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Systematics of the genus *Palaeictops* Matthew, 1899 (Mammalia: Leptictidae), with the description of two new species from the Middle Eocene of Utah and Wyoming

PAÚL M. VELAZCO¹ AND MICHAEL J. NOVACEK¹

ABSTRACT

Palaeictops is a genus of Early Cenozoic Leptictidae, currently comprising six species known from Eocene faunas in the United States and Canada. Two new species, *Palaeictops altimontis* and *P. robustus*, are represented by nearly complete skulls and mandibles from the Tepee Trail (Middle Eocene) and Uinta (Middle Eocene) formations of Wyoming and Utah, respectively. They are similar to other species of *Palaeictops* in having a single sagittal crest, small suprameatal foramen, and an expanded cochlear fossula. Phylogenetic analysis recovered a monophyletic *Palaeictops* and a sister relationship of *P. bicuspis* and *P. multicuspis* with *P. matthewi* sister to this clade. The subfamily Leptictinae is herein recognized to comprise *Blacktops*, *Leptictis*, *Megaleptictis*, and *Palaeictops*. This group is distinctive in having a number of features that indicate a less sectorial cheektooth dentition than in the nonleptictine *Prodiacodon* and *Myrmecoboides*. The leptictines *Palaeictops* and *Leptictis* are also known from postcranial elements, and these show features, such as the distally fused tibia and fibula, that distinguish them from the condition in *Prodiacodon*. The Late Cretaceous genus *Gypsonictops* is used as an outgroup for the phylogenetic assessment of leptictids herein, but it remains uncertain whether this taxon has a close relationship with other leptictids or lies outside the crown group Placentalia.

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INTRODUCTION

The Leptictidae is a diverse family of Paleogene mammals with an impressive fossil record that extends from the Early Paleocene to Late Oligocene (Novacek, 1977; McKenna and Bell, 1997; Gunnell et al., 2008). The phylogenetic affinities of this family have been long debated. The group has been associated with a variety of placentals, including Lipotyphla, Erinaceomorpha, Tupaiidae, Macroscelidea, Rodentia, Primates, Microsyopoidea, and Pantolestidae (Gregory, 1910; Butler, 1956; McDowell, 1958; Van Valen, 1965; Lillegraven, 1969; McKenna, 1969; Szalay, 1977; Novacek, 1986; O'Leary et al., 2013). Leptictids are found in North America, Europe, and Asia (Kellner and McKenna, 1996; McKenna and Bell, 1997), but some authors include all the European "leptictids" in a different family (Pseudorhyncocyonidae) (Morlo et al., 2004; Rose, 2012; Hooker, 2013). In North America approximately 27 species of leptictids are currently recognized and are grouped in 11 genera: *Amphigyion* Gingerich and Smith, 2006; *Blacktops* Meehan and Martin, 2010; *Euictops* Gunnell, Zonneveld, and Bartels, 2016; *Leptictis* Leidy, 1868; *Leptonysson* Van Valen, 1967; *Megaleptictis* Meehan and Martin, 2012; *Myrmecoboides* Gidley, 1915; *Palaeictops* Matthew, 1899; *Prodiacodon* Matthew, 1929; *Xenacodon* Matthew and Granger, 1921; and the unpublished Late Eocene–Oligocene taxon distinct from *Leptictis* (Novacek, 1977).

Palaeictops specimens have been recovered from Early to Middle Eocene faunas in Colorado and Wyoming in the United States and Saskatchewan in Canada (Russell, 1965; Novacek, 1977; Storer, 1995). Currently six species are recognized for *Palaeictops*: *P. bicuspis* (Cope, 1880); *P. borealis* (Russell, 1965); *P. bridgeri* (Simpson, 1959); *P. matthewi* Novacek, 1977; *P. multicuspis* (Granger, 1910); and *P. pineyensis* (Gazin, 1952) (Novacek, 1977; Gunnell et al., 2008). Here we provide a revised diagnosis of *Palaeictops* and its species and describe two new species from Utah and Wyoming.

MATERIALS AND METHODS

The dental notation used here for *Palaeictops* follows McKenna (1975): I1/i1, I2/i2, I3/i3, C/c, P1/p1, P2/p2, P4/p4, P5/p5, M1/m1, M2/m2, M3/m3. The majority of specimens were measured with an Ehrenreich photo-optical "shopscope," and in the case of *Palaeictops borealis* and *P. robustus*, with a Mitutoyo absolute digital caliper. The following criteria were used for dental measurements (fig. 1; see Novacek, 1997: fig. 2):

ANTERIOR-POSTERIOR AXIS (A-P)

Lower premolars: long axis of tooth.

Lower molars: line drawn through the apices of the metaconid and the entoconid.

Upper premolars: line extended from the anteriormost point of the anterolabial lobe to the posteriormost point of the metastylar lobe.

Upper molars M1–M3: line drawn through the apices of the paracone and metacone.

LENGTH (L)

Lower premolars: total length of crown, i.e., greatest dimension measured parallel to A-P axis.

Lower molars: total distance from the anterior face of the paraconid to the posterior talonid along a line parallel to the A-P axis (anterior cingulum not included in measurement).

Upper premolars and molars: greatest dimension parallel to the A-P axis of the tooth.

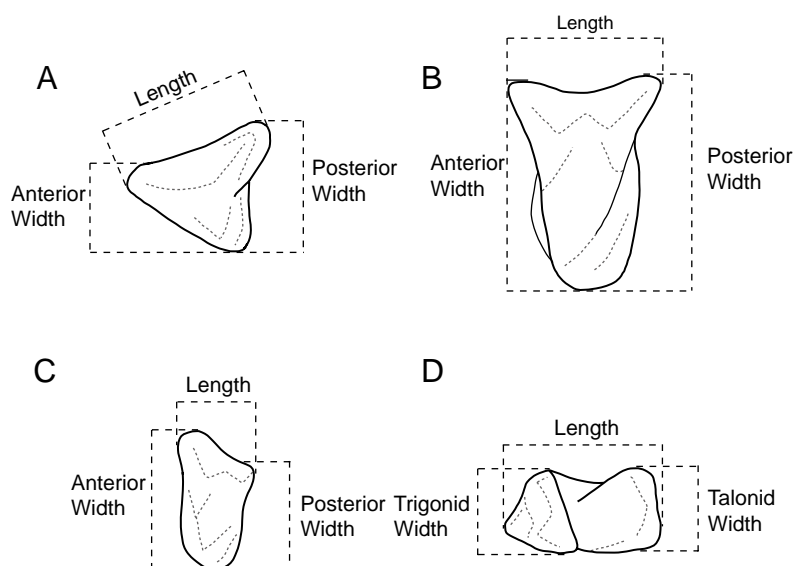


FIG. 1. Diagram showing criteria for dental measurements of **A**, upper posterior premolars, **B**, upper molars, **C**, upper last molar (M3), and **D**, lower posterior premolars and molars. See text for explanation.

WIDTH (W)

Lower premolars: widest part of crown; greatest dimension measured at right angles to A-P axis.

Lower molars: (two width measurements) trigonid width (WTR) and talonid width (WTA), widest part of each of these sections of the crown measured at right angles to A-P axis.

Upper premolars and molars: (two measurements) anterior width (AW), the distance from the labialmost point of the anterolabial corner of the crown to the lingualmost point of the protocone; and posterior width (PW), the distance from posterolabialmost point of meta-stylar lobe to lingualmost point of protocone, both width measurements taken at right angle to the A-P axis.

Specimens examined for this study are housed in the following collections:

AMNH American Museum of Natural History, New York, New York

CM Carnegie Museum of Natural History, Pittsburgh, Pennsylvania

FMNH Field Museum of Natural History, Chicago, Illinois

ROM Royal Ontario Museum, Toronto, Ontario, Canada

RSM Royal Saskatchewan Museum, Regina, Saskatchewan, Canada

USNM United States National Museum, Washington, D.C.

YPM VP Division of Vertebrate Paleontology, Yale Peabody Museum of Natural History, New Haven, Connecticut

YPM VPPU Division of Vertebrate Paleontology Princeton University Collection, Yale Peabody Museum of Natural History, New Haven, Connecticut

To assess the phylogenetic relationships of all the *Palaeictops* species, we analyzed variation in 50 cranial, dental, and postcranial characters (appendix 1 and 2). We used “New Technology” search options, using sectorial search, ratchet, tree drift, and tree fusing of TNT version 1.5 (Goloboff et al., 2003; Goloboff et al., 2008), using unordered states. The topologies of the short-

est-length trees were then subjected to bootstrap analysis (1000 replicates) and Bremer support. The matrix is available online (<http://www.morphobank.org>) (O'Leary and Kaufman, 2012); project: P2545, Systematics of the genus *Palaeictops* Matthew, 1899 (Mammalia: Leptictidae), with the description of two new species from the Middle Eocene of Utah and Wyoming.

SYSTEMATIC PALEONTOLOGY

ORDER LEPTICTIDA MCKENNA, 1975

FAMILY LEPTICTIDAE GILL, 1872

Subfamily Leptictinae Gill, 1872

EMENDED DIAGNOSIS: Leptictids with large, distinct hypocones on P5 (vestigial or absent in nonleptictines). Anteroposteriorly more elongated P5 and upper molars with lower paracones, protocones, and metacones (taller cusps in nonleptictines). Upper molars with slightly more labially situated conules, absence of a twinned paraconule, and variably developed ectoflexi, but less deeply infolded than in nonleptictines. Upper molar parastylar spurs poorly developed. Elongated p5, with large, projecting paraconid. Skeletons (known in *Leptictis dakotensis* and *Palaeictops matthewi*) with distinct distal fusion of tibia and fibula, head of humerus semilunar with sharply defined medial border, head of femur strongly canted to long axis of shaft, and deep trochanteric fossa of femur.

INCLUDED TAXA: *Blacktops* Meehan and Martin, 2010; *Leptictis* Leidy, 1868; *Megaleptictis* Meehan and Martin, 2012; and *Palaeictops* Matthew, 1899.

DISTRIBUTION: Early Eocene (Wasatchian)–Late Oligocene (Whitneyan), North America.

REMARKS: Postcranial evidence offers compelling evidence for the monophyly of Leptictinae. Unfortunately, only two species in this group are represented by skeletal material. For the present, the dental features alone must serve to group all species of the subfamily.

Genus *Palaeictops* Matthew, 1899

Stypolophus Cope, 1880: 746.

Parictops Granger, 1910: 250–251.

GENOTYPIC SPECIES: *Palaeictops bicuspis* Cope, 1880 (described as *Diacodon bicuspis* by Matthew, 1918).

REFERRED SPECIES: *Palaeictops borealis* (Russell, 1965), *P. bridgeri* (Simpson, 1959), *P. matthewi* (Novacek, 1977), *P. multicuspis* (Granger, 1910), *P. altimontis* (new, this paper), and *P. robustus* (new, this paper).

DIAGNOSIS: Leptictine differing from other members of this subfamily (i.e., *Leptictis* and *Megaleptictis*) in having single sagittal crest (known in *Palaeictops bicuspis*, *P. altimontis*, and *P. robustus*); shallow suprameatal fossa (known in *P. altimontis* and *P. bicuspis*); more trans-

versely flared basioccipital that overlaps ventrally the promontorium of the petrosal (known in *P. altimontis*); shallow groove on the paraoccipital process for the digastric muscle (known in *P. altimontis* and *P. robustus*); a paraoccipital process that is less extensive, so that the distance is shorter between stylomastoid foramen and posterior margin of basicranium (known in *P. altimontis* and *P. robustus*); and a small postglenoid process (known in *P. altimontis* and *P. robustus*). Expanded cochlear fossula (in *P. altimontis* and *P. robustus*). Lingually swollen protocones on P5 and M1–M3. Similar to *Leptictis* but different from *Prodiacodon* in having more bunodont cusps on posterior premolars and molars. Similar to *Megaleptictis* in having a small suprameatal foramen; lacking the posterior concavity in the coronoid process; and short talonid on p5. Differs from *Prodiacodon* in having slightly lower trigonids; well-developed hypocone on P5; shallow ectoflexi; elongate p5 with enlarged paraconid; less transverse M2; less developed parastylar spurs; and the presence of only one paraconule on the upper molars. Differs from *Myrmecoboides* in having well-separated paraconids and metaconids on p5–m3; less elongate, relatively wider talonids; and more closely spaced premolars. Pes in *P. matthewi* differs from that in all other leptictids where known in having a distinctly pear-shaped sustentacular facet on the astragalus and a very reduced fibular facet on the calcaneum.

DISTRIBUTION: Wind River, Bridger, Tepee Trail, Wasatch, and Willwood formations, Wyoming; DeBeque and Huerfano formations, Colorado; Uinta Formation, Utah; and Cypress Hills and Swift Current Creek formations, Saskatchewan, Canada. Lower–Middle Eocene (Wasatchian–Duchesnean NALMAs).

REMARKS: The above diagnosis documents the presence of cranial and postcranial traits that may exclude *Palaeictops* from a *Leptictis* grouping. It is noteworthy, however, that the posteriorly expanded nasals of *P. bicuspis* are primitive, but not universal for this genus. In *P. altimontis* the nasals are posteriorly constricted in a manner similar to that in *Leptictis*. There is, in fact, clear evidence that *Palaeictops* is closely tied to the history of the Late Eocene–Oligocene taxa. Postcranial features of *P. matthewi* also support this close phylogenetic relationship (e.g., distal fusion of tibia and fibula, head of femur strongly canted to long axis of shaft, and deep trochanteric fossa of femur).

Although there are distinct differences between *Palaeictops* and *Prodiacodon*, some of the criteria demarcating these taxa in Novacek (1977) have been questioned by Bown and Schankler (1982). The latter authors offered the following comparisons:

- (1) The two genera are not easily separated by the length-width dimensions of the upper molars (as used by Novacek, 1977), although Bown and Schankler noted (1982: 11) that “the upper molars of Paleocene *Prodiacodon* are more transverse than in early Eocene species of *Palaeictops*.”
- (2) Some referred specimens of *Palaeictops bicuspis* (e.g., Guthrie, 1971) have M2 ectoflexi that are intermediately deep between the type of *P. bicuspis* and the type of *Prodiacodon tauricinerei*.
- (3) A large individual from the Lysite biostratigraphic zone of the Willwood Formation has a mosaic of characters seen in teeth of both *Palaeictops* and *Prodiacodon*.

- (4) The conules of the few known upper molar specimens are positioned more lingually in *Prodiacodon tauricinerei*, as noted in Novacek (1977).
- (5) The type specimens of three *Palaeictops* species (*Palaeictops bicuspis*, *P. matthewi*, and *P. multicuspis*) show heavy wear, which precludes accurate assessment of cusp height. The trigonids of *Prodiacodon* may therefore not be much higher than those of *Palaeictops*.
- (6) p5 paraconids in *Palaeictops* are better developed than in *Prodiacodon* only because p5s of the former are larger and their anterior trigonids more elongate.

We address these remarks as follows:

- (1) The quotation of Bown and Schankler (1982) given above supports the original demarcation of *Palaeictops* and *Prodiacodon* based on dimension of upper molars. Some variation in these dimensions among specimens and species is expected. The significant character in this context is the markedly more transverse, anteroposteriorly compressed M2 relative to M1 in *Prodiacodon*, a feature definitely lacking in *Palaeictops* (Novacek, 1986: fig. 4).
- (2) Variation in the depth and configuration of the ectoflexi of M2 is expected. The types of *Palaeictops bicuspis*, *P. matthewi*, and *P. altimontis* are clearly distinguished in this character from the types of *Prodiacodon tauricinerei* and *P. puercensis* (M2s of *P. crustulum* were not definitely identified; see Novacek, 1977; and Clemens, 2015).
- (3) New specimens with a mosaic of dental features found in both *Palaeictops* and *Prodiacodon* is expected. Perhaps the “large-toothed” specimen from Willwood is a new taxon.
- (4) We concur with Bown and Schankler’s (1982) agreement with Novacek’s (1977) initial observation concerning the relative position of the upper molar conules in *Palaeictops vis a vis Prodiacodon*. We now emphasize, however, that the significant feature of the conules is the twinned paraconule, a feature of *Prodiacodon* definitely lacking in *Palaeictops*.
- (5) We acknowledge that elevation of the trigonids is difficult to assess in the worn types of *Palaeictops bicuspis*, *P. matthewi*, and *P. multicuspis*. The trigonids are, however, definitely lower in the relatively less worn teeth of *P. bridgeri* and *P. altimontis* than in *Prodiacodon* (Novacek, 1986: fig. 4). We agree with Bown and Schankler (1982) that the lower trigonids are possibly shared specializations developed by the Middle Eocene *Palaeictops*. The case is moot until better-preserved molars of Early Eocene *Palaeictops* are known.
- (6) The greatest difference in p5 paraconid size is between the type series of *Palaeictops* (*P. bicuspis*) and *Prodiacodon* (*P. puercensis*). We agree with Bown and Schankler (1982) that *Prodiacodon tauricinerei* approaches *Palaeictops* (especially the Middle Eocene species) in development of the p5 paraconid. However, the difference in development is worthy of recognition. The size of the p5 paraconid in *P. bicuspis* refers to its relatively robust proportions; it is not simply a function of overall tooth size. Moreover, the relationships between a larger paraconid and a more elongate anterior portion of the trigonid are hardly surprising; this portion of tooth is occupied by little more than a paraconid.

These considerations lead us to retain the generic separation of *Palaeictops* and *Prodiacodon*. We acknowledge that *Prodiacodon tauricinerei* has features that resemble the dental morphology characteristic of *Palaeictops* more closely than other species of *Prodiacodon*. *Prodiacodon tauricinerei* is, however, clearly referable to *Prodiacodon* based on features of the molars (e.g., P5 and upper molars transverse, anteroposteriorly compressed with sharp cusps; precingula on P5 and molars long, nearly reaching anterolingual corner of crown; M1 and M2 paraconules twinned and paraconules lingual to metaconules; lower molars with sharp cusps, trigonids relatively high and anteroposteriorly compressed). These features, as well as a nearly contemporaneous age, exclude *Prodiacodon tauricinerei* as a possible ancestor of *Palaeictops bicuspis* or other species of this genus. This view runs contrary to the argument of Bown and Schankler (1982: 11) that *P. tauricinerei*, persisting into Lysitean time, may have given rise to a second lineage that ultimately led to *Palaeictops*.

Palaeictops bicuspis (Cope, 1880)

Figures 2–5A, table 1

Stypolophus bicuspis Cope, 1880: 746.

Ictops bicuspis Cope, 1881: 192; Cope, 1885: pl. 29a, figs. 2, 3. Name combination.

Palaeictops bicuspis Matthew, 1899: 31, 35. First use of current name combination.

Diacodon bicuspis Matthew, 1918: 574–576. Name combination.

Diacodon pineyensis Gazin, 1952: 19. Name combination.

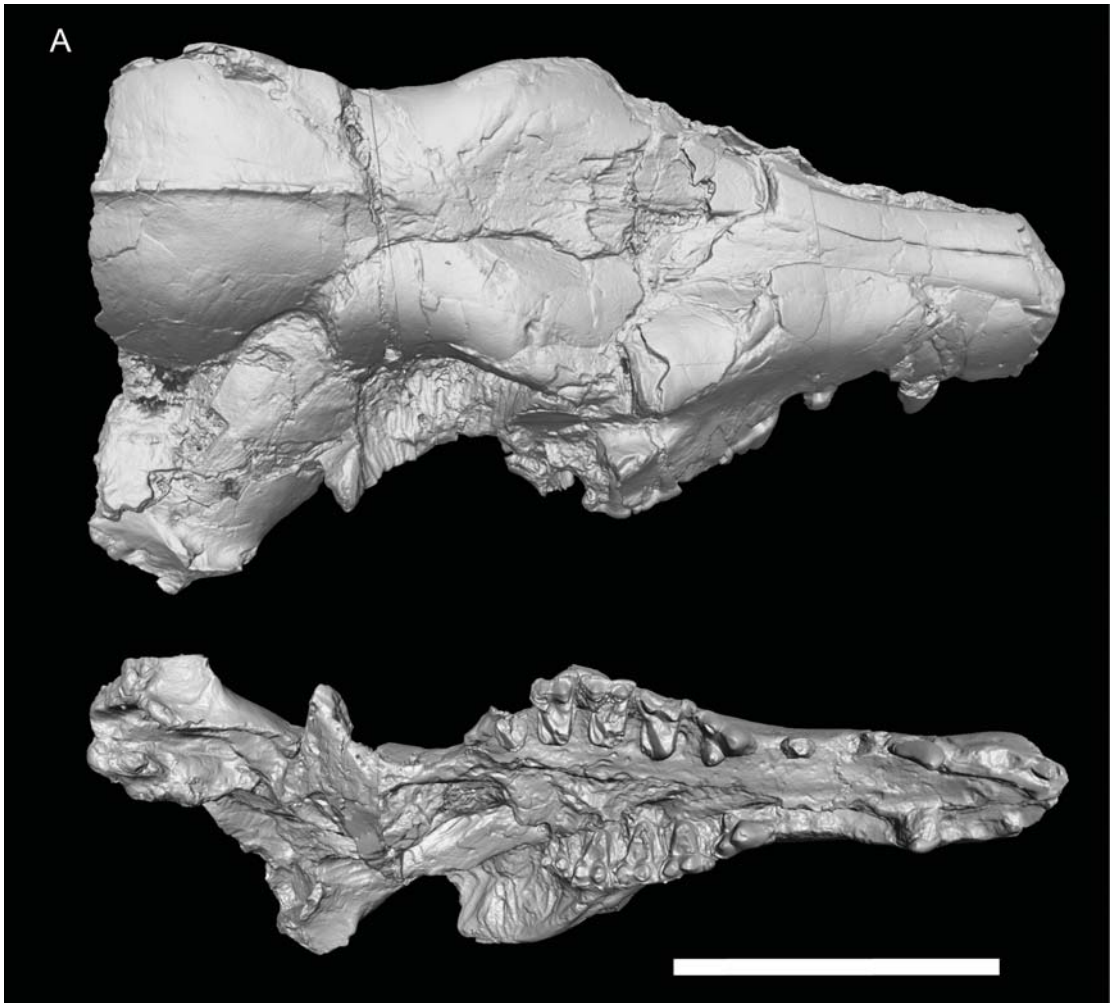
Palaeictops pineyensis Van Valen, 1967: 232. Name combination.

HOLOTYPE: AMNH 4802 (fig. 2A–B), consisting of a partial skull that retains C, P4–P5, M1–M3 on the left side; the right side retains two incisors possibly corresponding to I2 and I3 (both are broken), as well as P2 (broken), P4–P5, M1–M2, and M3 (broken). Left ramus with p5–m3 and roots of p1, p2, and p4 (fig. 3). Right ramus with p4–m2 and roots of i?, c, p1, and p2 (fig. 4).

TYPE LOCALITY: Wind River Basin, Wyoming. Wind River Formation, Lower Eocene (Wasatchian NALMA).

DIAGNOSIS (revised from Novacek, 1977: 14): Differs from other species of *Palaeictops* in having a large, swollen and anteriorly extended paracone of P4 (paracone less anteriorly projecting in *P. altimontis* and *P. matthewi*); tricuspid p4 with large anterior cusp on the heel and lack of a cusp anterior to main cusp (p4 in *P. multicuspis*, *P. matthewi*, and *P. altimontis* with cusp anterior to main cusp, but lacking a large anterior cusp on the heel). Differs from *P. bridgeri* in its smaller size, in lacking a broad prefossid between paraconid and metaconid on p5, and in having a more lingually positioned hypoconulid on m3. P4 and p4 less tall and trenchant than in *P. multicuspis* (p4) and *P. matthewi*. P4 more anteriorly extended than in *P. altimontis* (fig. 5).

DISTRIBUTION: Wind River Formation (Lost Cabin and Lysite members), Wasatch Formation (Knight Member), Willwood Formation, Wyoming, Lower Eocene (Wasatchian NALMA).



REFERRED MATERIAL: AMNH 4255, left ramus with broken m1, m2–m3 and, provisionally, several other specimens from the Willwood Formation, Bighorn Basin, Wyoming, described by Bown and Schankler (1982: 19) (see remarks below). YPM VPPU 13436, jaws with upper and lower cheektooth dentition and several other specimens described by Guthrie (1971: 54–55) from the Lost Cabin Member, Wind River Formation, Wyoming. Provisionally, USNM 19204, left ramus with damaged p5, m1–m3, from the Knight Member, Wasatch Formation, Big Piney La Barge Fauna, Sublette County, Wyoming. Described as the type of *Diacodon pineyensis* by Gazin, 1952, and referred to *Prodiacodon tauricinerei* by Novacek (1977: 26). YPM VPPU 13419, upper and lower jaws with cheektooth dentitions and associated distal humerus fragment (described as *Palaeictops pineyensis* by Guthrie, 1967) from the Lysite Member, Wind River Formation, Wyoming.

REMARKS: The most distinctive feature of *Palaeictops bicuspis* is the enlarged, anteriorly positioned paracone on P4 (fig. 5). This tooth is unknown in *P. borealis*, *P. bridgeri*, *P. multi-*

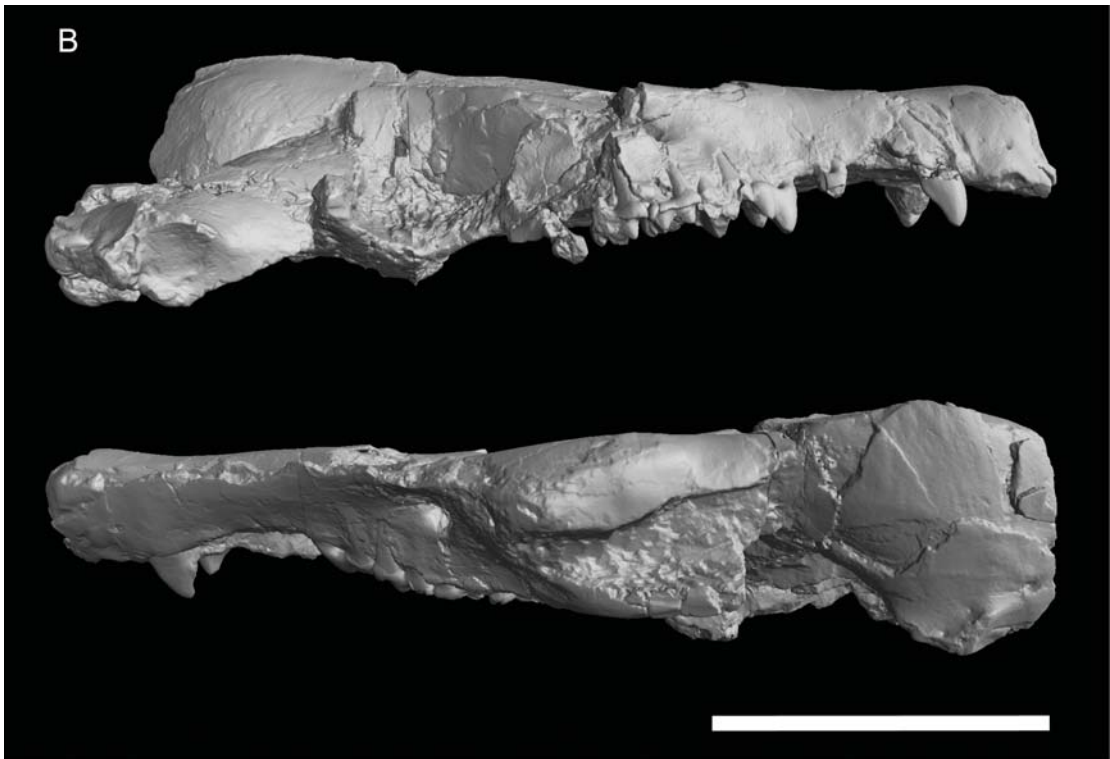


FIG. 2. The skull of *Palaeictops bicuspis* AMNH 4802 (holotype), containing C, P4–P5, M1–M3 on the left side; the right side retains two incisors possibly corresponding to I2 and I3 (both are broken), as well as P2 (broken), P4–P5, M1–M2, and M3 (broken). **A**, (opposite page) dorsal (top) and ventral (bottom) views and **B**, (above) right lateral (top) and left lateral (bottom) views. Scale bar = 2 cm.

cuspis, and *P. robustus*, and the combination of features cited above must be used to separate *P. bicuspis* from all other members of the genus.

We support Guthrie's (1971) identification of YPM VPPU 13436 from the Lost Cabin Member of the Wind River Formation as *Palaeictops bicuspis*. The characteristic P4 is clearly present in this specimen.

Bown and Schankler (1982: 16) gave statistical comparisons of tooth measurements for several species of *Prodiacodon* and *Palaeictops*. These suggest that the type of *Palaeictops* (*Diadacodon*) *pineyensis* (Gazin, 1952) is closer to *P. bicuspis* than to *Prodiacodon tauricinerei*, as suggested by Novacek (1977). The type is badly preserved, and assignment is uncertain. At present, we provisionally accept its transfer to *P. bicuspis*. Also referable to this species are the *Palaeictops pineyensis* specimens described by Guthrie (1967) from Lysite Member of the Wind River Formation.

Bown and Schankler (1982: 18) identified AMNH 48763, a ramus with p5–m1, as *Palaeictops bicuspis*. This assignment is contradicted by the morphology of the specimen. The p5 paraconid is lower, less anteriorly positioned, and has a slightly concave posterior face continuous with the lingually opened prefossid. The m1 has a very distinct entoconulid, a feature



FIG. 3. Left ramus of *Palaeictops bicuspis* AMNH 4802 (holotype), containing p5–m3 and roots of p1, p2, and p4, in (clockwise from upper left) medial, occlusal, and lateral views. Scale bar = 2 cm.

shared by *Prodiacodon* and *Myrmecoboides*. AMNH 48763 is retained within *Prodiacodon tauricinerei*, as proposed by Novacek (1977: 26).

The nomenclatural history of *Palaeictops bicuspis* is reviewed in Novacek (1977).

Palaeictops borealis (Russell, 1965)

Figure 6, table 1

Protictops? borealis Russell, 1965: 7–8, pl. 1, figs. 1, 2.

Palaeictops borealis Storer, 1984: 22–26: figs. 2A–B. First use of current name combination.

HOLOTYPE: ROM 1676, right M1 (fig. 6B).

TYPE LOCALITY: Swift Current, Saskatchewan. Swift Current Creek Formation, Middle Eocene (Uintan NALMA).

DIAGNOSIS: *Palaeictops borealis* can be easily distinguished from other species of the genus by its size (larger than *P. altimontis*, *P. bicuspis*, *P. bridgeri*, *P. multicuspis*, and *P. mat-*



FIG. 4. Right ramus of *Palaeictops bicuspis* AMNH 4802 (holotype), containing p4–m2 and roots of i?, c, p1, and p2, in (clockwise from upper left) lateral, occlusal, and medial views. Scale bar = 2 cm.

thewi, but smaller than *P. robustus*). Like *P. matthewi* in having P5 with a more extensive precingulum in lingual region (less extensive precingulum present in *P. altimontis* and *P. bicuspis*). Differs from *P. altimontis*, *P. bicuspis*, and *P. matthewi* in having the upper molars with a more extensive precingulum in lingual region. Like *P. altimontis* and *P. bridgeri* in having the lower molars with lower trigonids (higher trigonids present in *P. bicuspis*, *P. matthewi*, and *P. multicuspis*).

DISTRIBUTION: Cypress Hills and Swift Current Creek Formations, Saskatchewan, Canada. Middle Eocene (Uintan–Duchesnean NALMAs).

REFERRED MATERIAL: RSM P1654.220, right DP5; RSM P1654.221–222, right P5; RSM P1654.226, right m1; ROM 23595, left m1; RSM P1654.225, right m2; ROM 1685, right m2; RSM P1654.223–224, left m1 or m2; Swift Current Creek Formation, Saskatchewan, Middle Eocene. RSM P1899.1472, right DP4; RSM P1899.1486, left M1 or M2; and P1899.1450, left m1 or m2; Cypress Hills Formation, Saskatchewan, Middle Eocene.

REMARKS: Russell (1965) could not assign with certainty the holotype of *Palaeictops borealis* to a specific locus (P5 or M1), but subsequently Storer (1984) considered the holotype to be an M1, an assignment with which we agree. Likewise, other teeth were not assigned to a specific locus by Russell (1965) and Storer (1984); ROM 1685, ROM 23595, and RSM P1654.223–226 could not be assigned as either an m1 or m2. Based on our revision of all the *Palaeictops* material we were able to assign four of the six teeth to either m1 or m2 (see Referred Material), but we were not able to do this for RSM P1654.223 and RSM P1654.224 because of their poor

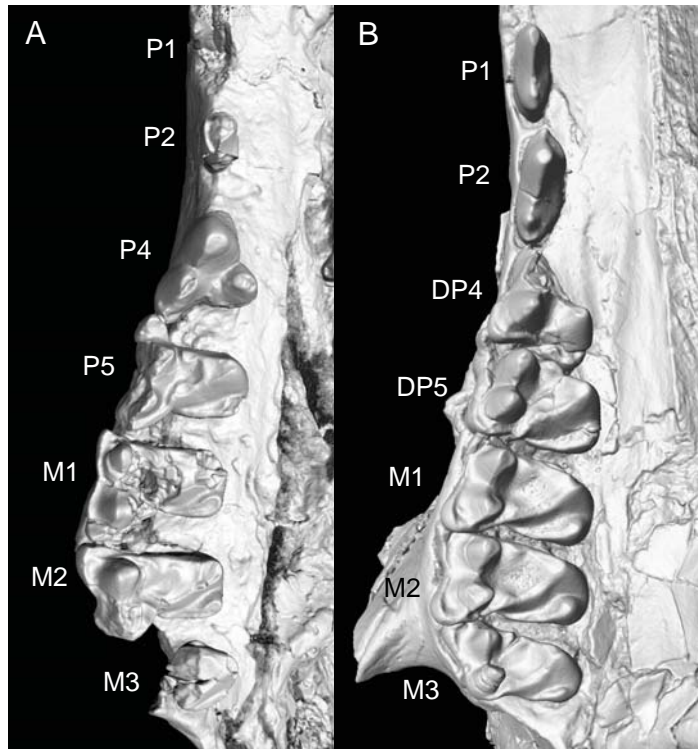


FIG. 5. Right maxilla in occlusal view, scaled to approximately the same size for comparison. **A**, *Palaeictops bicuspis* AMNH 4802 (P1 [missing], P2 [broken], P4–P5, M1–M2, M3 [broken]); **B**, *Palaeictops altimontis* AMNH 96250 (P1–P2, DP4–DP5, M1–M3).

preservation. We were not able to review the material from the Cypress Hill Formation (RSM P1899.1472, right DP4; RSM P1899.1486, left M1 or M2; and P1899.1450, left m1 or m2), but from the illustration it is clear that at least one specimen (RSM P1899.1450) belongs to *P. borealis* (Storer, 1995: fig. 1a).

Palaeictops bridgeri (Simpson, 1959)

Figure 7, table 1

Diacodon bridgeri Simpson, 1959: 1–4, fig. 1.

Palaeictops bridgeri Van Valen, 1967: 232. First use of current name combination.

HOLOTYPE: AMNH 56032, consisting of a right ramus that retains p5–m3 (fig. 7).

TYPE LOCALITY: Locality 6 (Misery Quarry) of McGrew (1959) in the vicinity of Tabernacle Butte, Wyoming. Upper Bridger Formation, Middle Eocene (Bridgerian NALMA).

DIAGNOSIS: Like *Palaeictops altimontis* (see diagnosis below) and unlike other species of the genus in having a p5 with a low paraconid bordered posteriorly by a distinctly opened, lingual prefossid, a shortened talonid, and a deeply excavated talonid basin opened lingually

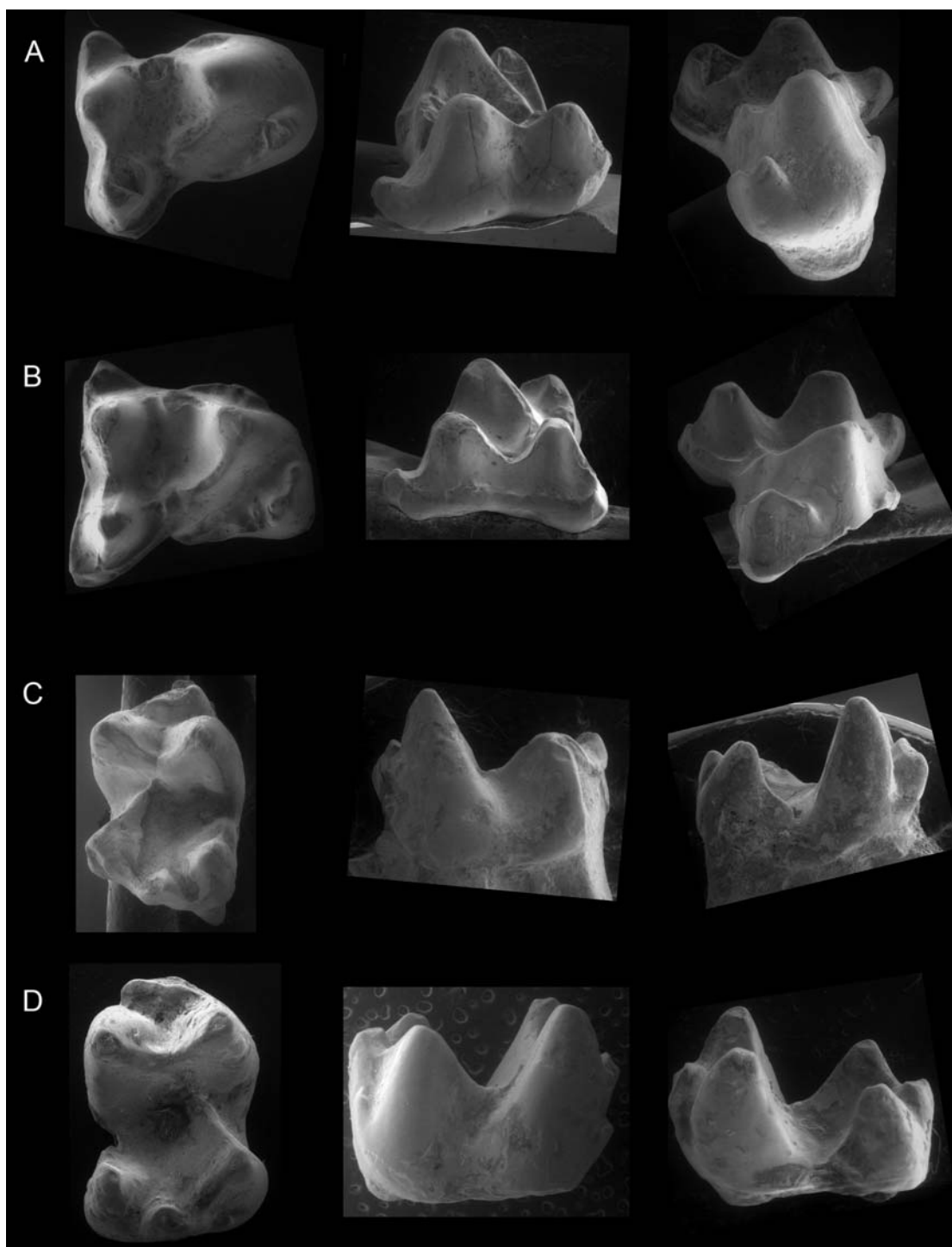


FIG. 6. *Palaeictops borealis*, occlusal (left), labial (center), and lingual (right) views of: **A**, right P5 (RSM P1654.221); **B**, right M1 (ROM 1676, holotype); **C**, left m1 (ROM 23595); **D**, right m2 (RSM P1654.225).

TABLE 1. Measurements of the cheekteeth of *Palaeictops*. All measurements are in millimeters.

Upper teeth				Lower teeth			
Element	L	AW	PW	Element	L	WTR	WTA
<i>Palaeictops bicuspis</i>							
AMNH 4802 type							
LP4	5.25	2.80		Lp5	3.92	1.55	2.14
LP5	3.40	4.40	3.86	Lm1	3.11	2.15	2.35
LM1	3.07	3.81	4.11	Lm2	3.00		
LM2	2.72	3.97	3.75	Lm3	3.27	2.37	1.70
LM3	2.44	3.17	2.65				
AMNH 4255							
				Lm2	3.09	2.00	2.45
				Lm3	3.40	2.30	2.14
<i>Palaeictops bridgeri</i>							
AMNH 56032 type							
				Rp5	4.25	2.31	2.22
				Rm1	3.65	2.52	2.47
				Rm2	3.58	2.69	2.64
				Rm3	4.00	2.39	2.03
<i>Palaeictops borealis</i>							
ROM 1676 type							
RM1	4.45	4.60	4.70				
RSM P1654.220							
RDP5	4.00	4.80	4.36				
RSM P1654.221							
RP5	4.38	5.03	5.15				
RSM P1654.222							
RP5	4.30	5.11	5.21				
ROM 23595							
				Lm1	4.04	2.15	2.42
				RSM			
				P1654.226			
				Rm1			2.47
				RSM			
				P1654.225			
				Rm2	4.27	2.28	2.50
				ROM1685			
				Rm2	3.98	2.40	2.70

<i>Palaeictops matthewi</i>							
FMNH 26904 type							
RP4	3.26	2.50		Lp4	4.02	1.60	
RP5	2.80	3.21	3.56	Lp5	3.90	2.05	1.84
RM1	2.90	4.03	4.17	Rm1	3.10	2.36	2.04
RM2	2.82	4.41	4.16	Rm2	3.21	2.36	2.13
RM2		3.60					
FMNH 26481							
RP4	3.57	3.06					
<i>Palaeictops multicuspis</i>							
				AMNH 14741 type			
				Lp2	3.66	1.42	
				Lp4	4.42	1.74	
				Lp5	4.21	2.41	2.21
				Lm1	3.20	2.67	2.63
				Lm2	3.27	2.65	2.47
				Lm3	3.40	2.50	2.09
<i>Palaeictops altimontis</i> , new species							
AMNH 96250 type							
RDP4	3.33	2.90		Lp5	3.55	2.17	2.07
RDP5	2.59	3.57	3.47	Lm1	3.15	2.65	2.47
LP5	3.34	3.36	3.65	Lm2	2.87	2.97	2.76
LM1	2.85	3.95	4.34	Lm3	3.16	2.60	2.16
LM2	2.80	4.12	4.33				
LM3	2.08	3.80	2.90				
<i>Palaeictops robustus</i> . new species							
CM 11954 type ^a							
LP1	3.23	1.83					
RP4	5.77	4.12					
RP5	5.55	5.38	5.86				
RM1	4.80	6.23	6.93				

^a The dentition of this specimen is worn down, approximate measurements are given for size comparison with the other species.



FIG. 7. Right ramus of *Palaeictops bridgeri* AMNH 56032 (holotype), containing p5–m3, in (clockwise from upper left) lateral, occlusal, and medial views. Scale bar = 1 cm.

and bordered posteriorly by steep faces of the entoconid and hypoconid (fig. 7). Both the types of *P. bridgeri* and *P. altimontis* have slightly worn, but low trigonids on m1–m3. Differs from *P. altimontis* in larger size (length of m1–m3 in *P. bridgeri* equals 11.23 mm, length in *P. altimontis* equals 9.18 mm.), and in having a p5 metaconid positioned more posteriorly relative to the protoconid and a more anteroposteriorly “opened” trigonid due to a more salient paraconid on m2. M2 possibly referable to *P. bridgeri* is more transverse with a shallower ectoflexus than M2 of *P. altimontis*.

DISTRIBUTION: Bridger Formation, Bridger Basin, western Wyoming, Middle Eocene (Bridgerian NALMA).

REFERRED MATERIAL: AMNH 9873, left M2, Main locality, Tabernacle Butte, Sublette Co., Wyoming. Upper Bridger Formation.

REMARKS: *Palaeictops bridgeri* was clearly described and illustrated by Simpson (1959) who first noted the distinctive characters of its lower, last premolar. The new *Palaeictops altimontis* species from the Tepee Trail locality (see below) is most similar to *P. bridgeri*, but the two species differ in size and in details of the lower dentition. More-

over, the possibility that a leptictid M2 (AMNH 98731) from Tabernacle Butte is referable to *P. bridgeri* provides further evidence for the distinction of this species from *P. altimontis*.

Palaeictops matthewi Novacek, 1977

Figure 8–10, table 1

HOLOTYPE: FMNH P26904 (fig. 8A–B), consisting of a damaged skull that retains P2–P5 (broken), M1–M2 (roots), and M3 (broken) on the left side; the right side retains roots of C–P1, P2 (broken), P4–P5, and M1–M3. Right ramus with c–p1 (broken), p2–p5, m1–m2 (broken), and root of i2 (fig. 9). Left ramus with c (broken), p1, p2 (broken), p4–p5, m1–m3 (broken), and root of i2 (fig. 10). Partial skeleton including lumbar and caudal vertebrae, pelvis, femur, tibia, carpals, tarsals, and phalanges.

TYPE LOCALITY: Exposure near top of Buzzard Pass, Mesa Co., Colorado. De Beque Formation, Rifle Member, Lower Eocene (Wasatchian NALMA).

DIAGNOSIS (modified from Novacek, 1977): Similar to *Palaeictops multicuspis* in having tall, trenchant p4 but differs from *P. multicuspis* in slightly smaller size and in having a more slender ramus; p2 with only one main, trenchant cusp and a basal posterior cusplule; p4 with anterior main cusp larger than posterior main cusp and a short transverse ridge on the posterior heel separated from the rest of the crown by a transverse trough (figs. 9, 10). P4 trenchant tooth, taller than P5 with a very prominent paracone, smaller metacone and low protocone (fig. 8B). Species has postcranial features used to diagnose *Palaeictops* (see above diagnosis).

DISTRIBUTION: De Beque and Huerfano formations, Colorado, Lower Eocene (Wasatchian NALMA).

REFERRED SPECIMENS: AMNH 17555, skull fragment, partial lower jaws and partial skeleton. Garcia Canon region, Colorado. Lower beds of Huerfano Formation.

REMARKS: Bown and Schankler (1982: 11–12) stated that *Palaeictops matthewi* is probably conspecific with *P. multicuspis*, because differences in size and p2 morphology are trivial. Synonymy is, however, unwarranted. The jaw proportions and p2 and p4 in these species are clearly distinct as described in the diagnosis of each species (this paper). Bown and Schankler (1982) maintained that such characters might be insignificant and subject to intraspecific variation. There is, however, no sample evidence supporting this assessment and, in absence of data to the contrary, *P. matthewi* is here recognized as diagnosed above.

Palaeictops multicuspis (Granger, 1910)

Figures 11–12, table 1

Parictops multicuspis Granger, 1910: 250–251.

Palaeictops multicuspis Van Valen, 1967: 232. First use of current name combination.

HOLOTYPE AND ONLY SPECIMEN: AMNH 14741, a left ramus with p2–m3 and a right ramus with p4–m3 and alveoli for a double-rooted p2, single rooted canine, and three inci-



sors (figs. 11, 12).

TYPE LOCALITY: Alkali Creek (Buck Springs) of Wind River Basin, Wyoming. Lost Cabin Member, Wind River Formation, Lower Eocene (Wasatchian NALMA).

DIAGNOSIS: Differs from other species of the genus (except *P. robustus*) in its large size and deeper ramus. Also differs from other species (including *P. robustus*) in having a trenchant p2 with four anteroposteriorly aligned cusps; p4 with very small anterior accessory cusps, two main cusps and two low cusps on the shortened heel; p5 with small, but distinct, cuspule at labial base of the paraconid. Similar to *Palaeictops matthewi* in having a trenchant p4 taller than p5 but differs from *P. matthewi* in having greater number of cusps on p2 and p4. Similar to *Prodiacodon* and *Myrmecoboides* in having lower molar entoconulids, but differs from these taxa in showing characters that diagnose *Palaeictops* (e.g., large, swollen p5 paraconid).

REMARKS: See Novacek (1977).

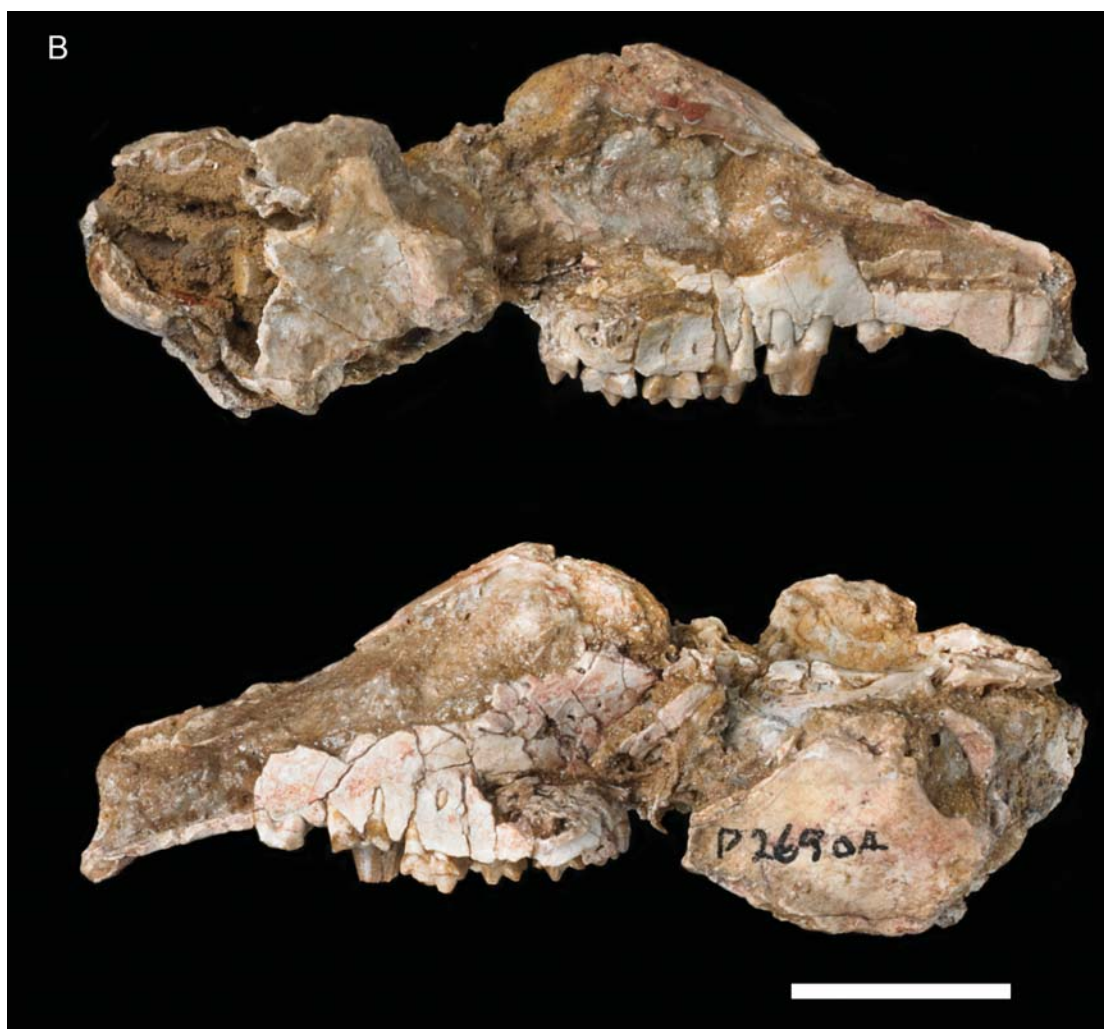


FIG. 8. The skull of *Palaeictops matthewi* FMNH P26904 (holotype), containing P2–P5 (broken), M1–M2 (roots), and M3 (broken) on the left side; the right side retains roots of C–P1, P2 (broken), P4–P5, and M1–M3. **A**, (opposite page) dorsal (top) and ventral (bottom) views and **B**, (above) right lateral (top) and left lateral (bottom) views. Scale bar = 1 cm.

***Palaeictops altimontis*, new species**

Figures 5B, 13–15, table 1

Palaeictops sp. Novacek, 1977: 21.

HOLOTYPE: AMNH 96250 (figs. 5B, 13B), consisting of a nearly complete skull that retains P1–P2, DP4–DP5, M1–M3 on the left side; the right side retains P5–M3. Left ramus with p2, and p4–m3 (fig. 15A–B). Right ramus with p4, p5 (damaged), and m1–3 (fig. 15B).

REFERRED SPECIMENS: AMNH 88400, right ramus with p4–5; AMNH 101955, left ramus with P2, P5; AMNH 105032, left ramus with p4, m3; AMNH 99301, left maxilla with P4–M3;



FIG. 9. Right ramus of *Palaeictops matthewi* FMNH P26904 (holotype), containing c–p1 (broken), p2–p5, m1–m2 (broken), and root of i2, in (clockwise from upper left) medial, occlusal, and lateral views. Scale bar = 1 cm.

AMNH 113880, left ramus with p4–m3. All from the type locality.

TYPE HORIZON AND LOCALITY: Unit 24 (bone bed A) East Fork Basin, northeast of Dubois, Fremont Co., Wyoming, about 500 feet above the local base of the Tepee Trail Formation (see McKenna, 1980: 337), Middle Eocene (Uintan NALMA).

ETYMOLOGY: From the Latin: *altus*, “high,” and *mons*, “mountain.” Refers to the dramatic montane settings of the type locality (see Love, 1939; McKenna, 1980).

DIAGNOSIS: Like *Palaeictops bridgeri* in having p5 with open prefossid and shortened talonid, but differs in smaller size, in lacking an anterior accessory cuspule at labial base of paraconid; p5 metaconid aligned less obliquely relatively to protoconid; more anteroposteriorly compressed trigonid on m2; and less transverse M2 with a deeper ectoflexus. Differs from *P. bicuspis*, *P. multicuspis*, and *P. matthewi* in having smaller, more anteriorly separated paraconid on p5 and lower trigonids on m1–3. Skull like *P. bicuspis* but unlike *Leptictis* in having single sagittal crest (fig. 13A). Skull like *Leptictis* but unlike *P. bicuspis* in having posteriorly narrow nasal elements. Basicranium differs from *Leptictis* (cf. fig. 14 and Novacek, 1986: fig. 22) in having: (1) a postglenoid foramen positioned more laterally and farther from the anteroexternal edge of the tympanic cavity; (2) a more transversely flared basioccipital that overlaps ventrally the promontorium of the petrosal; (3) shallower grooves on the promontorium for the promontory and stapedial branches of the internal carotid artery; (4) a posterior lacerate foramen only slightly larger than the stapedius fossa (much larger and more oval than stapedius fossa in *Leptictis*); (5) a cochlear fossula with a more expanded, dorsal rim; (6) a narrower bridge of the mastoid tubercle of the petrosal extending from ventral rim of the cochlear fossula between the stylomastoid foramen



FIG. 10. Left ramus of *Palaeictops matthewi* FMNH P26904 (holotype), containing c (broken), p1, p2 (broken), p4–p5, m1–m3 (broken), and root of i2, in (clockwise from upper left) medial, occlusal, and lateral views. Scale bar = 1 cm.

and stapedius fossa; (7) a paraoccipital process that is less extensive, so that the distance is shorter between stylomastoid foramen and posterior margin of basicranium; and (8) a shallower groove on paraoccipital process for the digastric muscle.

DESCRIPTION AND COMPARISONS: The front of the skull of *Palaeictops altimontis* (AMNH 96250) is badly damaged (fig. 13A–B), and the premaxillae are not preserved, except for a small nasal process on the right side of the skull. Most of the paired nasal elements can be seen in dorsal view (fig. 13A). Posteriorly the nasals are narrow, as in *Leptictis*. However, unlike the latter, the contact of the nasal and the frontal is along a more obliquely oriented suture (fig. 13A). It is difficult to ascribe much taxonomic significance to this difference, as the form of this suture varies to some degree in *Leptictis*. On the right side of the skull, the maxilla has been displaced laterally, and the contact of this element with the nasal is marked by a faint ridge that divides the dorsal (horizontal) process of the nasal from a more vertically oriented process (fig. 13A). From this, it is clear that the maxilla overlaps the nasal for a considerable extent on the skull roof and nasal-facial exposure (fig. 13A). Differential growth of the maxilla and nasal may thus account for the relatively narrowed nasal exposure in *Palaeictops* and *Leptictis*.

The maxilla has a broad contact with the frontal along an oblique suture (fig. 13A). The condition resembles that in *Leptictis*. In *Palaeictops bicuspis* this contact is narrower, because the posterior nasals are much broader in their contact with the frontals (fig. 2A). The antorbital fossa is distinct, though shallower than in *Leptictis*. The ventral border of the fossa is marked by a pronounced ridge. The anterior foramen of the infraorbital canal (preserved only on the right side of the skull) is a circular, but somewhat smaller, opening



FIG. 11. Left ramus of *Palaeictops multicuspis* AMNH 14741 (holotype), including p2–m3, in (clockwise from upper left) medial, occlusal, and lateral views. Scale bar = 1 cm.

than in the *Leptictis* (fig. 13A–B). As in the latter, the infraorbital canal is relatively short in length; it opens above M1 (fig. 13A–B). Unfortunately, the important relationships of the maxilla with other elements of the orbital region cannot be seen due to poor preservation.

The palatine has a basically similar construction as that in *Leptictis*. Its posterior margin (coincident with the posterior margin of the palate) lies between the last molars (fig. 13B). The margin is biconcave with a distinct, rounded postpalatine torus (fig. 13A–B). The minor palatine foramen is a large opening in the pars perpendicularis that meets the pterygoid (fig. 13A–B). The dorsally trending route of the minor palatine foramen cannot be traced as orbital foramina are obscured by damage. It appears, however, that the dorsal exit of the minor palatine foramen and the sphenopalatine foramen were in closed proximity within a shallow depression, a condition also seen in *Leptictis*.

The lacrimal is a small triangular element vaguely demarcated on both sides of the skull (fig. 13A–B). As in *Leptictis*, the lacrimal foramen is confined fully within the orbit. It faces posteriorly and lies directly below the dorsal ridge of the lacrimal (fig. 13A–B). A lacrimal tubercle is present, though it appears much weaker than this structure in *Leptictis*.

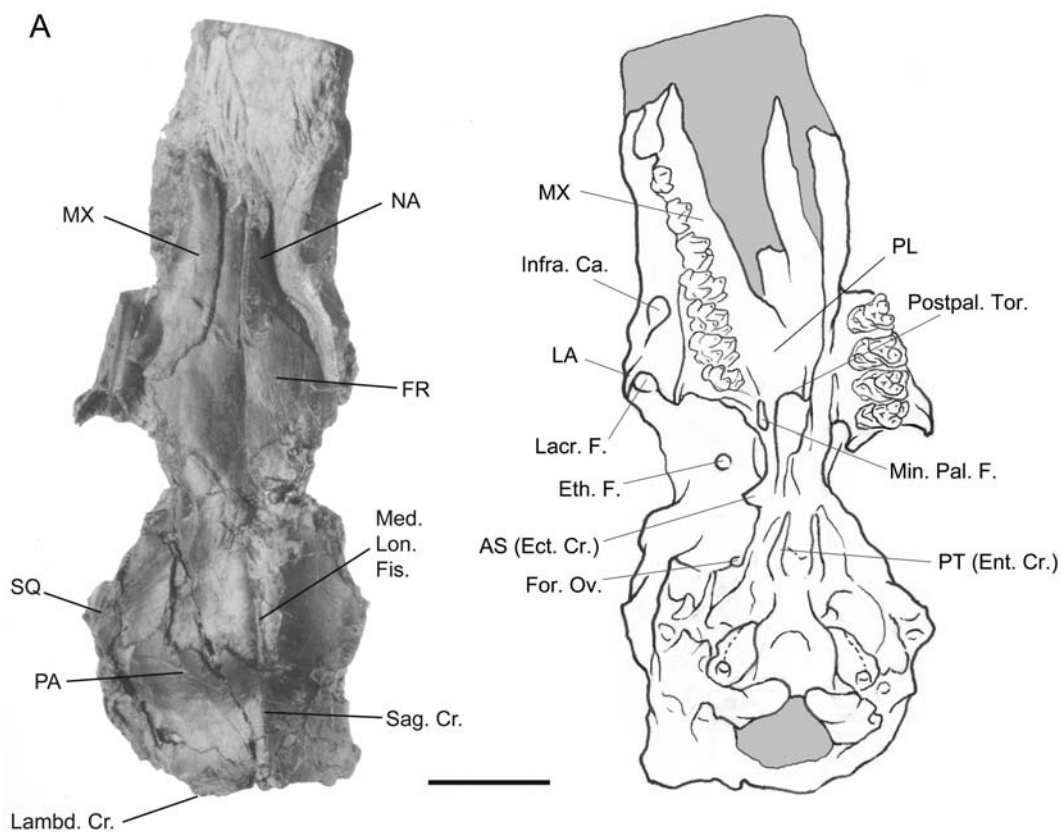


FIG. 12. Right ramus of *Palaeictops multicuspis* AMNH 14741 (holotype), including p4–m3 and alveoli for a double-rooted p2, single rooted canine, and three incisors, in (clockwise from upper left) lateral, occlusal, and medial views. Scale bar = 1 cm.

The jugal is not preserved, but a broken, rugose surface on the anterior root of the zygoma suggests that this element contacted the lacrimal (a common and probably primitive eutherian trait seen in other leptictids).

The frontal is poorly demarcated in the orbit, so it is impossible to determine whether it was isolated from the orbital process of the maxilla by the intrusive palatine. Its separation from the maxilla, however, seems likely, because the palatine-maxillary boundary lies directly above the pars perpendicularis of the palatine. This relationship is like that in *Leptictis*. Accordingly, it's probable that *Palaeictops* shared with the latter the same orbital mosaic. A small ethmoidal foramen is preserved near the frontal-orbitosphenoid suture in the right side of the skull (fig. 13A–B).

The most notable feature of the skull roof is the single sagittal crest, which is best exposed in the posterior parietal near the junction of the sagittal and lambdoidal crests (fig. 13A). More anteriorly, bone is missing and the brain endocast underneath shows the medial longitudinal fissure (fig. 13A). In addition to having only a single median sagittal crest, this skull differs



from *Leptictis* in showing much less sculpturing for attachment of the temporalis muscle on the parietal and squamosal. This, in combination with the comparatively smaller postglenoid process, suggests a weaker development of the temporalis complex of the jaw-closing apparatus. As noted in Novacek (1986), *Leptictis* shows a strong emphasis of orthal shear.

Another interesting feature of the skull roof in *Leptictis* is the extension of the parietal around the lambdoidal crest and its exposure as a small triangular process on the occiput. On the left side of the skull of *Palaeictops altimontis*, there is a break that may indicate the boundary between the parietal and interparietal, suggesting that the parietal in this form also developed an occipital process. Unfortunately, because of poor preservation, this rather anomalous mammalian condition is not clearly identified in *Palaeictops*.

Features of the orbitosphenoid and alisphenoid in the orbit are not clearly preserved (fig. 13B). The presphenoid appears to have a ventral median keel as in *Leptictis*. On the left side of the skull, there appears to be a short, but badly damaged alisphenoid canal just anterior to the foramen ovale.

The pterygoid shows prominent, vertical, entopterygoid crests that form the medial walls of the ectopterygoid fossae (fig. 13A–B). Although this region is damaged, there is evidence for the presence of lateral ectopterygoid crests of the alisphenoid, indicated by the extensive development of the fossae and the flaring of a ridge on the right side of the skull that lies lateral to

B

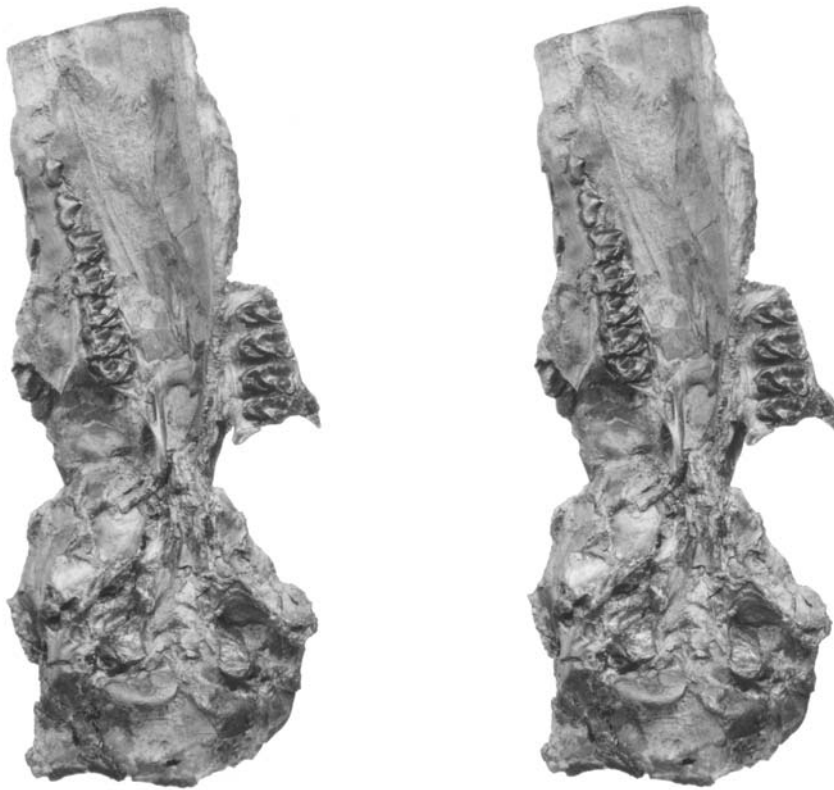


FIG. 13. The skull of *Palaeictops altimontis* AMNH 96250 (holotype): **A**, dorsal view and **B**, stereograph of ventral view with accompanying line drawing. Abbreviations: **AS (Ect. Cr.)**, ectopterygoid crest of the alisphenoid; **Eth. F.**, ethmoidal foramen; **For. Ov.**, foramen ovale; **FR**, frontal; **Infra. Ca.**, infraorbital canal; **LA**, lacrimal; **Lacr. F.**, lacrimal foramen; **Lambd. Cr.**, lambdoidal crest; **Min. Pal. F.**, minor palatine foramen; **Med. Lon. Fis.**, medial longitudinal fissure; **MX**, maxilla; **NA**, nasal; **PA**, parietal; **PL**, palatine; **Post-pal. Tor.**, postpalatine torus; **PT (Ent. Cr.)**, entopterygoid crest (of pterygoid); **Sag. Cr.**, sagittal crest; **SQ**, squamosal. Scale bar = 1 cm.

the entopterygoid crests (fig. 13A–B). As noted in Novacek (1986: 45) it is probable that the manner in which the internal pterygoid muscles originated from the skull is quite similar in *Palaeictops* and *Leptictis*.

The basisphenoid is closely fused with adjacent elements. In ventral view it forms a trapezoidal platform with weak sculpturing for pharyngeal grooves and rectus capitis muscles (fig. 13A–B).

The squamosal is strongly distorted by the dorsoventral flattening of the skull (fig. 13A). However, a few features of interest are recognizable. As noted above, there is no marked rugosity or ornamentation of the lateral moiety of the squamosal in the temporal region. Unlike *Leptictis* the suprameatal fossa behind the zygomatic process of the squamosal is quite shallow. A small opening lies directly above this fossa on the left side of the skull. This is likely the suprameatal foramen. In *Leptictis*, the suprameatal foramen is much larger and is situated more ventrally, well

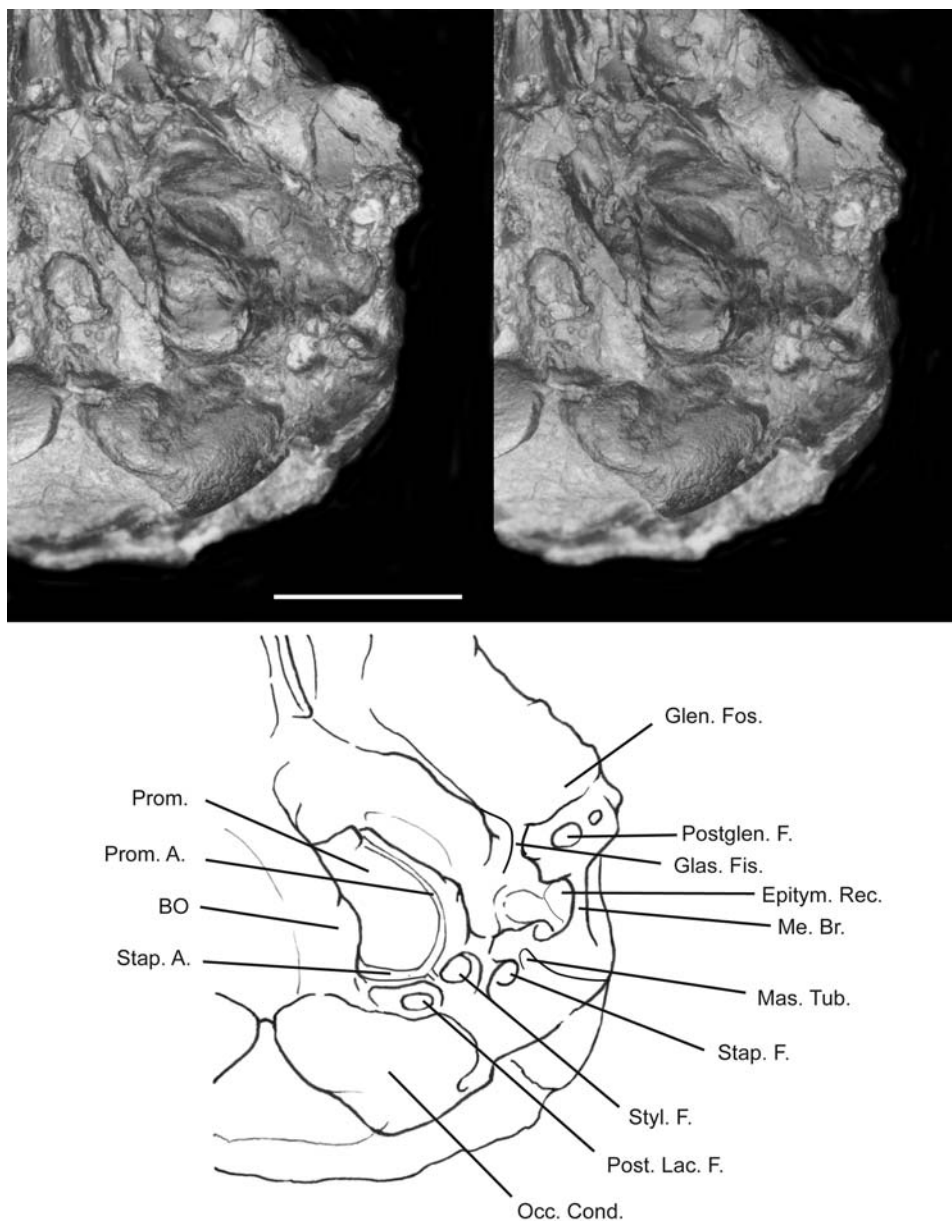


FIG. 14. Stereograph of the left ear region of *Palaeictops altimontis* AMNH 96250 (holotype) in ventral view with accompanying line drawing. Abbreviations: **BO**, basioccipital; **Epitym. Rec.**, epitympanic recess; **Glas. Fis.**, glaserian fissure; **Glen. Fos.**, glenoid fossa; **Mas. Tub.**, mastoid tubercle; **Me. Br.**, meatal bridge of the squamosal; **Occ. Cond.**, occipital condyle; **Postglen. F.**, postglenoid foramen; **Post. Lac. F.**, posterior lacerate foramen; **Prom.**, promontorium; **Prom. A.**, canal for promontory artery; **Stap. A.**, canal for stapedial artery; **Stap. F.**, stapedius fossa; **Styl. F.**, stylomastoid foramen. Scale bar = 1 cm.

within the deep suprameatal fossa. The glenoid fossa for articulation with the lower jaw is a shallow, broad surface, somewhat more extensive and less concave than in *Leptictis* (fig. 14). Although the skull on both sides is damaged in the region of the postglenoid process, it is clear that this feature is smaller than in *Leptictis*. There is only a very narrow bridge of bone representing the root of the postglenoid process. Furthermore, the postglenoid foramen lies posterior and slightly lateral to this area (fig. 14). In *Leptictis* the foramen has shifted to a more medial position, presumably repositioned by the marked expansion of the swollen postglenoid process.

The tympanic region of AMNH 96250 is remarkably well preserved and, thus, shows much more detail than other regions of the skull. There are some obvious departures from the condition in *Leptictis*. The promontorium of the petrosal is more smoothly rounded and does not taper as distinctively in its anterior region (cf. fig. 14 and Novacek, 1986: fig. 22). The regularity in surface features of the promontorium is the result of two other characteristics. The sulci for the promontory (= internal carotid) and stapedial arteries are very narrow and faint, whereas in *Leptictis* they form distinctly deep troughs (cf. fig. 14 and Novacek, 1986: fig. 22). In addition, the petrosal crest that arcs on the medial surface of the promontory is only a weak flange, whereas in *Leptictis* it develops as a distinct and prominent ridge with a rugose contact surface with the entotympanic bulla. Despite the weaker petrosal crest in *Palaeictops altimontis*, it is likely that this form also had an entotympanic bulla. Although this structure is not present in the specimen, it is also commonly not preserved in skulls of *Leptictis*, so it seems to be a feature readily lost during burial. Another feature of the promontorium peculiar to *P. altimontis* is the very broad development of the dorsal lip of the cochlear fossula (fig. 14), which overhangs the fenestra rotunda. In *Leptictis* this feature is also distinct but is less prominent.

There is, as in *Leptictis*, a distinct glaserian fissure in the lateral tympanic roof of AMNH 96250. Lateral to the region of the excavated facial canal, there appears to be an epitympanic recess, although its size is uncertain, because the meatal bridge of the squamosal has collapsed (fig. 14). This bridge, the suprameatal surface of the squamosal, is much narrower than in *Leptictis* (cf. fig. 14 and Novacek, 1986: figs. 20, 21). Moreover, the posttympanic process, which forms the posterior buttress for the roof of the meatus, is weaker in *Palaeictops*. Behind this buttress, the paraoccipital process of the petrosal is somewhat broader in exposure, and it lacks the distinctive groove for the digastric muscle seen in *Leptictis*.

Posterior to the facial canal is a very well-defined stylomastoid foramen. This opening seems even somewhat larger than in *Leptictis*, though the difference here is of dubious significance. In the left tympanic region, there is a small process that arises from the mastoid just medial to the posttympanic process and extends below the facial canal just short of contact with the promontorium in the region of the fenestra vestibuli. This process is likely that of the mastoid tubercle, which may also represent the fusion of the tympanohyal with the petromastoid (fig. 14). The cup-shaped ventral depression on this tubercle characteristic of *Leptictis* is not present, although the tubercle is so badly damaged that presence of this fossa in *Palaeictops* cannot be ruled out. The posterior lacerate foramen is, as in *Leptictis*, merged with the jugular foramen, so there is only one exit for the internal jugular vein and cranial nerves IX, X, and XI. Because the ventral lip of the cochlear fossula is so expanded, there is no narrow trough

between the stapedius fossa and the posterior lacerate foramen (fig. 14). This latter feature is distinctly present in *Leptictis*.

The occiput in *Palaeictops altimontis* is badly compressed and damaged, but it is apparent that there was a prominent mastoid exposure in this region. The anterior edge of the ventral occipital condyles has the sigmoid curvature seen in *Leptictis* and lipotyphlans.

The mandible is deepest below m1 (fig. 15). There is a small mental foramen located below p2 and below the posterior root of p4. At the back of the jaw the masseteric fossa is well excavated. The coronoid process shows some tapering dorsally (fig. 15), but does not show the extreme posterior concavity seen in *Leptictis* (figs. 15 and Novacek, 1986: fig. 1). Because the extremity of the coronoid process is missing, it is uncertain whether the process had a hooklike outline as in *Prodiacodon tauricinerei* or a more bluntly round curved process as in *Palaeictops robustus* (fig. 17). The angular process is damaged in both right and left mandibles. The articular surface of the jaw condyle is slightly broader medially than laterally. The surface features of the condyle are poorly preserved.

There are no upper incisors or canines preserved in AMNH 96250 (fig. 13). The canine alveolus is present on the right side of the skull. P1 is bicuspid, single rooted, and triangularly shaped in lateral outline. P2 is tricuspid, double rooted, and triangularly shaped in lateral outline. The central cusp of P2 is dominant while the most anterior cusp is very minute (fig. 5B).

AMNH 96250 shows a remarkable condition, wherein the right DP4–5 are present and only moderately worn, and the left P5 is already erupted (left P4 is missing) (figs. 5B, 13B). DP4 is roughly triangular in occlusal view with well-developed, somewhat inflated paracone, metacone, and protocone (fig. 5B). There is also a crenulated postcingulum. DP5 is molariform with well-developed paraconule, metaconule, and postcingulum in addition to three inflated main cusps (fig. 5B). There is a pronounced parastylar spur that is overlapped ventrally by the metastylar spur of DP4 (fig. 5B).

A P4 is preserved in AMNH 99301, but it is badly worn. The tooth is roughly triangular in occlusal view, although its parastylar spur is very strong, as is typical of leptictids. P5 is fully molariform with distinct conules. The hypocone is also well developed to nearly a third the height of the protocone. P5 has a strong parastylar spur, but the labial margin of the tooth shows no appreciable invagination.

The upper molars are essentially like P5 although they have broader crowns, more inflated cusps and conules, and (except for M3) relatively larger hypocones and talon basins (fig. 5B). The general construction of the dentition is very like that in other species of *Palaeictops* and in *Leptictis*. The labial margins of the upper molars have shallow inflexions in contrast to the condition in *Prodiacodon*. There is no evidence of a doubling of the paraconule as in the upper molars of *Prodiacodon* (fig. 5B; cf. Novacek, 1986: fig. 4B).

Lower incisors, canine, and p1 are missing from all specimens (fig. 15). The p2 is elongate, trenchant, and two rooted, with a small anterior cuspule, a large central cusp, and a low heel (fig. 15). The p4 resembles p2 but has four cusps: a small anterior cuspule, a large “central” cusp, a small cuspule on the posterior ridge of the central cusp, and a low cuspid heel (fig. 15). The p5 is molariform with a moderately developed paraconid well separated from the metaconid and protoconid and has an elongated talonid basin bordered by three cusps. The crista oblique con-

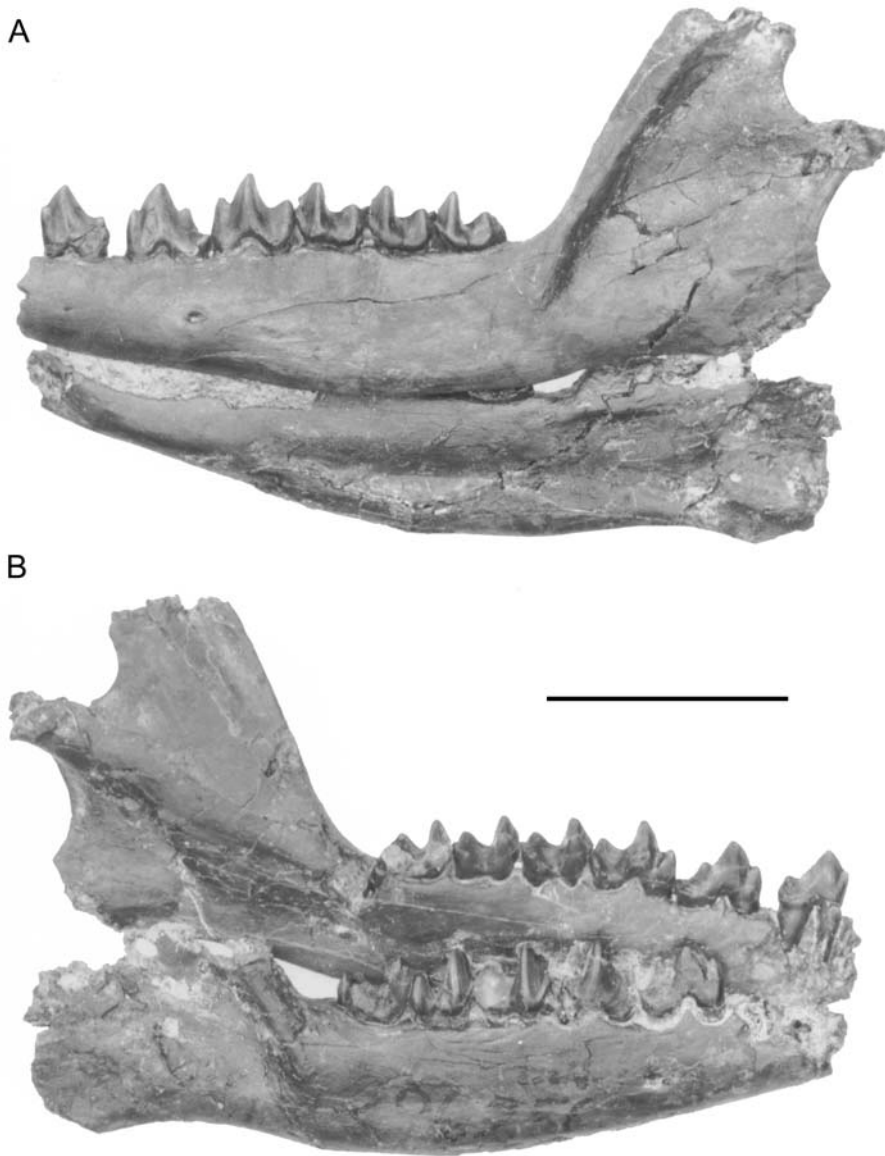


FIG. 15. The mandible of *Palaeictops altimontis* AMNH 96250 (holotype), containing left p2, and p4–m3 and right p4, p5 (damaged), and m1–m3. A, left lateral and B, right lateral views. Scale bar = 1 cm.

tacts the posterior wall of the trigonid nearly directly below the posterior trigonid notch. As noted above the p5 resembles *Palaeictops bicuspis* in having a very open trigonid due to the salient paraconid. The metaconid is less oblique in its alignment with the protoconid than in *P. bicuspis*. The lower molars are very characteristic of *Palaeictops* and *Leptictis* as a whole (see Novacek, 1986: 17), although the trigonid of m2 is notably compressed due to the crestiform paraconid.

REMARKS: The upper cheek teeth of *Palaeictops altimontis* resemble more closely the corresponding teeth of *Leptictis* than any other Paleocene or Eocene leptictid. *Palaeictops altimontis* lacks, however, the distinctive trenchant p4 of *Leptictis*, a condition more closely approached in *P. matthewi*. In addition, *P. altimontis* retains the single sagittal crest and several basicranial characters that are clearly modified in *Leptictis*. Aspects of molar morphology are specializations that separate all known species of *Palaeictops* from *Leptictis*.

Palaeictops bridgeri and *P. altimontis* are thus far known only from Middle Eocene assemblages. They depart from Early Eocene *Palaeictops* species in the structure of the p5 paraconid.

***Palaeictops robustus*, new species**

Figures 16–18, table 1

HOLOTYPE: CM 11954, consisting of a damaged skull that retains P1–P2, P4–M3 on the left side; the right side retains one incisor possibly corresponding to I2, as well as P4–M1 (fig. 16A–B). Left ramus with i1–3, c, p1, p2, and edentulous right ramus (figs. 17, 18).

TYPE HORIZON AND LOCALITY: Leland Bench Wash, 4 mi. west of Ouray, Utah; Wagonhound Member, Uinta B horizon, Middle Eocene (Uintan NALMA).

ETYMOLOGY: From Latin *robustus*, “hard” or “strong.” Refers to the notably large size of the skull.

DIAGNOSIS: Teeth (badly worn) less transverse than in *Prodiacodon* or *Myrmecoboides*. Single sagittal crest unlike *Leptictis* but like *Palaeictops altimontis* and *P. bicuspis* (figs. 2A, 13A, 16A; Novacek, 1986: fig. 2). Significantly larger than all other North American leptictid species (see table 1; cf. Novacek, 1977: table 2).

DESCRIPTION AND COMPARISONS: The skull of *Palaeictops robustus*, despite its poor condition, reveals several features of taxonomic interest. It possesses traits that are shared with *Palaeictops altimontis* but differ in *Leptictis*. There is only a single sagittal crest (fig. 16A). The postglenoid process (though damaged) is weak and confined to the lateral glenoid region. The postglenoid foramen is posterior (rather than posteromedial) to the postglenoid process (fig. 16A). The promontorium is broad and rounded, with a very weak median petrosal crest. There is a broadly expanded dorsal lip of the cochlear fossula.

The right side of the skull shows the base of a large canine. Anterior to this tooth, there is a damaged alveolus and, more anteriorly, the base of an incisor. Beyond the incisor, the premaxilla protrudes to form the floor to the external nares. There is no clear evidence of additional incisor alveoli, so it is likely that the tooth in question is I2, and as in other leptictids, there were only two upper incisors. The dorsal rim of the coronoid process of the mandible is rounded, rather than the hooklike dorsal coronoid process of *Leptictis* and *Prodiacodon tauricinerei* (figs. 17, 18).

REMARKS: The teeth in this specimen are so badly worn that reference to Leptictidae is open to question. However, the last upper premolar is of dimensions that suggest its molari-form construction (fig. 16A–B). Otherwise, *Palaeictops robustus* might just as well be a pantolestid. This species marks the youngest occurrence of *Palaeictops*.

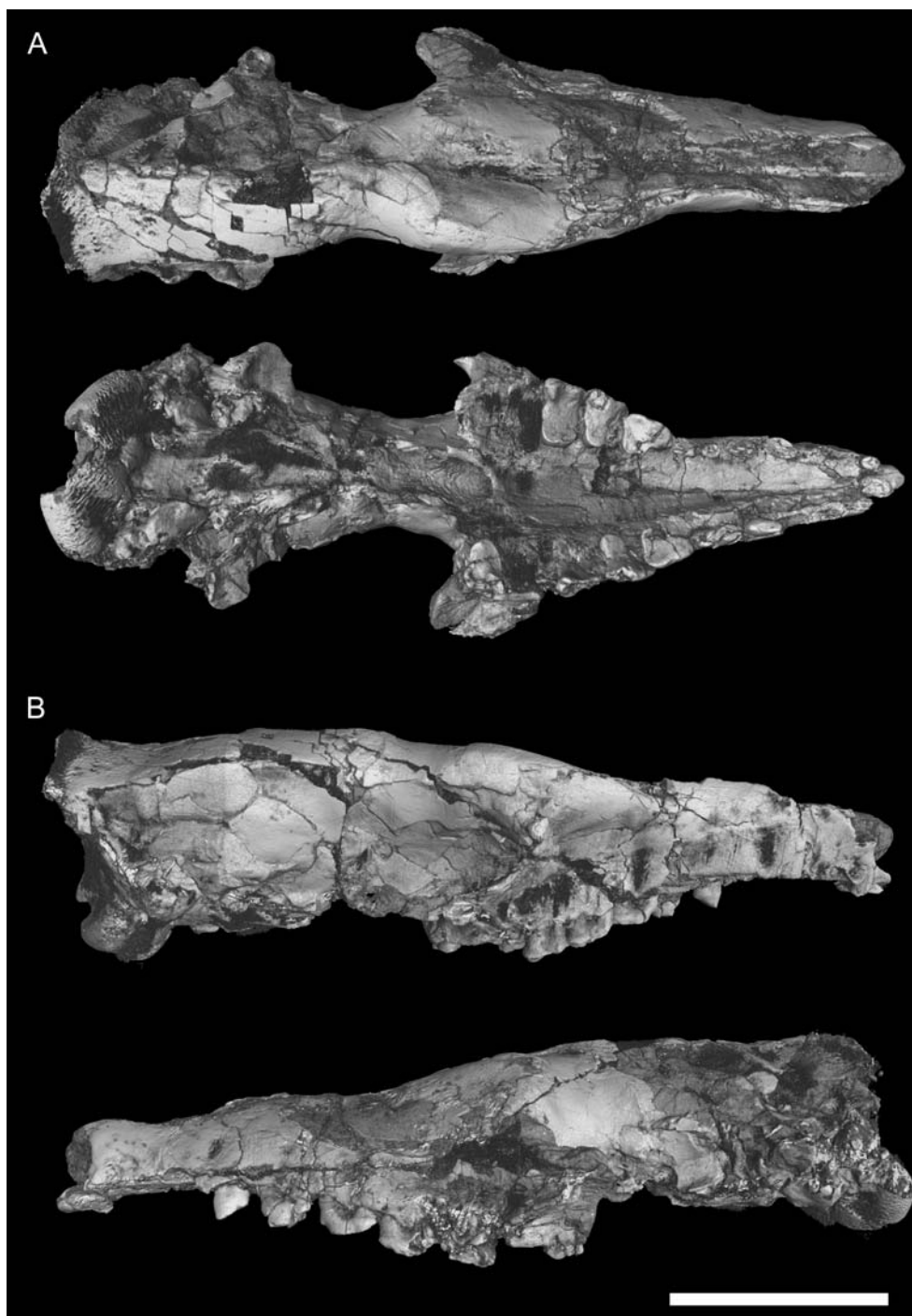


FIG. 16. The skull of *Palaeictops robustus* CM 11954 (holotype), containing P1–P2, P4–M3 on the left side; the right side retains one incisor possibly corresponding to I2, as well as P4–M1. **A**, dorsal (top) and ventral (bottom) views and **B**, right lateral (top) and left lateral (bottom) views. Scale bar = 2 cm.



FIG. 17. Left ramus of *Palaeictops robustus* CM 11954 (holotype), containing i1–3, c, p1, and p2, in medial (top) and lateral (bottom) views. Scale bar = 2 cm.

Palaeictops spp.

REMARKS: Two designated species from Middle Eocene beds are clearly leptictids, but their validity as separate taxa is dubious. The species are *Hypictops syntaphus* described by Gazin (1949) from a maxilla with a right P1–M3 (USNM 13445) found north of Lone Tree in the Bridger Basin of Wyoming, and *Viverravus? nitidus* Marsh (1872), known only from a left dp5 (YPM VP 11888) from Henry's Fork, also in the Bridger Basin.

The teeth of *Hypictops syntaphus* are badly worn (Gazin, 1949: fig. 1), but they are comparable in size to upper teeth that would occlude with the lower dentition of the holotype of *Palaeictops bridgeri* (contra Simpson, 1959). The M2 of “*Hypictops*” is also similar to the M2 from Tabernacle Butte referred here to *P. bridgeri*.

Matthew (1909: 342) remarked that YPM VP 11888, the type of *Viverravus? nitidus* Marsh, 1872, was probably a deciduous last lower premolar of a leptictid. McKenna et al. (1962) sug-



FIG. 18. Right ramus of *Palaeictops robustus* CM 11954 (holotype) in lateral (top) and medial (bottom) views. Scale bar = 2 cm.

gested that this tooth could be a permanent p4 (equals p5 of this paper) of *Hypictops syntaphus*. Either assessment might be correct. The posterior position of the metaconid in YPM VP 11888 is very similar to the condition of the p5 in *Palaeictops bridgeri*. Some differences are apparent, however, and perhaps this is related to differences found between deciduous and permanent teeth of the same taxon.

Thus, there is a strong possibility that *Viverravus? nitidus*, *Hypictops syntaphus*, and *Palaeictops bridgeri* are one and the same taxon. Synonymy would unfortunately establish YPM VP 11888, a single enigmatic tooth, as the type for *Palaeictops nitidus*, and the only specimen referable to *Hypictops* is too badly worn to allow positive identification. It seems best to resist the action of synonymy in these cases.

PHYLOGENETIC ANALYSIS

Our phylogenetic analysis of the 50 character matrix (appendix 2) identified five most parsimonious trees of 70 steps. The majority rule consensus recovered *Megaleptictis altidens* sister to a monophyletic *Palaeictops* (fig. 19). The only clades recovered within *Palaeictops*

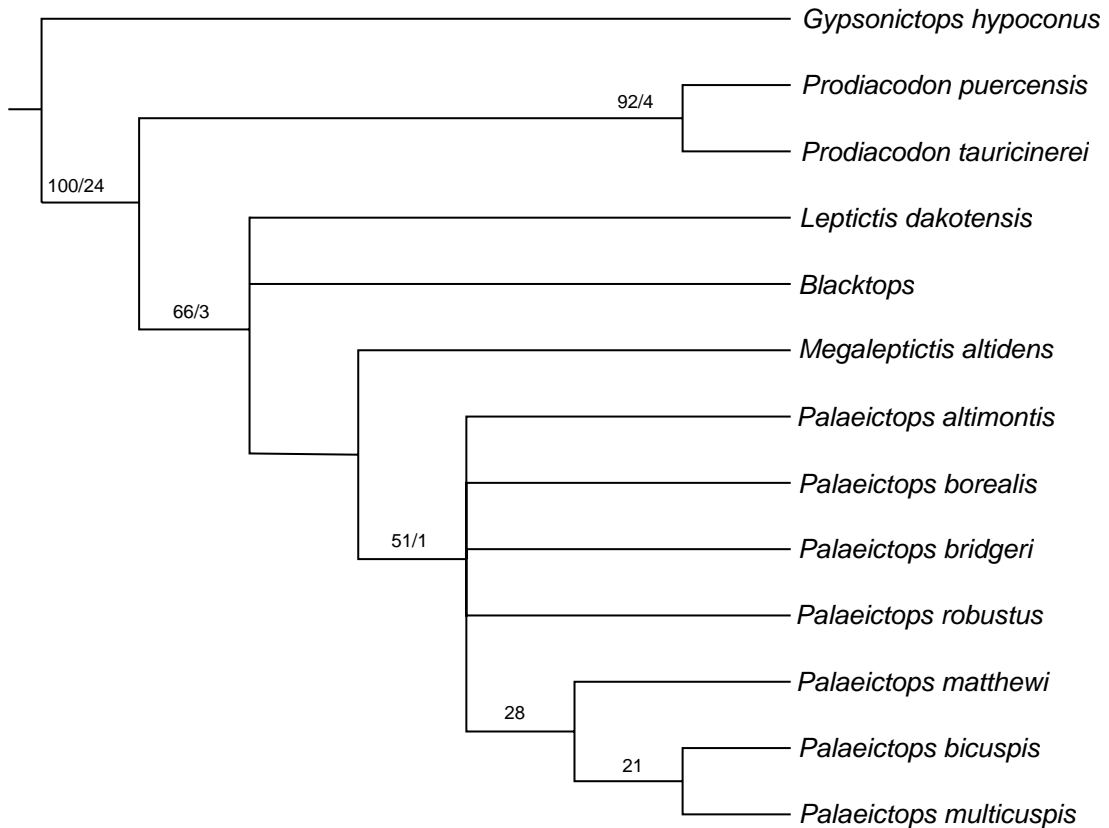


FIG. 19. Majority rule consensus of five most parsimonious trees generated in a phylogenetic analysis of *Palaeictops* species. Support for nodes are shown as MP bootstrap values/Bremer support values.

were a sister relationship of *P. bicuspis* and *P. multicuspis* with *P. matthewi* sister to this clade. The remaining species of the genus form a polytomy at the base of the clade (fig. 19). The support for *Palaeictops* monophyly and the clades within the genus are based on characters noted below.

DISCUSSION

The Leptictida is a key group for understanding crown placental relationships and time of origin. The Late Cretaceous *Gypsonictops* (Gypsonictopidae) has been variously proposed as a member of this group (Van Valen, 1967; Lillegraven, 1969; Clemens, 1973), although Novacek (1977) excluded it from the clade represented by Paleogene leptictids. *Gypsonictops* is known only by partial maxillae, mandibles, and upper and lower teeth. Unlike Paleogene leptictids and recognized crown placentals, it has five premolars (Clemens, 1973). Phylogenetic studies place Leptictidae either within (Asher et al., 2003; O'Leary et al., 2013) or outside crown Placentalia (Wible et al., 2007, 2009). O'Leary et al. (2013) recovered Leptictidae, represented by *Leptictis*, nested within

Afrotheria. If the addition of *Gypsonictops* to their analysis results in the grouping of *Gypsonictops* with Paleogene leptictids and in retention of these species within crown Placentalia, this would extend the time of origin of crown Placentalia into the Cretaceous and would also expand the membership of Placentalia to include taxa with five premolars. Resolution of this question requires a more comprehensive analysis of *Gypsonictops* along with other Cretaceous therians now underway (Velazco et al., in prep.). In this study *Gypsonictops* is included as an outgroup for purposes of phylogenetic analysis of incontrovertible leptictid taxa (fig. 19), acknowledging that it might prove to be positioned outside Leptictida and all other crown group Placentalia.

Members of the family Leptictidae are relatively small mammals with long snouts and body masses that range from about 200 to 700 g (Rose, 1999). The largely sectorial dentitions in leptictids suggest adaptations to insectivory. One of the two new species described here, *Palaeictops robustus*, with a condylobasal skull length of approximately 84 mm and an estimated p5–m3 length of 23 mm is the largest species of North American leptictids. The next two largest North American species in the family are *Leptictis douglassi* (p5–m3 length = 18.86 mm) (Novacek, 1976) and *Megaleptictis altidens* (condylobasal skull length = 68 mm; p5–m3 length = 13.5 mm) (Meehan and Martin, 2012). These two species are easily distinguishable from *P. robustus*: *M. altidens* has a paired sagittal crest whereas *P. robustus* has only one sagittal crest and in the case of *L. douglassi* by its trenchant P4 (less trenchant in *P. robustus*).

At the generic level, few phylogenetic analyses have included *Palaeictops* as part of their study taxa. In his evaluation of the phylogenetic relationships of Pseudorhyncocyonidae, Hooker (2013) found Leptictidae (represented by *Palaeictops* and *Prodiacodon*) to be sister to the clade formed by Pantolestidae and Palaeonodonta. Gunnell et al. (2008) found *Prodiacodon* sister to a clade containing *Palaeictops* and *Leptictis*. Our analyses, which included all known species of *Palaeictops*, as well as *Blacktops*, *Leptictis dakotensis*, *Megaleptictis altidens*, *Prodiacodon puercensis*, *P. tauricineri*, and *Gypsonictops hypoconus*, identified *Palaeictops* and *Megaleptictis* as sister taxa, but this relationship lacked support (fig. 19). Consistent with Gunnell et al. (2008), our analysis identified *Prodiacodon* as sister to a clade that includes *Leptictis* and *Palaeictops*.

The one previous study (Novacek, 1977) that evaluated relationships among species of *Palaeictops* accounted for four species (*P. bicuspis*, *P. bridgeri*, *P. matthewi*, and *P. multicuspis*) and found support for the monophyly of the genus. Our analysis includes seven species of *Palaeictops* (two described here), and also supports monophyly, indicating several characters that separate *Palaeictops* from *Leptictis* and *Prodiacodon* (e.g., single sagittal crest, shallow suprameatal fossa, small suprameatal foramen, shallow groove on the paraoccipital process for the digastric muscle, and protocones lingually swollen on P5–M3).

At the specific level, Novacek (1977) found the four *Palaeictops* species included in his analysis grouped into two clades: *P. bridgeri* + *P. bicuspis* and *P. matthewi* + *P. multicuspis*. The grouping of *P. matthewi* and *P. multicuspis* was supported by the enlargement and proliferation of cusps of p4. In our study, the multicuspsate condition (four or more) of the p4 is also shared with *P. altimontis*. The two clades within *Palaeictops* recovered in our analysis (*P. bicuspis* + *P. multicuspis*,

with *P. matthewi* sister to this clade) are supported by single characteristics of p5 morphology. The sister relationship of *P. bicuspis* + *P. multicuspis* is supported by an anterior accessory cuspule at the labial base of the paraconid on p5. The other clade, which includes *P. bicuspis*, *P. matthewi*, and *P. multicuspis*, is supported by the presence of a strongly developed p5 paraconid.

With the two new species described here, as well as the taxa recently described by Meehan and Martin (2010, 2012), the diversity of North American leptictids increases to 29 species. That number is likely to be augmented by further consideration of several putative species potentially referable to *Palaeictops*, *Prodiacodon*, *Myrmecoboides*, or *Xenacodon*, as well as a possible new genus (Gunnell et al., 2008).

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APPENDIX 1

CHARACTERS IN THE PHYLOGENETIC ANALYSIS

1. Sagittal crest morphology: (0) single sagittal crest, or (1) paired sagittal crests.
2. Lacrimal tubercle on anterior edge of orbit: (0) weakly developed, or (1) well developed.
3. Nasal posterior expansion: (0) absent, or present.
4. Suprameatal fossa, located behind the zygomatic process of the squamosal: (0) deep, or (1) shallow.
5. Suprameatal foramen: (0) large, or (1) small.
6. Basioccipital that overlaps ventrally the promontorium of the petrosal: (0) less expanded, or (1) more transversely flared.
7. Grooves on the promontorium; these grooves are for the promontory and stapedial branches of the internal carotid artery: (0) deep, or (1) shallow.
8. Posterior lacerate foramen: (0) much larger than stapedius fossa, or (1) only slightly larger than the stapedius fossa.
9. Bridge of the mastoid tubercle of the petrosal; this bridge extends from dorsal rim of the cochlear fossula between the stylomastoid foramen and stapedius fossa: (0) wide, or (1) narrow.
10. Groove on the paraoccipital process for digastric muscle: (0) deep, or (1) shallow.
11. Paraoccipital process size: (0) large, or (1) small.
12. Postglenoid process: (0) large, or (1) small.
13. Postglenoid foramen position: (0) posteromedial to postglenoid process, or (1) posterior to postglenoid process.
14. Median petrosal crest of the promontorium: (0) well developed, or (1) weakly developed.
15. Fossula cochlea dorsal rim: (0) less expanded, or (1) more expanded.
16. Mandibular ramus: (0) slender, or (1) deep.
17. Posterior concavity of coronoid process: (0) absent, or (1) present.
18. Extremity of coronoid process: (0) hooklike, or (1) rounded.
19. P4 anterior extension: (0) less anteriorly projected, or (1) anteriorly extended.
20. Trenchant P4: (0) less developed, or (1) well developed.
21. P4 paracone development: (0) well developed and swollen, or (1) less developed.
22. P5 and upper molars occlusal anteroposterior length: (0) more elongated, or (1) less elongated.
23. P5 and upper molars (paracones, protocones, and metacones): (0) shorter crowns, or (1) taller crowns.
24. P5 and upper molar crowns (hypocone development): (0) moderately developed, or (1) well developed.
25. Upper molar protocones lingually swollen: (0) less, or (1) more.
26. Upper molar trigonids: (0) higher, or (1) lower.
27. Upper molar parastylar spur development: (0) less developed, or (1) more developed.
28. Precingulum in lingual region of upper molars: (0) less extensive, or (1) extensive.

29. Upper molars “doubled” paraconule: (0) absent, or (1) present.
30. M2 ectoflexi: (0) shallow, or (1) deep.
31. p2 number of cusps: (0) two cusps, (1) three cusps, or (2) four cusps.
32. p4 anterior cusp presence: (0) absent, or (1) present.
33. Trenchant p4: (0) less developed, or (1) well developed.
34. p4 number of cusps: (0) three cusps, (1) four cusps, or (2) five cusps.
35. p5 length: (0) elongate, or (1) short.
36. Prefossid between paraconid and metaconid on p5: (0) small, or (1) large.
37. p5 paraconid: (0) weakly developed, (1) moderately developed, or (2) strongly developed.
38. p5 paraconid anterior accessory cuspule at labial base: (0) absent, or (1) conspicuous.
39. p5 trigonid: (0) open, or (1) closed.
40. p5 metaconid and protoconid alignment: (0) metaconid aligned less obliquely relative to protoconid, or (1) metaconid positioned more posteriorly relative to the protoconid.
41. p5 talonid: (0) short, or (1) large.
42. p5 talonid: (0) open lingually, or (1) closed lingually.
43. m1–m3 trigonids: (0) lower, or (1) higher.
44. m3 hypoconulid location: (0) less lingually, or (1) more lingually.
45. Angle between the sacral vertebrae and the long axis of the ilium: (0) less acute, or (1) more acute.
46. Anterior inferior gluteal eminence: (0) small, or (1) large .
47. Rim of the acetabulum: (0) weakly developed, or (1) well developed.
48. Projection of the ischium above the level of the acetabulum: (0) less dorsal, or (1) more dorsal.
49. Anterior ilium: (0) not flared in lateral direction, or (1) distal flaring in lateral direction.
50. Tibia and fibula fusion: (0) distal one-third fused, or (1) not fused.

APPENDIX 2

DATA MATRIX

Character matrix employed in this paper for assessing the phylogenetic relationships among *Palaeictops* species. Character description and coding are listed in appendix 1. Missing or unknown characters are represented by “?”. An electronic version of this matrix is available online (<http://www.morphobank.org>), project: P2545, Systematics of the genus *Palaeictops* Matthew, 1899 (Mammalia: Leptictidae), with the description of two new species from the Middle Eocene of Utah and Wyoming).

	5	10	15	20	25	30	35	40	45	50
<i>Gypsonictops hypoconus</i>	?????	?????	?????	0??00	01110	11001	01011	00000	1011?	?????
<i>Prodiacodon puercensis</i>	?????	?????	?????	0??10	11100	01111	?1011	10110	10101	11111
<i>Prodiacodon tauricinerei</i>	1?1??	?????	?????	00010	11100	01011	01011	10100	1110?	?????
<i>Blacktops</i>	110??	0?01?	0????	????00	10010	10001	?????	?????	?????	?????
<i>Leptictis dakotensis</i>	11000	00000	00000	01010	10010	10001	00101	00010	11000	00000
<i>Megaleptictis altidens</i>	11001	0?0??	00???	00100	10010	10001	001?1	?00?0	0?0??	?????
<i>Palaeictops altimontis</i>	00011	11111	11111	00???	?0011	10001	11010	11000	0000?	?????
<i>Palaeictops bicuspis</i>	0?111	?????	?????	00?10	00011	10001	?0000	02101	0011?	?????
<i>Palaeictops borealis</i>	?????	?????	?????	?????	?0011	1010?	?????	?????	??0??	?????
<i>Palaeictops bridgeri</i>	?????	?????	?????	0????	?????	?????	?????	11001	0000?	?????
<i>Palaeictops matthewi</i>	?????	?????	?????	0??01	00011	10000	01110	02001	001?1	11110
<i>Palaeictops multicuspis</i>	?????	?????	?????	1????	?????	?????	21120	02101	0010?	?????
<i>Palaeictops robustus</i>	01???	????1	11111	001??	?0011	10???	?????	?????	?????	?????

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