A Revision of the Tertiary Multituberculata

By Walter Granger and George Gaylord Simpson

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INTRODUCTION

The present revision of the Tertiary Multituberculata is the outcome of studies made some years ago, by the senior author, on the extensive collections in the American Museum, and of more recent studies, by the junior author, on the European material, followed by an examination of practically all of the American material. Both authors have also studied the known Mongolian material, originally described by Matthew, Granger and Simpson. All Tertiary multituberculate types have thus been studied, including the Paleocene forms from North America, Europe, and Asia, and the Lower Eocene forms from North America. The paper is not limited to a taxonomic revision in scope, but includes detailed morphological descriptions of all forms.

Previous revisions of the later multituberculates begin with Cope, who, in his Tertiary Vertebrata (1884), gave what was then known of

the American forms. In the same year, in his paper on Tertiary Marsupialia, he gave a brief revision of all then known genera of Paleocene multituberculates. Osborn and Earle, in 1895, revised the *Tæniolabis* (*Polymastodon*) group, and Gidley, in 1909, revised the *Ptilodus* group. Teilhard has recently (1922) given a brief statement of what is known regarding European forms.

With its many types, the Cope collection of multituberculates from the classic Paleocene locality in northern New Mexico forms the nucleus of the American Museum collection of these forms, but the museum expeditions into this region in 1892 and 1896 under Wortman, and in 1912, 1913, and 1916 under Granger, have not only added a great amount of additional material but have done much toward clearing up the stratigraphy of the region. This combined material forms the chief basis for the present revision of the American forms.

We wish to acknowledge our indebtedness to Professor M. Boule for giving access to the Lemoine Collection in the Muséum d'Histoire Naturelle in Paris; to Prof. C. Depéret for the opportunity to examine the undescribed material collected by him and now in the Université de Lyon; to Dr. W. O. Dietrich for giving access to material in the Museum für Naturkunde in Berlin; to Mr. August Peterson of the Carnegie Museum of Pittsburgh for the loan of the type of *Ptilodus montanus* Douglass; and to Dr. W. D. Matthew for examining the manuscript of this paper and giving some critical comments thereon.

The figures were drawn by Sydney Prentice from the original specimens, except Figs. 37–40 drawn by Prentice from pencil drawings by Simpson, Figs. 4–6, 19–26, and 31–32 by Mrs. L. M. Sterling, Figs. 34–36 and 42–43 by John Germann, and Fig. 41 by Mrs. John Germann. Figs. 15 and 16 are from photographs by G. Van Ingen.

AMERICAN TERTIARY MULTITUBERCULATES

The American Paleocene mammalian faunas are at present much better known than those of any other part of the world, and the multituberculates, which constitute one of the most striking elements of Paleocene faunas generally, are also known in the greatest variety and morphological detail from American strata. At present, at least three distinct faunas are known, the lower, middle, and upper Paleocene. The lower Paleocene is represented only by the Puerco of the San Juan Basin, New Mexico; the middle Paleocene by the Torrejon of New Mexico and by at least part of the Fort Union of the more northern Rocky Mountains and plains region, especially Montana; and the

upper Paleocene (approximately equivalent to the Thanetian of Europe) by the Tiffany of Southwestern Colorado, the Clark Fork of Wyoming, and part or all of the Paskapoo Formation of Alberta. Each of these horizons has its own multituberculates.

The following artificial key will serve for the recognition of the families and genera occurring in the American Paleocene :

I.   Premolars $\frac{1}{1}$, last lower premolar reduced, not trenchant . . . . Tæniolabididæ.
  A.   Lower molars narrower, cusps not more than 6:5, 4:2 . . . . *Catopsalis*.
  B.   Lower molars broader, cusps not less than 7:6, 5:4 . . . . . . *Tæniolabis*.
II.   Premolars $\frac{4}{2} \stackrel{-}{=} \frac{3}{1}$, last lower premolar enlarged, trenchant, serrated . . Ptilodontidæ.
  A.   Lower incisor not gliriform, P_3 present.
    1. P^4 with outer tubercles numerous . . . . *Ptilodus*.
    2. P^4 with outer tubercles 1 or 2 in number . . . . *Ectypodus*.
  B.   Lower incisors gliriform, P_3 absent, P^4 with 3 or 4 outer tubercles.
    . . . . *Eucosmodon*.

TÆNIOLABIDIDÆ, new name

SYNONYM.—Polymastodontidæ Cope, 1884.

DEFINITION.—Dental formula $\frac{2 \cdot 0 \cdot 1 \cdot 2}{1 \cdot 0 \cdot 1 \cdot 2}$. Enlarged incisors rooted but extremely hypsodont, with enamel confined to an anteroexternal band except at the tip. Premolars relatively small, non-trenchant, with a single subconical main cusp and various accessory cuspules. M^1 with three cusp rows, generally of equal length. M^2 with two cusp rows and slight indication of a third, outer, cusp row. Molar cusps generally not markedly crescentic, sharp when unworn but usually overlapping broadly in occlusion so as to be quickly worn down to bluntness. First molars much larger than second. Skull very heavy, somewhat depressed, with widely expanded rather square zygomata. Mostly animals of relatively large size.

TYPE.—*Tæniolabis* Cope.

Tæniolabis Cope, 1882

  1882.   *Tæniolabis*, Cope, Am. Nat., XVI, p. 604.
  1882.   *Polymastodon*, Cope, Am. Nat., XVI, p. 684.

TYPE.—*T. sulcatus* Cope, 1882.

DISTRIBUTION.—Known only from the Puerco of the San Juan Basin, New Mexico.

DIAGNOSIS.—Basic cusp formula: M_1 7-8: 6-7; M_2 5-6: 4-6. Molar cusps transversely elongated. M_1 relatively wider than in *Catopsalis*. Species relatively large.

This is the genus universally called *Polymastodon*. Most authors have considered *Tæniolabis* and *Polymastodon* as synonymous, which is unquestionably correct (see the specific revision below), but have used the latter name. *Tæniolabis*, however, was described in July, 1882, *Polymastodon* in August, and the prior name must necessarily be used. This change also involves changing the family name to Tæniolabididæ.

DENTITION

As has often been remarked, the dentition of *Tæniolabis* is rodent-like in habitus. The incisors are functionally gliriform, although not of continuous growth, and have limited enamel bands which led to the maintenance by wear of a chisel-like working edge. They were used only in the most anterior position of the jaw and were not in contact when the low-crowned but broad and heavy molars were in use. The motion of the jaw was almost purely anteroposterior, although there may have been some degree of lateral play when the molars were somewhat worn down.

The lower incisors are limited to one in each side and are much enlarged and very long, each forming an arc of a large circle. The working edge was throughout life at a point a little below the molar level, about 2 to 2.5 cm. of the tooth, as measured along the anterior face, protruding from the alveolus. The intra-alveolar portion is much longer. Until late maturity the root extends back beneath M_2. With the further advance of age the tooth continues to move forward, but the root is no longer lengthened and its end must therefore also move forward in the jaw. Growth is long continuing but not continuous throughout life. In younger specimens the root is widely open and the pulp cavity large, but in older ones continued dentine deposition reduces the size of the pulp cavity, completely obliterating it in the enamel-bearing portion, and the root becomes restricted and almost closed posteriorly.

The unworn tip is not known, but from very young specimens it appears to have been simply pointed. The median surface of the tooth is flattened and has a broad, shallow, longitudinal concavity. Inferiorly there is a sharp angulation between this and the outer surface; superiorly the transition is rounded. The outer surface is convex save for a small longitudinal groove above the enamel. The enamel is confined to a longitudinal band covering about a third of the section of the tooth. It extends for a short distance onto the median face, covers the lower face completely, and extends up on the external face. The enamel band does not widen posteriorly as does the tooth, so that while it covers the entire external face anteriorly, posteriorly it only covers about half. Deposition of enamel apparently continued for a time after the tooth was in use, but it finally ceased abruptly. This is shown by the fact that in young individuals the enamel band is very long, extending far down inside the alveolus, while in older ones it becomes progressively shorter and finally may be almost entirely lacking, not even reaching the mouth

of the alveolus. Osborn and Earle (1895, p. 14) considered this limitation of the enamel to be characteristic of the more robust species here called *T. triserialis*, but the large amount of material now available shows that it is not a taxonomic character, occurring in very old individuals regardless of species. The enamel is fluted longitudinally and there are also smaller longitudinal rugosities, while, especially posteriorly, there are numerous transverse lines of growth.
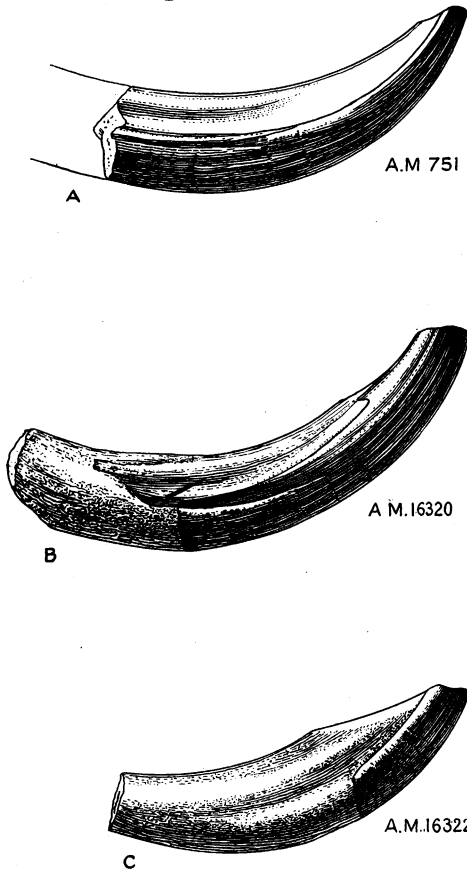

Fig. 1. *Tæniolabis*. Lower incisors showing successive stages of wear. A, Young. B, Adult. C, Senile. Natural size.

The small median upper incisors known to have occurred in the Triassic *Tritylodon* and in the Plagiaulacidæ of the upper Jurassic, are absent in *Tæniolabis*. The remaining two teeth are therefore I^2 and I^3. As in all multituberculates, I^2 is much enlarged and I^3 small. I^2 is similar

in general to the lower incisor, but there are many differences of detail. Like the lower, it is a large curved tooth with open root in the young, later becoming restricted, and with an enamel band of considerable length ending abruptly at the largest part of the tooth. The unworn apex is preserved in several specimens. The tip was bifid with two sharp points, one, slightly smaller, directly external to the larger one. On the posterior edge about one centimeter from the unworn apex is a distinct small accessory cusp. Although apparently so different in the usual state of preservation, this very hypsodont tooth thus shows in a remark-
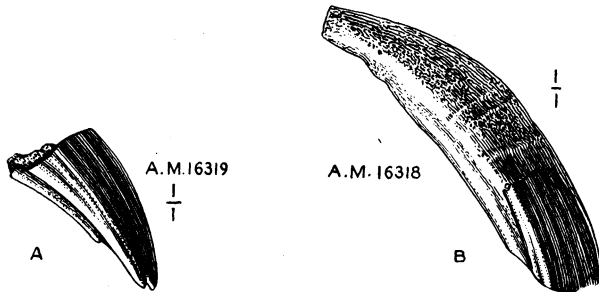

Fig. 2. *Tæniolabis.* Upper incisors showing stages of wear. A, Tip of unworn tooth. B, Old tooth. Natural size.

ably conservative way the same basic pattern as the homologous brachyodont teeth in the remotely structurally ancestral Jurassic plagiaulacids. The tip is completely covered with enamel but that on the posterointernal face is much thinner and begins to disappear medially about 10 to 12 mm. from the tip, although on the anterior and posterior edges it runs on for nearly 10 mm. farther. It is soon worn off and is not seen in old individuals. On the tip there is a sharp anterointernal vertical angulation and also a posteroexternal one passing just external to the posterior accessory cusp, but both become obsolete just above this point.

The thick enamel of the anteroexternal face of the tip becomes limited above this to a band about 12 mm. wide and passes back about 30 mm. (as measured along the curve) to the point where the enamel abruptly stops. Unlike that on the lower incisor, this enamel band is limited to the anteroexternal face, which it does not quite cover, and is not seen in the internal aspect of the tooth. The enamel surface is marked in the same way as that of the lower incisor.

The mouths of the alveoli of the lower incisors are close together, and these teeth are in contact throughout their extra-alveolar portions,

but the alveoli of the enlarged upper incisors are widely separated so that they project anterointernally and are in contact only at the tip.

I^3 is very small and is preserved in only one specimen (A. M. No. 970), although its alveolus is present in other premaxillary fragments. It is somewhat compressed anteroposteriorly and slightly recurved, with a simple tip. It is heavily enameled anteriorly and apparently has also a thin film of enamel on the posterior face near the tip.

Turning to the premolars, it seems highly probable that the single lower premolar of *Tæniolabis* is derived from a trenchant tooth something like that of *Ptilodus*, but the two are very unlike. In the present genus the crown is a somewhat elongated triangle in plan, with the base posterior. There is one main cusp at the apex and posterior to this there is a single small heel-like accessory cusp, usually somewhat transverse. Unless removed by wear, there is always also a still smaller postero-external basal cuspule, and there may be a small cuspule immediately anterior to the main cusp on the apex of the crown. The tooth is implanted by two stout roots. The alveolar border descends rapidly in front of it, so that part of the anterior root is exposed, and the enamel descends considerably farther anteroexternally than elsewhere.

This tooth cannot be called trenchant either in form or in function, but it did shear up internal to the upper premolar, as attested by the external wear surface. The heaviest wear is on the apex, however, which soon becomes truncated.

The single upper premolar is a wide plump tooth which has lost all shearing character although still efficient in grasping and no doubt also in limiting the lateral play of the jaw when the cheek teeth were in contact. It extends a little below the molar level and is ovoid, somewhat elongated in the direction of the jaw and wider posteriorly. Anterior to the main apex are one or two accessory cusps in the same longitudinal line and two or three ridges descend the crown posteriorly. There is also a posteroexternal basal accessory cusp, and a more or less cuspidate cingulum skirts the posterior end of the tooth. Wear from the lower premolar is slight, but M_1 reaches its posterointernal portion in anterior excursions of the mandible, and a large facet of wear is soon developed here. The enamel is rugose in some cases, nearly smooth in others.

The molars of *Tæniolabis* are highly variable, making separation into species difficult and hazardous. Not only do they vary in structure, size, and proportions, even the two sides of the same individual seldom being perfectly symmetrical, but their aspect is materially changed with advance of age and its attending wear. The general plan

is well known: the molars have broad crowns with numerous tubercles arranged in parallel rows. The details, however, are less well known, and, although much has been written on the subject, the rich material here available demands some emendation and amplification.

The lower molars have two rows of large cusps. M_1 is an elongate tooth rounded at the ends and slightly constricted in the middle so as to be composed of two subequal lobes. The number of cusps varies, but there is what may be thought of as the basic cusp number, normal for the genus, additional cusps being usually smaller, often more conical, added at the ends of the cusp rows or rather clearly intercalated. For M_1 the basic cusp number appears to be 7:6—that is, seven external and six internal cusps,—but there are usually small accessory cuspules anterior to one or both rows, while the number of more posterior cusps may be secondarily increased. In *T. triserialis* this tendency towards the addition of secondary cuspules is especially noticeable, and the main cusps may be increased to 8:7. Most striking, however, in this species is the distinct development of a row of small cuspules, which, starting posterior to the posterointernal main cusp, passes around the posterior end of the tooth and then curves anteriorly, outside the external cusp rows, for a short distance before disappearing. There may also be other cuspules intercalated between the outer bases of the external cusps of this species anterior to this accessory cusp row.

The shape of the main cusps has been variously described as quadrate, rounded, block-like, etc., but in fact when unworn they are tall and sharply pointed. The apices are inclined a little backward and usually have posterolateral sharp angulations, probably indicating a more truly selenodont ancestry. On anterior, posterior, and median faces each cusp usually has one, or seldom more, vertical grooves. The base of the cusp is thus rounded laterally, then constricted and passing into two internal ridges. The figures make this pattern clear. The unworn enamel is marked by fine vertical wrinkles.

Wear quickly truncates the cusps. In the early stages wear is much as in the ptilodonts, tending to retain or to emphasize the two longitudinal, cuspidate ridges and median valley, correlated with the three cusp rows and two valleys of the upper molars. With more advanced wear the median groove widens, and eventually there is only a single large plane of wear, concave transversely, convex longitudinally, and somewhat skewed so that it slopes inward posteriorly and is nearly horizontal or slopes somewhat outward anteriorly. Wear is greatest on the posterior part of the tooth. In mature individuals the crown is covered with

rings of enamel, corresponding to the cusps, of irregular outline due to the grooving of the cusps and surrounding lakes of dentine—a very complex pattern of great efficiency for grinding. The teeth are brachyodont, however, and as wear progresses further the enamel rings unite and eventually disappear so that in old age there is only a large surface of dentine surrounded by a crenulated rim of enamel. This limit to the useful age of the cheek teeth apparently coincided with that of the incisors and marked the maximum life span of an individual.

The second lower molar varies even more than the first, but in general is a much shorter and usually slightly wider tooth of ovoid shape, wider anteriorly than posteriorly. The inner cusp row extends some-
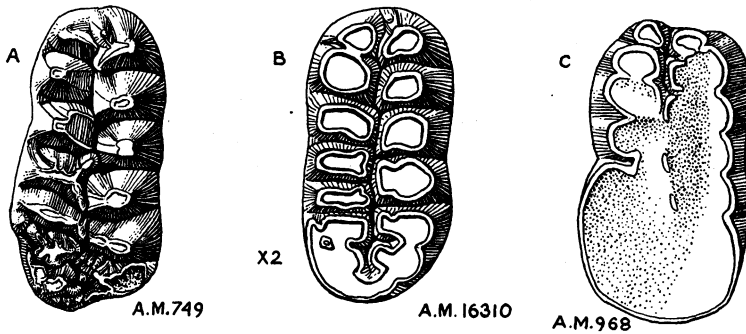

Fig. 3. *Tæniolabis taöensis*. First lower molars, showing successive stages of wear. A, Young (Type of "*Polymastodon selenodus*"). B, Adult. C, Senile. Twice natural size.

what farther anteriorly and the outer somewhat farther posteriorly. The basic cusp formula is 5:4 but it varies from 6:6 in an unusually robust *T. triserialis* to an individual belonging to *T. taöensis* which nearly reaches 5:3 through the reduction of the fourth inner cusp and enlargement of the first. In shape the cusps are like those of M_1 save that they tend to be shorter and wider. In *T. taöensis*, intercalated cusps are rare; in *T. triserialis* they are common, occurring even in the posterior part of the midgroove, and in addition there is a continuous row of cuspules, even stronger than on M_1, running from the posterointernal cusp around the posterior end of the tooth and for a greater or lesser distance anteriorly outside the external cusp row. In most specimens the external main cusp row is not quite so wide as the internal one, and this reaches an extreme in *T. triserialis* which may even appear to have three cusp rows diminishing in size from internal to external—an approach toward a three-rowed lower molar unique among Multituberculata.

The first upper molar is a broad and long tooth with three rows of cusps. Contrary to the usual, but not universal, condition in the Ptilodontidæ, these three rows are nearly equal in length. Outer and middle rows are uniform and subequal, but the inner row narrows anteriorly and the cusps become smaller. A median constriction of the tooth is indicated but is less definite than on M_1. The number of main cusps is variable, 8:9:10 probably being basic for the species *T. taöensis* or for the genus, but adventitious cusps, especially at the anterior end of the inner row and at both ends of the outer row, may increase the total number by three or four, and a lesser formula of 8:9:9 occurs rarely. The cusp structure of the outer and inner rows resembles that of the lower molars, while the cusps of the median row are symmetrical, bifid at both external and internal ends and somewhat restricted anteroposteriorly in the middle.

Even when unworn, the crown of M^1 is strongly arched, concave anteroposteriorly. The lower cusps are wider than the upper longitudinal grooves, so that as wear progresses they soon truncate the upper cusps. Even very old teeth, however, usually show broad shallow grooves for the lower cusp rows. The anteroexternal corner is least worn and usually projects above the general surface.

M^2, unlike the homologous tooth in the Ptilodontidæ, is essentially two-rowed, the outer, third, row consisting of but a single cusp which is not wholly external to the midrow. There are usually cuspules and ridges which make a count of the main cusps more or less subjective, but the formulæ 1:3:4, 1:4:5, 1:4:4, 1:3:6, and others do occur and the only possible general formula is 1:3-5:4-6. Variation is remarkably great. In A. M. No. 16321, for instance, the formula for M^2 right is 1:4:5 and for M^2 left of the same individual 1:4:6, so that despite the wide range it is impossible to assign the upper molars to different species with any degree of certainty. The outer cusp and the inner row are united across the front of the tooth by a ridge which bears three or four small tubercles. This may be disconnected and then has the aspect of a short transverse anterior cusp of the middle row. The first cusp of the midrow back of this ridge is usually internal to the single outer cusp, although when the latter is exceptionally small this cusp may reach the outer border. The next cusp of the midrow always reaches the external border back of the vestigial (or incipient?) outer row and is followed by a single cusp, usually the largest of the tooth, which is more or less crescentic, the crescent opening forward. The general contour of the crown is subtriangular, with the outer side oblique so that the tooth narrows posteriorly.

OSTEOLOGY

The lower jaws of *Tæniolabis* were adequately known to Cope (1884A) and to Osborn and Earle (1895). Cope also referred to *Catopsalis pollux* (*Tæniolabis taöensis*) certain skeletal fragments, including two fragmentary humeri, a vertebra, part of an ulna, and an astragalus. These bones, however, are so unlike those known to belong to multituberculates and, so far as characteristic, so like those of associated ungulates that their reference to *Tæniolabis* must be considered incorrect and no postcranial material is now known for any tæniolabid. With the skull the case is better. The type of *Tæniolabis taöensis* includes a number of skull fragments, although they are not in contact, so that the restoration by W. D. Matthew published by Gregory (1910, p. 170) was inevitably incorrect in some particulars. The American Museum Expedition of 1913 was fortunate in finding a nearly complete skull of *T. taöensis* which was described in detail by Broom (1914), and there are various other skull fragments in the Cope Collection and in the American Museum Collections of 1892 and 1913 which help to elucidate the structure of the skull and mandible in this most specialized of known multituberculates (with the possible exception of the little-known *Sphenopsalis*).

The mandible is deep and powerful with strongly marked muscle insertions. The masseteric insertion is especially marked, broad and deep and extending onto a great posteroexternal flange of bone. The coronoid process, in contrast, is relatively small and weak. The symphysis is short but deep, the two rami not coossified. Possibly they retained some degree of independent movement. The incisor and symphysis are internal to the longitudinal line of the cheek teeth, while the coronoid and, still more, the condyle are external to it. The coronoid arises external to M_2. Back of and below this molar is a deep fossa, at the anteroinferior end of which is the dental foramen. The mental foramen is very small and is just above the root of the incisor below the diastema.

All early writers on the Multituberculata referred to the "strongly inflected angle of marsupial type," and in spite of occasional protests (Broom 1914, Simpson 1926) this view is still widely accepted. The term "angular process" means a definite projection on the posteroinferior part of a mandible for the insertion of the internal pterygoid muscle. It may project downward, as in almost all placentals and in *Tarsipes*, or more or less inward as in most marsupials and some insectivores. In placentals it usually and in marsupials always projects somewhat backward and is separated from the body of the mandible

posteriorly and from the condyle by a distinct notch. In *Tæniolabis*, several specimens of which have this region quite undamaged, there is no definite projection for the internal pterygoid. It is inserted on the ridge which runs forward to or onto the main body of the horizontal ramus. In this specialized genus but not in the more primitive forms of the order, its point of insertion is marked by a distinct thickening, in no way resembling an angular process save in function. It is an accurate statement that in *Tæniolabis*, and in multituberculates generally, there

A.M.16321 (P⁴16323)

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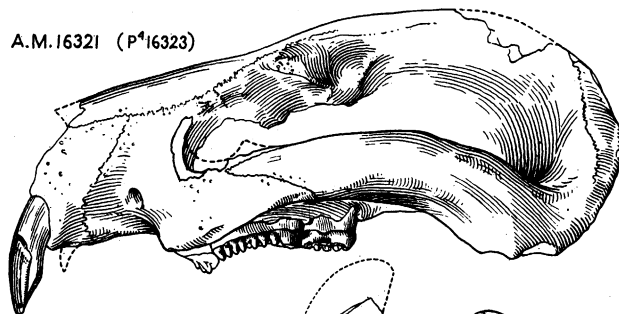
A.M.16310 (Condyle 745)

A

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A.M.16321

B
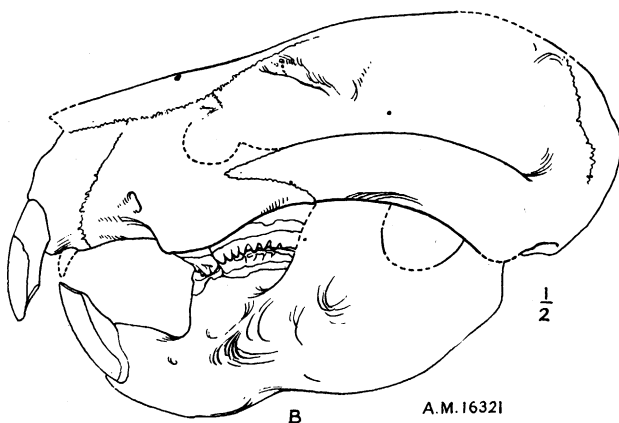
Fig. 4. *Tæniolabis taöensis.* Skull and jaw, composite. A, Left side, teeth separated. B, Left side, diagrammatic, teeth in occlusion. One half natural size.

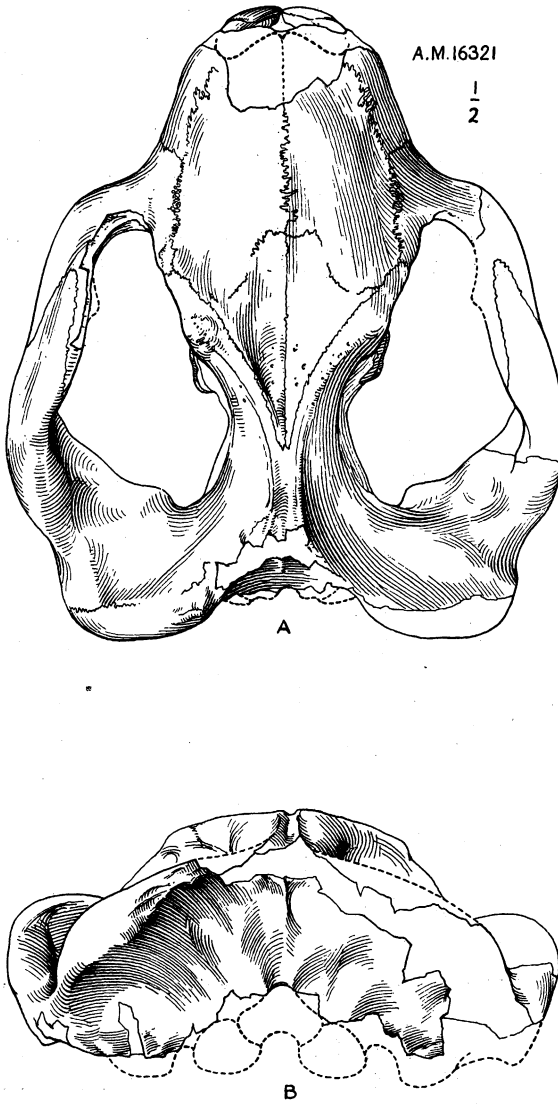A.M.16321

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A

B

Fig. 5. *Tæniolabis taöensis*. Skull, A, Superior view. B, Posterior view. One half natural size.

is no angular process, strictly speaking, and this region is fundamentally distinct from either marsupials or placentals.

The skull has been carefully described by Broom, and its morphology, so far as known, is also clearly shown in the new figures here published, so that a complete description is not necessary, although a few points may be added. The anterior palatine foramina were oval, about 15 mm. long, and quite lateral in position, just internal to I^3. The maxillary portion of the palate is greatly arched or domed, reaching its greatest height between the premolars. Broom (1914, p. 128) states that there is a small oval vacuity. This region is not well seen in the

A.M. 16321

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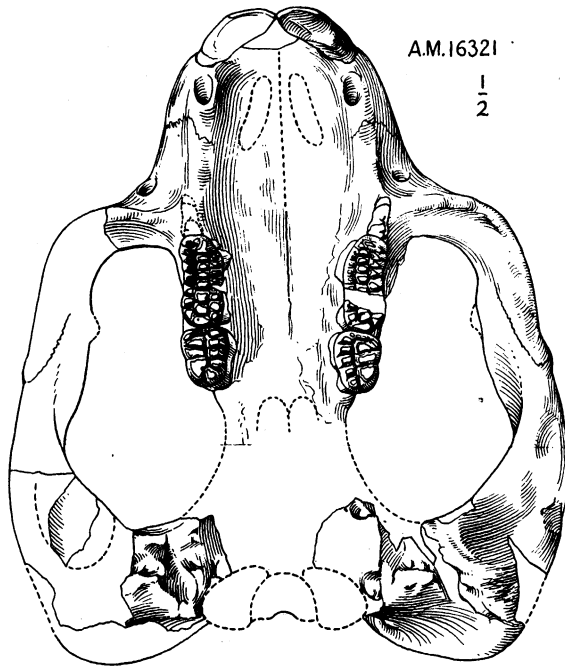
Fig. 6. *Tæniolabis taöensis*. Skull. Palatal view. One half natural size.

skull described by him (A. M. No. 16321), but another specimen (A. M. No. 3041) seems positively to indicate that palatal vacuities were not present in *Tæniolabis*.

Unfortunately very little is known of the basicranial region, but certain very important inferences as to the ear are permissible. The glenoid surface is broad and shallow, concave from side to side, the external portion passing anteriorly onto the base of the zygoma. It is

bounded externally by a low longitudinal process.   Posteriorly it ends just below the lower end of the lambdoid crest, forming an emargination directly below the angle between the squamous and zygomatic portions of the squamosal.   The surface posterointernal to the glenoid surface passes rapidly into the lateral part of the occiput.   There is no post-glenoid process or any other projection in this region, nor are there any meati, grooves, or notches.   The occiput begins directly back of the articular surface.   One is thus forced to the conclusion that the middle and inner ear was wholly internal to the glenoid fossa, as it is in cynodont reptiles and in monotremes, and that the external auditory meatus opened on the inferior surface of the skull.   In *Ornithorhynchus* the meatus of the external ear passes under the posterior end and then up to a point just back of the eye.   In *Echidna* the opening is farther back and lower on the head.   In the cynodonts the passage runs upward in a well-marked groove beginning back of the articulation for the lower jaw.   The conditions in *Didelphis* and, with progressively greater modifications, in higher mammals, are readily derivable from those in cynodonts through the lengthening of the postglenoid region and attend-ant changes.   In *Tæniolabis*, as in the monotremes, this lengthening did not occur.   It is impossible to say whether the monotreme specializa-tion of the external ear occurred, although there is no reason to suppose that it did.   A faint but definite small groove internal to the posterior end of the zygoma may well indicate that the cartilaginous meatus passed just back of the articulation for the lower jaw, as in cynodonts, but without the large, broad groove seen in the latter.

A fragment of squamosal surely belonging to *Tæniolabis* (A. M. No. 3041) suggests that the squamosal ended inferiorly just posterointernal to the glenoid fossa and articulated with another bone, presumably the petrosal or mastoid, by a large vertical surface running anteroposteriorly, but this is not very certain.   In the complete skull this region is so cracked and broken that nothing can surely be made out.

<div align="center">Taxonomy</div>

<div align="center">**Tæniolabis sulcatus** Cope, 1882</div>

July, 1882.   *T. sulcatus*, Cope, Am. Nat., XVI, p. 604.
1884.   *T. scalper*, Cope, Tert. Vert., p. 193.   (New name for same specimen).
Type.—Amer. Mus. No. 3038.   Single I² right.   Cope Coll., collected by D. Baldwin.
Horizon and Locality.—Puerco, San Juan Basin, New Mexico.

Discussion.—When this tooth was found, similar multituberculate incisors associated with cheek teeth were unknown and it was referred

to the Tæniodonta. Cope later (1885) recognized that *Tæniolabis* and *Polymastodon* are synonyms, but he retained the later name. There can be no possible doubt that *Tæniolabis* is the correct name for the genus so long known as *Polymastodon*. It is probable that *T. sulcatus* is synonymous with *T. taöensis*, but here the latter better-known name may reasonably be retained. At present it is not practicable to attempt to place the known upper jaws in more than one species, so that one cannot reach a positive conclusion as to whether *T. sulcatus* shows the definite specific character of *T. taöensis*. Until such time, therefore, as more abundant associated material makes it possible to determine the specific characters shown by I^2, it is proposed to apply the little known name *T. sulcatus* only to the type.
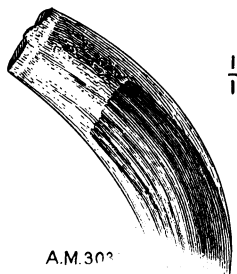
Fig. 7.   *Tæniolabis sulcatus*.   Right upper incisor.   External view.   Type.   Natural size.

Tæniolabis taöensis Cope, 1882

August, 1882.   *Polymastodon taöensis*, Cope, Am. Nat., XVI, p. 684.

August, 1882.   *Catopsalis pollux*, Cope, Am. Nat., XVI, p. 685.

April, 1885.   *Polymastodon latimolis*, Cope, Am. Nat., XIX, p. 385.

May, 1885.   *Polymastodon attenuatus*, Cope, Am. Nat., XIX, p. 494.

Feb., 1895.   *Polymastodon selenodus*, Osborn and Earle, Bull. A. M. N. H., VII, p. 12.

TYPE.—Amer. Mus. No. 3036. Parts of right and left maxillæ and fragments of skull. Cope Coll., collected by D. Baldwin, 1882.

TYPES OF SYNONYMS.—

Catopsalis pollux: A. M. No. 3036. Lower jaws associated with the type of *T. taöensis*. Cope Coll., collected by D. Baldwin, 1882.

Polymastodon latimolis: A. M. No. 3045. Badly preserved right lower jaw. Cope Coll., collected by D. Baldwin, 1885.

Polymastodon attenuatus: A. M. No. 3046. Right lower jaw. Cope Coll., collected by D. Baldwin.

Polymastodon selenodus: A. M. No. 749. Fragment of left lower jaw with premolar and M$_1$. Amer. Mus. Exp., 1892.

HORIZON AND LOCALITY.—Upper level of the Puerco, San Juan Basin, New Mexico.

DIAGNOSIS.—Lower molars generally less robust, with few or no accessory cuspules.

This is the common species, including about two-thirds of the determinable lower jaws. There appear to be two groups which grade into one another and which are not sufficiently distinct for specific differentia-

tion. One, including the types of *T. taöensis, attenuatus*, and probably *selenodus*, is characterized by rather smaller molars, especially M_2, which is little if any wider than M_1. The other group, possibly including the poorly preserved type of *latimolis*, has M_2 slightly enlarged and more distinctly wider than M_1. The number of specimens referable to each group is about equal, and this suggests that the difference may be sexual. There are no constant morphological differences.
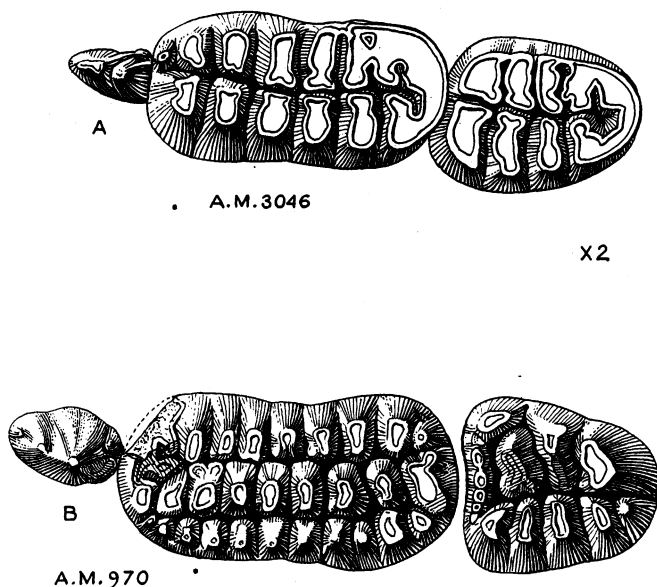

. A.M.3046

X2

B

A.M.970 .

Fig. 8. *Tæniolabis taöensis.* A, Lower cheek teeth, right side, crown view (type of "*Polymastodon attenuatus*"). B, Upper cheek teeth, left side, crown view. Twice natural size.

The few specimens which include associated upper and lower teeth all belong to this species. As there are no constant differences on which to separate the upper teeth into two species, it is probable that most or all of those known belong to *T. taöensis*, and in any event they must be so referred until found in association with lower jaws belonging to *T. triserialis*.

Catopsalis pollux, as Cope later recognized, was based on the associated lower dentition of the type of *Polymastodon taöensis*. The upper jaws were at first supposed to be lowers, but the error was soon discovered.

Polymastodon latimolis was based on a poorly exposed and broken specimen. M_1 was said to be shorter than in *taöensis* and only 1½ times

as long as M_2, but M_1 is broken, and its roots show that it was as long as in *taöensis*. This tooth was also said to have only five tubercles on the inner side, but this is also due to its being broken—a possibility recognized by Cope. Finally, the widths of M_{1-2} were said to be distinctive, but these teeth were heavily encased in a concretionary coating which prevented accurate measurement. We have had these teeth cleaned as well as practicable and find that they cannot have been wider than in typical specimens referred to *taöensis*.

Polymastodon attenuatus was based on an excellent lower jaw. The supposed specific distinctions were:

1. Upper and lower incisors compressed. There were no actually associated upper incisors, and those referred are all crushed. The compressed character of the lower incisor is not very distinctive and is due to the fact that it is young, the heaviest part not yet in use, and that it is somewhat crushed laterally.

2. Lightness of ramus. The ramus is actually deeper than in the type of *T. taöensis*. There is less transverse relief, but this and the increased depth are both clearly due to compression after burial. Although the jaw is well preserved, it has obviously suffered lateral crushing.

3. Superior incisors more rapidly acuminate, without facets on inner side. This simple describes young *T. taöensis* incisors.

4. Cutting edge of incisors anteroposterior rather than transverse. The edge is not really anteroposterior, nor is it really transverse in *T. taöensis*. In both it is oblique, and the somewhat greater obliquity in "*attenuatus*" is due to the youth of the type and the slight crushing which it has suffered.

To these, Osborn and Earle added that the molars are compressed in the mid-region, which is true of all specimens of *Tæniolabis*, and that the cusp formula is M_1 9:6-7, M_2 5:4 and three cuspules, a formula which also occurs in *taöensis*, while the actual formula of the *attenuatus* type, 7-8:6, 5:4, is even more typical of *taöensis*. They also supposed that the extension of the enamel down into the alveolus is characteristic of this species, but this is another juvenile character.

Polymastodon selenodus.—This was based on a very young, unworn, slightly crushed lower premolar and first molar of *T. taöensis*. The lateral compression has not significantly altered the molar width from that of *taöensis*, while the apparently more crescentic character of the cusps is due entirely to their being unworn. All stages from this one to the complete removal of the crown enamel are represented in the collection, which has been greatly augmented since Osborn and Earle made their revision of this genus. The cusp formula of M_1 is 7:6, typical of *taöensis*, as Osborn and Earle recognized, and the length, about 19.5 mm. (Osborn and Earle's "2 mm." is an obvious misprint for 2 cm. or 20 mm.), is exactly that of many *taöensis* molars.

MEASUREMENTS

The following measurements are of type specimens and of referred specimens which show the extremes of variation.

M_1			M_2		M^1			M^2	
A. M. No.	Length	Width	Length	Width	A. M. No.	Length	Width	Length	Width
3036	....	9.7	13.0	9.8	3036	22.3	10.4	14.6	11.4
3046	19.5	10.0	13.3	10.0	970	22.06	11.4	12.8	11.4
3045	....	ca. 9.5	13.0	ca. 11.0	16323	21.2	10.8	....	10.1
749	19.5	10.0	....	....	16305	23.7	11.7	....	....
16310	19.1	9.7	14.7	11.0	16321	23.	10.9	14.8	12.5
16306	20.2	10.6	13.6	10.8					
16308	20.3	10.0	14.7	114.					

Tæniolabis triserialis, new species

TYPE.—Amer. Mus. No. 725, part of left lower jaw with broken M_1 and complete M_2. Amer. Mus. Exp., 1892.

PARATYPES.—Amer. Mus. No. 748, right lower jaw nearly complete, with I and M_2. Amer. Mus. No. 727, fragment of right lower jaw with P_4 and M_1. Both of same origin as type.

HORIZON AND LOCALITY.—Upper level of Puerco, San Juan Basin, New Mexico. Type and paratypes from Coal Creek Canyon.

DIAGNOSIS.—Lower molars generally more robust, cusp number tending to increase. Molars with numerous accessory cuspules and especially a row passing around the posterior end of the tooth and then for a short distance forward outside the external main cusp row, developed to a greater or less degree on both M_1 and M_2.

Osborn and Earle recognized the presence of two distinct forms among the common species of *Tæniolabis*, one more robust than the other. In the absence of the Cope types, they naturally inferred that *taöensis* was the more and *attenuatus* the less robust species, and they so labeled and described their material. Now that the combined collections may be compared, however, *taöensis* and *attenuatus* prove to be synonymous and to belong to the generally less robust form. Unfortunately all the trivial names so far assigned to this genus prove to be synonyms of *taöensis*, and none can be used for the present species.

The type, chosen because of its clear preservation and obvious distinction from *taöensis*, is aberrant in one particular—M_2 is unusually long and has two cusps at the anterior end of the inner row where most specimens have only one larger one, but here, as in *taöensis*, one clearly must allow a great deal of latitude for individual variation. The formula for the main cusps is in the type: M_2 6:6, in No. 748: M_2 5:5, in No. 727: M_1 8:7 (or 9:8—there is a cuspule at the posterior end of each row). These figures are all larger than the normal *T. töôensis* formula 7:6, 5:4,
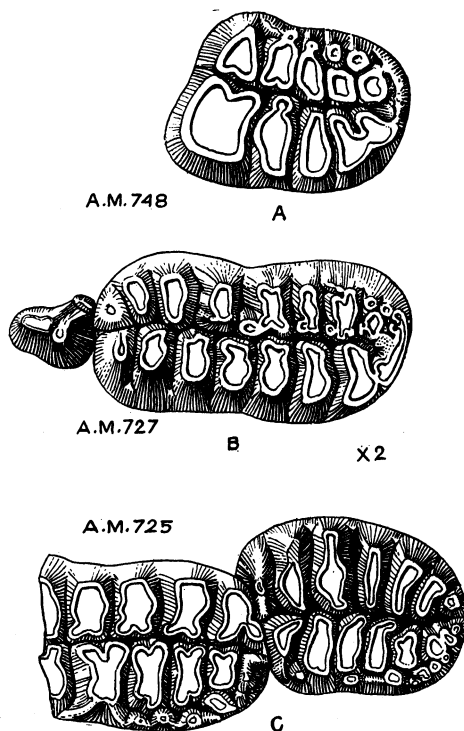
Fig. 9. *Tæniolabis triserialis.* A, Right. M₂, crown view, paratype. B, Right P₄-M₁, crown view, paratype. C, Left M₁₋₂, crown view, type. Twice natural size.

but the latter formula does occur in *triserialis*, and the increase in cusp number is a tendency rather than a hard and fast rule which would make classification easier, but probably less true. The smallest *triserialis* molars are about the size of the largest referred to *taöensis*, yet a morphological gap does exist, and the average specimens of the two species are very distinct.

MEASUREMENTS

The following measurements in millimeters are of the type and paratypes.

A. M. No.	M₁		M₂	
	Length	Width	Length	Width
725	....	10.8	15.7	11.8
748	....	....	14.9	11.8
727	21.4	10.2	....	....

Catopsalis Cope, 1882

May, 1882. *Catopsalis*, Cope, Am. Nat., XVI, p. 416.
TYPE.—*C. foliatus* Cope, 1882.
DISTRIBUTION.—Torrejon of New Mexico and Paskapoo of Alberta.
DIAGNOSIS.—Basic cusp formula: M_1 5-6:4-5; M_2 3-4:2. M_1 relatively longer and narrower than in *Tæniolabis*, cusps less inclined to transverse elongation, nearly square in section.

Although *Catopsalis* was based on an adequate type and proposed before either *Tæniolabis* or *Polymastodon*, it was abandoned by Cope in favor of *Polymastodon*, and almost all subsequent writers have followed this indefensible lead.   If *Catopsalis* and *Tæniolabis* were really synonymous, the former would be the correct name and *Polymastodon* would be doubly antedated, but *Catopsalis* appears to be a distinct, although closely related form.   It includes not only the genotype *C. foliatus* but also *C. fissidens*, originally placed in this genus but later removed to *Polymastodon*, and the recently described *C. calgariensis*.   There has been some doubt as to the horizons of the two New Mexican species, but both are now believed to be from the Torrejon, while *C. calgariensis* is from the Paskapoo and probably a little later in age.   *Catopsalis* generally is thus a later genus than *Tæniolabis*, despite the fact that it appears to be somewhat more primitive.
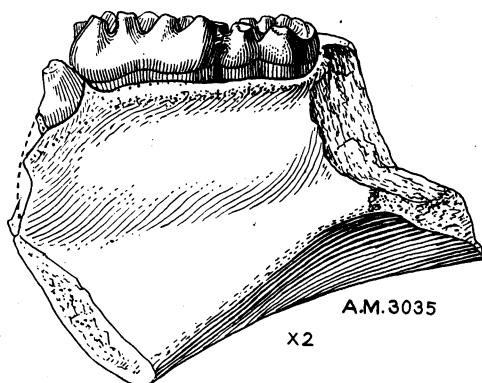

A.M. 3035
X 2

Fig. 10. *Catopsalis foliatus*. Right lower jaw. Internal view. Type. Twice natural size.

Catopsalis foliatus Cope, 1882

May, 1882. *C. foliatus*, Cope, Am. Nat., XVI, p. 416.
1884. *Polymastodon foliatus*, Cope, Am. Nat., XVIII, p. 688.
TYPE.—Amer. Mus. No. 3035. Fragment of right lower jaw with P_4, M_{1-2}.
Cope Coll., collected by D. Baldwin.
HORIZON AND LOCALITY.—Torrejon, San Juan Basin, New Mexico.

DIAGNOSIS.—Cusp formula: M_1, 5:4; M_2, 4:2. Molar lengths of type; M_1, 10.7 mm.; M_2, 6.6 mm. No internal accessory cuspules on M_2.

The type of this species was collected at a time when the Puerco and Torrejon were not clearly distinguished. It has always been listed as from the lower Puerco of Cope, i.e., the Puerco proper, but it is from a Torrejon locality, and later collecting has brought to light no specimens of this species or genus from the Puerco, while one specimen, referable with little doubt to *C. foliatus*, is definitely from the Torrejon. The genus is not positively known to occur at all in the Puerco. Inasmuch as there appear to be no other cases of species common to Puerco and Torrejon, and very few of genera, it seems reasonably certain that *C. foliatus* is a Torrejon species. Its reference to the Puerco did not rest on field data and was undoubtedly influenced by its erroneous inclusion in "*Polymastodon*"—a genus confined to the Puerco.

The lower incisor is known only from part of the root, apparently differing from *Tæniolabis* only in its smaller size. P_4 is also apparently similar to that of the older genus and of about the same relative size, although smaller absolutely. The surface is not well preserved and the tooth not fully protruded, the individual apparently being young. The high and more or less pointed molar cusps appear at first sight to distinguish the genus, but this, too, is largely due to the immaturity of the type the cusps not being higher than in young specimens of *Tæniolabis*. It is possible that wear was more nearly confined to the groove and less general than in *Tæniolabis*, but this could easily be illusory and more material is necessary.

On M_1 there are five distinct and well separated outer cusps, the first two somewhat more slender than the others. From the postero-external angle of the fifth cusp a definite ridge curves backward and inward along the posterior edge of the tooth, closing the median valley posteriorly and joining the posterointernal cusp. There are four subequal internal cusps, each larger than the external cusps, the posterior one somewhat elongated. All of the cusps are very nearly as long as wide, giving them a square appearance unlike that of the *Tæniolabis* cusps; The molar is constricted slightly in the middle.

M_2 is slightly wider than M_1 and much shorter. There are four outer cusps, the first two large and well separated, the last two smaller and not distinct externally. The last is the smallest cusp on the tooth and narrower than the preceding one. From it a ridge similar to that of M_1 passes around the posterior end of the tooth. There are only two cusps in the internal row, each relatively large and stout. The tooth is

subtriangular in outline. This more definite triangularity, together with the shortness of M_2 relative to its breadth, are common to all known species of *Catopsalis* and in distinction from *Tæniolabis*. The chief measurements of the type teeth follow.

M₁		M₂	
Length	Breadth	Length	Breadth
10.7	4.9	6.6	5.8

Catopsalis fissidens Cope, 1884

1884. *C. fissidens*, Cope, Proc. Am. Phil. Soc., XXI, p. 322.

1884. *Polymastodon fissidens*, Cope, Am. Nat., XVIII, p. 688.

TYPE.—Amer. Mus. No. 3044. Part of right lower jaw in matrix, with M_{1-2}. Cope Coll., collected by D. Baldwin.

HORIZON AND LOCALITY.—Torrejon, San Juan Basin, New Mexico.

DIAGNOSIS.—Cusp formula: M_1 6:5; M_2 apparently 3:2. Molar lengths of type: M_1 14.0 mm.; M_2 9.2 mm. Accessory row of tubercles on M_2 internal to the second main row.

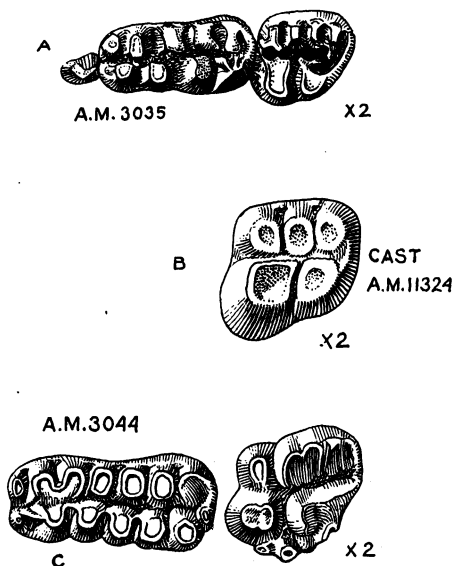A.M. 3035   X 2

B   CAST
A.M.11324
X 2

A.M.3044

C   X 2

Fig. 11. A, *Catopsalis foliatus*, right P_4-M_2, crown view, type. B, *Catopsalis calgariensis*, right M_2, crown view, plastotype. C, *Catopsalis fissidens*, right M_{1-2}, crown view, type. Twice natural size.

This species, at first referred to *Catopsalis*, was placed in *Polymastodon* when *Catopsalis* was considered as synonymous with the

latter genus. The specimen is registered as from the Torrejon, but has occasionally been listed in the Puerco fauna, apparently under the impression that a mistake had been made. There seems no reason to doubt the field data, however, for *C. fissidens* differs from the Puerco *Tæniolabis* and agrees with the apparently Torrejon *C. foliatus* in generic characters. Its reference to the Torrejon agrees with all the other data tending to show that in the known material *Tæniolabis* is the earlier, *Catopsalis* the later representative of the Tæniolabididæ.

The matrix on the type is an exceedingly hard ironstone, but the teeth have been completely exposed, although they are heavily worn and somewhat crushed. On M_1 the ridge from the posteroexternal cusp ends in a minute cuspule just back of the posterointernal cusp, and there is also a minute cuspule at the anterior end of each main cusp row, the external one a little the larger. M_2 is somewhat broader relative to its length than in *C. foliatus*. The outer cusp row is obscure as the posterior cusps tend to merge with wear, but it is very probable that there were only three outer cusps. The internal cusps are two, as in *Catopsalis* generally, and are very massive. Internal to these along the base of the crown is a row of four or five small but distinct tubercles. The second of these is below the notch between the two internal main cusps and is the largest of the series. Measurements in millimeters follow.

M_1		M_2	
Length	Breadth	Length	Breadth
14.0	6.3	9.2	8.6

Catopsalis calgariensis Russell, 1926

1926. *C. calgariensis*, Russell, Am. Jour. Sci., XII, p. 230.

TYPE.—Formerly in the possession of L. S. Russell, now lost. Isolated M^2 right.

PLASTOTYPE.—A. M. No. 11324.

HORIZON AND LOCALITY.—Paskapoo Formation, Alberta. Type found about thirty feet above the water level on the Elbow River at Calgary.

DIAGNOSIS.—Cusp formula, M_2, 3:2. The size of the base of the crown almost exactly that of *C. fissidens*, but apex more restricted (although this may be due in large part to difference in wear). No internal row of accessory cuspules. Internal cusp row broader relative to outer than in *C. fissidens* M_2.

Unfortunately the type of this interesting species was recently lost in the mail, but very clear and exact casts are at hand, and drawings (Russell, 1926, Fig. 1) and a photograph (Simpson, 1927, Fig. 1) have been published. The species appears to be very close to *C. fissidens*, so far as

one may judge from an isolated tooth, indeed the original diagnosis did not differentiate the two species, although they are quite surely distinct. The relatively more robust internal cusp row and absence of the internal accessory tubercles appear to be sufficiently distinctive with respect to *C. fissidens*, and the size and proportions at once exclude *C. foliatus*.

<h3 style="text-align:center">PTILODONTIDÆ Simpson, 1927</h3>

DEFINITION.—Dental formula $\frac{2}{1} \cdot \frac{0}{0} \cdot \frac{3}{1} \cdot \frac{4}{2} \cdot \frac{2}{2}$. Enlarged incisors rooted, with extra-alveolar portion almost completely enameled or with restricted enamel band. P$_3$, when present, small, one-rooted, fitting into a notch in P$_4$. P$_4$ always very large, laterally compressed, trenchant, with serrate edge and curving ridges and grooves on sides. Anterior upper premolars not opposed by any lower teeth, grasping, with three to six conical cusps. Only the last upper premolar shearing in function, enlarged. M^1 with three cusp rows, the inner usually incomplete anteriorly; M^2 with three cusp rows, the outer always incomplete posteriorly. Molar cusps more or less definitely crescentic. Wear generally not reducing molar surfaces to planes but accentuating the longitudinal ridges and grooves. First molars much larger than second. Skull notably triangular in outline as seen from above. Animals of relatively small size.

TYPE.—*Ptilodus* Cope.

This large and widespread family occurs in the Cretaceous of Mongolia and North America, in the Paleocene of Europe, Mongolia and North America, and in the Lower Eocene of North America. It has usually been included in the family Plagiaulacidæ, the type of which occurs in the Jurassic. It is, however, certainly entitled to the rank of a separate family, whether from the standpoint of the morphological variety which it includes or of the numerous differences from the Jurassic forms which its included genera share. The above definition is designed to separate the family not only from the partly contemporaneous Tæniolabididæ but also from the Plagiaulacidæ, as redefined to include only Jurassic and lower Cretaceous forms. The genera *Ptilodus, Eucosmodon*, and *Ectypodus* occur in North America.

<h3 style="text-align:center">Ptilodus Cope, 1881</h3>

1881. *Ptilodus*, Cope, Am. Nat., XV, p. 921.

1884. *Chirox*, Cope, Proc. Am. Phil. Soc., XXI, p. 321.

TYPE.—*Pt. mediævus* Cope, 1881.

DISTRIBUTION.—Torrejon of New Mexico, Fort Union of Sweetgrass County, Montana, possibly also in the Paskapoo of Alberta.

DIAGNOSIS.—Dental formula $\frac{2}{1} \cdot \frac{0}{0} \cdot \frac{4}{2} \cdot \frac{2}{2}$. Lower incisors long and slender, pointed, not gliriform. P$_3$ present. P^1 with three cusps, P^2 with four. P^3 narrower than P^2 and with 4–6 cusps. P^4 with two complete longitudinal rows of cusps and an incipient anteroexternal third row. Upper molars with the inner row of M^1 incomplete. Cusps moderately crescentic.

This genus, the type and best-known member of the family, is characteristic of the American Torrejon and its equivalents. Recent work in Alberta suggests that *Ptilodus* there occurs at a horizon probably somewhat later, and it may eventually be found to range through both middle and upper Paleocene.

<div align="center">DENTITION</div>

The lower incisors of *Ptilodus* are long slender curved teeth with slightly rounded tips. The extra-alveolar portion is almost completely enamel-covered, although the enamel is thin on the superinternal face and does not here extend quite so far back as on the external face. This face is somewhat excavated and is bounded below by a sharp longitudinal ridge. The external face is evenly convex and has a smooth, fairly thick enamel covering. The root is long, free of enamel, and, at least in the adult, closed. Wear on these incisors is not excessive and they are seldom deeply truncated, in contrast with *Eucosmodon* (below). This tooth is followed by a large diastema and P_{1-2} of the Jurassic *Ctenacodon* are absent. P_3 is present but it is very small, one-rooted, styloid, fitting closely into a distinct notch in the anterior base of P_4, which it appears to strengthen and buttress. P_4 is very much enlarged and it serves alone the shearing function shared by P_{2-4} in earlier forms. The anteroexternal part of the base extends far down and is somewhat gibbous, the anterior root being distinctly stouter than the posterior. The shearing edge is sharp and bears a number of projections, usually 12–16, from each of which there normally passes downward a curved sharp ridge on each side of the crown. In the correct orientation of the jaw these ridges are nearly vertical, but with the lower end somewhat anterior to the upper. On the most posterior part of the tooth these ridges are often quite irregular. They may here anastomose, often run posteroinferiorly instead of anteroinferiorly, and sometimes have no obvious relationship to the serrations of the cutting edge. On unworn specimens there is a very minute basal accessory cuspule at the extreme posteroexternal angle—possibly a vestige of the row of cuspules present on the outer face of P_4 in the plagiaulacids.

The proportions of the lower molars show marked differences from those of the Jurassic prototypal forms, M_1 being relatively elongate, M_2 relatively reduced. Each has two longitudinal cusp rows. The individual cusps may be broadly described as crescentic, with the wings of the crescents pointing backward, but this usual characterization gives an inadequate conception of their rather complicated nature. Each cusp sends downward into the central longitudinal groove two or more ridges,

and these ridges, coming from cusps on opposite sides of the groove, meet and anastomose in the bottom of the groove, forming a complicated wrinkled pattern not readily obliterated by wear. On M_4 the postero-external cusp is the largest and generally has four or more small ridges running down its internal face. The basic cusp formula for the genus appears to be, M_1, 6:4, M_2, 4:2, but variations of one cusp more or less may occur. The bases of the cusps are confluent, and when worn the cusp rows may appear as continuous longitudinal ridges, and the number of small transverse ridges on the original cusps may be mistaken for that of the true cusps, although the latter are only about half as numerous. M_2 is generally of rounded triangular form, the external side longer than the internal one.

I^1 is probably absent. I^2 is a pointed, curved tooth of moderate size. It does not appear to have a bifid apex or a basal accessory cusp, although their absence may be due to wear in the known material. Back of I^2 is a smaller tooth of the same form which Gidley took to be the canine. In this he was probably mistaken, for the tooth has all the characters and the position of the normal multituberculate I^3, and a canine is not known to occur in any member of this order.

Ptilodus has four upper premolars. Since the structurally ancestral type in the Jurassic has five, we were at first inclined to call those of *Ptilodus* P^{2-5}, just as the remaining lower premolars have been called P_{3-4}. In the case of the lower teeth, however, there can be no reasonable doubt that it is P_{1-2} of *Ctenacodon* that are absent, while in the upper jaw it is not at all certain that it is P^1 that is lost. In *Ptilodus* itself it is the third premolar which is undergoing reduction and which would presumably be the next to be lost, and in the Jurassic forms, also, P^3 often seems in process of reduction. The remaining upper premolars of *Ptilodus* may be homologous with P^{1-2} and P^{4-5} of the plagiaulacids, but until more is known of intermediate forms it seems best to call them P^{1-4}, numbering them according to actual position and without implication as to homologies.

P^1 is a triangular tooth with three subequal cusps, one anterior and two posterior and opposite. P^2 is somewhat larger and has four cusps in two opposite pairs. P^3 is smaller and more variable. It may closely resemble P^2 save in size, or it may have a posterior shelf back of the four cusps, or it may have six distinct cusps in three opposite pairs.

The next upper tooth was at one time commonly referred to the molar series. Gidley (1909, pp. 617–8) called it a premolar in *Ptilodus gracilis*. By Broom (esp. 1914, pp. 120–1) the formula in the Jurassic
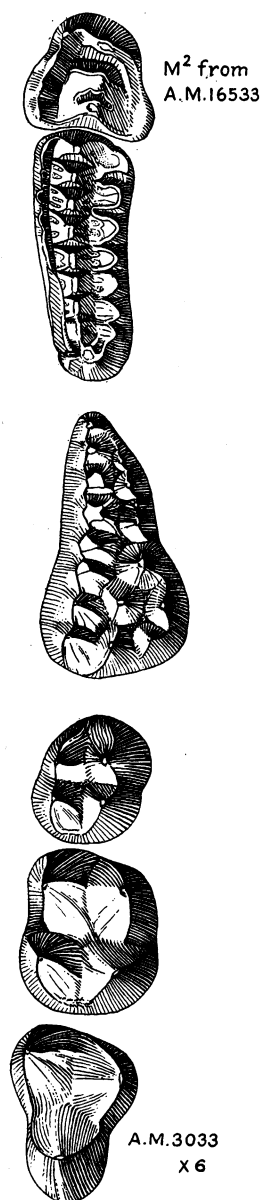
M² from
A.M.16533

A.M.3033
X 6

Fig 12. *Ptilodus mediævus.*
Right upper cheek teeth, crown view. Premolars and M¹ from A. M. No. 3033. M² from A. M. No. 16533. Six times natural size.

Ctenacodon ("*Plioprion*") is given as $\frac{3.0.4.3}{1.0.3.3}$, and *Ptilodus* is said to have $P\frac{3}{1}$ $M\frac{3}{3}$, but it has elsewhere been shown that these formulæ appear to be based on a fallacious analogy and are in opposition to the known morphological facts (Simpson, 1928). We believe there to be no reasonable basis for giving the formula of *Ctenacodon* as other than $\frac{3.0.5.2}{1.0.4.2}$, or of *Ptilodus* as other than $\frac{2.0.4.2}{1.0.2.2}$.

In the Plagiaulacidæ the last two upper premolars are of equal size and share the shearing function, whereas in the Ptilodontidæ the last upper premolar is much the largest and is the only one concerned with shearing. Simple reduction from the anterior end, such as took place in the lower jaw, will not explain this change, since in both cases the shearing teeth are preceded by three functional grasping teeth. P⁴ of *Ptilodus* has two main longitudinal rows of cusps, the inner row with eight or nine subequal cusps, the outer with six or seven, of which the second or third from the anterior end is the largest on the tooth, the ones posterior to it becoming rapidly smaller. In addition there is a tendency to form a third row. There may be, as in *Pt. gracilis*, an anteroexternal cingulum, or there may be, as in *Pt. mediævus*, two well-developed anteroexternal cusps. At first sight it seems little probable that such a tooth would oppose the great shearing tooth of the lower jaw, and it was chiefly for this reason that Cope and Osborn maintained that *Chirox*, based on an upper jaw, and *Ptilodus*, based on a lower, were distinct genera, or even members of different families. Gidley's description of actually associated upper and lower jaws (1909) proved that *Chirox* and *Ptilodus* are synonymous. P₄ shears just internal to P⁴, the inner surface of the latter tooth being smooth and accommodated to the shape of the lower shearing tooth. The cusps of the inner row of P⁴ form a serrated margin which opposes the

functionally similar but morphologically different serrated edge of P_4.

The cusps of all the upper premolars are quite different from those of the molars. They are more or less conical, their enamel marked by vertical wrinkles. Some of the cusps are made more or less angulate by the presence of one or two sharp crests, the character of which is more readily gathered from the illustration than from a verbal description.

The cusps of the upper molars, are very similar to those of the lowers, save that the poorly marked crescents open forward rather than backward. M^1 and M^2 have three cusp rows, the middle being the longest in each case. The outer row of M^1 and inner of M^2 are nearly as long as the midrow, but on M^1 the inner row narrows and disappears anteriorly and on M^2 the outer row similarly narrows and disappears posteriorly. This unusual apparent lack of harmony in the morphology of M^1 and M^2 seems to be due to the still more remarkable conditions in the Jurassic plagiaulacids, a problem elsewhere briefly discussed (Simpson, 1928). The basic cusp formula appears to be, M^1, 8:9:6, M^2, 2:3:4, but wear soon makes these difficult to count and there is probably much individual and specific variation.

Osteology

What is known of the osteology of *Ptilodus* has been given by Gidley (1909) and further discussed by Broom (1914). Our own material does not permit any additions, although some questionable points are mentioned below in dealing with *Eucosmodon*, a genus which appears to have been rather similar in skeletal structure.

Taxonomy
Ptilodus mediævus Cope, 1881

1881. *Ptilodus mediævus*, Cope, Am. Nat., XV, p. 921.
1884. *Chirox plicatus*, Cope, Proc. Am. Phil. Soc., XXI, p. 321.
1909. *Ptilodus plicatus*, Gidley, Proc. U. S. Nat. Mus., XXXVI, p. 614.
TYPE.—Amer. Mus. No. 3019. Right P_4. Cope Coll., collected by D. Baldwin.
HORIZON AND LOCALITY.—Torrejon, San Juan Basin, New Mexico.
DIAGNOSIS.—Length P_4 8.5–9.0 mm., 12 serrations on edge. Length M_1 (referred specimen, slightly smaller than type) 3.7 mm., cusp formula 6:4, anteroexternal cusp minute. P^3 with four cusps, P^4 with eight cusps in inner main row, six in outer main row, and two anteroexternal accessory cusps.

Pt. mediævus was founded on a single P_4 which happens to be the largest P_4 of this genus yet known. The referred specimens are all 0.4–0.6 mm. shorter, a difference insufficient in itself for specific distinction, although as great as that which separates *Pt. montanus* from *Pt. mediævus* and greater than that between *Pt. montanus* and *Pt. gracilis*. Gidley

(1909, p. 613) cites as a neotype the original of Cope, 1884, Tert. Vert., Pl. xxiiid, Fig. 1. This figure, however, is a composite from three separate specimens, A. M. Nos. 3021, 3022, and 3022a, which do not agree in all respects. Nos. 3021 and 3022 are closely similar and agree well with the type save in being respectively 0.5 and 0.4 mm. shorter. No. 3022a,
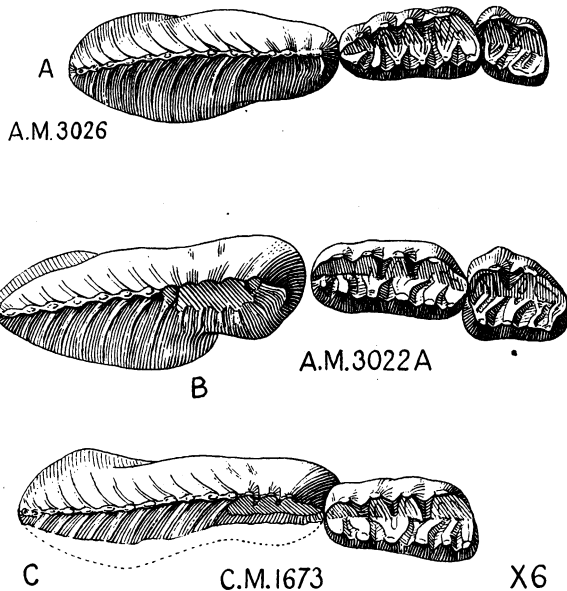

Fig. 13. A, *Ptilodus trovessartianus*, left P_4-M_2, crown view, neotype. B, *Ptilodus ?montanus*, left P_4-M_2, crown view, referred specimen from the Torrejon Formation. C, *Ptilodus montanus*, left P_4-M_1, crown view, type. Six times natural size.

however, is still smaller, P_4 being 1.2 mm. shorter than in the type. It cannot be distinguished from *Pt. montanus* by any character, and is provisionally referred to that species.

In referring the upper teeth hitherto known as *Chirox* or *Ptilodus plicatus* to *Pt. mediævus*, we differ from Gidley, who says, "The species, however, is probably distinct from *P. mediævus*, apparently representing a larger form." In the latter part of this statement, at least, he is mistaken. In *Pt. gracilis* the length ratio $\frac{P_4}{P_4}$ is 1.52. The ratio for P_4 of the *Pt. mediævus* type and P^4 of "*Chirox plicatus*" is 1.61, hence the latter is somewhat small, not large, for this species. But, as already noticed, the type of *Pt. mediævus* is considerably the largest specimen referred to the species. Using the most common figure for the length of

P_4 in *Pt. mediævus*, 8.5 mm., the ratio becomes 1.52, exactly the same as in *Pt. gracilis*. The ratio for P_4 of *Pt. trovessartianus*, the only other species certainly known to occur in the Torrejon, and P^4 of "*Chirox plicatus*" is 1.03 to 1.05, in wide disagreement with the known ratio in *Pt. gracilis*. Probabilities are strongly against any Torrejon species
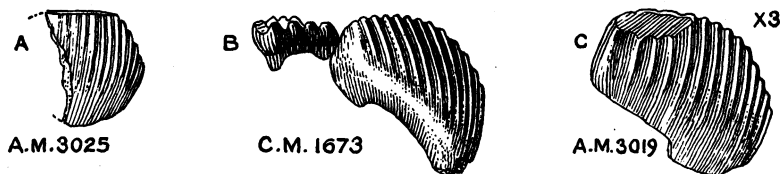

Fig. 14. A, *Ptilodus trovessartianus*, broken right P_4, external view, type. B, *Ptilodus montanus*, left P_4-M_1, internal view, type. C, *Ptilodus mediævus*, right P_4, external view, type. Three times natural size.

being known only from upper jaws, as the lowers are about three times as abundant in our collections. Taken together, all these facts seem to us to demand the conclusion that *Chirox plicatus* is not distinct, but is the upper dentition of *Ptilodus mediævus*. The five known Torrejon upper jaw fragments of this genus show some variation, but not more than in the lower jaws referred to *Pt. mediævus*.

Ptilodus trovessartianus Cope, 1882

1882. *Pt. trovessartianus*, Cope, Am. Nat., XVI, p. 686.

TYPE.—Amer. Mus. No. 3025. Fragment of right lower jaw with broken P_4. Cope Coll., collected by D. Baldwin.

PARATYPES.—Amer. Mus. Nos. 3025*b*, 3025*c*. Isolated P_4's. Same history.

NEOTYPE.—Amer. Mus. No. 3026. Left ramus with root of I and with P_{3-4}, M_{1-2}, and associated right ramus with P_4. Cope Coll., collected by D. Baldwin.

HORIZON AND LOCALITY.—Torrejon, San Juan Basin, New Mexico.

DIAGNOSIS.—Length of P_4 5.8-5.9 mm., 13 or 14 serrations. Length M_1 (referred specimen) 3.1 mm., cusp formula 6:4, anteroexternal cusp stronger than in *Pt. mediævus*. Length M_2 1.7 mm. Cusp formula 3:2, M_2 smaller relative to M_1 than in other known species, and M_1 relatively larger and more slender.

In his revision, Gidley stigmatizes this species as poorly character-ized "except for its small size," but he does not mention the excellent neotype, figured by Osborn (1893, p. 315). From a systematic point of view, the species is really on a very strong basis and is certainly distinct from any other known. The molar proportions are especially char-acteristic.

Fig. 15. *Ptilodus mediævus*. Palate. Inferior view. A. M. No. 3033. Five '
times natural size.

Ptilodus montanus Douglass, 1908   .

1908. *Pt. montanus*, Douglass, An. Carn. Mus., V, p. 14.

TYPE.—Carnegie Museum No. 1673. Left ramus with P_4, M_1. Collected by
A. C. Silberling.

HORIZON AND LOCALITY.—Fort Union, Sweetgrass County, Montana. Possibly
also present in the Torrejon of New Mexico.

DIAGNOSIS.—Length P_4 (type) 8.0 mm., 14 serrations. Length M_1 3.5 mm.,
cusp formula 6:4, anteroexternal cusp minute.

This species is at present in a very unsatisfactory position, although
the publication of further material may be expected to demonstrate its
distinctiveness. The differences of *Pt. montanus* from *Pt. mediævus* on

the one hand and *Pt. gracilis* on the other are relatively slight, and while the latter two species appear to be distinct, although closely related, *Pt. montanus* cannot be surely differentiated from either on the basis of the type specimen alone.   It is smaller than *Pt. mediævus*, but the difference is slight, specimens of intermediate size are known, and there are no other definite differences.   The possible differences from *Pt. gracilis*, which was named later, are mentioned below.
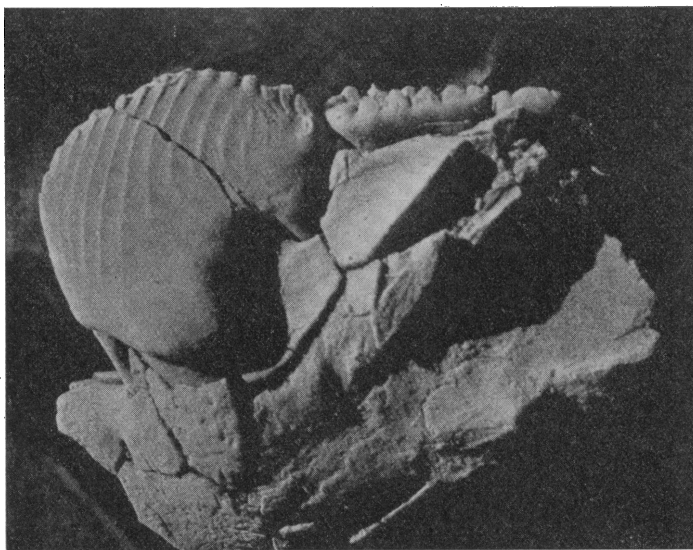

Fig. 16.   *Ptilodus trovessartianus.*   Left lower jaw.   External view.   A. M. No. 3026, neotype.   Seven times natural size.

There are two Torrejon specimens which cannot at present be distinguished from *Pt. montanus*, Nos. 3022a, with P_{3-4} and M_{1-2}, and 3023, with P_4.   On 3022a M_1 is a little narrower and on both the number of serrations is two less than in the type, but these differences may be due in part to wear or state of preservation and in any event are not in themselves of specific value.   In 3022a M_2 is relatively larger than in *Pt. trovessartianus*, having more the proportions seen in *Pt. gracilis*.

Ptilodus gracilis Gidley, 1909

1909. *Pt. gracilis,* Gidley, Proc. U. S. N. M., XXXVI, p. 616.
TYPE.—U. S. N. M. No. 6076.   Skull, lower jaws, and part of skeleton.
HORIZON AND LOCALITY.—Fort Union, Sweetgrass County, Montana.

DIAGNOSIS.—(Based on Gidley). Length P_4 7.6 mm., serrations 14. Length M_1 3.3 mm., cusp formula 5:4. Length M_2 2.4 mm., formula 3:2. P^4 with non-cuspidate anteroexternal shelf, seven cusps in outer main row and nine in inner. P^3 with six cusps.

This species is well characterized as against *Pt. mediævus* by the smaller size and the several differences in the upper premolars (assuming *Chirox plicatus* to represent the upper dentition of *Pt. mediævus*). The distinction from *Pt. montanus* from the same horizon and locality is not so clear, although it will perhaps be confirmed by the description of further material of the latter species. The size difference is only about 5%. The lower jaw of *Pt. gracilis* is said to be more slender, a statement apparently based on referred specimens of *Pt. montanus* which we have not studied. The difference in cusp formula in M_1, 5:4 for *Pt. gracilis* and 6:4 for *Pt. montanus*, is probably not a trustworthy criterion, as the anteroexternal cusp of the latter is very small and would readily be obscured or worn off, even if no allowance for individual variation be made.

MEASUREMENTS OF ALL SPECIES OF PTILODUS

Numbers	Length P_4	Length M_1	Length M_2
Pt. mediævus			
A. M. 3019	9.0	....	....
A. M. 3022	8.6	3.7	....
A. M. 3021	8.5	....	....
Pt. sp. indet.			
A. M. 16535	8.2	.....	....
Pt. montanus			
C. M. 1673	8.0	3.5	....
Pt. ?montanus			
A. M. 3023	7.9	....	....
A. M. 3022a	7.8	3.4	2.5
Pt. gracilis			
U. S. N. M. 6076	7.6	.3.3	2.4
Pt. trovessartianus			
A. M. 3025	ca. 5.9	....	....
A. M. 3025a	.5.9	.....	....
A. M. 3025b	5.9	....	....
A. M. 3025c	5.8	3.1	1.7

Eucosmodon Matthew and Granger, 1921

1921. *Eucosmodon*, Matthew and Granger, Amer. Mus. Novitates, No. 13, p. 1.
TYPE.— *E.* ("*Neoplagiaulax*") *americanus* (Cope).

DISTRIBUTION.—Puerco and Torrejon of New Mexico, lowest true Wasatch (Sand Coulee) of Wyoming, possibly also Fort Union of Montana and Paskapoo of Alberta.

DIAGNOSIS.—P_3 absent, P_4 typically lower relative to length than in other ptilodontids. Lower incisors strongly compressed laterally, with enamel limited to a narrow longitudinal band. Species largest of this family.

This is an unusually long-lived genus, ranging from the Puerco into the Wasatch. Inasmuch as no other genus is known to continue through these four very distinct faunal assemblages, it is probable that later discoveries, especially of upper dentitions, will indicate that more than one genus is included, but they are inseparable on the basis of the material now known. The genus is further remarkable for including the largest known ptilodontids.

As noted more fully in discussing the European forms below, the same genus may occur in Europe, and it is possible that *Eucosmodon* is a synonym of *Liotomus* Cope, 1884 (*Neoctenacodon* Lemoine, 1891), but this awaits confirmation and in the meantime we continue to use the name *Eucosmodon* for American forms.

DENTITION

Eucosmodon is sharply distinguished from all other American ptilodontids by the character of the lower incisors. The unworn tip is unknown and may have been enamel-covered, but the main body of the tooth has only a narrow band of enamel covering less than half the external face and extending a little onto the lower part of the internal face. These teeth are very much compressed, high and narrow, the depth two to five times as great as the width. The median face is almost flat and is limited by a sharp longitudinal angulation inferiorly, while the outer face is rounded. Both enamel and dentine may show curved transverse lines of growth, but the enamel is not rugose. Wear is rodent-like, the hard enamel projecting strongly and a facet being formed above it in the softer dentine. The tip is always somewhat rounded, however, and does not form a transverse chisel-like edge. Growth was long-continued, but closed roots were formed late in life, as in *Tæniolabis*.

P_3 is absent, as may be seen even in isolated specimens of P_4 by the absence or slight development of the anterior basal notch on the latter seen in *Ptilodus*. P_4 is otherwise of the normal ptilodontid type, save that it is typically longer and lower than in *Ptilodus*, although in *E. teilhardi* it is short and high. M_1 also resembles that of *Ptilodus* in general character, the cusp number, so far as known, being 5-6:4. In *E. ultimus* there is some tendency to develop minute accessory tubercles along the

external margin. M₂ is inadequately known. Except for a specimen
(A. M. No. 3027) so poorly preserved as to cast little real light on the
problem, associated upper and lower dentitions of *Eucosmodon* are un-
known. There are several Torrejon specimens of the upper dentition,
however, which are larger than any species of *Ptilodus* and on morpho-
logical grounds cannot belong to that genus. Their reference to *Eucos-*
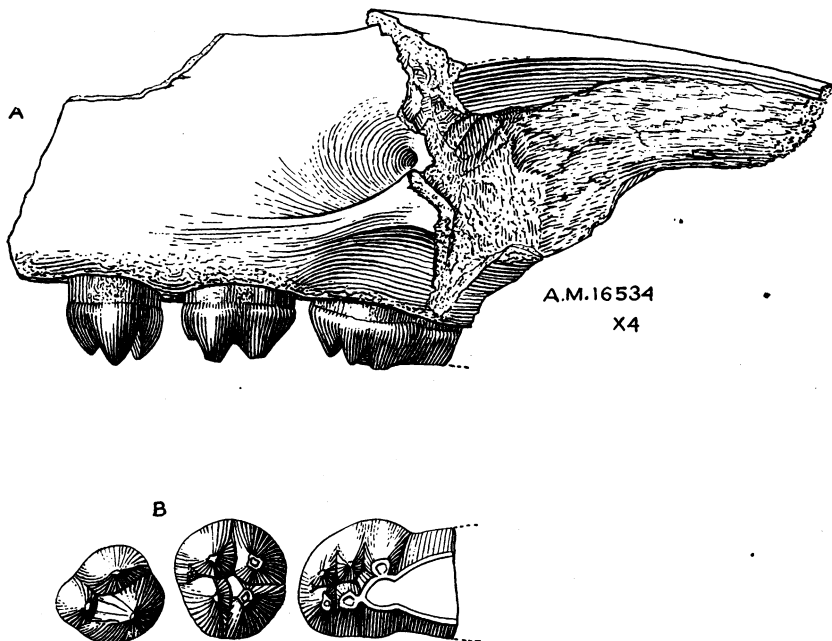

Fig. 17. *Eucosmodon* sp. A, part of skull, right lateral view. B, Premolars of
same specimen, crown view. Four times natural size.

modon is supported by these facts, and also by the badly preserved asso-
ciated material mentioned above, but their correlation with the species
based on the lower jaws is not now possible. In A. M. No. 16534 part of
the last premolar and all of the two preceding ones are preserved, as well
as part of the facial and frontal regions of the skull. There is a small
diastema in front of the first premolar present and then what appears
to be a suture, so that the number of upper premolars in this genus was
probably three. The first premolar is a small tooth with a low crown,
circular in outline, with three conical cusps, one external and two internal.
The external and posterointernal cusps are equal in size, but the antero-
internal cusp is much smaller.

The next premolar has four cusps of equal size, two external and two internal, and a minute anteromedian cuspule. The posterior end of the last premolar is broken away, but enough is preserved to show its character. It had a single main series of cusps, of which only the two anterior ones are now complete, as wear has deeply truncated the others, which may have been six or seven in number. Anteroexternally there are three additional cusps, vestiges or rudiments of a second cusp row, and there is no trace of a third row. It is possible that this upper dentition belongs to *E. teilhardi*, although the posterior upper premolar is a little more robust than would be expected in that species.

A second species, possibly *E. molestus*, is represented by several fragments (A. M. No. 17062). The penultimate premolar is larger and has three subequal external cusps, the inner half being broken away. The last premolar is also slightly larger than in No. 16534 and apparently
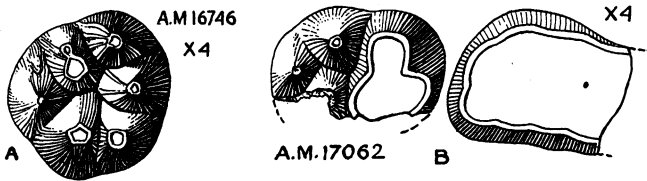

Fig. 18. *Eucosmodon* sp. A, isolated upper premolar, probably the penultimate, crown view. B, Broken last two premolars, crown view. Four times natural size.

of similar pattern, but it is deeply truncated by wear. A. M. No. 16746 is an isolated penultimate upper premolar, apparently of this same species. It is irregularly oval in outline with a cluster of six cusps on the crown. Four millimeters of the root above the enamel are preserved and in this distance it tapers but slightly and shows no sign of root division.

The only other known fragment of the upper dentition is a single incisor, probably I³, associated with the type of *E. teilhardi*, A. M. No. 16024. It is large for I³ but small for I² and certainly not what one would expect for I² in this genus, having a low crown which is completely enamel-covered. It is somewhat compressed transversely and has a posterior basal accessory cusp.

OSTEOLOGY

The skull of *Eucosmodon* is not well known, but it probably did not differ greatly from that of *Ptilodus*. In No. 16024, just mentioned, the only positively identifiable skull fragment is the posterior portion of the left zygoma with the glenoid surface. This region resembles *Ptilodus* and differs from *Tæniolabis* in many details. The glenoid surface is broad

and extends up onto the base of the zygoma. It is nearly flat transversely and convex anteroposteriorly, and the ectoglenoid process is seen only in a very slight ridge. The zygomatic arch was apparently not widely expanded. Gidley (1909, p. 619) stated that the jugal of *Ptilodus* extends back to the glenoid surface, but this statement was based on a cracked and crushed specimen. In *Tæniolabis* it certainly does not, and Broom, after an independent examination of Gidley's material, denied this feature in *Ptilodus* also (1914, p. 123). In *Eucosmodon* it is certain that the jugal not only did not reach the glenoid but had no part in the posterior portion of the zygoma. The same appears to be true of *Ectypodus* and probably was characteristic of all the Paleocene forms, at least.

Part of the skull is preserved in No. 16534. The zygoma arises opposite the anterior end of the last premolar, and the infraorbital foramen is just *above* the anterior root of the zygoma. The facial portion of the maxilla seems to have been relatively shorter than in *Ptilodus*. The orbit is large and is bounded by a sharp ridge superiorly.

The most important new material to be described in this paper is a specimen including most of the pelvis and both hind limbs as well as a number of vertebræ. This was found by Walter Granger in 1913 in the lower beds of the Puerco, three miles east of Kimbetoh, New Mexico. The bearing of this specimen on the relationships of the Multituberculata has been mentioned in an abstract of a paper read before the Paleontological Society (Granger, 1915) but no details or descriptions have been published.

The reference of the specimen to *Eucosmodon* seems very probable, although no teeth were found in association. That it is multituberculate is obvious. Only *Tæniolabis* and *Eucosmodon* are known to occur in the Puerco and it is much too small to belong to *Tæniolabis*. Furthermore it is from a level where *Tæniolabis* is not known to occur, while the specimens of *Eucosmodon americanus primus* are from the same level and locality. In *E. teilhardi*, a Torrejon species, a few fragments of associated limb material are known, and these agree exactly, save in size, with the comparable parts of the present specimen. The ratio of the width of the distal end of the femur to the length of P_4 at the alveoli in *E. teilhardi* is 1.92. The ratio of the same dimension of the present femur to the length of P_4 in *E. americanus primus* is 1.58, a sufficiently close agreement for distinct species of the same genus. The hind limbs in *Ptilodus gracilis* are much smaller relative to the dentition than in *Eucosmodon teilhardi*, and *Eucosmodon* may have been characterized by a relatively large skeleton and small skull.

A partial pelvis of *Ptilodus* has been described by Gidley (1909, p. 621). Broom (1914, pp. 123–5) redescribed the same specimen in detail, but he concluded that it was a shoulder girdle. In a note to the same paper (in Broom, 1914, p. 134) Granger pointed out that Broom's interpretation was incorrect and that the element in Gidley's material is a pelvis. This note was based on the specimen now to be described.

Parts of both right and left sides are preserved, the left with the ischium nearly complete, the greater part of the ilium, and a fragment of pubis. The right side is more fragmentary. There are several morphological differences from the *Ptilodus* pelvis of Gidley, due largely to generic character or different preservation, but possibly in part also to
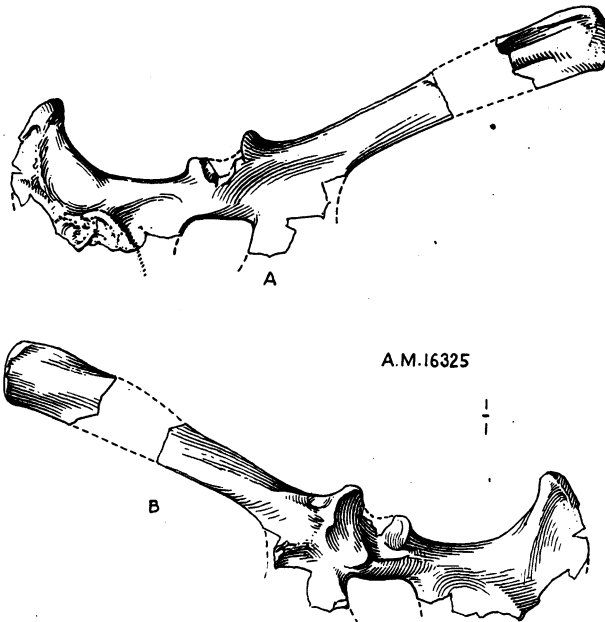

Fig. 19. *Eucosmodon* sp. Left side of pelvis. A, internal view. B, External view. Natural size.

variant interpretations. The ilium is long, straight, and rod-like, broadly oval in section at about a millimeter from the rim of the acetabulum and becoming flatter and laterally compressed more anteriorly. The rectus femoris origin is not marked by the usual spine (spina anterior inferior ilii) but by a small oval pit with raised rim, immediately anterior to the acetabulum. The superior and inferior rims of this pit merge anteriorly and continue forward as the very faint crista lateralis, which converges

slightly toward the lower border and becomes obsolete about 15 mm. from the rectus femoris pit. For the greater part of its course there is a second faint ridge above it, separated by a shallow longitudinal concavity. The sacro-iliac joint is not preserved but must have been short and at least 25 mm. from the acetabulum.

The acetabulum is quite unlike the simple unbroken cup shown by Gidley. There is a small acetabular fossa communicating with the large inferior incisura, which is overhung by the ends of the bilobed articular surface. The anterior part of this surface is much larger and more cupped than the posterior and is bordered by a stout, high rim on the ilium. The acetabulum is broadly and deeply emarginate superiorly, so that the connection between the anterior and posterior lobes of the articular surface is narrow.

Posteroinferiorly the ilium is expanded into a thin plate which bears rugosities for muscle attachment and which must have included part of the pubis or have passed into the pubis posteroinferiorly. The obturator foramen is below the acetabulum, hence somewhat farther forward than in *Ptilodus* as figured by Gidley, and its anteroposterior diameter is about the same as that of the acetabulum.

The most peculiar element in the pelvis is the ischium. Its superior border is very concave and it curves up to a sharp point posteriorly. Its lateral surface is broad and flat, but with the muscle areas marked.[1] The symphysial surface is long and strong and extends up to within six or seven millimeters of the posterosuperior angle. This surface is nearly parallel to that of the lateral surface of the ilium, a feature unique among mammals, so far as we have been able to determine. The opposite ischia, instead of meeting at a broad angle of nearly or quite 180°, as in other mammals, thus formed a very acute angle and were V-shaped as viewed posteriorly. From this and the great extent of the ischiatic symphysis it necessarily results that the axis of the ilium, continued by the anterior part of the ischium, was not parallel to the sacral axis or at a low angle to it, as in marsupials and placentals typically, but must have formed an angle of 45° or more, probably an even larger angle than in the monotremes. In the latter this is secondary[2] and has been correlated with a fossorial adaptation. *Eucosmodon* does not appear to be fossorial, and its pelvis is otherwise very different from that of the Monotremata. If also secondary in *Eucosmodon*, it must have been independently attained,

[1]The present morphological description is being supplemented elsewhere by an attempted restoration of the musculature by Simpson and Elftman.

[2]Howes, G. B. On the mammalian, pelvis, etc., Jour. Anat. Phys., XXVII, p. 543 seq.

but there is at least a possibility that it is primary and derived from the theriodont type in which the rotation primitive for all other mammals was not yet accomplished. In a few higher mammals, e.g., *Otocyon*, the iliac-sacral angle is also large, but here again this is secondary and independent of the superficially similar condition in monotremes and in *Eucosmodon*. The bearing of the narrow pelvis of *Eucosmodon* on reproduction is not clear. The oviparous monotremes have a relatively larger and more open pelvis than in many viviparous mammals, and there are no constant differences between marsupial and placental pelves which would serve to indicate the differences in reproduction.

Fig. 20. *Eucosmodon* sp. Pelvis. Superior view. Natural size.

The right femur is completely preserved, although the shaft is somewhat crushed posterodistally, and the proximal portion of the left femur is present. The articular surface of the head forms well over half of a nearly perfect sphere. There is no distinct pit for the ligamentum teres. The head projects sharply from the shaft, as in higher recent mammals, and like all the rest of the hind limb is on a definitely higher evolutionary level than in the monotremes. The neck is relati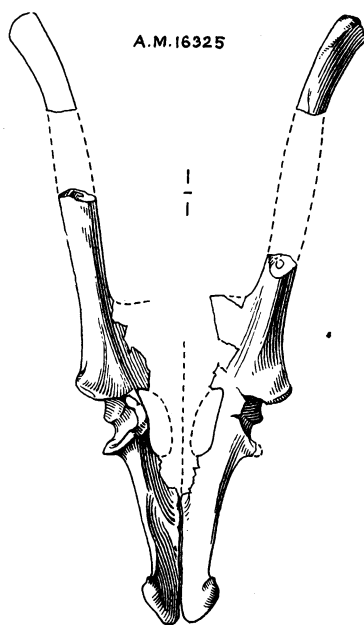vely long, sharply constricted and cylindrical. The greater trochanter is very large, projecting in the direction of the axis of the shaft to a point well above the top of the head and separated from the latter by a deep narrow notch. The apex of this trochanter is full and rounded, somewhat overhanging posterointernally, anteriorly, and anteroexternally and passing posteroexternally into a sharp crest running down the shaft of the femur to well below the middle. The intertrochanteric surface is nearly at right angles to the long axis of the shaft and bears between the two trochanters and the neck a small, well defined digital fossa. Lateral to the lesser trochanter and between it and the gluteal crest is another equally definite and larger elongated fossa which does not have any certain separate homologue on any other femur compared by us. This pit is separated from the true digital fossa by the inter-

trochanteric ridge, which is broad, rounded, and indefinite. The lesser trochanter is nearly median on the posterior face of the femur, much more external in position than in monotremes or even than in the more primitive marsupials and placentals. It is remarkably strong and independent, projecting sharply and having a definite restricted neck and expanded head, which overhangs the neck internally but not externally. It ends abruptly distally, not passing into a definite ridge as in most mammals.
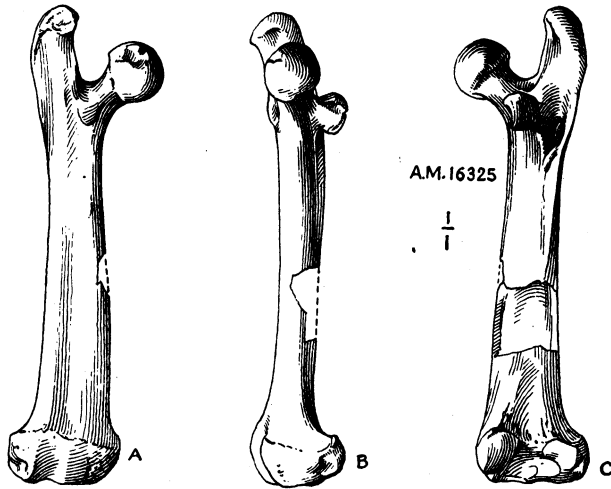

Fig. 21. *Eucosmodon* sp. Femur. A, Anterior. B, Internal. C, Posterior. Natural size.

On the anterior face of the femur just distal to the notch between the head and greater trochanter is a definite small projection. The shaft of the femur is crushed, but it appears to have borne only one sharp crest, the prolongation of the gluteal crest. There is no third trochanter.

The proximal epiphyses appear to be completely fused, but the boundaries of the distal epiphysis, agreeing in a general way with that of higher mammals, can still be made out. The articular surfaces of the condyles are relatively small and are separated on the posterior surface by a broad intercondylar notch. The patellar groove on the anterior surface is not continuous with the notch distally but is lateral in position, passing wholly onto the external condyle distally. The lateral epicondyle is large and rugose, the medial one less developed.

Sufficient is preserved of the tibiæ to give most of their characters with little doubt. The articular surface for the medial condyle of the

femur is small and is sharply bounded externally by the medial side of the intercondylar prominence, perhaps accentuated by crushing. Little is preserved of the lateral condylar surface. The posteroproximal portion of the shaft is deeply excavated. The central and distal portions are oval in section, compressed anterointernal-posteroexternally. The distal end is not very unlike the normal primitive therian type, with the surface for the trochlea rather small relative to the prominent internal malleolus.
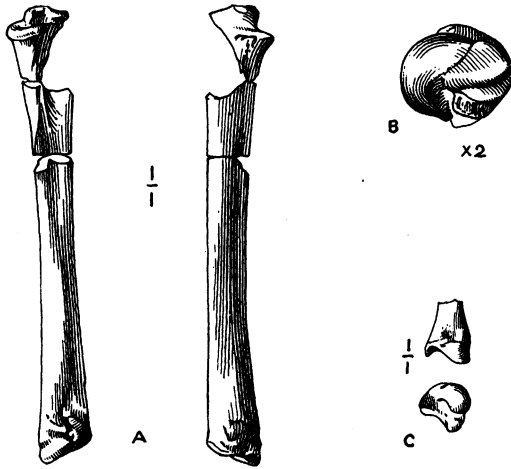

Fig. 22. *Eucosmodon* sp. A, Tibia, posterior and anterior views. B, Tibia, distal view. C, Distal end of fibula, anterior and distal views. A, C, natural size. B, twice natural size.

The fibulæ are represented only by the distal ends of both. They were not fused with the tibiæ, and each has a large convex articular facet, with a small sharp spine just posterior to it, and a small lateral process.
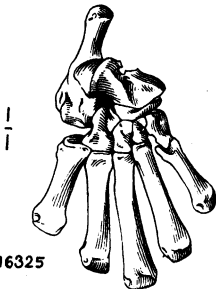
Fig. 23. *Eucosmodon* sp. Pes, without phalanges. Dorsal view. Natural size.

The tarsus consists of the usual seven elements, all separate. On the right side the ecto- and mesocuneiforms are absent, on the left the astragalus and entocuneiform, but the entire structure is displayed by the two sides considered together. As before, close comparison with the monotremes is impossible. The marsupio-placental pes gives the key for the interpretation of that of the multituberculates, although the differences are many and fundamental.

The astragalus has a roughly quadrate, oblong superior surface with two shallow slightly oblique grooves of nearly equal size. In the normal, oblique position of the bone the internal groove is considerably lower than the external, and apparently it articulates with the medial malleolus, but both grooves are roughly in the same plane. The calcaneo-astragalar facet, directly below the external crest of the trochlea, is large, markedly concave, elongate anteroposteriorly. It is nearly horizontal, a little higher externally, and is completely separated from the strongly inclined sustentacular facet by the irregular astragalar sulcus. The sustentacular facet is ovoid in shape, very gently concave, and forms the inferointernal face of the process for articulation with the navicular. The latter process is, of course, homologous with the head of the normal primitive therian astragalus, but here it has no neck and is not cut off from the main body of the bone. The navicular articulation is not rounded, as in primitive theria, but is formed by a groove with crests on both sides. This groove is shallow but long, forming a complete semicircle. It is curiously similar to the homologous feature of the artiodactyl astragalus, although its relationships to the rest of the astragalus are quite different. There is a relatively large astragalar foramen.

The calcaneum has a large, long tuberosity with a restricted neck and compressed transversely. The calcaneo-astragalar facet is dorsal, strongly convex, forming a prominent tuberosity. The sustentacular process is not prominent nor is it sharply distinguished from the body of the bone. Its facet is strongly oblique, but faces a little upward, and is separated only by a low sharp crest anteriorly from the vertical cuboid facet. The latter is concave and is distomedial, not purely distal. The external side of the distal part of the calcaneum is marked by a small nearly vertical groove, so deep that there is a tendency to bridge it over.

The navicular is transversely elongate. The whole proximal surface is taken up by the deep saddle-shaped surface for the astragalus. Distoexternally is the large cuboid facet, extending well around onto the plantar surface, and internal to this, continuous with it and with each other, are the three imperfectly differentiated convex cuneiform facets.

The cuboid articulates proximally about equally with calcaneum and navicular, internoproximally with the ectocuneiform, and distally with the whole of the proximal end of metatarsal IV and about half of that of metatarsal V. It is broadly emarginate along its external side, and there is a large gap here between the distal end of the calcaneum and the proximal end of metatarsal V.

Ecto- and mesocuneiforms are as in most primitive theria, articulat-

ing proximally with the navicular and with their neighbors on each side and distally with metacarpals III and II, respectively. The mesocuneiform is much the smaller. The entocuneiform is the largest and longest of the three. Proximally it has a concave facet for the navicular and a relatively small externoproximal facet for the mesocuneiform. Distally it is compressed laterally and expanded dorsoventrally and has a large saddle-shaped articulation for metatarsal I.
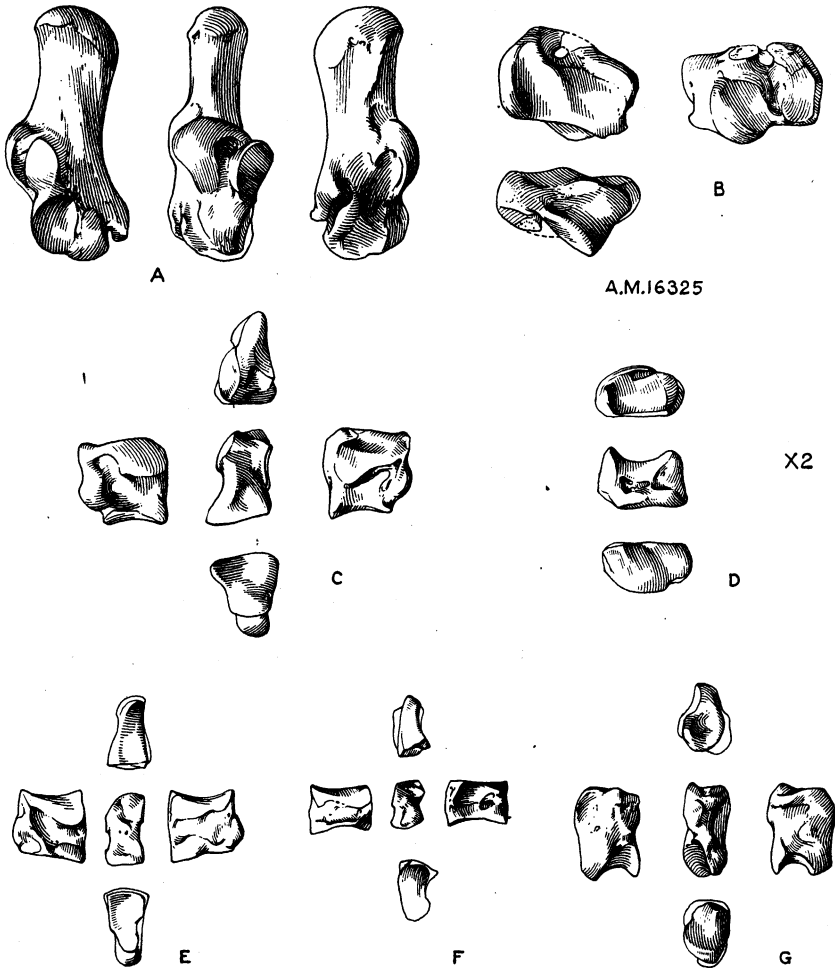

Fig. 24. *Eucosmodon* sp. Tarsus. A, Calcaneum. B, Astragalus. C, Cuboid. D, Navicular. E, Ectocuneiform. F, Mesocuneiform. G, Entocuneiform. Twice natural size.

All five metatarsals are present and they are well developed, stout bones of moderate length. The actual order of length is III, II, IV, V, I, but functionally the foot is perfectly mesaxonic, the proximal ends being so placed as to make the distal ends of I and V and of II and IV, respectively, equidistant from the posterior end of the foot; V is the largest and has a distinct prominence externoproximally. II–V are lightly in articulation with each other proximally and have nearly plane-surfaces for their tarsal articulations; I, however, is not in contact with the others and has a strong saddle-shaped articulation for the entocuneiform. The structure of this metatarsal and of the entocuneiform seems to show beyond a doubt that the first digit, while not markedly divergent, had much more freedom of motion than the others and was at least partially opposable. The articulations for the phalanges are simple, transversely cylindrical, with faint rudimentary keels at the extreme plantar ends of the articular surfaces.
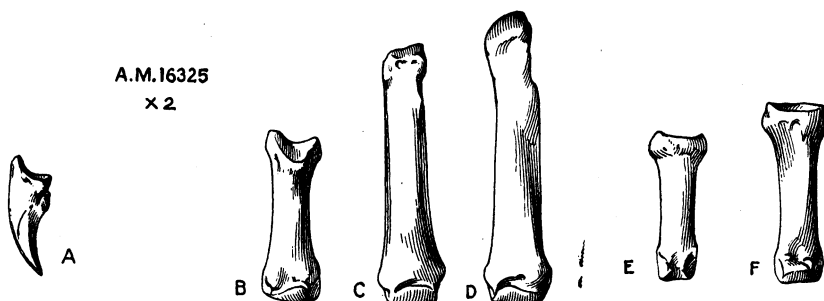

A.M. 16325
× 2

Fig. 25. *Eucosmodon* sp. Pes, A, Terminal phalanx, lateral view. B, Left metatarsal I, dorsal view. C, Left metatarsal II, dorsal view. D, Left metatarsal III, dorsal view. E–F, Isolated phalanges, dorsal views. Twice natural size.

The phalanges were not found in articulation but are represented by numerous isolated bones. They are of primitive type, the proximal articulations somewhat expanded, the distal ones grooved but not keeled. The terminal phalanges are stout, transversely compressed claws without fissures or hoods but with well-marked proximo-plantar tuberosities.

The multituberculate fore-limb is as yet poorly known. Gidley has described an imperfect humerus and radius in *Ptilodus*, while parts of scapula, humerus, metacarpals, and proximal phalanges are known in the Cretaceous *Djadochtatherium*. In *Eucosmodon* our only knowledge comes from No. 16024, the type of *E. teilhardi*, which includes both olecrana and a small fragment of the distal end of the humerus. The

latter agrees so far as it goes with *Ptilodus*. The olecrana are short but relatively stout, with expanded margins.

A. M. No. 16325 includes a number of fairly well preserved vertebræ, and No. 16024 also includes some centra. None of these are articulated or in unbroken sequence. With the first-mentioned specimen there are four fairly complete lumbars and six caudals, besides numerous fragments. In the lumbars the ends of the centra are nearly circular. The centra are excavated inferiorly and bear broad rounded longitudinal keels, each with a single small median foramen. The transverse processes are strong, taking their origin along the whole length of the centrum and extending forward and downward, their ends truncated, not pointed.
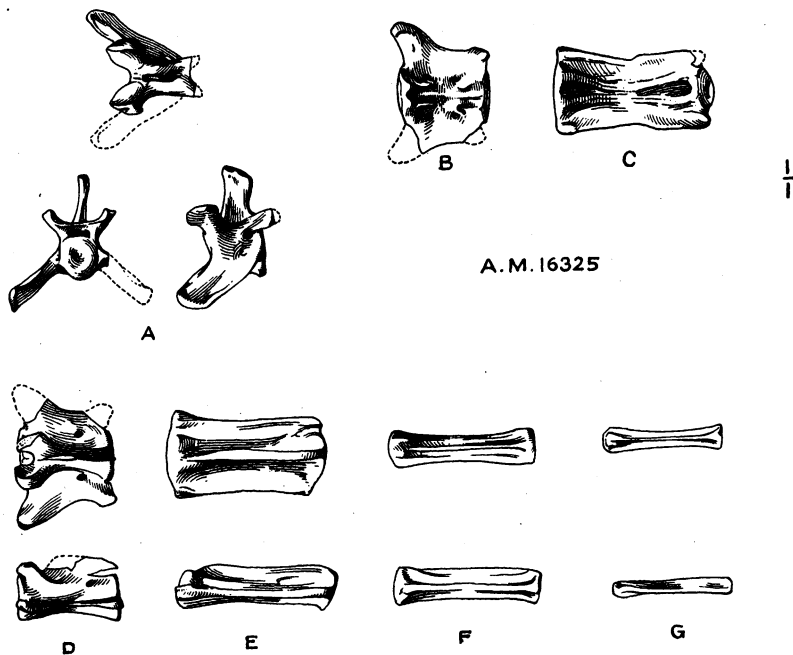

A.M. 16325

Fig. 26. *Eucosmodon* sp. Vertebræ. A, Lumbar. B–G, Caudals. Natural size.

Piercing the base of each transverse process slightly nearer its posterior edge is a small foramen or short canal, running nearly vertically, but a little more posterior above. The zygapophyses are large, the prezygapophyses having the articular surfaces concave transversely and inclined toward the midline. On at least one of the lumbars the neural spine is inclined forward and seems to be pointed, but on one, possibly more

posterior, it is truncate and inclined slightly backward. The spinal nerves issue through posterior notches.

An apparent anterior caudal has the centrum equal in diameter to those of the lumbars but much more elongate. The inferior surface is marked by an anterior and a posterior pair of small longitudinal ridges. The transverse processes are horizontal plates of the type familiar in this region in many primitive mammals, with anteriorly directed projections at their anterolateral angles and similar but smaller posterior ones. These processes are pierced by small vertical canals as in the lumbars. Prezygapophyses are well developed, but the postzygapophyses are not distinguishable from the posterior end of the long and probably low neural arch. Posterior to this vertebra the centra apparently become still more elongate for some distance and gradually more slender, the various processes becoming simpler. A long and heavy tail is indicated.

The fragments with No. 16024 also appear to include lumbars and caudals, all with the processes broken off and the centra mostly crushed. A dorsoventrally crushed fragment of sacrum is present and it shows that this consisted of at least two fused vertebræ.

<div align="center">Taxonomy</div>

Eucosmodon americanus (Cope, 1885)

1885. *Neoplagiaulax americanus*, Cope, Am. Nat., XIX, p. 493.

1921. *Eucosmodon americanus*, Matthew and Granger, Am. Mus. Novitates, No. 13, p. 1.

Type.—Amer. Mus. No. 3028. Under this number are included five fragments representing more than one individual and including a right P_4 in jaw, left P_4 in jaw, right M_1 and fragment of P_4 in jaw, apex of right incisor, and fragment of left jaw with root of incisor. Of this material the left P_4 in fragment of jaw with root of incisor may be considered as a lectotype. All Cope Coll., collected by D. Baldwin, 1885.

Horizon and Locality.—Upper horizon of Puerco, San Juan Basin, New Mexico.
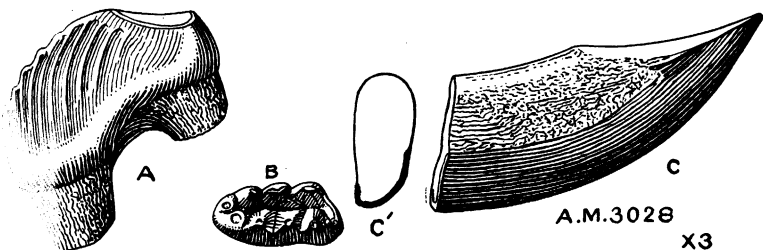

Fig. 27. *Eucosmodon americanus.* Cotypes. A, Left P_4, external view. B, Right M_1, crown view. C, Right lower incisor, external view. C′, Transverse section of lower incisor. Three times natural size.

DIAGNOSIS.—P_4 with not less than 12 serrations, 10.6 mm. long in type. Maximum height of incisor 6.0 mm., width 2.7 mm.; ratio height: width ca. 2.22. Length M_1 5.6 mm., width 2.6 mm., cusp formula 5:4.

The number of serrations on P_4 was probably greater than 12, the posterior ones being very vague. As in other ptilodontids, wear soon truncates this tooth posteriorly. On M_1 the anterior cusps of both rows are small, and the posteroexternal cusp is somewhat elongated. The two posterointernal ones are small and connate at their bases. A fragment of M_2 showing two large outer cusps is preserved.

Eucosmodon americanus primus, new subspecies

TYPE.—Amer. Mus. No. 16327, isolated P_4. Amer. Mus. Exp. 1913.

PARATYPE.—A. M. No. 16328, tip of left lower incisor. Amer. Mus. Exp., 1913.

HORIZON AND LOCALITY.—Lower horizon of Puerco, three miles southeast of Kimbetoh, New Mexico.

DIAGNOSIS.—Incisor smaller than in *E. americanus*, max. height 4.2 mm., width 1.9 mm., ratio ca. 2.21. P_4 shorter than in *E. americanus* and with only nine serrations.

These specimens are notable as coming from the lower horizon of the Puerco, multituberculates being very rare at this level. The type and paratype were not found in undoubted association, but both differ from *E. americanus* in being smaller, the incisor relatively more so, and P_4 also differs in being definitely simpler. It is 9.7 mm. in length. At the
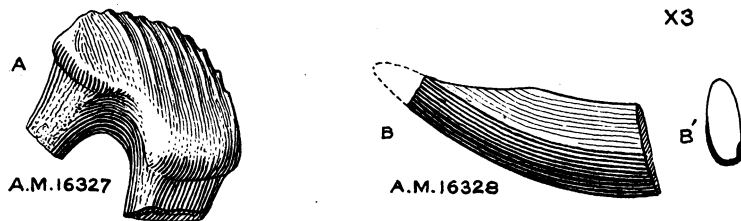

Fig. 28. *Eucosmodon americanus primus*. A, Right P^4, external view, type. B, Left lower incisor, external view, paratype, B', Same, transverse section. Three times natural size.

same level and general locality were found the pelvis and hind limbs described above, and they may belong to this subspecies, although not found in association with the teeth. Also at this level and near Kimbetoh was found No. 16529, a still smaller incisor with short enamel band. It may possibly be an upper incisor of this form.

Eucosmodon molestus (Cope, 1886)

1886. *Neoplagiaulax molestus,* Cope, Am. Nat., XX, p. 451.

TYPE.—Amer. Mus. No. 3029. Isolated left P_4. Cope Coll., collected by D. Baldwin.

NEOTYPE.—A. M. No. 17063. Parts of right and left rami with both incisors and left P_4. Amer. Mus. Exp., 1916.

HORIZON AND LOCALITY.—Torrejon, San Juan Basin, New Mexico.

DIAGNOSIS.—Incisor max. height 5.8 mm., width 2.6 mm., ratio 2.23. Length P_4 ca. 15.0 mm., with about 15 serrations.
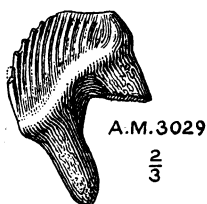

A.M.3029

$\frac{2}{3}$

Fig. 29. *Eucosmodon molestus.* Left P^4. External view. Type. Two-thirds natural size.

This highly distinctive and relatively very large species has incisors of almost exactly the same size and proportions as in *E. americanus,* although P_4 is about 50% larger. The neotype incisors are closed posteriorly and have the enamel band definitely limited to the anterior part of the tooth, showing that in this species, and probably in the whole genus, they are not rootless or nearly so as at first supposed.

Cope referred a toothless left ramus (A. M. No. 3030), but this is from the Puerco, while all the other material is from the Torrejon. Furthermore, the length of P_4 at the alveoli was over 15% greater
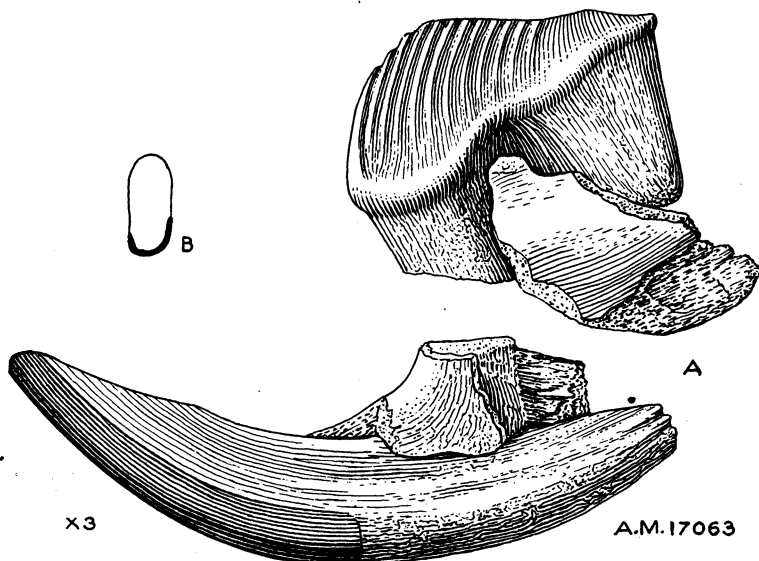

Fig. 30. *Eucosmodon molestus.* Neotype. A, Parts of left lower jaw with incisor and P_4. B, Transverse section of incisor. Three times natural size.

in the type than in this referred specimen, and the jaw of the latter is much larger and heavier than in the neotype, so that the reference is surely incorrect. The Puerco specimen is a multituberculate, but its relationships are entirely problematical.

Eucosmodon teilhardi, new species[1]

TYPE.—A. M. No. 16024, both lower jaws, incomplete, with roots of teeth, associated with I^3 and numerous skeletal fragments. Amer. Mus. Exp., 1912.

PARATYPES.—A. M. No. 2375, right ramus with broken P_4 and part of I. Collected by B. Brown, expedition of 1896. A. M. No. 16023, right ramus with I complete. Amer. Mus. Exp., 1912.

HORIZON AND LOCALITY.—Torrejon Formation, San Juan Basin, New Mexico. Type and No. 16023 are from the Arroyo Torrejon.

DIAGNOSIS.—Incisor, max. height 5.2 mm., width 1.6 mm., ratio 3.25. Length P_4 at alveoli 5.5 mm. P_4 relatively short and high.

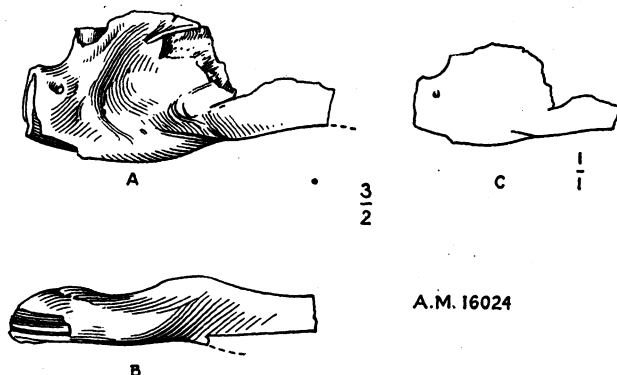A   • $\frac{3}{2}$ C |

A.M. 16024

B

Fig. 31. *Eucosmodon teilhardi.* Left lower jaw. Type. A, External view. B, Inferior view. C, External view, outline. A, B, one and one half times natural size. C, natural size.

A.M. 16024

Fig. 32. *Eucosmodon teilhardi.* Type. A, Olecranon, superior view. B, Same, lateral view. C, Upper incisor? Natural size.

The much more strongly compressed and more arcuate incisor and the short high P_4 mark this species off very strongly from all others referred to the genus. Further material may even justify generic separation, but the relationship to *Eucosmodon* must be close.

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[1] We dedicate this species to Dr. P. Teilhard de Chardin, author of "Les Mammifères de l'Éocène inférieur Français et leurs Gisements."
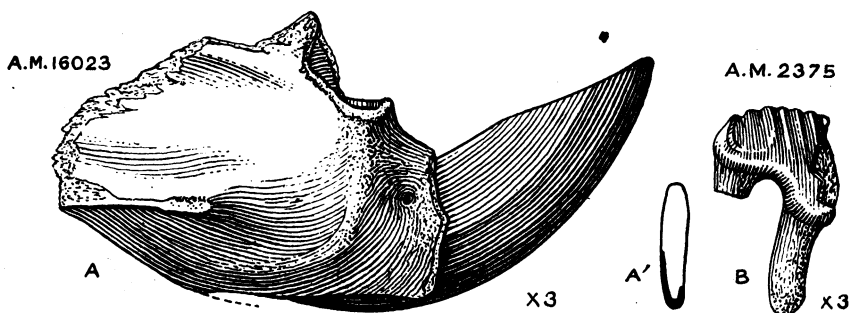
Fig. 33. *Eucosmodon teilhardi*. Paratypes. A, Part of right lower jaw, external view. A′, Transverse section of incisor. B, P₄, right, external view. Three times natural size.

Eucosmodon ultimus Granger and Simpson, 1928

1928. *E. ultimus*, Granger and Simpson, Amer. Mus. Novitates, No. 312, p. 2.

Type.—A. M. No. 16103, part of left ramus with P₄ and M₁, and associated right P₄. Collected by Walter Granger, 1912.

Horizon and Locality.—Sand Coulee beds, Wasatch formation, Clark Fork Basin, Wyoming.

Diagnosis.—Length P₄ 11.4 mm., fourteen serrations on margin, relatively long and low. Length M₁ 7.3 mm., width 3.7 mm., cusp formula 6:4.

This species is definitely post-Paleocene. The premolar differs but little from that of *E. americanus*, but the molar is larger, with more cusps, and with the anterointernal cusp elongate instead of being reduced. P₄ is considerably smaller than in *E. molestus* and longer and lower than in *E. teilhardi*. Two different types of incisor are known from the Sand Coulee beds—both belong to *Eucosmodon*, but it is uncertain which belongs with this species. One is much like that of *E. americanus* but with a wider enamel band, and the other is larger and more compressed.

Ectypodus Matthew and Granger, 1921

1921. *Ectypodus*, Matthew and Granger, Amer. Mus. Novitates, No. 13, p. 1.

Type.—*E. musculus* Matthew and Granger, 1921.

Distribution.—Tiffany beds, Southwest Colorado.

Diagnosis.—Dental formula $\frac{?2}{1}\cdot\frac{0}{0}\cdot\frac{4}{2}\cdot\frac{2}{2}$. P⁴ elevated posteriorly, with only one main row of cusps but with one or two small cuspules at the anteroexternal end of the main row. P¹⁻² tricuspid. P³ quadricuspid. Lower teeth much as in *Ptilodus*.

Although known only from a single small mass of matrix—the Mason pocket of the Tiffany beds—over a dozen individuals are at hand, and they make our knowledge of the dentition very satisfactory. This is all the more fortunate as *Ectypodus* is one of the smallest of all Tertiary

mammals and might be quite overlooked in the course of ordinary collecting. The variation shown is very slight, much less than in most species of which a comparable number of individuals is known,—an interesting fact suggesting that these remains may well be those of animals which were closely related individually.

The genus may also occur in a more robust species in the French Thanetian (see below). The question turns on the correct association of isolated elements in the French fauna, and so much doubt enters in,
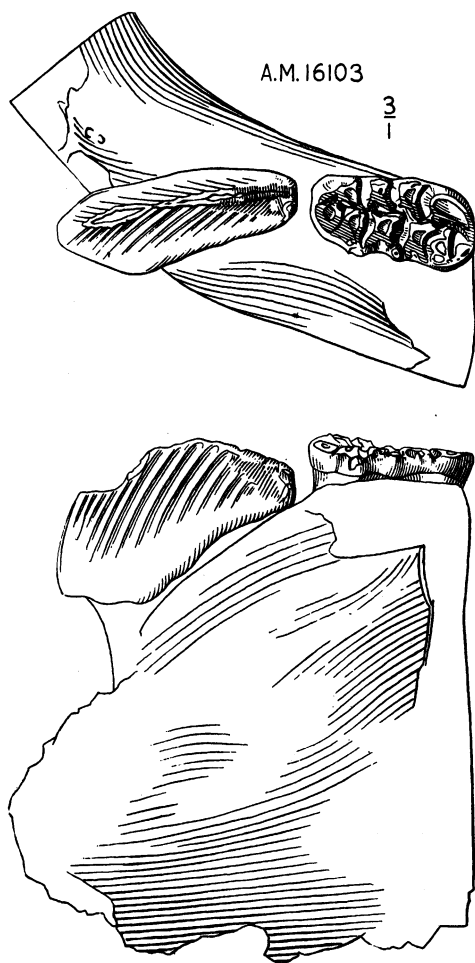

A.M. 16103

$\frac{3}{1}$

Fig. 34. *Eucosmodon ultimus.* Part of right lower jaw with P_4 and M_1. Crown and external views. Type. Three times natural size.

that at present it seems preferable to retain *Ectypodus* as a distinct and monotypic genus.

The premaxilla is not clearly preserved in any case, but no doubt there were two pairs of upper incisors as in other ptilodontids. Of these only I² has been recognized in the dissociated material. This tooth has a long root and short enameled crown separated into three distinct faces by three sharp vertical angulations: an evenly convex anteroexternal face, a concave internal face, and a posterior face excavated at the sides and with a prominent basal cusp above it.
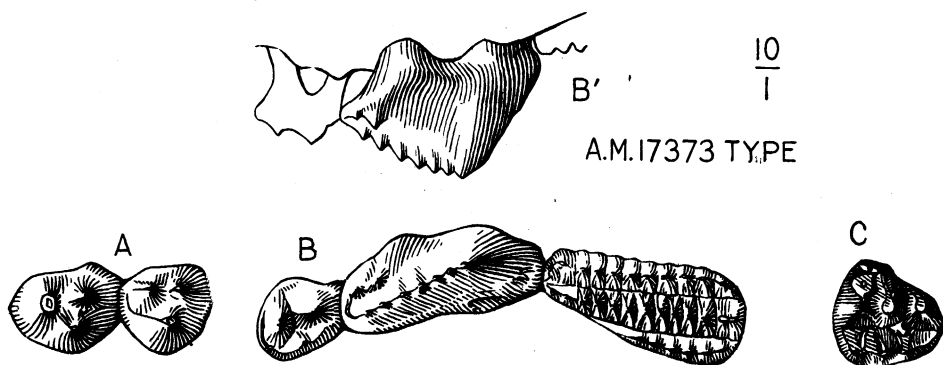

Fig. 35. *Ectypodus musculus*. Type. A, First two right upper premolars, crown view. B, Last two left upper premolars and first molar, crown view. B', Last left upper premolar, external view. C, Last left upper molar, crown view. All ten times natural size.

P¹⁻² have three cusps arranged in a triangle with one cusp external and two internal and with a posterior basal expansion or cuspless heel. They are similar except that P¹ is slightly compressed transversely and appears to have a slightly larger basal expansion than P². P³ has four small conical cusps, two external and two internal, and also has a posterior basal expansion.

P⁴ is very unlike anything else in the American Paleocene, and it was on this tooth that the genus was chiefly erected. It is more obviously trenchant than in other American Paleocene ptilodontids (although P⁴ actually is a shearing tooth in all). There is a single shearing edge with seven small cusps or serrations. This series rises sharply so that the seventh is farthest from the alveoli. It is still some distance in front of the posterior end of the tooth, which is triangular in lateral contour, with a long base next to the alveoli, a slightly shorter oblique cuspidate anterior edge, and a still shorter, more nearly vertical, non-cuspidate

posterior edge. The inner face is flat or slightly concave. The external face bears two (or in two specimens apparently only one) small accessory cuspules at the anterior end. Just posterior to these the face is hollowed out, but farther back it is convex.

M^1 has three cusp rows, the inner one incomplete anteriorly, and is much like the same tooth in *Ptilodus*. The cusp number is apparently 12:13:10, although this may not be quite exact, as the cusps are excessively minute and rather worn. M^2 is short and triangular, with apparently a single narrow anteroposterior outer cusp, three well separated median cusps, and four inner ones, their bases connate.

The lower incisor was like that of *Ptilodus*. P_3 was stated by Matthew and Granger to be absent, but from the distinct notch in the anterior end of P_4 and from rather obscure signs of an alveolus, we believe that it was present. P_4 differs from that of *Ptilodus* only in being a little longer relative to its height. M_1 is unusually long and slender, its length just two and one half times its breadth. There are eight external cusps, the anterior one or two very small, and six internal ones, the most posterior somewhat the longest. M_2 is subtriangular. It has five or six external cusps, all very closely crowded together and with bases more or less connate so as to appear to be so many apices on a continuous ridge, and two internal ones, the posterior elongate and with several ridges running into the midgroove.

The lower jaw is very like that of *Ptilodus* on a reduced scale and the skull was apparently similar, although not well shown by the badly crushed material.

Ectypodus musculus Matthew and Granger, 1921

1921. *E. musculus*, Matthew and Granger, Amer. Mus. Novitates, No. 13, p. 1.
TYPE.—Amer. Mus. No. 17373, upper jaw with P^{3-4} and M^1, and other possibly associated parts of upper and lower dentition. Amer. Mus. Exp. 1916.
HORIZON AND LOCALITY.—Tiffany Beds, Ignacio, Colorado.
DIAGNOSIS.—Length P_4 4.0 mm., P^4 2.7 mm. Cusp formula of M_1, 8:6.

The characters of this species are those given in describing the genus. The following measurements are taken from various individuals; none differs more than 0.1 mm. from any of these dimensions.

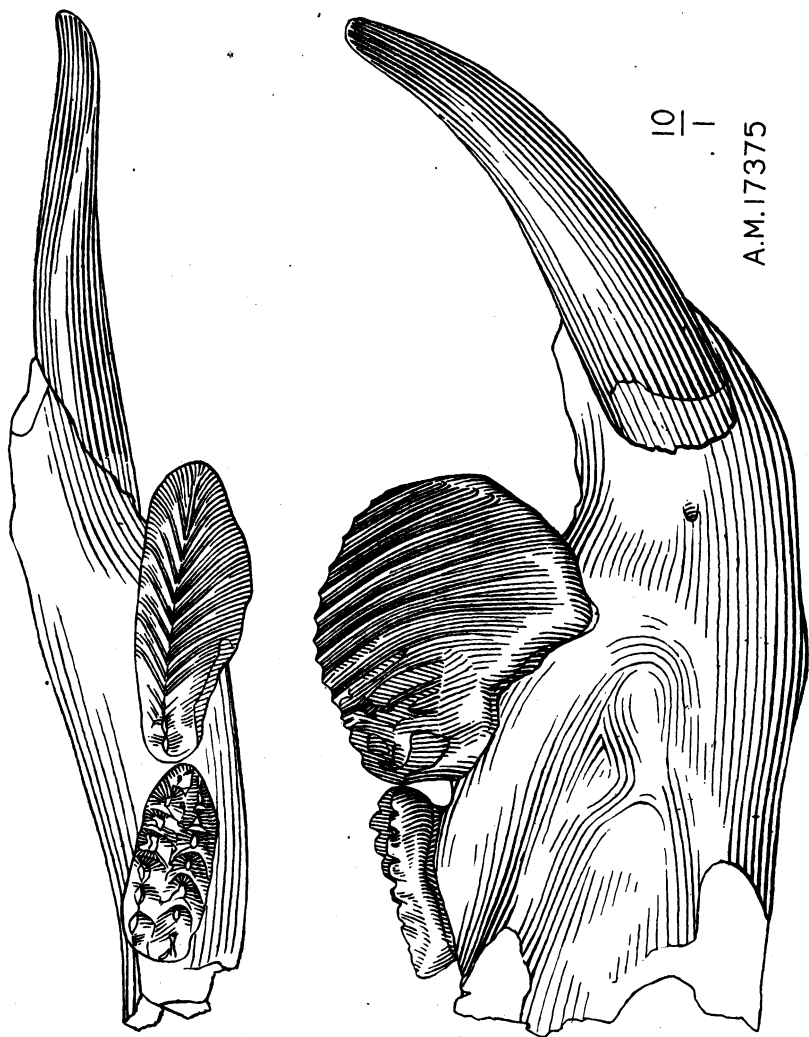|		
P_4 Length—4.0		P^4 Length—2.7
M_1 { Length—2.5		M^1 { Length—3.1
{ Width —1.0		{ Width —1.4
M_2 { Length—1.4		M^2 { Length—1.2
{ Width —1.1		{ Width —1.3

Fig. 36. *Ectypodus musculus.* Topotype. Right lower jaw with incisor, P4, and M1, crown and external views. Ten times natural size.

A.M.17375

$\frac{10}{1}$

Undescribed Genus and Species

Since the manuscript of the present paper was completed, Mr. G. L. Jepson of Princeton University has discovered a new multituberculate in the Gray Bull beds of Northern Wyoming. Coming from a distinctly later horizon even than *Eucosmodon ultimus,* this is now the latest known multituberculate. The species, which has not yet been published (October, 1928) is distinct, but apparently of a new genus related to *Ectypodus.*

It seems quite probable that the lower Eocene (as distinct from the Paleocene) will eventually prove to be characterized by several types of multituberculates.

EUROPEAN PALEOCENE MULTITUBERCULATES

Paleocene multituberculates are known from only one horizon in Europe, the Thanetian. The important mammalian fauna of this age from Cernay-les-Reims in the department of the Marne in France is the oldest in Europe save for those from far down in the Mesozoic, and the name Cernaysian is now in common use in the correlation of mammalian faunas.[1] This Thanetian fauna, long known to be equivalent in a general way to the American Paleocene, has recently been more carefully studied by Teilhard (1921-2), whose masterly analysis leads to the conclusion that it includes only the equivalent of the uppermost part of the American Paleocene, the Tiffany of southwestern Colorado and the Clark Fork of Wyoming.[2]

The multituberculates of the Thanetian are very poorly known, being represented only by two or three fragmentary jaws and a number of isolated teeth of very doubtful associations. A definitive revision is not now possible, but the conditions at the only fruitful locality, along the Mont de Berru just east of the village of Cernay-les-Reims, near Reims, do not hold out any promise for the immediate future, and an attempt at this time to correlate what little is known with the better knowledge of American forms may be of some use.

Two genera certainly occur, and there is probably also a third, although it cannot now be separated from *Neoplagiaulax.* The lower

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[1]This usage is rather firmly established, but it is open to objection, as the so-called Cernaysian fauna is probably typical of the whole Thanetian and not merely of the local bed to which alone the name Cernaysian properly applies. The great majority of Thanetian mammals known are from the so-called Cernaysian conglomerate, but typical "Cernaysian" fossils have also been found in other Thanetian deposits. See Teilhard, 1921, pp. 48-9. The term Thanetian, furthermore, is much more widely used and understood by stratigraphers generally, outside of mammalian specialists.

[2]The Paskapoo of Alberta has since been found also to be of this age, at least in part, and while the bulk of the Fort Union of Montana and elsewhere is apparently earlier, it probably also extends into the upper Paleocene.

incisors, lower premolars, and last upper premolars, taken separately, all agree in showing that there are at least three species and possibly one or two more. All of these appear to be very close to the ptilodontids of the Torrejon and Tiffany, and it is possible that one or even two genera are common to the two continents. Cope referred some American specimens to *Neoplagiaulax*, but in this he was mistaken. His "*Neoplagiaulax*" *americanus* is clearly distinct and was placed in the new genus *Eucosmodon* by Matthew and Granger. *Eucosmodon* may occur in the Thanetian, however.

PTILODONTIDÆ

Neoplagiaulax Lemoine, 1880

1880. *Neoplagiaulax*, Lemoine, Com. sur les Oss. Fos., etc., p. 12.

TYPE.—*N. eocænus* Lemoine, 1880.

DISTRIBUTION.—Thanetian, France.

PROVISIONAL DIAGNOSIS.—Lower incisor not gliriform, enamel covering most of extra-alveolar portion. P3 absent.

This was the first described genus of post-Jurassic Multituberculata, but its true characters are stilll doubtful. The only definite distinction from *Ptilodus* or *Ectypodus* lies in the absence of P3, from *Eucosmodon* in the *Ptilodus*-like incisors. Except for the two types of incisors, and presence or absence of P3, all ptilodontids are essentially similar in the lower jaws, while the upper premolars may be widely different.[1]

Lemoine created two species on the basis of lower jaws. In the first, *N. eocænus*, the length of P4 varies from 3.8 to 4.2 mm., and in the second, *N. copei*, from 5.0 to 5.6 mm. A census of specimens in Paris, Lyons, and Berlin shows the latter to be about three times as abundant as the former. No intermediates between 4.2 and 5.0 mm. were seen, and the species are probably quite distinct. The larger species also tends to have more serrations, for, although the numbers vary and overlap somewhat, *N. eocænus* generally has 13–14 and *N. copei* 15–16. The molars of the type of *N. eocænus* are not basined, as one might suppose from Lemoine's figures, but are of strictly ptilodontid type. M1 is broken and its cusp number uncertain. M2 is little if any wider. The cusp number, so far as obtainable on the worn tooth, is 5:2.[2] There are other fragmentary molars, upper and lower, but their association is uncertain, and they agree rather well with those of *Ptilodus* already described.

The difficulties of the whole question lie in the upper premolars. These are the most characteristic teeth in this family and must eventually

[1]Teilhard (p. 14, especially footnote 2) notes this stereotyped structure, but it did not extend to the whole dentition.

[2]Teilhard gives for M1 7:5, mentioning that study is difficult. This number is probably about correct. For M2 he gives 5:5, but there appear really to be only two distinct internal cusps. These are ridged in the usual ptilodontid way and give the impression of a greater number, but study of unworn teeth of the same family suggests correction to 5:2.

become the chief basis of taxonomic distinction in a group otherwise so uniform, but in the Cernaysian they are known only from a few specimens associated neither with other upper teeth nor with lowers. The anterior premolars are almost hopeless, from a systematic point of view. The main types have been figured by Teilhard, and we give new figures of the two most distinctive. They consist of three or four cusps with a slight basal extension on one side, and closely resemble corresponding teeth of *Ptilodus* and *Ectypodus*. The three-cusped ones probably include P^1 and possibly P^2, the four-cusped P^3, and possibly also P^2.
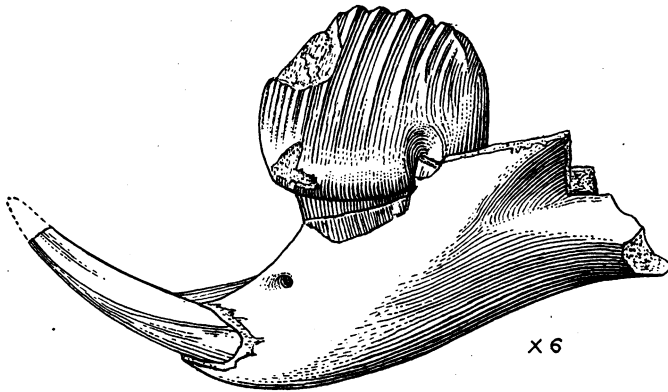

Fig. 37. *Neoplagiaulax copei*. Left lower jaw. External view. In the Depéret Collection, Université de Lyon. Six times natural size.

There are three distinct types of P^4, Teilhard's E, F, and G (p. 15). His F is typical of *Liotomus marshi* and is discussed under that genus. His E and G, of which we give new figures, are of a size suitable to be associated with the species here necessarily referred to *Neoplagiaulax*. We have spent much time trying in every way possible, by comparison with American forms, the use of all conceivable ratios, etc., to obtain some clue to their proper association with the lower jaws on which the taxonomy is based, but all the results are most vexatiously inconclusive. The ratio $P_4:P^4$ is apparently of taxonomic value in the Ptilodontidæ and is approximately constant for a given species, but it varies widely within the limits of a genus, and still more between different genera. These two types of P^4 obviously belong to different species, probably to distinct genera, and this, together with the fact that the size difference between them is markedly less than between P_4 of *N. eocænus* and of *N. copei*, makes invalid the simple and at first sight promising course of referring

the smaller P⁴ to the species with the smaller P₄. One of these premolars, the smaller, is so like that of *Ectypodus* that true generic separation may be impossible. It differs in being considerably larger than P⁴ of *Ectypodus*

Fig. 38. Cernaysian multituberculates. Upper premolars. Lemoine Collection. Museum d'Histoire Naturelle, Paris. Six times natural size.

musculus, in having nine rather than seven tubercles on the cutting edge, and in being less elevated posteriorly, but the general agreement is striking.
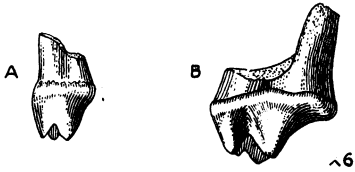
There are, so far as we are aware, only two specimens of the larger and three of the smaller among the known materials.

The larger type of P⁴ has only six stout cusps in the main series and four stout but lower cusps in the external accessory series. The last of these is opposite the fifth of the main row. The posterior main cusps are truncated by wear.

Neoplagiaulax eocænus Lemoine, 1880

1880. *N. eocænus*, Lemoine, Com. sur les Oss. Fos., etc., p. 12.
Type.—Lemoine Collection, Museum d'Hist. Nat., Paris. Part of left mandible with P₄ and M₁₋₂.
Horizon and Locality.—Thanetian, Cernay-les-Reims, Marne.
Diagnosis.—Length P₄, 3.8-4.2 mm., 13-14 serrations.

As figured by Lemoine, the incisor and much of the posterior part of the mandible were present, but these are now absent and may have been restored from other specimens. The apparent condyle in his figures must have been accidental, as the condyle never occurs in this position in any multituberculate.

Neoplagiaulax copei Lemoine, 1891

1891. *N. copei*, Lemoine, Bull. Soc. Geol. France, (3) XIX, p. 289.
Lectotype.—Part of right mandible with base of incisor and P₄. Lemoine also included a fragment of a left ramus with P₄ in his original description, but the right P₄ was considered as the type by Teilhard. Lemoine Collection, Museum d'Hist. Nat., Paris.
Horizon and Locality.—Thanetian of Cernay-les-Reims, Marne.
Diagnosis.—Length P₄ 5.0-5.6 mm., 14-16 serrations.

Liotomus Cope, 1884

1884. *Liotomus*, Cope, Am. Nat., XVIII, p. 691.
1891. *Neoctenacodon*, Lemoine, Bull. Soc. Geol. Fr., (3) XIX, p. 289.

TYPE.—*L. (Neoplagiaulax) marshi* (Lemoine, 1883.)

DISTRIBUTION.—Thanetian, Marne, France.

DIAGNOSIS.—Last upper premolar with a single, curved, multicuspidate shearing edge. Anteroexternal cusp or cusps small or vestigial. Edge not elevated posteriorly. Lower incisor probably compressed and with limited enamel band, but association not proven.

Neoctenacodon Lemoine is a strict synonym of *Liotomus* Cope. Both these authorities believed the tooth in question, type of *Neoplagiaulax marshi*, to be a lower premolar and urged its generic distinction on the basis of its manifest differences from the lower premolars of *Neoplagiaulax eocænus*. In his recent revision, Teilhard (pp. 15–16) recognized that the tooth is actually a last *upper* premolar and concluded that both generic and specific "denominations n'ont plus aucune raison d'être conservées." In this we cannot follow him. The type of this species differs in characters usually considered generic from all other known species of
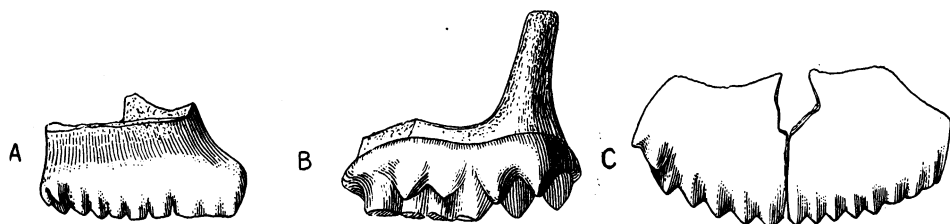
Fig. 39. Cernaysian multituberculates. Last upper premolars. External views. A, Cf. *?Ectypodus*, Teilhard's Type G. B, Teilhard's Type E. C, *Liotomus marshi*, lectotype, Teilhard's Type F. Lemoine Collection. Museum d'Histoire Naturelle, Paris. Six times natural size.

upper premolars, certainly could not pertain to the type species of *Neoplagiaulax*, and is probably to be associated with lower teeth which also show generic distinctions from *Neoplagiaulax*. The original definition was, to be sure, incorrect, but is not invalid on that account. Under the circumstances, however doubtful the status of the genus may be aside from this one tooth, one has no choice but to accept it.

The simple tooth which constitutes the type needs little description. It is about 7.0 mm. in length and has a single cutting edge with 14 projections, the anterior ones somewhat larger. Ridges from these projections run straight up on the tooth, but die out almost at once, leaving the greater part of the lateral surfaces smooth. The edge is evenly curved and does not rise to a point posteriorly. There is a single accessory cusp at the extreme anteroexternal angle of the tooth.

Even in the lack of association, it appears probable that the largest last lower premolars of the Thanetian belong to this species.[1] There are no other known lower premolars large enough to belong here, and the ratio P_4:P^4 would be 1.2, quite usual for a member of this family. There is a P_4 in Paris about 8.3 mm. in length and with 18 serrations, the last two very faint. In Berlin there is a specimen of the same length but with only 14 serrations clearly distinguishable. Both may well belong here, and we also doubtfully place here another tooth in Berlin which has 16 serrations and is notably larger, 9.6 mm. in length. These three specimens fall into a group differing sharply in size from those referred to *N. copei*, the largest of which is only 5.6 mm. in length.

Only one incisor is known which seems large enough to belong to this robust form. This is in the Depéret collection at Lyons and is a stout tooth, strongly compressed laterally, with limited enamel band covering about half the external face and about one fourth of the internal.[2] This
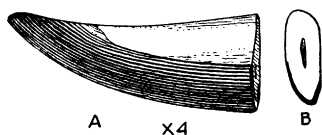

Fig. 40. Left lower incisor of a Cernaysian multituberculate. Depéret Collection. Université de Lyon. A, External view. B, Transverse section. Four times natural size.

tooth at once suggests *Eucosmodon*, but it is not in itself sufficient to establish generic identity. P^4 in the Torrejon material doubtfully referred to *Eucosmodon* differs from the type of *Liotomus* in being larger, more robust, with three antero-external cusps. It is a possibility that *Liotomus* and *Eucosmodon* are synonymous, but only future discovery can settle the point.

Teilhard suggests possible identity of this type of P^4 with *Ectypodus*, but it seems quite distinct, not only in its relatively huge size but also in its curved edge, not elevated posteriorly.

Liotomus marshi (Lemoine, 1883)

1883. *Neoplagiaulax marshi*, Lemoine, Bull. Soc. Geol. Fr., (3) XI, p. 261.
1884. *Liotomus marshi*, Cope, Am. Nat., XVIII, p. 691.
1891. *Neoctenacodon marshi*, Lemoine, Bull. Soc. Geol. Fr., (3) XIX, p. 289.
LECTOTYPE.—Last upper premolar. Lemoine also mentioned some other, uncharacteristic, material in his original description. Lemoine Collection, Mus. d'Hist. Nat., Paris.

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[1]Teilhard (p. 14) mentions these large lower premolars and figures one (p. 13), noting that they are distinct from *N. eocænus* and *N. copei*, but not suggesting identity with *L. marshi*.

[2]This tooth was mentioned but not figured by Teilhard, p. 14, footnote 1. He notes its resemblance to *Eucosmodon* but ventures no opinion as to possible association with other Thanetian teeth.

HORIZON AND LOCALITY.—Thanetian of Cernay-les-Reims, Marne, France.

DIAGNOSIS.—Length P^4 6.9 mm., 14 cusps in main row and one external accessory cuspule.

MONGOLIAN PALEOCENE MULTITUBERCULATES

Only one Paleocene deposit has yet been discovered in Mongolia: the Gashato Formation, explored in 1923 and again in 1925 by the Central Asiatic (Third Asiatic) Expedition of the American Museum of Natural History. The exact age of the formation is not certain, the fauna being aberrant. It contains, however, a genus, *Palæostylops*, allied to but more primitive than the Wasatch *Arctostylops*, a primitive uintathere close to one known from the Clark Fork (upper Paleocene), and two genera of multituberculates suggestive of a Paleocene stage of evolution. The deposit is thus almost surely Paleocene and possibly upper Paleocene. The 1923 collection contained a single multituberculate lower jaw without teeth (Matthew and Granger, 1925), but that of 1925 included partial dentitions of the same form and isolated teeth of another (Matthew, Granger, and Simpson, 1928).

TÆNIOLABIDIDÆ

Prionessus Matthew and Granger, 1925

1925. *Prionessus*, Matthew and Granger, Amer. Mus. Novitates, No. 189, p. 6.

TYPE.—*P. lucifer* Matthew and Granger, 1925.

DISTRIBUTION.—Gashato Formation, Mongolia.

DIAGNOSIS.—Dental formula $\frac{?.?.?1.2}{1.0.1.2}$. Basic cusp formula: M_1, 5:4; M_2, 3:2; M^1, about 6:7:5; M^2, 3:2—the anterior cusp of the midrow an obscure transverse ridge. Lower premolar much reduced, styliform, not shearing, roots connate. Internal cusp row of M^1 narrow and not reaching the anterior end of the tooth. All cusps relatively slender and subquadrate, as in *Ptilodus* but simpler. Species very small relative to other members of the Tæniolabididæ.

Most of what is known of this genus has recently been published. Matthew and Granger suggested that *Prionessus* is possibly an ancestral type of "catopsaline"—i.e., tæniolabid—and this surmise is supported by the later discoveries. The lower incisor, from its alveolus, must have been large and not strongly compressed; the ante-molar region is strongly abbreviated; P_3 is absent; P_4 is much reduced; the cusp number and arrangement, at least in the lower jaw, agree almost exactly with *Catopsalis;* the cusps are simpler than in ptilodontids; and the palate is without vacuities, as in *Tæniolabis.* .

If *Prionessus* is correctly referred to this family, it may be its most primitive known member. The premolars, especially important in this connection, are little known, but the lower premolar may be specialized
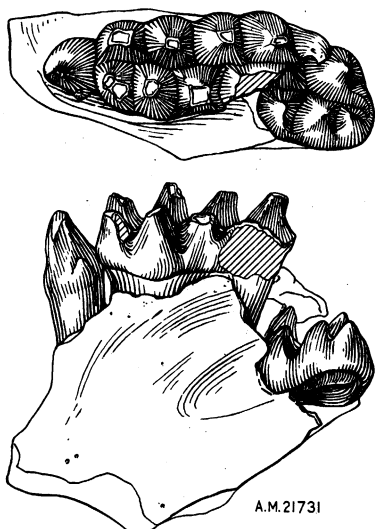
Fig. 41. *Prionessus lucifer*. Topotype. Left lower jaw with P₄, M₁₋₂. Crown and external views. Young individual with M₂ still in crypt. Five times natural size.
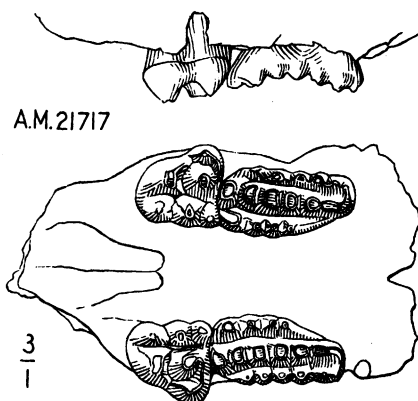
Fig. 42. *Prionessus lucifer*. Topotype. Palate with all molars, right external and crown views. Three times natural size.

in being more reduced than in *Catopsalis*. The molars, however, are primitive. The cusp number, as in *Catopsalis*, is smaller than in *Tæniolabis*. The internal row of cusps on M¹ is incomplete, surely a primitive character. The cusps themselves are unspecialized in form, and the occlusional relationships have departed less from the multituberculate norm than in *Tæniolabis* or *Sphenopsalis*, for example. The small size of the known species may also be primitive.

Prionessus is not an ancestral tæniolabid in any strict sense, for it is associated with a very advanced probable member of the family and, whatever the exact age, can hardly have been early enough to be ancestral to the Puerco *Tæniolabis*.

Prionessus lucifer Matthew and Granger, 1925

1925. *P. lucifer*, Matthew and Granger, Amer. Mus. Novitates, No. 189, p. 6.
    TYPE.—Amer. Mus. No. 20423, part of right lower jaw with alveoli of all teeth. Central Asiatic Expedition, 1923.
    HORIZON AND LOCALITY.—Gashato Formation, Shabarakh Usu, Mongolia.
    DIAGNOSIS.—Sole known species of the genus. Length M¹⁻² (topotype); 10 mm.

Sphenopsalis Matthew, Granger and Simpson, 1928

1928. *Sphenopsalis,* Matthew, Granger and Simpson, Amer. Mus. Novitates, No. 331, p. 2.

TYPE.—*S. nobilis* Matthew, Granger, and Simpson, 1928.

DISTRIBUTION.—Gashato Formation, Mongolia.

DIAGNOSIS.—Dental formula unknown. Basic cusp formula of M^2, 1:2:4. Cusps developed into narrow sharp crests, simply oblique in most cases but anterointernal cusp of M_2 (ref.) strongly crescentic, without any other complication. Known species large.

This genus is based on a few broken teeth, but it is so distinctive as to be quite unmistakable. Its affinities are inevitably dubious. What is known, however, permits tentative reference to the Tæniolabididæ, although the inclusion of this genus and of *Prionessus* involves a broader and less clear-cut conception of the family than might be based on *Tæniolabis* and *Catopsalis* alone. *Sphenopsalis* and *Tæniolabis,* indeed, represent opposite extremes of adaptation, and their wider systematic separation may be necessary when the former is better known.

A.M. 21736   A

A.M. 21715 B

A.M. 21713 C
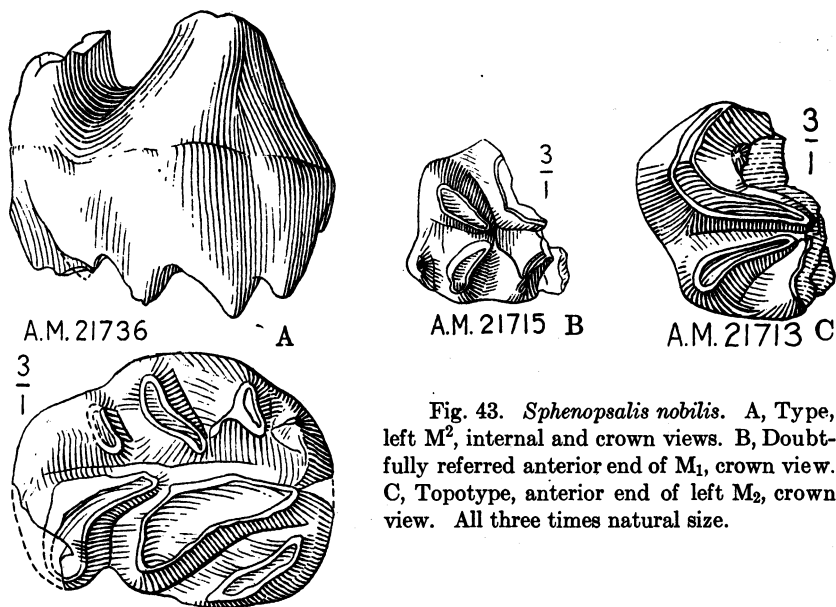
Fig. 43. *Sphenopsalis nobilis.* A, Type, left M^2, internal and crown views. B, Doubtfully referred anterior end of M_1, crown view. C, Topotype, anterior end of left M_2, crown view. All three times natural size.

In *Tæniolabis* the cusps are of a relatively heavy, quadrangular, grinding type; in *Sphenopsalis* they are slender, compressed, shearing. In the former they are almost as much complicated by secondary folds as in the ptilodontids and are relatively numerous; in the latter they are

extremely simple and are relatively few in number so far as known. But when unworn the cusps of *Tæniolabis* are fairly high, sharp, and crested, although not to the same degree as in the Mongolian form. *Catopsalis* is quite surely allied to *Tæniolabis*, but its cusps are more slender, less numerous, and have a more definite shearing function, thus somewhat more nearly approaching *Sphenopsalis*. An animal with much the structure of *Prionessus* might have given rise to all three of the larger genera.

Meniscoëssus is adaptively similar to *Sphenopsalis*, but its more numerous, more complex, strongly selenodont cusps are on the whole less similar in detail than are those of *Prionessus* or *Catopsalis*. The question remains open and might be settled by discovery of premolars and incisors.

In any event, *Sphenopsalis* is a very peculiar form and quite different from any other known multituberculate.

Sphenopsalis nobilis Matthew, Granger, and Simpson, 1928

1928. *S. nobilis*, Matthew, Granger and Simpson, Amer. Mus. Novitates, No 331, p. 2.

Type.—Amer. Mus. No. 21736, isolated left M^2. Central Asiatic Expedition, 1925.

Horizon and Locality.—Gashato Formation, Shabarakh Usu, Mongolia.

Diagnosis.—Sole known species of the genus. Length M^2 about 14 mm. Width, 11.0 mm.

RELATIONSHIPS AND DISTRIBUTION OF THE TERTIARY MULTITUBERCULATES

The American Paleocene multituberculates have been seen to belong to two very distinct groups, the Tæniolabididæ and the Ptilodontidæ. An attempt to relate these forms to the earlier Lance multituberculates and, through them, to the Jurassic plagiaulacids, was made by Osborn in 1893. He concluded that there were two main types of Lance multi-tuberculates, a smaller (*Cimolomys, Cimolodon*, etc. of Marsh) generically identical with *Ptilodus*, and a larger, *Meniscoëssus* Cope (*Dipriodon* Marsh) ancestral to *Tæniolabis* ("*Polymastodon*"). Further discoveries now necessitate some change in these views.

The various Cretaceous genera necessarily grouped under *Cimolomys* are certainly ptilodontids and possibly include the direct ancestors of *Ptilodus* and *Ectypodus* (although not of *Eucosmodon*) but the genus *Ptilodus* is distinct and does not occur in the Lance. · The lower jaws are very similar, as are those of all ptilodontids, but of the many Lance last upper premolars known, none could be included in *Ptilodus*. They

all differ generically in having but a single main row of cusps with one incomplete accessory row. As these must include the last upper premolars of the lower jaws formerly referred to *Ptilodus*. it is apparent that this reference cannot be sustained. In some respects they are closer to *Ectypodus*, although not generically identical. The small Lance and Paleocene multituberculates thus belong to distinct but possibly closely related genera of the same family. An attempt at more exact determination of ancestral relationships would be futile until more complete associated Lance upper dentitions are known.

The indication of special affinity between *Tæniolabis* and *Meniscoëssus* also seems to be opposed by later discoveries. The evidence has never been presented in much detail, but may fairly be said to be chiefly that the molar cusps of *Tæniolabis* retain traces of a selenodont ancestry (Osborn and Earle, 1895, p. 15), that the cusp formula is not far from that of *Meniscoëssus* (pp. 14–15), that the premolars of *Meniscoëssus* appear to have been somewhat reduced (Osborn 1893, p. 319), and that *Meniscoëssus* is a relatively large form. It is also necessary to remember that at that time *Tæniolabis* was considered as the latest known multituberculate. The more detailed zoning of the Paleocene since attained has shown that *Tæniolabis* occurs only in the lowest Paleocene, the Puerco. It hence immediately followed the Lance or even, according to the suggestion of Matthew (with which we are not in agreement), may be contemporaneous with the latter. In any event the time break between *Meniscoëssus* and *Tæniolabis* is so small, the morphological break so large, that this alone makes a directly ancestral relationship entirely impossible.

Even aside from this, there now seems no good reason for considering the two genera as especially related. *Tæniolabis* was undoubtedly derived from a ptilodontid. This was the essential feature of Osborn's discovery, and our work amply supports it, but *Meniscoëssus* cannot be the particular genus which unites the two families. It is evolving in the wrong direction. The ptilodontid shearing apparatus, almost unrecognizably changed in form and in function in *Tæniolabis*, is strongly and typically developed in *Meniscoëssus*. The molar cusps of *Tæniolabis* retain traces of the selenodont ancestry, but they are losing their crescentic character, whereas in *Meniscoëssus* this character is becoming more accentuated and the cusps are more highly crescentic than in any other known multituberculate. This genus, far from showing a *Tæniolabis*-like broadening and overlap of the cusps, represents the extreme of the opposite tendency. M^2 does not show any advance toward the broadening of the inner rows and reduction of the outer, so character-

istic of *Tæniolabis*.[1] The incisors of *Meniscoëssus*, also, are specialized in a direction diametrically opposed to *Tæniolabis*. They are slender, pointed, laterally compressed teeth with completely enameled crowns and with no enamel band on the intra-alveolar portion, no excessive wear at the apex, and no long-continued growth. The ancestry of *Tæniolabis* must be sought in some probably mid-Cretaceous ptilodontid, near the origin of the latter from plagiaulacids or the like, and the tæniolabids are probably immigrants when they first appear in North America.

The remark of Matthew that the "distribution of the species of [multituberculates] . . . is peculiar" in the American Paleocene (1897, p. 265) may be repeated with even greater force. In 1895, when Osborn and Earle wrote, it was still possible to regard the highly specialized *Tæniolabis* as the last survivor of its order. It is now known, however, that it not only occurs earlier than the more primitive of the Ptilodontidæ, but is even earlier than the less specialized genus of its own family, *Catopsalis*. Within the Ptilodontidæ the specialized *Eucosmodon* first appears at an earlier time than the more primitive *Ptilodus*. These anomalies are due in part to migrations between different regions, our materials being from a relatively small area, in part (as almost surely in the cases of *Ptilodus* and *Eucosmodon*) to differences in facies of the fossiliferous formations, causing absence in a given deposit of animals which were nevertheless present in the general region, and, finally, also no doubt in part to mere accidents of collecting. In no case, except doubtfully for some species of *Eucosmodon*, do we find any species which are probably or even possibly ancestral to any known species of a later horizon.

What little can be inferred as to relationships between the multituberculates of the different continents, North America, Europe, and Asia, has been sufficiently considered above. The remains outside of North America are too scanty to serve as a basis for any very far-reaching deductions.

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[1] With only isolated material for comparison, it was impossible to anticipate the anomalous arrangement of the upper molars of the Ptilodontidæ, and in Osborn's figures (1893, Pl. VII, Figs. 4 and 8) M^1 is placed on the wrong side. His left M^1 is really from the right side, and *vice versa*.

The known distribution is summed up in the following table:

North America	Paleocene			Eocene	
.	Puerco	Fort Union	Paskapoo	Wasatch	
		Torrejon	Tiffany	Sand Coulee	Gray Bull
Tæniolabis	——				
Catopsalis		——			
Ptilodus		——	....?.....		
Ectypodus					
Eucosmodon	——		....?.....		
New Genus					——

France			Thanetian	Sparnacian	
Neoplagiaulax			——		
Liotomus			——		
		?		?	

Mongolia		Gashato	
Prionessus		——	
Sphenopsalis		——	

The Fort Union and Paskapoo probably have a longer time range than is indicated by this table, only the accepted ages of the particular horizons from which multituberculates are now known having been taken into consideration. Some teeth, probably of Tiffany-Clark Fork age, indicate the probable presence in the Paskapoo of *Ptilodus* and possibly also of *Eucosmodon*, but the specimens so far known are too imperfect for certain identification.

REMARKS ON THE AFFINITIES OF THE MULTITUBERCULATA

The problem of multituberculate affinities has been treated rather fully elsewhere (Simpson, 1928), and it is not necessary to go into great detail here. The joint conclusion of the present authors is the same as that previously expressed by each of us singly, and the new evidence here adduced was taken into consideration in the work cited, although

not there given in detail. Among the many opinions which have been expressed since the first multituberculate was described over seventy years ago, the most striking are: (1) that they were ancestral to some or all diprotodonts (Falconer, Cope, 1884); (2) that they were diprotodonts but not ancestral to later forms (Gidley); (3) that they were an extinct group of marsupials (Owen, Marsh, Osborn, 1888); (4) that they were ancestral to the monotremes (Cope, 1888, Broom); (5) that they were prototherians but not necessarily ancestral to the living monotremes (Osborn, 1907); (6) that they were ancestral to both monotremes and marsupials (Hennig); (7) that they were ancestral to the placental mammals (Hinton); (8) that they were ancestral to rodents and perhaps to some other forms (Forsyth Major, Ameghino); and (9) that they represent a separate subclass not ancestral nor belonging to any other larger or smaller group of mammals, but having advanced beyond the remote, possibly reptilian, common ancestry about as far as have the marsupials as a whole (Granger, Matthew,[1] Simpson). The most orthodox view at present is that they are either non-ancestral marsupials or ancestral monotremes. After the careful work of Broom (especially 1914) and the recent vigorous claim of Abel that *Desmostylus* is an actual intermediate form, the theory of monotreme relationship is especially worthy of consideration.

Five chief lines of evidence are available:

1. Morphology of the teeth.
2. Histology of the teeth.
3. Structure of the skull.
4. Structure of the skeleton.
5. Distribution and evolutionary history.

1. The morphology of the teeth is unique. The closest approach, as Forsyth Major and M. A. C. Hinton have insisted, is seen in some rodents, but even here the resemblance does not go beyond the possession of enlarged incisors and of elongate molars with numerous cusps. The resemblances are surely due to similar habitus only. The dental formulæ are different and not derivable from each other; the detailed structure of the teeth is very different. The skull and lower jaw are fundamentally unlike those of any rodent. Even the distant resemblance in the teeth is seen only in rodents which occur late in geological time. The first known rodents, contemporaneous with the last known multituberculates, are even less like the latter than are recent rodents. Furthermore, these earliest rodents strongly support the view, which rests on the most ex-

[1]Matthew, 1915, p. 263, footnote 75; 1928, p. 949.

haustive research in rodent anatomy and history, that this group had an ultimate common root with the other placentals—and that the placentals as a whole were derived from the multituberculates (although even this has been claimed) could hardly be urged by anyone really familiar with the latter group. The multituberculates took the ecological position of the rodents in the Mesozoic and especially in the Paleocene, but there is no real zoological affinity.

On the other hand, the cheek tooth structure has been claimed by Cope and by many writers after him to be comparable with that of the monotremes and to indicate relationship with this group. Closer analysis, however, shows that the teeth not only are inadequate evidence of this view (as first recognized by Osborn) but that they strongly, even conclusively, oppose it. Broom (1914), although strongly favoring ancestral relationship to the monotremes, does not lay emphasis on the tooth structure.

2. The histology of the teeth, which has been described in part by Carter (1922) and which is clearly brought out in his thin sections and in others studied by us, is highly characteristic and important. The enamel is penetrated in greater or less degree by tubules from the dentine, a character almost universal in marsupials and also seen in many placentals of various orders. This character is not in itself decisive as to relationships, since tubular enamel is either primitive for mammals as a whole or else has often been independently acquired, and we cite it chiefly to point out that it does *not* indicate marsupial relationships, as might be thought. More important is the fact that etching brings out certain remarkable crescent-shaped figures, apparently sections of spiral bands (Carter), which are dilated at the ends and often enclose granular areas. This pattern, with numerous generic variations, seems to be characteristic of the order but occurs in no other known mammals. Here as elsewhere the multituberculates are distinguished by important, unique characters, developed on a substratum consisting only of the minimum common mammalian heritage. In passing it may be pointed out that there is no trace of the very characteristic rodent enamel character, and that *Desmostylus*, the enamel of which we have also studied, is equally characteristic and distinct.

3. The skull structure, first shown in its broader features by Gidley, was studied in more detail by Broom, who refuted Gidley's suggestion of marked marsupial resemblance in this region, and advanced it as his chief argument for monotreme ancestry. It has elsewhere been pointed out that the resemblances to monotremes, undoubtedly present, are

either primitive characters or else superficial and open to an entirely different interpretation (Simpson, 1928). The most important feature with respect to relationship to later marsupials or placentals is the position of the glenoid fossa and of the ear region. Even in the latest multituberculates this is substantially as in the cynodont reptiles, and such modification as has occurred is clearly quite the opposite of that in marsupials or placentals.

4. The chief new evidence in the present paper concerns the postcranial skeleton. Its importance is mainly in showing that the multituberculates cannot be ancestral or closely related to monotremes. Different as they are, the skull and teeth might be considered as equivocal, since in the living monotremes these parts are highly specialized in various ways and might be supposed to be unsafe bases for a positive conclusion as to *absence* of relationship. The limbs, however, are hardly open to such objections. They, too, naturally show a degree of specialization; but the myological and osteological researches of many workers have shown that their chief peculiarities in the monotremes are due to the retention of many of the characters in which the cynodont reptiles differ from the higher mammals. The multituberculates do not retain these same characters. They are clearly on a higher evolutionary plane than the monotremes in so many and such involved features of limb and girdle structure that the principle of irreversibility of evolution cannot be conceived of as open to exception in this case. The more primitive postcranial skeleton of the monotremes cannot be derived from the more advanced skeleton of the multituberculates. The limb structure of the latter is peculiar, it is specialized in its own way, it does not indicate relationship to the Metatheria in a taxonomic sense, but the degree of evolution is metatherian. The posture of the monotremes would also seem to be inherited in large part from the reptilian ancestry, and here again the multituberculates are more highly evolved.

5. The geological distribution and evolutionary history of taxonomic groups are as much "characters" as are any anatomical peculiarities, and, in view of the great changes which frequently take place in geologic time, are always of vital importance in classification, although too often neglected or undervalued by students of recent mammals. In the Multituberculata we have one of the greatest of all mammalian orders. World-wide in distribution (for they almost surely occurred also in Australia and South America although not yet known in these two land masses), they appear in the Rhætic and do not disappear until after the beginning of the true Eocene—a known range greater

than that of any other mammalian order. They are the first known mammals to appear in the geological record. In the Jurassic they occur together with other and quite different mammals which resemble the later marsupials and placentals in many respects and which appear to be structurally ancestral to both of the latter groups. Following the multi-tuberculate stock on the one hand and the marsupio-placental stock on the other into the Paleocene, we see that each makes great strides in development and in differentiation, and that each is following its own path, diverging rather than approaching or paralleling one another, but diverging from a point which clearly lies far back of the upper Jurassic. Nor do the multituberculates approach or parallel the monotremes in the course of their evolution—the later forms are just those in which we know the general structure to have been much more advanced than in the monotremes.

Whether on the basis of anatomical structure or of what is known of evolutionary history, the point of divergence of the three groups, multi-tuberculates, monotremes, marsupio-placentals, must have been in the Triassic, at latest, and must have been in a group of animals which, by our present definitions, would necessarily be classified as reptiles. Most of the characters which tie these three great stocks together do, in fact, occur in the cynodont reptiles, however typical these characters may be of modern mammals as opposed to modern reptiles. It may be urged that this is a polyphyletic view of mammalian origin and that it logically necessitates either referring monotremes and multituberculates to the Reptilia (or to a new class) as distinct orders, or referring the cynodonts to the Mammalia. This, however, would be a mere quibbling over terms. Whatever the ultimate logical aim of classification, the first necessity is that it should be practical. It is used as a means to express truths or what are believed to be truths, but it has no objective reality. Whether we conceive of mammals as derived through three different lines from a circumscribed group of advanced reptiles or by the same three lines from a similar group of earliest mammals, the essential unity of the Class Mammalia is not questioned. To transfer the cynodonts to the Mammalia would simply increase our difficulties by necessitating that a line be drawn at the beginning of the cynodont group, at present much less sharply limited than the cynodont-mammal line, and to place the cynodonts and their allies in a new class, as has been done by at least one student, increases the difficulties exactly two-fold without any practical gain.

In conclusion, it seems most in keeping with what is now known of

them to place the multituberculates in a single order, Multituberculata, of a distinct subclass of the class Mammalia. This subclass may properly receive the name Allotheria of Marsh, originally applied to the order.

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