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MULTITUBERCULATES (MAMMALIA, ALLOTHERIA) FROM THE EARLIEST TIFFANIAN (LATE PALEOCENE) DOUGLASS QUARRY, EASTERN CRAZY MOUNTAINS BASIN, MONTANA

BY

CRAIG S. SCOTT[1] AND DAVID W. KRAUSE[2]

Abstract—Highly fossiliferous sequences from the eastern Crazy Mountains Basin, south-central Montana, have figured importantly in current understanding of mammalian evolution during the middle and late parts of the Paleocene epoch in the Western Interior of North America, and are crucial for intra- and interbasinal biostratigraphic correlation, particularly those localities of early Tiffanian (late Paleocene) age. One of these localities, Douglass Quarry, documents mammals of earliest Tiffanian age, an important but poorly represented interval in mammalian evolution. Notable among the specimens from Douglass Quarry are well-preserved teeth of multituberculates, a long-lived group of herbivorous or omnivorous mammals. Neoplagiaulacidae are particularly abundant, and are represented by species of *Mesodma*, *Ectypodus*, and two species of *Neoplagiaulax*, one of which, *Neoplagiaulax donaldorum*, is new. Two species of the cimolodontid *Anconodon* are identified, with *Anconodon cochranensis* being the most abundant multituberculate in the local fauna. The Douglass Quarry multituberculate fauna closely resembles that from the Cochrane 2 locality, Paskapoo Formation, Alberta, also of earliest Tiffanian age. Multituberculate evolution in the Western Interior of North America during the early part of the Tiffanian is characterized by higher taxonomic diversity among neoplagiaulacids and, especially, ptilodontids when compared with localities from the late Torrejonian, and increased generic and specific diversity toward more northerly latitudes.

INTRODUCTION

Multituberculata were a geologically long-ranging, primarily Laurasian group of mammals with an abundance and diversity that peaked during the Paleocene, but declined thereafter until their extinction in the late Eocene (Krause, 1986). Multituberculates were common members of

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North American early Tertiary terrestrial vertebrate communities, and may have been among the first mammals to enter an herbivorous (Fox, 1971; Novacek and Clemens, 1977), or at least omnivorous (Krause, 1982c), adaptive zone. The multituberculate record from the Western Interior of North America is among the best known and densest stratigraphically in the world, with a temporal range spanning the Middle? or Late Jurassic to the late Eocene, and geographically from southern Texas to Ellesmere Island (see summaries in Weil, 1999; Kielan-Jaworowska et al., 2004).

The Tiffanian record (the term "Tiffanian" refers to a North American Land Mammal Age or NALMA that is approximately equivalent to the early late Paleocene; see Lofgren et al., 2004) of multituberculates in the northern part of the Western Interior of North America is especially rich, with numerous localities preserving multituberculate fossils (e.g., Granger and Simpson, 1929; Simpson, 1937a-b; Jepsen, 1930, 1940; Gazin, 1956; Holtzman and Wolberg, 1977; Krause, 1977, 1982a; Rose, 1981; Sloan, 1987; Fox, 1990a, 2005; Lofgren et al., 2002; Higgins, 2003a-b; Scott, 2003a-b; Kihm et al., 2004; and summaries in Archibald et al., 1987 and Lofgren et al., 2004).

The earliest Tiffanian biochron (Ti-1) is a particularly important interval in that it represents a period of significant faunal turnover and possibly climatic change in North America, in addition to documenting the earliest occurrences of a number of higher-level mammalian taxa, including *Phenacodus-Ectocion* phenacodontid condylarths, apheliscine apheliscid condylarths, and titanoideid pantodonts (e.g., Rose, 1981; Archibald et al., 1987; Krause and Maas, 1990; Secord, 1998; Higgins, 2003a; Zack et al., 2005). Although the mammalian fossil record documenting the latest Torrejonian (To-3) in the Western Interior of North America is rich (e.g., Simpson, 1936, 1937a; Rose, 1981), the earliest Tiffanian is comparatively poorly known, with the majority of Ti-1-aged local faunas represented by only a few specimens, or remaining undescribed (see Lofgren et al., 2004 for summary).

Multituberculates are taxonomically diverse and abundant during the Torrejonian, and remain so through the early part of the middle Tiffanian (Ti-3; e.g., Scott, 2003b, 2005), yet their record during the earliest Tiffanian, like those of other contemporaneous mammals, remains obscure. The largest and potentially most informative local faunas of earliest Tiffanian age are from the Cochrane 2 locality of south central Alberta, Canada (Cochrane II of Russell, 1932; see Fox, 1990a; Scott et al., 2002), the Keefer Hill/Twin Buttes ("Shotgun") locality of Wyoming, and the Breaks localities of south central Wyoming (Youzwyshyn, 1988; Gunnell, 1989; Fox, 1990a; Scott et al., 2002; Higgins, 2003a), but the bulk of these local faunas remains undescribed.

Studies on fossil mammals from an important series of localities in the eastern Crazy Mountains Basin, Montana, have contributed to knowledge of Paleocene mammalian evolution and biochronology in the Western Interior of North America (see, e.g., Simpson, 1935, 1936, 1937a-b; Rose, 1981; Krause, 1982a, 2004; Krause and Gingerich, 1983; Archibald et al., 1987 and references therein; Krause and Maas, 1990; Hartman and Krause, 1993; Silcox et al., 2001; Lofgren et al., 2004 and references therein; Zack et al., 2005), with the ages of these local faunas being further refined by ongoing magnetostratigraphic work (see, e.g., Butler et al., 1987; Boyer et al., 2004a). The Crazy Mountains Basin localities preserve a succession of mammalian faunas spanning middle/late Torrejonian (To-2) through the early part of middle Tiffanian (Ti-3) time, with the three principal localities (Gidley, Silberling, and Scarritt quarries) and their associated mammalian faunas having been thoroughly described by Simpson (1935, 1936, 1937a-b).

Douglass Quarry (Locality 63 of Simpson, 1937a), a fourth locality in the eastern part of the Crazy Mountains Basin, is one of the few localities in the region that documents mammals of earliest Tiffanian age. Two other localities, Bingo Quarry in the eastern part of the basin and Bangtail Quarry in the western part, have yielded exceptionally well-preserved specimens that are briefly discussed elsewhere (see, e.g., Gingerich et al., 1983; Boyer, 2003; Boyer et al., 2004b). It was discovered in 1902 by field parties from Princeton University, and was quarried for fossil vertebrates in 1940 primarily by John Bell, for a senior thesis project at Princeton University, and Albert C. Silberling, a local fossil collector. These collections, now housed at Yale University, as well as a small sample collected during a reconnaissance expedition from Stony Brook University in 1982, were described by Krause and Gingerich (1983). Intensive collecting from Douglass

Quarry by field parties from Stony Brook University was initiated in 1983 and continued into the early 1990s. This effort augmented the earlier collections by an order of magnitude, substantially increased the number of taxa known from the locality, and further clarified Paleocene mammalian diversity near the beginning of the Tiffanian NALMA in the Western Interior. A preliminary faunal list was presented by Krause and Maas (1990: table 3).

Included among the new specimens from Douglass Quarry are numerous isolated teeth and jaw fragments of multituberculates, together representing a diverse assemblage of cimolodontan, microcosmodontid, and eucosmodontid taxa. Our objectives here are to report on new and previously undescribed multituberculate specimens, focusing on the non-ptilodontids; compare the multituberculate fauna from Douglass Quarry with those from other penecontemporaneous localities in the Western Interior of North America; and comment briefly on larger-scale patterns of multituberculate evolution that occurred during the late Torrejonian and early Tiffanian in North America. The ptilodontids from Douglass Quarry and other localities of Paleocene age are under study by Krause (2004, in prep.).

GEOLOGICAL SETTING

Douglass Quarry is located in the eastern Crazy Mountains Basin, south-central Montana, on the east side of US Highway 191. It is in north-facing exposures of a south-to-north tributary of Sadie Creek in the NW¼ of Section 18, Township 5 North, Range 15 East, Sweetgrass County (see location maps in Simpson, 1937a, locality 63, plate 1; and Hartman and Krause, 1993, fig. 1; and photographs in Krause and Gingerich, 1983, fig. 1). Douglass Quarry occurs approximately 400 m above the base of the Melville Formation, Fort Union Group (Hartman and Krause, 1993). The Melville Formation, named for exposures near the town of Melville (located west of US 191 roughly halfway between Harlowton to the north and Big Timber to the south), is approximately 1500 m thick and consists primarily of "a basal, yellow to off-white sandstone overlain by olive-green shales and sandstones" (Hartman and Krause, 1993, p. 76). The two dominant lithologies in the quarry were described by Krause and Gingerich (1983, p. 158) as (1) an indurated, greenish-grey, fine-grained quartz sandstone, and (2) a mottled orange/brown/green conglomerate with a fine-grained quartz sand matrix and angular to rounded, dark, greenish-grey mudstone clasts." The vast majority of fossil mammal specimens, as well as a small molluscan assemblage (Hartman and Krause, 1993), were recovered from the conglomeratic beds.

Douglass Quarry is the type locality for the plesiadapiform primate *Plesiadapis praecursor*, an index fossil that characterizes the *Plesiadapis praecursor* Range Zone (earliest Tiffanian biochron Ti-1) of Gingerich (1975), more recently called the *Plesiadapis praecursor/Plesiadapis anceps* Lineage Zone (Archibald et al., 1987; Lofgren et al., 2004). Douglass Quarry lies stratigraphically below Scarritt Quarry (Ti-2) and above Bingo and Glennie quarries (Ti-1), all in the Melville Formation, and above Gidley and Silberling quarries (To-2), in the Lebo Formation (Hartman and Krause, 1993, table 2). Paleomagnetic samples collected from Douglass Quarry by Butler et al. (1987), as well as from Bingo Quarry (Boyer et al., 2004a), have been correlated to chron 26r. The age of Douglass Quarry, based on current litho-, bio-, and magnetostratigraphic evidence, is estimated to be between 60 and 60.5 million years (Lofgren et al., 2004).

SAMPLE COMPOSITION, TERMINOLOGY, MEASUREMENTS, AND ABBREVIATIONS

Sample.— The sample analyzed in this report consists of non-ptilodontid multituberculates, primarily neoplagiaulacids and cimolodontids; the ptilodontid fraction is under study by one of us (DWK) and will be published elsewhere. The non-ptilodontid multituberculate assemblage from Douglass Quarry reported upon here consists of 89 specimens, of which almost all are isolated upper and lower fourth premolars. A single dentulous jaw containing P_4, M_{1-2} of a neoplagiaulacid comprises the only articulated specimen in the sample. Of the 89 specimens, 82 were identifiable

to at least family level. Taxa were identified on the basis of the morphology of complete or nearly complete upper and lower fourth premolars, the teeth most often used in previous diagnoses of multituberculate taxa, or incisors and molars where these teeth are diagnostic (e.g., microcosmodontids, eucosmodontids). The incisors, anterior premolars, and molars of neoplagiaulacids and cimolodontids are often closely similar between taxa and were not identified. Multituberculate classification follows Kielan-Jaworowska and Hurum (2001).

Dental terminology.— Dental terminology follows that of Krause (1977, 1982a, 1987). Following the results of Hahn (1987), we consider the enlarged, blade-like tooth in the lower dental row to be the lower fourth premolar (P$_4$) rather than the "molar blade" ("M$_b$"; contra Schiebout, 1974; Sloan, 1981, 1987; Secord, 1998). Dental measurements follow Krause (1987) and Scott (2003a); width of P$_4$ was not measured (Krause, 1977, following the rationale of Ramaekers, 1975). "Exodaenodont lobe" refers to the ventral projection of enamel on the labial side of the anterior root on the P$_4$ of many multituberculates. Outline drawings of lower fourth premolars were made with the aid of a camera lucida following the methodology of Jepsen (1940) and Krause (1977). Baseline of standard measurement refers to a line that extends from the apex of the anterobasal concavity posteriorly to the point where the posterolabial shelf intersects the posterior margin of the crown (see Krause, 1982a for details).

Tooth positions.— Incisor, premolar, and molar tooth positions are abbreviated I, P, and M, respectively, with superscript numerals indicating particular upper teeth and subscript numerals indicating particular lower teeth.

Multituberculate cusp formulae.— Cusp number and their expression in formulae follow the methods and rationale of Krause (1977). P^4 and upper molar cusp formulae of the form x:y:z designate cusps of the labial (x), middle (y), and lingual (z) rows, respectively. Lower molar cusp formulae of the form x:y designate cusps of the labial (x) and lingual (y) rows, respectively.

Measurements and statistical abbreviations.— *C,* cusp formula; *S,* serration count; *L,* length of tooth; *W,* width of tooth; *D,* depth of incisor; *M,* mean; *OR,* observed range; *SD,* standard deviation; *CV,* coefficient of variation; *N,* number. An asterisk (*) indicates the measurement or count is an estimate. All measurements are in millimeters (mm).

North American Land-Mammal Ages (NALMAs).— *Pu,* Puercan, subdivided into early, *Pu-1*; middle, *Pu-2*; and late, *Pu-3* biochrons. *To,* Torrejonian, subdivided into early, *To-1*; middle, *To-2*; and late, *To-3* biochrons. *Ti,* Tiffanian, subdivided into earliest, *Ti-1*; early, *Ti-2*; early middle, *Ti-3*; late middle, *Ti-4*; late, *Ti-5*; and latest, *Ti-6* biochrons.

INSTITUTIONAL ABBREVIATIONS

AMNH — American Museum of Natural History, New York
MCZ — Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts
UALVP — Laboratory for Vertebrate Paleontology, University of Alberta, Edmonton
UM — Museum of Paleontology, The University of Michigan, Ann Arbor
USNM — United States National Museum of Natural History, Washington, D. C.

SYSTEMATIC PALEONTOLOGY

Class MAMMALIA Linnaeus, 1758
Subclass ALLOTHERIA Marsh, 1880
Order MULTITUBERCULATA Cope, 1884
Suborder CIMOLODONTA McKenna, 1975
Superfamily PTILODONTOIDEA (Sloan and Van Valen, 1965)
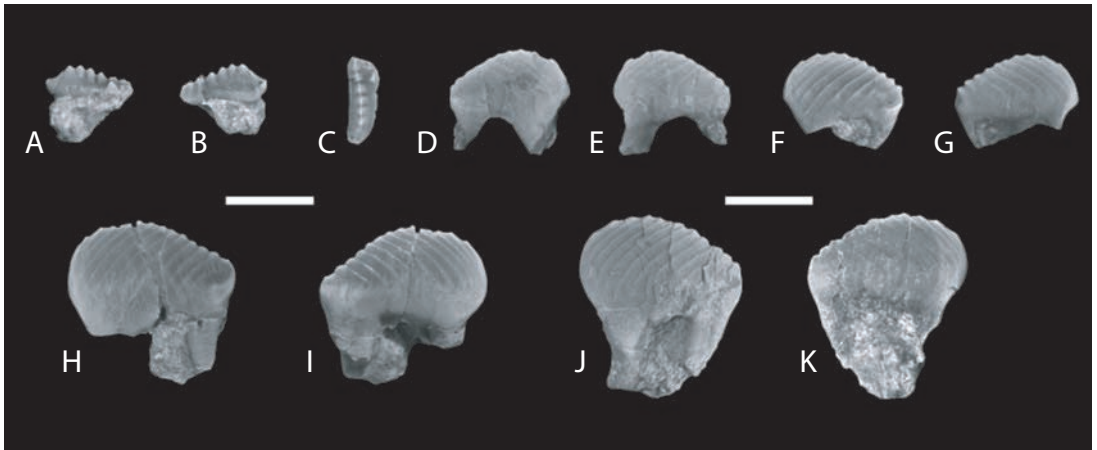Family NEOPLAGIAULACIDAE Ameghino, 1890

FIG. 1 — Multituberculates from the earliest Tiffanian (Ti-1, late Paleocene) Douglass Quarry, eastern Crazy Mountains Basin, Montana. A-G are *Mesodma pygmaea* Sloan, 1987, and H-K are *Ectypodus* sp. . A-C, left P^4, UM 84196, in labial (A), lingual (B), and occlusal (C) views; D and E, right P_4, UM 84194, in labial (D) and lingual (E) views; F and G, left P_4, UM 84195, in labial (F) and lingual (G) views. H and I, left P_4, UM 84198, in labial (H) and lingual (I) views; J and K, left P_4, UM 84197, in labial (J) and lingual (K) views. Scale = 2 mm.

Genus *Mesodma* Jepsen, 1940

Mesodma Jepsen, 1940, p. 267.

   Type species.— *Mesodma ambigua* Jepsen, 1940.
   Type locality.— Mantua Lentil locality (early Puercan, Pu-1, Lofgren et al., 2004), Fort Union (= Polecat Bench) Formation, Bighorn Basin, Wyoming, USA.

Mesodma pygmaea Sloan, 1987
Figure 1A-G

Mesodma sp. P, Krishtalka, 1973, p. 15; Krause, 1977, p. 20; Holtzman, 1978, p. 25.
Mesodma pygmaea Sloan, 1987, p. 188.

   Holotype.— AMNH 35298, incomplete left dentary with P_4, M_{1-2} (Sloan, 1987, p. 188, fig 10).
   Type locality.— Gidley Quarry (middle Torrejonian, To-2, Lofgren et al., 2004), Lebo Formation, eastern Crazy Mountains Basin, Montana, USA.
   Referred specimens.— Left P^4: UM 84196 (L = 2.0, W = 0.7). Left P_4: UM 84195 (L = 2.6, S = 10). Right P_4: UM 84194 (L = 2.7, S = 10).
   Description.— **P^4**: Cusp formula ?2:6:0 (N = 1). P^4 is short and low, with little elevation of the crown posteriorly. The crown is only slightly wider anteriorly than posteriorly, with the poorly developed anterolabial lobe supporting two cusps: a large conical cusp is developed adjacent to the second cusp of the middle row, while a second, smaller cusp is developed anterior and slightly lingual to the first; additional cusps may have been developed anterior to the second cusp, but the crown in this area is damaged. The cusps of the middle row are approximately equal to one another in size and height (as measured from cusp base to apex), and are arranged in a faintly arcuate line that is convex labially. The anterior slope is straight, with the ultimate and penultimate cusps

together being highest above the base of the crown. The posterior slope is short, shallow, and slightly concave; a posterobasal cusp is not developed.

P$_4$: The profile of P$_4$ is low and asymmetrical, with the anterior margin slightly convex, the dorsal crest smoothly arcuate, and the posterior slope virtually straight. Except for the weakly developed posterolabial shelf, the labial side of the crown is flat, and the faintly swollen exodaenodont lobe is both narrow and deep. The anterobasal concavity is shallow, and the anterior root bears a vertical groove. The anterior margin of the crown inclines steeply to the low first serration, and when the tooth is held with the baseline of standard measurement in a horizontal position, the apogee of the dorsal crest occurs at the third serration, and the height of the first serration above the anterobasal concavity is approximately one-third the length of the crown. The cutting edge bears 10 serrations (N = 2), the first of which is set off anteriorly from the succeeding serrations; the apices of the remaining serrations are equidistant from one another, and their bases become stouter posteriorly. The crown below the serrations bears well-developed labial and lingual ridges that extend anteroventrally in a gentle arc; anteriorly the ridges are closely spaced and coarse, but become further separated from one another and weaker towards the posterior parts of the crown, disappearing below the last three serrations.

Discussion.— The coronal features of the referred teeth are consistent with Sloan's (1987) diagnosis of the species and resemble teeth of *Mesodma pygmaea* from other localities in the Western Interior of North America. The P$_4$ of *M. pygmaea* from Douglass Quarry most closely resembles those referred to this species from the late Torrejonian Who Nose? locality and the earliest Tiffanian Cochrane 2 locality, both known from southwestern Alberta, Canada (Youzwyshyn, 1988; Scott, 2003a), and differing from P$_4$ of *M. pygmaea* from the late middle Tiffanian Roche Percée localities of Saskatchewan primarily in having a deeper and more swollen exodaenodont lobe (Krause, 1977).

Mesodma pygmaea is a stratigraphically long-ranging taxon (late Torrejonian through late Tiffanian) that appears to be restricted to the northern part of the Rocky Mountain Interior (Fig. 7) (the single record of *M. pygmaea* from the Black Peaks Formation, Texas, Schiebout, 1974, has been questioned; Krause, 1977).

Genus *Ectypodus* Matthew and Granger, 1921

Ectypodus Matthew and Granger, 1921, p. 1.
Charlesmooria Kühne, 1969, p. 200.

Type species.— *Ectypodus musculus* Matthew and Granger, 1921.
Type locality.— Mason Pocket locality (late middle Tiffanian, Ti-4; Lofgren et al., 2004), Animas Formation, San Juan Basin, Colorado, USA.

Ectypodus sp.
Figure 1H-K

Referred specimens.— Left P$_4$: UM 84197 (L = 3.6, S = 11), UM 84198 (L = 3.8, S = 10).

Description.— **P$_4$**: The lateral profile of UM 84197 and 84198 resembles that of P$_4$ of *Mesodma*, *Mimetodon*, and other basal neoplagiaulacids in being asymmetrically arcuate, with a weakly convex to straight anterior margin and a long, straight posterior slope. The referred P$_4$ differ from those of *Neoplagiaulax* in having a more arcuate profile (rather than more nearly trapezoidal), with a more convex anterior margin and more anteriorly positioned coronal apogee. The anterior margin of the crown does not project anteriorly as in P$_4$ of more basal neoplagiaulacids (see, e.g., P$_4$ of *Mesodma thompsoni* Clemens, 1964, or *Mimetodon silberlingi* (Simpson, 1936)); rather, the anterior edge forms a smooth arc extending from the base of the narrow and deep exodaenodont lobe to the high first serration, or to a slightly lower incipient serration (i.e., projection on the

anterior margin of the apical crest and which lacks ridges; see Johnston and Fox, 1984). With the exception of the weakly developed posterolabial shelf, the labial side of the crown is virtually flat, while the lingual side is weakly convex. The cutting edge bears 11 or 12 serrations (N = 2), that become larger and more nearly conical posteriorly; the apogee of the crown is at the third or fourth serration. Obliquely oriented labial and lingual ridges are developed below the serrations; the ridges become weaker towards the posterior part of the crown, and are undeveloped below the penultimate and ultimate serrations. The anterobasal concavity is shallowly excavated for reception of P_3.

Discussion.— UM 84197 and 84198 resemble P_4 of basal neoplagiaulacids in their asymmetrical profile, and in this regard are similar to P_4 of *Mesodma* and particularly *Mimetodon*, the taxon to which these specimens were originally questionably referred (Krause and Maas, 1990). The referred P_4s differ from those of *Mesodma* and *Mimetodon*, however, in being higher-crowned, in having a more broadly arcuate anterior margin, and in having a relatively higher first serration, features more consistent with those on P_4 of *Ectypodus* (e.g., relative height of P_4 is approximately 50 percent standard length; Sloan, 1981). UM 84197 and 84198 resemble P_4 of the late Torrejonian *E. szalayi* Sloan, 1981 and especially the early middle Tiffanian *E. elaphus* Scott, 2005, differing from the latter only in their larger size and narrower exodaenodont lobe. While UM 84197 and 84198 probably represent a new species of *Ectypodus*, we defer its formal naming and diagnosis, pending the discovery of additional, better-preserved material. *Ectypodus* sp. is also known from fragmentary specimens from the earliest Tiffanian Cochrane 2 and Aaron's localities, Paskapoo Formation, Alberta (CSS, pers. obs.).

<center>Genus Neoplagiaulax Lemoine, 1882</center>

Plagiaulax Lemoine, 1880, p. 12.
Neoplagiaulax Lemoine, 1882, p. 1011.

Type species.— *Neoplagiaulax eocaenus* (Lemoine, 1880).
Type locality.— Lemoine Quarry (Cernaysian, Savage and Russell, 1983; Lofgren et al., 2004), Cernay Conglomerate, northeastern Paris Basin, France.

<center>***Neoplagiaulax donaldorum*** n. sp.
Figure 2A-K; Tables 1, 2</center>

Neoplagiaulax new species, Krause and Maas, 1990, p. 84, table 3.

Holotype.— UM 84178, incomplete left dentary with P_4, M_{1-2} (L P_4 = 4.2, S = 12; L M_1 = 2.6, W M_1 = 1.2; L M_2 = 1.6, W M_2 = 1.4).
Typodigm.— Left P^4: UM 84192. Right P^4: UM 84190-UM 84191. Left P_4: UM 84185-84189. Right P_4: UM 84179-84184.
Type locality.— Douglass Quarry, Melville Formation, eastern Crazy Mountains Basin, Montana, USA.
Age and distribution.— Earliest Tiffanian (Ti-1) of Montana (type locality) and Alberta (Cochrane 2 locality, see Youzwyshyn, 1988; and Aaron's locality, see Fox, 1990a).
Diagnosis.— Differs from most other species of *Neoplagiaulax* in combining a short, relatively low crowned P_4 with a more arcuate profile (i.e., the profile is more nearly circular than trapezoidal), and in having a more pronounced and projecting anterior margin; differs further in P_4 having modally fewer cusps in the middle row. Differs from *N. macintyrei* Sloan, 1981, ?*N. burgessi* Archibald, 1982, and *N. paskapooensis* Scott, 2005 in having a proportionately higher crowned and more arcuate P_4. Differs from *N. jepi* Sloan, 1987 in being proportionately lower crowned. Differs from *N. kremnus* Johnston and Fox, 1984, *N. hunteri* (Simpson, 1936), *N. hazeni*
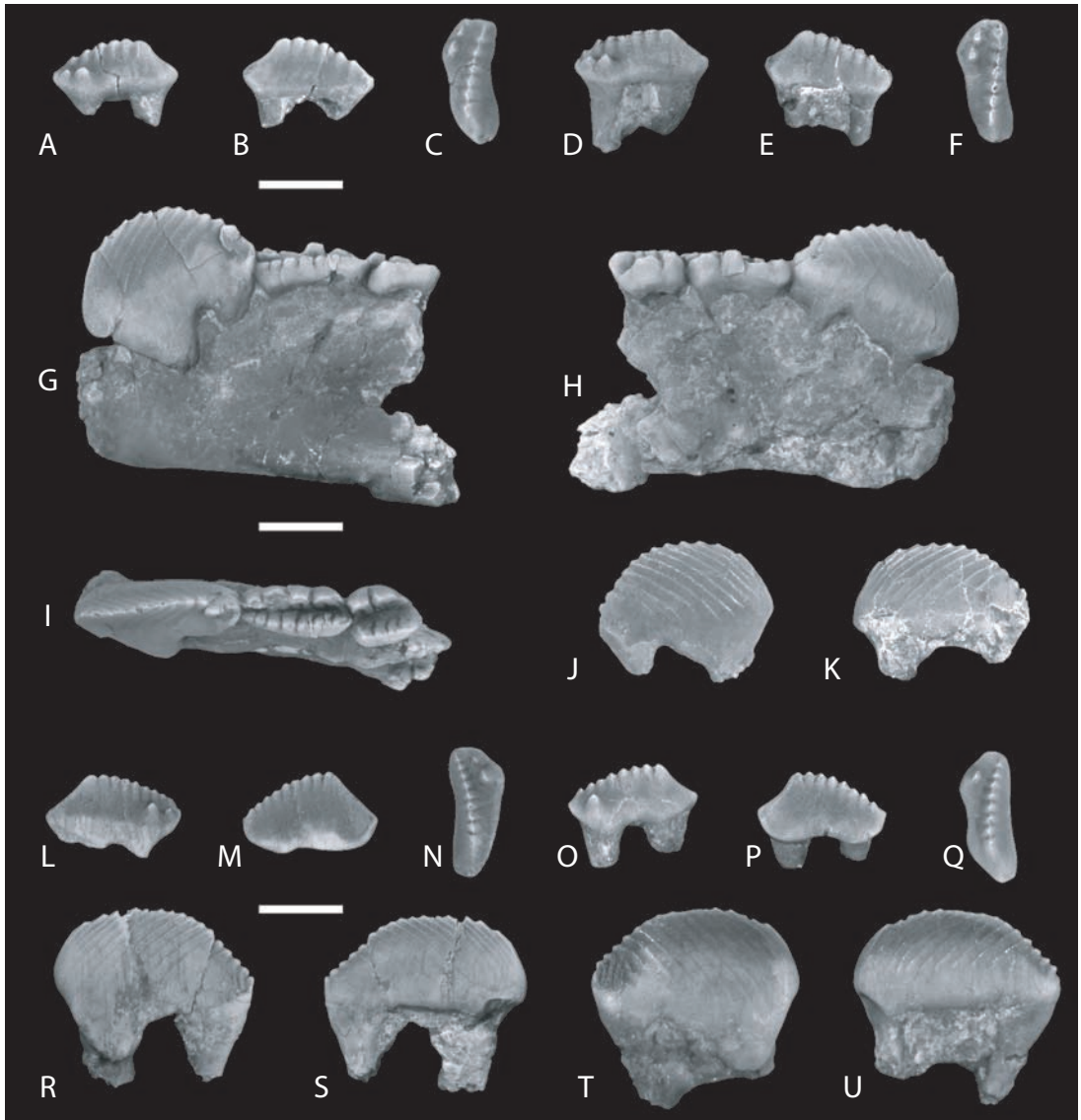
FIG. 2 — Multituberculates from the earliest Tiffanian (Ti1, late Paleocene) Douglass Quarry, eastern Crazy Mountains Basin, Montana. A-K are *Neoplagiaulax donaldorum* n. sp, and L-U are *Neoplagiaulax hunteri* (Simpson, 1936). A-C, right P^4, UM 84190, in labial (A), lingual (B), and occlusal (C) views; D-F, right P^4, UM 84191, in labial (D), lingual (E), and occlusal (F) views; G-I, incomplete left dentary with P_4, M_{1-2}, UM 84178 (holotype), in labial (G), lingual (H), and occlusal (I) views; J and K, right P_4, UM 84182, in labial (J) and lingual (K) views. L-N, left P^4, UM 84170, in labial (L), lingual (M), and occlusal (N) views; O-Q, right P^4, UM 84173, in labial (O), lingual (P), and occlusal (Q) views; R and S, left P_4, UM 84157, in labial (R) and lingual (S) views; T and U, right P_4, UM 84166, in labial (T) and lingual (U) views. Scale = 2 mm.

(Jepsen, 1940), and *N. mckennai* Sloan, 1987 in P_4 and P^4 being lower crowned and in P_4 being less trapezoidal in profile. Differs from *N. serrator* Scott, 2005 in having fewer serrations on P_4, and fewer cusps on P^4.

TABLE 1 — Measurements and descriptive statistics for upper fourth premolars (P4) of *Neoplagiaulax donaldorum* n. sp., Douglass Quarry locality, earliest Tiffanian (Ti-1), Melville Formation, Montana.

Specimen	L	W	C
UM 84190	2.8	1.2	2:6:0
UM 84191	3.0	1.2	2:7:0
UM 84192	2.9	1.1	2:-:-
Mean:	2.90	1.17	—
Standard deviation:	0.10	0.06	—
Coefficient of variation:	3.4	5.1	—

TABLE 2 — Measurements and descriptive statistics for lower fourth premolars (P4) of *Neoplagiaulax donaldorum* n. sp., Douglass Quarry locality, earliest Tiffanian (Ti-1), Melville Formation, Montana.

Specimen	L	S
UM 84178	4.2	12
UM 84179	—	12*
UM 84180	4.0	12
UM 84181	4.3	12
UM 84182	4.0	12
UM 84183	4.3	12
UM 84184	3.9	11
UM 84185	4.1	12*
UM 84186	4.0	12
UM 84187	4.1	12
UM 84188	4.2	13
UM 84189	4.1	12
Mean:	4.11	—
Standard deviation:	0.13	—
Coefficient of variation:	3.2	—

Etymology.— In reference to the Donald family, on whose land Douglass Quarry occurs, in recognition of and gratitude for their hospitality and innumerable acts of assistance to Stony Brook University field crews.

Description.— **P4**: Cusp formula 2:6-7:0 (N = 2). The P4 of *N. donaldorum* is moderately high crowned, with the ultimate or ultimate and penultimate cusps of the middle row highest above the base of enamel. The anterolabial lobe is weakly developed, and the labial row bears two cusps that increase in size posteriorly; a small cuspule can be developed at the anterior edge of the anterolabial lobe. The cusps of the middle row increase in size and height posteriorly, and are arranged anterolingually-posterolabially. In profile, the anterior slope is shallow and convex, while

the posterior slope is long and weakly concave. Neither accessory roots nor an interradicular crest are present.

P_4: The P_4 of *N. donaldorum* is subovate in profile, with a smoothly arcuate cutting edge. Because the exodaenodont lobe is swollen and juts labially, the labial side of the crown is slightly concave, whereas the lingual side is convex. The exodaenodont lobe narrows to a conspicuous point ventrally, and its ventral apex is positioned more posteriorly when compared to P_4 of other species of *Neoplagiaulax*, with its deepest part below the level of the third true serration (crown height at the exodaenodont lobe is approximately 80 percent of the standard length). A short, poorly developed posterolabial shelf occupies the area immediately beneath the ultimate serration. The anterobasal concavity is shallowly excavated and the anterior surface of the anterior root of P_4 on the holotype, as well as those on the referred P_4, bears a vertical groove. The anterior slope is shallow and reclined posteriorly, ascending posterodorsally at approximately 50 degrees from horizontal to the high first serration; the anterior margin of the exodaenodont lobe meets the anterior slope above the anterobasal concavity, with the two edges forming a sharp angle (the anterior part of the crown appears "pinched" or "beaklike" in profile, similar to P_4 of *N. macintyrei* and *N. burgessi*). The cutting edge can bear 11, 12, or 13 serrations (mode = 12; N = 12) that become larger and more conical posteriorly, and the apogee occurs at the third and fourth serrations. The labial and lingual surfaces of the crown bear coarse, obliquely oriented ridges that become shorter and more widely spaced posteriorly, eventually fading out below the last two or three serrations.

Lower molars: M_1 cusp formula 7:4; M_2 cusp formula 4:2. The lower molars of *Neoplagiaulax donaldorum* are known only from the holotype. The crown of M_1 is subrectangular in occlusal aspect, with the two cusp rows diverging posteriorly. The labial row supports seven low cusps that increase in height posteriorly to the fifth cusp, after which they remain subequal; the cusps are subpyramidal anteriorly but become more crescentic posteriorly. Unlike M_1s of many other species of *Neoplagiaulax*, grooving is not present on either the labial or lingual surfaces of the labial cusps. The two undamaged cusps of the lingual row are tall with flat labial and convex lingual sides, with the ultimate cusp nearly twice the length of the preceding cusp; the valley-facing sides of the lingual cusps are deeply grooved. The labial cusps on M_2 are crescentic, whereas the two lingual cusps are taller, subpyramidal, and bear strong grooves on their valley-facing sides.

Discussion.— The genus *Neoplagiaulax* is badly in need of revision, with numerous species known from Europe and North America that together encompass a morphological range exceeding that of most other neoplagiaulacid genera. Furthermore, *Neoplagiaulax* may not be monophyletic (a conclusion alluded to by Weil, 1999). In any case, the P_4 of *N. donaldorum* exhibits most of the features of *Neoplagiaulax* considered diagnostic by Sloan (1981; although the wide range of dental morphologies in *Neoplagiaulax* as currently conceived complicates even this most general of diagnoses): the relative height of the first serration is approximately 50 percent of the standard length; the angle formed by the planes of molar occlusion and the anterior margin of P_4 exceeds 90 degrees; and the length of P_4: length of M_1 ratio is 1.58, near the lower extreme of the range documented by Sloan (1981) for *Neoplagiaulax*. In contrast, the apogee of the crown of P_4 of *N. donaldorum* occurs at the third serration, slightly anterior to that in other species of *Neoplagiaulax*.

In a phenetic sense, the teeth of *Neoplagiaulax donaldorum* most closely resemble those of *N. kremnus* from the Puercan of Saskatchewan, and to a lesser extent of *N. "nelsoni"* from the late Puercan through early Tiffanian of Alberta, Montana, and Wyoming (we note here that *N. "nelsoni"* was not diagnosed by Sloan, 1987; as such, we consider the specific name a *nomen nudum* and refer to it herein by the use of quotation marks). Johnston and Fox (1984) considered the dental morphology of *N. kremnus* closest to that of *N. "nelsoni"* (= *N.* cf. *hunteri* of Rigby, 1980) and *N. hunteri* from Scarritt Quarry; we believe the resemblances in the morphology of P_4, *N. kremnus*, are closest to the former, and these together resemble P_4, *N. donaldorum*: all have a serrate crest with the leading edge somewhat reclined posteriorly, a projecting anterior margin (appearing "pinched" or "beaked"), and similar relative heights. The P_4 of *N. donaldorum* differs from those of *N. kremnus* and *N. "nelsoni"*, however, in being relatively lower crowned, in having a more ovate, rather than trapezoidal profile, and in having modally fewer serrations. Among other species of *Neoplagiaulax*, *N. burgessi* and *N. macintyrei* both have P_4 that are relatively low-crowned,

and have a low and arcuate cutting edge, features that may be plesiomorphic for *Neoplagiaulax* and neoplagiaulacids generally (assessed through comparison with P_4 of Late Cretaceous/Paleocene *Mesodma thompsoni* Clemens, 1964 and *M. formosa* (Clemens, 1964), both considered to be among the most basal neoplagiaulacids known (see, e.g., Clemens, 1964; Fox, 1971; Sloan, 1981), and with P_4 of taxa in the so-called "*Paracimexomys* group", a cohort of basal cimolodontans; Archibald, 1982; Eaton, 1995; Kielan-Jaworowska and Hurum, 2001). The P_4 of *N. donaldorum*, although having a low and arcuate cutting edge, is higher crowned than those of *N. burgessi* or *N. macintyrei*. Of potentially greater importance is the shallow, posteriorly leaning anterior margin on P_4 of *N. donaldorum*: this feature is also developed on P_4 of *N. burgessi* and *N. macintyrei* (but the anterior margin leans posteriorly to an even greater degree in these taxa), and is derived compared to the shorter, steeper anterior margin on P_4 of more basal cimolodontans (e.g., *Mesodma* and *Cimexomys* Sloan and Van Valen, 1965). Vianey-Liaud (1986) and Sloan (1987) considered the morphology of P_4, *N. macintyrei*, potentially ancestral to that of later species of *Neoplagiaulax*: in this scheme, P_4 of *Neoplagiaulax* are initially low-crowned, with arcuate cutting edges and shallow anterior margins, but become increasingly high-crowned and trapezoidal in profile, and the anterior slope becoming steeper in some species (e.g., P_4 of *N. mckennai*, *N. jepi*, *N. hunteri*).

Pending a thorough analysis and revision of *Neoplagiaulax*, the P_4 morphology in *N. donaldorum* is probably best considered intermediate between *N. burgessi* and *N. macintyrei* on the one hand, and *N. kremnus* and *N. "nelsoni"* on the other: 1) the P_4 of *N. donaldorum* has an anterior margin that is slightly steeper than those of *N. burgessi* and *N. macintyrei* but clearly shallower than those of other *Neoplagiaulax*; 2) although the P_4 crown is subovate in *N. donaldorum*, rather than trapezoidal, it is higher relative to those of *N. burgessi* and *N. macintyrei*, more closely approximating that of *N. kremnus*; 3) the P_4 cutting edge on *N. donaldorum* usually bears 12 serrations, a slightly greater number than those of *N. burgessi* and *N. macintyrei*, but fewer than in most other species of *Neoplagiaulax*; 4) the P^4 of *N. donaldorum* is relatively lower than those of later species of *Neoplagiaulax*, and bears fewer cusps (in these regards the P^4 of *N. donaldorum* most closely resembles that of *N. macintyrei*).

N. donaldorum is also known from the earliest Tiffanian Cochrane 2 locality (*N. "nelsoni"* of Youzwyshyn, 1988 and Fox, 1990a) and Aaron's locality, both from the Paskapoo Formation of Alberta.

<p style="text-align:center">*Neoplagiaulax hunteri* (Simpson, 1936)</p>
<p style="text-align:center">Figure 2L-U; Tables 3, 4</p>

Ectypodus hunteri Simpson, 1936, p. 6-7.
Neoplagiaulax hunteri Sloan in Van Valen and Sloan, 1966, p. 270.

Holotype.— AMNH 33865, incomplete right dentary with I_1, P_4, M_{1-2} (Simpson, 1936, pp. 6-7, figs. 1-2).

Type locality.— Scarritt Quarry (early Tiffanian, Ti-2, Lofgren et al., 2004), Melville Formation, eastern Crazy Mountains Basin, Montana, USA.

Referred specimens.— Left P^4: YPM-PU 14637, UM 84170-84171. Right P^4: UM 84172-84175. Left P_4: YPM-PU 23581, UM 84155-84160. Right P_4: UM 84161-84166, UM 84176.

Description.— P^4: Cusp formula 1-2:8-9:0 (mode = 1:8:0; N = 7). The crown of P^4 is high relative to its length and forms an asymmetrical triangle in profile. The middle cusp row is slightly convex labially in occlusal view, and the crown is wider anteriorly than posteriorly. The anterolabial lobe is well developed and supports a single large, conical cusp opposite the second or third cusp of the middle row; a smaller cusp can be developed anterior to the large anterolabial cusp. The anterior slope is long and weakly convex in profile, and extends to the high ultimate cusp of the middle row, while the posterior slope is steep and straight to slightly concave. The cusps of the middle row are subequal in size, and increase in height posteriorly to the apogee of the crown at the slightly enlarged ultimate or penultimate and ultimate cusp.

TABLE 3 — Measurements and descriptive statistics for upper fourth premolars (P^4) of *Neoplagiaulax hunteri*, Douglass Quarry locality, earliest Tiffanian (Ti-1), Melville Formation, Montana. Values for YPM-PU specimen from Krause and Gingerich (1983).

Specimen	L	W	C
YPM-PU 14637	3.0	1.3	1:9:0
UM 84170	3.0	1.3	2:9:0
UM 84171	3.1	1.3	2:8:0
UM 84172	3.0	1.1	1:8:0
UM 84173	3.0	1.2	1:8:0
UM 84174	3.2	1.0*	2:9:0
UM 84175	—	1.1	1:8:0
Mean:	3.05	1.22	—
Standard deviation:	0.08	0.10	—
Coefficient of variation:	2.6	8.2	—

TABLE 4 — Measurements and descriptive statistics for lower fourth premolars (P$_4$) of *Neoplagiaulax hunteri*, Douglass Quarry locality, earliest Tiffanian (Ti-1), Melville Formation, Montana. Values for YPM-PU specimen from Krause and Gingerich (1983).

Specimen	L	S
YPM-PU 23581	4.3	16
UM 84155	—	—
UM 84157	4.5	16
UM 84158	4.4*	15*
UM 84159	4.4	15
UM 84160	4.5	15
UM 84161	4.8	—
UM 84162	4.5	15
UM 84163	4.8	15
UM 84164	—	—
UM 84165	4.3	15
UM 84166	4.5	15
UM 84176	—	—
Mean:	4.51	—
Standard deviation:	0.18	—
Coefficient of variation:	4.0	—

P$_4$: The crown of P$_4$ is high relative to its length and nearly trapezoidal in profile; the labial side is slightly convex, similar to P$_4$ of *N. hunteri* from the late middle Tiffanian Roche Percée locali-ties of Saskatchewan (Krause, 1977). The exodaenodont lobe is anteroposteriorly long and deep,

and its ventral margin is smoothly rounded; the posterolabial shelf is weakly developed below the ultimate and penultimate serrations. The anterobasal concavity is deeply excavated for reception of P_3. The leading edge of the serrate crest is weakly reclined posteriorly and strongly convex, ascending posterodorsally to the low first serration. The dorsal margin of the serrate crest is horizontal, with the apogee occurring between the fourth and seventh serrations; the cutting edge bears 15-16 serrations (mode = 15; N = 9), consistent with P_4 of *N. hunteri* from the early to late middle Tiffanian Judson and Brisbane localities of North Dakota (Holtzman, 1978) and the Roche Percée localities (Krause, 1977). The posterior slope of the cutting edge is virtually straight, descending posteroventrally at approximately 65 degrees from horizontal, slightly shallower than on P_4 of *N. hunteri* from the early Tiffanian Scarritt Quarry and Roche Percée. The ridges on the labial and lingual surfaces of the crown below the serrations are coarse and are oriented steeply posterodorsally-anteroventrally.

Discussion.— Excepting the few minor differences noted previously, the referred teeth from Douglass Quarry closely resemble those of *N. hunteri* from Scarritt Quarry and Roche Percée: compared with teeth of *N. hunteri* from these localities, the crowns of P^4 and P_4 from Douglass Quarry are slightly lower relative to their length; the anterolabial lobe on P^4 is weaker, and bears a smaller cusp; the anterior margin of P_4 is steeper; and the exodaenodont lobe on P_4 is less swollen. In these respects, the Douglass Quarry teeth approach comparable teeth of *N. serrator* Scott, 2005, from the early middle Tiffanian of Alberta but differ in being higher crowned relative to their length and in having fewer cusps/serrations.

The few differences between teeth of *N. hunteri* from Douglass Quarry and those from other localities are considered slight, and the variation is easily accommodated in the much larger topotypic sample from Scarritt Quarry. *N. hunteri* is among the dentally best-known late Paleocene multituberculates, with a stratigraphic range extending from the late Torrejonian through the late Tiffanian.

Family CIMOLODONTIDAE Marsh, 1889

Genus *Anconodon* Jepsen, 1940

Anconodon Jepsen, 1940, p. 289.

Type species.— *Ptilodus? gidleyi* Simpson, 1935.
Type locality.— Gidley Quarry (middle Torrejonian, To-2; Lofgren et al., 2004), Lebo Formation, Crazy Mountains Basin, Montana, USA.

Anconodon cochranensis (Russell, 1929)
Figure 3A-M, 4, 5; Tables 5, 6

Ptilodus trovessartianus? Russell in Rutherford, 1927, p. 41.
Ptilodus cochranensis Russell, 1929, p. 172.
Ectypodus cochranensis Russell, 1932, p. 49.
?Ectypodus russelli Simpson, 1935, 1937a, p. 99.
?Ectypodus grangeri Simpson, 1937a, in part, p. 99.
Anconodon russelli Jepsen, 1940, in part, p. 290.
Ectypodus cochranensis Jepsen, 1940, p. 299, tables 9-10.
Anconodon cochranensis Van Valen and Sloan, 1966, p. 269.
Liotomus russelli Vianey-Liaud, 1986, p. 141.
Anconodon lewisi Sloan, 1987, p. 195.

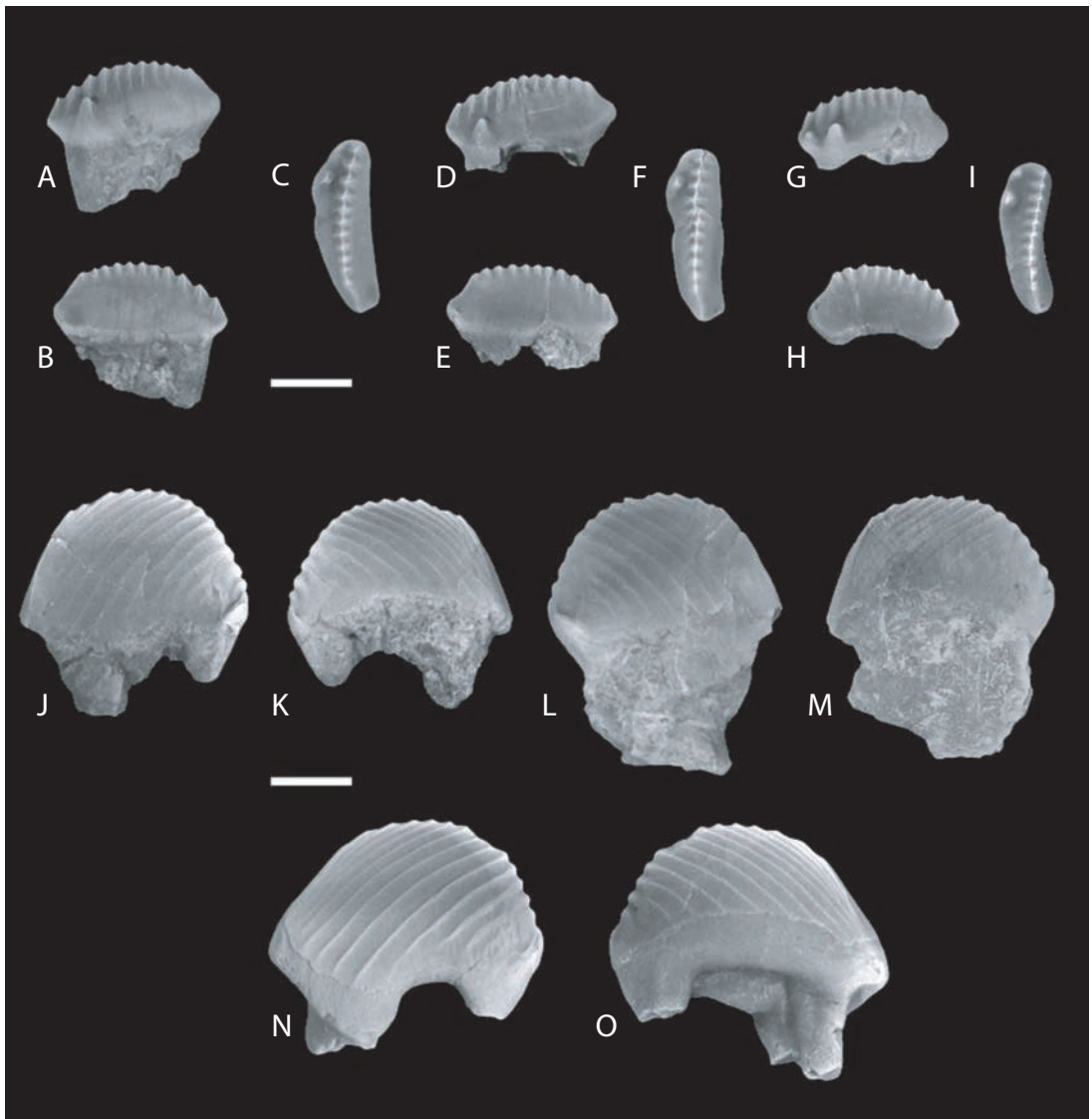*Holotype.*—UALVP 129, left P_4 (Russell, 1929, p. 172, fig. 1).

FIG. 3 — Multituberculates from the earliest Tiffanian (Ti1, late Paleocene) Douglass Quarry, eastern Crazy Mountains Basin, Montana. A-M are *Anconodon cochranensis* (Russell, 1929), and N and O are *Anconodon gidleyi* (Simpson, 1935). A-C, right P⁴, UM 84153, in labial (A), lingual (B), and occlusal (C) views; D-F, right P⁴, UM 84154, in labial (D), lingual (E), and occlusal (F) views; G-I, right P⁴, UM 84143, in labial (G), lingual (H), and occlusal (I) views; J and K, left P₄, UM 84131, in labial (J) and lingual (K) views; L and M, right P₄, UM 84117, in labial (L) and lingual (M) views. N and O, left P₄, UM 84146, in labial (N) and lingual (O) views. Scale = 2 mm.

Type locality.— Cochrane 1 locality (late Torrejonian, To-3; Fox, 1990a; Lofgren et al., 2004), Paskapoo Formation, Alberta Syncline, Alberta.

Referred specimens.—Left P⁴: UM 84136, UM 84138, UM 84139, UM 84150, UM 84151. Right P⁴: UM 84140-84144, UM 84152-84154. Left P₄: UM 84130-84135. Right P₄: UM 84117-84124, UM 84125-84126, UM 84128-84129.
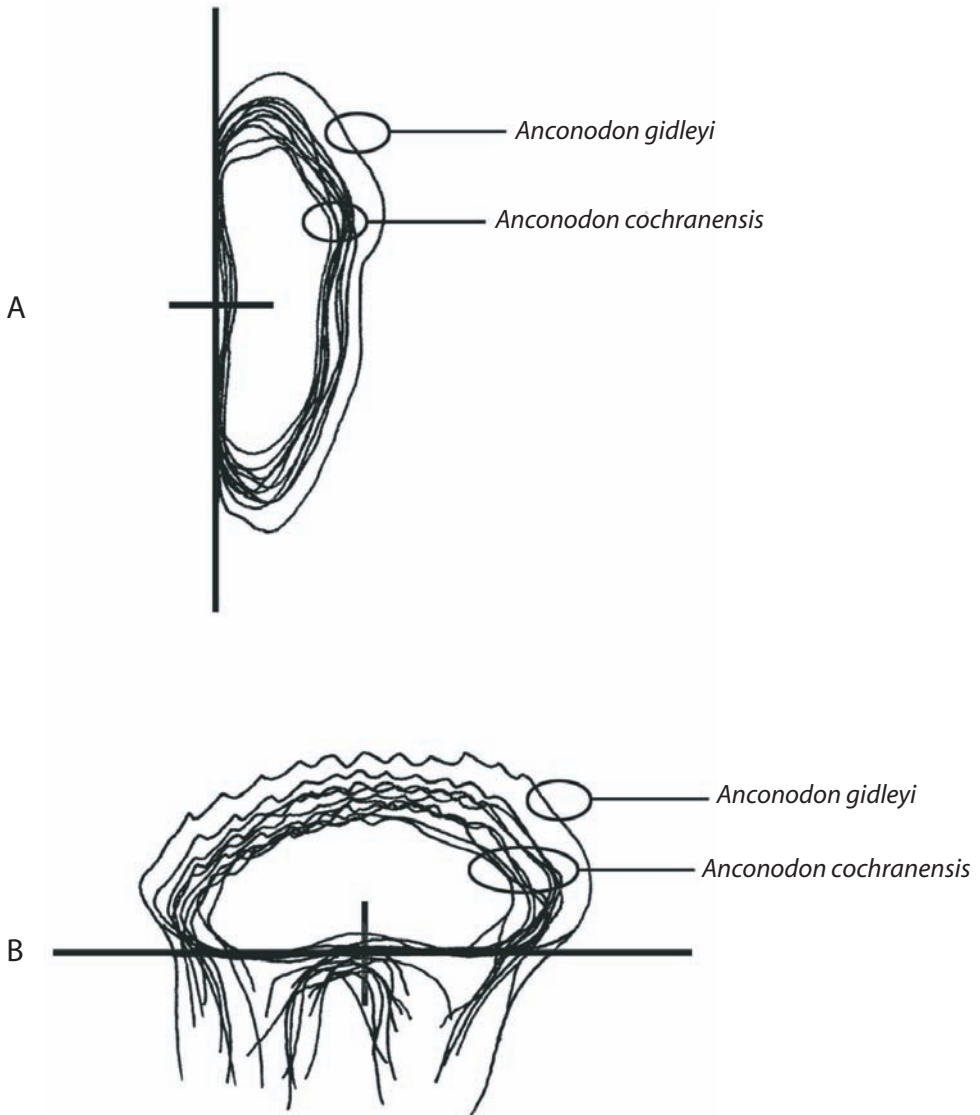
FIG. 4 — Outline drawings of occlusal (A) and lingual (B) views of P⁴s of *Anconodon cochranensis* (Russell, 1929) from the earliest Tiffanian (Ti-1, late Paleocene) Douglass Quarry, eastern Crazy Mountains Basin, Montana. UALVP 24488, P⁴ of *Anconodon gidleyi* (Simpson, 1935) from the earliest Tiffanian (Ti-1, late Paleocene) Cochrane 2 locality, Alberta Basin, Alberta is included for comparison (represented by the larger outlines). Both sets of outlines approximately X15. The P⁴s are oriented along a line running parallel to the lingual margin of the crown (occlusal view), or along a line running just below the lingual base of the enamel (lingual view). Both sets of outlines were registered at the midpoint of the crown.

Description.— **P⁴**: Cusp formula 1-2:9-11:0 (mode = 1:11:0; N = 12). The referred P⁴ are long and low crowned, with little elevation of the anterior and posterior slopes. The crown is straight to slightly convex labially in occlusal view; the long anterior slope is convex, while the steeply inclined posterior slope is short and straight to weakly concave. The anterolabial lobe is poorly developed, forming only a weak labial bulge on most specimens, and most often bears a single large, coarse cusp; a second, smaller cusp is present at the anterior margin of the lobe on one speci-

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TABLE 5 — Measurements and descriptive statistics for upper fourth premolars (P4) of *Anconodon cochranensis*, Douglass Quarry locality, earliest Tiffanian (Ti-1), Melville Formation, Montana.

Specimen	L	W	C
UM 84136	3.9	1.4	1:10:0
UM 84138	—	1.4	1:9:0
UM 84139	3.7	1.3	2:11:0*
UM 84140	—	1.2	2:10:0*
UM 84141	3.5	—	-:10:0
UM 84142	3.6	1.3	2:11:0
UM 84143	3.3	1.2	2:10:0
UM 84144	3.9	1.3	2:10:0
UM 84150	4.1	1.4	1:11:0
UM 84151	4.5	1.4	1:11:0
UM 84152	4.4	1.5	1:11:0
UM 84153	4.2	1.5	1:11:0
UM 84154	4.1	1.4	1:11:0
Mean:	3.93	1.35	—
Standard deviation:	0.38	0.09	—
Coefficient of variation:	9.6	6.7	—

men (UM 84144). The cusps of the middle row are coarse and well-separated from one another anteriorly, but become increasingly smaller and more crowded posteriorly; the cusps are nearly the same height for much of the row, with the apices of only the first three or four cusps becoming progressively lower. The third or fourth through seventh cusps of the middle row are highest above the base of the enamel.

P4: The P4 profile is high and arched, with the crown subcircular in outline and leaning posteriorly. The anterior margin of the crown is nearly straight, reclining slightly as it ascends to the high first serration. The labial side is flat, with the exception of the short posterolabial shelf, while the lingual side is slightly convex. The anterior part of the crown dorsal to the anterobasal concavity is broad and flat, and is skewed lingual to the midline; as a result, the anterior margin of the crown, including the anterobasal concavity and anterior root, faces somewhat lingually. The exodaenodont lobe is long, shallow, and swollen. The smoothly arcuate cutting edge can bear 13, 14, or 15 serrations (mode = 13; N = 14), and the posterior margin descends abruptly at the sixth or seventh serration. The apogee of the serrated edge occurs at the level of the fifth through seventh serrations. The first serration, or the first and second serrations together, are set off anteriorly from the remaining serrations, while successive serrations become larger, more conical, and remain equidistant from one another. Short, well-developed labial and lingual ridges are developed below the first serration: the labial ridge extends anteriorly, terminating just anterior to the anterobasal concavity, while the lingual ridge curves a short distance anterolingually, becoming more indistinct towards the base of the crown; the two ridges together delimit the broad, flat anterior surface of the crown. The remaining labial ridges are oriented obliquely posterodorsally-anteroventrally, the distance between successive ridges increasing towards the posterior parts of the crown. The lingual ridges are crowded near the anterior margin of the crown, with the first and second, second and third, or third and fourth ridges joining one another anteriorly. Ridges are not developed below the posterior two or three serrations on either the labial or lingual side of the crown. The anterobasal concavity is wide, deeply notched, and overhung dorsally by a prominent enamel shelf.
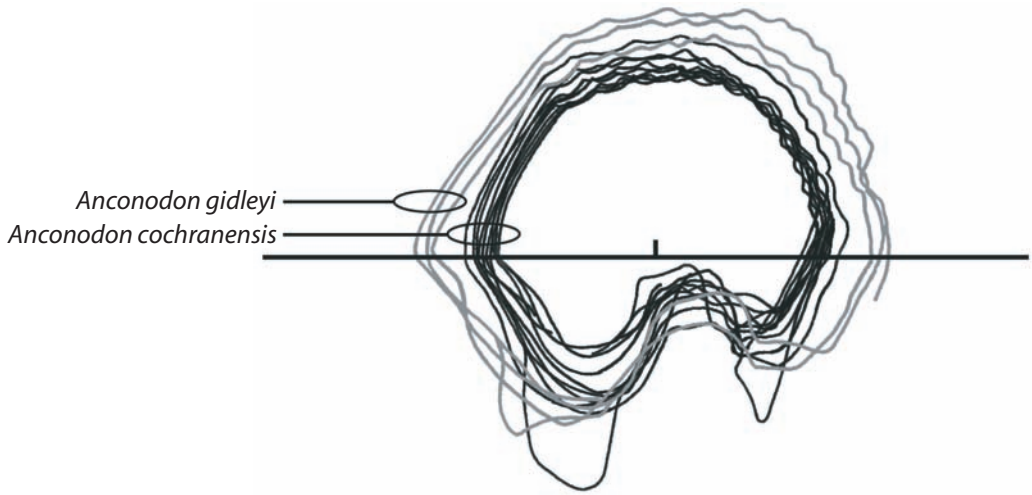
FIG. 5 — Outline drawings of P$_4$s of *Anconodon cochranensis* (Russell, 1929) and *Anconodon gidleyi* (Simpson, 1935) from the earliest Tiffanian (Ti-1, late Paleocene) Douglass Quarry, eastern Crazy Mountains Basin, Montana. Both outlines approximately X10. The P$_4$s are oriented along a line passing through the peak above the anterobasal concavity and the base of the posterolabial shelf, and registered at the midpoint of the crown.

Discussion.— Although *Anconodon cochranensis* has suffered a muddled taxonomic history, studies by Youzwyshyn (1988) on samples of *Anconodon* from the Cochrane 2 locality of Alberta and Douglass Quarry have provided clarification. *A. cochranensis* was founded on UALVP 129, an isolated P$_4$ collected from the late Torrejonian Cochrane 1 locality, Paskapoo Formation, Alberta, by R. L. Rutherford (Russell in Rutherford, 1927; Youzwyshyn, 1988; Fox, 1990a). Although Russell (in Rutherford, 1927) initially referred UALVP 129 to *Ptilodus trovessartianus?*, he later considered the specimen as representing a new species of *Ptilodus* (*P. cochranensis*; Russell, 1929). Still later, and on the basis of new specimens from the earliest Tiffanian Cochrane 2 locality, Russell (1932) referred UALVP 129 to a new species of *Ectypodus, E. cochranensis*.

In describing new specimens from the Fort Union of Montana, Simpson (1935) tentatively referred a number of teeth to a new species of *Ectypodus*, ?*E. russelli*. Simpson (1935, 1937a) compared teeth of ?*E. russelli* with specimens of *E. cochranensis*, noting similarities in the coronal structure of P$_4$, but maintained taxonomic separation of the two species on the basis of structure of the anterobasal concavity (as Russell had noted in 1929 for *Ptilodus cochranensis*). He maintained this distinction in his review of the Fort Union faunas (Simpson, 1937a).

Jepsen (1940) named *Anconodon* for specimens from Paleocene horizons of Montana and Wyoming, designating Simpson's *Ptilodus? gidleyi* as the type species and including ?*E. russelli* as a valid species. Although Jepsen continued to regard *E. cochranensis* as a species of *Ectypodus*, it was subsequently transferred to *Anconodon* (and to the Cimolodontidae) by Van Valen and Sloan (1966). Krause and Gingerich (1983) suggested that *A. russelli* is a junior synonym of *A. cochranensis*, a view adopted by Hartman (1986) and Sloan (1987) and confirmed by Youzwyshyn (1988, p. 61), who demonstrated that the difference in structure of the anterobasal concavity of P$_4$ cited by Russell (1929) and Simpson (1935, 1937a) "is a variable feature easily accommodated in the larger sample of *A. cochranensis* from Cochrane 2." In the most recent review of the affinities of *Anconodon* and Cimolodontidae, Vianey-Liaud (1986) considered *A. russelli* a species of the primarily European multituberculate *Liotomus* Cope, 1884, and transferred *Liotomus* from the Cimolodontidae to the Neoplagiaulacidae. Furthermore, Vianey-Liaud (1986) retained *A. gidleyi*

TABLE 6 — Measurements and descriptive statistics for lower fourth premolars (P4) of *Anconodon cochranensis*, Douglass Quarry locality, earliest Tiffanian (Ti-1), Melville Formation, Montana.

Specimen	L	S
UM 84117	4.5	14
UM 84118	4.5	13
UM 84119	4.5	13
UM 84120	4.2	15
UM 84121	4.9	15
UM 84122	5.0	14
UM 84123	4.4	14
UM 84124	3.9	—
UM 84125	4.7	14
UM 84126	4.4	13
UM 84128	—	—
UM 84129	4.3	13
UM 84130	5.1	13*
UM 84131	4.2	14
UM 84132	4.8*	15*
UM 84133	—	—
UM 84134	—	—
UM 84135	4.8	13
Mean:	4.51	—
Standard deviation:	0.34	—
Coefficient of variation:	7.6	—

as a valid species of *Anconodon* (within Cimolodontidae), and considered the similarities in P4 structure between *A. gidleyi* and *Liotomus* (including *A. russelli*) a result of parallelism.

Although there are superficial coronal similarities in P4 of *A. cochranensis* and *L. marshi* (e.g., long, straight, shallow anterior profile, broad exodaenodont lobe), we expand upon Youzwyshyn's (1988) observations and note the following important differences:

(1) The P4 of *A. cochranensis* is smaller and proportionately less elongate;
(2) The slope of the anterior margin of P4, *A. cochranensis*, is shorter and considerably steeper than that of *L. marshi*; we note further that an elongate and reclined anterior slope is developed independently in P4 in other lineages of multituberculates, including *Parectypodus sinclairi* (Simpson, 1935) (but see Vianey-Liaud, 1986, for a different opinion on the taxonomic position of *Parectypodus sinclairi*), *Parectypodus simpsoni* Jepsen, 1930, and *Neoplagiaulax cimolodontoides* Scott, 2005; and
(3) The cutting edge of P4, *A. cochranensis*, is high, arcuate, and descends abruptly towards the posterior part of the crown, whereas that of *L. marshi* is longer, relatively lower, and more smoothly arcuate posteriorly.

Additionally, the P4 of *A. cochranensis* described here differs from those of *L. marshi* as illustrated by Russell (1964, pl. II, figs. 1d, 8a-b) and Vianey-Liaud (1986, pl. 2, figs. 13-14) in being smaller, proportionately wider, and in having a less vertical posterior slope. As Youzw-

yshyn (1988) had already pointed out, and as our analysis of specimens of *A. cochranensis* from Douglass Quarry and Cochrane 2 confirms, these differences are, in both size and morphology, comparable to those distinguishing other genera of cimolodontan multituberculates. Although the systematic positions of *Liotomus* and *Anconodon* within Cimolodonta are beyond the scope of the present study, we note that the similarities between the two genera may be indicative of a close relationship (consistent with the views of Van Valen and Sloan, 1966, Sloan, 1979, McKenna and Bell, 1997, and Kielan-Jaworowska and Hurum, 2001), and we continue to regard both as cimolodontids pending a more comprehensive analysis of Cimolodontidae.

The specimens of *A. cochranensis* from Douglass Quarry exhibit a large range of variation in linear dimensions, particularly in the lengths of P^4 and P_4 (Tables 5, 6), with coefficients of variation of 7.6 and 9.6, respectively. These values fall within, but towards the high end of the range, for CVs documented for single species of extant mammals (e.g., Simpson et al., 1960; Gingerich and Winkler, 1979; but see Plavcan and Cope, 2001) and for what are regarded to be single species samples of multituberculates (e.g., Krause, 1982a). Despite these somewhat high values, there is no evidence of bimodality in the size, shape, serration count, cusp formula, or any other aspect of morphology of P^4 or P_4 in the sample of *A. cochranensis* from Douglass Quarry (Figs. 4, 5) and therefore to suggest the presence of a third species of *Anconodon* at the locality (in addition to *A. cochranensis* and *A. gidleyi*). As such, we adopt a conservative approach and consider only two species of *Anconodon* to be represented in the Douglass Quarry sample, with one of these species (*A. cochranensis*) being unusually variable.

An interesting corollary of recognizing the high degree of variation in *A. cochranensis* bears importantly on the taxonomic status of a small putative species of *Anconodon* from the earliest Tiffanian of Wyoming. Sloan (1987) described specimens of *Anconodon* from the Shotgun local fauna of Wyoming (and see Lofgren et al., 2004) and referred them to a new species, *A.* "*lewisi*". He distinguished the species from congeners primarily on the basis of its smaller size. We note, however, that although the P_4s referred to *A.* "*lewisi*" by Sloan (1987; M = 4.4, OR = 4.1 - 4.7, N ≤ 12) are shorter than the holotype (UALVP 129; L = 4.9 mm, S = 14; data from Russell, 1932) of *A. cochranensis* from Cochrane 1 and referred specimens from Rock Bench (M = 5.3, OR = 5.1 - 5.4, N = 3) and Gidley quarries (M = 5.0, OR = 4.9 - 5.1, N = 3), the length of P_4 (and P^4) of *A.* "*lewisi*" falls entirely within that for *A. cochranensis* from the much larger samples from Douglass Quarry (M = 4.51, OR = 3.9 - 5.1, N = 15) and Cochrane 2 (M = 4.69, OR = 4.4 - 5.0, N = 14). We note further that the P_4 of *A.* "*lewisi*" is virtually identical to that of *A. cochranensis* in profile and serration count (modal serrations, *A.* "*lewisi*" = 13, OR = 12 - 15; modal serrations, *A. cochranensis*, Douglass Quarry = 13; OR = 13 - 15). Given these close similarities, we consider *A.* "*lewisi*" a subjective synonym of *A. cochranensis*. The two P^4s assigned to *A.* "*lewisi*" from Shotgun (Sloan, 1987) are atypical of *Anconodon*: the crown is extremely low, with virtually no elevation to the middle row, and the middle row bears seven cusps, two fewer than the lowest number recorded for P^4 of *A. cochranensis* from Douglass Quarry and Cochrane 2. Furthermore, the occlusal outline of P^4, *A.* "*lewisi*", does not resemble that of either *A. cochranensis* or *A. gidleyi* (e.g., the antero-labial lobe is prominent in *A.* "*lewisi*", weak in other *Anconodon*). On the basis of the illustration provided by Sloan (1987, fig. 15), the taxonomic identity of the two P^4s referred to *A.* "*lewisi*" is uncertain, although they are not, we believe, referable to *Anconodon.* Their low profile, prominent anterolabial lobe, and low number of cusps in the middle row are suggestive of P^4 of some ptilodontids (e.g., *Ptilodus gnomus* Scott, Fox, and Youzwyshyn, 2002, fig. 1).

The specimens of *A. cochranensis* from Douglass Quarry differ little from those at Cochrane 2. *A. cochranensis* is known from numerous localities in the Western Interior of North America, with a stratigraphic range spanning the middle Torrejonian to early middle Tiffanian (Lofgren et al., 2004).

Anconodon gidleyi (Simpson, 1935)
Figure 3N, O, Figure 5; Table 7

?Ptilodus gidleyi Simpson, 1935, p. 225.

TABLE 7 — Measurements and descriptive statistics for lower fourth premolars (P$_4$) of *Anconodon gidleyi*, Douglass Quarry locality, earliest Tiffanian (Ti-1), Melville Formation, Montana. Values for YPM-PU specimens from Krause and Gingerich (1983).

Specimen	L	S
YPM-PU 14619A	6.2	14
YPM-PU 14619B	5.6	14
UM 84145	—	—
UM 84146	5.7	13
UM 84147	5.5	14
UM 84148	6.0	15
UM 84149	6.0	14
Mean:	5.83	—
Standard deviation:	0.27	—
Coefficient of variation:	4.6	—

Anconodon gidleyi Jepsen, 1940, p. 290.
Anconodon? sp. Jepsen, 1940, p. 292-293.
Ectypodus cochranensis Russell, 1958, p. 96-98.
Anconodon cochranensis Krause and Gingerich, 1983, in part, p. 162.

Holotype.— USNM 9763, incomplete left dentary with P$_4$, broken M$_1$ (Simpson, 1935, p. 225; 1937a, pp. 95-97, fig. 9b).
Type locality.— Gidley Quarry (middle Torrejonian, To-2, Lofgren et al., 2004), Lebo Formation, eastern Crazy Mountains Basin, Montana, USA.
Referred specimens.— Left P$_4$: YPM-PU 14619A, UM 84146. Right P$_4$: YPM-PU 14619B, UM 84145, UM 84147-84149.
Description.— **P$_4$**: The P$_4$ crown of *A. gidleyi* resembles that of *A. cochranensis* in its high and arcuate serrate crest, weak exodaenodont lobe, and truncated posterior margin. The anterior margin of the crown protrudes in a "beaklike" manner, a result of the union between the posteriorly reclined leading edge of the serrate crest with the anterior edge of the exodaenodont lobe. The lobe itself is short, shallow, and slightly swollen. As with the P$_4$ of *A. cochranensis*, the anterior part of the P$_4$ crown of *A. gidleyi* dorsal to the anterobasal concavity is broad and flat, and is skewed lingually, resulting in the anterior side of the crown, including the anterobasal concavity and anterior root, facing slightly lingually. The labial side of the crown is virtually flat, with the posterolabial shelf only weakly developed; in contrast, the lingual side of the crown is strongly convex. The arcuate dorsal crest can bear 13, 14, or 15 serrations (mode = 14; N = 6) that become larger and more conical posteriorly, with the apogee occurring between the fourth and sixth serrations; the posterior margin of the serrate crest abruptly descends posteroventrally at the sixth serration. Coarse ridges are developed below the serrations: those on the labial side of the crown are oblique and run towards the exodaenodont lobe, while the lingual ridges are more nearly horizontal and considerably more widely spaced posteriorly than anteriorly. The anterobasal concavity is deeply excavated. A weak interradicular crest is developed on one specimen (UM 84146).
Discussion.— The P$_4$ of *Anconodon gidleyi* from Douglass Quarry closely resemble those described by Simpson (1935, 1937a) and Jepsen (1940) from the late Torrejonian of Montana and Wyoming but are, on average, slightly smaller. The P$_4$ of *A. gidleyi* differs from that of *A. cochranensis* in its larger size, straighter and more posteriorly reclined anterior margin, proportionately lower crown, and less swollen exodaenodont lobe (Fig. 4). Accordingly, the two P$_4$ (YPM-PU
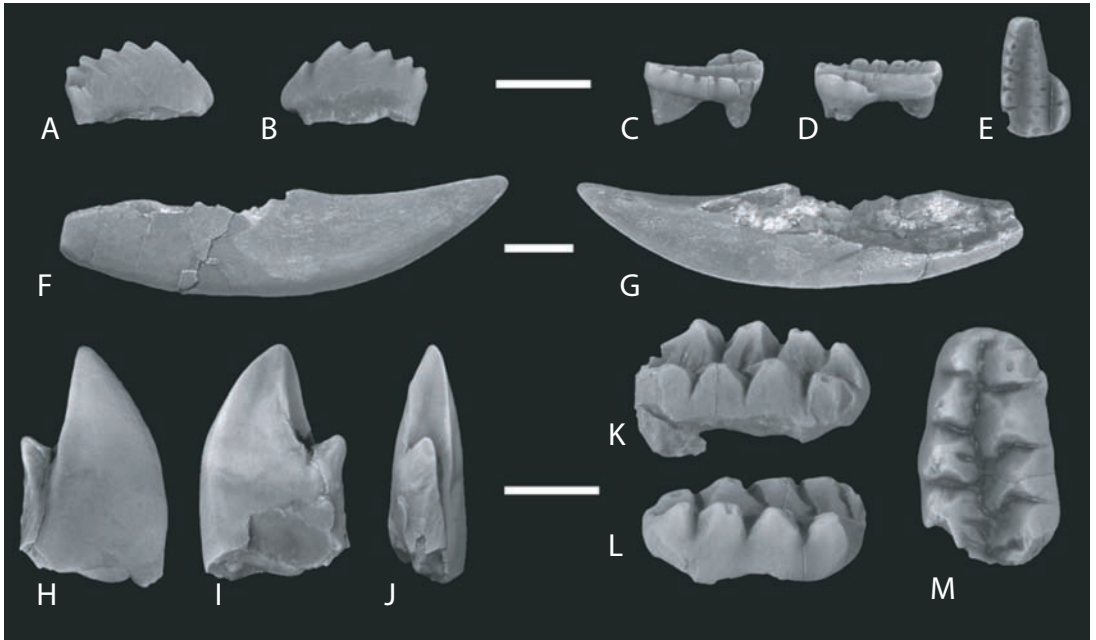
FIG. 6 — Multituberculates from the earliest Tiffanian (Ti-1, late Paleocene) Douglass Quarry, eastern Crazy Mountains Basin, Montana. A-E are *Allocosmodon woodi* (Holtzman and Wolberg, 1977), F-G are ?Microcosmodontidae, genus and species indeterminate, and H-M are ?Eucosmodontidae, genus and species indeterminate. A and B, right P_4, UM 84199, in labial (A) and lingual (B) views; C-E, right M^1, UM 84200, in labial (C), lingual (D), and occlusal (E) views. F and G, right I_1, UM 84201, in labial (F) and lingual (G) views. H-J, left I^2, UM 84202, in distal (H), mesial (I), and occlusal (J) views; K-M, incomplete right M_1, UM 84077, in labial (K), lingual (L), and occlusal (M) views. Scale = 2 mm.

14619A and 14619B) from Douglass Quarry allocated to *A. cochranensis* by Krause and Gingerich (1983, fig. 3C-D) are referred here to *A. gidleyi* on the basis of their larger size and longer, lower anterior margin.

A. gidleyi is also known from the earliest Tiffanian Cochrane 2 and Aaron's localities (Youzwyshyn, 1988; Fox, 1990a), as well as from the Torrejonian of New Mexico (Sloan, 1981). Following Youzwyshyn (1988), an isolated P_4 from the late Torrejonian Calgary 2E/7E locality (NMC 9104), referred to "*Ectypodus cochranensis*" by Russell (1958) is referred here to *A. gidleyi* on the basis of its larger size (L = 5.6 mm, 15 serrations; data from Russell, 1958) and shallower anterior margin.

Family MICROCOSMODONTIDAE (Holtzman and Wolberg, 1977)

Genus *Allocosmodon* Fox, 2005

Allocosmodon Fox, 2005, p. 55.

Type and only species.— *Microcosmodon woodi* Holtzman and Wolberg, 1977.
Type locality.— New Anthill locality (anthill "L"; earliest Tiffanian, Ti-1; Lofgren et al., 2004), Fort Union Formation, Wind River Basin, Wyoming, USA.

Allocosmodon woodi (Holtzman and Wolberg, 1977)
Figure 6A-E

Microcosmodon woodi Holtzman and Wolberg, 1977, p. 6; Weil, 1998, p. 7.
Allocosmodon woodi Fox, 2005, p. 56.

Holotype.— MCZ 19963, right P_4 (Holtzman and Wolberg, 1977, p. 6, fig. 2.1-2.8)

Type locality.— New Anthill locality, anthill "L"; (earliest Tiffanian, Ti-1, Lofgren et al. , 2004), Fort Union Formation, Wind River Basin, Wyoming, USA.

Referred specimens.— Right P_4: UM 84199 (L = 3.4, S = 6). Right M^1: UM 84200 (L = 2.7, W = 1.6, C = 6:8:2).

Description.— **P_4**: The crown of P_4 is long and low, and bears six robust serrations connected to one another by a sharp keel. The labial side of the crown is virtually flat, whereas the lingual side is convex. Although the exodaenodont lobe has been broken away, the parts that remain indicate it was anteroposteriorly long, and probably short ventrally, as in P_4 of *A. woodi* from the early middle Tiffanian DW-2 locality of Alberta (Fox, 2005). The conspicuous posterolabial shelf is pocket-like and positioned below the ultimate serration. The steep leading edge of the serrate crest extends posterodorsally from the apex of the deeply excavated anterobasal concavity to the first serration, and the apogee of the cutting edge occurs at the second or third serration. The first serration is slightly displaced lingually from the anteroposterior axis of the crown and anteriorly from the succeeding serration. Two strong ridges extend from the apex of the first serration: the first ridge runs as a sharp keel along the anterior face of the crown, fading as it nears the apex of the anterobasal concavity; the second ridge is weaker and descends the lingual side of the crown a short distance before fading out. The remaining serrations (dorsal serrations of Fox, 2005) are coarse and nearly equal in size and height through to the ultimate serration, which is both smaller and lower. Coarse lingual ridges are developed below the second through fourth serrations, and extend anteroventrally a short distance down the face of the crown, while the labial side of the crown bears weaker, anteroventrally oriented labial ridges.

M^1: Cusp formula estimated at 6:8:2. The coronal outline of UM 84200 is roughly P-shaped, with a transverse anterior and broadly rounded posterior margin. The crown is slightly concave ventrally and bears three parallel rows of cusps separated from one another by wide intercusp valleys; the labial and middle cusp rows converge slightly at the anterior margin of the crown. The apices of the cusps are heavily worn, erasing much of their original features. The bases of the labial cusps are convex labially, and the cusps were likely conical while the middle cusps are square at their bases and increase in size posteriorly. The two cusps of the lingual row are large and convex lingually. The lingual cusp row and is separated from the middle cusp row by a wide intercusp valley, ending abruptly at the fourth cusp of the middle row. Accessory roots are not developed.

Discussion.— In his recent review of North American Microcosmodontidae, Fox (2005) referred all specimens pertaining to the Tiffanian *Microcosmodon woodi* Holtzman and Wolberg, 1977 to a new genus, *Allocosmodon*. UM 84199 is nearly identical to P_4 of *A. woodi* from the middle Tiffanian DW-2 locality of Alberta (Fox, 2005), differing only in its slightly larger size (length P_4, *A. woodi*, Douglass Quarry = 3.4 mm versus mean length P_4, *A. woodi*, DW-2 = 3.16 mm, OR = 3.0 - 3.3, N = 9). Similarly, the size, cusp formula, cusp shape, and width of the intercusp valleys of UM 84200 are nearly identical to those on M^1s of *Allocosmodon woodi* from the early middle Tiffanian DW-2 locality of Alberta. The only significant difference appears to be the abruptly truncated lingual cusp row on UM 84200. M^1s previously referred to *A. woodi*, by contrast, have a lingual cusp row that joins the middle cusp row further anteriorly and less abruptly and which therefore appears less convex lingually (Fox, 2005). The abbreviated lingual cusp row in UM 84200, however, is here interpreted as a wear feature, consistent with the fact that the rest of the occlusal surface in this specimen is heavily worn. Fox (2005) has documented that molar wear in microcosmodontids does not differ radically from that in *Ptilodus* (Krause, 1982c). It is not unusual in aged individuals of *Ptilodus* for the length of the lingual cusp row of M^1 to be

progressively truncated (from anterior to posterior) by wear as the posterolabial face of P_4 slides posterodorsally, posteriorly, and then posteroventrally against the lingual surfaces of P^4 and M^1 during the power stroke of the grinding cycle (see Krause, 1982c, figs. 9-11). The specimens of *A. woodi* from Douglass Quarry represent the only occurrence of the taxon from the earliest Tiffanian of Montana.

?MICROCOSMODONTIDAE, genus and species indeterminate
Figure 6F, G

Referred specimen.— Right I_1: UM 84201 (as preserved: W = 1.9, D = 3.0).

Description.— Although the referred incisor is badly damaged posterodorsally, the parts that remain indicate that it is deep, laterally compressed, and gently curved dorsally. The medial surface is flat, but becomes more nearly convex ventrally and laterally. The crown is faintly sinusoidal in dorsal view, with the tip curving medially. Strong carinae are developed dorsolaterally and ventromedially, extending an unknown distance posteriorly from the tip. The enamel is thickest ventrally and laterally, but thins considerably dorsally and medially, where it forms no more than a thin veneer.

Discussion.— UM 84201 most closely resembles I_1s of microcosmodontids, which are, where known, disproportionately large compared to body size. The similarities are strongest to those of *Allocosmodon* and *Microcosmodon*, although the crown of UM 84201 is both larger and deeper than in known species of these two genera. The crown of UM 84201 is only faintly curved dorsally, differing from the more arcuate I_1s of microcosmodontids and ptilodontids (compare with, e.g., I_1 of *Microcosmodon conus,* e.g., Fox, 2005, pl. 5), suggesting the tooth may have been more procumbent than in these taxa, and in these regards seems closer to I_1s of the eucosmodontid *Stygimys* Sloan and Van Valen, 1965. UM 84201 clearly differs from lower incisors of *Stygimys* and other eucosmodontids, however, in having a more even distribution of enamel over the surface of the crown, rather than a distinct, anteroinferiorly restricted enamel band. Although UM 84201 more closely resembles I_1s of microcosmodontids than those of eucosmodontids, a better assessment of its taxonomic affinities must await discovery of more complete specimens.

Family EUCOSMODONTIDAE Jepsen, 1940

?Eucosmodontidae, genus and species indeterminate
Figure 6H-M

Referred specimens.— Left I^2: UM 84202 (as preserved: L = 5.0, W = 1.2, D = 3.2); Right M_1: UM 84077 (L = 4.2, W = 3.1).

Description.— **I^2**: The crown of I^2 is large, dorsoventrally deep, and slightly curved; the biting surface is bifid, bearing a single large apical cusp and a smaller posterior accessory cusp. Insofar as can be determined, the enamel is evenly distributed on the crown and does not form a restricted band along the anterolabial surface. Three well-developed crests originate from the apex of the main cusp: the first runs dorsally and slightly medially along the anterior side of the crown, but quickly terminates a short distance from the apex of the main cusp. The remaining two crests extend posterodorsally along the occlusal surface of the crown: the more medial of these crests runs a short distance to the base of the accessory cusp, while the lateral crest extends posterodorsally, fading out posterior, dorsal and lateral to the accessory cusp. The valley formed between the two crests is deeply concave, with its posterior margin limited by the conical accessory cusp. A small crest is developed along the lateral side of the accessory cusp.

M_1: UM 84077 preserves only the anterior part of a right M_1. The two cusp rows converge at the anterior margin, and bear large, robust cusps. The four stout, pyramidal cusps of the labial row are swollen at their bases, increase in size posteriorly, and are weakly grooved on their val-

ley-facing surfaces; the first lingual cusp is small, short, and subconical, whereas the remaining lingual cusps increase in size and height posteriorly; the third and fourth cusps are deeply grooved on their valley-facing surfaces. The cusps of the labial and lingual rows are staggered (i.e., are not transversely opposed to one another), and the valley between the cusp rows is narrow, with the enamel on its floor extensively folded.

Discussion.— The referred specimens are sufficient to document the presence of at least one large eucosmodontid at Douglass Quarry, but little more. The I^2 is closest to those of *Stygimys* and *Eucosmodon* Matthew and Granger, 1921, differing from I^{2}s of microcosmodontids and taeniolabidids in having an approximately uniform distribution of enamel on the crown, rather than a restricted band or anterolabial thickening, or a limited distribution on the medial surface (Simmons, 1993; Fox, 2005). The M$_1$ differs from those of ptilodontids, with which it may be confused, in its larger size, more robust proportions, and pyramidal cusp shape.

Large-bodied eucosmodontids are generally uncommon in the late Paleocene: *Eucosmodon* is known from the Puercan and Torrejonian of the Western Interior of the United States and Canada (see, e.g., Granger and Simpson, 1929; Simpson, 1935, 1937a; Russell, 1958), while the enigmatic *Neoliotomus* Jepsen, 1930, considered a eucosmodontid by some (e.g., Krause, 1980, 1982b; McKenna and Bell, 1997), a ptilodontoid by others (e.g., Kielan-Jaworowska and Hurum, 2001), or associated with the European genus *Boffius* Vianey-Liaud, 1979 by still others (see, e.g., Simmons, 1993; Rougier et al., 1997), is more common in the latest Tiffanian, Clarkforkian, and Wasatchian. Isolated and fragmentary teeth from the Torrejonian and Tiffanian of Alberta have been referred to *Stygimys* or *Eucosmodon* (see, e.g., Russell, 1929; Scott, 2003a) or to *Neoliotomus*-like multituberculates (see, e.g., Youzwyshyn, 1988), but none are complete enough for a more precise referral. The teeth from Douglass Quarry are most similar to undescribed specimens from the earliest Tiffanian Cochrane 2 locality of Alberta ("Eucosmodontinae, unidentified genus and species" of Fox, 1990a, p. 59), but their fragmentary condition prevents a more precise referral.

TEMPORAL AND LATITUDINAL DIVERSITY IN LATE TORREJONIAN/EARLY TIFFANIAN MULTITUBERCULATES

When Krause and Gingerich (1983) described the Douglass Quarry local fauna, three multituberculate species were identified: the neoplagiaulacid *Neoplagiaulax hunteri*, a new species of the ptilodontid *Ptilodus*, and the cimolodontid *Anconodon cochranensis*. Subsequently, Krause and Maas (1990) added to the local fauna, identifying eight more multituberculates in a preliminary faunal list. At present, 10 species in six genera are known confidently or tentatively from Douglass Quarry: five of these are stratigraphically long ranging continuations of lineages known from at least as early as the late Torrejonian and five are first known from the earliest Tiffanian (Figure 7). All of the multituberculates identified to species level from Douglass Quarry, with the exception of *Allocosmodon woodi*, also occur at Cochrane 2 (Ti-1), Paskapoo Formation, Alberta (Figure 8). Of particular importance are the neoplagiaulacids *Ectypodus* sp. and *Neoplagiaulax donaldorum*; both are apparently restricted to the earliest Tiffanian (at Douglass Quarry, Cochrane 2, Aaron's locality) and may be useful in correlation, particularly for local faunas where plesiadapid primates and other age-diagnostic taxa are poorly known.

Comparisons of taxonomic composition between two or more fossil assemblages have the potential to offer insight into paleocommunity structure, paleoecological reconstructions, and, importantly, changes in taxonomic diversity and biogeographical distribution through time (e.g., Simpson, 1960; Rose, 1981; Gingerich, 1989; Krause and Maas, 1990; Alroy, 2000; Alroy et al., 2000; Secord, 2004). We investigated the potential temporal and latitudinal effects on multituberculate taxonomic diversity during the Paleocene in the Western Interior by first comparing the Douglass Quarry multituberculates with those from other well-sampled earliest Tiffanian (Ti-1) localities, and then examining multituberculate faunal composition from a number of local faunas
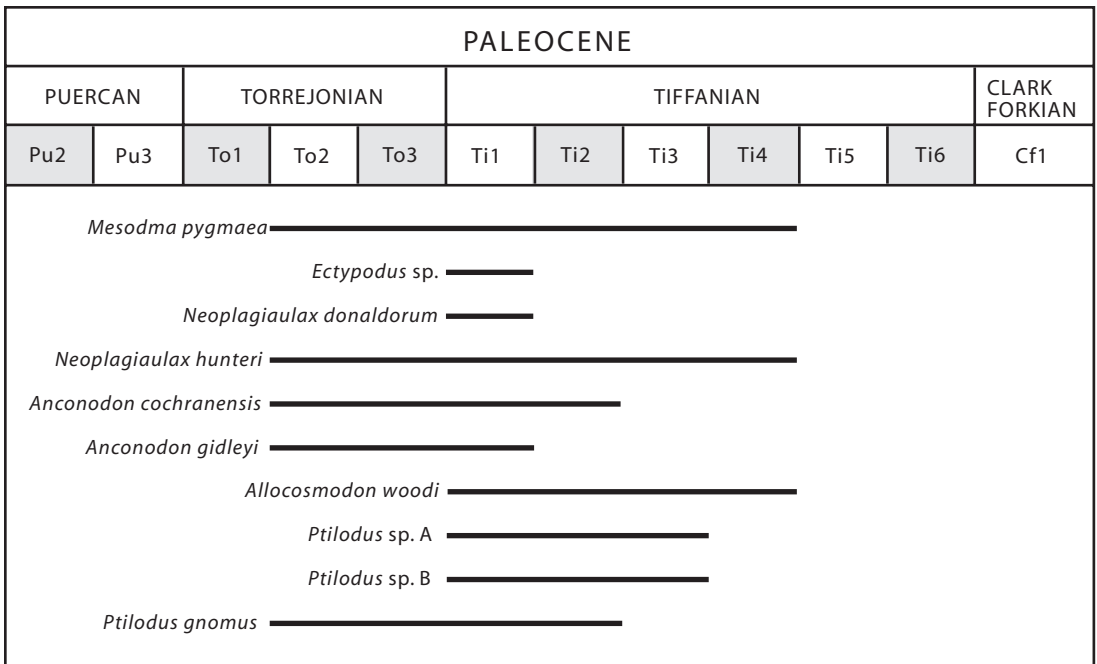
PALEOCENE											
PUERCAN		TORREJONIAN			TIFFANIAN						CLARK FORKIAN
Pu2	Pu3	To1	To2	To3	Ti1	Ti2	Ti3	Ti4	Ti5	Ti6	Cf1

Mesodma pygmaea

Ectypodus sp.

Neoplagiaulax donaldorum

Neoplagiaulax hunteri

Anconodon cochranensis

Anconodon gidleyi

Allocosmodon woodi

Ptilodus sp. A

Ptilodus sp. B

Ptilodus gnomus

FIG. 7 — Temporal distribution of multituberculates from the earliest Tiffanian (Ti-1, late Paleocene) Douglass Quarry, eastern Crazy Mountains Basin, Montana. North American Land-Mammal Ages and their constituent biochronologic zones follow Lofgren et al. (2004). Although taxonomic ranges (solid bars) are depicted as extending from the beginning of the earliest zone from which they are known to the termination of the latest zone from which they are known, their actual ranges within these zones are unknown.

spanning the middle Torrejonian (To-2) through the early middle Tiffanian (Ti-3). Comparisons of taxonomic diversity are restricted here to genus and species level presence/absence (occurrence) data (essentially measures of unweighted species richness (Hurlbert, 1971)) based on taxonomic lists in the published literature, and are preliminary in the sense that abundance data, and estimates derived from such data (e.g., species evenness), are not taken into account. We acknowledge that a number of biases, particularly differences in sample size and size sorting, as well as differences in depositional environments, potentially may affect even these general observations. Biases such as these in fossil samples and their effects on estimating taxonomic diversity are well known and have been discussed at length (e.g., Rose, 1981; Badgley, 1986; Behrensmeyer, 1988; Wilson, 1996). The different sample sizes in this analysis warrant particular caution: although the multituberculates in many of the samples examined are represented by hundreds of identifiable specimens (e.g., Cochrane 2), some are not (e.g., Who Nose?); as species richness is strongly correlated with sample size (Hurlbert, 1971), the multituberculate taxonomic diversity in those local faunas with small sample sizes is likely to be underestimated. Despite these potential biases, significant information regarding the stratigraphic and geographic distributions of multituberculate taxa can be gleaned from presence/absence data, and this level of analysis (i.e., comparing only the presence or absence of particular taxa) is likely to be less sensitive to the effects of sample size than are estimates based on abundance data.

When compared with other well-sampled earliest Tiffanian local faunas from the northern part of the Western Interior, the multituberculates from Douglass Quarry are more taxonomically diverse than at Keefer Hill/Twin Buttes (Shotgun local fauna), Wind River Basin, Wyoming, but less so relative to Cochrane 2 (Figure 8). Cochrane 2 documents the most diverse Paleocene mamma-

lian local fauna known from the Western Interior (or anywhere in the world), with approximately 80 species identified so far (Youzwyshyn, 1988; Fox, 1990a; Scott et al., 2002), including 21 species of multituberculates in 13 genera. Collections made from Douglass Quarry, culminating in the present study, as well as from newly discovered localities in the Hanna Basin of south-central Wyoming (Secord, 1998; Higgins, 2003a), have increased the number of multituberculate taxa known from the earliest Tiffanian of Montana and Wyoming, suggesting the disparities in taxonomic diversity between Cochrane 2 and more southern localities ultimately may, at least in part, be owing to the effects of sampling error or local ecological factors (Fox, 1990a; Scott et al., 2002). Nonetheless, we note that multituberculate diversity during the middle Tiffanian of Alberta also remains markedly higher when compared to coeval local faunas from Montana and Wyoming (Scott, 2003b, 2004, 2005).

The early Tiffanian of North America is a poorly documented interval when compared to the late Torrejonian and middle to late Tiffanian: only a few of the well-sampled earliest Tiffanian (Ti-1) localities have been described, and the two best-known early Tiffanian (Ti-2) localities, Scarritt Quarry, Crazy Mountains Basin, Montana, and Saddle locality, Bison Basin, Wyoming, have not been reviewed since Simpson (1937b), Gazin (1956), Rose (1981), and Krause and Maas (1990). In spite of this, a growing body of information derived from recent collections from the northern part of the Western Interior of North America, as well as descriptions of previous collections, has shed some light on the taxonomic diversity and evolution of multituberculates during the earliest Tiffanian. A comparison of multituberculates from some of the better sampled localities spanning the late Torrejonian (To-2) through early Tiffanian (Ti-2) of Canada and the northern United States (Figure 8) suggests multituberculate diversity peaked during the earliest Tiffanian, with four cimolodontan families (Neoplagiaulacidae, Ptilodontidae, Cimolodontidae, Microcosmodontidae) each represented by at least three species.

Neoplagiaulacids are taxonomically diverse and abundant during the late Torrejonian and remain so into the early Tiffanian. Six genera (*Mesodma*, *Mimetodon*, *Ectypodus*, *Parectypodus*, *Neoplagiaulax*, *Xyronomys*) survive into the Tiffanian but two have not yet been recorded with certainty (*Xanclomys* Rigby, 1980, from the late Torrejonian Swain Quarry, southern Wyoming, and *Fractinus* Higgins, 2003b, from the late Torrejonian/earliest Tiffanian Breaks locality, south central Wyoming). In contrast, ptilodontid diversity increased at both the generic and specific levels from the late Torrejonian to earliest Tiffanian, with three genera (*Ptilodus*, *Prochetodon*, *Baiotomeus*) and five species from Cochrane 2, a diversity unmatched before or after. The cimolodontid *Anconodon*, documented by few specimens in middle and late Torrejonian local faunas in Montana and Wyoming (Rose, 1981), becomes much more numerically abundant, and is among the best represented multituberculate taxa in the earliest Tiffanian of Alberta and Montana.

Microcosmodontids also experienced a modest radiation during the early Tiffanian. They are first known from the Late Cretaceous of Saskatchewan (Fox, 1989, 2005), but remain poorly

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FIG. 8 (facing page) — Occurrence of multituberculate taxa from selected localities from the late Torrejonian (To-2) through early Tiffanian (Ti-2) of the Western Interior of North America, as depicted by black dots. Locality information and primary references are as follows: Rock Bench Quarry, Fort Union Formation, Bighorn Basin, Wyoming (Rose, 1981; Krause, 1987; Sloan, 1987); Gidley Quarry, Lebo Formation, Crazy Mountains Basin, Montana (Rose, 1981; Sloan, 1981; Krause, 1987; Sloan, 1987); Who Nose? locality, Paskapoo Formation, Alberta Basin, Alberta (Scott, 2003a); Keefer Hill/Shotgun local fauna, Fort Union Formation, Wind River Basin, Wyoming (Holtzman and Wolberg, 1977; Sloan, 1987; Gunnell, 1989); Cochrane 2, Paskapoo Formation, Alberta Basin, Alberta (Youzwyshyn, 1988; Fox, 1990a; Scott et al., 2002; Fox, 2005); Saddle locality, Fort Union Formation, Bison Basin, Wyoming (Gazin, 1956); Scarritt Quarry, Melville Formation, Crazy Mountains Basin, Montana (Krause and Maas, 1990).

	LOCALITIES							
TAXA	Rock Bench Quarry (To2)	Gidley Quarry (To2)	Who Nose? (To2)	Keefer Hill (Ti1)	Douglass Quarry (Ti1)	Cochrane 2 (Ti1)	Saddle Locality (Ti2)	Scarritt Quarry (Ti2)
Mesodma pygmaea	●	●	●	●	●	●	●	●
Mimetodon silberlingi	●	●	●	●		●		
Ectypodus sp.					●	●		
Ectypodus szalayi		●	●			●		
Ectypodus powelli								●
Ectypodus aphronorus	●	●		●				
Parectypodus corystes			●			●		
Parectypodus sylviae			●			●		
Parectypodus sinclairi		●				●		
Neoplagiaulax donaldorum					●	●		
Neoplagiaulax hunteri			●		●	●		●
Neoplagiaulax grangeri		●						
Neoplagiaulax "nelsoni"			●	●				
Xyronomys sp.			●			●		
Ptilodus montanus		●	●					
Ptilodus wyomingensis	●							
Ptilodus sp. A				●	●	●		●
Ptilodus sp. B					●	●		●
Ptilodus gnomus			●		●	●		
Prochetodon speirsae						●		
Baiotomeus rhothonion			●					
Baiotomeus russelli						●		
Baiotomeus douglassi	●	●						
Anconodon cochranensis	●	●	●	●	●	●	●	
Anconodon gidleyi	●	●			●	●		
Acheronodon vossae						●		
Allocosmodon woodi				●	●			
Pentacosmodon bowensis						●		
Stygimys jepseni		●						
Catopsalis calgariensis				●				

known during the early Paleocene (represented by rare specimens of "*Microcosmodon*" *arcuatus* Johnston and Fox, 1984, "*Microcosmodon*" *harleyi* Weil, 1998, and *Acheronodon garbanii* Archibald, 1982) and throughout the Torrejonian (represented by an isolated M_1 of Microcosmodontidae, indeterminate genus and species B of Fox, 2005 (= *Acheronodon* sp. of Scott, 2003a). In the earliest Tiffanian, two additional genera are known (*Allocosmodon*, *Pentacosmodon* Jepsen, 1940), but, even so, and with the exception of *Acheronodon vossae* from Cochrane 2 (Fox, 2005), they are never a large component of any early Tiffanian multituberculate fauna (e.g., *Allocosmodon* is represented by only two specimens from Douglass Quarry). Eucosmodontids and taeniolabidids are rare in the early Tiffanian, with only *Neoliotomus* surviving into the late Tiffanian.

Multituberculate diversity also appears to have varied latitudinally, with northerly faunas more diverse compared to coeval faunas from more southerly areas. For example, local faunas from Wyoming document lower multituberculate diversity at both the generic and specific levels compared with similarly aged faunas in Canada (compare, e.g., the taxonomic composition of the Shotgun local fauna with that from Cochrane 2, Figure 8), with the Montana sites documenting an intermediate diversity. Recent collections have helped to fill in this taxonomic "gap", however, and in this regard the newly described Breaks local fauna of southern Wyoming (Higgins, 2003a) is of particular importance in that it represents one of the few sequences of localities that records mammalian evolution during the late Torrejonian-earliest Tiffanian transition, a period of time that was critically important in multituberculate evolution.

When multituberculate taxa from the Breaks local fauna are considered (i.e., those taxa found in the "zone of overlap", Higgins, 2003a), taxonomic diversity in the earliest Tiffanian of Wyoming is increased. Following the opinion that taxonomic first appearances are more advantageous than last appearances for recognizing biochronologic units (e.g., Woodburne, 1987, 1996; Lofgren et al., 2004; but see Walsh, 1998 for a discussion on the utility of single- versus multiple-taxon definitions of biochronologic units), Higgins (2003a) considered the "zone of overlap" earliest Tiffanian in age, despite the presence of numerous taxa considered more "typical" of the Torrejonian NALMA (see Lofgren et al., 2004 for a listing of these taxa). As a result, multituberculate diversity in the earliest Tiffanian of Wyoming is closer to levels seen at Douglass Quarry. Interestingly, a comparable situation exists at the late Torrejonian Who Nose? locality, Paskapoo Formation, Alberta, but with different results. Based on the presence of *Pronothodectes matthewi* Gidley, 1923, Scott (2003a) suggested a late Torrejonian (To-3) age for the local fauna, yet a considerable portion of the fauna is more typical of the earliest Tiffanian, with strong similarities to the Cochrane 2 fauna (in other words, had the index taxon *Pronothodectes matthewi* not been present, the fauna may very well have been assigned an earliest Tiffanian age, with concomitant range extensions for Torrejonian "relicts" into the Tiffanian). In contrast, had the index taxon *Plesiadapis praecursor* not been present in the Breaks local fauna, the assemblage may have been assigned a late Torrejonian age with subsequent range extensions for typical Tiffanian taxa back into the Torrejonian (Higgins, 2003a; Lofgren et al., 2004). Perhaps a more conservative assessment of these transitional local faunas would be to consider them biochronologically ambiguous, particularly when relying on index taxa that are extremely rare (e.g., both *Pronothodectes matthewi* and *Plesiadapis praecursor* are geographically restricted and known from few specimens), or whose phylogenetic position and stratigraphic distribution are unclear (consider, e.g., the presence of *Pronothodectes* in local faunas of earliest and middle Tiffanian age in Alberta, contemporary with its supposed phyletic descendant *Plesiadapis* (Fox, 1990b), or the co-occurrences of *Pronothodectes* and *Plesiadapis* in the Breaks local fauna (Higgins, 2003a). In any case, the Breaks local fauna documents a diversity of multituberculates which exceeds that recorded at the penecontemporaneous Shotgun locality, and is consistent with the trends outlined previously regarding multituberculate evolution through the Torrejonian-Tiffanian boundary (i.e., neoplagiaulacids remain taxonomically diverse, ptilodontids increase markedly in diversity). This further emphasizes the importance of sampling error and its potential effects on current understanding of the evolutionary history of multituberculates during early parts of the Tiffanian.

ACKNOWLEDGMENTS

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