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# NEW ADAPISORICIDAE, PENTACODONTIDAE, AND HYOPSODONTIDAE (MAMMALIA, INSECTIVORA AND CONDYLARTHRA) FROM THE LATE PALEOCENE OF WYOMING AND COLORADO

By

Philip D. Gingerich

*Abstract.*—Three new genera and species of Adapisoricidae are described from middle Tiffanian Cedar Point Quarry: *Litocherus zygeus*, *Cedrocherus ryani*, and *Diacocherus meizon*. "*Litolestes*" *notissimus* Simpson and "*L.*" *lacunatus* Gazin are here referred to *Litocherus*. The type species of *Diacocherus*, new genus, is "*Diacodon*" *minutus* Jepsen. All of these species are grouped with *Leipsanolestes seigfriedti* Simpson, *Litolestes ignotus* Jepsen, and *Mckennatherium ladae* (Simpson) in a new adapisoricid subfamily Litocherinae. Litocherines resemble hyopsodontid condylarths, but differ in retaining stylar crests on upper molars and small cuspate or crestlike paraconids on lower molars. Most genera exhibit molar size reduction posteriorly.

One new species of Pentacodontidae, *Bisonalveus holtzmani*, is described from Cedar Point Quarry.

Two new genera and two new species of Hyopsodontidae are recorded from middle and late Tiffanian faunas. "*Haplaletes*" *diminutivus* Dorr is placed in a new genus *Dorraletes*. *Aletodon quadravus*, new species, is described from Cedar Point. The type and only specimen of "*Platymastus*" *mellon* Van Valen is an upper molar of *Aletodon* possibly conspecific with *A. conardae* Winterfeld. Finally, *Utemylus latomius*, new genus and species, is described from Mason Pocket in southern Colorado. Hyopsodontidae, in spite of these additions, are rare elements in late Paleocene mammalian faunas.

## INTRODUCTION

Adapisoricidae, Pentacodontidae, and Hyopsodontidae together include many early Cenozoic genera of small and presumably ground-living insectivorous and herbivorous mammals. The relationships of genera and species within each family are poorly known, and there is considerable discussion in the literature regarding allocation of particular genera to one or another of the three families. The ordinal positions of the families are themselves not known with certainty. This confusion is due, in part, to the close relationship and modest differentiation of many placental mammals in the Paleocene, and it is also due to limited documentation of the morphological diversity known to exist within each family. The purpose of this paper is to record a number of new genera and species of Adapisoricidae, Pentacodontidae, and Hyopsodontidae collected by University of Michigan field parties in recent years or, in some cases, discovered in undescribed Princeton University collections. The paper began as a review of late Paleocene Hyopsodontidae, but it was necessarily expanded to include similar groups that may or may not be related to hyopsodontids. Adapisoricidae, Pentacodontidae, and Hyopsodontidae are

appropriately treated together because of past confusion in the allocation of genera, species, or individual specimens to one or another of the families.

Nomenclature used to describe mammalian teeth is outlined by Van Valen (1966) and Krishtalka (1976). The biostratigraphic framework utilized to subdivide the Tiffanian Land-Mammal Age and correlate various localities is documented in Gingerich (1976). Institutional abbreviations used in this paper are as follows: AMNH, American Museum of Natural History (New York); PU, Princeton University Museum of Natural History (Princeton, N.J.); UM, University of Michigan Museum of Paleontology (Ann Arbor); USNM, United States National Museum of Natural History (Washington); and UW, University of Wyoming Geological Museum (Laramie).

## SYSTEMATIC PALEONTOLOGY

### Order INSECTIVORA Bowdich, 1821
### Family ADAPISORICIDAE Schlosser, 1887
### Subfamily **LITOCHERINAE,** new subfamily

*Type genus.*—*Litocherus*, new genus.

*Included genera.*—*Cedrocherus* new genus, *Diacocherus* new genus, *Leipsanolestes* Simpson, *Litocherus* new genus, *Litolestes* Jepsen, and *Mckennatherium* Van Valen.

*Age and distribution.*—Middle Paleocene to early Eocene of North America.

*Diagnosis.*—Differ from Adapisoricinae in having less reduced anterior premolars and less molarized posterior premolars, with the metacone on $P^4$ unusually small or absent and the talonid on $P_4$ small and flat or shallowly basined. Upper molars are transversely broader than they are long, with a distinct cuspate hypocone. Lower molars have a trigonid of moderate size, with a reduced paraconid. Molar talonids are moderately large and basined. Differ from Dormaaliinae in having less reduced anterior premolars, smaller hypocones on upper molars, unbasined or shallowly basined talonids on $P_4$, and reduced paraconids on all lower molars.

*Discussion.*—*Litocherus* ("*Litolestes*") *notissimus* (Simpson, 1936) and *L. lacunatus* (Gazin, 1956) were both originally described as hyopsodontids. Subsequently, Van Valen (1967, p. 261) transferred *Litolestes* to Adapisoricidae without discussion. Russell et al. (1975, p. 165) studied "*Litolestes*" *notissimus* and "*L*". *lacunatus*, noting resemblances to Condylarthra. They retained *Litolestes* in Adapisoricidae, but indicated that it might prove advisable to place *Litolestes*-like adapisoricids in a subfamily distinct from both Adapisoricinae and Dormaaliinae. Their suggestion is followed here in grouping *Litocherus*, *Litolestes*, and their allies in a new subfamily Litocherinae. The principal dental characteristics of litocherine genera are compared in Table 1.

Litocherines differ from small hyopsodontids, with which they are often confused, in possessing small but distinct stylar crests associated with the paracone and/or metacone on upper molars (preparacrista and postmetacrista, respectively, extending onto the stylar shelf). In addition, litocherines differ from hyopsodontids in retaining small but distinct paraconids on most lower molars and in exhibiting a more marked gradient of posterior molar size reduction.

European *Adunator* Russell (1964) is sometimes included in discussions of North American genera here grouped in Litocherinae. However, *Adunator* appears to have much more molarized upper premolars, like those of *Adapisorex*, and larger, more lingual hypocones. Relationships suggested by the conservatism of preserved lower cheek teeth are clearly contradicted by the upper cheek teeth allocated to *Adunator* by Russell. Whatever the systematic position of *Adunator*, it does not belong in North American Litocherinae.

TABLE 1 — Comparison of dental morphology in six genera of Paleocene Litocherinae, new subfamily of Adapisoricidae. Note that genera are presently distinguished primarily by the conformation of lower premolars and the relative size and form of posterior molars.

| Tooth position | *Leipsanolestes* Simpson, 1928 | *Litolestes* Jepsen, 1930 | *Mckennatherium* Van Valen, 1965 | *Litocherus* new genus | *Cedrocherus* new genus | *Diacocherus* new genus |
|---|---|---|---|---|---|---|
| UPPER DENTITION | | | | | | |
| $P^3$ | --- | Reduced, small protocone and no metacone. | --- | Reduced, small protocone and no metacone. | --- | Reduced, distinct metacone, no protocone. |
| $P^4$ | --- | Large paracone, small protocone, no metacone. | --- | Large paracone, small protocone, no metacone. | --- | Moderate protocone and paracone, distinct metacone. |
| $M^1$-$M^2$ | --- | Similar in size, strong postmeta-crista, distinct conules, small hypocone. | --- | Similar in size, strong postmeta-crista, moderate preparacrista, distinct conules, small hypocone. | --- | Similar in size, weak postmeta-crista, distinct conules, small hypocone. |
| $M^3$ | --- | --- | --- | Reduced in size, no hypocone. | --- | Reduced in size, no hypocone. |
| LOWER DENTITION | | | | | | |
| $C_1$ | --- | Reduced, incisi-form. | --- | Projecting. | --- | --- |
| $P_3$ | --- | Short, broad, small paraconid, no metaconid. | Moderate length, narrow, paraconid small or absent, no metaconid. | Moderate length, narrow, paraconid small or absent, no metaconid. | --- | Moderate length, narrow, small paraconid, no meta-conid. |

TABLE 1, cont.

| Tooth position | *Leipsanolestes* Simpson, 1928 | *Litolestes* Jepsen, 1930 | *Mckennatherium* Van Valen, 1965 | *Litocherus* new genus | *Cedrocherus* new genus | *Diacocherus* new genus |
|---|---|---|---|---|---|---|
| LOWER DENTITION | | | | | | |
| $P_4$ | Moderate length, narrow, semi-molariform, distinct paraconid and metaconid, moderate basined talonid with small entoconid and hypoconid. | Short, broad, premolariform, small paraconid and metaconid, very short talonid. | Moderate length, narrow, semi-molariform, low paraconid and small metaconid on open trigonid, talonid basined with distinct entoconid and hypoconid. | Moderate length, narrow, premolariform, low paraconid, metaconid small or lacking, moderate talonid. | --- | Moderate length, narrow, semi-molariform to submolariform, paraconid may be as high as metaconid, talonid basined with distinct entoconid and hypoconid. |
| $M_1$-$M_2$ | $M_2$ slightly smaller than $M_1$, both with prominent crestlike paraconids, acute entoconid, weak hypoconulid, and angled talonid basin. | $M_2$ smaller than $M_1$, both with prominent crest-like paraconid, acute entoconid, and angled talonid basin. | $M_2$ smaller than M, trigonids have large metaconid, slightly smaller protoconid, small paraconid near metaconid, talonid basins rounded. | $M_2$ smaller than $M_1$, paraconid on $M_2$ reduced and crestlike, rounded entoconid and rounded talonid basin. | $M_2$ much smaller than $M_1$, paraconid is cuspate on $M_1$, crest-like on $M_2$, entoconid squared on $M_1$, rounded on $M_2$ | $M_2$ as large or larger than $M_1$, paraconid reduced, crestlike, and joined to enlarged metaconid on $M_2$. |

TABLE 1, cont.

| Tooth position | *Leipsanolestes* Simpson, 1928 | *Litolestes* Jepsen, 1930 | *Mckennatherium* Van Valen, 1965 | *Litocherus* new genus | *Cedrocherus* new genus | *Diacocherus* new genus |
|---|---|---|---|---|---|---|
| LOWER DENTITION | | | | | | |
| $M_3$ | Smaller than $M_2$, prominent crest-like paraconid, distinct entoconid, hypoconulid, and hypoconid on angular talonid. | Smaller than $M_2$, prominent crest-like paraconid, distinct entoconid, hypoconulid, and hypoconid on angular talonid. | Longer and narrower than $M_2$, trigonid with small paraconid near large metaconid, talonid basin rounded with projecting hypoconulid. | Smaller than $M_2$, reduced crest-like paraconid, rounded entoconid, rounded talonid basin. | Much smaller than $M_2$, paraconid crest-like, entoconid and hypoconulid rounded, talonid basin rounded. | Smaller than $M_2$, very reduced crest-like paraconid, rounded entoconid, rounded talonid basin. |

## *Litocherus*, new genus

*Litolestes* (in part), Simpson, 1936, p. 23. Gazin, 1956a, p. 41.

*Type species.*—*Litocherus zygeus*, new species.

*Included species.*—*Litocherus notissimus* (Simpson, 1936); *L. zygeus*, new species; and *L. lacunatus* (Gazin, 1956).

*Age and distribution.*—Early through late Tiffanian Land-Mammal Age (late Paleocene) of central Montana and central and western Wyoming.

*Diagnosis.*—Differs from *Litolestes* in having large projecting canines, longer and narrower lower premolars, reduced, often crest-like paraconids, and a more rounded talonid basin with more rounded talonid cusps on lower molars. Differs from other small litocherine genera in having a simple premolariform $P_4$ with a small narrow talonid. Lower molar length decreases moderately from $M_1$ to $M_3$.

*Etymology.*—*Litos*, small, simple, and *cherus* (Gr., masc.), hedgehog; in allusion both to the small size and simple dental structure of this genus, and to its probable erinaceoid affinities.

### *Litocherus notissimus* (Simpson)

*Litolestes notissimus* Simpson, 1936, p. 23, figs. 14, 15; 1937a, p. 9.

*Holotype.*—AMNH 33831, left dentary with $P_2$-$M_3$ and associated left and right maxillae with $C^1$-$M^3$.

*Type locality.*—Scarritt Quarry in the Crazy Mountain Basin of south central Montana.

*Age and distribution.*—*L. notissimus* is presently known only from the early Tiffanian Land-Mammal Age (late Paleocene) at Scarritt Quarry (type locality).

*Diagnosis.*—Smallest and oldest species of the genus. Differs from middle Tiffanian *L. zygeus*, new species, in being about 18% smaller. Differs from middle to late Tiffanian *L. lacunatus* (Gazin) in being about 27% smaller in linear dimensions.

*Discussion.*—*Litocherus notissimus* is fully described by Simpson (1936, 1937a). Most of the Scarritt Quarry specimens of this species are in the American Museum of Natural History, but there is also a significant sample in the University of Michigan collection.

### ***Litocherus zygeus***, new species
Figure 1

*Litolestes lacunatus* (in part), Holtzman, 1978, p. 35, Pl. 6, fig. 5-14.
*Litolestes* sp. nov., Rose, 1981, p. 152.

*Holotype.*—UM 64508, right dentary with $P_3$-$M_3$ intact.

*Type locality.*—Cedar Point Quarry in the northern Bighorn Basin, northwestern Wyoming.

*Age and distribution.*—*L. zygeus* is known from middle Tiffanian Cedar Point Quarry (type locality) and from the Brisbane and Judson localities in western North Dakota.

*Diagnosis.*—Differs from earlier *L. notissimus* in being about 22% larger. Differs from later *L. lacunatus* in being about 11% smaller in linear dimensions and in having relatively narrower lower molars.

*Etymology.*—*zygos*, yoke (Gr.); in allusion to the intermediate morphological and stratigraphic position of this species linking early Tiffanian *L. notissimus* to late Tiffanian *L. lacunatus*.

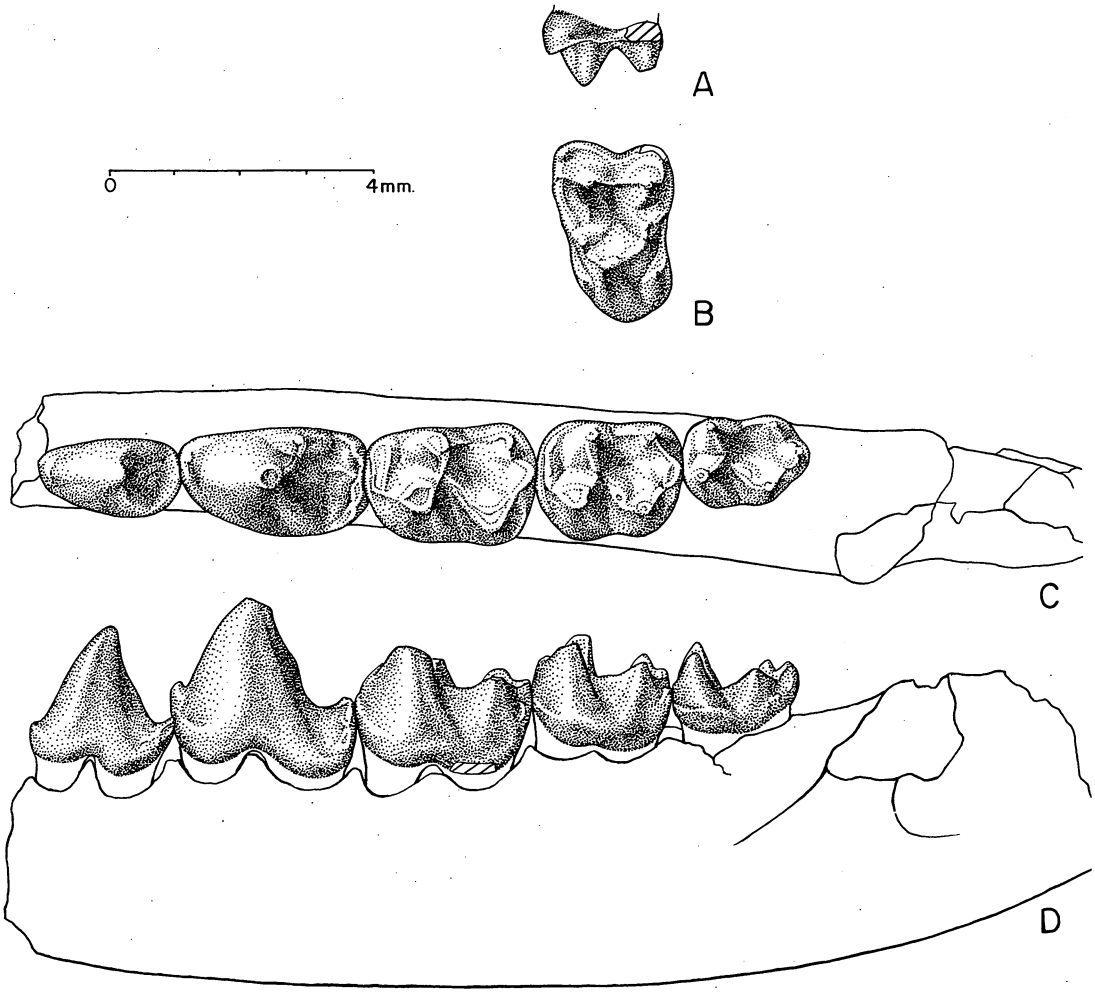


FIG. 1— Dentition of *Litocherus zygeus*, new genus and species, from Cedar Point Quarry (middle Tiffanian), northern Bighorn Basin, Wyoming. *A*, UM 82026, left $M^2$ in lateral view; *B*, same specimen in occlusal view. *C*, UM 64508 (holotype), left dentary with $P_3$-$M_3$ in occlusal view; *D*, same specimen in lateral view.

*Description.*—The only upper molar known from the type sample is an $M^2$, UM 82026 (Fig. 1A,B), with a prominent protocone and paracone, and a slightly reduced metacone. It has prominent conules and a distinct hypocone on the posterior cingulum. The anterior cingulum terminates lingually in a small cusp as well. The labial cingulum is indented, with the parts of this shelf associated with the paracone and metacone being approximately equal in size. There are no stylar cusps. The preparacrista is very small, running directly forward along the front of the paracone. The postmetacrista is more prominent, curving posterolabially onto the labial cingulum. A maxilla of *L. zygeus* illustrated by Holtzman (1978, Pl. 6, fig. 7) preserves $M^1$ and $M^2$ intact. $M^2$ resembles $M^1$ closely, differing principally in being shorter anteroposteriorly and both relatively and absolutely broader labiolingually.

An alveolus for a moderately large lower canine is preserved in UM 71831. This specimen also shows $P_1$ to have been single-rooted and the remaining lower premolars double-rooted. Mental foramina are present below the anterior root of $P_2$ and the posterior root of $P_3$. The crown of $P_3$ is preserved in the holotype, UM 64508, and it is moderately long and narrow with a simple protoconid and no accessory cusps. The talonid of $P_3$ is very short and unbasined. $P_4$ in the holotype is moderately long and narrow with a large simple central protoconid. A very small paraconid is present at the base of the protoconid, and a distinct metaconid is located on the lingual side of the protoconid about half way up the crown. Development of a metaconid on $P_4$ is variable. There is no metaconid on $P_4$ in UM 64425 and 71831, and a metaconid is only weakly developed on $P_4$ in UM 64516. The remaining three specimens preserving $P_4$ resemble the holotype in having a distinct metaconid on this tooth. The talonid on $P_4$ is short. It is divided into labial and lingual parts by a faint anteroposteriorly aligned crest. The labial part of the talonid is broad and sloping, and the lingual part is narrow and more nearly flat.

The crowns of $M_1$-$M_3$ decrease progressively in size posteriorly. $M_{(1-2)}$ are moderately high crowned, with the talonid almost as high as the trigonid. On $M_1$ the protoconid is the largest cusp, and the metaconid is slightly smaller. The paraconid is much smaller but it too is a distinct cusp. On $M_2$ and $M_3$ the metaconid is slightly larger than the protoconid and the paraconid is usually reduced to a transverse crest on the preprotocristid. This transverse crest occasionally bears a very small cuspate paraconid. The talonid is completely enclosed by the hypoconid, hypoconulid, and entoconid, and by crests connecting these cusps to each other and to the trigonid. All of the talonid cusps are rounded, and the basin they enclose is rounded as well (unlike the more angled basins on molars of *Litolestes*). There are no lingual cingulids on the lower molars.

The length and width of the lower cheek teeth of UM 64508 (holotype) are as follows (all measurements in mm): $P_3 = 2.2$ x 1.2, $P_4 = 2.8$ x 1.7, $M_{1p} = 2.6$ x 1.9, $M_2 = 2.1$ x 1.8, $M_3 = 2.0$ x 1.4, and the depth of the mandibular ramus below $M_1 = 3.6$. Measurements of the type sample of *Litocherus zygeus* are summarized in Table 2.

*Typodigm.*—UM 63106, 63107, 64417, 64428, 64508, 64516, 71831, 71835, 82026 and 82027 are all from Cedar Point Quarry. Additional specimens from the type locality are present in the Princeton University collection.

## *Litocherus lacunatus* (Gazin)
Figure 2

*Litolestes lacunatus* Gazin, 1956, p. 41, Pl. 11, figs. 3, 4. Winterfeld, 1982, p. 86.
*Haplaletes* near *H. disceptatrix*, Dorr, 1958, p. 1224.
*Litolestes lacunatus*, Winterfeld, 1982, p. 86.

TABLE 2 — Summary of measurements of the upper and lower dentition of *Litocherus zygeus*, new genus and species, from Cedar Point Quarry (type locality), based on all specimens in the University of Michigan collection. *L* = crown length, *W* = crown width, *N* = sample size, *OR* = observed range, $\bar{x}$ = mean, *S* = standard deviation, and *V* = coefficient of variation.

| Tooth position | | N | OR | $\bar{x}$ | S | V |
|---|---|---|---|---|---|---|
| UPPER DENTITION | | | | | | |
| $M^2$ | L | 1 | 2.0 | - | - | - |
| | W | 1 | 2.9 | - | - | - |
| LOWER DENTITION | | | | | | |
| $P_3$ | L | 2 | 2.1-2.2 | 2.15 | - | - |
| | W | 2 | 1.2-1.3 | 1.25 | - | - |
| $P_4$ | L | 8 | 2.5-2.8 | 2.63 | 0.13 | 4.9 |
| | W | 8 | 1.5-1.8 | 1.69 | 0.10 | 5.9 |
| $M_1$ | L | 6 | 2.3-2.6 | 2.40 | 0.11 | 4.6 |
| | W | 6 | 1.6-1.9 | 1.72 | 0.12 | 6.8 |
| $M_2$ | L | 5 | 1.9-2.1 | 2.02 | 0.08 | 4.1 |
| | W | 5 | 1.6-1.8 | 1.66 | 0.09 | 5.4 |
| $M_3$ | L | 4 | 1.8-2.0 | 1.90 | 0.08 | 4.3 |
| | W | 4 | 1.3-1.4 | 1.35 | 0.06 | 4.3 |

*Holotype.*—USNM 21016, left dentary with $P_4$-$M_1$.

*Type locality.*—*Titanoides* locality in the Bison Basin, central Wyoming.

*Age and distribution.*—*Litocherus lacunatus* is known from the late Tiffanian *Titanoides* locality in central Wyoming (type locality), and from the Rock Springs Uplift in southwestern Wyoming. It is also reported here from two middle Tiffanian localities, Battle Mountain and Type Chappo, in western and southwestern Wyoming.

*Diagnosis.*—Differs from *L. notissimus* (Simpson) in being about 30% larger. Differs from *L. zygeus*, new species, in being about 13% larger in linear dimensions and in having relatively broader lower cheek teeth.

*Discussion.*—*Litocherus lacunatus* is sometimes confused with the hyopsodontid condylarth *Haplaletes disceptatrix* because of its similar size and quadrate lower molars. However, *Litocherus* has more sharply crested cheek teeth, and it also has a postmetacrista curving onto the stylar shelf that is lacking on upper molars of *Haplaletes*. There are no labial cingula on lower molars as there are in *Haplaletes*. One specimen (UM 34776; Fig. 2A,B) from Battle Mountain identified as *Haplaletes* near *H. disceptatrix* by Dorr (1958), and another specimen collected recently (UM 80803; fig. 2C,D) are here referred to *L. lacunatus*. In addition, two specimens (UM 81120 and 81139) from the Type Chappo locality are here referred to *L. lacunatus*. These records extend the stratigraphic range of *L. lacunatus* from the late Tiffanian back to the middle Tiffanian.

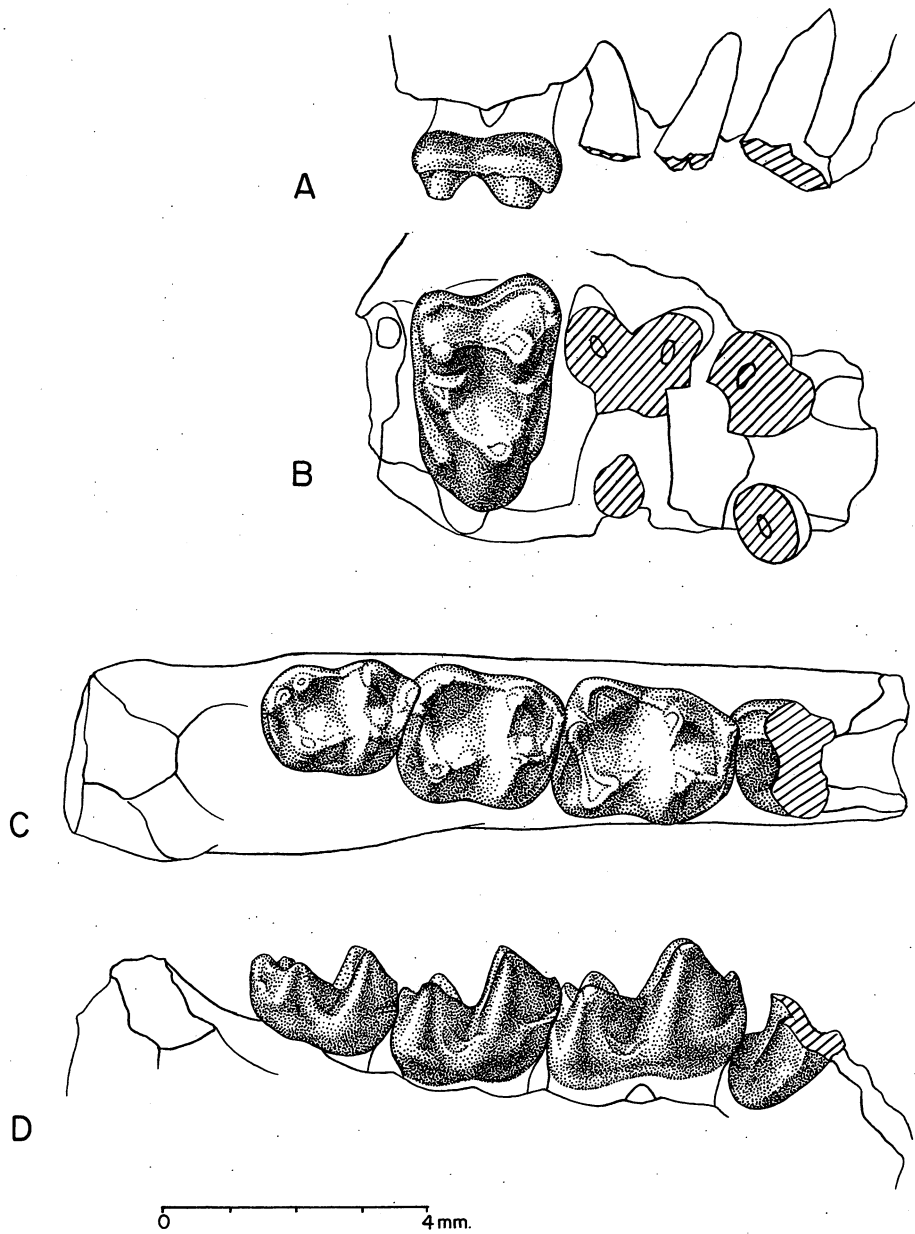


FIG. 2— Dentition of *Litocherus lacunatus* (Gazin) from Battle Mountain (middle Tiffanian), Hoback Basin, Wyoming. *A*, UM 34776, right maxilla with $M^2$ in lateral view; *B*, same specimen in occlusal view. *C*, UM 80803, right dentary with $M_{1-3}$ in occlusal view; *D*, same specimen in lateral view.

## *Cedrocherus*, new genus

*Type species.*—*Cedrocherus ryani*, new species.

*Included species.*—Type species only.

*Age and distribution.*—Middle Tiffanian Land-Mammal Age (late Paleocene) of northwestern Wyoming.

*Diagnosis.*—Differs from all other Litocherinae in having a very steep gradient of decreasing molar crown size from $M_1$ to $M_3$. Also differs in combining a squared entoconid on $M_1$ with a more rounded entoconid on $M_2$.

*Etymology.*—*Cedrus*, cedar, and *cherus* (Gr., masc.), hedgehog; in reference to the type locality of the only known species and to its probable erinaceoid affinities.

### *Cedrocherus ryani*, new species

Figure 3

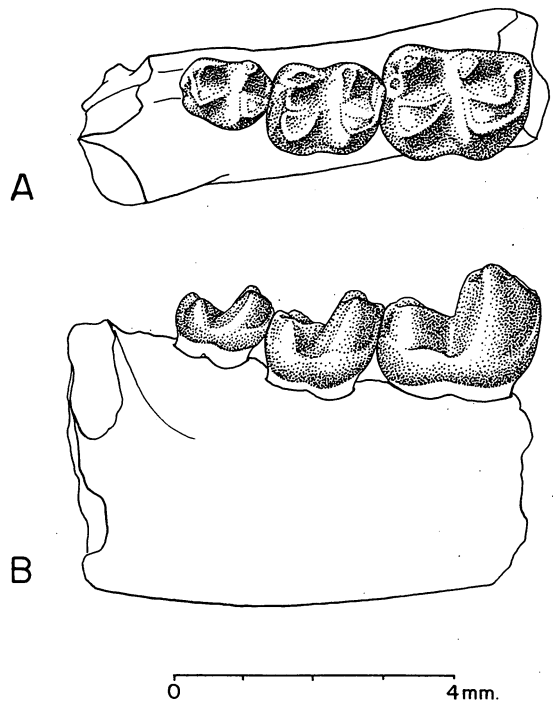


FIG. 3— Dentition of *Cedrocherus ryani*, new genus and species, from Cedar Point Quarry (middle Tiffanian), northern Bighorn Basin, Wyoming. *A*, UM 82028 (holotype), right dentary with $M_{1-3}$ in occlusal view; *B*, same specimen in lateral view.

*Holotype.*—UM 82028, right dentary with $M_{1-3}$.

*Type locality.*—Cedar Point Quarry in the northern Bighorn Basin, northwestern Wyoming.

*Age and distribution.*—*C. ryani* is presently known only from middle Tiffanian Cedar Point Quarry (type locality) of northwestern Wyoming.

*Diagnosis.*—As for the genus.

*Etymology.*—Named for Mr. William J. Ryan who found and collected the type specimen.

*Description.*—The type and only specimen, UM 82025, is a right dentary with $M_{1-3}$. The crowns of the molars decrease markedly in size from front to back. All three molars are relatively high crowned. The protoconid is worn on each of the molars, but it appears to have been the largest trigonid cusp in each case. The metaconid is only slightly smaller than the protoconid on all three molars. The paraconid on $M_1$ is a distinct cusp well separated from the metaconid. On $M_2$ and $M_3$ the paraconid is more reduced and crest-like, although it remains distinct from the metaconid. The hypoconid, hypoconulid, and entoconid enclose a talonid on each molar that is lower than the trigonid but nearly equal to it in occlusal area. The hypoconid is the largest talonid cusp and the hypoconulid is the smallest on all three molars. The entoconid and hypoconid are more acutely angled on $M_1$ than they are on $M_2$ or $M_3$, and the posterior border of the talonid on $M_1$ is nearly straight. The hypoconid and entoconid are more rounded and the hypoconulid projects posteriorly to a greater degree on $M_2$ and $M_3$.

The length and width of the lower molars of UM 82025 (holotype) are as follows (all measurements in mm): $M_1 = 2.0 \times 1.6$, $M_2 = 1.5 \times 1.4$, and $M_3 = 1.3 \times 1.0$. Mandibular depth below $M_1$ is 3.3 mm.

*Typodigm.*—UM 82028 (holotype) is the only known specimen.

## ***Diacocherus***, new genus

*Diacodon* (in part), Jepsen, 1930, p. 511.

*Type species.*—*Diacodon minutus* Jepsen, 1930.

*Included species.*—Type and *Diacocherus meizon*, new species.

*Age and distribution.*—Middle to late Tiffanian Land-Mammal Age (late Paleocene) in western Wyoming.

*Diagnosis.*—Differs from all other litocherines in having $M_2$ equal in size or larger than $M_1$. Distinctive also in retaining a metacone on $P^3$ and $P^4$, and in having a more reduced paraconid closely appressed to the metaconid on $M_2$ and $M_3$. Resembles *Mckennatherium* but differs in having $M_2$ larger relative to $M_1$. Also differs in possessing a more molarized $P_4$: the paraconid on $P_4$ tends to be higher and closer to the protoconid (it is submolariform rather than semimolariform in the terminology of Krishtalka, 1976).

*Discussion.*—The entire described sample of *Mckennatherium* consists of fragmentary dentaries from a single Torrejonian locality, Gidley Quarry. Lower cheek teeth appear to be relatively conservative in litocherines, limiting the number of characters available to differentiate *Diacocherus* (and other litocherines) from *Mckennatherium*. Nevertheless, *Diacocherus* differs from *Mckennatherium* and other litocherines in a number of important characteristics justifying its recognition as a distinct genus.

*Diacocherus minutus* (Jepsen)
Figure 4A, B

*Diacodon minutus* Jepsen, 1930, p. 511, Pl. 9, figs. 7-9.
*Leptacodon packi* (in part), Dorr, 1952, p. 78, Pl. 5, figs. 6-7.
*Leptacodon* near *L. ladae*, Dorr, 1958, p. 1226.
*Elpidophorus minutulus* Dorr, 1958, p. 1226, Pl. 2, figs. 5-7.
"*Diacodon*" *minutus* (in part), Krishtalka, 1976, p. 10, fig. 3.
*Scenopagus*? *proavus* Winterfeld, 1982, p. 87, figs. 3L-N.
*Adunator minutus* (in part), Winterfeld, 1982, p. 106.

*Holotype.*—PU 13360, left dentary with $M_{1-3}$.

*Type locality.*—Princeton Quarry in the northern Bighorn Basin, northwestern Wyoming.

*Age and distribution.*—*Diacocherus minutus* is known from several late Tiffanian faunas in western Wyoming. Clarkforkian specimens referred to this species by Rose (1981, p. 44) are larger and probably represent a distinct species.

*Diagnosis.*—Differs from *D. meizon*, new species, in being about 8% smaller. $P_4$ usually submolariform. Differs also in having much less elevated paraconids on $M_2$ and $M_3$.

*Description.*—The dentition of *Diacocherus minutus* is adequately, if briefly, described by Jepsen (1930, p. 511). A partial upper dentition of *D. minutus* is illustrated in Figure 4A,B in comparison with that of *Litolestes ignotus* (Fig. 4C,D). Upper premolars have not been described previously. $P^3$ and $P^4$ are distinctive in having prominent metacones. It should be noted too that upper molars of *Diacocherus* differ from those of condylarths in having stylar crests (a small preparacrista and a slightly more prominent postmetacrista extending onto the labial cingulum).

*Discussion.*—Dorr (1952, 1958, see also 1978) referred small insectivores from Dell Creek Quarry to three genera and species: *Leptacodon packi*, *Leptacodon* near *L. ladae*, and *Elpidophorus minutulus*. All three are very similar in size and form to *Diacocherus minutus* (Jepsen). Dell Creek and Princeton quarries are both latest Tiffanian in age (Gingerich, 1976), and it is likely that all of the small insectivores from Dell Creek represent a single species, *D. minutus*.

Most discussion of "*Diacodon*" *minutus* (e.g., Krishtalka, 1976; Bown and Schankler, 1982) has been confined to the lower dentition. Winterfeld (1982) described an isolated upper molar from the Rock Springs Uplift in southwestern Wyoming (UW locality V-77059) as a new species "*Scenopagus*?" *proavus*. He described other isolated upper and lower molars from the same locality as "*Adunator*" *minutus*. Identification of isolated molars of *Diacocherus minutus* (or any other insectivore) is very difficult without associated premolar and molar teeth preserved in series in jaws. I hesitate to include "*S.*?" *proavus* in *Diacocherus minutus* without making direct comparisons of the Rock Springs Uplift holotype with specimens from Princeton Quarry. However, the fact that Winterfeld himself identified a number of cheek teeth of insectivores from V-77059 as *Diacocherus* (= "*Adunator*") *minutus* without discussing the possibility that the single isolated tooth serving as type of "*Scenopagus*?" *proavus* might belong here as well is surprising. The holotype of "*S.*?" *proavus* lacks the enlarged hypocone characteristic of upper molars of *Scenopagus*, and it appears from Winterfeld's discussion and illustrations to be the correct size and form to represent an $M_2$ of *Diacocherus minutus*. Hence, *Scenopagus*? *proavus* is provisionally synonymized with *Diacocherus minutus* (Jepsen).

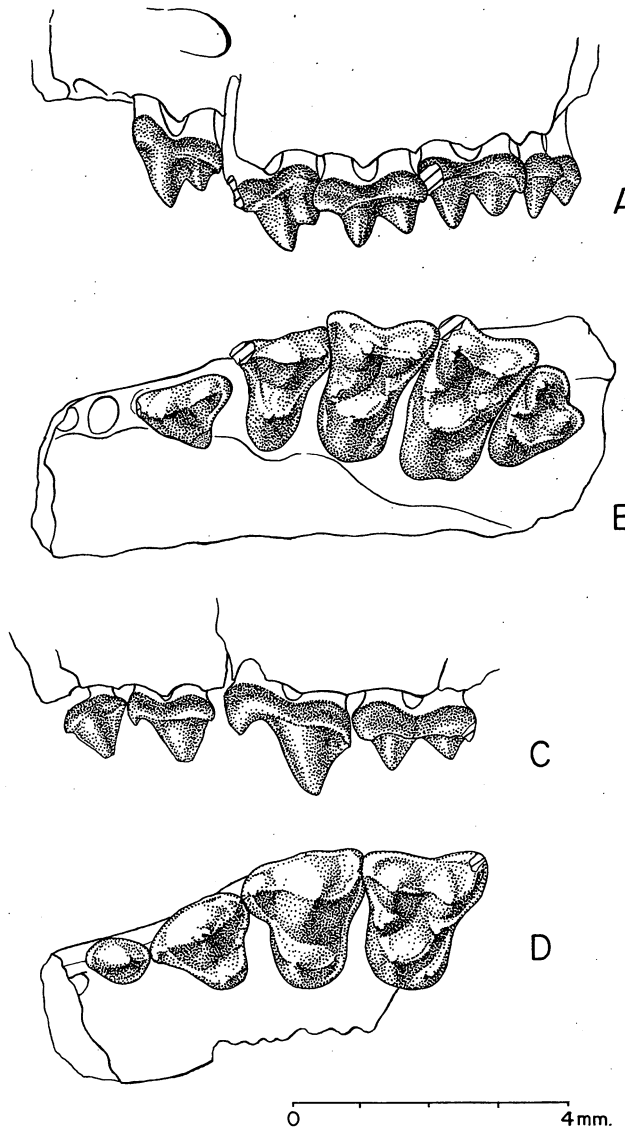


FIG. 4— Comparison of the upper dentitions of *Diacocherus minutus* (Jepsen) and *Litolestes ignotus* Jepsen, both from Princeton Quarry (late Tiffanian), Clark's Fork Basin, Wyoming. *A*, PU 14371, left maxilla of *D. minutus* with $P^3$-$M^3$ in lateral view; *B*, same specimen in occlusal view. *C*, PU 21193, left maxilla of *L. ignotus* with $P^2$-$M^1$ in lateral view; *D*, same specimen in occlusal view.

***Diacocherus meizon***, new species
Figure 5

*Mckennatherium* cf. *ladae*, Rose, 1981, p. 152.

*Holotype.*—UM 82023, right dentary with $P_3$-$M_3$ (talonid of $P_4$ slightly damaged).

*Type locality.*—Cedar Point Quarry in the northern Bighorn Basin, northwestern Wyoming.

*Age and distribution.*—*Diacocherus meizon* is known only from middle Tiffanian Cedar Point Quarry (type locality).

*Diagnosis.*—Differs from *Diacocherus minutus* in being about 8% larger in most linear dimensions. Differs also in having much more elevated paraconids on $M_2$ and $M_3$. $P_4$ tends to be semimolariform rather than submolariform, with the paraconid usually positioned anteriorly and well below the level of the metaconid.

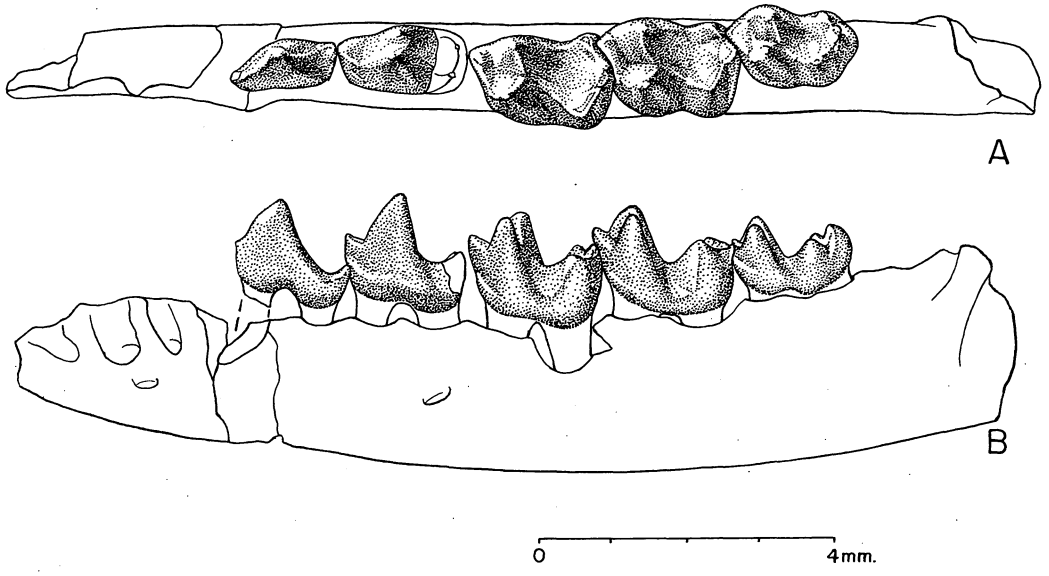


FIG. 5— Lower dentition of *Diacocherus meizon*, new genus and species, from Cedar Point Quarry (middle Tiffanian), northern Bighorn Basin, Wyoming. *A*, UM 82023 (holotype), left dentary with $P_3$-$M_3$ in occlusal view; *B*, same specimen in lateral view. Talonid of $P_4$ is partially reconstructed from UM 64566.

*Etymology.*—*Meizon* (Gr.), larger; in reference to the larger tooth size and more elevated paraconids on lower molars of this species.

*Description.*—The holotype, UM 82023, is the most complete specimen of *Diacocherus meizon*. It preserves alveoli for a single-rooted $P_1$ and double-rooted $P_2$, but the crowns of these teeth are not preserved. $P_3$ has a moderately long narrow crown with a high central protoconid, a very small cuspule in the position of a paraconid, no metaconid, and a narrow flat talonid of moderate length. $P_4$ also has a long narrow crown with a high central protoconid. There is a distinct paraconid positioned low on the crown, well anterior to the protoconid. A moderately

large metaconid is present high on the lingual side of the protoconid. The metaconid is much higher and closer to the protoconid than is the paraconid. The talonid of $P_4$ is damaged in the holotype, but it is well preserved in UM 64566 where it is moderately long and basined, with a very small hypoconid and entoconid on the posterior margin. The talonid is approximately equal in total length to the trigonid.

The trigonid of $M_1$ is dominated by the protoconid and a slightly larger metaconid. The paraconid is a small cusp at the lingual end of a sharply flexed preprotocristid. The paraconid is directly in front of, and slightly separated from the metaconid. A distinct hypoconid, hypoconulid, and entoconid are present on the talonid. Together they enclose a rounded basin. $M_2$ resembles $M_1$ but differs in being slightly larger and in having the paraconid joined to the metaconid high on the anterior surface of the latter cusp. $M_3$ resembles $M_2$ in having an elevated paraconid joined to the metaconid, but it differs in being much narrower and in having a more posteriorly projecting hypoconulid.

Measurements of the type specimen of *D. meizon*, UM 82023, are as follows (all measurements in mm): $P_3$ = 1.6 x 0.7, $P_4$ = —x 0.9, $M_1$ = 1.8 x 1.3, $M_2$ = 1.8 x 1.4, and $M_3$ = 1.7 x 1.1. Measurements of the type sample of *Diacocherus meizon* are summarized in Table 3.

*Typodigm.*—UM 63115, 63117, 64556, 64571 and 82023 (holotype). Additional specimens from Cedar Point are conserved in the Princeton University collection.

*Discussion.*—*Diacocherus meizon* is intermediate in form and stratigraphic position between the type samples of *Mckennatherium* and *Diacocherus*. *D. meizon* has a semimolariform $P_4$ very much like that of *Mckennatherium ladae*, but this appears to be a primitive characteristic of litocherines in general. It is included in the genus *Diacocherus* because it shares a morphological characteristic presumed to be advanced, $M_2$ as large or larger than $M_1$, with *Diacocherus minutus*.

TABLE 3 — Summary of measurements of the lower dentition of *Diacocherus meizon*, new genus and species, from Cedar Point Quarry (type locality), based on all specimens in the University of Michigan collection. Abbreviations as in Table 2.

| Tooth position | | N | OR | $\bar{x}$ | S | V |
|---|---|---|---|---|---|---|
| $P_3$ | L | 1 | 1.6 | - | - | - |
| | W | 1 | 0.7 | - | - | - |
| $P_4$ | L | 1 | 1.7 | - | - | - |
| | W | 2 | 0.9-1.0 | 0.95 | - | - |
| $M_1$ | L | 3 | 1.71.8 | 1.73 | 0.06 | 3.3 |
| | W | 3 | 1.2-1.3 | 1.23 | 0.06 | 4.7 |
| $M_2$ | L | 3 | 1.7-1.8 | 1.73 | 0.06 | 3.3 |
| | W | 3 | 1.4 | 1.40 | - | - |
| $M_3$ | L | 3 | 1.7 | 1.70 | - | - |
| | W | 3 | 1.1-1.2 | 1.13 | 0.06 | 5.1 |

## Family PENTACODONTIDAE Simpson, 1937
## *Bisonalveus* Gazin

*Bisonalveus* Gazin, 1956a, p. 17.

*Type species.*—*Bisonalveus browni* Gazin, 1956.

*Included species.*—Type, and *Bisonalveus holtzmani*, new species.

*Age and distribution.*—Early through middle Tiffanian Land-Mammal Age (late Paleocene) of Wyoming and western North Dakota.

*Diagnosis.*—Differs from other pentacodontids in having a more generalized $P_4$ retaining a small paraconid and a distinct posterolingual entoconid. Lower cheek teeth of *Bisonalveus* are high crowned and with a massive protoconid and metaconid on the trigonid. Paraconids on $M_1$ and $M_2$ are moderately large and lingually placed; hypoconulids are indistinct.

### ***Bisonalveus holtzmani***, new species
Figure 6

*Bisonalveus* sp., Holtzman, 1978, p. 39, Pl. 7, figs. 5, 6, 8.
Cf. *Protoselene* sp., Rose, 1981, p. 152.

*Holotype.*—PU 20795, left dentary with $M_{1-2}$.

*Type locality.*—Cedar Point Quarry, northern part of Bighorn Basin, northwestern Wyoming.

*Age and distribution.*—Middle Tiffanian of northwestern Wyoming and western North Dakota.

*Diagnosis.*—Differs from *Bisonalveus browni* in being about 30% larger in linear dimensions.

*Etymology.*—Named for Dr. Richard Holtzman in appreciation of his exemplary monographic treatment of the Paleocene mammals of North Dakota. Holtzman described the first tooth referable to this species.

*Description.*—The holotype is a left dentary preserving $M_1$ and $M_2$. Judging from the shallowness of the mandibular ramus and the cancellous texture of the bone itself the type represents a juvenile individual. $M_1$ and $M_2$ exhibit very slight occlusal wear. The protoconid and metaconid are massive on $M_1$ and $M_2$. A paraconid is also well developed. $M_2$ is distinctive in having a trigonid both relatively and absolutely broader than that of $M_1$. There is a large hypoconid and entoconid on the talonid of $M_1$ and $M_2$, but there is only a small and indistinct entoconid, partially obscured by wear, on the curving posterior margin of each talonid.

Measurements of the holotype of *Bisonalveus holtzmani*, PU 20795, are as follows (all measurements in mm): $M_1 = 3.1 \times 2.4$, $M_2 = 3.4 \times 3.0$.

*Typodigm.*—PU 20795 (holotype) is the only specimen known from the type locality.

*Discussion.*—The presence of a prominent paraconid well separated from the metaconid distinguishes lower molars of *Bisonalveus* from those of similar sized hyopsodontid condylarths like *Protoselene*, with which they might otherwise be confused. The tooth described by Holtzman (1978, p. 39) from Brisbane, in North Dakota, is an $M_1$ somewhat smaller than $M_1$ in PU 20795 from Cedar Point, and it is possible that the Brisbane tooth represents a third species of *Bisonalveus* intermediate in size between *B. browni* and *B. holtzmani*. However, considering

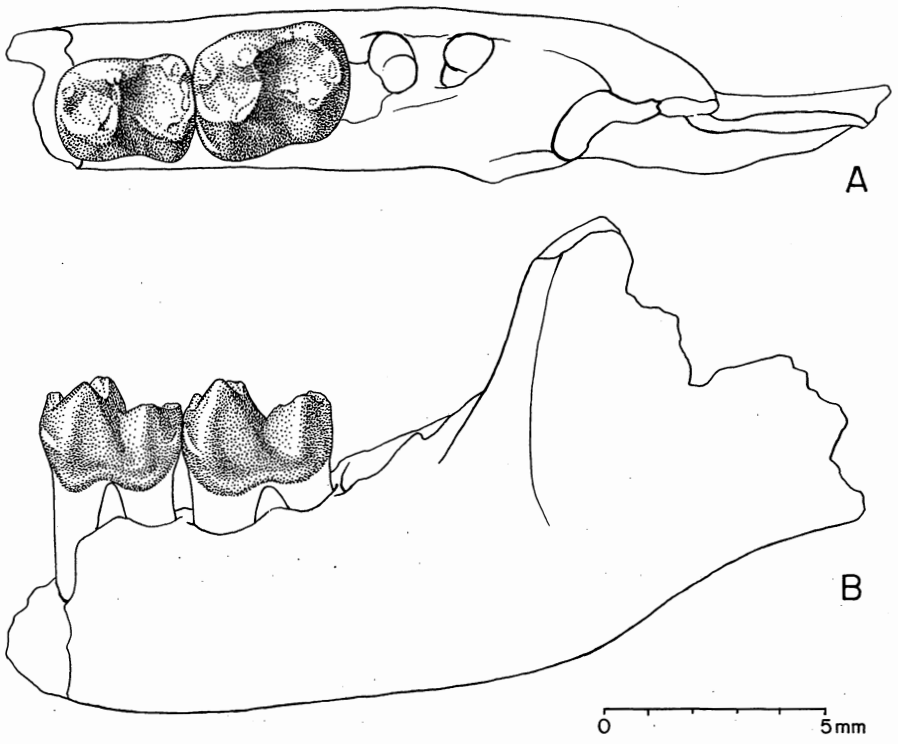


FIG. 6— Lower dentition of *Bisonalveus holtzmani*, new species, from Cedar Point Quarry (middle Tiffanian), northern Bighorn Basin, Wyoming. *A*, PU 20795 (holotype), left dentary with $M_{1-2}$ in occlusal view; *B*, same specimen in lateral view.

independent faunal evidence that Brisbane and Cedar Point are similar in age, and the impossibility of characterizing variation in *Bisonalveus* from either locality based on single specimens, both are here grouped together in the same species.

## Order CONDYLARTHRA Cope, 1881
## Family HYOPSODONTIDAE Lydekker, 1889
## ***Dorraletes***, new genus

*Haplaletes* (in part), Dorr, 1952, p. 86.

*Type species.*—*Haplaletes diminutivus* Dorr, 1952.

*Included species.*—Type species only.

*Age and distribution.*—Middle to late Tiffanian Land-Mammal Age (late Paleocene) of Wyoming and western North Dakota.

*Diagnosis.*—Differs from *Haplaletes* in being much smaller and in having a more symmetrical $M^1$ and $M^2$, each with a small hypocone posterior to the protocone and often with a smaller

pericone anterior to the protocone. $P_4$ is relatively longer and narrower. $M_1$ has a much more open trigonid, with the paraconid well anterior to the metaconid. There is no paraconid on $M_2$ or $M_3$, and all lower molars lack a labial cingulid. $M^3$ and $M_3$ are markedly reduced in size by comparison with $M^2$ and $M_2$. The occluding cusps and basins on all molars are more rounded and less angular than those of *Haplaletes*. This combination of characteristics distinguishes *Dorraletes* from other hyopsodontid condylarths as well.

*Etymology.*—Named for Dr. John A. Dorr, Jr., in recognition of his many contributions to the study of Paleocene mammals interpreted in their broadest geological perspective; combined with *aletes* (Gr., masc.), grinder or millstone, a common stem of hyopsodontid generic names.

## *Dorraletes diminutivus* (Dorr)
Figures 7, 8

*Haplaletes diminutivus* Dorr, 1952, p. 86, fig. 7, Pl. 5, figs 12-13.
*Haplaletes diminutivus*, Holtzman, 1978, p. 57, Pl. 10, figs. 9-13.
Erinaceoid sp., Dorr and Gingerich, 1980, p. 107.
Hyopsodontid sp. small, Dorr and Gingerich, 1980, p. 107.

*Holotype.*—UM 27231, left maxilla with $P^4$-$M^2$.

*Type locality.*—Dell Creek Quarry in the Hoback Basin, western Wyoming.

*Age and distribution.*—Middle to late Tiffanian (late Paleocene) of Wyoming and western North Dakota.

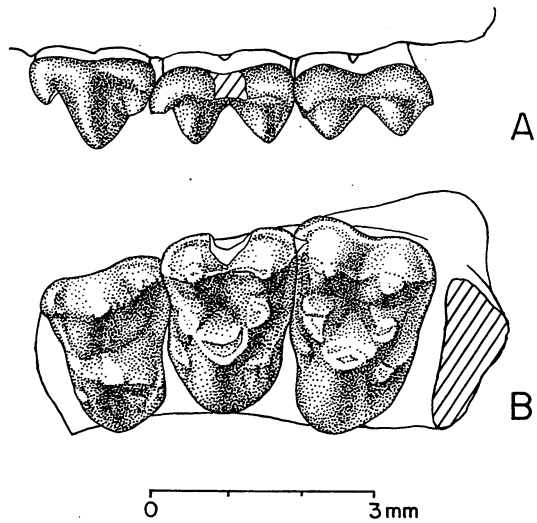


FIG. 7— Upper dentition of *Dorraletes diminutivus* (Dorr) from Dell Creek Quarry (late Tiffanian), Hoback Basin, Wyoming. *A*, UM 27231 (holotype), left maxilla with $P^4$-$M^2$ in lateral view; *B*, same specimen in occlusal view.

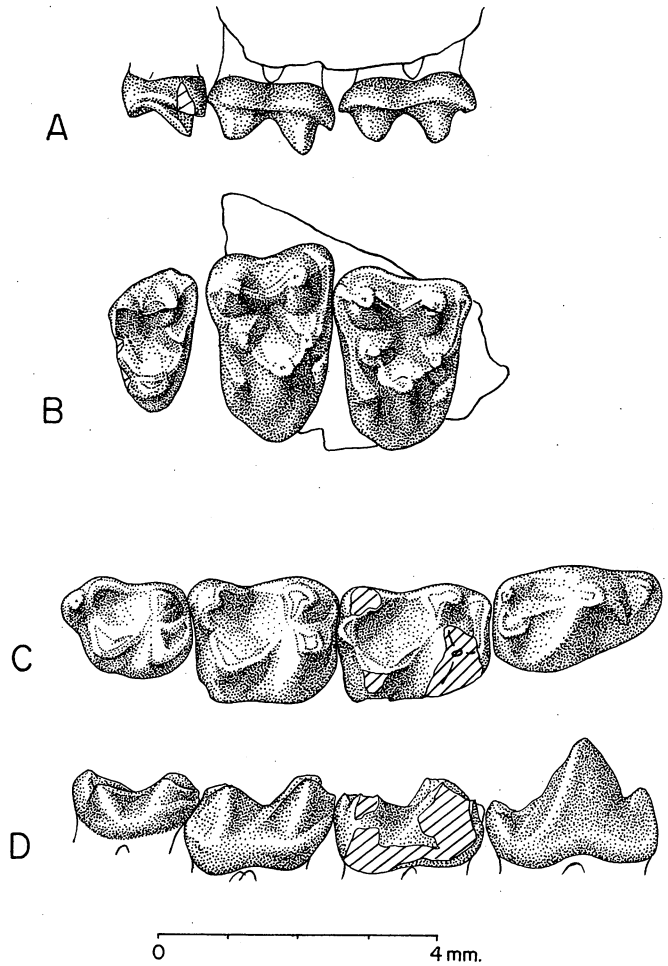


FIG. 8— Dentition of *Dorraletes diminutivus* (Dorr) from the Type Chappo locality (middle Tiffanian), Green River Basin, Wyoming. *A*, UM 72069, right maxilla with $M^{1-2}$, and UM 72073, right $M^3$, in lateral view; *B*, same specimens in occlusal view. *C*, Composite right lower dentition, based on UM 81133 ($P_4$), 81098 ($M_1$), 81105 ($M_2$), and 81115 ($M_3$), in occlusal view; *D*, same specimens in lateral view.

*Diagnosis.*—As for the genus.

*Description.*—The holotype, UM 27231 (Fig. 7), preserves $P^4$-$M^2$ in sequence in a maxillary fragment. $P^4$ has a large protocone and paracone, and a very small metacone. There is a distinct cuspule anterior to the paracone. $M^1$ and $M^2$ both have a prominent paraconule and metaconule in addition to a larger protocone, paracone, and metacone. The hypocone is small cusp directly posterior from the protocone, and there is a very small pericone anterior to the protocone. These accessory cusps are positioned at the lingual end of small but distinct anterior and posterior cingula. $M^2$ differs from $M^1$ only in being relatively broader transversely. Several isolated $M^3$'s are known from the Type Chappo locality (e.g., UM 72077; Fig. 8). These are all reduced in size by comparison with $M^2$. The metacone on $M^3$ is much reduced in size, and there is no metaconule or hypocone on $M^3$.

Lower teeth of *Dorraletes* are moderately common in washing concentrate collected from the Type Chappo locality (Fig. 8). Molars are very similar to those described by Holtzman (1978) from Judson in North Dakota. $P_4$ is described here for the first time. It is a long narrow semimolariform tooth with a low paraconid positioned well forward of the protoconid. There is a small but distinct metaconid lingual to the protoconid. The talonid is moderately long, with a hypoconid and entoconid enclosing two sides of a basin; the talonid basin remains open lingually. The trigonid of $M_1$ has a prominent protoconid and metaconid, with a very small paraconid. The latter cusp is positioned forward of the metaconid, at the lingual end of a sharply curved paracristid. The hypoconid is the largest cusp on the talonid. There is a small hypoconulid near the entoconid. $M_2$ differs from $M_1$ in having an anteroposteriorly shorter trigonid, with no paraconid and a paracristid joining the anterior surface of the metaconid. The talonids on both $M_1$ and $M_2$ are open lingually. $M_3$ is reduced in size by comparison with $M_2$. It has the short trigonid characteristic of $M_2$, and a narrow talonid with a moderately large projecting hypoconulid.

Measurements of the type specimen of *Dorraletes diminutivus* are as follows (all measurements in mm): $P^4 = 1.8 \times 2.3$, $M^1 = 1.9 \times 2.5$, $M^2 = 1.9 \times 3.0$. Measurements of the Type Chappo sample of *D. diminutivus* are summarized in Table 4.

TABLE 4 — Summary of measurements of the upper and lower dentition of the Type Chappo locality sample of *Dorraletes diminutivus*, new genus and species, based on specimens in the University of Michigan collection. Abbreviations as in Table 2.

| Tooth position | | N | OR | $\bar{x}$ | S | V |
|---|---|---|---|---|---|---|
| UPPER DENTITION | | | | | | |
| $M^1$ | L | 1 | 2.0 | - | - | - |
| | W | 1 | 2.6 | - | - | - |
| $M^2$ | L | 3 | 1.9-2.1 | 2.00 | 0.10 | 5.0 |
| | W | 3 | 3.0-3.2 | 3.07 | 0.12 | 3.8 |
| $M^3$ | L | 3 | 1.3-1.5 | 1.37 | 0.12 | 8.4 |
| | W | 3 | 2.0-2.1 | 2.07 | 0.06 | 2.8 |
| LOWER DENTITION | | | | | | |
| $P_4$ | L | 2 | 2.4-2.5 | 2.45 | - | - |
| | W | 2 | 1.4-1.5 | 1.45 | - | - |
| $M_1$ | L | 5 | 2.0-2.1 | 2.06 | 0.06 | 2.7 |
| | W | 5 | 1.4-1.7 | 1.56 | 0.13 | 8.6 |
| $M_2$ | L | 7 | 2.0-2.2 | 2.07 | 0.08 | 3.7 |
| | W | 7 | 1.6-1.9 | 1.74 | 0.13 | 7.3 |
| $M_3$ | L | 3 | 1.8-2.1 | 1.97 | 0.15 | 7.8 |
| | W | 3 | 1.3-1.4 | 1.33 | 0.06 | 4.3 |

*Typodigm.*—UM 27231 (holotype) is the only specimen known from the type locality. An important supplementary collection of *D. diminutivus* was described by Holtzman (1978) from the Judson locality in North Dakota. Another important collection includes material described here from the Type Chappo locality, including: UM 68375, 72069, 72073, 72074, 72077, 81098-81101, 81105, 81107, 81109, 81110, 81112, 81115, 81123-81126, 81128-81130, 81132, 81133, and 81136.

*Discussion.*—The holotype was the only specimen known when *Dorraletes diminutivus* was first described. Dorr (1952) conservatively retained it in the well known Torrejonian genus *Haplaletes.* Discovery of lower cheek teeth in washed samples yielding upper molars of *D. diminutivus* (Holtzman, 1978; this report) indicates that this species differs markedly from the type and other species of *Haplaletes.* Specimens of *D. diminutivus* from the Type Chappo locality previously identified as "Erinaceoid sp." and "Hyopsodontid sp. small" are illustrated in Figure 8. They differ from Erinaceoidea in lacking stylar crests on upper molars, in having more rounded cusps, and in having no trace of a paraconid on $M_2$ or $M_3$.

## *Aletodon* Gingerich

*Aletodon* Gingerich, 1977, p. 238.
*Platymastus* (in part), Van Valen, 1978, p. 56.

*Type species.*—*Aletodon gunnelli* Gingerich, 1977.

*Included species.*—Type; *A. mellon* (Van Valen), 1978; *A. conardae* Winterfeld, 1982; and *A. quadravus*, new species.

*Age and distribution.*—Middle Tiffanian (late Paleocene) through Clarkforkian (early Eocene) land-mammal ages in Colorado, Wyoming, and western North Dakota.

*Revised diagnosis.*—Differs from *Litomylus* and other hyopsodontids in having more massive cusps on upper and lower cheek teeth. $P^4$ simple, with only two major cusps: a bulbous protocone and paracone. Upper molars relatively narrow labiolingually with prominent conules and a large hypocone. $P_4$ simple, with a large bulbous protoconid and, primitively, a small metaconid lost in later species. Lower molars broad, with a massive protoconid and metaconid on a trigonid little elevated above the talonid. Talonid has a large hypoconid, small hypoconulid, and large entoconid. A very small paraconid is present in early species, but this was subsequently lost.

### ***Aletodon quadravus***, new species
Figure 9A-D

*Litaletes* sp., Dorr, 1958, p. 1223.
*Litomylus? ishami* (in part), Gingerich, 1977, p. 238. Winterfeld, 1982, p. 102, fig. 5A.
Condylarth indet., Holtzman, 1978, p. 60, Pl. 11, fig. 19.
*Litomylus* sp. A, Rose, 1981, p. 152.
*Litomylus* sp. B, Rose, 1981, p. 152.

*Holotype.*—UM 82024, right dentary with unworn $M_{1-2}$.

*Type locality.*—Cedar Point Quarry in the northern Bighorn Basin, northwestern Wyoming.

*Age and distribution.*—Middle Tiffanian (late Paleocene) of Wyoming and western North Dakota.

*Diagnosis.*—Differs from *A. conardae* and *A. mellon* in being about 15% smaller in linear dimensions and in having relatively broader upper and lower molars. $P_4$ relatively short and broad compared to $M_{1-2}$, with a massive protoconid and traces of a very small paraconid and small metaconid. *A. quadravus* is most easily confused with middle Tiffanian *Litomylus? ishami* Gazin, but differs in having relatively longer and narrower lower molars, with lower and more rounded cusps.

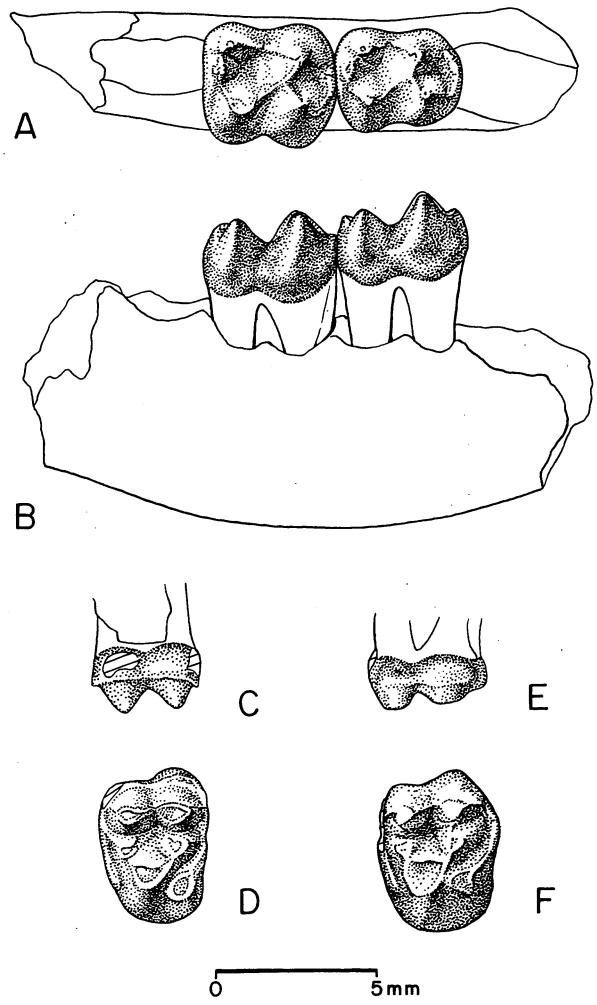


FIG. 9— Dentition of *Aletodon quadravus*, new species, from Cedar Point Quarry (middle Tiffanian), northern Bighorn Basin, and Battle Mountain (middle Tiffanian), Hoback Basin, Wyoming, compared with *A. mellon* (Van Valen) from arkosic sandstone 50 m above Mason Pocket (late Tiffanian), San Juan Basin, Colorado. *A*, UM 82024, holotype of *A. quadravus* from Cedar Point Quarry, right dentary with $M_{1-2}$ in occlusal view; *B*, same specimen in lateral view. *C*, UM 34775, *A. quadravus* from Battle Mountain, left $M^2$ in lateral view; *D*, same specimen in occlusal view. *E*, AMNH 56293; *A. mellon* from above Mason Pocket, left $M^2$ in lateral view; *F*, same specimen in occlusal view.

*Etymology.*—*Quadra* (L.), square, and *avus*, grandfather; in reference to the quadrate lower molars of this species and its probable ancestral relationship to later *Aletodon.*

*Description.*—The maxillary dentition of *Aletodon quadravus* is poorly known. One isolated $P^4$ is illustrated by Holtzman (1978, Pl. 11, fig. 19). It has a large simple protocone and paracone with no trace of a metacone. An isolated $M^1$, UM 34775, is illustrated in Figure 9C,D. $M^1$ is rectangular in outline, with large conules and a large hypocone in addition to the three principal upper molar cusps.

Several dentaries are known preserving two or more teeth. The holotype is unique in preserving unworn $M_1$ and $M_2$ intact (Fig 9A,B). $P_4$ is a moderately short, broad tooth with a single large protoconid cusp and a very small hypoconid dividing it into sloping labial and lingual portions. The lingual portion occasionally has a very small entoconid, giving it a slightly basined appearance. $M_1$ has a narrower trigonid than talonid. The trigonid is little elevated above the talonid. It has a low massive protoconid and metaconid. The paraconid is a very small cuspule centered on the paracristid. There is a large hypoconulid and a smaller entoconid and hypoconulid on the talonid. The hypoconulid is positioned closer to the entoconid than it is to the hypoconid. $M_2$ differs from $M_1$ in having a broader trigonid than talonid and in lacking a distinct paraconid. $M_3$ has a narrow trigonid otherwise similar in form to that on $M_2$. The talonid of $M_3$ is also narrow, with a moderately large entoconid projecting posteriorly.

Measurements of the holotype, UM 82024, are as follows (all measurements in mm): $M_1 = 3.8$ x 3.4, $M_2 = 4.0$ x 3.9, mandibular depth below $M_1 = 6.6$. Measurements of the entire sample of *A. quadravus* from Cedar Point Quarry are summarized in Table 5.

TABLE 5 — Summary of measurements of the lower dentition of *Aletodon quadravus,* new genus and species, from Cedar Point Quarry (type locality), based on all specimens in the University of Michigan and Princeton University collections. Abbreviations as in Table 2.

| Tooth position | | N | OR | $\bar{x}$ | S | V |
|---|---|---|---|---|---|---|
| $P_4$ | L | 3 | 4.2-4.6 | 4.43 | 0.21 | 4.7 |
| | W | 3 | 2.9-3.0 | 2.97 | 0.06 | 1.9 |
| $M_1$ | L | 6 | 3.7-4.2 | 3.93 | 0.23 | 5.9 |
| | W | 6 | 3.0-3.4 | 3.30 | 0.16 | 4.7 |
| $M_2$ | L | 8 | 3.8-4.3 | 3.96 | 0.17 | 4.2 |
| | W | 8 | 3.5-4.0 | 3.74 | 0.18 | 4.7 |
| $M_3$ | L | 1 | 3.9 | - | - | - |
| | W | 1 | 3.0 | - | - | - |

*Typodigm.*—The type sample of *Aletodon quadravus* from Cedar Point Quarry comprises the following specimens: PU 19963, 20009, 21449, 21450, 22016, UM 64638, and 82024 (holotype). In addition, UM 34775 and 80804 from the Middle Tiffanian Battle Mountain locality, and UM 74005 from the middle Tiffanian Type Chappo locality represent *A. quadravus.*

*Discussion.*—In a previous report (Gingerich, 1977), I referred the Cedar Point specimens described here to Gazin's (1956b) species *Litomylus? ishami.* The holotype of *L? ishami* consists of the talonid of $M_1$ and an intact crown of $M_2$, both little worn. Detailed comparison of this specimen with the Cedar Point sample of *A. quadravus* suggests that the two are not conspecific

as previously suggested. *L? ishami* differs consistently from all Cedar Point specimens of *A. quadravus* in having relatively narrower lower molars with sharper trigonid cusps and the trigonid more elevated above the talonid.

Rose (1981) concluded that two species of "*Litomylus*" are present in the Cedar Point collection, however study of all specimens available to him together with new material suggests that a single species is represented. The observed variation in dental measurements of the entire sample is well within that characteristic of single species (see Table 5).

Finally, it should be noted that most of the specimens Winterfeld (1982) referred to *Litomylus ishami* are significantly larger than those of *Aletodon quadravus*. Winterfeld's specimens have broad crowns like those of primitive *Aletodon*, and they may represent a new species intermediate in size between *A. quadravus* and *A. conardae*, or they may represent the smaller end of the size range of *A. conardae* itself.

*Aletodon mellon* (Van Valen)
Figure 9E,F

*Platymastus mellon* Van Valen, 1978, p. 56, Pl. 2, fig. 7.

*Holotype.*—AMNH 56293, isolated left $M^2$.

*Type locality.*—Tiffany, Colorado. The holotype was found in an arkosic sandstone approximately 50 m above the level of Mason Pocket quarry.

*Age and distribution.*—Late part of the late Tiffanian (late Paleocene) in southwestern Colorado (see Butler et al., 1981, p. 309, for discussion of the age of this locality).

*Diagnosis.*—Differs from *A. quadravus*, new species, in being larger and in having the paracone and metacone more closely joined. Differs from *A. gunnelli* Gingerich in being smaller. Cannot be compared at present with *A. conardae* Winterfeld.

*Description.*—AMNH 56293 is an isolated upper molar identified as $M^2$ on the basis of its metacone slightly smaller than the paracone. It is moderately rectangular in occlusal outline. All six upper molar cusps, including a relatively large paraconule, metaconule, and hypocone, are low and rounded. The position of the metacone relative to the paracone is variable in *Aletodon gunnelli*. These cusps are sometimes well separated, as in UM 65059 (Gingerich, 1977, fig. 2), but they are also sometimes positioned close to each other (as in PU 19850). The holotype of *A. mellon* has the external cusps joined like those of the latter specimen.

The entire labial part of the holotype tooth is damaged in such a way that tooth size cannot be measured accurately. Van Valen (1978, p. 56) estimated the length and width of the holotype $M^2$ to have been 3.8 x 5.5 mm, respectively.

*Discussion.*—It is difficult to be certain of the systematic position of a species based on a single broken tooth. In this particular case, the holotype of "*Platymastus*" *mellon* is closely similar to $M^2$ of the slightly larger *Aletodon gunnelli*, and "*P.*" *mellon* may be referred to *Aletodon* with some confidence. However, reference of "*P.*" *mellon* to *Aletodon* makes the systematic position of *Aletodon conardae* problematical. Both are from the late part of the late Tiffanian (*Plesiadapis simonsi* or *Plesiadapis fodinatus* zone of Gingerich, 1976), and both are similar in size. Each is based on a unique specimen, an upper molar and a dentary with $P_4$-$M_2$, respectively, that cannot be compared directly. I suspect that *A. conardae*, based on the more informative type specimen, may unfortunately be a junior synonym of *A. mellon*.

## *Utemylus*, new genus

*Type species.*—*Utemylus latomius.*

*Included species.*—Type species only.

*Age and distribution.*—Late Tiffanian Land-Mammal Age (late Paleocene) of southwestern Colorado.

*Diagnosis.*—Differs from all Hyopsodontidae except *Haplomylus* in having a postprotocingulum in place of a hypocone. Resembles *Haplomylus*, but differs in lacking any trace of a metacone on $P^4$, in having more rounded, bunodont molar cusps, in having relatively broader $M^1$ and $M^2$, and in having a more rounded $M^3$ with a distinct posterior cingulum.

*Etymology.*—*Ute*, Amerindian people of western North America, and *mylos* (Gr., masc.), mill or grinder. The type species of this genus comes from a locality on reserved land of the Southern Ute tribe.

## *Utemylus latomius*, new species

Figure 10A,B

*Holotype.*—PU 14583, left maxilla with $M^{1-3}$ intact.

*Type locality.*—Mason Pocket near the town of Tiffany in the northern San Juan Basin of southwestern Colorado.

*Age and distribution.*—Known only from late Tiffanian Mason Pocket (type locality) in southwestern Colorado.

*Diagnosis.*—As for the genus.

*Etymology.*—*Latomos* (Gr.), stone-cutter or mason; in reference to the type locality, Mason Pocket.

*Description.*—$P^4$ has a prominent protocone and paracone but no trace of a metacone. There is a distinct crest curving posterolabially from the protocone in the position of a postprotocingulum. $M^1$ has a large protocone, paracone, and metacone, with distinct conules and anterior, labial, and posterior cingula. A postprotocingulum connects the protocone to the posterior cingulum. $M^2$ differs from $M^1$ in being larger and in having a slightly reduced metacone. $M^3$ is much reduced by comparison with $M^1$ or $M^2$, and it has very low rounded cusps, a very reduced metacone and metaconule, and no postprotocingulum.

Measurements of the teeth of *U. latomius* are as follows (all measurements in mm): $P^4 = 3.6$ x 4.6, $M^1 = 4.0$ x 5.0, $M^2 = 4.1$ x 6.0, and $M^3 = 2.9$ x 4.0.

*Typodigm.*—Two specimens are known, both from the type locality: PU 14583 ($M^{1-3}$, holotype), and AMNH 101509 ($P^4$).

*Discussion.*—*Utemylus latomius* is noteworthy in being the first hyopsodontid condylarth to be reported from Mason Pocket. The holotype, PU 14583, was collected in 1940 by Jepsen and Bott. AMNH 101509 is an isolated $P^4$ found among miscellaneous teeth in the American Museum collection from Mason Pocket. It fits almost perfectly onto the type maxilla and there is little question that the tooth belongs to the same species. However, it overlaps the type slightly in preserved parts and thus cannot actually be a part of the same specimen.

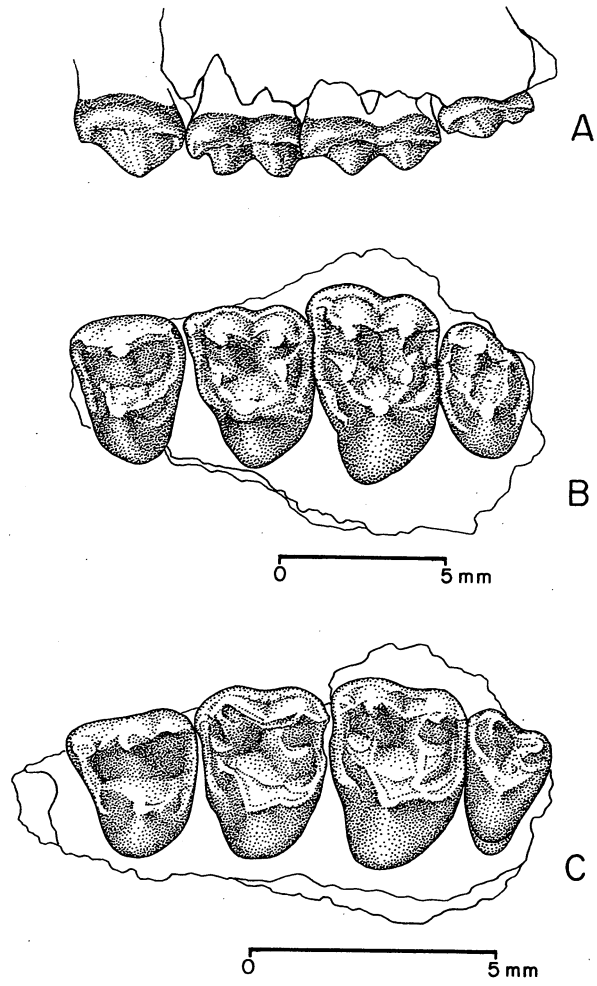


FIG. 10— Composite upper dentition of *Utemylus latomius*, new genus and species, from Mason Pocket (late Tiffanian), San Juan Basin, Colorado, compared to early Wasatchian *Haplomylus speirianus* (Cope). *A*, PU 14583 (holotype), right maxilla with $M^{1-3}$, and AMNH 101509, right $P^4$, in lateral view; *B*, same specimens in occlusal view. *C*, UM 65692, left maxilla of *Haplomylus* with $P^4$-$M^3$ in occlusal view. Note postprotocingulum present on $M^{1-2}$ of both genera.

## CHANGING COMPOSITION OF TIFFANIAN FAUNAS

Analysis of the stratigraphic ranges of small Paleocene hyopsodontid and hyopsodontid-like mammals of the families Adapisoricidae, Pentacodontidae, and Hyopsodontidae, reveals several interesting patterns of faunal change during the Tiffanian Land-Mammal Age (late Paleocene). Litocherine Adapisoricidae were apparently represented by a single genus, *Mckennatherium*, during the Torrejonian Land-Mammal Age (middle Paleocene). Three genera, *Litocherus*, *Cedrocherus*, and *Diacocherus*, representing three distinct evolutionary lineages, were present in the middle Tiffanian Land-Mammal Age (late Paleocene). Two genera, *Diacocherus* ("*Diacodon*") and *Leipsanolestes*, are known from the Clarkforkian Land-

Mammal Age (latest Paleocene to early Eocene; Rose, 1981), and litocherines were replaced by dormaaliine Adapisoricidae in the Wasatchian Land-Mammal Age (early Eocene). Litocherine Adapisoricidae apparently reached their maximum diversity in the middle Tiffanian.

Three genera of Pentacodontidae are known from the late Torrejonian of Wyoming and Montana (*Aphronorus*, a new *Aphronorus*-like genus, and *Coriphagus*). *Bisonalveus* replaced *Coriphagus* in the early Tiffanian, and *Aphronorus* and the *Aphronorus*-like genus became extinct. *Bisonalveus* itself apparently became extinct in the middle Tiffanian. Thus the history of Pentacodontidae is one of decline and extinction during the Tiffanian.

Hyopsodontidae are represented in late Torrejonian faunas by four genera (*Litaletes*, *Haplaletes*, *Litomylus*, and *Promioclaenus*) that collectively account for about 20% of the total number of individuals in particular faunas (Rose, 1981, p. 146). Most middle Tiffanian localities, even quarries as well sampled as Cedar Point (with a total of more than 2,000 specimens representing a minimum of more than 500 individuals; Rose, 1981, p. 152), have a single genus and species of hyopsodontid, *Aletodon quadravus*. It is, in addition, a rare faunal element. The entire Cedar Point collection includes only fifteen specimens representing a minimum of six individuals of *A. quadravus*. Screen washed samples from sites of similar age (Judson, Type Chappo) have at most one additional hyopsodontid, *Dorraletes diminutivus*. However, unlike the pentacodontid example of declining Tiffanian diversity, *Aletodon* and *Dorraletes* persisted and an additional hyopsodontid lineage, represented by *Phenacodaptes*, was added to Wyoming faunas in the late Tiffanian. *Utemylus* was apparently added to southern faunas as well. Three genera, *Apheliscus*, *Haplomylus*, and *Aletodon* were present through most of the Clarkforkian in Wyoming (Rose, 1981). *Aletodon* was replaced by *Hyopsodus* in the Wasatchian, and hyopsodontids then underwent a second major radiation.

These three patterns of changing diversity in Adapisoricidae, Pentacodontidae, and Hyopsodontidae were undoubtedly coordinated with other changes in overall faunal composition and with extrinsic environmental conditions during the Tiffanian. It may be no coincidence that the radiation of Plesiadapidae, to take one distantly related group as an example, coincided with a temporary restriction in the diversity of Hyopsodontidae. Hyopsodontidae and Plesiadapidae may have filled similar adaptive roles in faunas associated with different floral and climatic regimes. However, much remains to be learned about faunal composition in the Tiffanian, and much also remains to be learned about the cranial and postcranial morphology and adaptations of the mammalian families discussed here. Consequently it is not yet possible to frame a comprehensive hypothesis to explain the changing composition of Tiffanian mammalian faunas.

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