

<sup>2</sup> See Flower, W. H., 1882, Proc. Zool. Soc. London, pp. 358-367.

Klinckowström, Axel, 1895. Zur Anatomie der Edentata. Jena, 1895.

Weber, M., 1904, Die Säugethiere, pp. 412 and ff. Jena, 1904.

Smith, Elliott, 1899. The brain in the Edentata. Trans. Linn. Soc. London (2).

Windle, B. G., and Parsons, F. G., 1899. Myology of the Edentata, Proc. Zool. Soc. London, p. 314 and ff.

Mitchell, Chalmers, 1905. Intestinal tract of mammals. Trans. Zool. Soc. London. See pp. 453-458 and 529-530.

Gregory, W. K., 1910. The orders of mammals. Bull. Amer. Mus. Nat. Hist., XXVII, pp. 332-341.

<sup>3</sup> The arrangement was based upon the view that the diphyodontism of placental mammals was secondarily acquired, a view which Thomas himself withdrew a few years later (Ann. and Mag. Nat. Hist., 1892, p. 308) in consequence of later investigations by Kükenthal and others.

<sup>4</sup> Scott, W. B., 1913. *Loc. cit.*, p. 94.

*Manis* and *Orycteropus* and their supposed relatives in the Tertiary of Europe, and with the primitive placentals of the early Tertiary (Eocene and Paleocene, chiefly known from North America), making in this comparison a due allowance for the relative geological age of the various types under consideration, adds a great deal to the evidence for solving the much disputed problems of the origin, relationship and taxonomy of the "edentate" orders, and clears up several obscure and difficult points.

**Geological and Geographical Distribution of Palæanodonta,  
Xenarthra and Pholidota**

	EUROPE, ETC.	NORTH AMERICA	SOUTH AMERICA
Recent	<i>Manis</i> (all Oriental and Ethiopian)	<i>Tatusia</i> (Texas, Mexico)	<i>Bradypus</i> <i>Dasypus</i> <i>Tatusia</i> <i>Cholæpus</i> <i>Chlamydophorus</i> , etc. <i>Myrmecophaga</i> , etc.
Pleistocene		<i>Megatherium</i> (Tex., Fla.) <i>Mylodon</i> , <i>Megalonyx</i> <i>Nothrotherium</i> (Cal.) <i>Chlamydothorium</i> (Fla.) <i>Glyptodon</i> , etc. (Fla. & S.)	<i>Megatherium</i> <i>Dasypus</i> <i>Eutatus</i> <i>Mylodon</i> <i>Chlamydothorium</i> <i>Scelidothorium</i> <i>Glyptodon</i> <i>Panochtus</i> <i>Nothrotherium</i> <i>Dædicurus</i> etc.
Pliocene		<i>Megalonyx</i> <i>Glyptotherium</i> ..... Some doubtful fragments of ground-sloths	<i>Scelidodon</i> <i>Chlamydothorium</i> <i>Promegatherium</i> <i>Proeuphractus</i> , etc. <i>Palæohoplophorus</i> <i>Neuryurus</i> <i>Lomaphorus</i>
Miocene	<i>Galliatatus</i>	(Absent)	<i>Hapalops</i> <i>Stegotherium</i> <i>Eucholæops</i> <i>Proeutatus</i> , etc. <i>Nematherium</i> <i>Prozædyus</i> etc. <i>Peltephilus</i> <i>Propalæohoplophorus</i> <i>Metopotoxus</i>
Oligocene	<i>Necrodasypus</i> etc.	(Absent)	Ground-sloths doubtful Armadillos imperfectly known
Eocene		<i>Metacheiromys</i> ..... <i>Palæanodon</i>	Some doubtful fragments of Armadillos .....
Paleocene		<i>Palæanodon</i>	

*Summary of Diagnostic Characters of Palæanodon.*—Setting aside generalized or unimportant characters, the following features of the skull and skeleton appear to have principal weight as evidence for the affinity of *Palæanodon*.

1. The cheek teeth appear from their alveoli to have been of armadillo type and considerably reduced in number and size (as in *Tatusia*, *Stegotherium*, etc.), and to have been partly replaced by a horny pad.

2. The front teeth are unknown in this genus. In *Metacheiromys* the canines are large enamelled tusks.

3. The basicranial region is broad and flat; the paroccipital, mastoid, and posttympanic processes are not prominent; and the tympanic region agrees with the general loricate type but also with *Manis*.

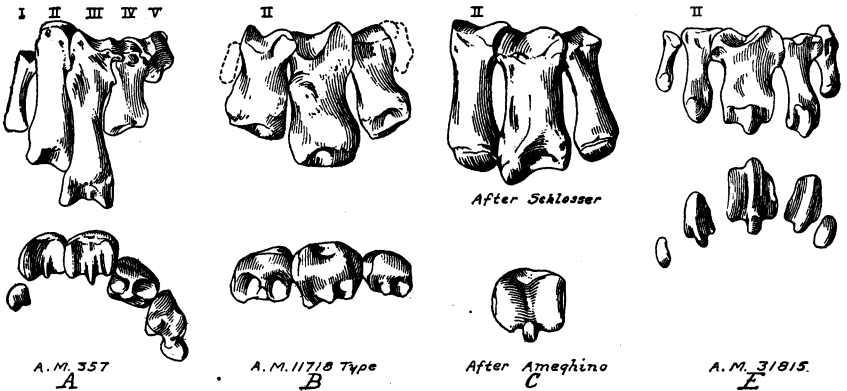


Fig. 64. Comparative views of metacarpals in *Dasypus*, *Melacheiromys*, *Gallizetatus* and *Manis*. The first and the last from the same skeletons as Figs. 61 and 62. The *Melacheiromys* is from the type of *M. dasypus*; the *Gallizetatus* is copied from Schlosser and Ameghino. All natural size.

4. The occiput is broad and low as in *Dasypus*, but the resemblance in this respect is convergent, since the construction in *Dasypus* is decidedly different and the broadening evidently a secondary specialization.

5. The mastoid exposure is extensive both posteriorly and inferiorly, more extensive than in any of the modern armadillos or in *Manis* but of generally similar construction.

6. The foramina for the posterior cranial nerves (condylar and for. lac. post.) are of the primitive insectivore-creodont type, more nearly retained in *Manis* than in the Loricata.

7. The glenoid articulation is like that of the armadillos; the condyle of the jaw is not expanded transversely, the post-glenoid process is vestigial, the socket is more deeply buried than in *Tatusia*, less than in *Dasypus*.

8. The proportions of the lower jaw are armadilloid, somewhat heavier than in *Tatusia*, and the angle projects backward in a sharp process (a primitive character). The front of the jaw is unknown in this genus; presumably it was as in *Metacheiromys*.

9. The cervicals are decidedly short and wide, somewhat as in *Tatusia*, except that  $C_{2-4}$  are separate.

10. The dorsals and lumbers are primitive, the zygapophyses with (1) simple flat facets, (2) no accessory facets (i. e. nomarthral), (3) no zygapophysial spines, (4) the spinal nerves making their exit through a notch

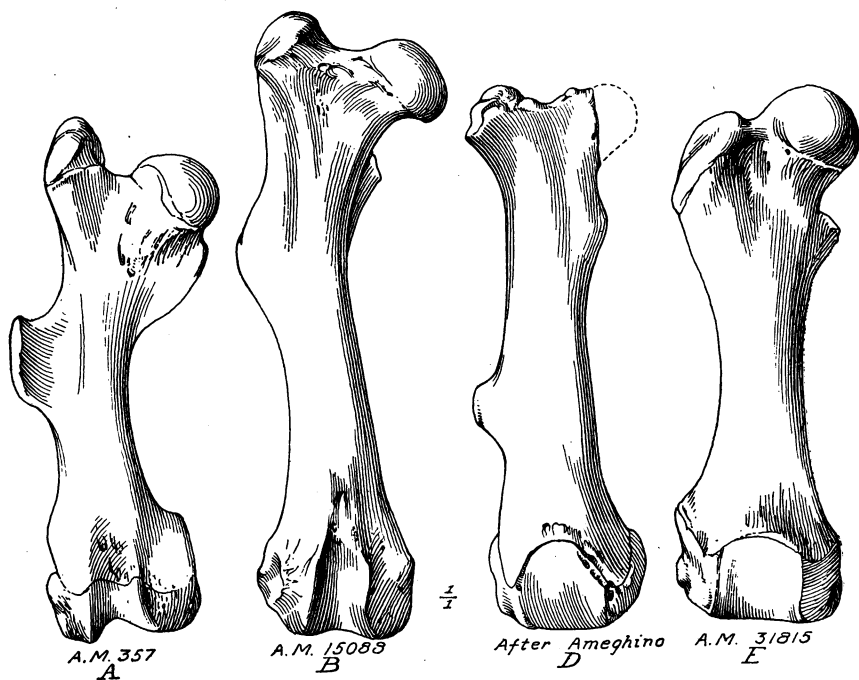


Fig. 65. Comparative views of right femora of *Dasyus*, *Palaeonodon*, *Necromanis* and *Manis*. From same specimens as preceding figures; the *Necromanis* after Ameghino. All natural size.

behind the base of the arch, not through enclosed foramina. In all these points they agree with the primitive type, in all except the first with *Manis*, in all except the third with *Metacheiromys*.

11. The caudal vertebræ are likewise primitive but accord much better with the armadillos than with *Manis*; but the tail was very long and heavy.

12. The pelvis is distinctly xenarthral in the long slender anteriorly placed pubis, but the ischium is of primitive type, i. e., long, slender, and not united to the caudal vertebræ.

13. The humerus is distinctly armadilloid in various characteristic details cited in the description, especially the peculiar deltoid crest, prominent supinator crest, and wide shallow trochlea. But the deltoid crest projects forward as in primitive mammals generally, instead of outward as in the armadillos.

14. The ulna is armadilloid in the long, straight, heavy, *Tatusia*-like olecranon and broad flat shaft, but has a reduced and oblique distal facet as in primitive placentals, instead of a wider, transversely set distal facet as in the armadillos.

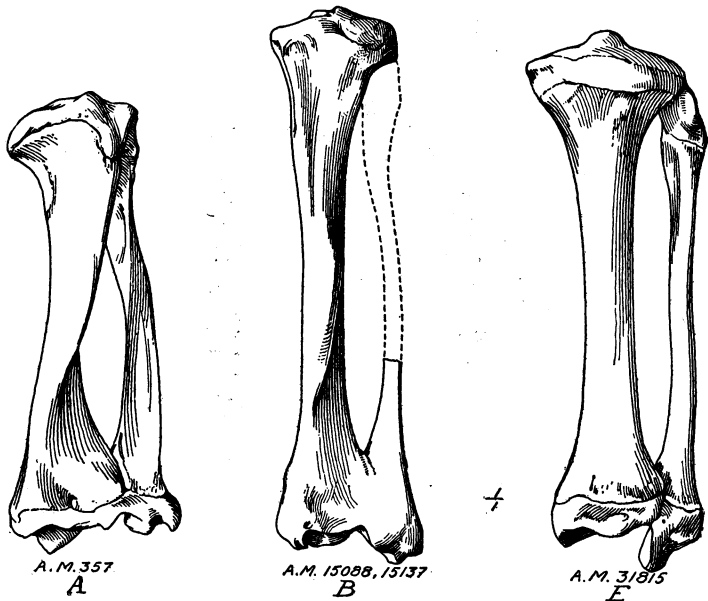


Fig. 66. Comparative views of left tibiae in *Dasypus*, *Palæanodon* and *Manis*; front view, natural size, same specimens as preceding figures.

15. The radius resembles *Tatusia* in the extremely prominent sharp anterior crest extending from the proximal part of the shaft to the distal end of the bone, the quadrate double distal facet, etc. The crest is directed more anteriorly than in the armadillos (it is higher than in *Dasypus*).

16. The metacarpals are characteristically armadilloid, although more primitive than in *Metacheiromys* or in modern armadillos. This is especially seen in the peculiar distal articulations, the short heavy shafts with prominent dorso-external process, etc. But they retain considerable of the primitive type.

17. The phalanges are armadilloid, about as much specialized in the

manus as *Tatusia*, save that they allow only of a more restricted movement. The unguals, however, are high, narrow and compressed, more of the Miocene ground-sloth type, and not very different from some Eocene creodonts and Insectivora. They are not fissured, save possibly at the very tip.

18. The femur compares well with that of the armadillos, save that the three trochanters are less prominent than in *Tatusia* or *Dasypus*.

19. The tibia is characteristically armadilloid in the forward bowing of the shaft, the high cnemial crest extending along its whole length, the sutural union with the fibula at the lower end, the peculiar form of the astragalar trochlea, etc. It is primitive in lack of proximal union with the upper end of the fibula.

20. The astragalus is like that of the armadillos except that the trochlea is less shortened anteroposteriorly. It is of the primitive insectivore-rodent-edentate type, distinguished by sharp symmetrical crests, no astragalar foramen, wide flattened-oval head, short distinct neck, etc. The

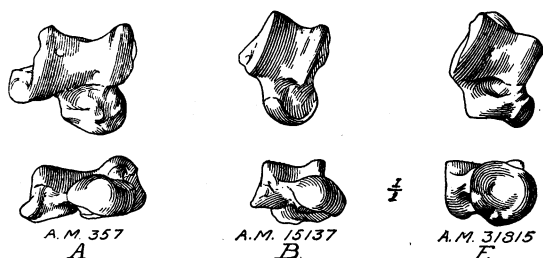


Fig. 67. Dorsal view of right astragalus, natural size, in *Dasypus*, *Palæanodon* and *Manis*. Same specimens as preceding figures.

armadillo-glyptodont astragalus is obviously a specialization from this type; the astragalus in the *Gravigrada* or in *Manis* also appears to be a derivative in a diverse line of specialization. The astragalus of *Orycteropus* appears to be derived not from this type but from the creodont-condylarth type.

21. The metatarsals in *Palæanodon* are very like those of *Metacheiromys*, the internal digit small and slender, the external digit short and stout, the three intermediates being the chief functional digits. This unusual type of lateral digital reduction is characteristic of armadillos. The distal ends of the metatarsals and the phalanges are much like *Dasypus*, etc., but in some respects more primitive.

*Relationship to Metacheiromys.*—This hardly calls for extended discussion. *Metacheiromys* is more specialized in various particulars but there is no question of its being closely related to, and either directly or approximately descended from *Palæanodon*. The cheek teeth are much more

reduced; the tympanic bulla is completely ossified in the larger species; the limbs and feet more abbreviated, the limb bones, metapodials and phalanges more like those of *Dasypus* or *Tatusia* in various respects; the lumbar zygapophyses develop the characteristic spine of the armadillos,

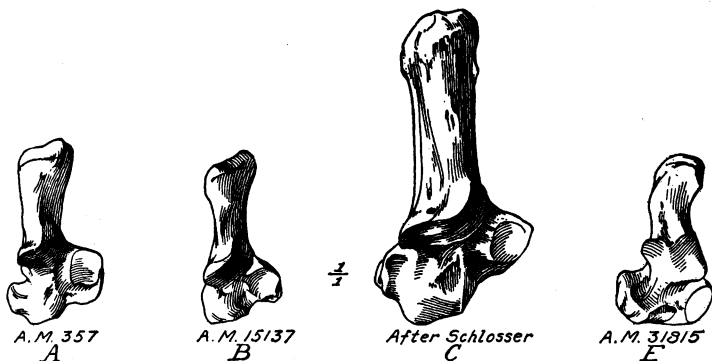


Fig. 68. Dorsal view of right calcaneum, natural size, in *Dasypus*, *Palæanodon*, *Gallizetatus* and *Manis*. Same specimens as preceding figures.

although their facets remain flat and the notch for exit of the spinal nerves is not bridged over. The smaller *M. tatusia* retains many of the primitive characters of *Palæanodon* in the basicranial region, vertebræ, and limb bones. It is somewhat smaller than *P. parvulus*, whereas *M. dasypus* is a little larger and much more robust than *P. ignavus*.

The largest *Metacheiromys* is an undescribed species from the Upper Bridger; it is unknown from any later formation.

*Relations to the Xenarthra.*—From the above list of skeletal characters it appears beyond question that *Palæanodon* is related to the armadillos, although it retains numerous primitive characters that have been lost in varying degree by the late Tertiary and modern genera, and has not developed certain obviously specialized characteristics of all the South American edentates (Xenarthra). It is generally believed, and I think quite rightly, that the armadillos represent most nearly the primitive type from which the sloths and anteaters, as well as the glyptodonts, were derived; and if this be so, the xenarthral articulations of the vertebræ, which appear to be degenerating in the sloths, must have been acquired previous to their splitting off from the common ancestral stock of the Xenarthra, but subsequent to the splitting off of the metacheiromyids from the primitive Edentate stock.

Save for the reduction of the cheek teeth and the supposed character of the canines (the last inferred from the near relationship to *Metacheiromys*),

I see nothing in the skeleton structure against regarding *Palæanodon* as a direct ancestor of the South American Tertiary and modern Loricata, or indeed of all the Xenarthra. It is of course much more primitive; it lacks many of the specializations which are already fully developed in the Santa Cruz genera. But it must be kept in mind that it is a very much older type. It is a contemporary of *Eohippus*. The earliest South American armadillos of which we know the skull or skeleton were contemporaries of *Merychippus* or approximately of that age. Now *Merychippus* is very characteristically equid in numerous features that have not yet appeared or are only vaguely foreshadowed in *Eohippus*, and we must expect to see corresponding differences of degree in phyletic specialization when we compare Lower Eocene with late Miocene representatives in any other phylum. I see no reason to believe that the Lower Eocene and Paleocene ancestors of the Xenarthra were any more specialized than is *Palæanodon* and I believe that they were quite closely related to it. But we know next to nothing of their intervening stages up to the Santa Cruz; for the plates and fragments of isolated bones which Ameghino has described from the Deseado and Casamayor formations and made types of various new genera are too uncertain either of provenience or of association to throw any real light upon the pre-Miocene South American history of the Xenarthra.

For geographic and faunal reasons I do not think that *Palæanodon* was directly ancestral to the Xenarthra even though there were no structural difficulties in the way. The early Tertiary faunas of South America cannot be directly derived from any Tertiary fauna of North America, for they wholly lack true Carnivora, while in the North American faunas from Puerco onward this order was well represented. They must be derived apparently from some late Cretacic fauna, unknown to us but presumably inhabiting some part of North America, and containing the immediate ancestors of our Paleocene and Lower Eocene Condylarthra, Taligrada, marsupials, edentates, notoungulates and perhaps primates and rodents, but not the creodonts, perissodactyls or artiodactyls, Amblypoda or true Insectivora.

*Comparison with Manis.*—A preliminary comparison of the skeleton of *Manis* with *Palæanodon* and the armadillos had brought me to the conclusion that the pangolins had little or nothing to do with the true Xenarthra, the many points of resemblance in their structure to one or another of the xenarthral groups being due to convergence. A more careful reconsideration and interpretation of the data, and especially the evidence afforded by the supposed "edentate" remains of the Oligocene and Miocene of France and Germany has materially modified that view.

So far as the skull is concerned, there is nothing to prevent our regarding

*Palæanodon* as a direct ancestor of *Manis*. The cheek teeth are evidently degenerating in the *Metacheiromyidæ*; in *Manis* they have disappeared; in the lower jaw of the pangolin there is a little bony process very suggestive in character and position of a vestigial remnant of the lower canine tusk of the *Metacheiromyidæ*. There is a great deal of resemblance in the basi-cranial region; the loss of occipital crest in *Manis* is evidently secondary.

The presacral vertebræ of *Manis* agree fairly well with those of *Palæanodon* except that the lumbar zygapophyses are strongly convex, presumably a specialization. The caudals, however, appear more primitive, extraordinarily so indeed, retaining a uniformly simple, flattened, spine-like transverse process throughout the whole series, while in *Palæanodon*, as also in the armadillos, the same diversity of type in the transverse processes of anterior, median and distal caudals is seen, as in most other primitive mammals and those in general with long heavy tails. But this peculiarity of *Manis* is perhaps reversionary rather than primitive; indeed it points back quite too far to be regarded as truly primitive, for *Manis* is after all a true placental, descended from primitive placental stock, and this character is reptilian and would indicate, if it really were persistently primitive, an independent line of descent back to early Mesozoic Reptilia.

The pelvis of *Manis* lacks that peculiarly xenarthral type of pubis, already indicated in *Palæanodon*; but perhaps this also is secondary, as the incipient union between ischium and transverse processes of the caudals would seem to be; the one character departs from the xenarthral type, the other parallels it.

The limb bones differ greatly from those of palæanodonts and armadillos, and appear at first to be more simple and primitive. But this apparent simplification (decrease of humeral crests, of femoral trochanters, of cnemial crest of tibia, etc.) may also be secondary, and that it is truly so seems to be quite definitely shown in the fossil *Manidæ* of the European Tertiary, in which intermediate stages are shown.

The peculiar type of astragalus in *Manis* and the prominent distal keels of the metapodials both resemble very closely the Miocene ground-sloths, and differ widely from palæanodonts and armadillos. But these peculiarities in the ground-sloths are undoubtedly derived from the more primitive armadillo type; it is reasonable to conclude that in *Manis* they are also derived from the primitive armadilloid type seen in *Palæanodon*; and here again the European Tertiary genera afford confirmatory evidence, for in *Galliatatus* the metacarpals appear to be quite armadilloid, although the limb bones of the same skeleton are far advanced toward the type of *Manis*.

On the whole, I can find no very conclusive evidence against deriving *Manis* as well as the *Loricata* (and through them the remaining *Xenarthra*)

from the primitive type represented by *Palæanodon*. Just how direct the ancestors may be in each case is a highly speculative matter. But I think that we are well warranted in concluding that there is, after all, a real affinity between the Pholidota and Xenarthra. They may not necessarily be included in a single order but they do clearly belong in the same natural superorder Edentata.

*Orycteropus*, however, does not belong in this natural group. So far as I am able to judge, it has no particular relations to the edentate-insectivore group, but is descended rather from the creodont-condylarth group of the primitive placentals. I can find nothing in the skull or skeleton that seems to be characteristically edentate, as distinguished from merely primitive. The teeth are unique in structure and there is no hint of their origin in any other mammalian type as far as I know. Lönnberg's interpretation,<sup>1</sup> according to which they represent the root, not the crown, of the ordinary mammal tooth, is the most plausible theory of their origin that I have seen.

It seems to be generally agreed by comparative anatomists that there is no definite evidence in *Orycteropus* to indicate any real affinity with the Xenarthra, nor with *Manis*. Elliott Smith<sup>2</sup> believes that the brain indicates affinities rather with the primitive ungulates than with unguiculates; and there is some support for this view in the skeleton, at least in so far as condylarthran affinities are suggested. The astragalus has some resemblance to that of the typhotheres and some other notoungulates, which would be in accord with this derivation.

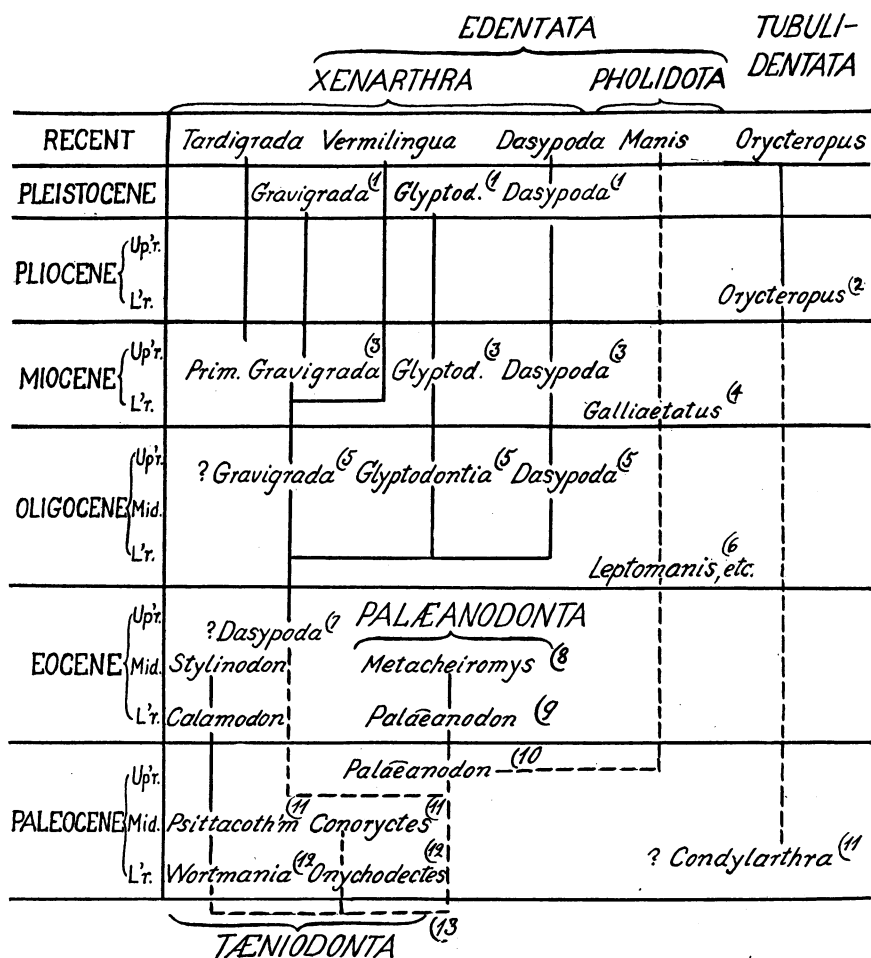
#### *Distributional Notes to Accompanying Table*

- 1) Pampean formation; South America and North America generally.
- 2) Samos, Maragha; probably Mediterranean region in general.
- 3) Santa Cruz formation, Patagonia; probably South America generally.
- 4) Solenhofen, Bavaria (fissure filling); probably Europe and Asia generally.
- 5) Pyrotherium fauna (Deseado) of Patagonia; probably South America in general.
- 6) Phosphorites, France; probably Europe and Asia.
- 7) Notostylops fauna (Casamayor) of Patagonia; presumably widely distributed in South America. The armadillos are represented only by isolated plates of the carapace and by parts of bones of questionable refer-

<sup>1</sup> Lönnberg, Einar, 1906. On a new *Orycteropus*, etc. Arkiv. for Zoöl., k. sv. vet. Stockholm, III, No. 3, pp. 1-35.

<sup>2</sup> Smith, Elliott, 1899, Trans. Linn. Soc. London, (2) Zoöl., VII, p. 387 and ff.

## PHYLOGENY OF THE EDENTATA



ence. It is somewhat doubtful whether they really belong in this fauna which has been much confused by Ameghino with the later horizons.

8) Bridger formation of Wyoming. Presumably widely distributed in North America.

9) Wasatch and Wind River, Wyoming and New Mexico. Presumably widely distributed in North America. The scanty Sparnacian fauna of Europe is identical, so far as it goes, with the Wasatch, and there is no valid evidence against extending the distribution of *Palæanodon* to Europe and Asia at this time — nor any proof that it did so extend.

10) Clark Fork, Tiffany, ?Fort Union in part, of Wyoming, Colorado and Montana. Probably widely distributed in North America. The Cernaysian fauna of France is a near equivalent, and in part closely related, but only in part. The most abundant types of the one fauna are absent from the other. This may mean that the Holarctic faunas at this stage were more provincial than in the Lower Eocene when the cosmopolitan Coryphodon fauna replaces them. The great migration between Paleocene and Eocene may have initiated the dispersal and differentiation of the edentate groups.

11) Torrejon of New Mexico, ?Fort Union in part. Probably widespread in North America. The Cernaysian of France is a near equivalent, but apparently somewhat later. There is no sufficient evidence to indicate whether the Phenacodontidæ ever reached Europe, but *Orycteropus* might be derived from this family, although not from *Phenacodus* itself.

12) Puerco of New Mexico. Unknown elsewhere, but presumably widespread in North America, perhaps throughout the northern world. No trace of this fauna has been detected in the Fort Union, which immediately and without any serious stratigraphic or floral break overlies the Lance formation containing a fauna of dinosaurs, multituberculates and didelphoid marsupials. This has suggested that the Puerco fauna is really of equivalent age to the Lance or even older, but represents a different habitat facies. The formation is underlain by beds equivalent to the Belly River, an older horizon of the Upper Cretaceous.

13) Primitive 'Insectivora' related to the *Leptictidæ* and *Pantolestidæ*. Unknown but presumably Holarctic.

