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A REVIEW OF PALEOCENE AND EOCENE LEPTICTIDAE
(EUTHERIA: MAMMALIA) FROM NORTH AMERICA

by

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ABSTRACT

Abundant and widely distributed fossils demonstrate a diversity of leptictid species in North America during the Paleocene and Eocene epochs. The late Cretaceous genus *Gypsonictops* markedly contrasts with the Tertiary leptictids, but is recognized as the most closely related sister taxon of the latter. The genus *Diacodon* is removed from the Leptictidae because the type species, *D. alticuspis*, more closely resembles adapisoricid insectivores. Three major leptictid lineages are known from the Paleocene and Eocene of North America. One lineage, the genus *Prodiacodon*, shows the retention of primitive sectorial features in the dentition. The second lineage, *Palaeictops*, shows a more derived "bunodont" condition. *Palaeictops*, particularly *P. matthewi* (n. sp.), is undoubtedly closely related to the Oligocene *Leptictis*. *Myrmecoboides* represents the third early divergent lineage not closely related with other leptictid genera. A new species, *Prodiacodon crustulum*, from the Puercan of Montana shows a combination of dental characters intermediate between *Gypsonictops* (*Hypocoenus*) and *Prodiacodon puercensis*.

INTRODUCTION

The Leptictidae is an archaic family of eutherian mammals with a long evolutionary history. Earliest undoubted members are known from the early Paleocene of North America and the family persisted with reasonable diversity until the end of the middle Oligocene. Records of the group in Europe are fewer with cited occurrences from the later Paleocene of Germany (Russell, 1964), the middle Eocene of Germany (Tobien, 1962) and the late Eocene or early Oligocene of France (Filhol, 1892).

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The primitive nature of the Leptictidae has long been recognized and the family has been cited as a central stock from which a number of important eutherian groups might be derived (Lillegraven, 1969; Clemens, 1973). Others (Szalay, 1968; Clemens, 1974) have concluded that leptictids were not direct ancestors of such groups as primates. Leptictids have been included in the Order Insectivora in many classifications (e.g., Simpson, 1945; Van Valen, 1967). However, as Butler (1956, 1972) and McDowell (1958 and unpublished studies) have pointed out, the family does not share with undoubted insectivores such specializations as a loss of a medial internal carotid artery, the absence of the entotympanic as a bullar component, the crowding out of palatine by the maxillary bone in the orbital region of the skull, and the loss or reduction of a jugal bone. Accordingly, Butler (1972) has proposed the recognition of the order Proteutheria from Romer's (1966) suborder and the inclusion of the Leptictidae within it. Butler (1972) acknowledged that his establishment of the Proteutheria was a matter of practicality. The majority of similarities between members of this group merely represent shared-primitive eutherian characters. Thus the order replaces the Insectivora as a "waste-basket" category. More recently, McKenna (1975) has proposed that Tertiary leptictids belong to the superorder Leptictida also comprising anagalids, macroselidids, and lagomorphs. Other members of Butler's Proteutheria were relegated by McKenna to various eutherian "supergroups". McKenna's Leptictida is a stimulating concept, in part suggested by evidence from the skull, dentition, and postcranial skeleton. Nevertheless this idea has yet to be tested rigorously with a careful analysis of the available morphological evidence. Such a critique is not the subject of this review, and, in recognition of the current controversy on the matter, I have not formally assigned leptictids to any of proposed higher categories. An assignment will be made following a detailed study of the broader affinities of the Leptictidae (Novacek, unpublished data). The aims of the present paper are confined to a characterization of the family and taxonomic revision of its Paleocene and Eocene members.

DISTRIBUTION

Fig. 1 shows the localities where North American Paleocene and Eocene leptictids described in this report have been recovered. The figure is accompanied by Table 1 listing the land mammal age, formation, and leptictid taxa represented at a particular locality. It is evident that leptictids had a widespread distribution throughout much of the Rocky Mountain region of western North America during early Cenozoic times.

METHODS

The dental nomenclature employed here follows that of Rich (1971: 4).

All specimens were measured on an Ehrenreich Photo Optical "shop-scope." Measurements were in millimeters and were rounded off to

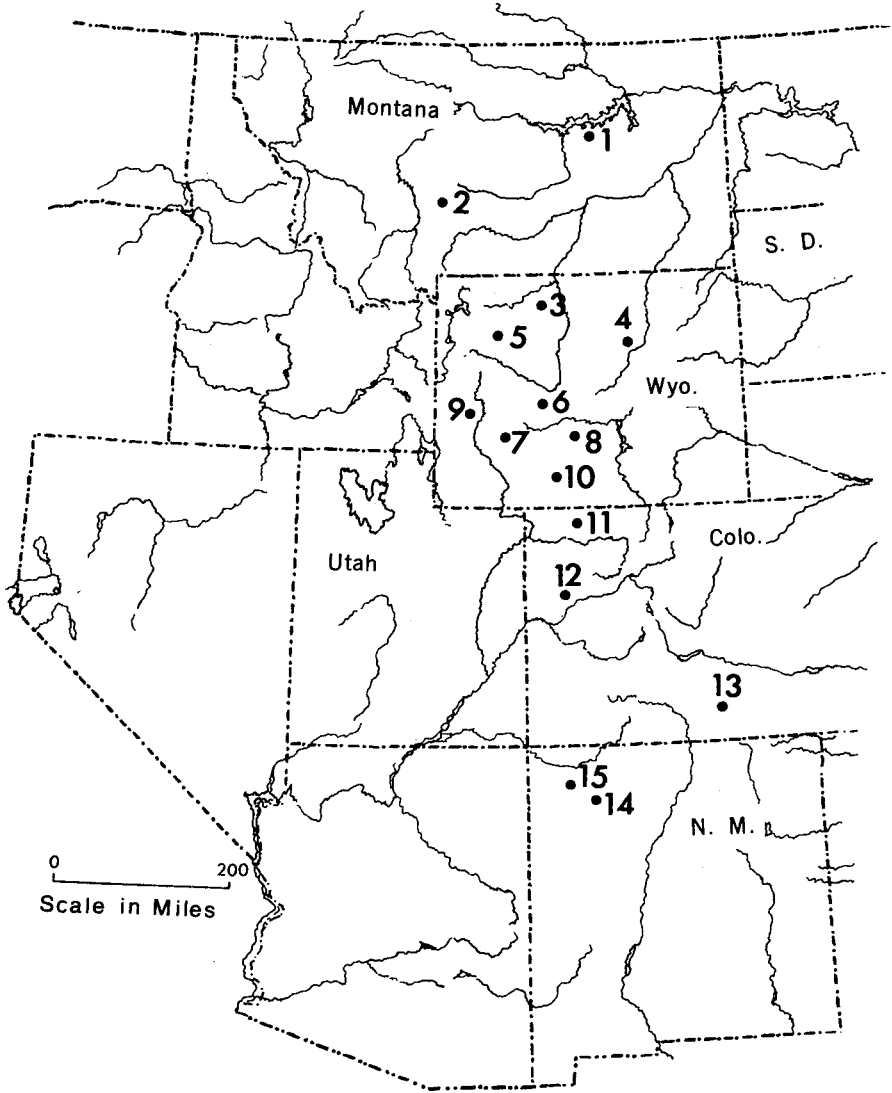


FIG. 1. Map showing Paleocene and Eocene North American localities where leptictids described in this report have been recovered. Numbers refer to localities listed in Table 1.

TABLE 1. North American Paleocene and Eocene localities where leptictids described in this report have been recovered.

Locality	Age	Formation	Taxa
1. Garbani	Puercan	Tulloch	<i>Prodiacodon crustulum</i>
2. Crazy Mtn. Field, Gidley Quarry	Torrejonian	Fort Union	<i>Myrmecoboides montanensis</i> <i>Prodiacodon concordiarcensis</i> <i>Prodiacodon furor</i>
3. Bighorn Basin	Wasatchian	Willwood	<i>Prodiacodon tauricinerei</i> <i>Palaeictops bicuspis</i>
4. Powder River	Wasatchian	"Wasatch"	<i>Prodiacodon tauricinerei</i>
5. Tepee Trail	Uintan	Tepee Trail	<i>Palaeictops</i> sp.
6. Wind River Basin, Bridger Creek	Wasatchian	Wind River	<i>Palaeictops bicuspis</i> <i>Palaeictops multicuspis</i> <i>Prodiacodon tauricinerei</i>
7. Tabernacle Butte	Bridgerian	Bridger	<i>Palaeictops bridgeri</i>
8. Bison Basin	Tiffanian	Fort Union	<i>Prodiacodon concordiarcensis</i>
9. Big Piney	Wasatchian	Wasatch	<i>Prodiacodon tauricinerei</i>
10. Bitter Creek	Wasatchian	Wasatch	<i>Prodiacodon tauricinerei</i>
11. Four Mile, East Alheit Pocket	Wasatchian	Wasatch	<i>Prodiacodon tauricinerei</i>
12. Cherard Park	Wasatchian	Wasatch	<i>Palaeictops matthewi</i>
13. Garcia Canon	Wasatchian	Huerfano	<i>Palaeictops matthewi</i>
14. Arroyo Blanco	Wasatchian	San Jose	<i>Prodiacodon tauricinerei</i>
15. San Juan Basin, Torrejon Arroyo	Torrejonian	Nacimiento	<i>Prodiacodon puercensis</i>

the nearest one-hundredth of a millimeter. The following orientation for measuring cheek teeth (Fig. 2) were used in this report.

ANTEROPSTERIOR AXIS ("A-P") AXIS

Lower posterior premolars - long axis of tooth.

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

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

Upper molars (M¹⁻²) - line drawn through the apices of the paracone and metacone.

Upper molars (M³) - line drawn at right angles to a line which divides the tooth into equal anterior and posterior halves.

LENGTH

Lower posterior 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 back of the talonid along a line parallel to the "A-P" axis (anterior cingulum not included in measurement).

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

WIDTH

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

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

Upper posterior premolars and upper molars - two measurements anterior width, distance from the labialmost point of the anterolabial corner of the crown to the lingualmost point of the protocone; posterior width, distance from posterolabialmost point of metastylar lobe to lingualmost point of protocone, both width measurements taken at right angles to the "A-P" axis.

The dental measurements of all specimens studied are given in Table 2.

ABBREVIATIONS

- AMNH - American Museum of Natural History
- CMNH - Chicago (Field Museum) of Natural History
- LACM - Los Angeles County Museum
- PU - Princeton University
- UCMP - University of California Museum of Paleontology
- CIT - California Institute of Technology

DENTAL IDENTIFICATIONS

The primitive eutherian dental formula is traditionally recognized as $\frac{1.2C1P4M3}{3143}$. McKenna (1975) has proposed a novel hypothesis of dental evolution in the Eutheria, maintaining that the

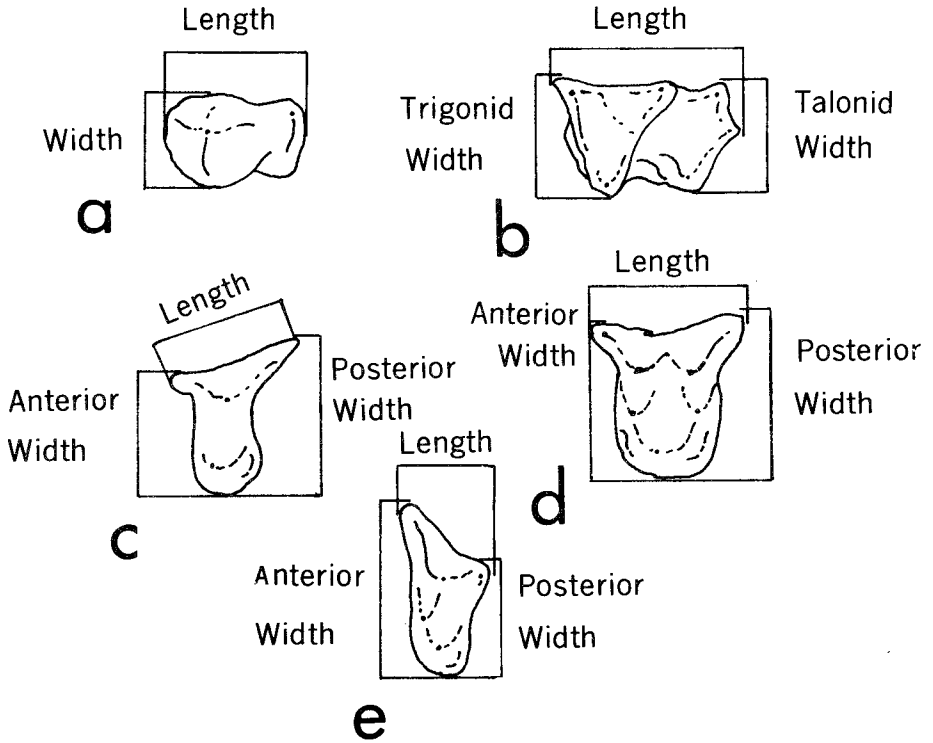


FIG. 2. Diagram showing criteria for dental measurements of a) lower posterior premolars, b) lower molars, c) upper posterior premolars, d) upper molars, and e) upper last molar (M_3). See text for explanation.

most primitive members of the infraclass had 5 upper and lower premolars. He identifies the dental formula in these forms as $\begin{matrix} 1 & 1 & 2 & 3 & 1 & 1 & 2 & 3 & 1 & 1 & 2 & 3 \\ \hline 1 & 2 & 3 & 1 & 2 & 3 & 1 & 2 & 3 & 1 & 2 & 3 \end{matrix}$. There is evidence that a (unknown) lineage which gave rise to Tertiary leptictids had such a dental formula. Lillegraven (1969, p. 57) and Clemens (1973, p. 6) described specimens of the late Cretaceous genus *Gypsonictops* with five lower premolar loci, reduction to four in number occurring through loss of the reduced tooth at the third premolar locus (P_c of Clemens' and Lillegraven's notation) in at least one known specimen. In all Tertiary leptictids where a complete dental row is known, only four premolars are present. McKenna (1975) identifies these as $P_1P_2P_4P_5$, arguing that P_3 (and, or DP_3) were lost in leptictids. It is recognized in this study that *Gypsonictops* is closely related to Tertiary leptictids. McKenna's dental hypothesis is thus more compatible with this phylogenetic picture than traditional dental designations. In this paper $P_5 =$ tradi-

TABLE 2. Measurements of cheek teeth of North American Paleocene and Eocene leptictids described in this report. All measurements are in millimeters.

Element	Upper Cheek Teeth			Element	Lower Cheek Teeth		
	Length	Width	Width		Length	Width	Width
AMNH 4802 Type of <i>Palaeictops bicuspis</i>							
LP ⁴	5.25	2.80		LP ₅	3.92	1.55	2.14
LP ⁵	3.40	4.40	3.86	LM ₁	3.11	2.15	2.35
LM ₁	3.07	3.81	4.11	LM ₂	3.00		
LM ₂	2.72	3.97	3.75	LM ₃	3.27	2.37	1.70
LM ₃	2.44	3.17	2.65				
AMNH 4255							
				LM ₂	3.09	2.00	2.45
				LM ₃	3.40	2.30	2.14
<i>Palaeictops bridgeri</i>							
AMNH 56032 Type							
				RP ₅	4.25	2.31	2.22
				RM ₁	3.65	2.53	2.47
				RM ₂	3.58	2.69	2.64
				RM ₃	4.00	2.39	2.03
<i>Palaeictops multicuspis</i>							
AMNH 14741 Type							
				LP ₂	3.66	1.42	
				LP ₄	4.42	1.74	
				LP ₅	4.21	2.41	2.21
				LM ₁	3.20	2.67	2.63
				LM ₂	3.27	2.65	2.47
				LM ₃	3.40	2.50	2.09
<i>Palaeictops matthewi</i>							
CMNH 26904 Type							
RP ⁴	3.26	2.50		LP ₄	4.02	1.60	
RP ⁵	2.80	3.21	3.56	LP ₅	3.90	2.05	1.84
RM ₁	2.90	4.03	4.17	RM ₁	3.10	2.36	2.04
RM ₂	2.82	4.41	4.16	RM ₂	3.21	2.36	2.13
RM ₃		3.60					
CMNH 26481							
RP ⁴	3.57	3.06					

TABLE 2. Continued.

Element	Upper Cheek Teeth			Element	Lower Cheek Teeth		
	Anterior Length	Posterior Width	Posterior Width		Trigonid Length	Trigonid Width	Talonid Width
<i>Myrmecoboides montanensis</i>							
USNM 8037 Type							
				LP ₅	2.95	1.46	1.12
				LM ₁	2.37	1.63	1.40
				LM ₂	2.42	1.65	1.40
				LM ₃	2.67	1.75	1.35
<i>Prodiacodon puercensis</i>							
AMNH 16011 Type							
RP ₅	2.62	4.00	4.40				
AMNH 16748							
RP ₄	3.50	3.03		LP ₅	3.90	2.13	2.04
RP ₅	3.31	3.87	4.28	LM ₁	3.45	2.80	2.56
RM ₁	3.15	4.67	5.14	LM ₂	3.48	3.13	2.36
RM ₂	3.40	5.15	5.33	LM ₃	3.80	2.81	1.93
RM ₃	2.33	4.14	3.67				
<i>Prodiacodon tauricinerei</i>							
PU 13104 Type							
LP ₄	2.75	2.39		RP ₄	2.96	1.41	
LP ₅	2.10	3.25	2.95	RP ₅	3.10	1.65	1.59
LM ₁	2.65	3.48	3.53	RM ₅	2.39	1.83	1.72
LM ₂	2.66	3.99	3.85	RM ₁	2.46	1.92	1.77
				RM ₂	2.77	1.70	1.30
				RM ₃			
PU 14726							
AMNH 80695							
LP ₄	3.01	2.11		LP ₅	3.06	1.53	1.47
LP ₅	2.81	2.87	3.01	LM ₅	2.53	1.75	1.39
LM ₁	2.65	3.23	3.27				
LM ₂	2.34	3.82	3.55				
LM ₃	2.10	3.40	2.71				

TABLE 2. Continued.

Lower Cheek Teeth				Lower Cheek Teeth			
Element	Trigonid	Talonid		Element	Trigonid	Talonid	
	Length	Width	Width		Length	Width	Width
<i>Prodiacodon tauricinerei</i>							
				AMNH 48763			
AMNH 80023				LP ₅	3.09	1.22	1.56
				LM ₁ ⁵	2.42	1.85	1.63
RP ₅	2.96	1.65	1.51				
RM ₁	2.97	1.97	1.22	USNM 19204			
RM ₂	2.41	2.52	1.85				
RM ₃	2.82	1.95	1.51	LM ₂	2.72	2.25	1.91
				LM ₃	2.94	2.07	2.57
<i>Prodiacodon concordiarcensis</i>							
USNM 9637 Type				USNM 35693			
LP ₅	2.14	1.29	1.02	RM ₁	2.06	1.45	1.29
LM ₃	1.95	1.43	1.47	RM ₂	1.83	1.51	1.13
				RM ₃	1.89	1.40	1.00
USNM 20970							
LP ₅	2.40	1.67	1.25				
LM ₁	2.15	1.85	1.40				
<i>Prodiacodon furor</i>							
AMNH 35291 Type				AMNH 35289			
RP ₅	3.09	1.68	1.40	LP ₅	2.39	1.57	1.20
				LM ₁ ⁵	2.29	2.00	1.13
				LM ₂	2.16	1.82	1.45
AMNH 35290							
RM ₁	2.54	1.91	1.73				
RM ₂	2.52	1.98	1.62				
Upper Cheek Teeth							
Element	Anterior		Posterior				
	Length	Width	Width				
<i>Prodiacodon crustulum</i>							
UCMP 114990				UCMP 114993			
LM ¹	2.4 *	4.0 *	4.08 (Type)	DP ₅	3.74	1.47	1.44

TABLE 2. Continued.

Element	Upper Cheek Teeth			Element	Lower Cheek Teeth		
	Anterior Length	Posterior Width	Width		Trigonid Length	Talonid Width	Width
<i>Prodiacodon crustulum</i>							
LACM 32970				UCMP 114991			
RM ¹	2.67	3.75	3.82	LM ₁ or 2	2.81	2.25	1.83
UCMP 114980				UCMP 114985			
LM ^x	2.40	3.99	3.9 *	LM ₃	3.27	1.79	1.57
UCMP 114976				UCMP 114992			
RM ^x			3.99	LM ₁ ?	2.84	2.04	1.72
UCMP 114979				UCMP 114981			
LP ⁴	3.45	2.21		LM ₂ ?	2.74	1.94	1.80
UCMP 114974				UCMP 114986			
LP ⁴	3.19	2.23		RM ₂ ?	2.91	2.09	1.79
UCMP 114972							
LP ⁵ ?	2.58	3.14	3.38				
* Tooth damaged, measurement approximate							
x Position in tooth row unknown							

tional P_4^4 , P_4^4 = traditional P_3^3 , and P_3^3 are thought to be absent. All other dental identifications correspond to their traditional designations. P_1^1 may actually be DP_1^1 as there is no evidence of replacement at this locus in primitive eutherians.

SYSTEMATIC PALEONTOLOGY
Family LEPTICTIDAE Gill, 1872

Diagnosis.-- Dental formula $\frac{1-2}{3-2} C 1 P_1^1$ (or DP_1^1) $\frac{P_2^2 P_4^4 P_5^5 M_1-3}{2^2 4^4 5^5 1-3}$. Canines and (D) P_1^1 single rooted. P_4^4 double rooted, usually trenchant without a basined talonid. P_5^5 molariform with paraconid and basined talonid with three or more cusps. Molar trigonids anteroposteriorly compressed. Molar talonids with large shallow basins. Entoconulid often present. M_3 with salient hypoconulid. P_4^4 with paracone, metacone, protocone (protocone secondarily lost in *Leptictis haydeni*), anterior accessory cuspule, and posterior cingulum. Molariform P_2^2 (hypocone reduced, vestigial, or absent in some forms) with posterior and anterior cingula. Upper molars with labially positioned paracone and metacone, very narrow ectocingulum, paraconule and metaconule, pre- and postcingula and a hypocone. Skull (where known) with

elongate snout, elongate nasal bones, and small lacrimal foramen. Infraorbital canal short. Jugal bone present. True postglenoid process well developed. Subsquamosal foramen present. Maxilla with large orbital wing. Auditory bulla formed by entotympanic bone, not completely covering tympanic cavity. Medial branch of the internal carotid artery present, but small. Flange of the periotic at the posterior wall of tympanic chamber absent and the fenestra rotunda fully exposed. Stylomastoid foramen not isolated from the tympanic chamber by the tympanohyal. All known leptictid skeletons have the following diagnostic features: Forelimb much shorter than hindlimb. Enlarged deltoid crest present on anterior surface of humerus. Hindlimb with elongate tibia, fibula, and pes. Tibia-fibula contact broad or bones fused distally. Sternum enlarged with prominent keel. Strong pubic symphysis. Astragalar foramen present ventrally, but not dorsally. Elongate metatarsals and phalanges. Plantigrade.

Age and Distribution.-- Early Paleocene - late Oligocene, North America; late Paleocene-?late Eocene, Europe (see Fig. 1, Table 1 for distribution of North American Eocene and Paleocene leptictids).

Genera excluded.-*Diacodon* (type *D. alticuspsis*) has long been considered a leptictid. The type specimen of *D. alticuspsis*, USNM 1098 from San Jose Formation, New Mexico, (See Cope, 1875, Matthew and Granger, 1918), a very poorly preserved lower jaw, has a broken last premolar which is uncharacteristically submolariform. Excellent undescribed cranial and dental material of *Diacodon alticuspsis* from the San Jose Formation further demonstrates that this species is not a leptictid. *Diacodon alticuspsis* differs from leptictids in having 1) a last premolar with a small metaconid, a paraconid that does not project far anteriorly, and a very shortened talonid with only one or two cusps; 2) lower molars with low trigonids which lean slightly forward toward their apices, a very low cristiform paraconid, a reduced, centrally positioned hypoconulid, and a hypoconid that is worn flat and much lower than the entoconid; 3) a penultimate upper premolar that is minute relative to the last one and has only one main cusp; 4) a last upper premolar that is submolariform, lacking a definite hypocone and having a small metacone on the posterior shoulder of the paracone, a strong postmetacrista leading to the posterolingual corner of the crown, and a protocone much lower than the paracone and metacone; 5) upper molars that are not transverse but anteroposteriorly broad with prominent parastylar and metastylar lobes, and strong postmetacristae. In these features *D. alticuspsis* more closely resembles *adapisoricids* and the similarity of this species to *Scenopagus edenensis* (Robinson, 1966) and *S. mcgrewi* (McKenna and Simpson, 1959) is striking.

Other species of *Diacodon* have either been removed from the Leptictidae (see Robinson, 1966, and Van Valen, 1967) or referred to other leptictid genera (see below).

Leptonysson basiliscus Van Valen (1967) from the medial Paleocene (Torrejonian) Crazy Mountain Field Fauna of Montana is here excluded from the Leptictidae in agreement with arguments presented by Clemens (1973, p. 29-30). *Diacodon packi* (originally described as *Leptacodon packi* by Jepsen, 1930a) has a submolariform last lower premolar and is probably a nyctitheriid related to *Leptacodon tener* (McKenna, 1968).

Remarks. -- The most recent review of the Leptictidae was published by Van Valen (1967) who subdivided the family into three subfamilies - Procerberinae, Gypsonictopinae and Leptictinae. The Gypsonictopinae includes only the late Cretaceous genus *Gypsonictops*, whose reference to the Leptictidae has been questioned (Butler, 1972). Clemens (1973) considered the relationship of *Gypsonictops* in detail and referred this genus to the Leptictidae but pointed out such action requires a substantially broader definition of the family. Unlike all Cenozoic leptictids, *Gypsonictops* variably has 5 lower premolars set closely in the jaw, the paraconid of P_2 is small or absent, and the P_2 and upper molars usually lack distinct hypocones. In all specimens where the posterior region of the mandible is preserved an inflected angular process is present. The ectocingulum or styler shelf on the upper molars is much broader than that in Cenozoic leptictids. Lillegraven (1969, p. 58) and Clemens (1973, p. 33) have also remarked on the significant difference in occlusal pattern between *Gypsonictops* and other leptictids. Since four upper and lower premolars, a molariform P_2 , and molar hypocones are key diagnostic characters of all leptictids excepting *Gypsonictops*, strong argument is provided for removing the latter from the family. It presently seems best to regard *Gypsonictops* as the most closely related sister group but not as a definite member of the Leptictidae. The possible relationships of *Gypsonictops* with other eutherian families has been considered at length by Szalay (1968), Lillegraven (1969), Clemens (1973) and McKenna (1975).

Van Valen's (1967) leptictid subfamily Procerberinae has been shown by Lillegraven (1969) to be more properly allied with *Cimolestes* and other early palaeoryctids, the latter may, however, be related to leptictids through such forms as *Kennalestes* and *Asioryctes* (Kielan-Jaworowska, 1969, 1975; McKenna, 1975 and pers. comm.).

Several European genera, *Diaphyodectes*, *Adapisoriculus*, and *Adunator* (medial and late Paleocene Cernay and Walbeck faunas), were recognized by Russell (1964) as leptictids. Guth (1962) described an exquisitely preserved leptictid skeleton from late Paleocene beds at Menat Basin, France, but made no formal assignment of the specimen. The aberrant *Pseudorynchoeyon* from the early Oligocene Quercy Phosphorites was recently assigned by Sige (1974) to a new leptictid subfamily, the Pseudorynchoeyoninae. Sige (1974) also allocated the medial Eocene *Leptictidium* to his newly established subfamily. A detailed consideration of the

relationships of the alleged European leptictids to North American forms is presented elsewhere (Novacek, unpublished data).

Genus *Palaeictops* Matthew, 1899

Stypolophus Cope, 1880

Ictops: Cope, 1881

Parietops Granger, 1910

Diacodon: Matthew and Granger, 1918

Diagnosis.-- P₅ and upper molars not transverse nor anteroposteriorly compressed, with low bulbous cusps very narrow styelar shelves, small but distinct hypocones, very short anterior cingula, and conules situated labially at base of paracone and metacone. M₂ not significantly transversely wider than M₁. Parastylar spurs not strongly developed and ectoflexi not deep on M₂ and M₃. Paraconid on P₅ well developed. Molar trigonids not as elevated as in *Prodiacodon*. Skull (where known) with a single median sagittal crest and a very narrow zygomatic arch.

Type species.-- *Palaeictops bicuspis* (Cope, 1880) described as *Diacodon bicuspis* by Matthew and Granger (1918).

Geologic range.-- Wasatchian (early Eocene)-early Uintan (later Eocene).

Remarks.-- Species of *Palaeictops* can easily be distinguished from other known Paleocene and Eocene leptictids by their notable lack of such sectorial features as very transverse, anteroposteriorly compressed molars with sharp, elevated cusps, which indicate an emphasis on shearing and piercing in occlusion. The major difficulty arises in conveniently separating *Palaeictops* from the Oligocene leptictid *Leptictis* (Leidy, 1868). There are definite dental differences between the two genera but a series of species here referred to *Palaeictops* represent intermediate stages that grade easily into the condition represented in *Leptictis* (see below). The type species of *Palaeictops*, *P. bicuspis*, however, is clearly different from *Leptictis* in the presence of a single sagittal crest rather than double parasagittals, and in having nasal bones which are enlarged posteriorly. Van Valen (1967) expressed doubt as to whether parasagittal crests were universally present in *Leptictis* but this feature is in fact present without exception in the large sample (200 skulls) representing the genus. The double parasagittal crest therefore appears to be a useful diagnostic character in separating *Leptictis* from *Palaeictops*. Unfortunately, the single sagittal crest is clearly preserved only in *P. bicuspis*. Reference of other species to *Palaeictops* is based primarily on dental evidence, and consequently the assignment of species like *P. matthewi* is somewhat arbitrary. This is to be expected. *Palaeictops* is undoubtedly very closely related to *Leptictis* and one of its lineages probably gave rise to the latter.

Palaeictops bicuspis (Cope, 1880) Matthew, 1899

Fig. 3

Stypolophus bicuspis Cope, 1880, p. 746*Ictops bicuspis*: Cope, 1881, p. 192; Cope, 1885, Pl. XXIXa, figs. 2 and 3*Palaeictops bicuspis* Matthew, 1899*Diacodon bicuspis* Matthew and Granger, 1918, p. 574-576, figs. 3-5

Diagnosis.-- P_4^h with large, swollen paracone, very small anterior accessory cuspule, and small protocone. Styler shelf on P_2 only present external to metacone. Hypocone present on P_5 . Pre-cingulum on P_2 and upper molars not extensive, terminating far short of lingual edge of protocone. P_4^h lacking an anterior accessory cusp. P_4 heel is very small. P_5 with large bulbous paraconid, and minute cuspule at labial base of paraconid. Lower molars with bulbous rather than piercing cusps, trigonids not greatly elevated relative to talonids. M_2 with salient hypoconulid. Skull with single sagittal crest and nasals swollen posteriorly.

Type.-- AMNH 4802, skull and jawsType locality.-- Wind River Basin, Wyoming. Wind River Fm., Wasatchian (early Eocene).Referred material.-- AMNH 4255, left mandible with broken M_1 , M_{2-3} from Willwood Fm., Bighorn basin, Wyoming. Wasatchian.

Remarks.-- Cope (1880) originally described *Palaeictops bicuspis* as a species of *Stypolophus*, a taxon also containing several creodonts, and later (1881) transferred the species to the Oligocene genus *Ictops* (now considered a junior synonym of *Leptictis*; see Van Valen, 1967). The name *Palaeictops* was assigned by Matthew (1899) in a footnote of a biostratigraphic review. Matthew and Granger (1918) referred the species to *Diacodon*, but was later taken out of synonymy by Gazin (1952) who recognized the very reduced talonid of P_4 in *Diacodon alticuspis* as a character denoting its generic separation from *Palaeictops*.

The type of *Palaeictops* is a badly crushed skull, and the reconstruction of the specimen provided by Matthew and Granger (1918, Fig. 3 and 5, p. 575) takes some rather strong creative liberties. For example, the reconstruction shows the presence of three incisor alveoli in the upper jaw, while only two can actually be discerned on the specimen. The reconstruction of the skull shape is based primarily on the Oligocene *Leptictis* and its accuracy seems doubtful. However, at least the diagnostic cranial features of *P. bicuspis*, the single sagittal crest and the posteriorly flared nasal bones, are readily recognizable in the original specimen.

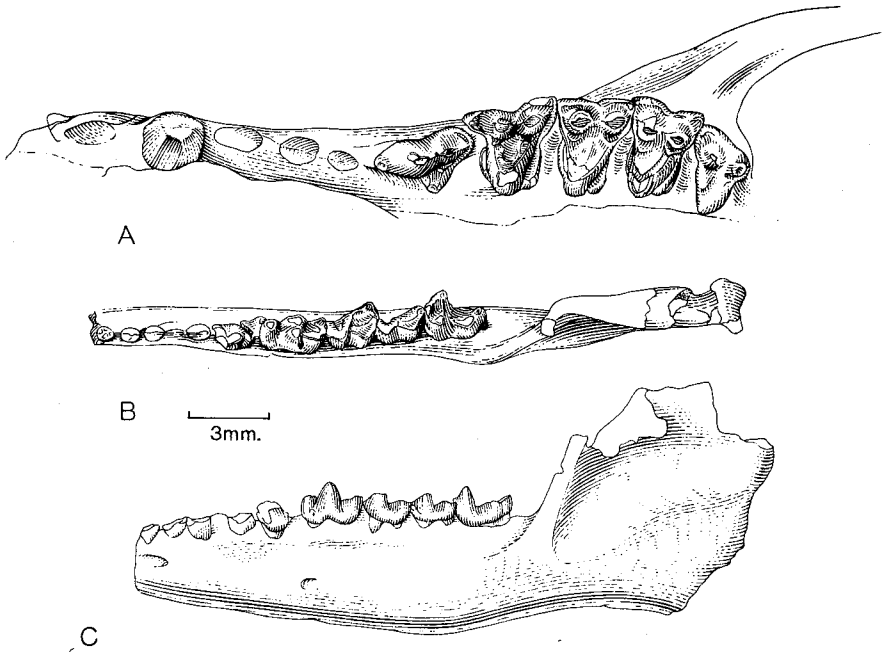


Fig. 3. *Palaeictops bicuspis* AMNH 4802 Type. A. Left maxilla with C, P₅, M¹⁻³ and alveoli for I³, (D) P¹, P², occlusal view. B. Left mandible with P₄ fragment, P₅, M₁₋₃ and alveoli for (d) P₁, P₂, occlusal view. C. Same specimen as B, lateral view.

Palaeictops bridgeri (Simpson, 1959) Van Valen, 1967

Diacodon bridgeri Simpson, 1959; p. 1-5, fig. 1.

Diagnosis.-- Very similar to *Palaeictops bicuspis* in dental features but approximately 15% larger and P₅ with a distinctly more open prefossid as a result of the anterolingual projection of the paraconid and the position of the metaconid more posterior to that of the protoconid. Talonid basins relatively broader than in *P. bicuspis*.

Type Specimen.-- AMNH 56032, a right lower jaw with P₅-M₃.

Type locality.-- Locality 6 of McGrew (1959) in the vicinity of Tabernacle Butte, Wyoming. Bridger Formation, Bridgerian (medial Eocene).

Remarks.-- In his original description of *Palaeictops bridgeri*, Simpson (1959) noted the strong similarity between this species and *P. bicuspis*. If not for its distinctive P_7 characteristics *P. bridgeri* would be synonymous with the genotypic species. At the least, the two species appear to be very closely related. Simpson (1959) remarked that the trigonids in *Palaeictops bridgeri* are not particularly short or square; but this is not entirely accurate as the trigonids in this species have the relatively lower profile characteristic of *Palaeictops* in contrast to the higher, more piercing trigonid cusps of *Prodiacodon*.

Palaeictops bridgeri shows a close resemblance to the *Leptictis* species, *L. haydeni*, and *L. dakotensis* in lower cheek tooth morphology. However this Bridgerian species is distinguished from *Leptictis* in details characteristic of *Palaeictops*, namely a P_7 paraconid set more lingually rather than central on the antero-posterior axis of the crown, less conical paraconids, and a more salient hypoconulid on M_3 .

Palaeictops multicuspis (Granger, 1910) Van Valen, 1967
Fig. 4

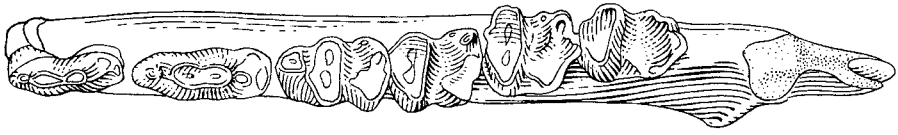
Parietops multicuspis Granger, 1910

Diagnosis.-- Large *Palaeictops* species with much deeper ramus than other species referred to the genus. Mental foramen below anterior root of P_7 . P_7 trenchant with four cusps. P_4 very large tooth; higher than P_5 , trenchant with very small, low anterior accessory cusps, two main cusps, and at least two low cusps on the shortened heel. All cusps aligned along the anteroposterior axis of the tooth. P_5 with strong paraconid and minute cuspule at labial base of paraconid. P_7 paraconid large, not well separated from metaconid, with prefossilid interrupted labially by close approximation of paraconid with protoconid. Paraconid on molars set quite lingually and closely approximated to metaconid. M_3 hypoconulid not so posteriorly projecting as in *Palaeictops bicuspis*.

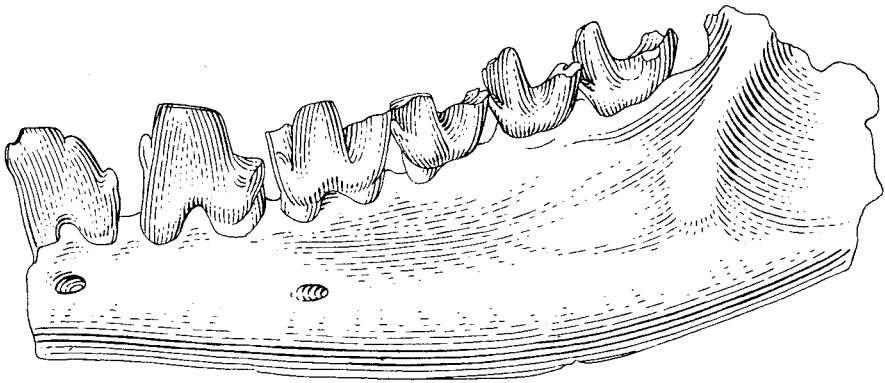
Type Specimen.-- AMNH 14741, a left ramus with P_2, P_4, P_5, M_1-3 and a right ramus with P_4, P_5, M_1-3 and alveoli for double-rooted P_2 and single rooted canine, and three incisors.

Type locality.-- Alkali Creek, (Buck Springs) of Wind River Basin, Wyoming. Lost Cabin beds, Wind River Formation, Wasatchian (early Eocene).

Remarks.-- The reference of this species to *Palaeictops* is provisional; it is primarily based on the low profile of the molar trigonids and the similarity of the P_7 to that of *P. bicuspis* in the strong development of the paraconid and the presence of a minute cuspule at the labial base of the paraconid. Unfortunately, heavy wear on the molars renders an accurate estimate of trigonid elevation impossible. As is evident from the diagnosis of



A
4mm.



B

FIG. 4. *Palaeictops multicuspis*. AMNH 14741 Type. Left mandible with P_{4-5} , M_{1-3} . A. Occlusal view. B. Lateral view.

Palaeictops, upper molars are much more useful for purposes of identification than are lower molars.

The P_{2} and P_{4} of *Palaeictops multicuspis* are unique in their large size and in the development of several cusps. As in the dentitions of species of *Prodiacodon*, an anterior accessory cusp is present on P_{4} but the great size of this tooth relative to P_{5} differs from the condition observed in all *Prodiacodon* species.

I concur with Van Valen (1967, p. 235) that the characters of P_{2} and P_{4} (= Van Valen's P_{3}) do not warrant recognition of *Palaeictops multicuspis* as a distinct genus.

Palaeictops matthewi new species

Figs. 5, 6

Diagnosis.-- Species of *Palaeictops* with lower dentition similar to *P. multicuspis* but 8% smaller and P_2^2 simpler in morphology with only one main trenchant cusp and a basal posterior cuspsule. P_4^1 very large double-rooted tooth much higher than P_5^1 with a minute anterior basal cuspsule, a very large main cusp broadly connected with a slightly smaller, more posterior cusp, and a short transverse ridge on the posterior heel separated from the rest of the crown by a transverse trough. Trigonids in P_5^1 and lower molars not greatly elevated relative to talonid. P_5^2 metaconid set posterior to protoconid but not to the degree present in *P. bridgeri*. P_4^1 high, enlarged tooth (relatively much higher than P_2^2) with a very prominent paracone, smaller metacone, and low protocone. Apex of protocone set directly opposite the notch between the paracone and metacone. Very narrow cingula present anterior to paracone and posterior to metacone. P_2^2 with very narrow styler shelf continuous along labial border of crown and slight ectoflexus. Postcingulum well developed. Small parastyle and parastylar lobe, conules set labially at bases of paracone and metacone. Upper molars with labial conules. Precingula not elongate, terminating lingually nearly directly below the midpoint of the preprotocrista. M_1M_2 with distinct parastylar and meta-stylar spurs. Hypocones larger than in *Prodiacodon* but not so developed as in *Leptictis*. Tibia-fibula fused for most of their shaft lengths, as in *Leptictis*. Nasals swollen posteriorly (?) as in *Palaeictops bicuspis*.

Type specimen.-- P26904 (CMNH) lower mandible with C-M₇, badly damaged skull with cheek teeth, partial skeleton including lumbar and caudal vertebrae, pelvis, femur, tibia, carpals, tarsals and phalanges.

Type locality.-- Cherard Park, Garfield Co., Colorado. Shire Member?, Wasatch Formation, Wasatchian (early Eocene).

Referred specimens.-- AMNH 17555. Skull fragments, partial lower jaws, and partial skeleton from Garcia Canon region, Colorado. Lower beds of Huerfano Formation, Wasatchian (early Eocene). P26481, fragmentary upper jaw with DP_4^1 , P_2^2 .

Etymology.-- Named after Dr. William D. Matthew, late 19th-early 20th century paleontologist who made significant contributions to the study of leptictids and many other Tertiary mammals.

Remarks.-- *Palaeictops matthewi* is an interesting species because it exhibits a dental morphology transitional between other species of *Palaeictops* and the Oligocene *Leptictis haydeni* and *L. dakotensis*. The similarity between the $P_2^2P_4^1$ morphology of the latter species and *P. matthewi* is striking. The only significant difference is the lack of an anterior accessory cusp in the P_4^1 of *Leptictis*. The overall morphology of $P_2^2P_4^1$ is unique within the

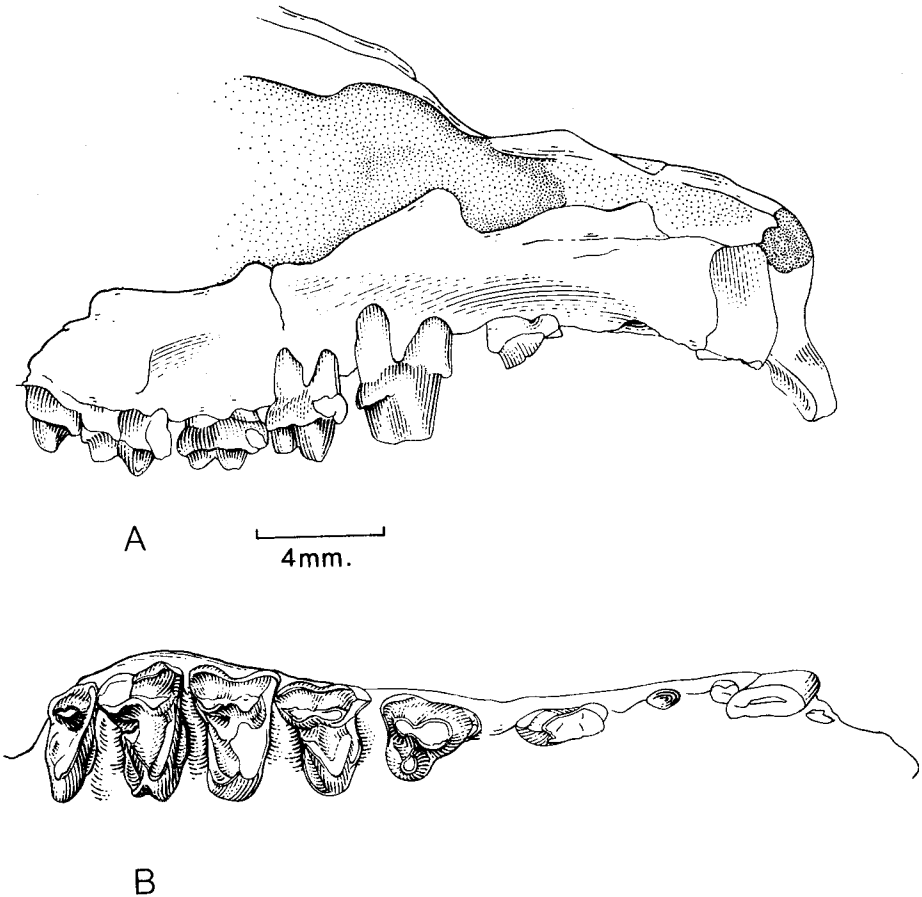


FIG. 5. *Palaeictops matthewi*. n.sp. CMNH 26904 Type. Fragmentary skull with canine root, P² fragment, P⁴⁻⁵, M¹⁻³ and alveolus for (D)P¹. A. Lateral view. B. Occlusal view.

Leptictidae to *Leptictis* and *P. matthewi* and is here interpreted as a shared-derived character. Skeletal features in *P. matthewi* also strongly resemble those in *Leptictis*; particularly interesting is the common possession of tibia-fibula fusion for almost the total length of the shaft, a distinct departure from the more primitive condition represented in *Prodiacodon* where only the distal ends of the tibia-fibula are fused. There is, in fact, a strong enough resemblance of *P. matthewi* to *Leptictis* to make the generic assignment of this form somewhat arbitrary. However,

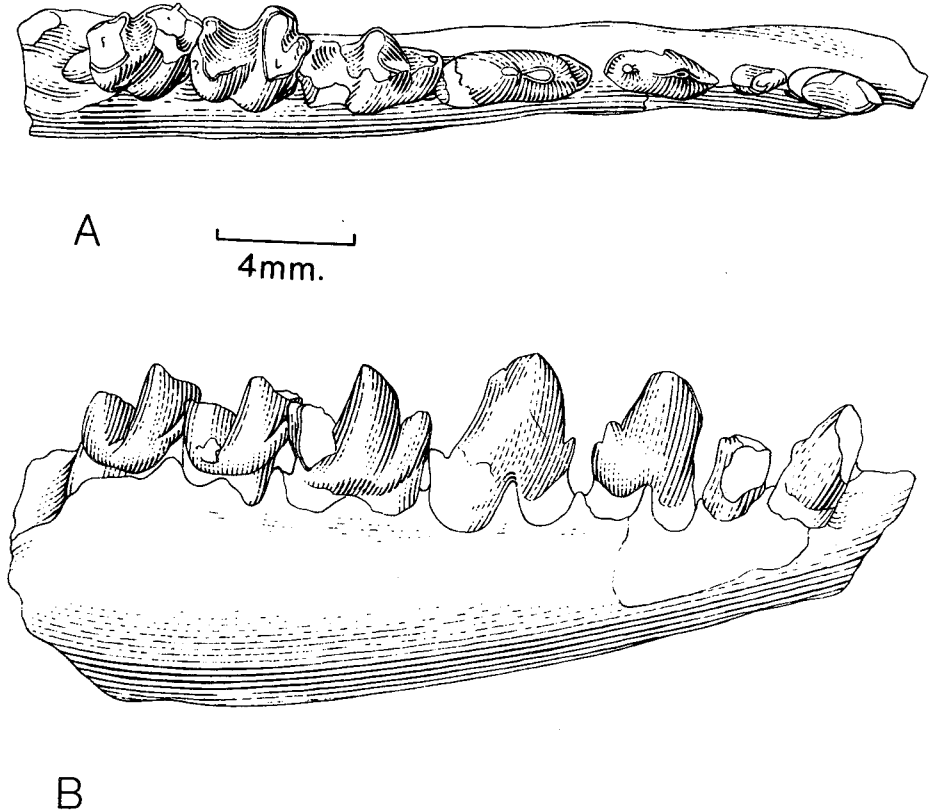


FIG. 6. *Palaeictops matthewi* n.sp. CMNH 26904 Type. Right mandible with (d)P₁, P₂, P₄₋₅, M₁₋₂. A. Occlusal view. B. Lateral view.

P. matthewi has not yet made the full transition in molar specializations: unlike *Leptictis* and like other species of *Palaeictops* the upper molars do not show the exaggerated swelling of the molar cusps, the strongly developed hypocones, the row of small cuspsules on the posterior cingulum, and the lack of prominent parastylar and metastylar spurs on M₁₋₂. These differences are slight, to be sure, but would be expected when sampling forms that possibly represent intermediates between two major taxa. Unfortunately, the type skull of *P. matthewi* is too badly damaged to provide useful taxonomic information. It is not known, for instance, if *P. matthewi* had double parasagittal crests as in *Leptictis* or a single one as in *P. bicuspis*. The nasal bones appear to be enlarged posteriorly (as in *P. bicuspis* but not as in known skulls

of *Leptictis*), however this observation may not be reliable due to damage in this region of the skull.

Palaeictops multicuspis resembles *P. matthewi* in having an enlarged P_4 of very similar structure. However, the P_7 in *P. multicuspis* is quite distinct in morphology, and this coupled with its significantly larger size seems sufficient evidence for keeping *P. multicuspis* specifically separate from *P. matthewi*.

Palaeictops sp.

A partial leptictid skull and jaws with dentition has been recovered from unit 24 (A beds) of the type section of the Tepee Trail Formation in the East Fork Basin, Fremont County, Wyoming (see Love, 1939; McKenna, 1972 for locality descriptions). This specimen and two other jaw fragments were kindly loaned to me for study by Dr. Malcolm McKenna, who is currently conducting field work and faunal analysis in the East Fork Basin. My interpretation that the specimens represent a new species of *Palaeictops* will be supported elsewhere with detailed descriptions, comparisons and illustrations.

Myrmecoboides Gidley, 1915

Myrmecoboides montanensis Gidley, 1915

Fig. 7

Diagnosis.-- Anterior premolars well spaced. P_1 very small, single-rooted. P_4 with paraconid and heel with basin and posterior cusp (D?) P_7 paraconid considerably salient, prefossilid open labially and lingually, heel elongate very narrow without hypoconulid. Molar trigonids not nearly as elevated as in *Prodiacodon*, paraconids situated very lingually, closely appressed to metaconid producing a "twinned" appearance. Molar paraconids and metaconids much higher than protoconids. M_2 talonid elongate with salient hypoconulid. Entoconulid present on P_5 and lower molars.

Type species.-- *Myrmecoboides montanensis*, middle Paleocene (Torrejonian) described by Gidley (1915) and later by Simpson (1937, p. 115-118, figs. 17-18).

Type specimen.-- USNM 8037. Left lower jaw with P_1 - M_3 .

Type locality.-- Gidley Quarry, Crazy Mountain Field, Sweetgrass County, Montana. Fort Union Formation, Torrejonian (middle Paleocene).

Referred material.-- USNM 9552, P^5 - M^3 (see discussion below).

Remarks.-- In the original description of *Myrmecoboides*, Gidley (1915) allocated this genus to the Marsupialia, noting its strong similarities with *Myrmecobius*. Simpson's (1937) re-analysis

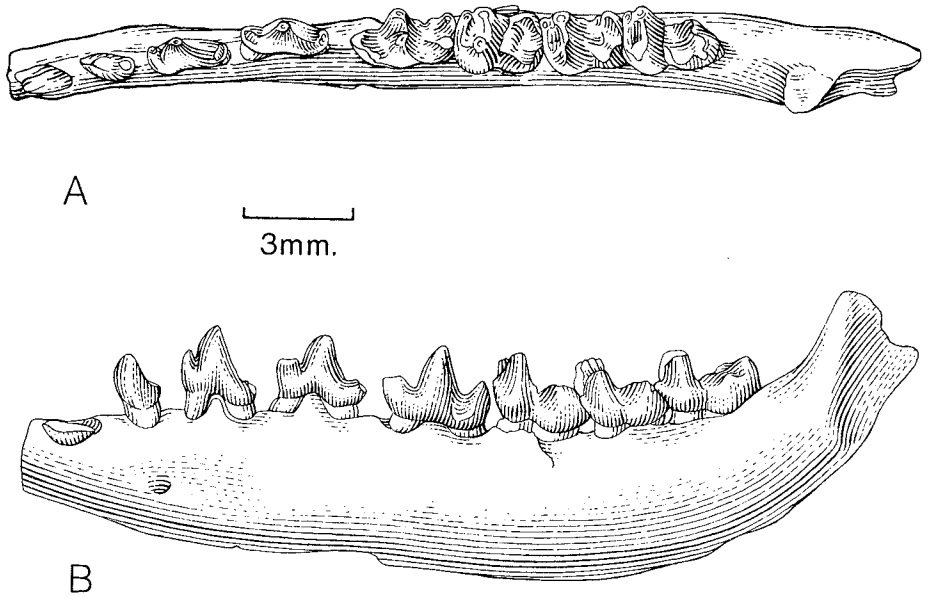


FIG. 7. *Myrmecoboides montanensis* USNM 8037 Type. Left Mandible with (D)P₁, P₂, P₄₋₅, M₁₋₃. A. Occlusal view. B. Lateral view.

demonstrated that *Myrmecoboides* is best referred to the Leptitidae, but as he noted, its position in the family is isolated. Particularly striking is the unique structure of the molar trigonids, namely, the lingual position of the paraconid and its close appression to the metaconid and the much higher relief of the "twinned" metaconid and paraconid relative to the protoconid.

An upper dentition (P⁵-M³, USNM 9552) from Gidley Quarry referred by Simpson (1937) to *Myrmecoboides montanensis* shows a strong resemblance to corresponding teeth in *Prodiacodon puericensis*, thus suggesting a relationship with the latter. I suspected (in agreement with the unpublished opinions of Craig Wood) the reference of this upper set of cheek teeth to *M. montanensis* was erroneous. Percy Butler (personal communication) has however carefully analyzed the occlusal relationships of the upper and lower dentition and convinced me that the association is probably valid. I am still open to the possibility that USNM 9552 might represent the upper cheek teeth of *Prodiacodon furor*, a new species from Gidley Quarry (see below).

Prodiacodon Matthew, 1929*Diacodon*: Matthew and Granger, 1918; Gazin, 1952*Palaeictops*: Van Valen, 1967

Diagnosis.-- P^5 and molars transverse, anteroposteriorly compressed with sharp piercing cusps. P^2 hypocone vestigial or absent. Conules set lingually, not at the base of paracone and metacone as in *Palaeictops* and *Leptictis*. Precingula on P^2 and molars long, nearly reaching anterolingual corner of the crown. Hypocone on upper molars very short relative to protocone. Paraconule lingual to metaconule on M^1M^2 . Paraconule "doubled" where upper molars are known. Parastylar lobes on M^1 and M^2 prominent and ectoflexi deep. Lower molars with sharp cusps. Trigonids high and anteroposteriorly compressed. Paraconid not closely "twinning" with metaconid and not higher than protoconid as in *Myrmecoboides*.

Type species.-- *Prodiacodon puercensis*.

Remarks.--*Prodiacodon* is a broadly defined genus which includes forms emphasizing a sectorial mode of occlusion. The molar cusps are high and piercing. Except for the development of the hypocones and the lingual cingula, the complexity of the P^4 and the molariform structure of P^2 , *Prodiacodon* resembles other early eutherians in the general structure of the molar morphology, and it is quite plausible that the molar structure in *Prodiacodon* is more primitive than that seen in *Palaeictops* and *Leptictis*.

It follows that the concept of *Prodiacodon* presented here is based primarily on dental characters which are primitive for the Leptictidae. However, all species of *Prodiacodon* can be separated from their most closely related plesiomorphic sister taxon, *Gypsonictops*, in the common possession of characters derived relative to the latter—narrow styler shelves, hypocones invariably present on the upper molars, paraconids always present on P^5 , and only 4 premolars.

Prodiacodon has been traditionally recognized as a monotypic genus, but here includes various species formerly allocated to both *Diacodon* and *Palaeictops* (see Van Valen, 1967).

Prodiacodon puercensis (Matthew and Granger, 1918) Matthew, 1929

Fig. 8

Diacodon (*Palaeolestes*) *puercensis* Matthew and Granger, 1918, p. 576, 579, figs. 6-9.

Diagnosis.-- P^4 paracone not greatly swollen anteriorly. P^4 protocone subequal with metacone in height; anterior and posterior accessory cuspules present. P^2 with paracone and metacone broadly joined, and hypocone vestigial or absent but pre- and postcingula present. Molars with very small hypocones and elongate pre-

cingula. "Doubled" paraconules present on M_2^2 . P_4 with small anterior accessory cusp, large bulbous medial cusp, small posterior cusp, and a short heel with a small cuspule. P_5 paraconid very small; talonid with 4 cusps. Entoconulids present on lower molars. M_3 talonid with 5 cusps. Skeleton differs from that in *Leptictis* in 1) tibia-fibula fused only at the distal ends, shafts being wholly free, 2) distal parts of astragalus and calcaneum considerably shorter, and 3) first digit longer.

Type specimen.-- AMNH 16011, maxillary fragment with P_5^2 , edentulous lower jaw fragments, humerus, femur, tibia, fibula, tarsals, carpals, and phalanges.

Type locality.-- Torrejon Arroyo, San Juan Basin, New Mexico. Nacimiento Formation, Torrejonian (middle Paleocene).

Referred material.-- AMNH 16748, maxillary with P_2^2 - M_3^2 , mandible with P_4 - M_3 ; partial skeleton. AMNH 16598 mandible with P_5 - M_3 and associated maxillary with partial P_2^2 , M_1^{1-3} , Torrejon Arroyo.³ AMNH 703, left femur, astragalus. Rio Torrejon, San Juan Basin, Nacimiento Formation.

Remarks.-- *Prodiacodon puercensis* was originally recognized as a subgenus of *Diacodon* by Matthew and Granger (1918) who assigned the (subgeneric) name *Palaeolestes*. Matthew (1929) later raised this form to generic rank and named it *Prodiacodon*, as the name *Palaeolestes* was preoccupied.

The overall similarities of the skeleton of *Prodiacodon* to that of *Leptictis* were noted by Matthew and Granger (1918). These authors viewed *Prodiacodon puercensis* as "...an ancestral type of the leptictine phylum", but details of dental morphology, such as the 5-cusped talonid in M_3 , the multi-cusped P_4 , and the "doubled" paraconule in M_1^{1-3} , preclude an argument for its direct ancestry to *Palaeictops* or other species of *Prodiacodon*. *P. puercensis* is best viewed as early offshoot of the *Prodiacodon* group. It is interesting to note that the above cited "primitive" features in the skeleton of *P. puercensis* correspond with the hypothesis based on dental evidence that *Prodiacodon* is a primitive leptictid genus.

Prodiacodon tauricinerei (Jepsen, 1930b)

Diacodon tauricinerei Jepsen, 1930b, p. 124-126, pl. III, fig. 1-4.

Palaeictops tauricinerei Van Valen, 1967

Diacodon pineyensis Gazin, 1952

Palaeictops pineyensis Van Valen, 1967

Diagnosis.-- Similar to *Prodiacodon puercensis* but smaller with more transverse and anteroposteriorly compressed molars. Hypocone present on P_2^2 . P_2^2 stylar shelf very narrow but present external to metacone. Paracone and metacone on P_5^2 not broadly joined. Like *P. puercensis* "doubled" paraconule present on M_2^2 .

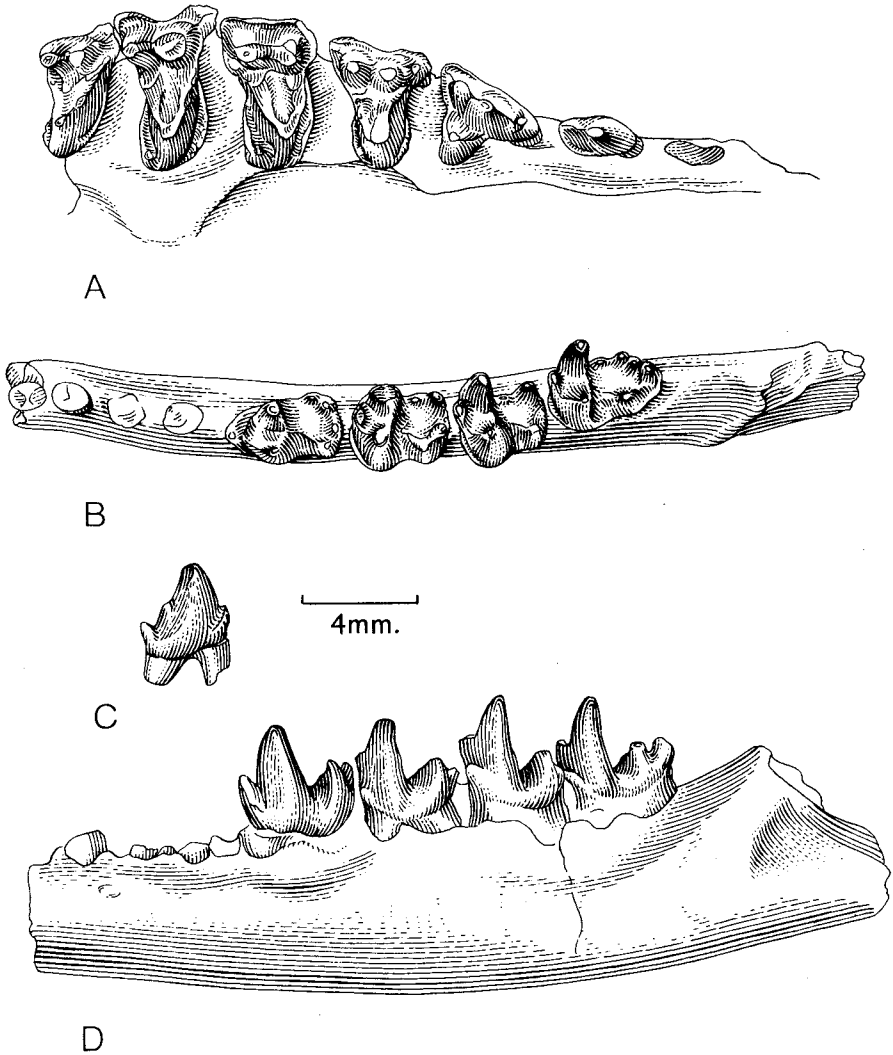


FIG. 8 *Prodiacodon puercensis* AMNH 16748. A. Right maxillary fragment with P², P⁴⁻⁵, M¹⁻³ and alveolus for (D)P¹, occlusal view. B. Left mandible with P⁵, M¹⁻³ and alveoli for P², P⁴, occlusal view. C. Right P⁴, lateral view. D. Same specimen as C, lateral view.

(d) P_1 and P_2 closely situated and procumbent. P_4 with five cusps, second cusp from anterior largest; heel longer than *P. puercensis*. Anteriormost cusp on P_4 small, but larger than in *P. puercensis*. P_5 paraconid larger than in *P. puercensis*, well separated from protoconid and metaconid, prefossid open both labially and lingually. P_5 talonid with 4 cusps. Metaconids higher than protoconids on M_{1-2} .

Type specimen.-- PU 13104, right and left? lower jaw with C-M₃. Maxillary with I²-M², crushed skull.

Type locality.-- "Shale Pocket" one and one-half miles south of Dorsey Creek, and two miles south of Otto-Basin road, Bighorn Basin, Bighorn County, Wyoming. Gray Bull beds, Willwood Formation, Wasatchian (early Eocene).

Referred specimens.-- PU 13267, lower jaw, incisors preserved on right side. Locality same as type (Jepsen, 1930b). PU 14726, maxillary with right and left C-M₂. AMNH 80023, right mandible fragment with P_5 -M₃, East Alheit Pocket, Four Mile Creek, Moffit County, Colorado. Wasatch Formation. AMNH 80695, left mandible fragments with partial P_4 , P_5 , M_7 , M_7 . S. Elk Creek, Bighorn Basin, Wyoming. Wasatchian. AMNH 48763, right mandible P_5 , M₃. 88 Quarry, Arroyo Blanco, New Mexico. San Jose Formation, Wasatchian. AMNH 12831, left mandible with P_5 -M₃ right maxillary fragments with right P_2 , M₂; left maxillary fragments with M₁₋₃. Bridger Creek, Wind River Basin, Wyoming. Wind River Formation, Wasatchian (See Matthew and Granger, 1918, p. 572-573). USNM 19204, left mandible with fragments of P_5 , M₁₋₃. Big Piney, Sublette County, Wyoming. Knight Member, Wasatch Formation, Wasatchian. Described as the type of *Diaecodon pineyensis* by Gazin, 1952. Five isolated teeth from Powder River local fauna. Wasatchian (Delson, 1971, p. 324-325).

Remarks.-- *Prodiacodon tauricinerei* was first described by Jepsen (1930b) who noted that "Compared with other Diacodons, this species has molars with unusually small anteroposterior diameters and great linguo-labial dimensions". This character is more exaggerated than in *P. puercensis* but the dental differences between the two forms are less than generic. *P. tauricinerei* differs from *P. puercensis* in having smaller, more transverse molars, a greater number of cusps and a longer heel on P_4 , and other characters noted in the above diagnosis.

It appears that many variously named early Eocene leptictids are referable to *Prodiacodon tauricinerei*. These include an upper and lower jaw in association from the Wind River Basin (AMNH 12831) referred by Matthew and Granger (1918) to *Diaecodon alticuspis* and *Diaecodon pineyensis* (Gazin, 1952). The latter was represented only by a fragmentary P_5 and M₁₋₃ but these teeth are nearly identical to corresponding teeth in the type of *P. tauricinerei*, although they are slightly larger with a more anteroposteriorly compressed trigonid on M₂. Such differences are ascribed here to intraspecific variation.

Prodiacodon concordiarzensis Simpson, 1935, p. 228

Fig. 9, 10

Diacodon concordiarzensis (Gazin, 1956) Van Valen, 1967.

Diacodon pearcei Gazin, 1956

Diagnosis.-- Much smaller than *Prodiacodon puercensis* and *P. tauricinerei*. dP_1 - P_2 - P_4 trenchant "mitten shaped" in lateral view. P_2 and P_4 with minute anterior accessory cuspule, large middle cusp, and small, very low posterior cusp. P_1 much lower than P_5 . P_4 heel separated anteriorly from main cusp by a continuous transverse trench. P_5 talonid anteroposteriorly shorter than *P. puercensis* and *P. tauricinerei*. P_5 and molars with three (not four) cusps on talonids. M_3 trigonid with paraconid more nearly central in position than in *P. puercensis* and *P. tauricinerei*.

Type.-- USNM 9637, left mandible fragment with P_2 , P_5 , and M_3 .

Type locality.-- Gidley Quarry, Crazy Mountain Field, Sweetgrass County, Montana. Fort Union Formation (Lebo Member). Torrejonian (middle Paleocene).

Referred specimens.-- AMNH 35693, right mandible with $P_{1,2,4}$, M_{1-3} , from type locality. AMNH 35694, right lower jaw with $P_{2,4}$ from type locality. USNM 20970, left mandible fragment with P_2 - M_1 from Saddle Locality, Bison Basin at South Rim County, Wyoming. Fort Union Formation. Tiffanian (later Paleocene). Described as the type of *Diacodon pearcei* by Gazin, 1956.

Remarks.-- *Prodiacodon concordiarzensis* is the smallest known leptictid and is easily distinguishable from other species of *Prodiacodon* by this character. The curious "mitten-shaped" morphology of $P_{1,2,4}$ and the reduced size of P_2 relative to P_4 in this species are also unique specializations for the family and a close affinity with later members of *Prodiacodon* seems unlikely.

In his discussion of "*Diacodon pearcei*" Gazin commented (1956, p. 17) on "the closeness of resemblance between *D. (Diacodon) concordiarzensis* and *D. (Diacodon) pearcei*". The similarity between the two species is indeed too great to keep them specifically separate and *D. pearcei* is here made a junior synonym of *P. concordiarzensis*. Thus evidence is provided for a leptictid lineage that probably underwent major reduction in size by Torrejonian times, a trend seen to occur in some later leptictid lineages as well.

Prodiacodon furor new species

Fig. 11

Diagnosis.-- Similar to *Prodiacodon concordiarzensis* but 28% larger with P_2 and P_4 of simpler construction, consisting only

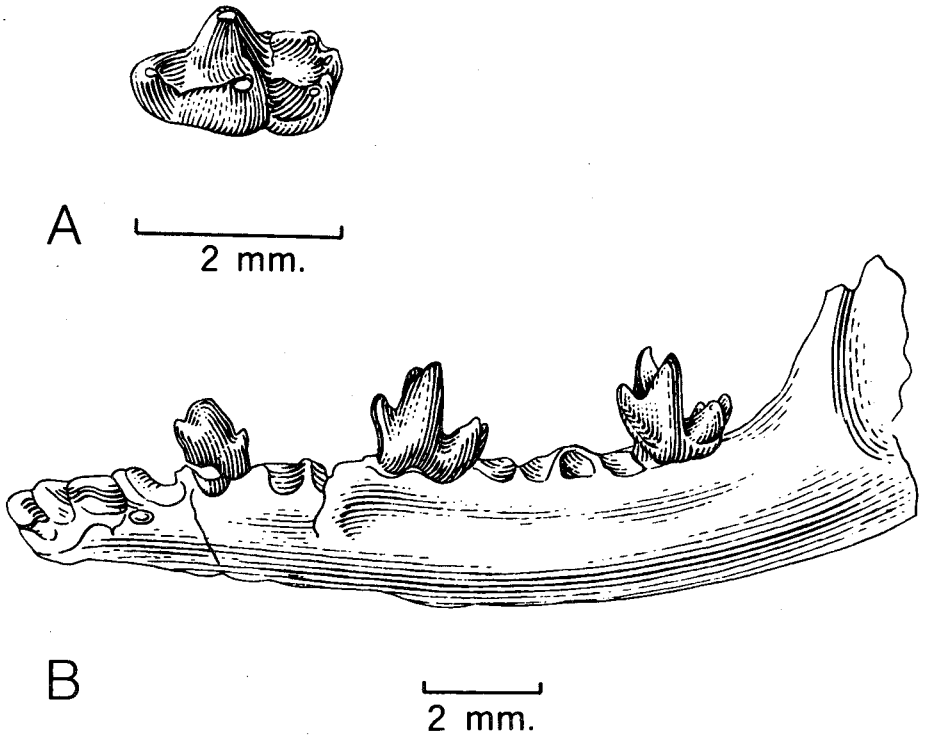


FIG. 9. *Prodiacodon concordiacensis* USNM 9637 Type. A. Left P_5 , occlusal view. B. Left mandible with P_2 , P_5 , M_3 , lateral view.

of a high recurved cusp and a minute basal posterior heel. P_2 subequal to P_4 in height. P_4 slightly lower than P_5 . Paraconid in P_5 blade-like, directly anterior to protoconid. P_5 Talonid of P_5 and molars short anteroposteriorly as in *P. concordiacensis* but not in *P. puercensis* or *P. tauricinerei*. P_5 metaconid of much larger basal dimensions and situated more posteriorly than protoconid. Metaconid on lower molars much higher and more swollen than protoconid. Four cusps are present on molar talonids as in *P. puercensis* and *P. tauricinerei*.

Type specimen.-- AMNH 35291, partial right mandible with P_2 , P_4 , P_5 .

Type locality.-- Gidley Quarry, Crazy Mountain Field, Sweetgrass County, Montana. Lebo Unit of Fort Union Formation, Torrejonian (middle Paleocene).

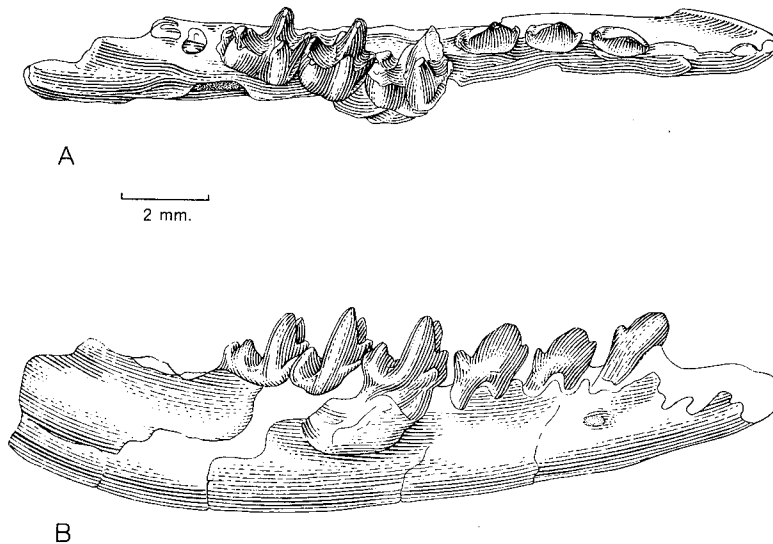


FIG. 10. *Prodiacodon concordiarcensis* AMNH 35693, right mandible with P_2 , P_4 , M_{1-3} . A. occlusal view. B. Lateral view.

Referred specimens.-- AMNH 35290, partial right mandible with M_{1-2} . AMNH 35289, partial left mandible with P_5 , M_{1-2} . Both from type locality.

Etymology.-- *furor* L. craziness. Refers to general region where specimens were collected. All known specimens are from Gidley Quarry in Crazy Mountain Field, Montana.

Remarks.-- With the recognition of *Prodiacodon furor*, Gidley Quarry shows a diversity of leptictids. At least two other species, *Myrmecoboides montanensis* and *P. concordiarcensis*, are also represented at this locality. It is quite possible that the upper dentition from Gidley Quarry referred by Simpson (1937) to *M. montanensis* might belong to *P. furor*, as the upper teeth are of proper size and shape for occlusion with the lowers. This would explain the strong resemblance of this specimen to upper molars of *P. puercensis*.

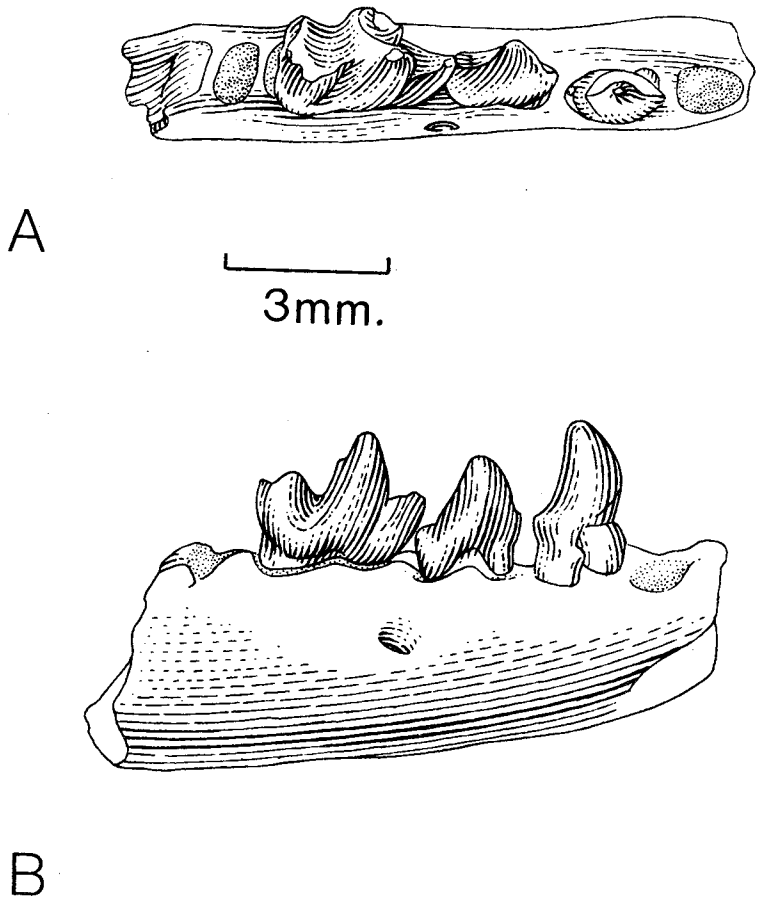


FIG. 11. *Prodiacodon furor* n. sp. AMNH 35291 Type, right mandible fragment with P_2 , P_{4-5} , and alveolus for (D) P_1 . A. Occlusal view. B. Lateral view.

P. furor shows a strong similarity to *P. tauricinerei*, suggesting a possible close relationship with this younger early Eocene species. However, the enlarged and posteriorly situated $P_{\frac{1}{4}}$ metaconid, in *P. furor* a character here considered as derived on the basis of its uniqueness within the Leptictidae, precludes any direct ancestor-descendant relationship between the two species.

Prodiacodon crustulum new species

Figs. 12, 13

Diagnosis.-- Upper molars similar to those in *Prodiacodon puercensis* but smaller with wider styler shelves, smaller hypocones, shorter and smaller (in basal dimensions) metacones relative to paracones. A small cusp (stylocone) is present in some specimens on the labial edge of the crown at the junction with the preparacrista. Conules well developed and situated on the pre- and postprotocrista closer to the apex of the protocone than to the paracone and metacone bases. Paraconule higher than the metaconule. As in *Prodiacodon puercensis*, a small cusplule is present adjacent and anterolabial to the paraconule. Precingulum "crenulated" with series of folds. P_2^2 with pre- and postcingula. M_1^1 and M_2^2 talonids differ from those in *P. puercensis* in having only three cusps, lacking an entoconulid. Entoconulid present on M_3^3 .

Type specimen.-- UCMP 114990, left M_1^1 .

Type locality.-- V-74122, Biscuit Springs locality, Garfield County, Montana, Tullock Formation, Puercan (early Paleocene).

Referred material.-- LACM 32970, right M_1^1 from V-72134, Garbani Locality #9, Tullock Formation, Garfield County, Montana. UCMP 114993, left broken P_5^5 , UCMP 114991-2, lower molars from V-74123 Yellow San Hill #1, Tullock Formation. UCMP 114971, 114973, 114975, 114976, 114977, 114980, 114988, upper molars. UCMP 114972, left P_5^5 . UCMP 114974, 114979, left ? P_2^2 's. UCMP 114978, right P_5^5 fragment. UCMP 114981, 114986, M_1^1 's or M_2^2 's. UCMP 114985, left M_3^3 from V-74122 - type locality. All localities from Tullock Formation, Puercan, (early Paleocene).

Etymology.-- *crustulum* L. biscuit. Refers to the type locality, Biscuit Springs.

Remarks.-- Although only isolated teeth can be referred to this new Puercan species, enough characters are present to indicate its possible affinities and provide some insight on the relationship of very early leptictids. Most interesting is its close resemblance in some features of the upper molars to *Gypsonictops hypoconus* (Simpson, 1927). In both species a small cusp (?stylocone) is present posterior to the parastyle and labial to the paracone, the styler shelf is moderately wider than those in *Palaeictops* or other species of *Prodiacodon*, and the hypocone is a very low cusp. Unlike *G. hypoconus* and like *Prodiacodon puercensis*, the precingulum has a slight rise or crest, the conules are more lingual in position, and the paraconule is "doubled", the main cusp being bordered anterolingually by a smaller cusp. In fact, *P. crustulum* shows a strong overall dental similarity to *P. puercensis* while representing a stage of dental development intermediate between that observed in *Gypsonictops hypoconus* and that

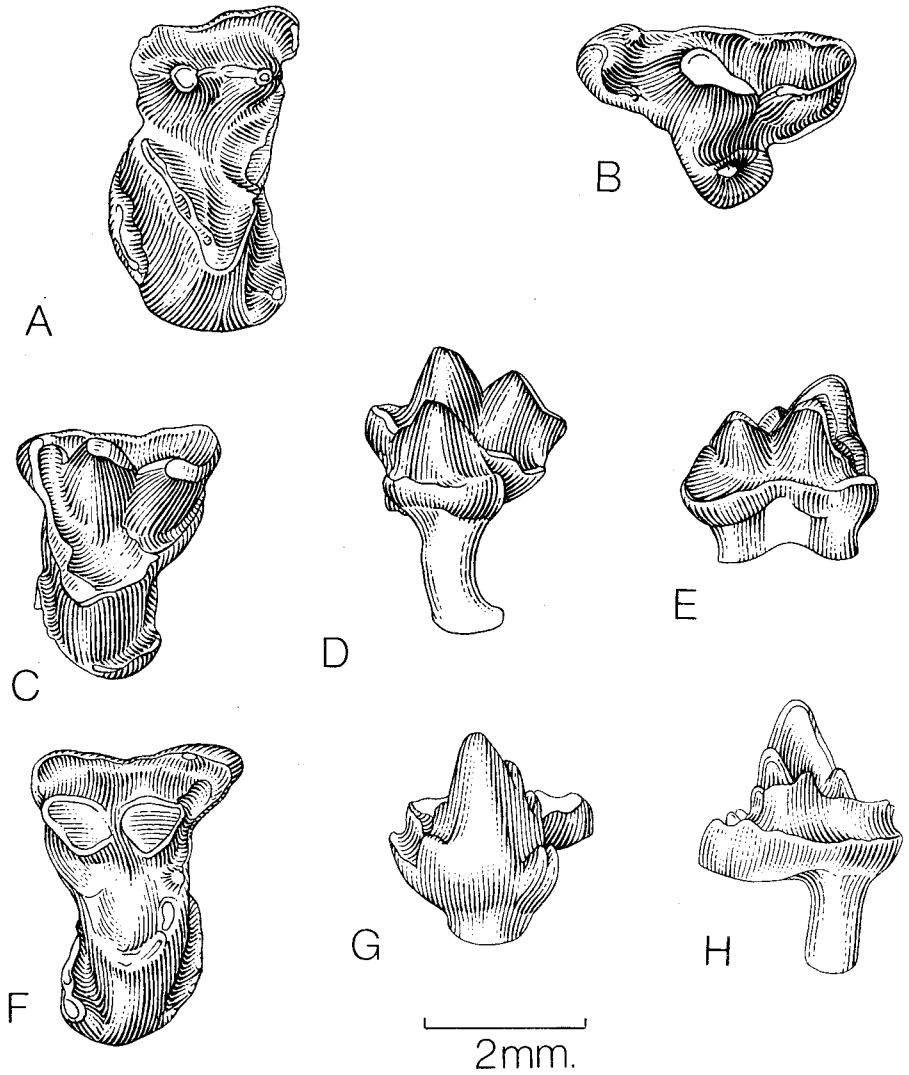


FIG. 12. *Prodiacodon crustulum* n. sp. A. UCMP 114990 Type, M^1 , occlusal view. B. UCMP 114979, left P^4 , occlusal view. C. UCMP 114972, left P^5 ?, occlusal view. D. Same, lingual view. E. Same, labial view. F. UCMP 32970, right M^1 , occlusal view. G. Same, lingual view. H. Same, labial view.

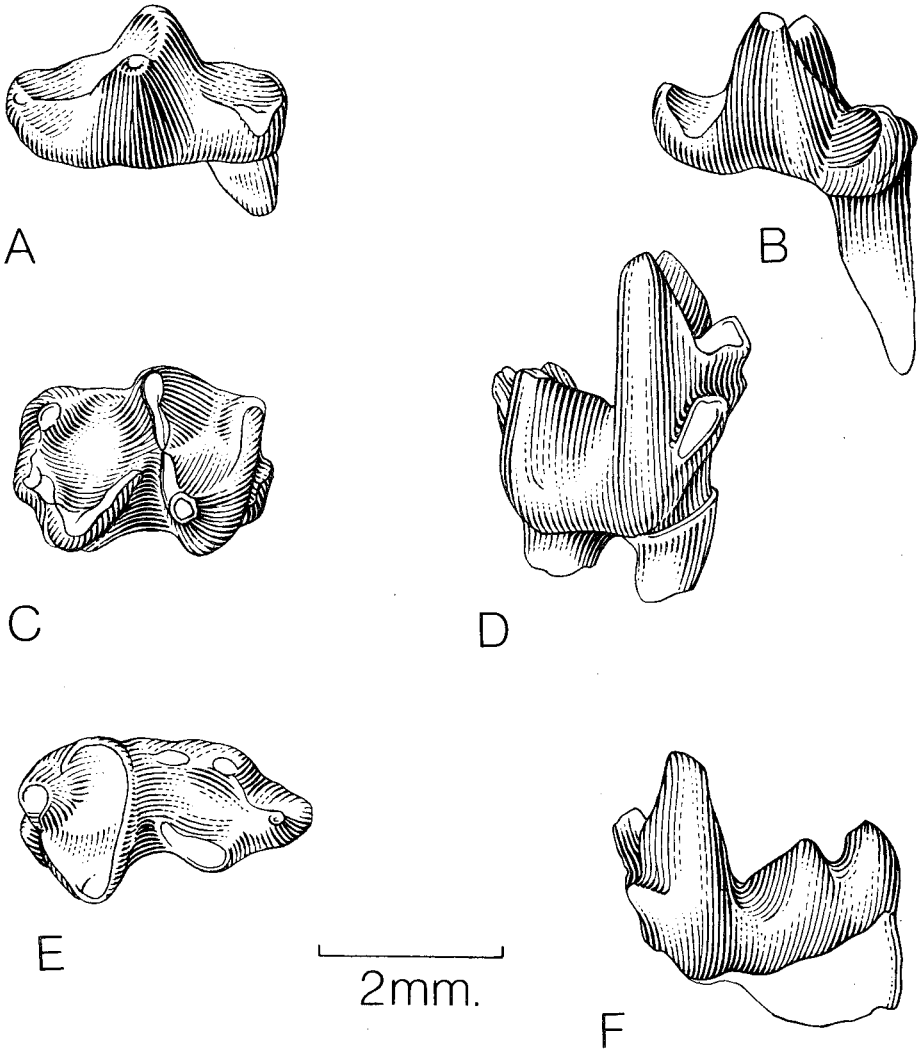


FIG. 13. *Prodiacodon crustulum* n.sp. A. UCMP 114982, left P₅?, occlusal view. B. Same labial view. C. UCMP 114986, right M₂, occlusal view. D. Same, labial view. E. UCMP 114985, left M₃, occlusal view. F. Same, labial view.

in *Prodiacodon*. Accordingly, *P. crustulum* is regarded here as the most primitive known Tertiary leptictid.

Leptictidae?

A few named leptictids are not recognized in this study because the referred material is too poor to allow any definite assignment. Russell (1929, p. 173-175) named a species *Diacodon septentrionalis* from the late Paleocene Cochrane 1 locality of Alberta. The referred material consists of an M_3 and an M_1 or M_2 . The high relief of the trigonid cusps suggests a reference to *Prodiacodon* rather than *Palaeictops*, but on the basis of the meager material it is impossible to determine whether these molars are assignable to a new species, *P. puercensis*, *P. tauricinerei*, *D. alticuspis*, or a pantolestid.

Gazin (1949) described a new genus and species, *Hypictops syntaphus*, from Bridgerian of western Wyoming based on a right upper cheek tooth dentition (USNM 13445). The outline and dimension of the teeth are so strikingly similar to those of *Leptictis dakotensis* as to suggest conspecificity, but the molars themselves are so badly worn that few, if any, important details are preserved. Even if well preserved, it is highly doubtful that this specimen would serve as evidence for a distinct genus.

Stock (1935) referred a fragmentary lower jaw with an M_3 (CIT 16791) from a Brea Canyon locality (CIT locality 150) Sespé Formation, "late" Eocene, southern California, to the Leptictidae, but unfortunately this specimen cannot be relocated in the present CIT collections (recently acquired by LACM). The identification of this specimen as a leptictid jaw is questioned because the published description and illustration of the M_3 does not eliminate the specimen from possible reference to palaeoryctids, adapisoricids, or geolabidines.

Phylogeny of the Leptictidae

Previous taxonomic arrangements of leptictids have reflected to a large extent the biostratigraphic occurrence of the various species (Douglass, 1905, Matthew and Granger, 1918, Scott and Jepsen, 1936). All Oligocene species were indiscriminantly lumped under *Leptictis* (= *Ictops*). Paleocene-early Eocene forms were assigned to *Palaeictops* and early and middle Eocene forms to *Diacodon*. Van Valen (1967) attempted a more phyletic arrangement of species and his results show some strong departures from previous classifications. Van Valen specified that his study was only preliminary and accordingly did not present rigorous definitions of the leptictid genera and species he considered. Further, he did not attempt to subdivide Oligocene leptictids into major lineages but noted that such a revision might be in order. It is evident that there are at least two major groups of Oligocene leptictids which can easily be separated at the generic level (Novacek, 1976). One of these (now being studied by the author)

shows phyletic relationships with *Prodiacodon*. The second group is represented by *Leptictis haydeni*, *L. dakotensis*, *L. douglassi*, and perhaps *L. wilsoni* (Novacek, 1976) and is most clearly related to *Palaeictops*, particularly *P. matthewi* and *P. multicauspi* from the dental and cranial similarities noted above. Thus the basic dichotomy seen in Oligocene forms might be traced as far back as the Paleocene.

Fig. 14 is a graphic representation of the hypothesized phylogeny of the Paleocene and Eocene North American Leptictidae. The numbers given at each node of the branches refer to proposed shared-derived (synapomorphic) characters which unite the groups stemming from them. The following characters separate leptictids from *Gypsonictops*:

1. Four lower premolars.
2. Narrow styler shelves.
3. Hypocones uniformly present on upper molars
4. P_5^- with a well developed paraconid.
5. Entoconulid present on M_3^- .

Recognition of the above characters as derived is based on interpretations of early therian dental evolution. Five premolars are variably present in *Gypsonictops* and *Kennalestes* and most likely represent a plesiomorphous condition in Eutheria (McKenna, 1975). All Tertiary leptictids (where complete postcanine dentitions are known) have only four premolars and, in agreement with McKenna (1975), it is hypothesized that they represent a derived evolutionary stage through loss of P_5^- . Characters 2 and 3 stem from the generally accepted conclusion that eutherians evolved from a primitive condition where the upper molars had wide styler shelves and lacked hypocones (Patterson, 1956; Slaughter, 1965, 1971; Crompton, 1971; Fox, 1975). In *Gypsonictops* the hypocone is vestigial or absent, and the styler shelves are wider than in Tertiary leptictids. P_5^- paraconids (character 4) are absent or small in *Gypsonictops*, but well developed in Tertiary leptictids. The polarity of this character is difficult to determine. Paraconids on the last premolar are uniformly lacking or weakly developed in a number of early primitive eutherians including *Kennalestes* (see Kielan-Jaworowska, 1969). However the paraconid is large in the P_5^- 's of *Procerberus* (see Lillegraven, 1969). It is tentatively argued here that a P_5^- with a very small (or absent) paraconid is primitive for eutherians but this feature may prove to be a derived specialization of *Gypsonictops*. Entoconulids on the M_3^- (5), a feature common to primitive species of *Prodiacodon* and *Myrmecoboides montanensis* but absent in *Gypsonictops*, is presumed to represent a derived character uniting Tertiary leptictids. It must be noted that certain other Cretaceous eutherians have lower molar entoconulids (e.g. *Cimolestes magnus*, see Lillegraven, 1969).

Myrmecoboides montanensis can be separated from all other leptictid clades by three unique specializations in the lower dentition:

6. Closely appressed metaconids and paraconids, producing a "twinning" effect of these two cusps.

7. Anteroposteriorly elongated talonids.

8. Widely spaced anterior premolars.

Although the isolated phyletic position of *Myrmecoboides* within the Leptictidae seems clear, it is not certain whether the divergence of this lineage occurred before or after the *Palaeictops-Prodiacodon* dichotomy.

Prodiacodon is the most primitive leptictid genus and does not show many derived characters other than those recruited to unite all members of the family. One possible derived character unique to *Prodiacodon* is the "doubled" paraconule (9) in the upper molars of *P. Puercensis*, *P. crustulum*, and *P. tauricinerei*. Definitely referable upper molars are not known in *P. furor* and *P. concordiarcensis*.

Palaeictops is regarded here as the most derived genus among the Paleocene-Eocene leptictids known from North America, distinguished by the following specializations:

10. P⁵'s and upper molars are more "bunodont", being more anteroposteriorly elongate and transversely compressed, with lower, more bulbous paracones, metacones, and protocones.

11. Parastylar spurs M²⁻³ are not prominent and ectoflexi are not deep.

12. Hypocones are well developed, being more than half the height of the protocones.

13. Conules are situated labially at the base of the paracone and metacone.

14. Molar trigonids are not greatly elevated.

15. P₅ paraconids are well developed.

16. Paracone on P⁴ is moderately to greatly enlarged.

17. Tibia and fibula are fused for most of their shaft lengths.

The central hypothesis argued in this study is that the sectorial features in the molars of *Prodiacodon*, namely high, piercing molar cusps on transverse molars with salient parastylar spurs, represent a primitive leptictid condition. This conclusion stems from the acknowledgment of the distribution of "sectorial" dental features among palaeoryctids, leptictids, and Cretaceous Mongolian eutherians. *Palaeictops* is removed from this condition in characters 10, 11, and 14 above. The derived

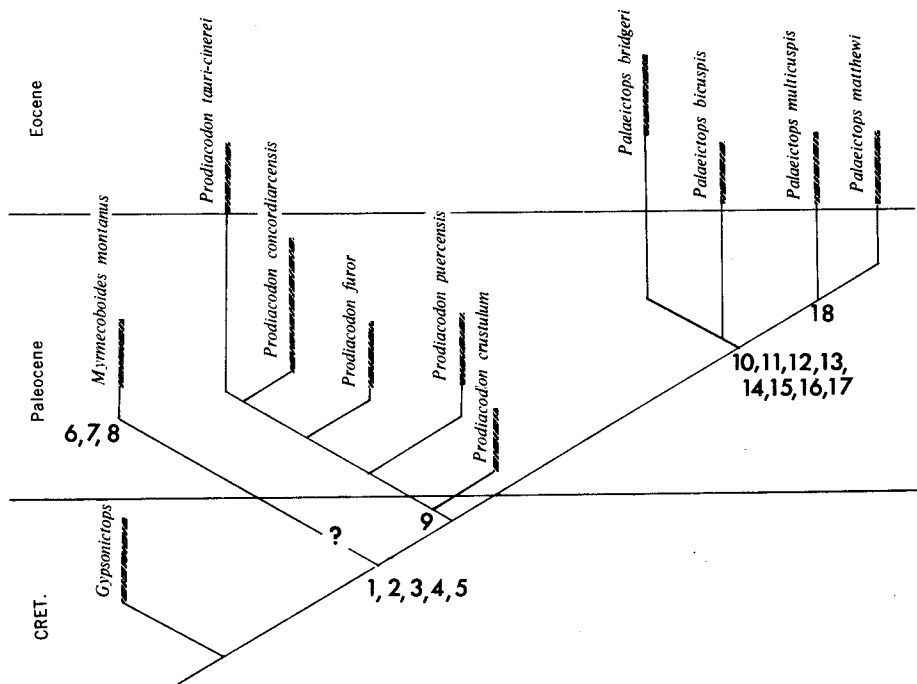


FIG. 14. Postulated phylogenetic relationships of the North American Paleocene and Eocene Leptictidae. Vertical bars with diagonal stripes represent the approximate geochronological occurrence of a particular taxon. The intersections of branches are only meant to reflect the relative sequence of splitting. The time of branching on a geochronologic scale is not intended to be represented here. Numbers refer to shared-derived characters discussed in the text.

states represented by characters 12 and 15 are recognized as tendencies for increased development of molar hypocones and P_5 paraconids already present in the most primitive leptictids. ⁵ The labial position of the upper molar conules in *Palaeictops* (character 13) represents a distinct departure from that in *Prodiacodon*. The lingual position of upper molar conules in *Prodiacodon* is recognized as a primitive condition for the Eutheria (Patterson, 1956; Slaughter, 1965, 1971; Turnbull, 1971; Fox, 1975). Enlargement of the P_4 paracone (16) in *Palaeictops* is variable. The P_4 paracone is distinctly enlarged in the Oligocene *Leptictis*. Character 17 is shared by *Palaeictops* (where known) and the Oligocene *Leptictis*, but the tibia and fibula are unfused in *Prodiacodon*.

Palaeictops multicuspis and *P. matthewi* are synapomorphic in the enlargement and proliferation of cusps on P_4 (character 18).

An effort was made to establish a phylogenetic scheme without reference to the age and occurrence of a particular taxon, but as is clearly demonstrated by Fig. 14 there seems to be little discrepancy between the hypothesized phylogenetic relations of taxa and the recorded age of their occurrence. Primitive species of *Prodiacodon* are recorded as far back as the early Paleocene, the new Puercan species *P. crustulum* showing dental characters intermediate between the late Cretaceous *Gypsonictops* and middle Paleocene species of *Prodiacodon*. Medial and later Eocene species of *Palaeictops* show the closest resemblance to the Oligocene *Leptictis*. There are, of course, exceptions (e.g. *Myrmecoboides*, *Prodiacodon concordiarvensis*) and these are interpreted as early divergently specialized lineages.

Although a number of major changes in leptictid taxonomy at the generic level have been proposed in this study, the overall number of species has not been reduced. I do not feel that this result is due directly to a subliminal desire on my part to "over split", but is a reflection of true diversity. Many of the species described above are represented by only one or two specimens but I doubt that larger referable samples and a better idea of dental variation would serve to unite these taxa, as the cited differences between them are generally very distinct. In the cases where larger samples of leptictids are available (e.g., *Leptictis dakotensis* from the Oligocene of North America) the variation in important comparative dental characters is clearly not great. Leptictids evidently were quite diverse, at least at the species level, throughout their Tertiary history.

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