MYLANODON ROSEI, A NEW METACHEIROMYID (MAMMALIA, PALAEANODONTA) FROM THE LATE TIFFANIAN (LATE PALEOCENE) OF NORTHWESTERN WYOMING

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ROSS SECORD, PHILIP D. GINGERICH, AND JONATHAN I. BLOCH

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Abstract — Mylanodon rosei is a new genus and species of late Paleocene metacheiromyid palaeanodont from a new late Tiffanian locality, Y2K Quarry, in the Clarks Fork Basin, Wyoming. The type is an adult dentary with P_4 and a molariform double-rooted M_1. This provides the first evidence that molariform teeth were retained in early Metacheiromyidae. A second specimen is a juvenile dentary with a partial P_3 and an unerupted P_4. This is the first juvenile dentition known for a Paleocene metacheiromyid. The new specimens enable determination of dental homologies. Reduction of teeth in early metacheiromyids took place from back to front, opening the characteristic posterior diastema. Both *Mylanodon* and *Propalaeanodon*, a slightly older metacheiromyid, are intermediate morphologically and temporally between the older Tiffanian epoicotheriid *Amelotabes* and the younger Clarkforkian and Wasatchian metacheiromyid *Palaeanodon*. *Propalaeanodon* has a single-rooted M_1, a derived characteristic not found in *Mylanodon*, suggesting that two lineages are involved and *Propalaeanodon* was not ancestral to *Mylanodon*.

INTRODUCTION

Palaeanodonta are a group of Paleocene, Eocene, and Oligocene mammals with numerous postcranial characteristics indicating a fossorial habitus. Digging specializations include short, robust forelimb bones, with restricted mobility and conspicuously enlarged areas for muscle attachment (Rose and Emry, 1983; Rose et al., 1992). Palaeanodonts are usually allied with either Xenarthra (Simpson, 1931; Szalay, 1977), Pholidota (Emry, 1970; Rose and Emry, 1993), or both (Matthew, 1918; Rose, 1978; Rose, 1979). Relationships between these taxonomic groups remain uncertain. We follow current practice and refer Palaeanodonta questionably to Pholidota.

Three palaeanodont families are now recognized: Escavadodontidae, Epoicotheriidae, and Metacheiromyidae. Escavadodontidae contains a single species from the late Torrejonian land-mammal age (middle Paleocene) of the San Juan Basin, New Mexico (Rose and Lucas, 2000). Epoicotheriidae is first represented by *Amelotabes*, collected just south of Croc Tooth Quarry in the Bighorn Basin, Wyoming (Fig. 1; Rose, 1978). It came from a stratigraphic interval at or near the level of the quarry itself, in the *Plesiadapis churchilli* zone (Ti-4) of the middle Tiffanian land-mammal age (late Paleocene; Fig. 2). Metacheiromyidae is first represented by *Propalaeanodon*
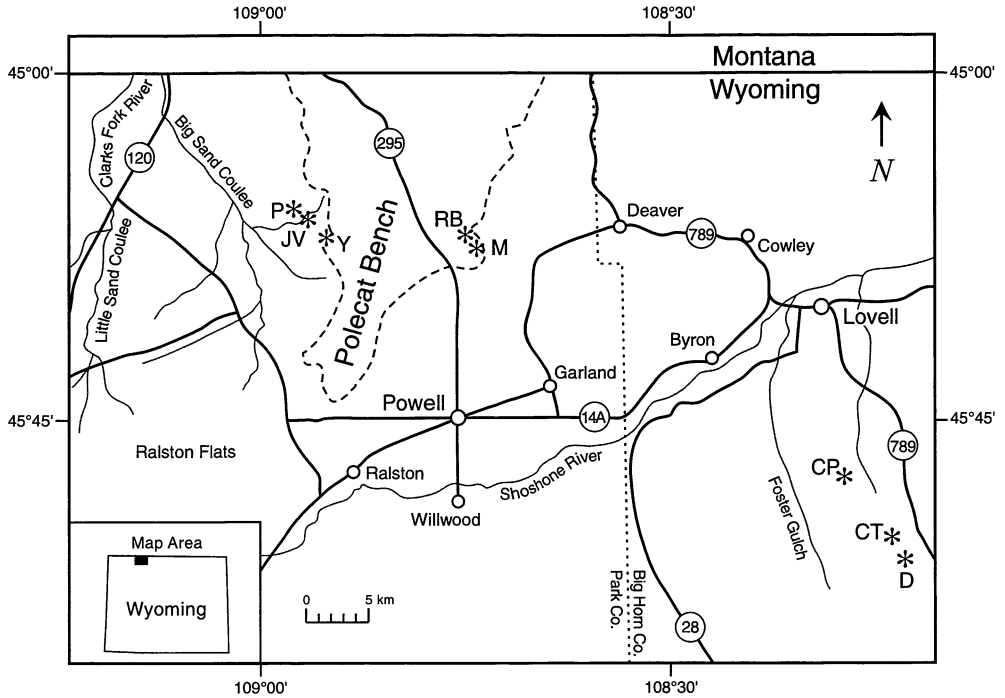
FIG. 1 — Location of some important Paleocene quarry sites in the Clarks Fork and northern Bighorn basins of northwestern Wyoming. The type and referred specimens of *Mylanodon rosei* described here are from Y2K Quarry. Abbreviations: *CP* = Cedar Point Quarry; *CT* = Croc Tooth Quarry; *D* = Divide Quarry; *JV* = Jepsen Valley Quarry; *M* = Mantua Quarry; *P* = Princeton; *RB* = Rock Bench Quarry; and *Y* = Y2K Quarry. Map adapted from Bloch et al. (2001).

from Jepsen Valley Quarry in the Clarks Fork Basin (Fig. 1; Rose, 1979). The quarry is within the *Plesiadapis fodinatus* zone (Ti-5) of the late Tiffanian (late Paleocene; Fig. 2). Tiffanian biozones are defined stratigraphically in Gingerich (2001).

Metacheiromyidae retain a more conservatively generalized mammalian postcranial skeleton than epoicotheriids, but have a more specialized and simplified dentition, while epoicotheriids retain a more generalized dentition, but have a postcranial skeleton more specialized for digging (Rose et al., 1992; Gunnell and Gingerich, 1993). Palaeanodont remains are rare in the Paleocene and the specimens described here represent some of the earliest metacheiromyid fossils known.

Specimens described here were recovered from Y2K Quarry, a new locality near the western edge of Polecat Bench in the Fort Union Formation of the Clarks Fork Basin (Fig. 1; Secord, 2002). Mammalian fossils are preserved in a thin siltstone layer (2-12 cm thick) along with snail shells and carbonized plant material. The site was discovered by R. Secord in the summer of 2000, and it has yielded more than 80 mammalian jaws and jaw fragments as well as hundreds of isolated teeth recovered by quarrying and screen-washing. Associated faunal elements and stratigraphic superposition in the sequence of localities along the western side of Polecat Bench indicate that Y2K Quarry is late Tiffanian in age, occurring in the *Plesiadapis simonsi* zone of the late Tiffanian (zone Ti-5; Fig. 2).

Y2K Quarry is about 80 m stratigraphically above Princeton Quarry, an important locality yielding a large mammalian fauna from the 'Silver Coulee beds' of Jepsen (1940) that lie to the west of Polecat Bench (Fig. 1; Rose, 1981). Princeton Quarry is late Tiffanian in age (zone Ti-5; Fig. 2), but has yielded only two palaeanodont humeri tentatively referred to *Propalaeanodon*

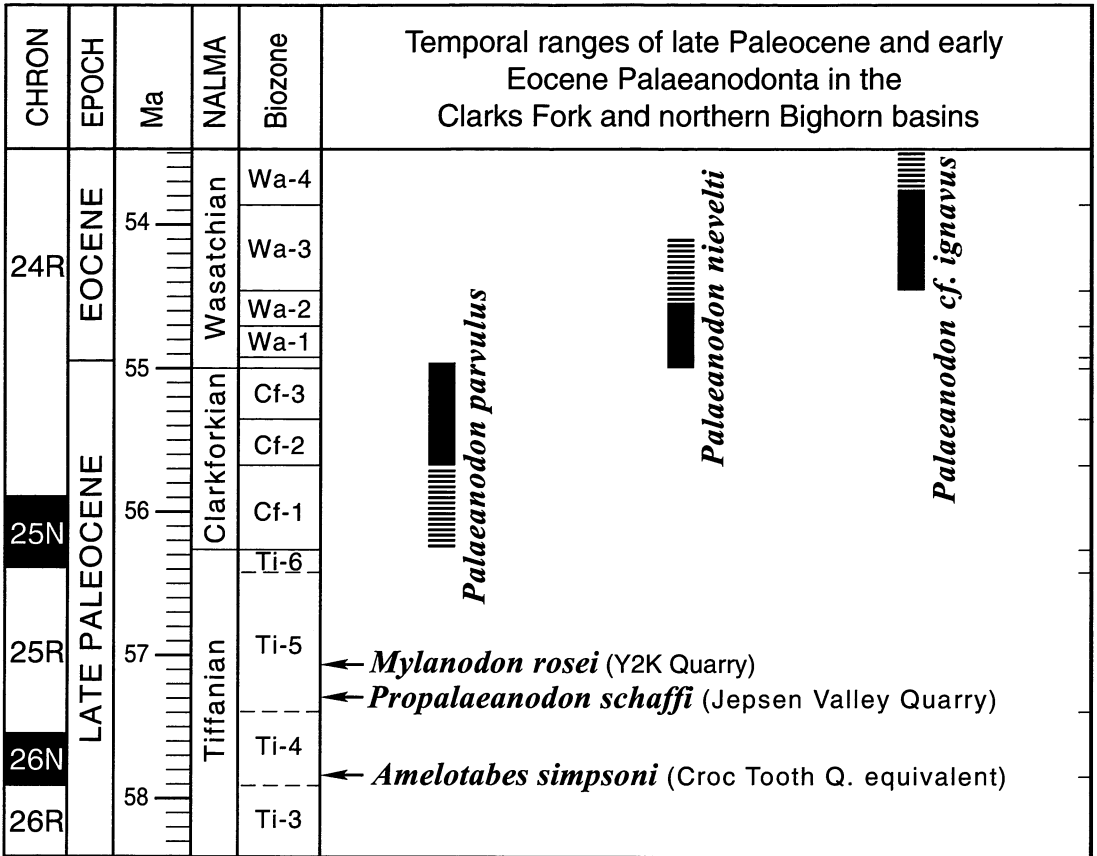| CHRON	EPOCH	Ma	NALMA	Biozone	Temporal ranges of late Paleocene and early Eocene Palaeanodonta in the Clarks Fork and northern Bighorn basins

FIG. 2 — Late Paleocene and early Eocene stratigraphic ranges of Palaeanodonta in the Clarks Fork and northern Bighorn basins. Biostratigraphy is from Gingerich (1989, 2000, 2001) and unpublished field work of R. S., calibrated temporally using the magnetostratigraphy of Butler et al. (1981, 1987) and the magnetochronology of Cande and Kent (1995).

schaffi (Rose, 1979; Rose, 1981). Jepsen Valley Quarry (Fig. 1; Schaff, 1985) yielded the type and only dentary of *Propalaeanodon schaffi* (Rose, 1979). Jepsen Valley Quarry appears to lie about 40 m stratigraphically above Princeton Quarry, but is below Y2K Quarry (Fig. 2).

The hypodigm of *Mylanodon rosei* includes both an adult and a juvenile dentary, the latter being the first juvenile metacheiromyid dentary described from the Paleocene. The only other described dental material that may belong to a juvenile metacheiromyid is a single unworn postcanine in a dentary fragment (UM 99720) from the Bridgerian (middle Eocene) that was tentatively referred to Metacheiromyidae (Gunnell and Gingerich, 1993).

We view *Amelotabes* as the most primitive late Paleocene palaeanodont, and consider it to represent the primitive condition of the dentition for both Epoicotheriidae and Metacheiromyidae. *Escavadodon* from the late Torrejonian (middle Paleocene) has postcranial specializations characteristic of palaeanodonts. It can be viewed as either the closest relative of Palaeanodonta or as the most primitive palaeanodont. Dental characteristics and some postcranial characteristics indicate possible affinity with insectivorous Leptictidae or Pantolestidae (Rose and Lucas, 2000).

INSTITUTIONAL ABBREVIATIONS

MCZ   — Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts
PU   — Princeton University collection at Yale Peabody Museum, New Haven, Connecticut
UM   — University of Michigan Museum of Paleontology, Ann Arbor, Michigan

SYSTEMATIC PALEONTOLOGY

Class MAMMALIA Linnaeus, 1758
Order ?PHOLIDOTA Weber, 1904
Suborder Palaeanodonta Matthew, 1918
Family Metacheiromyidae Wortman, 1903

Mylanodon, new genus

Types species.— *Mylanodon rosei*, new species.
Included species.— Genotype only.
Diagnosis.— Differs from all other Palaeanodonta in having (1) a molariform M_1 with a trigonid represented only by a protoconid and the talonid represented only by a hypoconid; and (2) a higher and more acute P_4, with a posterior vertical trough and a 'talonid.' Further differs from all Epoicotheriidae except *Dipassalus oryctes* in lacking enamel on postcanine teeth, and possessing a diastema between the last postcanine and the ascending ramus. Further differs from *Amelotabes* in having less complex post-canine teeth; longer intra-tooth diastemata; lacking M_3; having a diastema behind M_2; and having single-rooted P_2, P_3, and M_2.

Differs from other Metacheiromyidae and *Dipassalus oryctes* in having 6 postcanine teeth, with a double-rooted, molariform M_1. Further differs from *Propalaeanodon* in having a posterior diastema and in lacking M_3. Further differs from *Palaeanodon* in having a shorter posterior diastema and retaining M_2.

Etymology.— *Mylos*, mill, molar, grinding tooth; *an*, not, without; and *odous*, tooth (Gr., masc.). Name refers to the retention of broad *Amelotabes*-like molar teeth in this genus, while at the same time alluding, by adopting the nominal root, to conspicuous reduction of molars in contemporary *Propalaeanodon* and later *Palaeanodon*.

Mylanodon rosei, new species
Figs., 1-3, 4D

Holotype.— UM 109174, adult left dentary with partial P_4, M_1, and alveoli for P_2, P_3, and M_2. From Y2K Quarry (within UM locality SC-389), west side of Polecat Bench, Clarks Fork Basin, Wyoming.

Referred specimens.— UM 109530, juvenile left dentary with P_4 in a crypt in the jaw, the base of unerupted P_3, an associated partial crown of P_3, and alveoli for dP_{3-4}, and M_{1-2}. UM 110015 is a fragment of a right humerus.

Age and horizon.— Late Tiffanian *Plesiadapis simonsi* zone (Ti-5) of the Fort Union Formation in the Clarks Fork Basin, Wyoming (Gingerich, 2001).

Known distribution.— Y2K Quarry, Clarks Fork Basin, Wyoming.

Diagnosis.— As for the genus.

Etymology.— Named for Kenneth D. Rose of Johns Hopkins University in recognition of his many contributions to understanding of the evolution of Palaeanodonta.
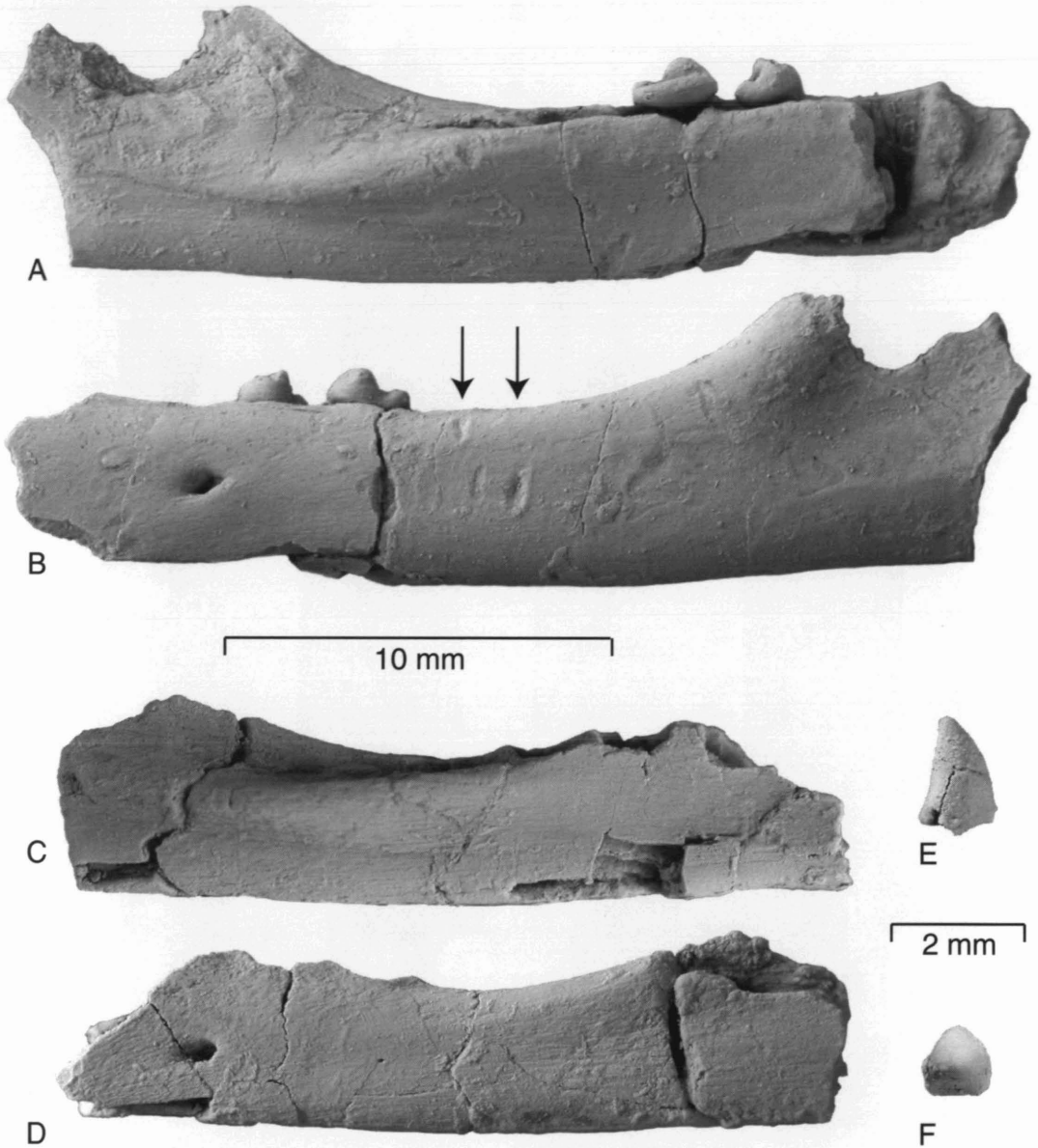
FIG. 3 — Photographs of holotype and referred specimen of *Mylanodon rosei*. A-B, UM 109174, left dentary (holotype), in lingual and labial views; arrows point to bite marks. C-D, UM 109530, left dentary (juvenile) in lingual and labial views. E-F, UM 109530, associated crown of P_3, in lingual and occlusal views, with anterior to right and top of page, respectively. Scale is in mm.

Description.— The dentary of the holotype contains a partial P_4, M_1, and alveoli for P_{2-3} and M_2 (Fig. 3A-B, 4A). It has a well developed medial buttress (a ridge present along the lingual face of the dentary) above an indistinct internal mandibular groove. A mental foramen is positioned below the diastema separating P_3 and P_4. A moderately long diastema is present between the M_2 alveolus and the base of the ascending ramus. Diastemata separate P_3-M_2 alveoli. Two parallel
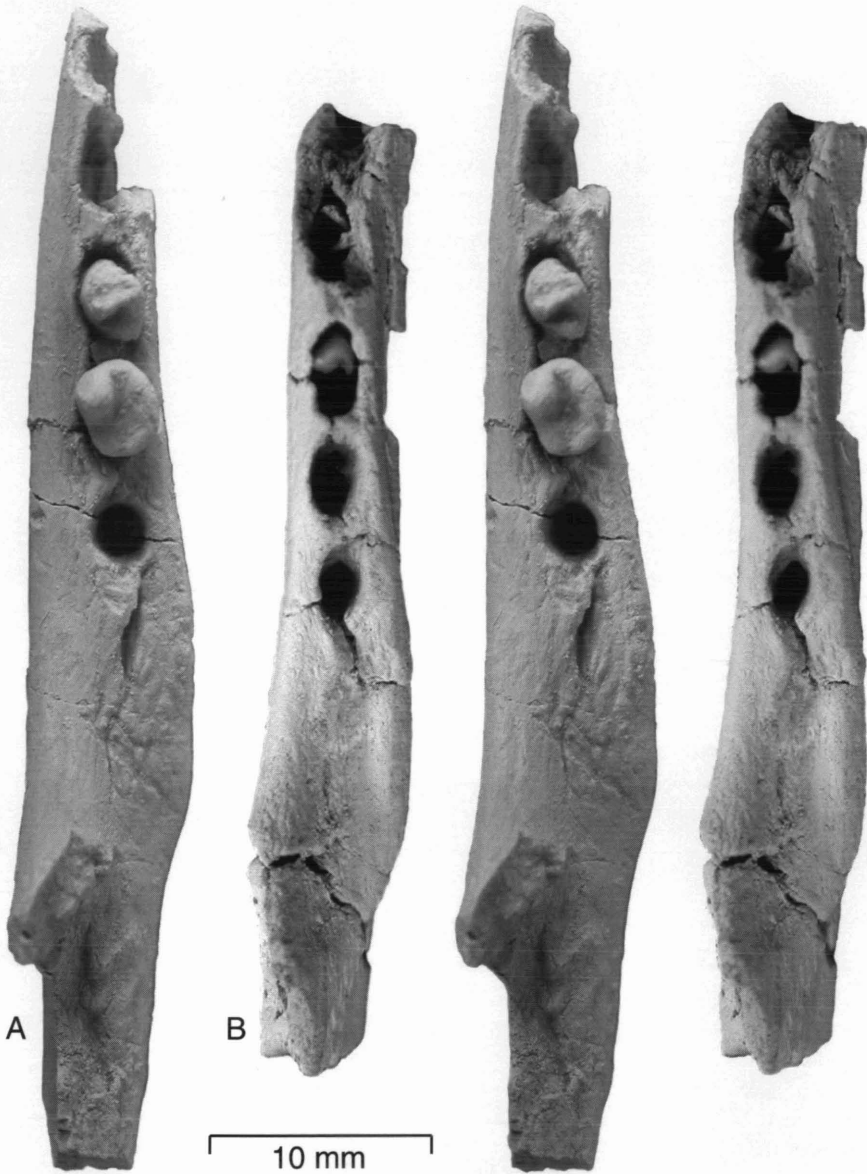
FIG. 4 — Stereophotographs of holotype and referred specimen of *Mylanodon rosei*. A, UM 109174, left
  dentary (holotype), in occlusal view. B, UM 109530, left dentary (juvenile), in occlusal view. Scale is in
  mm.

grooves that we interpret to be bite marks are present on the lingual surface of the dentary below
the alveolus for M_2 (Fig. 3).

The juvenile dentary (UM 109530) has the crown of P_4 preserved unerupted in its crypt in the
jaw, the base of an unerupted P_3, an associated P_3 partial crown, and alveoli for dP_{3-4}, and M_{1-2}
(Fig. 3C-F, 4B). The dentary is highly striated more or less parallel to its long axis, a feature
typical of incompletely ossified juvenile bone. A medial buttress is weakly developed and the
internal mandibular groove is indistinct. A mental foramen is situated below the posterior alveolus
of dP_3. A diastema is present between P_3 and P_4, but diastemata have not yet developed between
more posterior teeth. The juvenile dentary is smaller than the adult dentary (Table 1).

TABLE 1—Measurements of mandibles and teeth of *Mylanodon rosei* (UM 109174, 109530) and *Palaeanodon* cf. *P. ignavus* (UM 66243). All measurements in mm. Asterisk indicates estimate.

Tooth	Measurement	UM 109174 (holotype)	UM 109530 (juvenile)	UM 66243 (*P.* cf. *P. ignavus*)
P_3	Alveolus length	2.20	--	1.70
	Alveolus width	--	--	--
	Crown length	--	1.39*	1.57
	Crown width	--	1.10*	1.08
P_4	Crown length	1.74	1.70*	1.29
	Crown width	1.37	--	1.10
M_1	Alveolus length	1.80	1.70	1.80
	Alveolus width	1.20	1.10	--
	Crown length	2.15	1.50*	--
	Crown width	1.74	1.10*	--
M_2	Alveolus length	1.50	1.70	--
	Alveolus width	1.40	0.80	--
	Depth of dentary below M_1	4.50	4.20	6.40
	Maximum width of dentary	3.80	3.10	4.70

P_4 in the holotype is heavily worn (Figs. 3A-B, 4A). Comparison with the unerupted juvenile P_4 (UM 109530; Fig. 4B, 5, 6B) shows that occlusal wear reduced the principal cusp from an acute, pyramidal shape, to a lower, more rounded form. Comparison of cusp positions on P_4 with those of the P_3 of *Amelotabes* and with those of P_4 in the potential outgroups Leptictidae and Pantolestidae (Rose and Lucas, 2000), indicates that the principal cusp is a protoconid. A long vertical crest on the juvenile P_4 descends from below the protoconid apex along the lingual margin, where it is separated from the protoconid by a narrow vertical groove. Most of the crest is missing on the adult P_4, but enough remains to show that the ridge descended until it contacted the lingual side of a single-cusped 'talonid,' separated from the protoconid by the vertical trench. Figure 5 shows a composite reconstruction based on the morphology of P_4 in both specimens.

M_1 of the holotype (Fig. 3A-B, 4A, 7D) is simple, bunodont, and lacks enamel. A large protoconid and a small hypoconid rise from an otherwise nearly flat occlusal surface. A low, barely-discernable ridge follows the tooth's lingual margin from the protoconid to the hypoconid. A small flat surface that we interpret to be a wear facet is visible on the anterolabial surface of the protoconid. The M_1 root bifurcates distally into separate sockets (Fig. 6A). The crown of M_1 was partially dislodged from its alveolus during preparation. Comparison with the molar structure of *Amelotabes* (see below), however, leaves little doubt that the tooth was still in its original antero-posterior orientation.

An anterior portion of the juvenile dentary is broken open, revealing the base of an unerupted P_3 (Fig. 4B, 6B). A partial crown that appears to be the top of P_3 was found during preparation alongside the dentary in an inverted position (Fig. 5E-F). It probably is not part of a deciduous tooth, as it lacks the wear that might be expected for an erupted enamel-less tooth. P_3 is subtrigonal with an acute apex and flat posterior face. It appears to have been a single high cusp, similar in shape to the principal cusp of P_4.

Alveoli in the juvenile dentary are oval in outline, viewed occlusally, and taper ventrally (Fig. 4B, 6B). Small alveoli are present on the anterior and posterior sides of the P_4 crypt, indicating that dP_4 was double-rooted. The anterior margin of the P_3 crypt is mostly missing, but a small alveolus on its posterior margin clearly held a root of dP_3. Absence of most of the anterior crypt
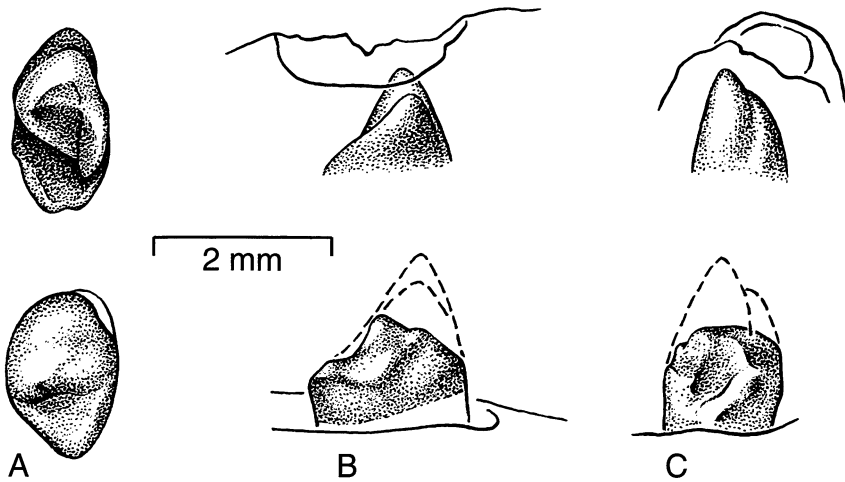
FIG. 5 — Composite reconstructions of the crown of P_4 in *Mylanodon rosei*, based on UM 109530 (juvenile; top) and UM 109174 (holotype; bottom). Drawings show occlusal (A), lingual (B), and posterior (C) views. Drawings of UM 109530 were made of tooth in crypt and are approximations. Scale is in mm.

means that we were unable to determine whether dP_3 was a single- or double-rooted tooth, although a gap between the anterior base of the P_3 crown and the basal crypt wall suggests a second root. In the juvenile specimen complete separation of M_1 roots had not yet occurred, but vertical ridges demarcating root boundaries are present on the lingual and labial surfaces of the alveolus. Alveoli for P_{2-3} and M_2 in the adult dentary held single, ventrally tapering roots (Fig 4A, 6A). Alveoli for P_{2-3} are oval in outline, like those of the juvenile, while the M_1 alveolus is round, unlike the oval M_1 alveolus of the juvenile.

Measurements of tooth crowns and alveoli are listed in Table 1.

DISCUSSION

Tooth Homologies

Determination of tooth homologies in metacheiromyids has been greatly impeded by the reduced number and simplified morphology of the teeth, and by uncertainties concerning the direction of tooth loss. Consequently, most descriptions of metacheiromyid dentitions refer to teeth posterior to the canine simply as postcanines. Fortuitous discovery of both adult and juvenile dentaries of *Mylanodon rosei* allows us to infer both tooth homology and direction of tooth loss for metacheiromyids.

The two unerupted postcanine teeth in the juvenile dentary had deciduous precursors, as discussed above, indicating that these teeth are premolars. There is no evidence, however, for precursors in the two posterior-most alveoli, suggesting that they held molars. Although it is conceivable that precursors were already replaced by permanent teeth, such a late stage of development for the two posterior teeth is unlikely given the early stage of development exhibited in the anterior premolars still in their crypts. Our interpretation is supported by the observation that leptictids, a probable sister group of Palaeanodonta (Rose and Lucas, 2000), have a dental eruption sequence of dP_1-M_1-M_2-M_3-P_2-P_4-P_3 (reconstructed from '*Ictops*' *bicuspis*; Slaughter et al., 1974). If this sequence is representative of Palaeanodonta, and either or both of the posterior teeth were premolars, the permanent tooth (or teeth) would still be in the crypt, because P_2 would still be unerupted. If either of the posterior teeth were premolars it would require the eruption of P_4 well before the
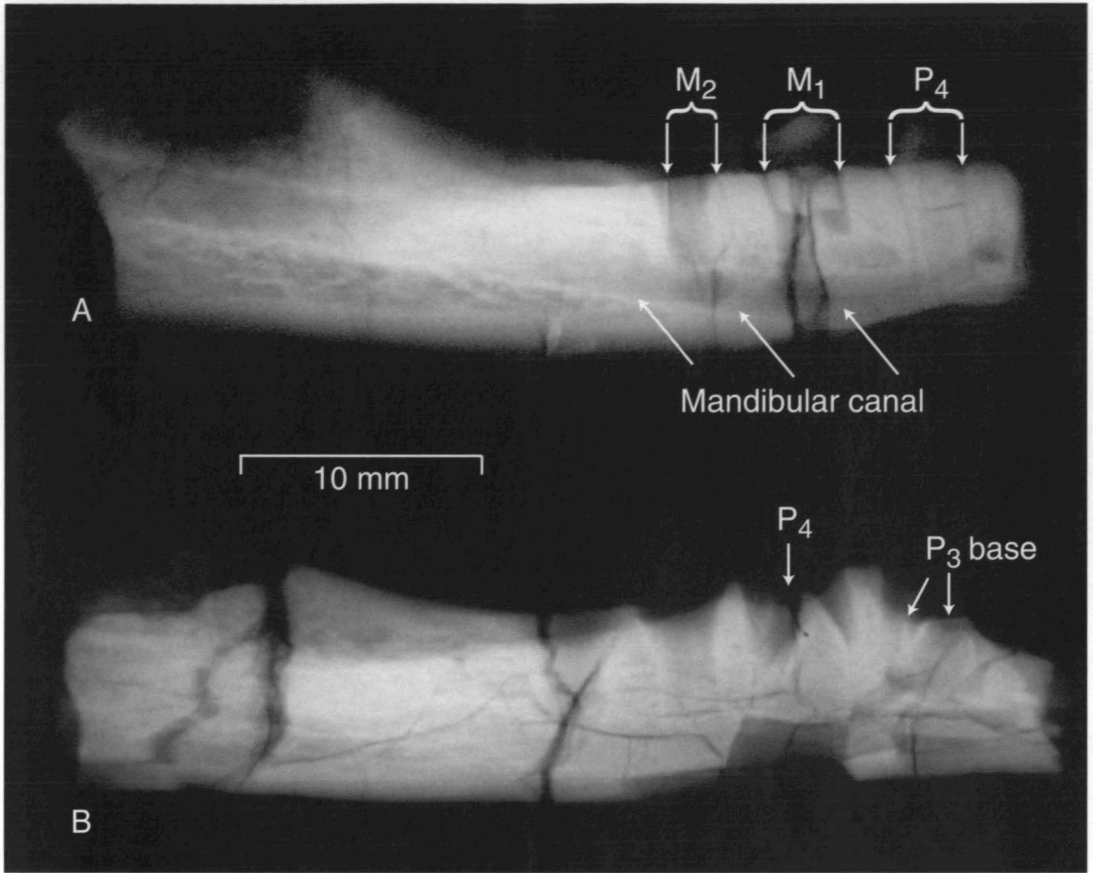
FIG. 6 — X-ray images of holotype and referred specimen of *Mylanodon rosei*. A, lateral view of dentary of UM 109174 (holotype) showing possible separation of P_4 roots, and distal bifurcation of M_1 roots. Arrows mark edges of alveoli. B, lateral view of dentary of UM 109530 (juvenile) showing P_4 in crypt and base of broken P_3. Scale is in mm.

anterior premolars that are still unerupted. For these reasons we believe it is unlikely that either of the posterior teeth had precursors, and we consider them molars. Our dental homologies are supported by the premolariform and molariform condition of P_4 and M_1, respectively, and by comparison with the more primitive, but closely related *Amelotabes* (Rose, 1978).

Amelotabes and *Propalaeanodon* have the general placental complement of seven postcanine teeth, which are recognizably four premolars and three molars (Rose, 1978, 1979), for a postcanine formula of 4:3. The total number of premolars in *Mylanodon* cannot be determined, but the number of molars is two, indicating that the number of postcanines was probably six, and the postcanine formula was probably 4:2. Thus tooth loss in early metacheiromyids proceeded from back to front. Retention of only five postcanine teeth in *Palaeanodon* (Rose, 1978, 1979) indicates that its postcanine formula was either 3:2 or 4:1. If there was a single direction of tooth loss in all of metacheiromyid evolution, then the postcanine formula of *Palaeanodon* was 4:1. This is consistent with the presence of a long posterior diastema following the last postcanine in *Palaeanodon*.

Palaeanodonts have been allied with both Xenarthra and Pholidota (Simpson, 1931; Szalay, 1977; Emry, 1970; Rose and Emry, 1993; Matthew, 1918; Rose, 1978; Rose, 1979). While absence of teeth in all known fossil and extant Pholidota precludes dental comparison, the simple conical teeth of most Xenarthra are similar to those of palaeanodonts. It is interesting that, unlike
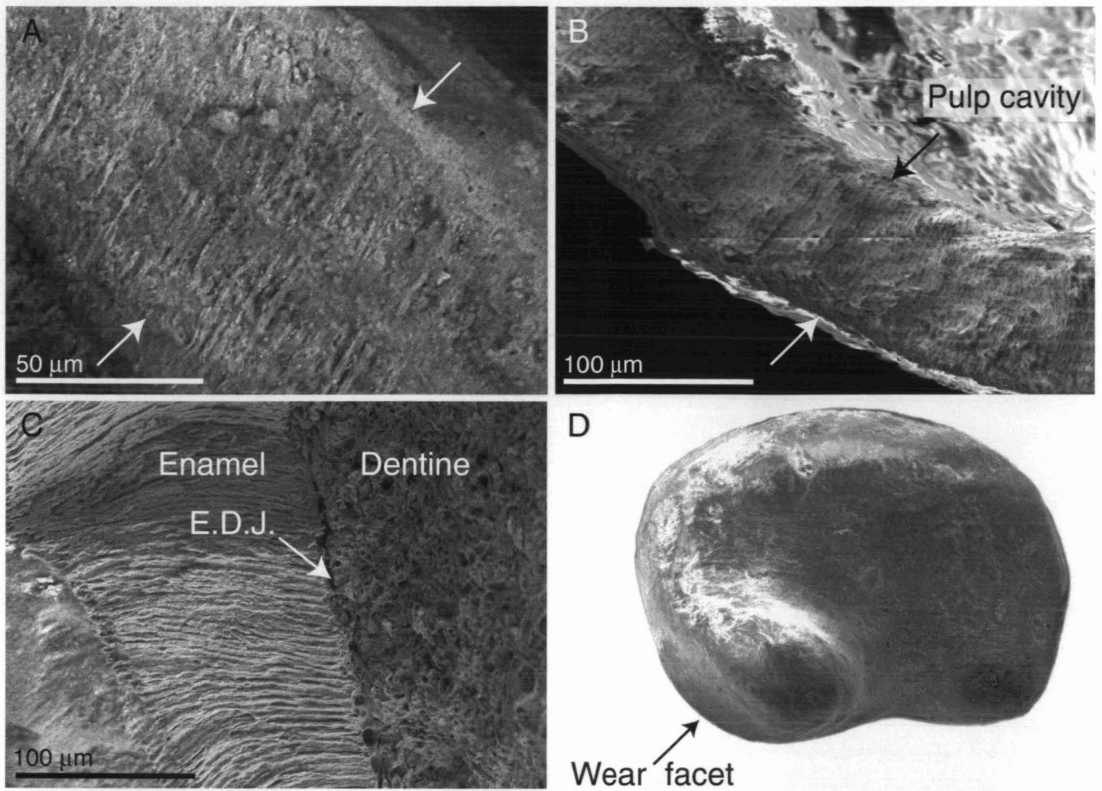
FIG. 7 — Scanning electron microscope images of holotype and referred specimen of *Mylanodon rosei*. A, cross-section of broken base of crown of P_3 in UM 109530 (juvenile; pulp cavity at upper right). B, cross-section of broken surface of crown of P_3 in UM 109530 (juvenile). C, cross-section of broken surface of crown of contemporary *Ectocion* molar, for comparison, showing enamel prisms and enamel-dentin junction (EDJ). D, crown of left M_1 of UM 109174 (holotype), in occlusal view with anterior to left (crown length 2.15 mm). Surfaces on A-C etched with 2 M HCl for 8 seconds. All surfaces uncoated. Arrows in A and B show boundaries of tooth wall.

extant Xenarthra, which are monophyodont (Martin, 1916; Veselovsky, 1966; Peyer, 1968), early metacheiromyids had two generations of teeth, probably reflecting a more primitive condition.

Tooth Structure and Wear

The exterior surface of the crown of P_4 in the juvenile dentary of *Mylanodon rosei* (UM 109530) is smooth and glossy, appears to be differentially hardened, and resembles enamel. Alternatively, the hard outer layer also resembles that of extant xenarthran teeth, which is usually composed of a thin layer of cementum (Peyer, 1968; Ferigolo, 1985). In order to clarify the character of the outer surface, we studied the P_4s, M_1, and broken surfaces of P_3 using scanning electron microscopy. We were unable to identify enamel prisms, an enamel-dentin junction, or a cementum-dentin junction (Fig. 7A-C). P_3 in the juvenile dentary has a large pulp cavity (Fig. 7B), rimmed by a layer of homogeneous material exhibiting radiating lineations. The lineations appear to mark the traces of dentinal tubules on the irregular broken surface (see, for example, Ferigolo, 1985). Alternatively,

the lineations could be interpreted as enamel prisms in an incompletely mineralized enamel layer. However, a mammal tooth consisting of a pulp cavity and enamel with no intermediate dentin layer would be highly unusual (see Koenigswald and Sander, 1997, for additional examples of enamel prisms and enamel-dentin junctions).

An x-ray image of the holotype of *Mylanodon* suggests that P_4 is double-rooted (Fig. 6A). The anterior and posterior edges of the roots are demarcated by dark vertical lines, probably indicative of space between the roots and alveolar wall. A darker area can be seen in the bottom half of the center of the alveolus, probably indicating lower-density bone separating the roots. Additionally, the dark vertical lines at the edges of the roots are approximately parallel, as would be expected for a double-rooted tooth. Single-rooted metacheiromyid teeth typically taper distally.

Wear facets have not been reported previously in metacheiromyids. A flat, oblique surface on the anterolabial surface of the M_1 protoconid (Fig. 7D) of the holotype of *Mylanodon rosei* appears to be a wear facet. We also note that a similar feature is present on the posteriolabial surface of the third postcanine in UM 66243 representing *Palaeanodon* cf. *P. ignavus*. The position of the facet on UM 66243 is similar to the position of a facet on the P_3 of *Amelotabes*. Facets may not be unique to *Mylanodon rosei*, and potentially could be found on relatively unworn teeth of other metacheiromyids. The singular occurrences of these facets, however, might indicate relatively minor and highly variable occlusal contact between upper and lower postcanines.

Comparison to Closely Related Taxa

Mylanodon is morphologically and temporally close to three known palaeanodonts: *Amelotabes*, *Propalaeanodon*, and *Palaeanodon* (Fig. 2). *Amelotabes* is a monospecific genus represented by a single dentary (Rose, 1978). *Mylanodon* shares a similar M_1 structure with *Amelotabes*, both species having low rounded cusps, and a dominant large protoconid, followed in size by a small, low hypoconid (Figs. 4A, 5A-B, 6A, 7D). The original morphology of the metaconid in *Amelotabes* is obscured by wear, but it appears to have been reduced. The metaconid was absent in *Mylanodon*. M_1 in *Mylanodon* differs from M_1 of *Amelotabes* in being smaller and less anteroposteriorly elongate (28% shorter, 6% narrower). Additionally, M_1 and M_2 of *Amelotabes* had an entoconid, greater basining of the talonid, and a paralophid, characteristics not present in *Mylanodon*. The M_1 roots in *Mylanodon* are fused below the crown, but distally bifurcate into separate sockets, while the M_1 roots of *Amelotabes* are separated for their entire length. In *Mylanodon* P_{2-3} and M_2 were single-rooted, while these teeth were double-rooted in *Amelotabes*. *Mylanodon* also differs from *Amelotabes* in its loss of tooth enamel, loss of M_3, and acquisition of inter-tooth diastemata. The dentary of *Mylanodon* is close in size and structure to that of *Amelotabes*. The medial buttress is slightly stronger on *Mylanodon*, but the mandibular groove is equally indistinct in both.

Mylanodon is similar to *Propalaeanodon*, a monospecific genus known from a single dentary and two tentatively referred humeri (Rose, 1979). However, *Mylanodon* differs in being larger (Table 1), in retaining a double-rooted M_1, and in having lost M_3. The crown of P_4 is not known in *Propalaeanodon*, but the alveolus for this tooth is long and narrow, and contains two roots. The alveolus of P_4 in *Mylanodon* is less elongate, and the number of roots is probably two. No molar crowns are known for *Propalaeanodon*. Rose (1979) described the M_1 of *Propalaeanodon* as having been single-rooted. This observation was confirmed by additional preparation of the M_1 alveolus in the holotype to rule out the possibility of distally bifurcating roots (Charles R. Schaff, personal communication, 2002). The M_1 root in the holotype of *Mylanodon* is single, fused, and incipiently bifurcated directly below the crown, but it bifurcates distally into separate roots (Fig. 6A). A single small alveolus for M_3 in *Propalaeanodon* indicates that, although M_3 was retained, it was significantly reduced. The dentary of *Propalaeanodon* is shallowest at the M_3 alveolus, while the dentary of *Mylanodon* tapers in height from the ascending ramus to M_1 (compare Fig. 3A-B with fig. 2 in Rose, 1979). Diastemata between postcanine teeth are longer in *Mylanodon*.

The only described specimen of *Palaeanodon* demonstrating the number of postcanine teeth is UM 66243, a dentary of *Palaeanodon* cf. *P. ignavus* figured by Rose (1978, 1979, 1981). Five

single-rooted postcanines are represented by alveoli, but only P_3 and P_4 have crowns preserved (dental homologies discussed above). The postcanines of *Palaeanodon* lack enamel and are reduced to rounded pegs. All postcanine alveoli are approximately the same size, and these are separated by relatively long diastemata. *Mylanodon* differs from *Palaeanodon* in having heteromorphic alveoli separated by shorter diastemata; having a larger P_3 alveolus; having a larger, more complex P_4; retaining M_2; and having a double-rooted, molariform M_1. The degree of development of the medial buttress is similar in both taxa.

Phylogenetic Considerations

Characteristics that have been used to distinguish metacheiromyids from epoicotheriids include: (1) loss of enamel on postcanine teeth; (2) presence of a posterior diastema between the last postcanine and base of the ascending ramus on the dentary; (3) presence of diastemata between postcanine teeth; (4) reduction in number of teeth; (5) reduction of teeth to simple peg-like structures; (6) alveoli larger than tooth crowns; (7) a more prominent medial buttress; and (8) absence of postcanine wear facets (Rose, 1978; Rose, 1979; Schoch, 1984; Rose et al., 1992; Gunnell and Gingerich, 1993). If *Amelotabes simpsoni* represents the primitive dental state for late Paleocene Palaeanodonta, then most or all of these characteristics are derived in Clarkforkian and later metacheiromyids.

We refer *Mylanodon rosei* to Metacheiromyidae because of its loss of postcanine tooth enamel, presence of a posterior diastema, loss of M_3, and presence of diastemata between postcanines that are proportionally longer than those in Epoicotheriidae. Other characteristics in *Mylanodon rosei* that suggest a close relationship to metacheiromyids, and particularly to *Palaeanodon*, are its near lack of postcanine wear facets, its single-rooted P_{2-3}, and its prominent medial buttress. A potential confounding factor in the use of some of these characteristics is that they may have been acquired or lost secondarily and independently in at least two Eocene palaeanodonts. Enamel is apparently present on specimens of *Brachianodon westorum*, a Bridgerian species tentatively referred to Metacheiromyidae (Gunnell and Gingerich, 1993). *Dipassalus oryctes*, a late Wasatchian species questionably referred to Epoicotheriidae based on postcranial features (Rose et al., 1992), has a reduced dentition, a long posterior diastema behind the last postcanine, and other dental characteristics either convergently derived, or indicative of metacheiromyid affinities. Although there may be homoplasy in both families, the characteristics in question are presumably of greater utility in determining relationships in earlier and more closely related palaeanodonts that have a less modified dentition, such as those compared here.

We consider *Amelotabes* to be the most primitive late Paleocene palaeanodont, and to represent the primitive condition for both Epoicotheriidae and Metacheiromyidae. Rose (1979) cited numerous characteristics shared by *Amelotabes*, the earliest and most primitive known epoicotheriid, and *Propalaeanodon*, the earliest metacheiromyid (Fig. 2), as evidence for a close relationship between metacheiromyids and epoicotheriids. Rose concluded that metacheiromyids were probably derived from an epoicotheriid near *Amelotabes*. *Propalaeanodon* appears to be a morphological intermediate between *Amelotabes* and *Palaeanodon* (Rose, 1979), a Clarkforkian and Wasatchian metacheiromyid. Similarly, *Mylanodon* can also be viewed as a morphological intermediate between *Amelotabes* and *Palaeanodon*. *Mylanodon* and *Propalaeanodon* do, however, exhibit different specializations.

The loss of M_3 and development of a posterior diastema in *Mylanodon* are derived conditions shared with *Palaeanodon*, but not with *Propalaeanodon*. Conversely, the single-rooted M_1 in *Propalaeanodon* is a derived condition shared with *Palaeanodon*, but not with *Mylanodon*. Although the number of roots could conceivably be variable in late Tiffanian palaeanodonts, both dentaries from Y2K Quarry have a double-rooted M_1. *Mylanodon* occurs stratigraphically above *Propalaeanodon* and both could potentially be part of a single lineage leading to *Palaeanodon*. If this is the case, however, a reversal from the derived single-rooted M_1 condition in *Propalaeanodon* to the primitive double-rooted M_1 condition in *Mylanodon* would be required. The general trend

in metacheiromyid evolution is toward reduction and simplification of the dentition, suggesting the presence of two metacheiromyid lineages in the late Tiffanian. We find no specializations in *Mylanodon* that would preclude it from being a direct ancestor to *Palaeanodon*, nor did we identify any specializations in *Amelotabes* that would preclude it from being directly ancestral to *Mylanodon*. Rose (1979) interpreted *Propalaeanodon* as a possible ancestor of *Palaeanodon*, but now *Mylanodon* is an equally viable candidate. Ongoing recovery of new palaeanodonts shows that their evolution was more complicated than might have been expected.

CONCLUSIONS

The new specimens described here represent the first juvenile dentary of a Paleocene palaeanodont, and provide a first look at the unworn P_4 and M_1 of a primitive metacheiromyid. The combination of characteristics observed in these dentaries is not found in any other metacheiromyid. Comparison of adult and juvenile dentaries allows determination of tooth homologies in *Mylanodon*, and suggests homologies for later *Palaeanodon*. The loss of M_3 in *Mylanodon* and appearance of a posterior diastema between M_2 and the ascending ramus indicates that tooth reduction proceeded from back to front in early metacheiromyids.

Mylanodon is morphologically intermediate between *Amelotabes* and *Palaeanodon* in: (1) number of postcanine teeth; (2) degree of tooth simplification; (3) number of double-rooted teeth; (4) lengths of intra-tooth diastemata; and (5) relative length of the posterior diastema between the last postcanine and the base of ascending ramus. *Mylanodon* is also stratigraphically intermediate between *Amelotabes* and *Palaeanodon* (Fig. 2). *Mylanodon* has no known specializations that would preclude it from being a direct ancestor of *Palaeanodon*. Similarly, *Amelotabes* has no derived characteristics that would preclude it from being a direct ancestor to *Mylanodon*. Although *Mylanodon* could be part of a single lineage including *Propalaeanodon* and *Palaeanodon* (Fig. 2), reversal from a single-rooted M_1 in the earlier *Propalaeanodon* to a double-rooted M_1 in *Mylanodon* would be required. Alternatively, two metacheiromyid lineages appear to have been present in the late Tiffanian. This idea can be tested by recovery of additional fossils.

ACKNOWLEDGMENTS

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