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Leptacodon, an American Paleocene Nyctithere (Mammalia, Insectivora)

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INTRODUCTION

The late Paleocene American insectivore genus *Leptacodon* was named and described as a member of the family Leptictidae by Matthew and Granger (1921, pp. 2, 3) on the basis of a lower jaw and crushed rostrum of a single individual, of which only the lower jaw and dentition were completely freed from the surrounding mudstone matrix. Recent work suggests that the genus may be more similar to one or another of the erinaceid-like insectivores of the American and European Paleocene and Eocene than to the leptictids (McKenna, 1960a, 1960b; Tobien, 1962; Russell, 1964; Robinson, MS).

Additional preparation of the type specimen (fig. 1) of the type species, *Leptacodon tener,* reveals many previously unknown details about the upper dentition. As Matthew and Granger noted, the type, A.M.-N.H. No. 17179, is badly crushed and is from a young adult with incompletely erupted P^4_4, but it has been possible to illustrate each upper tooth separately, combining the results in a single illustration (fig. 2). The depicted orientation of the teeth and the curvature of the dental row are entirely my own estimates, but the sequence of teeth and degree of separation of the teeth anterior to P^4 are believed to be accurate. In view of the phylogenetic significance of *Leptacodon* and the in-

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creased tempo of revisionary work on various primitive erinaceoids and soricoids, the reconstruction and a few comments are presented here in order to facilitate the research of others. Although *Leptacodon* has often been discussed, the discussion has frequently rested on referred species. No illustration of the upper dentition of the type species has previously been published.

The cusp nomenclature employed in this paper is adapted from that of Van Valen (1966, pp. 7–9). The abbreviations used are:

A.M.N.H., the American Museum of Natural History
C.M., Carnegie Museum, Pittsburgh
U.S.N.M., United States National Museum, Smithsonian Institution
Y.P.M., Peabody Museum of Natural History, Yale University

I am indebted to Drs. Leigh Van Valen, F. S. Szalay, R. E. Sloan, and Peter Robinson for comments and criticism. Mr. Chester Tarka prepared the illustrations with his usual virtuosity.

DESCRIPTION

MATERIAL: A.M.N.H. No. 17179, crushed rostrum with complete left upper dentition, fragmentary right anterior upper dentition, and fragmentary lower jaws with left M_1–M_3, right P_3–M_2, half of M_3.

LOCALITY: Mason Pocket, Tiffany Beds (?San José Formation), sect. 20, T. 33 N., R. 6 W.; north of Tiffany, La Plata County, Colorado.

AGE: Late Paleocene, Tiffanian.

The left upper dental series is preserved as a continuous sequence of teeth in crushed and rotated fragments of the maxilla and premaxilla. Parts of the right dental series are also preserved but have been transported along several planes of slippage to points some distance from their original positions.

For convenience and in order to avoid a built-in taxonomic bias, the teeth anterior to P^4 have been labeled from front to rear: A, B, C, D, E. A and B are single-rooted teeth; C, D, and E are double-rooted. All teeth are assumed here either already to have replaced deciduous predecessors at the time of the death of the individual or to belong to an animal the anterior teeth of which were not replaced in late ontogeny. M_3^3 were in use at death, but A and P_4 were not fully erupted, thus indicating a young adult. That A is a permanent replacement for B has been considered but rejected.

Right P^4–M^3 have been moved to the rear along a sagittal slippage plane, so that right P^4 lies opposite left M^1, right M^1 opposite left M^2, and right M^3 well to the rear of left M^3. A mashed cusp of right E lies dorsal to the root of the paracone of right P^4, but right D is closely

appressed to left D at present, suggesting a fracture and substantial postmortem separation of right D from right E. The left maxilla is crumpled anterior to left E, rotating left D almost at right angles to its position in life and medially displacing left C. The right dental series anterior to right D has been pulled apart, and right A, right B, and right C have been rotated to the left side of the animal in a symmetrical relationship with left A, left B, and left C. This separation has a possible significance, in that the separation may have occurred at the maxillary-premaxillary suture, and therefore right C and left C may be double-rooted canine teeth, but this question is far from solution.

Both right A and left A are still not fully erupted (if it be assumed that they have not been crushed back into their alveoli) and are closely appressed to right B and left B, respectively. The crowns are simple but are not identical. Right A possesses a crested tip of its crown, whereas left A has a simple conical apex. Neither tooth has a heel cusp. The root is single and approximately the same size as the root of right B and left B. Presumably, the difference between the crowns of right A and left A can be ascribed to chance variation; if not, then two kinds of incisor-like teeth occur anterior to B.

Right B and left B are distinguished by the presence of a small heel cusp and by the hooked curvature of the laterally compressed crown, which foreshadows the morphology of the crown of C. B has a single, long root, however, in contrast to the shorter, double-rooted condition of C.

C is double-rooted[1] and may be described as premolar-like, but it is possibly a double-rooted premolariform canine similar to the canines of various erinaceids. If it is the canine, however, the number of possible premolars would be three rather than the usual four in a Paleocene mammal, P^1 being presumed missing. A possibility more favored here is that C is P^1, the canine being either absent or represented by A or B, probably the latter.

D is present on both right and left sides. It is double-rooted, with the high apex ventral to the anterior root. The rounded anterior surface of the paracone is convex forward; the posterior edge is a nearly straight cutting crest which dies out dorsally near the base of the cusp.

[1] In *Macrocranion* of the German Lutetian all teeth anterior to P^4_4 are single-rooted, and there is a problem of homology of the anteriormost upper teeth. Possibly B of *Leptacodon* is the same as the large tooth identified by Tobien (1962) as the canine of *Macrocranion*. If so, the upper incisors of *Leptacodon* were relatively larger than those of *Macrocranion*.

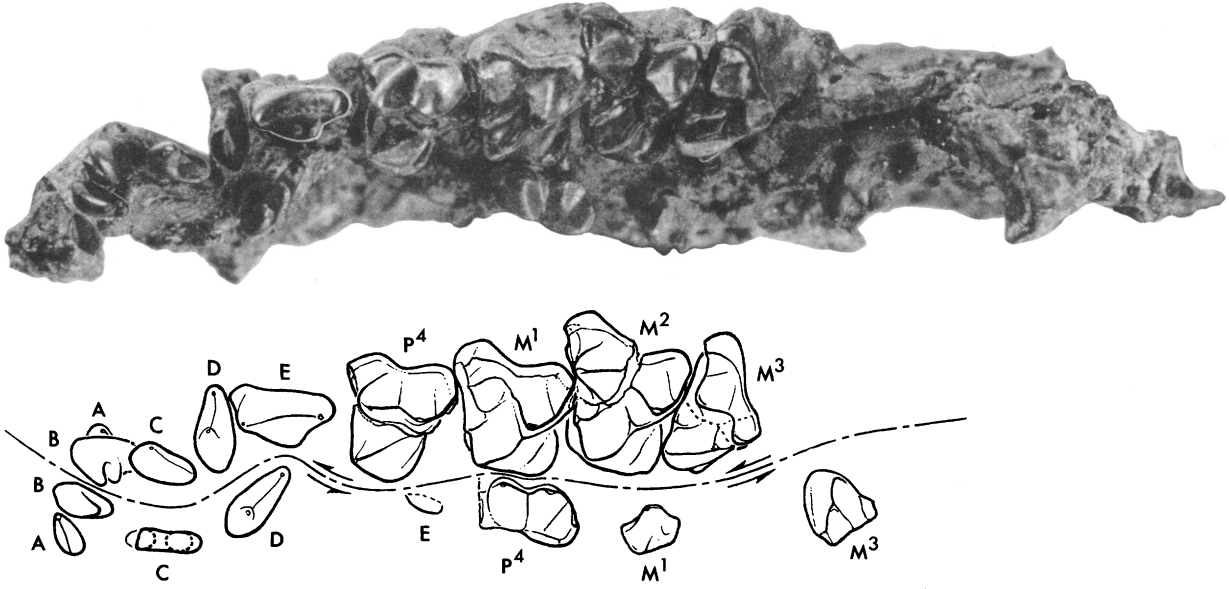

FIG. 1. Upper dentition of the type specimen, A.M.N.H. No. 17179, of *Leptacodon tener* Matthew and Granger, 1921. *Above:* Photograph of crushed rostrum as found in matrix of Mason Pocket. *Below:* Diagrammatic representation of the dentition as found, with position of left-lateral fault indicated by arrows. A, B. Single-rooted teeth. C–E. Double-rooted teeth. P^4–M^3. Fourth premolar to third molar, inclusive. Both $\times 13$.

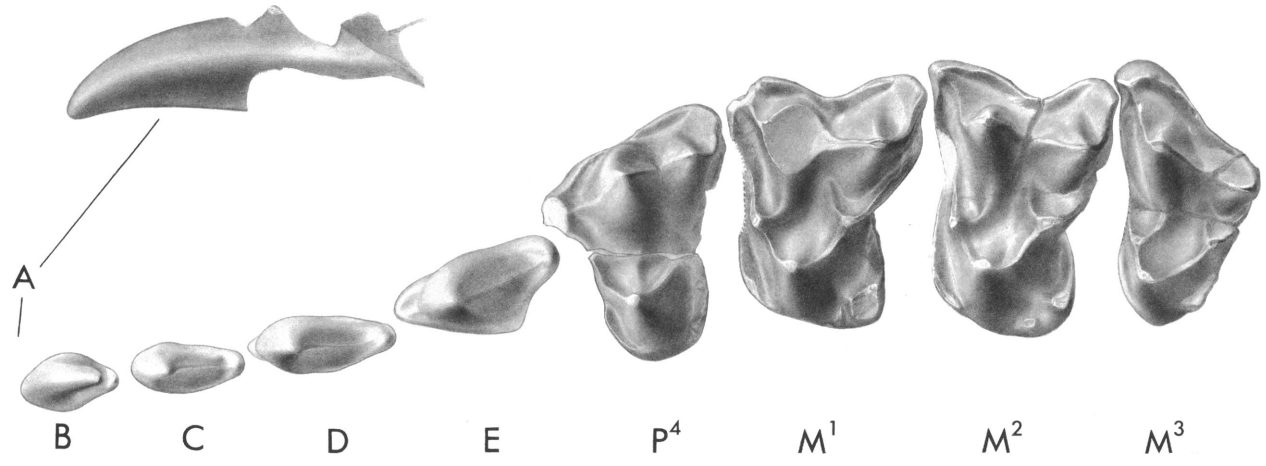

FIG. 2. Upper dentition of the type specimen, A.M.N.H. No. 17179, of *Leptacodon tener* Matthew and Granger, 1921, the type species of *Leptacodon*. A, B. Single-rooted teeth (inset, above, showing side view of A). C–E. Double-rooted teeth. P^4–M^3. Fourth premolar to third molar, inclusive. All teeth drawn separately; orientation, but not sequence, reconstructed. All ×20.

A small but distinct heel cusp lies at the rear of the tooth, ventral to the posterior root. Presumably D is P^2.

Left E was accidentally destroyed in the final stages of preparation, but fortunately a photograph of it had been taken beforehand. The drawing of it (fig. 2) and these comments were made entirely on the basis of the photograph (fig. 1). There is essentially a single cusp, the paracone, preceded and followed by low stylar cusps on shelves, to which crests on the front and rear of the paracone connect. The lingual base of the paracone is swollen, suggesting an incipient protocone, but no apex is present, in contrast to *Scenopagus edenensis* of the Bridgerian (McKenna and Simpson, 1959, p. 3; McKenna, Robinson, and Taylor, 1962, p. 26), *Geolabis* (McKenna, 1960b, p. 140), or *Tupaiodon morrisi* (Matthew and Granger, 1924). As in all three genera just mentioned there is no metacone, only a strong posterior crest and stylar cusp. Because of breakage, the orientation of the tooth is not known with certainty, but there is no evidence for a constricted snout at this point as there is in *Geolabis,* the P^3 of which is rotated about 45 degrees at the point where the snout narrows, or in *Nyctitherium* (C.M. No. 13726), in which P^3 is rotated about 20 degrees. The number of roots cannot now be determined, but, judged from the small protoconal swelling, there was at least no need for a third root lingually. Presumably E is a P^3, appropriately structurally ancestral to erinaceoid P^3's in which a metacone is lacking but to which a third root and small protocone were added.

P^4 is apparently newly erupted and is not dP^4. It has a very high conical paracone, the posterior slope of which is crested, followed by a lower metacone the apex of which is continuous with the metastylar crest as in *Nyctitherium* (U.S.N.M. No. 17653) and *Saturninia.* The lack of incorporation of the metacone in the metastylar crest would have resulted in the condition seen in Four Mile material referred to *Entomolestes* (McKenna, 1960a, p. 59). Incorporation could have led to the condition exhibited by *Macrocranion, Scenopagus edenensis,* and advanced erinaceoids and soricoids. An intermediate condition is shown by A.M.-N.H. No. 59678, P^4–M^2 of an undescribed species of *Scenopagus* from East Alheit Pocket Quarry in the earliest Eocene Four Mile fauna of Colorado. A strong protocone juts anterolinguad, but there is no incipient development of conules. The preprotocrista and postprotocrista are quite strong, and a very weak third crest lies between them, running labiad from the protocone apex. A cingulum foreshadowing that of *Nyctitherium* nearly surrounds the tooth, but no hint of a hypoconal broadening is present and the precingulum is not broadened at the base of

the protocone. There are no labial stylar cusps between the parastyle and metastyle. The latter cusps are small, the (broken) parastyle is a low eminence set low on a shelf, and the metastyle is merely the termination of the metastylar crest from the metacone.

M^1 and M^2 are not so wide transversely as in *Scenopagus*. They are rather similar to each other in stylar features, there being no tendency toward an enlargement of the metastyle of M^1 and the nearby parastyle of M^2. *Leptacodon tener* is thus similar in this feature to *Nyctitherium* and cf. *Entomolestes nitens* of the American early Eocene and *Adunator* (a leptictid), *Adapisorex, Messelina,* and *Macrocranion* of the European

TABLE 1

MEASUREMENTS (IN MILLIMETERS) OF A.M.N.H. NO. 17179, TYPE OF *Leptacodon tener*

Length, left lower jaw, M_1–M_3	3.7
Depth, left lower jaw, below M_2	1.5[a]
Depth, left lower jaw, coronoid to base of angle	4.7[a]
Length, right lower jaw, five preserved cheek teeth	6.2
Length, entire upper dentition as reconstructed	8.5[a]
Length, P^4–M^3, as reconstructed	4.7

[a] A fully adult individual would have a slightly greater measurement.

Paleocene and Eocene. In *Scenopagus* and *Saturninia* the metastyle of M^1 and parastyle of M^2 are somewhat enlarged, and in *Geolabis* and *Ankylodon*[1] very much so. Both M^1 and M^2 of *Leptacodon tener* have the usual three main cusps, the paracone, metacone, and protocone, supplemented by strong "conules" at the junctions of the preprotocrista and postprotocrista with the paracingulum and metacingulum, respectively. The paracingulum of each tooth is confined to the anterolingual side of the paracone base and does not have a projection entering the trigon basin. The metacingulum, however, extends completely around the lingual base of the metacone. Although broken and lost on M^1, the paracone in both teeth was about the same size as the metacone, perhaps a bit larger. In agreement with *Nyctitherium* but in contrast to *Scenopagus,* the protocone is uncompressed—a condition no doubt related to the weaker transverse molar shear in *Leptacodon.* The precingulum and postcingulum are quite strong on both M^1 and M^2 but do not meet each other lingual

[1] The upper dentition of *Ankylodon* has never been described, although at least one partial palate has reposed in a museum case since 1901 (C.M. No. 430). The complete lower and most of the upper dentition of *Ankylodon* will be discussed in a separate paper.

FIG. 3. Fragmentary left lower jaw with M_1–M_3 of the type specimen, A.M.N.H. No. 17179, of *Leptacodon tener* Matthew and Granger, 1921. *Above:* Labial view. *Below:* Lingual view. Both ×10.

to the protocone and do not fill the interdental embrasure as in *Nyctitherium* (Y.P.M. No. 15251). The postcingulum is notably wide and posterolingually projecting, forming a shelf with a raised edge terminating lingually in a tiny hypocone without an anterobuccal link to the protocone base. This condition is clearly ancestral to the hypocone of *Nyctitherium* and perhaps of *Saturninia,* but is also similar to the hypo-

FIG. 4. Right lower jaw of the type specimen, A.M.N.H. No. 17179, of *Leptacodon tener* Matthew and Granger, 1921. *Above:* Occlusal view. *Below:* Labial view. Both ×10.

cone of Four Mile *Entomolestes* and to that of *Scenopagus.* There is but a single lingual root on M^1 and M^2, a contrast to *Geolabis, Lanthanotherium,* and the Recent Echinosoricinae.

M^3 is provided with a relatively very large parastyle, but *Geolabis, Saturninia, Nyctitherium* (Y.P.M. No. 15251), and probably *Scenopagus* have similar parastyles. In *Tupaiodon* and *Adapisorex* the M^3 parastyle is somewhat reduced; from *Proterix, Galerix,* and later echinosoricines it is virtually absent, or completely so. Clearly, the large M^3 parastyle of *Leptacodon* is a primitive feature; it is almost as striking a projection as that of the M^3 referred to *Gypsonictops* (Simpson, 1929, p. 137, fig. 53, pl. 32; 1951, p. 9, fig. 3), *Diaphyodectes* (Russell, 1964), or *Myrmecoboides,* but is larger than on the M^3 referred to *Procerberus* (Sloan and Van Valen, 1965, p. 225) or in *Prodiacodon* or Eocene and Oligocene leptictids. The metacone of M^3 is smaller than the paracone and occupies the posterobuccal corner of the tooth. No metastyle lies beside it. The conules are both strong, in contrast to *Nyctitherium* (Y.P.M. No. 15251) from which the M^3 paraconule is absent and in which the metaconule is reduced. The protocone is lower on M^3 than on M^1 or M^2 and the precingulum and postcingulum are reduced, the latter strikingly so in comparison with that of M^1 and that of M^2, as in *Nyctitherium.* The hypocone is thus functionally absent from M^3. As in M^1 and M^2 the buccal cingulum is adorned by no important stylar cusps other than the low but widely projecting parastyle at the anterior end. Specifically, no *Nyctitherium*-like stylar cusp is present at the posterobuccal base of the paracone. In contrast to *Geolabis,* there is only one lingual root. The lingual enamel base of the crown in all teeth from P^4 to M^3 overhangs the lingual root in a manner reminiscent of *Nyctitherium.*

The mandible and lower dentition of *Leptacodon tener* (figs. 3, 4) were not illustrated or discussed thoroughly by Matthew and Granger (1921) but were depicted in a line drawing by Simpson (1935, fig. 4) and discussed in somewhat greater detail by him (1935; 1937). To the comments previously made, it can be added that the type individual was young and the jaw depth had not yet reached its greatest value. Preparation of the left lower jaw suggests that the condyle lies higher than the position originally inferred, more or less as in *"Leptacodon" packi* Jepsen, 1930. In addition to previous comments on the dentition it should be noted that the entoconids and hypoconulids of M_1–M_3 are rather close together, and M_3 has a strong separate hypoconulid. It is not possible to determine whether P_1 was single-rooted and large as it appears to be in nyctitheres, *Creotarsus,* and *"Leptacodon" packi* (alveolus only). The metaconid of P_4 is smaller and lower, and the trigonids of

all teeth were lower, than in leptictids, and the similarities to *Entomolestes siegfriedti* noted by Simpson (1935) are real. Even closer similarities can be seen to *Nyctitherium* (Matthew, 1918, p. 605, fig. 34; P. Robinson, MS).

COMMENTS

The primary purpose of this paper is to place on record certain previously unavailable details of the dentition of *Leptacodon tener,* a late Paleocene insectivore often thought to be allied with the Leptictidae but now generally regarded as an early erinaceoid. The new information, moreover, suggests that *Leptacodon* is perhaps best classified as an early member of the Nyctitheriidae,[1] a family that is itself divergent from early erinaceoids. The fascinating problem of the origin of various lineages of the Soricoidea might well be discussed at this point, but that subject is deliberately placed outside the scope of this paper.

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[1] As the result of Robinson's (unpublished) work, I now recognize a restricted family-group taxon based on *Nyctitherium* and several referred genera.

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