

NOTES ON THE FOSSIL MAMMALIAN GENUS *PTILODUS*, WITH DESCRIPTIONS OF NEW SPECIES.

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INTRODUCTION.

The recent fortunate discovery of a fine specimen of *Ptilodus*, in which the lower jaws and some other parts of the skeleton are associated with a nearly complete skull, not only adds materially to our knowledge of this genus, but makes possible the clearing up of much of the confusion still existing regarding the classification and relationships of the entire Multituberculate (Allotheria) group.

In view of the very fragmentary material hitherto representing this great group of mammals this new material is of more than usual interest and importance. The comparative completeness of the specimen permits for the first time a fairly accurate study of the morphology of the little creature, and makes it possible to determine its relationships with more certainty than has hitherto been done.

This interesting specimen represents a new species which is described below. It is from the Fort Union beds of Sweet Grass County, Montana, where it was found by Mr. A. C. Silberling in the spring of 1908 while collecting fossil mammals in that locality under a special grant from the United States Geological Survey. In this and subsequent collections obtained by Mr. Silberling through a continuation of the work by the U. S. National Museum, there are disassociated upper and lower jaws of several other individuals of this and a second species of the genus. The greater part of this collection, however, consists of numerous specimens, mostly teeth and jaws, representing a large number of genera and species of Basal Eocene mammals, many of them closely related to or identical with species from the Torrejon of New Mexico. Several of the forms are apparently new, and when studied will be published.

Before describing this new species of *Ptilodus* it seems desirable to first give a short history of the genus and a summary revision of the Torrejon and Fort Union species already referred to it.

Ptilodus, a genus of the Plagiaulacidae, was proposed by Cope in 1881, the type-species, *P. mediavrus*, being founded on a single lower premolar, p_1 , from the Torrejon beds of New Mexico. Other specimens, some representing the complete lower dentition, have since been referred to this species, but the upper dentition has not been known. In 1884 Cope proposed a second genus, *Chirox*, basing the type-species, *C. plicatus*, on a series of three upper premolars. This and a second specimen, consisting of a palate containing most of the upper dentition, which was later described and figured by Cope, constitute the principal material referred to this second genus. Both specimens are from the same beds as those from which the type of *Ptilodus mediavrus* was obtained. In 1887 Cope^a questioned whether the specimens referred to *Chirox* might not belong to *Ptilodus*, but deciding they did not, proposed a new family, the Chirogidae, for the former genus, which he considered allied to the Polymastodontidae, regarding the family as a connecting type between the Plagiaulacidae and the Polymastodontidae. In classifying the Allotheria in 1888, Osborn^b placed *Chirox* in the Bolodontidae, a family proposed by him in 1887.^c

It is thus evident that the uncertainty regarding the relationships and systematic position of these species has been considerable. The confusion, however, has been largely due to lack of associated material, therefore it is with more than ordinary interest that we come to examine the present specimen from Montana, in which the complete upper and lower dentition has for the first time been found in undoubted association. This specimen has the lower jaws and teeth of *Ptilodus* and the upper teeth of *Chirox*, a fact that has not been wholly unsuspected, though none the less interesting and important in the confirmation. Thus, in proving the synonymy of these two genera the family Chirogidae, proposed by Cope, is finally and satisfactorily disposed of. Incidentally, it also apparently confirms indirectly the opinion expressed by Marsh^d regarding the probable identity of the genera *Bolodon* and *Plagiaulax*. This opinion, which he gave in criticising Osborn's classification of the Mesozoic Mammalia, is expressed as follows: "A careful study, moreover, of the known species of the true Plagiaulacidae would have shown him the strong probability, at least, that the genus *Bolodon*, which he makes the type of a distinct family, is based on the upper jaws of *Plagiaulax*." This supposition now seems confirmed, for, as is generally conceded, *Ptilodus* bears an undoubtedly close relationship to the much older form *Plagiaulax*, known only from the lower teeth, while

^a Amer. Naturalist, XXI, 1887, p. 567.

^b Journ. Acad. Nat. Sci. Phila. (2), IX, Pt. 2, 1888, p. 219.

^c Proc. Acad. Nat. Sci. Phila., 1887, p. 285.

^d Idem, 1891, p. 239.

Chirox, now known to be *Ptilodus* also, has been shown by Osborn to hold a similar relationship to *Bolodon*, a contemporary of *Plagiaulax*, and similarly known only from the upper teeth. There seems, therefore, little doubt that, as in the case of *Ptilodus* and *Chirox*, the genera *Plagiaulax* and *Bolodon* were founded on the lower and upper teeth, respectively, of individuals representing the same species or, at least, species not generically distinct. If this be true, the family Bolodontidae is also invalid.

With the important addition to our knowledge of the Allotheria supplied by this more complete material from Montana, the necessity of a further revision and reclassification of the whole group becomes apparent. The present paper is intended, however, only as a preliminary communication, hence it is confined principally to the *Ptilodus* group.

Family PLAGIAULACIDÆ Gill.

Genus PTILODUS Cope.

Generic characters.—With the added characters shown in the new specimen described below, the genus *Ptilodus* may now be redefined as follows:

Dental formula.— i_1^1 , c_0^0 , pm_3^3 , m_3^3 . Incisors simple with sharp, pointed tips, upper and lower pairs not directly opposing each other; upper canine and first three premolars well developed and functional, though not directly opposing the teeth of the lower jaw; p^3 with 4 to 6 cusps; p^4 the largest tooth of the upper series, greatly elongated anteroposteriorly, multituberculate; m^1 multituberculate, with two complete rows of tubercles and a third vestigial row, confined to the posterior half, on the inner side of the crown; m^2 shorter and broader than m^1 , with three short rows of tubercles. In the lower jaw, p_1 and p_2 are wanting and p_3 is rudimentary, with a rounded bead-like crown, which fits into a depression at the anterior end of the large p_4 ; p_4 , the principal tooth of the lower series, greatly elongated and laterally compressed, forming a thin cutting blade with numerous (12 to 14) parallel ribs on either side.

PTILODUS MEDIÆVUS Cope.

Ptilodus mediævus COPE, Amer. Naturalist, XV, 1881, p. 921.

Type-specimen.—A single lower fourth premolar. (No. 3019, Amer. Mus. Nat. Hist. Coll.)

Neotype (Cope).—Portion of a right lower jaw representing the complete lower dentition. Amer. Mus. Nat. Hist. Coll.^a

Type-locality.—Northern New Mexico.

Horizon.—Torrejon formation.

^a Cope, Amer. Naturalist, 1884, p. 694; Rep. U. S. Geol. Surv. Terr., III, p. 1, 1884, pl. xxiii, fig. 1.

This species, the type of the genus, was founded on a single lower premolar and was later supplemented by portions of jaws of other individuals. The following definition is compiled from descriptions given by Cope and Osborn, which have been verified or corrected by a recent examination of the type-material:

Dental formula.— i_1 , c_0 , pm_2 , m_2 ; premolars 1 and 2 wanting; p_3 vestigial; p_4 greatly enlarged, with high compressed crown, which is developed into a sharp, serrated cutting blade, which has 12 (14?) parallel oblique ridges on either side; m_1 narrow and elongate, with 4 internal and 5 external tubercles; m_2 much shorter and somewhat broader than m_1 , with 2 inner and 3 outer tubercles. Upper dentition of this species not known.

Measurements of type.—Diameters of pm_4 : anteroposterior, 9 mm.; transverse, 3 mm.; height, 6 mm.

Measurements of neotype (after Cope).—Length of ramus to last true molar, inclusive, 20.5 mm. Diameters of m_1 : anteroposterior, 4 mm.; transverse, 2 mm. Diameters of m_2 :^a anteroposterior, 2.5 mm.; transverse, 2.2 mm. Diameters of pm_4 : anteroposterior, 8.5 mm.; transverse, 3 mm. Vertical diameter of pm_4 at middle, 4.5 mm.

PTILODUS TROUESSARTIANUS Cope.

Ptilodus trouessartianus COPE, Amer. Naturalist, XVI, 1882, p. 686.

Type-specimen.—A fourth lower premolar in a fragment of jaw. (No. 3025, Amer. Mus. Nat. Hist. Coll.) Paratypes: Two additional fourth lower premolars of other individuals.

Type-locality.—Northern New Mexico.

Horizon.—Torrejon formation.

The description, as given by Cope, is as follows:

This species is represented by three of the characteristic fourth inferior premolars, one of which stands on a part of the ramus, giving its depth. These differ from those of the *P. medivrus* in their uniformly smaller size and in their strongly serrate posterior edge. The number of lateral edges [ridges] is 12, as in *P. medivrus*. Length of fourth premolar, M. .0055; elevation of same, .0040; depth of ramus at P.-m. iv, .0057.

This species is known only from the material described above, and except for its small size is not well characterized. It represents a much smaller species than *P. medivrus*.

PTILODUS PLICATUS (Cope).

Chirox plicatus COPE, Proc. Amer. Phil. Soc., XXI, 1884, p. 321.

Type-specimen.—A series of three upper premolars, p^1 to p^3 . (No. 3032, Amer. Mus. Nat. Hist. Coll.)

Neotype.—The palate portion of the skull, containing the premolars and the first true molar of the right side, and premolars 1, 2,

^a Measurements for m_2 are taken from Cope's figure, Tertiary Vertebrata, Rept. U. S. Geol. Surv. Terr., 1884, pl. xxiii d, fig. 1b. For other measurements, see Cope, Amer. Naturalist, 1884, p. 694.

and 4 of the left side. (No. 3033, Amer. Mus. Nat. Hist. Coll.) A canine and incisor are represented by their fangs.^a

Type-locality.—Northern New Mexico.

Horizon.—Torrejon formation.

The description, as given by Cope, is as follows:

Char. gen.: These are known from three superior molars; viz; the last premolar and the second and third true molars.^b The fourth premolar has two external, and one internal cusps, and the true molars have four cusps each. * * * The second true molar resembles a convex body which has been divided by two cuts at right angles to each other, from which the quarters thus produced have spread away from each other subequally. The external faces of the cusps are convex.

Measurements (after Cope).

		M.
Diameters of P.m. iv [pm ¹]	anteroposterior.....	.0030
	transverse.....	.0038
Diameters of m. ii [pm ²]	anteroposterior.....	.0033
	transverse.....	.0035
Diameters of m. iii [pm ³]	anteroposterior.....	.0035
	transverse.....	.0030

The description of the Neotype, as given by Cope, is as follows:

This genus was described by the writer in 1883, from a few teeth of the upper jaw found in the Puerco [*Torrejon*] formation of New Mexico. Since then a palate with the entire molar series of one side and nearly all that of the other has been obtained. This shows that the teeth described are premolars, and that there are two true molars, which resemble those of *Polymastodon* and *Neoplagiaulax*. The premolars are a good deal like those of *Plagiaulax*, as described to me by Professor Osborn, and the question arises whether the dentition in question does not belong to *Ptilodus*. There are two reasons for answering this question in the negative. First, in *Plagiaulax* and *Neoplagiaulax*, according to Osborn and Lemoine, there is a tooth in the superior series resembling and opposing the peculiar-cutting fourth premolar of the inferior series; second, the only tooth which could oppose such an inferior premolar is the first molar, and this is not worn obliquely, as in *Plagiaulacide*, but transversely, as in *Polymastodon*. This and the second true molar support two and parts of a third longitudinal rows of cusps, which are, on the last tooth, worn by anteroposterior movement of an inferior tooth of corresponding form.

As previously mentioned, the genus *Chirox* is now known to have been founded on the upper dentition of *Ptilodus*. The species, however, is probably distinct from *P. medius*, apparently representing a larger form.

PTILODUS MONTANUS Douglass.

Ptilodus montanus DOUGLASS, Annals of the Carnegie Museum, V, No. 1, October, 1908, pp. 11 to 26, pls. x and xi.

Type-specimen.—A portion of the left lower jaw, containing the first molar and the last premolar. (No. 1673, Carnegie Museum Catalogue of Vertebrate Fossils.)

^a Cope, Amer. Naturalist, XXI, 1887, p. 566.

^b These are all premolars, as afterwards recognized by Cope.

Type-locality.—Sweet Grass County, Montana.

Horizon.—Fort Union formation.

The description as given by Douglass is as follows:

Crown of p_4 semi-elliptical in a lateral view; crown not high, and upper portion of cutting edge not extremely convex; eleven distinct and two posterior indistinct ridges on the crown; m_1 nearly one-half the length of p_4 , with four external ^a and six internal ^a tubercles; anterior portion of tooth narrower than posterior portion.

The last premolar is larger than that of *Ptilodus trouessartianus* Cope, but not so large as that of *P. mediavus* Cope.

Measurements of type (after Douglass).

	mm.
Length of p_4	7.5 [7.8] ^b
Length of m_1	3.7 [3.4]

This is the first species of *Ptilodus* described from the Montana Fort Union and is apparently quite distinct from the New Mexico Torrejon species described by Cope. In the National Museum collection there are portions of upper and lower jaws representing four individuals that are probably referable to this species. They are two left lower-jaw fragments, each containing p_4 ; a lower-jaw fragment containing p_4 and m_1 ; and an upper-jaw fragment containing the three anterior premolars. These are, respectively, Nos. 6077, 6078, 6079, and 6080, U. S. National Museum collection. They are from the same locality and horizon as the type of *P. montanus*.

PTILODUS GRACILIS, new species.

Type-specimen.—A partial skeleton, including a nearly complete skull and lower jaws, the greater portion of the pelvis, one femur, the distal portion of the humerus, a radius and portion of an ulna, the proximal end of a tibia, a terminal phalanx, portions of vertebrae, and other fragments. (Cat. No. 6076, U.S.N.M.)

Type-locality.—Sweet Grass County, Montana.

Horizon.—Fort Union formation.^c

General definition.—Dental formula, $i_1^1, c_1^1, pm_2^4, m_2^2$. In size this species is about intermediate between *P. mediavus* and *P. trouessartianus*. It is but slightly smaller than *P. montanus* Douglass. The lower jaw is far more slender in proportions than either *P. mediavus* or *P. montanus*; the fourth premolar is relatively higher and has 14 ridges on either side of the crown. Lower m_1 has but 5 tubercles in

^a This is evidently a typographical error and should read "four internal and six external tubercles."

^b In carefully remeasuring the type I find these measurements to be: Length of p_4 , 7.8 mm.; length of m_1 , 3.4 mm.

^c Other forms from these beds indicate that this horizon is about equivalent to, as reported by Douglass, or perhaps somewhat older than the Torrejon beds of New Mexico.

the outer row of cusps, as compared with 6 in *P. montanus*. The upper dentition of this species can at present be compared only with that of *Ptilodus plicatus* Cope, since the upper molariform teeth of other species of the genus are not known. The principal differences thus shown are: (1) The smaller proportions of *P. gracilis*, which is about one-fourth less in size; (2) the proportionately greater antero-posterior length of the cheek teeth; and (3) the greater number of cusps in p^3 , there being 6 cusps instead of 5, as in the type, or 4, as in the neotype of *P. plicatus*. The number of these cusps may be more or less variable, but are probably of specific importance.

DETAILED DESCRIPTION.

The dentition.—The teeth of the present specimen being fully adult and but little worn afford an excellent opportunity both for a detailed and general study of their characters.

The single upper incisor preserved is placed in the premaxillary near but not closely appressed to the median line. It is a relatively long, rounded and gently curved tooth, with a pointed tip. The crown is slightly compressed on the posterior face with lateral angles dividing the surface into two unequal areas, the posterior one being the smaller and less convex. Near the summit of the tooth the posterior area is subdivided obliquely by a sharp ridge running from the apex upward and outward to the outer main angle, so that the tip of the crown is roughly triangular in cross section.

The next tooth in the upper series, which from its position is apparently a canine, is separated from the incisor just described by a considerable diastema. It much resembles the incisor in general form, but is smaller, and a posterior oblique ridge runs to the inner main angle instead of the outer one. A considerable diastema separates the canine from the premolar series.

The first upper premolar, p^1 , is a triangular tooth composed of three nearly equal subpyramidal cusps whose apexes point slightly backward. Premolar² resembles p^1 , except that it is quadrate in outline and has four subequal cusps. This tooth is somewhat higher crowned than the others and is the largest of the anterior three premolars. Premolar³ equals p^2 in length, but is narrower and less robust. The crown is quadrangular and bears six cusps of nearly uniform size arranged in two longitudinal rows. The anterior pair is somewhat smaller than the others, and the cusps are closely joined to those of the median pair. This tooth strikingly resembles the upper true molars of *Plagiaulax (Bolodon)*. All the cusps of the anterior premolars have the peculiar wrinkled appearance noted by Cope, Marsh, and others.

In classing the next tooth of the upper series with the premolars. I differ from the opinions of Cope and Osborn, who called the cor-

responding tooth in *Ptilodus plicatus* the anterior true molar. However, a critical examination shows that, though resembling in general form the molar next behind it, it differs from that tooth in several important particulars, while in position and function it properly belongs with the antemolar series. Like the first true molar, p^1 is much elongated anteroposteriorly and is multituberculate, but here the real resemblances between the two teeth end. P^4 is made up of two rows of cusps of unequal length, the inner, composed of nine tubercles of nearly uniform size, being the longer, while the tubercles of the outer row, seven in number, are very unequal, some being larger and some smaller than those of the inner row. The third tubercle from the front in the outer row is the largest and principal cusp of the tooth; in consequence the transverse diameter of the crown is greatest at this point. This and the three other larger cusps of the outer row have the characteristic wrinkling of the enamel seen in the anterior premolars and is almost a duplicate of the outer main cusps of p^3 ; if detached, it might readily be mistaken for one of them. There is a marked difference in the character of these cusps and the smooth-surfaced tubercles of the true molars.

In contrast with p^4 , m^1 is composed of two subequal rows of tubercles of nearly uniform size and a third less prominent and much shorter inner row, which, in the present specimen and in *P. plicatus*, is developed only along the posterior half of the crown; thus the widest transverse diameter of this tooth is at the extreme posterior end instead of across the anterior half, as in p^4 . The last tooth of the series, m^2 , is wider transversely, but is much shorter than m^1 . It has three rows of tubercles, the inner and outer rows being fused into an almost undivided ridge. The cusps of the median row are slightly curved and point forward.

The lower incisors are comparatively long, slender, and moderately curved. They are oval in section at the base, but are somewhat flattened on the inner faces and are sublanceolate near the tips. A considerable portion of the tip is completely enamel-covered, although the enamel is thin on the posterior face and it does not continue to the base of the crown. When placed in their normal position the lower incisors come in contact with each other only along the sharp angles forming the anterior borders of their inner faces.

The lower premolars are reduced to two in number and are greatly specialized, p_3 being vestigial, while p_4 is the largest and most highly modified tooth of the lower series. It is set obliquely in the jaw, so that its fore-and-aft plane comes in direct line with the cheek-tooth row and parallel to that of its fellow of the opposite side; its normal position is well shown in Plate 70, fig. *c*. The tooth crown dips downward at a sharp angle anteriorly, so that its highest point is on a level with the low-crowned molars. This position brings the grooves

and ridges of its sides at right angles to the horizontal plane of the tooth row, and consequently in line with the direction of force brought to bear on the tooth in normal use. This position of the tooth in the jaw would explain the relatively large size of the anterior fang, which much exceeds the posterior one, since much the greater part of the strain would thus be transmitted to that portion of the tooth. It probably also accounts for the uniform persistence of the vestigial p_3 , as the latter is placed well under the anterior edge of p_4 in such a position as to receive part of the strain imparted to p_4 . Thus p_3 evidently served as a prop or supplementary buttress for the large cutting tooth.

The combined length of the two lower molars is somewhat less than that of the upper true molars which they directly oppose; but this discrepancy in length is compensated by the peculiar fore-and-aft movement of the jaw in chewing. Both molars are low-crowned, with two rows of subequal tubercles. M_1 has 5 cusps in the outer and 4 in the inner row, while m_2 has 3 in the outer and 2 in the inner row. M_2 is broader and shorter than m_1 .

The *skull* is relatively short and broad, its greatest width being across the posterior ends of the zygomatic arches. The zygomatic arch is moderately slender. It joins the maxillary opposite the anterior half of p^1 and extends backward nearly to the lambdoidal crest. The malar extends backward to the glenoid surface, and apparently joins the lachrymal bone anteriorly as in the living marsupials. The anterior extension of the malar, however, can not be made out with certainty, owing to the almost complete obliteration of suture lines in this region. The occiput extends but slightly beyond the posterior root of the zygoma; this, with the extreme backward extension of the cheek-teeth series, gives the basi-cranial region very short and broad proportions. The brain case is large, but comparatively smaller than that of living marsupials, and is marked anteriorly by a distinct but broad constriction of the skull. The nasals are relatively large and broad, expanding posteriorly. They join the frontals on a line slightly forward of the anterior margin of the orbits. The maxillaries are relatively very large and deep, and extend well backward to accommodate the long row of cheek teeth. The premaxillaries are short and widely separated from the frontals by the ascending portion of the maxillary. The relatively broad, high-arched palate is perforated by two pairs of foramina. The posterior pair are very large, occupying nearly one-half the entire length of the palate. The palate back of the muzzle is narrowest between the last pair of molars and widest between the third pair of premolars. The characters of the basicranial region can not be made out clearly, owing to crushing and breaking, but there appears to be an alisphenoid canal and a well-developed alisphenoid bulla.

The glenoid fossæ are broad, nearly flat, and extend well forward, giving free fore and aft movement to the lower jaws. The right occipital condyle is broken away, but the remaining one is broad and shows that the pair were set widely apart; the articular surface curves gently outward, backward, and upward. There is a distinct notch on the inferior inner border of the condyle, a character also observed in some of the living diprotodont marsupials.



FIG. 1.—LEFT HUMERUS OF PTILODUS GRACILIS. TYPE. ANTERIOR VIEW. TWICE NAT. SIZE.

A nearly complete cervical, probably the sixth or seventh, and parts of two or three broken caudals are practically all the elements preserved representing the *vertebral column*. The cervical vertebra is slightly longer than broad, indicating a moderately long neck. The caudals are relatively large, with well-developed processes, indicating a long and rather heavy tail.

The *humerus* (see fig. 1) is incomplete, but the head, the distal end, and a considerable portion of the shaft are preserved. These portions show some important characters. It is distinctly eutherian

throughout, and is very unlike that of any of the living Montremes. The head is relatively large, broadly oval in outline, and well rounded. The shaft is moderately long and slender, with well-developed but not highly specialized deltoid ridge. The distal end is moderately expanded, and the articular surface is divided into two well-defined ridges, the inner, or trochlea, being somewhat broader, especially on the anterior face, than the outer, or capitellum. The inner condyle occupies about one-third of the transverse diameter of the distal end of the humerus. The entepicondylar foramen is small, broadly oval in outline, and placed close to the trochlea. The olecranal fossa is deep and sharply defined.

The *radius* (see fig. 2) lacks the distal epiphysis, but is otherwise complete. The shaft is comparatively long and slender, slightly curved, and nearly round in cross section. The tuberosity for the attachment of the biceps muscle is well developed. The head is expanded into a broadly elliptical, almost circular disk, with a wide transversely convex facet for the articulation of the ulna. Its form indicates a perfectly free rotation of the forearm. Another long slender bone lacking the epiphysis of the distal end, and with the proximal end somewhat broken, represents the ulna.



FIG. 2.—RIGHT RADIUS OF PTILODUS GRACILIS. TYPE. *a*, VIEW OF PROXIMAL END; *b*, SIDE VIEW. TWICE NAT. SIZE.

The feet are represented by an ungual phalanx (fig. 3) and two or three portions of metapodials. These bones, which from their relatively small size apparently belong to the fore feet, are rather long and slender in proportions and not specialized. The ungual phalanx apparently supported a rather sharp claw.

The *pelvis* is proportionately large but primitive in structure. (See fig. 4.) The ilium is a long, slender, rod-like bone, somewhat flattened transversely. The ischium is moderately long and expanded.

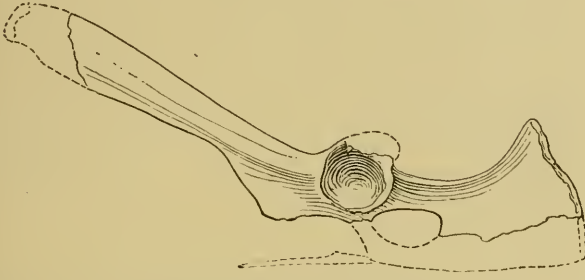


FIG. 4.—LEFT HALF OF PELVIS OF *PTILODUS GRACILIS*. TYPE. OUTER VIEW. TWICE NAT. SIZE.

Unfortunately the greater part of the pubis is broken away so that the presence or absence of marsupial bones can not be determined, although they probably were present. The obturator foramen, as indicated by its upper border, which is preserved, is comparatively small.

The *femur* (see fig. 5) is relatively large and stout as compared with the humerus. Both trochanters are well developed, the great trochanter extending considerably above the head of the femur. The lesser trochanter is a prominent tubercle, and is situated on the posterior face of the shaft near the base of the great trochanter as in the eutherian mammals. The shaft is nearly straight and is slightly flattened anteroposteriorly.



FIG. 5.—RIGHT FEMUR OF *PTILODUS GRACILIS*. TYPE. POSTERIOR OBLIQUE VIEW. TWICE NAT. SIZE.

The *tibia* and *fibula* (see fig. 6) are poorly preserved, but are represented by portions of the proximal ends. The tibia is much the larger bone. Both are large as compared with the radius and ulna. The relatively large proportions of

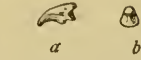


FIG. 3.—TERMINAL PHALANX OF *PTILODUS GRACILIS*. TYPE. *a*, SIDE VIEW; *b*, PROXIMAL END VIEW. TWICE NAT. SIZE.

the pelvis and hind limbs strongly suggest that *Ptilodus* was saltatorial in habits.



FIG. 6.—PROXIMAL PORTIONS OF TIBIA AND FIBULA OF *PTILODUS GRACILIS*. TYPE. POSTERIOR OBLIQUE VIEW. TWICE NAT. SIZE.

Measurements of type.

[Dimensions in millimeter's.]

	Anteroposterior.	Transverse.	
Diameters of p ¹ -----	2.5	2.1	
Diameters of p ² -----	2.5	2.5	
Diameters of p ³ -----	3	2	
Diameters of p ⁴ -----	5	2.5	
Diameters of m ¹ -----	4.6	2.1	
Diameters of m ² -----	2	2.3	
Total length of upper dental series-----			25
Length of molar-premolar series-----			19.5
	Anteroposterior.	Transverse.	Height.
Diameters of lower p ₁ -----	7.6	2.4	5.6
Diameters of lower m ₁ -----	3.3	1.8	1
Diameters of lower m ₂ -----	2.4	2	---
Total length of lower series, including incisor-----			20.8
Length of molar-premolar series-----			12.2
Length of lower jaw-----			26
Length of lower jaw, including incisor-----			31
Depth of lower jaw at m ₁ -----			6.8
Depth of lower jaw at p ₁ -----			5.5
Total length of skull-----			41
Greatest width of skull (across glenoid fosse)-----			31.6
Width of skull at p ⁴ -----			15.5
Width of palate between first premolars-----			8
Width of palate between last molars-----			8
Width of palate between fourth premolars-----			11
Distance from occipital condyle to posterior border of palate-----			15
Transverse diameter of occipital condyles-----			9.2
Distance from center of glenoid fossa to m ² -----			11
Distance from condyle of lower jaw to m ₂ -----			11
Length of humerus (estimated)-----			24
Length of distal portion preserved-----			16
Greatest diameter of head of humerus-----			4.9
Transverse diameter of shaft-----			2.6
Width across condyles-----			5.6
Width across articular surface (anterior)-----			3.4
Width across articular surface (posterior)-----			2.6
Anteroposterior diameter of trochlea-----			3.4
Total length of pelvis (estimated)-----			37
Length of ischium-----			12.5
Diameter of acetabulum-----			3.8
Length of femur-----			32+
Diameter of shaft-----			4

PTILODUS SERRATUS? ^a (Marsh).

A left lower fourth premolar (Cat. No. 6088, U.S.N.M.), found in the same deposits from which the types of *P. montanus* and *P.*

^a *Halodon serratus* Marsh, Amer. Journ. Sci., XXXVIII, 1889, p. 87, pl. III, fig. 14.

gracilis were obtained, represents a third and much smaller species of *Ptilodus* from these beds. This tooth is about the size of the type of *P. trouessartianus* Cope, but does not agree with it in proportions, the latter being relatively much lower crowned. In this respect it corresponds much more closely and agrees also in size with the type of "*Halodon serratus*" Marsh, from the Ceratops beds of Converse County, Wyoming. For the present I provisionally refer it to Marsh's species, although there are minor differences which indicate that it may later be placed in a new species.

• **PTILODUS FORMOSUS? ^a (Marsh).**

A fourth and still smaller species is represented in this collection from the Fort Union by two lower fourth premolars (Cat. Nos. 6089 and 6090, U.S.N.M.). These teeth, which are only 3.2 mm. in length, agree in size, proportions, and the number (12) of enamel ridges with Marsh's "*Halodon formosus*," from which they can not at present be distinguished. The type of this species is also from the Ceratops beds.

ZOOLOGICAL RELATIONS.

Owing to the absence of good material, well-defined characters other than those presented in the teeth have hitherto been wanting. In consequence there has been a wide diversity of opinions regarding the relation of the Multituberculates to other great groups of the Mammalia. Earlier writers, studying Jurassic forms, classed them with the *Marsupialia*. Marsh, in 1880,^b first proposed placing the group in a distinct order, which he named the *Allotheria*, although recognizing their marsupial affinities. In defining the order he said:^a "These characters alone do not indeed separate the *Plagiaulacidae* from some of the Marsupials, and future discoveries may prove them to belong in that group, where they would then represent a well-marked suborder." Later Cope^c proposed the name *Multituberculata* for this same group, which he considered a suborder of the *Marsupialia*. Still later he suggested their relationship to the *Monotremes*. At present most authorities rank the group as a full order, which is variously classed with the Marsupials or the *Monotremes*.

As has been stated by Osborn,^d the relationship of the group to the *Marsupialia*, which was first proposed by Falconer, had not been questioned until the discovery, by Poulton, of the early-shed multitubercular teeth of *Ornithorhynchus*. This led Cope to suggest the reference of the Multituberculates to the *Monotremata*, a view which

^a *Halodon formosus* Marsh, Amer. Journ. Sci., XXXVIII, 1889, p. 179, pl. VIII, fig. 36.

^b Amer. Jour. Sci., (3) XX, 1880, p. 239.

^c Amer. Naturalist, XVIII, 1884, p. 687.

^d The Structure and Classification of the Mesozoic Mammalia, Journ. Acad. Nat. Sci., Phila., (2), IX, 1888, p. 254.

has found rather wide acceptance. In his classification of the Mesozoic Mammals^a Osborn stated his own views as follows:

While the Multituberculata are widely separated from the mammals of the second group [including the Trituberculata forms] they are so closely related to each other by the unique structural and functional adaptations of the dentition, that the discovery in one genus of a single taxonomic character, which is distinctive, will probably determine their position either with the Monotremata or Marsupialia or in an independent order; * * *.

The separation of these genera from the Diprotodonts justifies the prediction, as a result of future discovery, that the Multituberculata will prove to be the last representative of a very ancient phylum which reached too great a degree of specialization and dental reduction at the close of the Cretaceous to survive or leave descendents in the recent period. Whether they are to be considered as a branch of the monotreme or of the marsupial stock is an unsettled question.



FIG. 7.—RIGHT LOWER JAW OF TRICHOSURUS VULPECULA KERR. CAT. NO. 85436, U. S. N. M. INNER VIEW. $\frac{1}{2}$ NAT. SIZE.

In his latest classification of the Mammalia,^b Osborn lists the Allotheria under the subclass *Protheria* as a doubtful order of uncertain systematic position.

Falconer and Owen referred *Plagiaulax* to the Diprotodontia, but differed in their opinions regarding its probable habits and taxonomic relations. Falconer compared *Plagiaulax* with *Hypsiprymnus* (*Potorous*) and sought to prove that the former was a salutory herbivorous marsupial, allied to the Rat-Kangaroos. Owen^c just as strongly contended that it was carnivorous in habits, and more probably related to the extinct carnivorous *Thylacoleo*.

Owen's conclusions regarding the carnivorous habits of *Plagiaulax* lose much of their force since it is now apparent, through a study of the present specimen of *Ptilodus*, that his principal arguments were based on an error in the interpretation of a most important factor, namely, the normal position of the jaw. Viewing the lower jaw of *Ptilodus*, properly articulated with the upper (see figs. 7 and 8), it is observed that passing forward it pitches downward at a considerable angle, bringing the plane of the tooth-row below the condyle, and the incisors into a semiprocumbant position as in the Diprotodonts. It will be noted also that the greater part of the thin cutting blade of p_1 does not come in contact with the upper teeth, but stands free in the mouth. If the lower jaw of *Plagiaulax* is thus placed



FIG. 8.—RIGHT LOWER JAW OF PTILODUS GRACILIS. TYPE. INNER VIEW. $\frac{3}{4}$ NAT. SIZE.

^a Journ. Acad. Nat. Sci. Phila. (2), IX, 1888, p. 254.

^b Evolution of the Mammalian Molar Teeth, 1907, p. 11.

^c Fossil Mammalia of the Mesozoic Formations, 1871.

(see fig. 9), here also the condyle is above the tooth-row and not below it, as stated by both Owen and Falconer. The premolar teeth likewise drop away from the level of the molar series, forward, so that the anterior ones could scarcely have come in contact with any teeth of the upper jaw. It is further observed that, as in *Ptilodus*, the ridges on the sides of the cutting blades viewed laterally run nearly at right angles to the plane of the molars; thus these ridges which have always been described as being "oblique" in the fossil forms, are after all placed in the same relative position in the mouth as those of the ridged premolars of living species. Assuming this position for the lower jaw and recognizing the fact that the blade-like premolars did not oppose teeth of like structure in the upper jaw, the carnivorous characters pointed out by Owen seem to disappear, while the general resemblances to the less specialized Diprotodonts become more than ever apparent.

The resemblances pointed out by Falconer^a between *Plagiaulax* and *Potorous* ("Hypsi-prymnus") a genus of the Macropodidæ, are in the main substantiated in the present specimen of *Ptilodus*, which also possesses some important characters in common with some of the Phalangeridæ, as *Trichosurus* and *Phalanger*. The specialization of the teeth, however, has been carried to a greater degree, both in reduction in numbers of the molars and in the development of the premolars, than in any of the living Diprotodonts.

This preliminary study leads apparently to the following conclusions regarding the zoological position not only of *Ptilodus* and the Plagiaulacidæ, but of the Allotheria in general. A fact of first importance is that neither in the skull nor skeleton of the Montana specimen are there any indications of affinities suggesting the Monotremes, while every character is marsupial, as shown in the general arrangement and function of the teeth and the development of the skull and skeleton. The unequal development of the fore and hind limbs, the character of the incisors, the form of the palate, and the position of the cheek-teeth all indicate definite affinities with the Diprotodonts. At the same time the reduction in numbers of the molars and the extreme specialization of the premolars confirms Osborn's conclusion regarding the philetic position of the group, namely, that the Multituberculata may be the last representatives of a very ancient phylum that became extinct in the early Tertiary.

From the foregoing therefore it appears that the Allotheria represent an extinct group of multituberculate eutherian mammals closely



FIG. 9.—RIGHT LOWER JAW OF *PLAGIAULAX BECKLESII* FALCONER. INNER VIEW. ABOUT NAT. SIZE.

^a Quart. Journ. Geol. Soci. London, XIII, 1857.

related with but not ancestral to the Diprotodont division of the Marsupialia, with which division they may be now classed as an Infraorder, or Superfamily, their relationship dating back to a common ancestry somewhere in the Jurassic or even to earlier Triassic times, as was suggested by Cope.

Regarding the probable character of the food, upon which *Ptilodus* and its related genera subsisted, the specimen from Montana described above seems to throw considerable light. An examination of the type of *P. gracilis* (Pl. 70) shows Cope's^a statement, that the grinding teeth are "weak in structure," is incorrect, and his supposition that it was necessary for the animal to swallow its food without mastication is not admissible. On the contrary it will be seen that the grinding area is comparatively very considerable, occupying nearly three-fourths of the actual contact space between the upper and lower dental series, and although the tooth-crowns are low they are relatively broad and massive. To add to their efficiency the molars are well supplied with an array of short stout tubercles, well adapted to crushing and grinding small hard substances but very poorly adapted to cutting or masticating meat. In specimens of old individuals the much worn condition of the tubercles of the molars as compared with that of the lower cutting-premolar suggests that the latter may have been used for the purpose of cutting only soft materials, such as the skin and pulp of fruit, while the molars were employed in grinding harder substances, such as seeds.

The evidence that *Ptilodus* and *Plagianax* were not carnivorous in habits seems rather conclusive, but as to whether they were insectivorous, herbivorous, or frugivorous there may still be some differences of opinion. I am inclined to consider them as frugivorous, since the incisors were well fitted for picking small fruits or berries, while the large cutting blades of the lower premolars were admirably adapted to cutting or slicing the rinds of tough-skinned berries, or to chopping up fleshy fruits held against the blunt-pointed premolars of the upper jaw. For masticating the seeds of such small fruits and berries the multituberculate molars were amply sufficient.

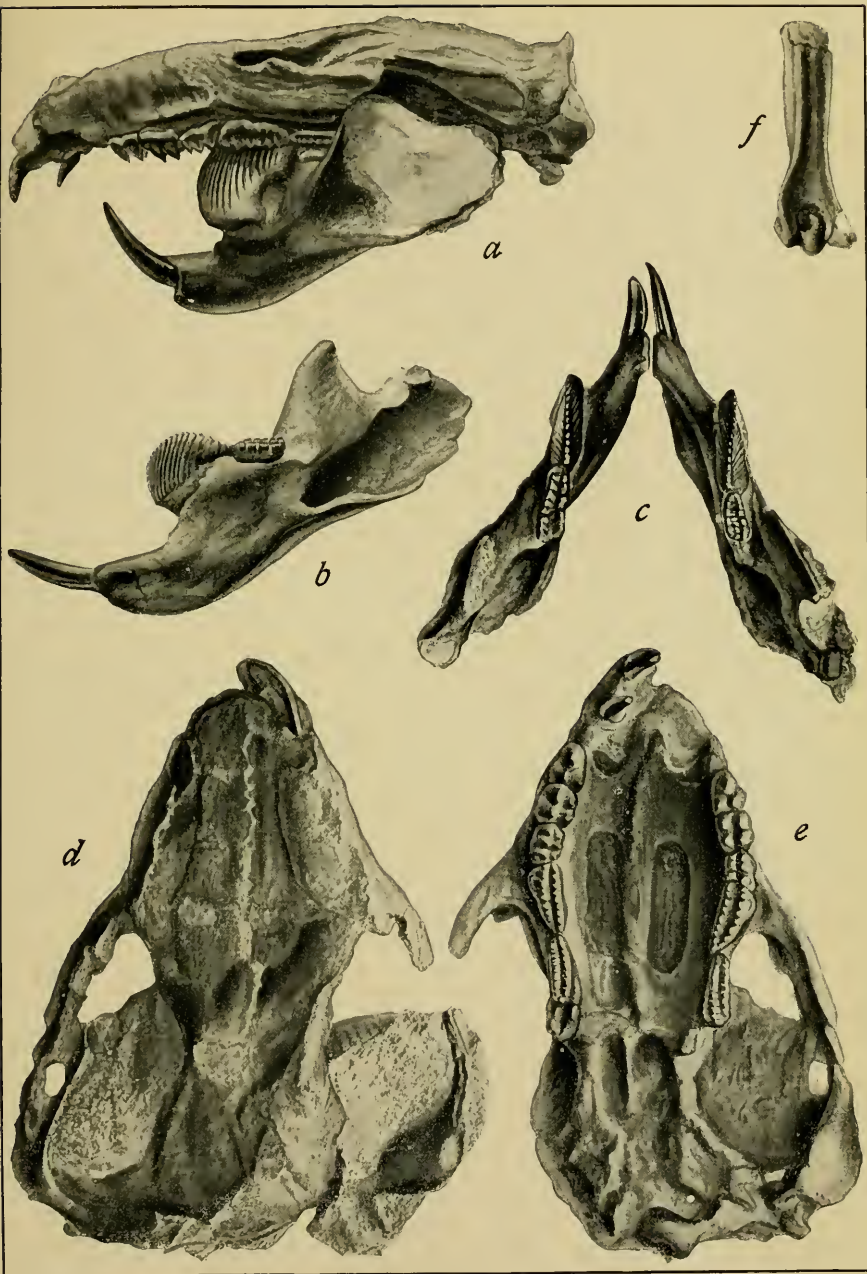
EXPLANATION OF PLATE 70.

Ptilodus gracilis Gidley.

(Type-specimen.—Cat. No. 6076, U.S.N.M. All figures twice natural size.)

- Fig. a. Skull with lower jaw in position, side view.
 b. Right ramus of lower jaw, inside view.
 c. Lower jaws in normal position, viewed from above.
 d. Skull, top view.
 e. Skull, palate view.
 f. Distal portion of left humerus, posterior view.

^a Cope, Tertiary Vertebrata. U. S. Geol. Surv. Terr., III, 1884, p. 170.



PTILODUS GRACILIS GIDLEY.

FOR EXPLANATION OF PLATE SEE PAGE 626.

