CONTRIBUTIONS FROM THE MUSEUM OF PALEONTOLOGY

THE UNIVERSITY OF MICHIGAN

Vol. 26, No. 9, p. 157-196

December 31, 1983

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MUSEUM OF PALEONTOLOGY THE UNIVERSITY OF MICHIGAN ANN ARBOR

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MAMMALIAN FAUNA FROM DOUGLASS QUARRY, EARLIEST TIFFANIAN (LATE PALEOCENE) OF THE EASTERN CRAZY MOUNTAIN BASIN, MONTANA

By

David W. Krause¹ and Philip D. Gingerich²

Abstract.—Douglass Quarry is the fourth major locality to yield fossil mammals in the eastern Crazy Mountain Basin of south-central Montana. It is stratigraphically intermediate between Gidley and Silberling quarries below, which are late Torrejonian (middle Paleocene) in age, and Scarritt Quarry above, which is early Tiffanian (late Paleocene) in age. The stratigraphic position of Douglass Quarry and the presence of primitive species of Plesiadapis, Nannodectes, Phenacodus, and Ectocion (genera first appearing at the Torrejonian-Tiffanian boundary) combine to indicate an earliest Tiffanian age. Earliest Tiffanian faunas are known from only four other localities in the Western Interior of North America.

One hundred seventy-eight specimens have been collected from Douglass Quarry and these represent seven orders, 13 families, and 23 species. The fauna is dominated by a phenacodontid condylarth, *Ectocion collinus* (17.9% of the individuals), and a ptilodontid multituberculate, *Ptilodus* n. sp. (12.5%). The fauna appears to be characterized by low species diversity and evenness, but it is still inadequately sampled.

Comparison of a new specimen of the pantolestid proteutherian *Paleotomus* senior from Douglass Quarry with that of the middle and late Tiffanian Niphredil radagesti indicates that Niphredil is a junior synonym of Paleotomus.

INTRODUCTION

The eastern part of the Crazy Mountain Basin of south-central Montana has figured prominently in the establishment of a biochronological subdivision of the Torrejonian (middle Paleocene) and Tiffanian (late Paleocene) Land-Mammal Ages. Simpson's (1935, 1936, 1937a, b) classic studies of the paleontology of the "Crazy Mountain Field" documented a sequence of mammalian faunas spanning the late Torrejonian through middle Tiffanian. Most of the material studied by Simpson came from three localities: Gidley, Silberling, and Scarritt quarries. As Simpson (1937b, p.30) remarked, "Were it not for its three principal quarries,... this field would be of little importance." Our objective in this report is to provide a full account of previously undescribed specimens from a fourth major locality in the Crazy Mountain Basin,

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Douglass Quarry, a locality known to Simpson (as Locality 63) but developed subsequent to his work in the area.

Douglass Quarry, named in honor of the paleontologist Earl Douglass, occurs in a small exposure in the NW ¼ of Sec. 18, T5N, R15E, Sweetgrass County, Montana. It is located just east of U.S. Highway 191 on the south side of a small drainage that enters the main northeast-southwest trending coulee from the east (see Figure 1 in this paper, and map in Plate 1 of Simpson, 1937b). The quarry consists of two major lithologies: 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. Most of the specimens of fossil mammals were found in the conglomeratic beds. Douglass Quarry lies at a level that is stratigraphically intermediate between the Gidley and Silberling quarries below and Scarritt Quarry above (Figure 2). Gidley and Silberling quarries are late Torrejonian in age [Pronothodectes matthewi biochron of Gingerich (1975, 1976)] and Scarritt Quarry has been accorded an early Tiffanian age (Plesiadapis anceps biochron).

Douglass Quarry was discovered in 1902 by Albert C. Silberling, a resident of nearby Harlowton. Silberling was then a member of a Princeton University field party headed by M. S. Farr. Silberling's efforts at Douglass Quarry in 1902 produced only a few isolated teeth and fragments thereof (Bell, 1941). In March, 1940 Silberling discovered several jaws and teeth in situ and later that year returned to the site with John A. Bell, then an undergraduate student at Princeton University, for seven weeks. They were joined briefly by Professor G. L. Jepsen of Princeton University and H. Bott, a student at the University of Utah. During the summer of 1940 approximately 170 specimens were recovered. These specimens were the subject of Bell's senior thesis at Princeton (Bell, 1941), an unpublished report now long out-dated. Additional specimens were collected by University of Michigan field crews during brief visits to the area in the summers of 1978, 1980, and 1982. The total sample of identifiable specimens from Douglass Quarry available for analysis includes 37 jaws with one or more teeth and 141 isolated teeth.

Only a small part of the mammalian fauna from Douglass Quarry has been described in the published literature. Simons (1960) tentatively assigned a specimen to *Titanoides zeuxis* (*Titanoides* sp. in this paper), West (1971) cited the occurrence of deciduous teeth of *Phenacodus bisonensis* and *Ectocion montanensis* (*E. collinus* in this paper), and Gingerich (1975, 1976) described the dentitions of *Nannodectes intermedius* and *Plesiadapis praecursor*. Our purpose here is to record the entire mammalian fauna known to date from Douglass Quarry, based principally on Silberling's and Bell's undescribed collections at Princeton University. The composition of the fauna now known from the quarry is summarized in Table 1. This study has provided the impetus for one of us (DWK) to initiate a field research program on late Torrejonian - early Tiffanian mammalian faunas from the Crazy Mountain Basin and elsewhere. Brief visits to Douglass Quarry indicate that the locality is still productive, and we anticipate that future collecting will produce a much larger sample than is currently known.

TERMINOLOGY AND ABBREVIATIONS

The terminology employed in the description of multituberculate dentitions is summarized in Krause (1977); for eutherian dentitions, Van Valen (1966) and Gingerich (1976) are followed. All measurements are in millimeters (mm) and are expressed as anteroposterior length (L) x labiolingual breadth (W). Specimens described or referred to in this report are housed in the American Museum of Natural History (AMNH), the Princeton University Museum of Natural



FIG. 1— Douglass Quarry, eastern Crazy Mountain Basin, Montana. Above, view looking eastward toward the coulee containing Douglass Quarry from U.S. Highway 191. Quarry is in right center of photograph. Below, view looking south at the quarry itself.

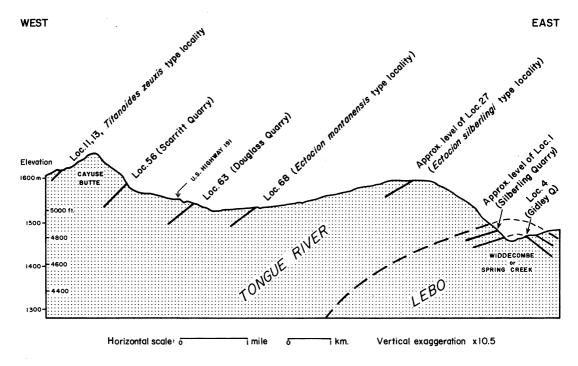


FIG. 2— Diagrammatic geologic cross-section of the eastern Crazy Mountain Basin showing the stratigraphic relationships of the principal fossil localities, as well as others that are discussed in the text. Stratigraphic levels are based on measurements provided by Simpson (1937b).

History (PU), the University of Alberta Laboratory for Vertebrate Paleontology (UA), the University of Michigan Museum of Paleontology (UM), and the National Museum of Natural History (USNM).

SYSTEMATIC PALEONTOLOGY

Class MAMMALIA Linnaeus, 1758
Order MULTITUBERCULATA Cope, 1884
Family NEOPLAGIAULACIDAE Ameghino, 1890
Genus Neoplagiaulax Lemoine, 1882
Neoplagiaulax hunteri (Simpson, 1936)
Figure 3A, B

Referred specimens.— PU 14637 (LP⁴) and PU 23581 (badly fragmented LP₄).

Description and discussion.—The two specimens here referred to Neoplagiaulax hunteri, although both are isolated teeth and only one is complete, are comparable in size and shape to specimens in the typodigm from Scarritt Quarry (Simpson, 1936).

PU 14637 is an isolated P⁴ that, like P⁴s of *N. hunteri* from Scarritt Quarry (Simpson, 1936) and Roche Percee (Krause, 1977), is high-crowned and has a cusp formula of 1:9:0, convex

TABLE 1 — Composition of the mammalian fauna from Douglass Quarry, eastern Crazy Mountain Basin, Montana.

Percent frequency is based on the minumum number of individuals (MNI) represented by the total sample of specimens known.

| Taxon | Number Specimen | | % Freq. (MNI) |
|---|--------------------|----|---------------|
| O A MAINTITUDED CHILATA | | | |
| Order MULTITUBERCULATA | | | |
| Family NEOPLAGIAULACIDAE | 2 | | 1.0 |
| Neoplagiaulax hunteri | 2 | 1 | 1.8 |
| Family CIMOLODONTIDAE | 5 | 2 | 3.6 |
| Anconodon cochranensis Family PTILODONTIDAE | 3 | 2 | 3.0 |
| Ptilodus, new species | 36 | 7 | 12.5 |
| Order PROTEUTHERIA | | | |
| Family Palaeoryctidae | | | |
| Palaeoryctidae incertae sedis | 1 | 1 | 1.8 |
| Family PENTACODONTIDAE | • | • | 1.0 |
| Bisonalveus browni | 11 | 4 | 7.1 |
| Cf. Aphronorus sp. | 4 | 3 | 5.4 |
| Family PANTOLESTIDAE | • | | 2 |
| Propalaeosinopa diluculi | 5 | 3 | 5.4 |
| Paleotomus senior | 1 | 1 | 1.8 |
| Order LIPOTYPHLA | | | |
| Family NYCTITHERIIDAE | • | | |
| Leptacodon munusculum | 1 | 1 | 1.8 |
| Order PRIMATES | | | |
| Family PLESIADAPIDAE | | | |
| Nannodectes intermedius | 11 | 4 | 7.1 |
| Plesiadapis praecursor | 6 | 2 | 3.6 |
| Order CONDYLARTHRA | | | |
| Family HYOPSODONTIDAE | | | |
| Litomylus dissentaneus | . 2 | 1 | 1.8 |
| Family PHENACODONTIDAE | | | |
| Ectocion collinus | 52 | 10 | 17.9 |
| Phenacodus bisonensis | 20 | 3 | 5.4 |
| Family ARCTOCYONIDAE | | | |
| Claenodon cf. montanensis | 1 | 1 | 1.8 |
| Claenodon? sp. | 1 | 1 | 1.8 |
| Mimotricentes fremontensis | 4 | 2 | 3.6 |
| Chriacus orthogonius? | 1 | 1 | 1.8 |
| Chriacus pelvidens | 2 | 1 | 1.8 |
| Chriacus sp. | 6 | 3 | 5.4 |
| Thryptacodon cf. demari | 2 | 2 | 3.6 |
| Order CARNIVORA | | | |
| Family MIACIDAE | • | 1 | 1 0 |
| Protictis sp. | 1 | 1 | 1.8 |
| Order PANTODONTA | | | |
| Family PANTOLAMBDIDAE Titanoides sp. | 3 | 1 | 1.8 |
| i nanotaes sp. | | | |
| | Totals 178 | 56 | 100.4 |

anterior slope, and concave posterior slope. The ultimate and penultimate cusps of the middle row are subequal in height and highest above the base of the crown.

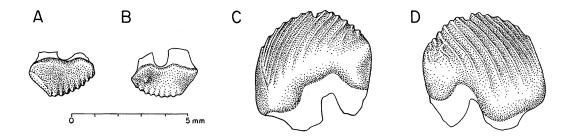


FIG. 3— Small multituberculates from Douglass Quarry. A and B, left P⁴ of Neoplagiaulax hunteri, PU 14637, in labial and lingual views. C and D, right P₄ of Anconodon cochranensis, PU 14619B, in lingual and labial views.

The single P_4 (PU 23581) has 16 serrations and, although badly damaged, has the cross-sectional outline characteristic of N. hunteri, being convex labially and flat lingually (Krause, 1977).

Measurements.— PU 23581: $P_4 = 4.3 \text{ mm long}$; PU 14637: $P^4 = 3.0 \text{ x } 1.3$.

Family CIMOLODONTIDAE Marsh, 1889 Genus Anconodon Jepsen, 1940 Anconodon cochranensis (Russell, 1929) Figure 3C, D

Referred specimens.—PU 14619A (LP₄), PU 14619B (RP₄), PU 14619C (poorly preserved LP₄), PU 14619D (anterior fragment of RP₄), and PU 23582 (fragmentary RP⁴ - questionably referred).

Description and discussion.—PU 14619A and 14619B, the best preserved specimens of P₄, exhibit the highly arched labial outline and long, straight anterior margin typical of P₄s of Anconodon. Both specimens have 14 serrations.

A poorly preserved and fragmentary P⁴ (PU 23582) may also be referable to this species. It is incomplete anteriorly and lingually, thus precluding precise measurement. PU 23582 is tentatively assigned to A. cochranensis because of its size and its similarity to isolated P⁴s that Jepsen (1940, pp. 292-293) questionably referred to Anconodon. The 10+ cusps of the middle row are arranged in a gently convex arc. This arc does not rise steeply posteriorly, as it does in neoplagiaulacids.

Although few specimens are known, the genus Anconodon is badly in need of revision. Three species are currently recognized in the literature: A. gidleyi from Gidley Quarry (Simpson, 1935, 1937b), Rock Bench Quarry (Jepsen, 1940), Keefer Hill (?A. gidleyi - Keefer, 1961), and Kutz Canyon KU locality 13 (Wilson, 1956; Sloan, 1981); A. russelli from Gidley Quarry (Simpson, 1935, 1937b), Rock Bench Quarry (Jepsen, 1940), and the Bison Basin Saddle locality (cf. A. russelli - Gazin, 1956); and A. cochranensis from Cochrane site I (Russell, 1929), Cochrane site II (Russell, 1932), and Calgary site 2E (Russell, 1932, 1958). [L. S. Russell (1967) also referred

several specimens from Swan Hills site 1 to A. cochranensis but they are clearly referable to other genera—see Krause (1977) for a discussion of some of these specimens.] If the above identifications are valid, the genus was apparently widely distributed and quite common in the late Torrejonian and early Tiffanian of the Western Interior. Unfortunately, useful diagnoses distinguishing the three species are lacking. A. gidleyi appears to have been slightly larger than A. russelli (Jepsen, 1940). When Jepsen (1940) diagnosed A. gidleyi and A. russelli, he accepted (p. 258) A. cochranensis as a valid species of Ectypodus. Only later (Van Valen and Sloan, 1966) was the species correctly allocated to Anconodon. Based on published descriptions and illustrations, A. russelli appears to be a junior synonym of A. cochranensis but we have not examined the original material of either species. In any case, the specimens from Douglass Quarry are of a size and morphology that accord well with A. cochranensis and they are therefore tentatively assigned to this species, pending a thorough revision of the genus.

Measurements.—PU 14619A: $P_4 = 6.2 \times 1.6$; PU 14619B: $P_4 = 5.6 \times 1.9$.

Family PTILODONTIDAE Gregory and Simpson, 1926 Genus Ptilodus Cope, 1881 Ptilodus new species Figure 4

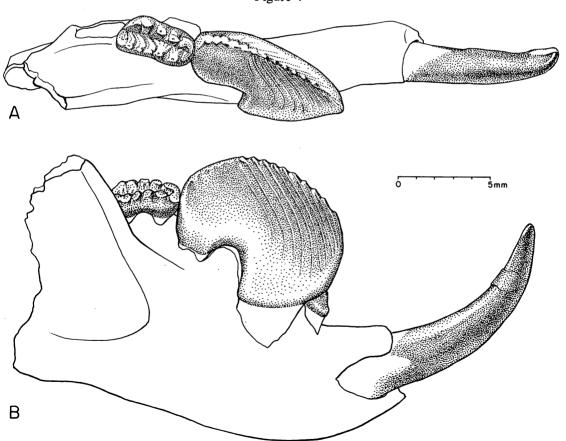


FIG. 4— *Ptilodus*, new species, from Douglass Quarry. (A) Occlusal and (B) labial views of PU 14584, right dentary with I₁P₃¬₄M₁.

Referred specimens.—PU 14584 (R dentary with $I_1P_{3-4}M_1$), 14586 (R dentary with I_1P_4), 14587 (R dentary with P_4), 14588 (R dentary with P_4), 14594 (R P_4), 14595 (fragmentary R P_4), 14596 (R P_4), 14597 (R P_4), 14598 (R P_4), 14599 (L P_4), 14600 (L P_4), 14601 (L P_4), 14602 (R P_4), 14615 (one L P_4 , one L P_4), one L P_4 , one L P_4 , one L P_4 , one L P_4 , one R P_4), 23572 (R dentary with P_4), 23573 (L dentary with P_4), 23574 (two R P_4), 23575 (several fragmentary P_4), 23576 (fragmentary L P_4), 23577 (fragmentary L P_4), 23578 (R P_4), 23579 (L P_4), and 23580 (fragmentary L P_4).

Discussion.—The species of Ptilodus from Douglass Quarry is new and will be described by Krause (in prep.) in his systematic revision of the Ptilodontidae. It is easily distinguished from other known species of Ptilodus on the basis of its large size alone.

Order PROTEUTHERIA Romer, 1966 Family PALAEORYCTIDAE (Winge, 1917) Palaeoryctidae, incertae sedis Figure 5

Referred specimen.—PU 23602 (fragmentary LM³).

Description and discussion.—PU 23602 is an isolated M³ that is missing the parastylar lobe, which, based on the pattern of breakage, was apparently large. The tooth is very short anteroposteriorly and broad transversely, the paracone is much larger and taller than the metacone, the conules are weak, the ectoflexus is deeply invaginated, and pre- and postcingula are absent.

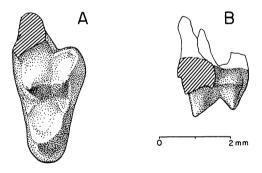


FIG. 5— Palaeoryctidae, incertae sedis, from Douglass Quarry. (A) Occlusal and (B) labial views of PU 23602, fragmentary LM³.

PU 23602 may be referable to the same species as USNM 9554, a left M² from Gidley Quarry. Simpson (1937b, p.110) questionably referred USNM 9554 to *Gelastops parcus*, an assignment that was also used, without question, by Van Valen (1966, p.15). Gingerich (1982b) suggested that USNM 9554 is an M² of a palaeoryctine rather than that of a didelphodontine.

Measurements.—PU 23602: $M^3 = 2.2 \times 4.5$.

Family PENTACODONTIDAE Simpson, 1937 Genus Bisonalveus Gazin, 1956 Bisonalveus browni Gazin, 1956 Figure 6

Referred specimens.—PU 14580 (R dentary with $P_{3-4}M_{1-3}$), PU 14581 (L dentary with $P_{3-4}M_1$ and trigonid of M_2), PU 14582 (L maxilla with M^{1-3}), PU 14582A (RM²), PU 14582B (RM²), PU 23583 (L dentary with M_2), PU 23584 (L dentary with M_2), PU 23585 (RM₁), PU 23586 (RM₁), and UM 80826 (unassociated RP₄ and LM₂).

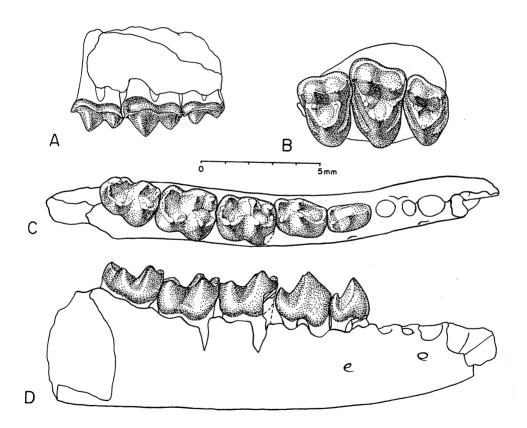


FIG. 6 — Bisonalveus browni from Douglass Quarry. (A) Labial and (B) occlusal views of PU 14582, left maxilla with M¹⁻³. (C) Occlusal and (D) labial views of PU 14580, right dentary with P₃₋₄M₁₋₃.

Description and discussion.—Bisonalveus, a monotypic genus, was represented in the typodigm from the Bison Basin Saddle locality by P_4M_{1-3} (Gazin, 1956). In addition, Holtzman (1978) referred an isolated M_1 from Brisbane to Bisonalveus sp. The material from Douglass Quarry therefore adds considerably to our knowledge of the genus. In addition to dentaries that contain P_3 and anterior alveoli, a maxilla with M^{1-3} (PU 14582) can now be referred to B. browni.

The lower dental formula of $B.\ browni$ is?.1.4.3. Breakage on PU 14580 and 14581 prevents us from counting the number of lower incisors. Judging from alveoli in these two specimens, the canine was enlarged and procumbent, P_1 was single-rooted and only slightly smaller than the canine, and P_2 was double-rooted. Mental foramina occur beneath P_1 and P_3 . P_3 is double-rooted and has a tall, single-cusped trigonid bearing both an anterior and a posterior crest. The anterior crest (the paracristid) veers lingually near the base of the crown and continues posteriorly as a variably developed cingulid (prominent on PU 14580 but indistinct on PU 14581) eventually joining the entocristid. The basined talonid on P_3 is dominated by a large hypoconid. No other distinct talonid cusps are developed along the crest that descends lingually from the hypoconid.

 P_4M_{1-3} of *B. browni* have been described by Gazin (1956) but several additional features can be noted with the larger sample now available. P_4 is much like P_3 but it is larger and distinctly more molariform in possessing a variably developed but always distinct metaconid and entoconid. There is no trace of a hypoconulid on any of the P_4 specimens.

The trigonids of the lower molars, particularly those of M_{2-3} , are wider than the talonids. Gazin (1956) observed that a small mesoconid was developed on M_3 only but several specimens in the sample from Douglass Quarry show slight development of this cuspule on M_{1-2} as well. The hypoconulid, although feebly developed on M_{1-2} , is frequently twinned, as shown by the presence of two small islands of exposed dentine on the postcristid. On M_3 of PU 14580 the hypoconulid is a large lobe that is separated from both the hypoconid and entoconid by distinct valleys along the postcristid.

PU 14582, 14582A, and 14582B are upper molars referred to *B. browni* on the basis of size, occlusal relationships with known lowers, and similarities to upper molars of other pentacodontids. The absence of any other small pentacodontids in the fauna makes the association of upper and lower dentitions proposed here reasonably certain.

The paracone on the upper molars of *B. browni* is considerably larger than the metacone, particularly so on M^2 . Conules are generally well-developed but the metaconule is reduced on M^{2-3} . Pre- and postcingula are prominent and, on M^{2-3} in particular, there is a faint swelling on the postcingulum in the position of the hypocone. The occlusal outline of M^1 is subrectangular but in M^2 the paracone is so large and in M^3 the parastylar lobe is so well-developed and the metastylar area so reduced that the labial margins of these teeth are strongly oblique in orientation. On M^{1-2} preparacristae are faint or absent and postmetacristae are distinct. On the only known M^3 (PU 14582), the preparacrista is distinct but the postmetacrista is absent.

Measurements.—See Table 2.

Genus Aphronorus Simpson, 1935 Cf. Aphronorus sp. Figure 7

Referred specimens.—PU 14620A-D (three L and one RM_{1?}).

Description and discussion.—Included in the fauna from Douglass Quarry is a pentacodontid that is represented by four isolated molars, probably M_1 s, only one of which has a complete

TABLE 2 — Statistical summary of dental variation in earliest Tiffanian *Bisonalveus browni* from Douglass Quarry, Crazy Mountain Basin, Montana. N = number of specimens, OR = observed range, x = mean, SD = standard deviation, CV = coefficient of variation. All measurements in mm.

| Tooth position | | N | OR | x | SD | CV |
|----------------|---------------|---|---------|------|------|-----|
| Maxillary den | tition L | 1 | 2.4 | | | |
| M | w | 1 | 3.1 | | | |
| 2.62 | L | 3 | 2.4-2.6 | 2.50 | 0.10 | 4.0 |
| M ² | w | 3 | 3.5-4.0 | 3.73 | 0.25 | 6.7 |
| | L | 1 | 1.8 | | | |
| M^3 | w | 1 | 3.1 | | | · |
| Mandibular d | entition L | 2 | 1.9-2.0 | 1.95 | | |
| P ₃ | w | 2 | 1.2-1.3 | 1.25 | | |
| | L | 3 | 2.3-2.5 | 2.37 | 0.12 | 5.1 |
| P ₄ | w | 3 | 1.5-1.7 | 1.63 | 0.12 | 7.4 |
| | L . | 4 | 2.3-2.6 | 2.48 | 0.13 | 5.2 |
| \mathbf{M}_1 | w | 4 | 1.7-1.9 | 1.80 | 0.08 | 4.4 |
| | L | 4 | 2.6-2.7 | 2.63 | 0.05 | 1.9 |
| M ₂ | w | 4 | 2.0-2.1 | 2.05 | 0.06 | 2.9 |
| | L | 1 | 2.6 | | | |
| M_3 | w | 1 | 1.8 | | | |

crown. The metaconid and protoconid are subequal in size and height but the paraconid is reduced to a small cuspule situated almost as far lingually on the trigonid as the metaconid. The paraconid is connected to the protoconid by an arcuate paracristid. The talonid is short and broad. The hypoconid is the largest and tallest talonid cusp; the entoconid can be either single (PU 14620C) or twinned (PU 14620D). The most striking feature of the Douglass Quarry form is the height of the molar crowns. In unworn or only slightly worn specimens the crown of M_1 is approximately as high as it is long.

The Douglass Quarry form is much larger than either Aphronorus simpsoni or A. fraudator, smaller than A. orieli, and approximately the same size as Winterfeld's (1982) new species A. ratatoski. It differs from all of these species in possessing remarkably high molar crowns and in having relatively lingually positioned paraconids. It further differs from A. simpsoni and A. fraudator in having more reduced paraconids.

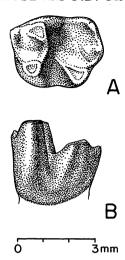


FIG. 7— Cf. Aphronorus sp. from Douglass Quarry. (A) Occlusal and (B) labial views of PU 14620C, LM₁₂,

The Douglass Quarry form resembles most closely an undescribed new species, and probably new genus, from Gidley Quarry (see Rose, 1981a, table 39). Unfortunately, only two specimens (AMNH 35293 - L dentary with heavily worn P_4M_{1-3} ; AMNH 35294 - R dentary with P_4M_{1-2}) are known from Gidley Quarry. The new taxon is not named here because the Douglass Quarry material is too fragmentary to permit an adequate diagnosis and because comparisons have not yet been made with an apparently closely related, but also undescribed, form from Rock Bench Quarry (see Rose, 1981a, Table 38).

Measurements.—PU 14620A: $M_{1?} = 2.8$ mm wide; PU 14620B: $M_{1?} = 2.8$ mm wide; PU 14620C: $M_{1?} = 3.5 \times 2.7$; PU 14620D: $M_{1?} = 3.6 \times 2.6$.

Family PANTOLESTIDAE Cope, 1884 Genus *Propalaeosinopa* Simpson, 1927 *Propalaeosinopa diluculi* (Simpson, 1935) Figures 8, 9

Referred specimens.—PU 14589 (R dentary with P_3M_{1-3}), PU 14590 (L dentary with P_4M_{1-3}), PU 14591 (R dentary with M_{1-2}), PU 14592 (R dentary with M_{1-2}), and UM 80828 (L maxilla with M^{2-3}).

Description and discussion.—Propalaeosinopa diluculi was assigned to Palaeosinopa when first described (Simpson, 1935) but it was later transferred to Bessoecetor (Simpson, 1937b). Bessoecetor, however, is a junior synonym of Propalaeosinopa (see Van Valen, 1967). The specimens from Douglass Quarry compare well in size and morphology to those of P. diluculi from Gidley and Swain quarries and also to those of P. "thomsoni" from Scarritt Quarry. The latter were described in detail by Simpson (1936). P. thomsoni was placed in synonymy with P. diluculi under the name P. albertensis by Van Valen (1967). We concur with Rose (1981a, p.150) in maintaining P. diluculi as a species distinct from P. albertensis.

Measurements.—See Table 3.

| TABLE 3 — Statistical summary of dental variation in earliest Tiffanian I | Propalaeosinopa diluculi from Douglass |
|---|--|
| Quarry, Crazy Mountain Basin, Montana. Abbreviations as in | Table 2. All measurements in mm. |

| Tooth 1 | position | N | OR | x | SD | CV |
|----------------|-----------|---|---------|------|------|-----|
| Maxillary den | ntition | | | | | |
| M^2 | L | 1 | 2.5 | | | |
| IVI | W | 1 | 3.5 | | | |
| M^3 | L | 1 | 2.3 | | | |
| | w | 1 | 3.7 | | | |
| Mandibular d | lentition | | | | | |
| | L | 0 | | | | |
| P ₄ | w | 2 | 1.2-1.3 | 1.25 | | |
| | L | 3 | 2.3-2.5 | 2.40 | 0.10 | 4.2 |
| M_1 | w | 4 | 1.6-2.0 | 1.75 | 0.17 | 9.7 |
| | L | 3 | 2.3-2.5 | 2.40 | 0.10 | 4.2 |
| M_2 | w | 3 | 1.8-2.1 | 1.93 | 0.15 | 7.8 |
| | L | 2 | 2.7-2.9 | 2.80 | | |
| M_3 | w | 2 | 1.8-2.2 | 2.00 | | |

Genus Paleotomus Van Valen, 1967 Paleotomus senior (Simpson, 1937) Figure 10

Referred specimen.—PU 14616 (R dentary with P₃₋₄M₂₋₃).

Description and discussion.—Paleotomus senior was previously known only from the holotype M₃ (AMNH 33990) and two referred upper molars (M¹, AMNH 33991; M², AMNH 33828), all of which were found at Scarritt Quarry. The new specimen described here adds considerably to knowledge of both the genus Paleotomus and the type species P. senior.

Judging from alveoli, P_2 was double-rooted like the following cheek teeth, but nothing remains of the crown of this tooth. The crown of P_3 is badly broken, but enough remains to permit a measurement of crown length. There is a distinct, trenchant hypoconid on the talonid of P_3 very much like that on P_4 . The crown of P_4 is intact, with only the tip of the principal cusp (protoconid) removed by apical wear. A distinct paraconid of moderate size is present directly anterior to the protoconid, and a small metaconid is present high on the talonid, posterior and slightly medial to the principal cusp. A large hypoconid forms a trenchant talonid directly posterior to the protoconid.

The crown of M_1 is missing and its length can only be estimated by measuring between the intact posterior surface of P_4 and the anterior surface of M_2 . Crowns of M_2 and M_3 are intact except for some slight breakage at the apices of cusps. M_2 and M_3 are both high crowned, with the

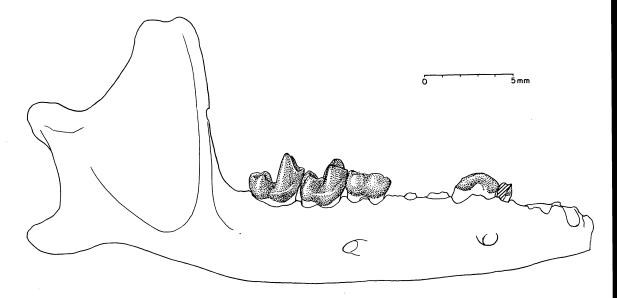


FIG. 8— Propalaeosinopa diluculi from Douglass Quarry. Labial view of PU 14589, right dentary with P3M1-3.

trigonids elevated well above the level of the talonids. The protoconid is the principal trigonid cusp on M_2 and M_3 , with the metaconid being next in size and the paraconid the smallest cusp. The paraconid and metaconid are close together, and in occlusal view the paracristid and protocristid form an acute angle of about 30°. Viewed from the front, the paracristid bends sharply at about 90° between the protoconid and paraconid. Viewed from the rear, the protocristid makes an acute angle estimated at about 70° between the protoconid and metaconid. The hypoconid is the principal cusp on the talonids of M_2 and M_3 . Other talonid cusps are broken and obscured by wear on M_2 , but the entoconid and hypoconulid are distinct and closely approximated on M_3 . The talonid is nearly as wide as the trigonid on M_2 , but it is distinctly narrower than the trigonid on M_3 (see following dental measurements). The mandibular ramus is robust and deep, and there is a distinct mental foramen below the anterior root of M_1 . The masseteric fossa is relatively deep.

The holotype of *Paleotomus senior* from Scarritt Quarry is a right M₃ that is very slightly smaller and narrower, but otherwise identical, to M₃ in the specimen described here. Van Valen (1967) removed *P. senior* from the pantolestid genus *Palaeosinopa* and placed it in *Paleotomus*, which he referred to the family Palaeoryctidae. M₃ of *Paleotomus* differs from that in *Palaeosinopa* principally in having a relatively higher trigonid. Van Valen (1967) retained Simpson's referred upper molars of *P. senior* from Scarritt Quarry in *Palaeosinopa*, naming a new species *P. simpsoni* to receive them. Gingerich (1980a, b) recognized the genus *Palaeosinopa* as being distinct from *Palaeosinopa*, but synonymized Van Valen's species *Palaeosinopa simpsoni* with *Paleotomus senior*. Upper molars of *P. simpsoni* differ from those of *Palaeosinopa* in being more constricted lingually and in having smaller hypocones. These differences are appropriate for occlusion with higher crowned lower molars.

Van Valen (1967) described *Paleotomus* as a didelphodontine palaeoryctid because of its reduced paraconid closely approximated to the metaconid, because of its distinct entoconid, and in spite of its high M₃ trigonid. In reuniting *Paleotomus senior* with *Palaeosinopa simpsoni*, Gingerich (1980a, b) returned *Paleotomus* to the family Pantolestidae. The new specimen

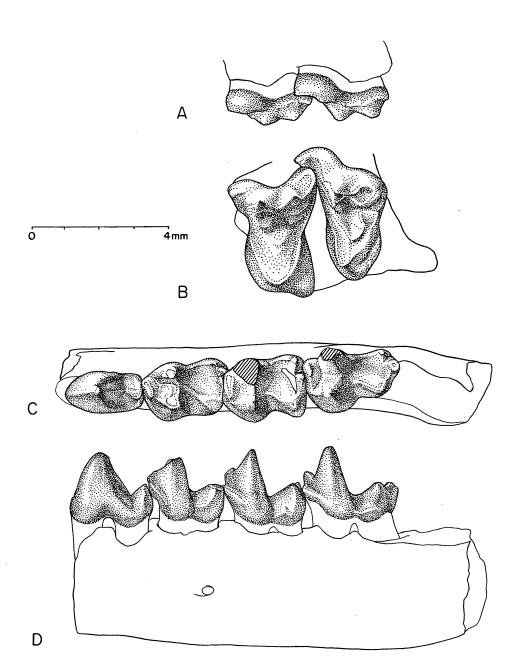


FIG. 9— Propalaeosinopa diluculi from Douglass Quarry. (A) Labial and (B) occlusal views of UM 80828, left maxilla with M^{2-3} . (C) Occlusal and (D) labial views of PU 14590, left dentary with P_4M_{1-3} .

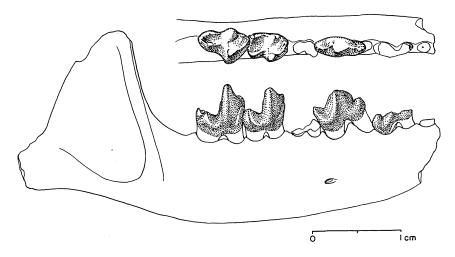


FIG. 10— Paleotomus senior from Douglass Quarry. (A) Occlusal and (B) labial views of PU 14616, right dentary with P₃₋₄M₁₋₃.

described here corroborates this assignment. Furthermore, comparison of the new specimen from Douglass Quarry with the middle and late Tiffanian pantolestid Niphredil radagesti indicates that Niphredil Van Valen, 1978, is clearly a junior synonym of Paleotomus Van Valen, 1967. M₁ is not yet known in Paleotomus, but the diagnostic characteristics of the dentition and position of the mental foramen described by Van Valen (1978, p. 66) match those of Paleotomus exactly. PU 21239 from Cedar Point Quarry is a topotype specimen of N. radagesti important in preserving unworn P₃ and P₄. These two teeth are larger but otherwise very similar to those in Paleotomus senior from Douglass Quarry. Both specimens have P₃ distinctly smaller than P₄, and the characteristically high metaconid cusp on P₄.

Measurements.— PU 14616: $P_3 = 4.8 \text{ x about } 2.0$, $P_4 = 5.8 \text{ x } 2.4$, $M_1 = \text{about } 3.4 \text{ mm long}$, $M_2 = 4.5 \text{ x } 3.3$, $M_3 = 5.5 \text{ x } 3.7$. Mandibular depth below $M_2 = 9.3$. For comparison, the holotype M_3 of P. senior measures 5.3 x 3.4.

Order LIPOTYPHLA Haeckel, 1866
Family NYCTITHERIIDAE Simpson, 1928
Genus Leptacodon Matthew and Granger, 1921
Leptacodon munusculum Simpson, 1935
Figure 11

Referred specimen.—PU 14593 (L dentary with P₄M₁₋₂ and trigonid of M₃).

Description and discussion.—PU 14593 is similar in size to specimens of both Leptacodon munusculum and L. tener, but is clearly smaller than those of L. packi. Krishtalka (1976) compared L. munusculum and L. tener as follows: "Relative to L. munusculum, P_4 of L. tener is less compressed labiolingually and has a wider talonid and a labially convex cristid obliqua. The paraconid on M_{1-3} of L. tener is more nearly cuspate, the talonid on M_3 is more elongate, and the talonid on M_{1-2} extends beyond the labial margin of the talonid." Except for the absence of the M_3 talonid because of breakage, PU 14593 exhibits the distinctive characteristics ascribed by Krishtalka to L. munusculum and it is here assigned to that species.

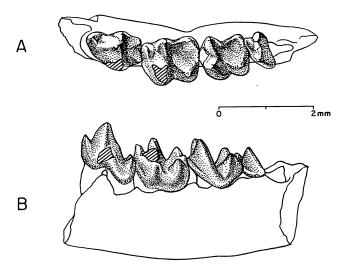


FIG. 11 — Leptacodon munusculum from Douglass Quarry. (A) Occlusal and (B) labial views of PU 14593, left dentary with P₄M₁₋₂ and trigonid of M₃.

L. munusculum is elsewhere known from Gidley Quarry (Simpson, 1937b), Cedar Point Quarry (Krishtalka, 1976), Bangtail (Gingerich et al., 1983), and probably also from Rock Bench Quarry (Rose, 1981a). A series of workers (McKenna, 1960; Krishtalka, 1976; Bown and Schankler, 1982) have suggested that L. munusculum is not closely related to the type species of Leptacodon, L. tener, and that it should be removed from that genus, although none has formally done so.

Measurements.—PU 14593: $P_4 = 1.3 \times 0.9$, $M_1 = 1.3 \times 1.1$, $M_2 = 1.3 \times 1.0$.

Order PRIMATES Linnaeus, 1758
Suborder PLESIADAPIFORMES Simons, 1972
Family PLESIADAPIDAE Trouessart, 1897
Genus Nannodectes Gingerich, 1975
Nannodectes intermedius (Gazin, 1971)
Figure 12A, B

Referred specimens.—PU 14623 (L dentary with $P_{3-4}M_{1-3}$), PU 14624 (L dentary with M_{1-3}), PU 14625 (L dentary with $P_{4}M_{1-3}$), PU 14627 (associated P_{1-3}), PU 14628 (R dentary with P_{2-3}), PU 14636 (P_{1-3}), PU 21577 (in part - P_{1-3}), PU 21578 (two P_{1-3}), PU 23587 (P_{1-3}), and P_{1-3} 0824 (P_{1-3} 0824 (P_{1-3} 0824).

Description and discussion.—The largest sample of Nannodectes intermedius is that described by Gazin (1971) and Gingerich (1976) from the type locality at Keefer Hill (Shotgun local fauna) in the Wind River Basin, Wyoming. The Douglass Quarry specimens extend the geographic range of N. intermedius to south-central Montana, but otherwise contribute little to knowledge of this species.

Nannodectes intermedius differs from a second Douglass Quarry plesiadapid, Plesiadapis praecursor, in being smaller and in retaining a lower canine. N. intermedius is similar in size to

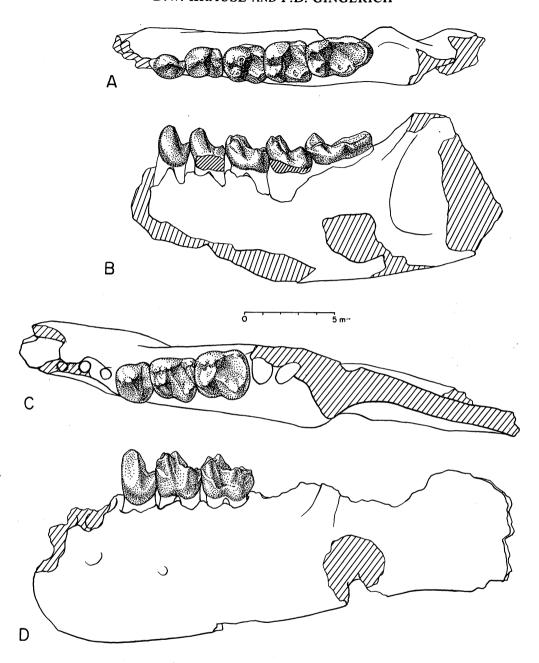
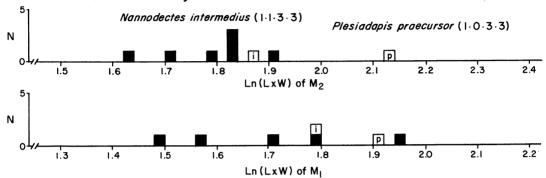


FIG. 12 — Plesiadapidae from Douglass Quarry. A and B, left dentary with P₃₋₄M₁₋₃ of Nannodectes intermedius, PU 14623, in occlusal and labial views. C and D, left dentary with P₄M₁₋₂ of Plesiadapis praecursor, PU 14512 (holotype), in occlusal and labial views.

late Torrejonian *Pronothodectes jepi* but differs in lacking I_2 . All three of these species are very similar in form at this stage of evolution, and all are evidently closely related phyletically. The distribution of tooth size in Douglass Quarry N. *intermedius* is compared to that of *Ples*. *praecursor* in Figure 13. The distribution of tooth size in Rock Bench Quarry *Pro. jepi* is included as well for comparison.

DOUGLASS QUARRY (Early Tiffanian)



ROCK BENCH QUARRY (Late Torrejonian)

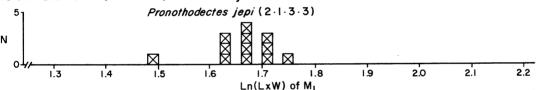


FIG. 13 — Comparison of tooth size distributions of late Torrejonian Rock Bench Quarry and early Tiffanian Douglass Quarry Plesiadapidae. Above, Nannodectes intermedius and Plesiadapis praecursor from Douglass Quarry (i and p refer to the type specimens of N. intermedius and P. praecursor, respectively). Below, Pronothodectes jepi from Rock Bench Quarry. Pronothodectes jepi is considered to be a good structural ancestor for both Nannodectes intermedius and Plesiadapis praecursor (Gingerich, 1976).

Nannodectes intermedius is known principally from gnathic remains and associated teeth at Keefer Hill and Douglass Quarry, but a partial skull of this species was recently described from Bangtail in the western Crazy Mountain Basin (Gingerich et al., 1983).

Measurements.—Measurements of the cheek teeth of Nannodectes intermedius from Douglass Quarry are compared with those of Plesiadapis praecursor in Table 4.

Genus Plesiadapis Gervais, 1877 Plesiadapis praecursor Gingerich, 1975 Figure 12C, D

Referred specimens.—PU 14512 (holotype - L dentary with P_4M_{1-2}), PU 14626 (L maxilla with $P^{3-4}M^1$), PU 21576 (L dentary with P_3), and PU 21577 (in part - unassociated LI^1 , LP_3 , and RM_3).

TABLE 4 — Comparison of dental measurements of cheek teeth of earliest Tiffanian Nannodectes intermedius and Plesiadapis praecursor from Douglass Quarry, Crazy Mountain Basin, Montana. Selected measurements are compared graphically in Figure 13. Abbreviations as in Table 2. All measurements in mm.

| Tooth p | Tooth position | | OR | $\overline{\mathbf{x}}$ | SD | CV | _ |
|------------------------|----------------|-----|---------|-------------------------|------|-------------|---|
| Nannodectes intermed | lius | | | | | | |
| Maxillary den | | | | | | | |
| M^1 | L | 1 . | 2.5 | | | | |
| | W | 1 | 3.5 | | | | |
| M^3 | L | 1 | 2.5 | | | | |
| M | w | 1 | 3.6 | | | | • |
| Mandibular d | entition | | | | | | |
| P_3 | L | 1 | 1.7 | | | | |
| 13, | w | 1 | 1.3 | | | | |
| | L | 2 | 1.9-2.2 | 2.05 | | | |
| P ₄ | w | 2 | 1.7-1.9 | 1.80 | | · . | |
| ., | L | 4 | 2.2-2.5 | 2.35 | 0.13 | 5.5 | |
| M_1 | w | 4 | 2.0-2.4 | 2.20 | 0.18 | 8.3 | |
| | L | 7 | 2.3-2.6 | 2.49 | 0.14 | 5.4 | |
| M_2 | W | 7 | 2.2-2.6 | 2.41 | 0.14 | 5.6 | |
| | L | 4 | 3.4-3.7 | 3.55 | 0.13 | 3.6 | |
| M ₃ | \mathbf{w} | 4 | 2.1-2.3 | 2.20 | 0.82 | 3.7 | |
| Plesiadapis praecursor | • | | | | | | |
| Maxillary den | tition | | | | | | |
| P^3 | L | 1 | 2.2 | | | | |
| | W | 1 | 3.0* | | | | |
| \mathbf{P}^4 | L L | 1 | 2.2 | | | | |
| P. | W | 1 | 3.7* | | | | |
| 2.41 | L | 1 | 2.7 | | | | |
| M^1 | W | 1 | 4.4* | | | | |

TABLE 4 cont.

| Tooth p | Tooth position | | OR | x | SD | CV | |
|----------------|----------------|---|---------|------|----|----|--|
| Mandibular d | | | | | | | |
| \mathbf{P}_3 | L | 2 | 2.1-2.2 | 2.15 | | | |
| * 3 | W | 2 | 1.7-1.8 | 1.75 | | | |
| _ | L | 1 | 2.1 | | | | |
| P ₄ | W | 1 | 2.3 | | | | |
| M | L | 2 | 2.6-2.7 | 2.65 | | | |
| M ₁ | w | 2 | 2.6 | 2.60 | | | |
| M | L | 1 | 2.9 | | | | |
| M_2 | w | 1 | 2.9 | | | | |
| M | L | 1 | 3.8 | | | | |
| M_3 | w | 1 | 2.5 | | | | |

^{*} Estimated

Description and discussion.—Four specimens of Plesiadapis praecursor, including the holotype, are known from Douglass Quarry. Ples. praecursor differs from contemporary early Tiffanian Nannodectes intermedius and late Torrejonian Pronothodectes jepi in being larger (Figure 13) and in having a reduced lower dental formula (1.0.3.3), lacking both I_2 and the canine. In addition to the type occurrence, Ples. praecursor is known from Keefer Hill (Gazin, 1971), where it is also associated with N. intermedius.

Measurements.—Measurements of the cheek teeth of Plesiadapis praecursor from Douglass Quarry are compared with those of Nannodectes intermedius in Table 4.

Order CONDYLARTHRA Cope, 1881 Family HYOPSODONTIDAE Lydekker, 1889 Genus Litomylus Simpson, 1935 Litomylus dissentaneus Simpson, 1935 Figure 14

Referred specimens.—PU 23588 (RM₂), PU 23589 (RM₃).

Description and discussion.—The two isolated molars referred here, although slightly larger than the small sample described by Simpson (1937b) from the type locality (Gidley Quarry), fall within the size range of a much larger sample from Swain Quarry (Rigby, 1980). Van Valen (1978) synonymized the Tiffanian forms L. scaphicus and L. scaphiscus from Bison Basin with L. dissentaneus, although Rigby (1980) questionably retained L. scaphicus as separate.

Measurements.—PU 23588: $M_2 = 3.5 \times 2.8$; PU 23589: $M_3 = 3.6 \times 2.5$.

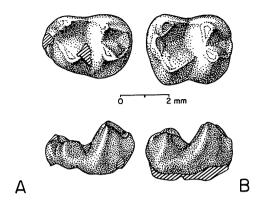


FIG. 14 — Litomylus dissentaneus from Douglass Quarry. A, occlusal view above and labial view below of PU 23589, RM₁, B, occlusal view above and labial view below of PU 23588, RM₂.

Family PHENACODONTIDAE Cope, 1881 Genus Ectocion Cope, 1882 Ectocion collinus Russell, 1929 Figures 15, 16

Referred specimens.—PU 14603 (R dentary with P_4M_{1-3}), PU 14604 (L maxilla with P^{3-4} M^{1-2}), PU 14605 (R dentary with M_{1-2}), PU 14606 (R dentary with M_{1-3}), PU 14607 (R dentary with M_{2-3}), PU 14608 (R dentary with P_4M_{1-2}), PU 14609 (R dentary with M_{1-2}), PU 14610 (R maxilla with M^{1-3}), PU 14611 (L maxilla with P^4M^{1-2}), PU 20417 (Rd P_4 and L M_3), PU 20418 (R $M^{1 \text{ or } 2}$), PU 20919 (L P_4), PU 20420 (L M_1), PU 20421 (R M_2), PU 20422 (R M^3), PU 20423 (two L M_1 s, one R M_1 , two L M_2 s, and three R M_2 s), PU 20424 (R $M^{1 \text{ or } 2}$), PU 20425 (L $M^{1 \text{ or } 2}$), R $M^{1 \text{ or } 2}$), PU 20426 (Ld P_4), PU 20427 (R $M^{1 \text{ or } 2}$), PU 20428 (R P_4 , Ld P^4), PU 20429 (L P^3 , L P^4), PU 20430 (R P_4 , L M^3), PU 20431 (R $M^{1 \text{ or } 2}$), PU 20432 (L $M^{1 \text{ or } 2}$ and fragments of upper Ps and Ms), PU 20433 (three L M^3 s, one R $M^{1 \text{ or } 2}$), and one R M^3), PU 20434 (L $M^{1 \text{ or } 2}$, R $M^{1 \text{ or } 2}$), PU 20435 (two L $M^{1 \text{ or } 2}$), UM 80706 (L P^3), UM 80827 (Ld P_4 , L M_3 , R P^2 , Ld P^3 , R P^4 , and tooth fragments).

Description and discussion.—The Douglass Quarry sample of Ectocion collinus is the largest and most representative sample of early Tiffanian Ectocion known to date. Species of Ectocion differ from those of earlier, probably ancestral Tetraclaenodon and from most contemporary species of Phenacodus in being smaller and in having more lophodont cheek teeth (Figure 15). Lower molars of Ectocion usually lack a distinct paraconid. There is a distinct mesostyle on the upper molars of Ectocion, and conules are less prominent than in Tetraclaenodon. Ectocion collinus is the oldest species of Ectocion known and it differs from later Ectocion, resembling species of Tetraclaenodon and Phenacodus, in having paracristids on the lower molars that curve medially and then posteriorly to join the metaconid. Ectocion collinus also differs from later species of Ectocion in having less molarized premolars (West, 1976), although some individual specimens of E. collinus from Douglass Quarry (e.g., PU 14611) approach E. wyomingensis and later species in this regard.

Douglass Quarry specimens of *Ectocion* are conservatively referred to *E. collinus* because this is the first early Tiffanian species of the genus to have been named, and because there is as yet no evidence to indicate that more than a single species representing a single lineage of *Ectocion* existed in the Western Interior during the early Tiffanian. The holotype of *E. collinus* (UA 118) is

an isolated right M³ from the early Tiffanian locality Cochrane I in southern Alberta (Russell, 1929; Gingerich, 1982a). It measures 5.9 mm in length and 8.7 mm in width. The holotype of E. collinus is significantly larger than any M³ of Ectocion known from Douglass Quarry (Figure 17, compare also measurements in Table 5) but we do not feel, in view of the small samples known at present and the great variability of third molars, that evidence is sufficient to indicate the existence of two early Tiffanian species or lineages. If additional specimens of Ectocion collinus from Cochrane I are found indicating that this species differs in other more important characteristics from the Douglass Quarry sample of Ectocion described here, then two species will have to be recognized. "Gidlevina" montanensis (Gidlev), here regarded as a synonym of Ectocion collinus, is based on a single specimen from beds underlying Douglass Quarry. It could be used as the species name for Douglass Quarry Ectocion if E. collinus proves to be inappropriate. The type specimen of E. montanensis is similar to specimens of Ectocion from Douglass Quarry (compare Figures 15 and 16 - see also Figure 17). The holotype of "Gidleyina" silberlingi also comes from early Tiffanian Tongue River beds in the vicinity of Douglass Quarry (Figure 2), and we regard this species as a junior synonym of both E. collinus and E. montanensis (Figure 17).

In reviewing the Phenacodontidae, West (1976, p. 47) synonymized "Tetraclaenodon" superior Simpson (1935) with Ectocion montanensis, but this species is larger and from Locality 11 or 13 at a much higher stratigraphic level than E. montanensis (Figure 2). Ectocion superior is more likely to be conspecific with E. wyomingensis Gazin (1956) than it is with E. collinus or E. montanensis.

Measurements.—See Table 5.

Genus Phenacodus Cope, 1873 Phenacodus bisonensis Gazin, 1956 Figure 18

Referred specimens.—PU 14633 (RM^{1 or 2}) and PU 14634 (19 isolated teeth: two LP₄s, one RP₄, two LM₁s, one RM₁, three LM₂s, one LM₃, two RM₃s, one RdP⁴, two RP⁴s, three LM^{1 or 2}, and two RM^{1 or 2}).

Description and discussion.—The Douglass Quarry sample of Phenacodus bisonensis is small, including a total of 20 isolated teeth representing a minimum of three individuals. Species of Phenacodus generally differ from those of earlier, probably ancestral Tetraclaenodon and from contemporary Ectocion in being larger (Figure 17) and in having more inflated cusps on the upper and lower cheek teeth. Upper molars usually have prominent parastyles and mesostyles. Phenacodus bisonensis is the oldest species of Phenacodus known. It resembles Tetraclaenodon puercensis and differs from later Phenacodus in having a less well developed metacone on P⁴ and in having a relatively narrower P₄ with a less open trigonid.

Gazin (1956) originally proposed the name *Phenacodus bisonensis* for specimens from the early Tiffanian Saddle locality in the Bison Basin, Wyoming, and this remains the only available species name for early Tiffanian *Phenacodus*. As shown in Figure 17, upper molars in the holotype maxilla of *P. bisonensis* agree well in size, as they do in form, with those in the Douglass Quarry sample.

Measurements.—See Table 6.

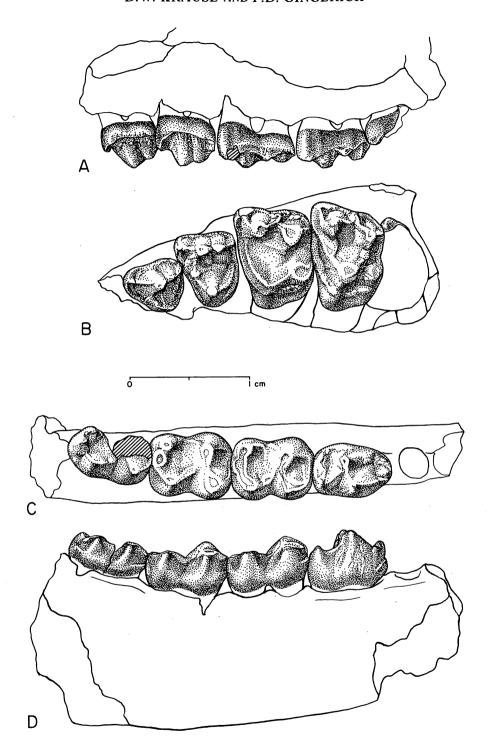


FIG. 15 — *Ectocion collinus* from Douglass Quarry. (A) Labial and (B) occlusal views of PU 14604, left maxilla with $P^{3-4}M^{1-2}$. (C) Occlusal and (D) labial views of PU 14603, right dentary with P_4M_{1-3} .

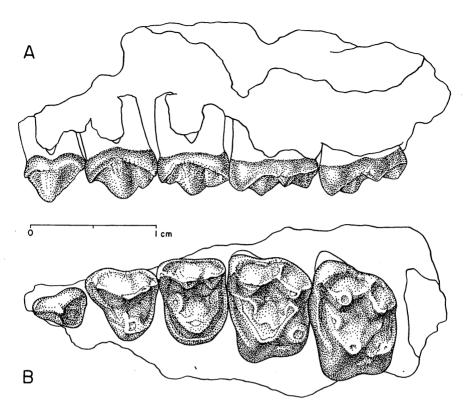


FIG. 16 — Holotype of *Ectocion* "montanensis" from Locality 68, eastern Crazy Mountain Basin, Montana. (A) Labial and (B) occlusal view of PU 12048, left maxilla with P²⁻⁴M¹⁻². Note that P², which is absent from previous illustrations of the holotype, has been added.

Family ARCTOCYONIDAE Murray, 1866

The arctocyonids from Douglass Quarry are a particularly difficult group. Most of the species are represented by only one or a few specimens, most of which are isolated teeth. As Rose (1981, p. 147) wrote in discussing Rock Bench Quarry arctocyonids: "Size and morphology are highly variable, and there is considerable intergradation, making consistent separation by size and structure exceedingly difficult."

Genus Claenodon Scott, 1892 Claenodon cf. montanensis (Gidley, 1919) Figure 19A, B

Referred specimen.—PU 14621 (L dentary with P₂₋₄M₁₋₃).

Description.— PU 14621 is a nearly complete left dentary that retains all of the cheek teeth except P_1 . P_1 was single-rooted and separated from P_2 by a small gap. P_{2-4} are tall, pointed teeth,

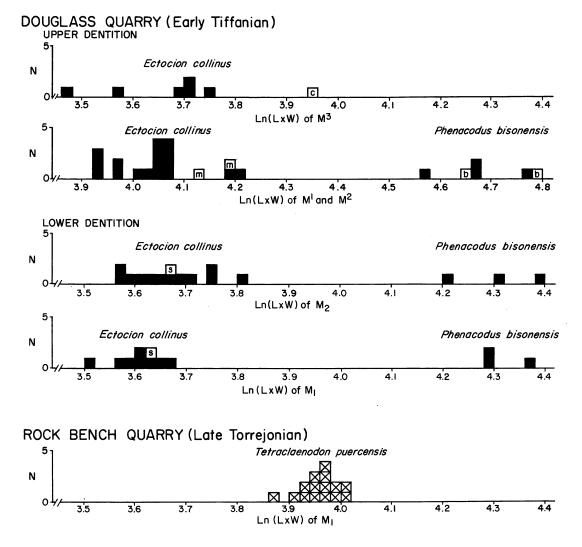


FIG. 17 — Comparison of tooth size distributions of late Torrejonian Rock Bench Quarry and early Tiffanian Douglass Quarry Phenacodontidae. Above, Ectocion collinus and Phenacodus bisonensis from Douglass Quarry (c, m, b, and s refer to the type specimens of Ectocion collinus, Ectocion montanensis, Phenacodus bisonensis, and "Gidleyina" silberlingi, respectively).

each with a small heel. The talonid on P_2 bears a single cusp; on P_{3-4} three distinct talonid cusps can be discerned (probably only because they exhibit very little wear), the middle one of which is largest and tallest. The crest that descends anteriorly and posteriorly from the apex of the protoconid becomes increasingly pronounced and papillate from P_2 to P_4 . Similarly, an ectocingulid becomes increasingly expressed from P_2 to P_4 . On P_4 the ectocingulid is well-developed and continuous from the heel to the anterior margin of the tooth, where it rises to a cusp-like eminence, and then continues for a short distance onto the lingual side of the crown.

Ectocingulids are also well-developed on M_{1-3} , particularly on M_2 . The trigonid of M_1 is considerably narrower than the talonid. On M_2 the trigonid is only slightly narrower than the talonid and, on M_3 , the reverse situation obtains. The paraconid is distinct only on M_1 , which has

TABLE 5 — Statistical summary of dental variation in earliest Tiffanian *Ectocion collinus* from Douglass Quarry, Crazy Mountain Basin, Montana. Isolated M¹ and M² cannot be distinguished consistently and the statistics given are based only on teeth in maxillae. Abbreviations as in Table 2. All measurements are in mm.

| Tooth 1 | osition | N | OR | x | SD | CV |
|----------------|---------|------------|---------|------|------|-------|
| Maxillary den | | | | | | - |
| dP^3 | L | 1 | 5.8 | | | |
| | W | 1 | 3.5 | | | |
| dP⁴ | L | 1 | 6.1 | | | |
| u. | w | 1 | 6.0 | | | |
| P^2 | L | 1 | 4.4 | | | |
| r | w | 1 | 2.4 | | | |
| P^3 | L | 3 | 5.5-6.0 | 5.77 | 0.46 | 8.0 |
| r | w | 3 . | 4.6-6.3 | 5.40 | 0.85 | 15.8 |
| P⁴ | L | 4 | 5.3-6.3 | 5.78 | 0.41 | . 7.1 |
| . P | w | 4 | 6.4-7.2 | 6.88 | 0.40 | 5.7 |
| \mathbf{M}^1 | L | 3 | 6.4-6.9 | 6.60 | 0.27 | 4.0 |
| IVI | w | 3 | 8.4-9.0 | 8.80 | 0.35 | 3.9 |
| M^2 | L | 2 | 6.1-6.6 | 6.35 | 0.35 | 5.6 |
| M | w | 2 | 8.8-9.4 | 9.10 | 0.42 | 4.7 |
| 1 | L | 7 | 5.2-5.6 | 5.40 | 0.14 | 2.6 |
| M ³ | w | 6 | 6.2-7.7 | 7.17 | 0.59 | 8.3 |
| Mandibular d | | | | | | · |
| dP₄ | L | 3 | 6.8-7.2 | 6.97 | 0.21 | 3.0 |
| | W | 3 | 4.2-5.0 | 4.60 | 0.40 | 8.7 |
| P_4 | L | 4 | 6.3-6.6 | 6.43 | 0.15 | 2.3 |
| 1 4 | w | 4 | 4.3-4.8 | 4.60 | 0.22 | 4.7 |
| M_1 | L | 9 | 6.2-7.0 | 6.67 | 0.22 | 3.4 |
| 1411 | w | 8 | 5.3-5.7 | 5.54 | 0.15 | 2.7 |
| M | L | 12 | 6.5-7.3 | 6.86 | 0.26 | 3.8 |
| M_2 | w | 12 | 5.1-6.2 | 5.68 | 0.29 | 5.0 |
| 14 | L | 5 | 6.9-7.8 | 7.36 | 0.38 | 5.1 ' |
| M ₃ | w | 5 | 4.6-5.6 | 4.92 | 0.40 | 8.1 |

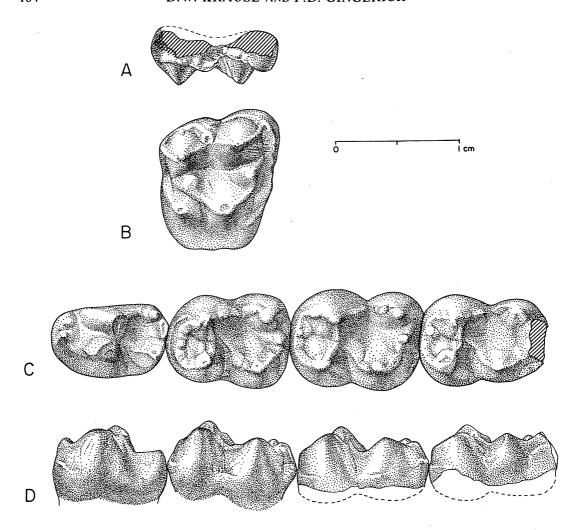


FIG. 18 — Phenacodus bisonensis from Douglass Quarry. (A) Labial and (B) occlusal views of PU 14633, RM^{1 or 2}. (C) Occlusal and (D) labial views of PU 14634, non-associated P₄ (left) to M₃ (right).

an anteroposteriorly expanded trigonid. The enamel is wrinkled on all of the cheek teeth preserved, but particularly so on the molars.

Discussion.—Van Valen (1978) made a number of new taxonomic assignments within the Arctocyoninae but his reasons for doing so have yet to be substantiated. Pending publication of an expanded version of Van Valen's telegraphic revision, PU 14621 is tentatively and conservatively referred to Claenodon cf. montanensis (Van Valen proposed that this species be transferred to the European genus Arctocyonides). C. montanensis is elsewhere known from Gidley Quarry in the Crazy Mountain Basin (Gidley, 1919; Simpson, 1937b) and probably also from the Saddle locality in the Bison Basin (Gazin, 1956) and Rock Bench Quarry in the Bighorn Basin (Van Valen, 1978; but see Rose, 1981a). PU 14621 is slightly larger than the few described specimens of C. montanensis but it is clearly smaller than C. ferox (M₂ length = 11.5-13.9, n=18; see Simpson, 1937b), which is known from a much larger sample.

| TABLE 6 — Statistical summary of dental variation in earliest Tiffanian Phenacodus bisonensis from Douglass |
|--|
| Quarry, Crazy Mountain Basin, Montana. Isolated M ¹ and M ² cannot be distinguished consistently and |
| both are combined here. Abbreviations as in Table 2. All measurements in mm. |

| Tooth position | | N | OR | $\bar{\mathbf{x}}$ | · SD | CV |
|-----------------|-----------|---|-----------|--------------------|------|-----|
| Maxillary den | tition | | | | | |
| dP⁴ | L | 1 | 9.4 | | | |
| dР | w | 1 | 8.4 | | | |
| ₽⁴ | L | 2 | 9.1-9.2 | 9.15 | | |
| P. | w | 2 | 9.4-9.7 | 9.55 | | |
| M^1 and M^2 | L | 4 | 8.9-10.2 | 9.43 | 0.56 | 5.9 |
| | w | 4 | 10.7-11.6 | 11.25 | 0.40 | 3.6 |
| Mandibular d | lentition | | | | | |
| | L | 3 | 8.9-9.2 | 9.07 | 0.15 | 1.7 |
| P_4 | w | 3 | 5.8-6.3 | 6.00 | 0.27 | 4.4 |
| | L | 3 | 9.5 | 9.50 | | |
| M_1 | w | 3 | 7.6-8.3 | 7.87 | 0.38 | 4.8 |
| | L | 3 | 9.2-10.2 | 9.67 | 0.50 | 5.2 |
| M_2 | w | 3 | 7.3-7.9 | 7.63 | 0.31 | 4.0 |
| | L | 2 | 9.3-10.7 | 10.00 | 0.99 | 9.9 |
| M_3 | W | 3 | 6.6-7.4 | 7.10 | 0.44 | 6.1 |

Gidley (1919) noted, as part of the diagnosis of C. montanensis, that P_3 and P_4 have "small, narrow, single-cusped heels." As described above, three cusps can be discerned on the heels of P_3 and P_4 on PU 14621 but the middle one is much the larger and it seems likely that the lingual and labial ones would become indistinct with even the slightest wear.

Measurements.—PU 14621: $P_2 = 6.1 \times 3.0$, $P_3 = 8.5 \times 4.8$, $P_4 = 10.1 \times 6.3$, $M_1 = 9.5 \times 8.1$, $M_2 = 10.6 \times 8.6$, $M_3 = 10.8 \times 7.0$.

Claenodon? sp. Figure 19C, D

Referred specimen.—UM 80825 (R upper canine).

Description and discussion.—UM 80825 is an isolated right upper canine that is clearly too large to belong to the same taxon as PU 14621, here referred to Claenodon cf. montanensis (see above). Although most of the crown is devoid of enamel, the tooth is provisionally assigned to Claenodon because of the presence of serrations along its posterior edge.

Measurements.—UM 80825 measures 57.5 mm from apex of crown to end of root.

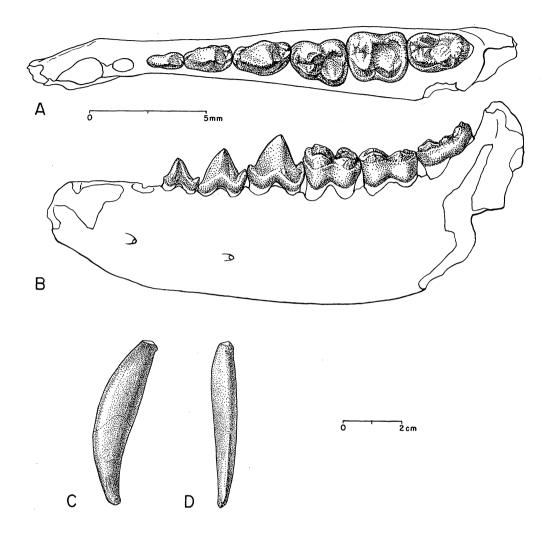


FIG. 19 — Large arctocyonids from Douglass Quarry. (A) Occlusal and (B) labial views of Claenodon cf. montanensis, PU 14621, left dentary with P₂₋₄M₁₋₃. (C) Lingual and (D) posterior views of Claenodon? sp., UM 80825, right C¹.

Genus Mimotricentes Simpson, 1937 Mimotricentes fremontensis Gazin, 1956 Figure 20A, B

Referred specimens.—PU 23590 (LM₂), PU 23591 (RM₂), PU 23592 (LM₃), PU 23593 (LM₃). Description and discussion.—Four isolated lower molars, two M₂s and two M₃s, are here allocated to Mimotricentes fremontensis. Although M. fremontensis and M. subtrigonus posterior lower molars are apparently very similar, those of M. fremontensis have a lower and weaker paraconid (Gazin, 1956); the Douglass Quarry specimens conform to the latter in this regard. M. fremontensis is also known from the Saddle, Ledge, and West End localities in Bison

Basin (Gazin, 1956; Gingerich, 1979) and from Cedar Point Quarry in the Bighorn Basin (Van Valen, 1978; Gingerich, 1979).

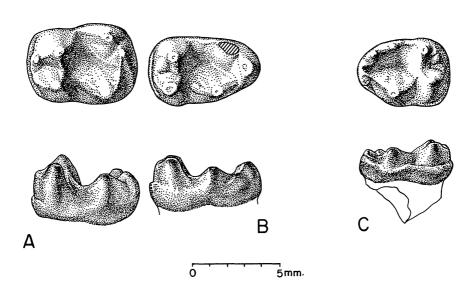


FIG. 20 — Mimotricentes fremontensis and Thryptacodon cf. demari from Douglass Quarry. Occlusal views above and labial views below for each tooth. (A) PU 23590, LM₂, and (B) PU 23592, LM₃, of Mimotricentes fremontensis. (C) PU 23604, RM₃, of Thryptacodon demari.

Although all four lower molars from Douglass Quarry referred to *M. fremontensis* are smaller than in the type specimen (USNM 20582) from Saddle, Gazin (1956) stated that the type "is a comparatively large individual."

Measurements.—PU 23590: $M_2 = 6.0 \times 4.6$; PU 23591: $M_2 = 6.1 \times 4.4$; PU 23592: $M_3 = 6.1 \times 3.7$; PU 23593: $M_3 = 6.1 \times 3.8$.

Genus Thryptacodon Matthew, 1915 Thryptacodon cf. demari Gazin, 1956 Figure 20C

Referred specimens.—PU 23603 (RM₃) and PU 23604 (RM₃).

Description and discussion.—The two M₃s referred here are short and broad, and have low, rounded cusps. The protoconid and metaconid are subequal in size and height but the paraconid is reduced to a vestige situated anterolabial to the metaconid. An ectocingulid extends from the anterior margin of the crown to the anterolabial base of the hypoconid to near the apex of the hypoconulid, where it terminates in a small, accessory cuspule. The hypoconid is the most massive of the talonid cusps. From it a crest extends posterolingually to the anterior base of the hypoconulid where it is met by a shorter crest descending posterolabially from the entoconid. The hypoconulid, about the same size as the entoconid, is much lower and projects posteriorly. An entoconulid is developed on PU 23603 but is indistinct on PU 23604.

PU 23603 and PU 23604 are tentatively referred to *Thryptacodon* on the basis of their occlusal outline, the configuration of the hypoconulid, and the position of the paraconid, which, although situated relatively labially, is not as far labial as in most other *Thryptacodon*. However, several workers have noted the variable form of *Thryptacodon* M₃s and, until better material is discovered, it seems best to refer the Douglass Quarry specimens to that genus. The specimens compare closely in size to Gazin's (1956) *T. belli*, which Van Valen (1978) placed in synonomy with *T. demari*.

Measurements.—PU 23603: $M_3 = 5.2 \times 4.2$; PU 23604: $M_3 = 5.2 \times 3.9$.

Genus Chriacus Cope, 1883 Chriacus pelvidens (Cope, 1881) Figure 21A, B

Referred specimens.—PU 23600 (LM¹) and PU 23601 (LM³).

Description and discussion.—PU 23600 (M¹) is very similar to M¹s assigned here to Chriacus sp. except that it is much larger, the parastylar area is not expanded into a wedge-shaped process, the hypocone is situated further lingually, and the cingulum is incomplete lingual to the protocone. PU 23600 closely resembles M¹s from Little Muddy Creek that Gazin (1969) assigned to Chriacus, cf. pelvidens except that it is slightly smaller. It does, however, fall within the range of M¹ sizes of C. pelvidens in the larger sample from Swain Quarry (Rigby, 1980).

PU 23601 (M^3) is questionably referred to C. pelvidens. It appears to be slightly too large to be associated with the M^1 (PU 23600) but, as Matthew (1897, p.273) noted, M^3 of C. pelvidens is not reduced. It is as wide as M^2 , which is considerably more transverse than M^1 . Also, by comparison with measurements of upper molars of C. pelvidens from Swain Quarry (Rigby, 1980), the size of PU 23601, although slightly longer, is not as transverse as the largest specimen from that locality.

Measurements.—PU 23600: $M^1 = 6.4 \times 7.2$; PU 23601: $M^3 = 5.6 \times 8.9$.

Chriacus orthogonius? Russell, 1929 Figure 21C

Referred specimen.—PU 23605 (LM¹).

Description and discussion.—PU 23605 is almost identical to UA 124, the type specimen of Chriacus orthogonius from Cochrane site II. Both are M²s and have the following features: rectangular occlusal outline, paracone and metacone subequal in size and height, conules well-developed but metaconule larger than paraconule, hypocone distinct and situated posterolingual to protocone, and cingulum developed around entire periphery of crown, including lingual to protocone. The most notable differences from UA 124 is that PU 23605 is smaller (UA 124 measures 5.0 x 7.0) and has a slightly more invaginated ectoflexus. Until a larger sample is discovered from Douglass Quarry, PU 23605 can be only questionably referred to C. orthogonius.

The taxonomic status of *C. orthogonius* is currently in question. Van Valen (1978) placed *Metachriacus punitor* into synonymy with *C. orthogonius*, thus extending the known distribution of the species to Gidley, Silberling, and Rock Bench quarries. Rose (1981a), however, retained *M. punitor* in *Tricentes*, which Van Valen (1978) regarded as a junior synonym of *Chriacus*.

Measurements.—PU 23605: $M^1 = 4.2 \times 6.0$.

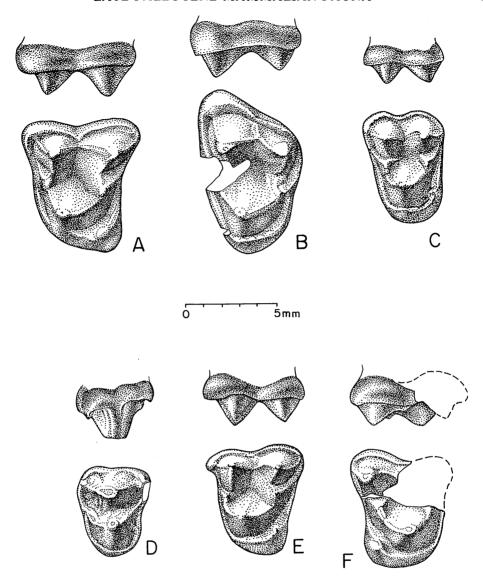


FIG. 21 — Chriacus from Douglass Quarry. Labial views above and occlusal views below for each tooth. (A) PU 23600, LM¹, and (B) PU 23601, LM³, of C. pelvidens. (C) PU 23605, LM¹, of C. orthogonius?. (D) PU 23599, RP⁴, (E) PU 23595, LM¹, and (F) PU 23598, RM², of Chriacus sp.

Chriacus sp. Figure 21D-F

Referred specimens.—PU 23594 (LM¹), PU 23595 (LM¹), PU 23596 (fragmentary LM¹), PU 23597 (fragmentary RM¹), PU 23598 (fragmentary RM²), and PU 23599 (RP⁴).

Description.—The crown of P⁴ is dominated by two major cusps: a large paracone labially and a smaller and lower protocone lingually. An indistinct separation suggests that a rudimentary metacone is closely appressed to the paracone. A small metaconule is developed but there is no

trace of a paraconule. The preprotocrista is strong; the postprotocrista is absent. A cingulum is developed to variable degrees around the entire periphery of the crown. The enamel on the sides of the major cusps is wrinkled.

The paracone and metacone of M^1 are subequal in size and height and the centrocrista between them is strong. Both conules are well-developed with strong conule cristae but the metaconule is the larger. The trigon cusps, the centrocrista, the conules, and the well-developed protocristae enclose a deep and broad trigon basin. The hypocone is distinct and about as large as the metaconule; it is situated posterior and slightly lingual to the protocone. A cingulum extends around the crown, including the margin lingual to the protocone. The parastylar area is prominent and extends as a wedge on the anterolabial corner of the crown. The enamel is wrinkled but not as much as on the single, referred P^4 .

The only M^2 preserved (PU 23598) is missing the anterolabial part of the crown. The area that remains closely resembles M^1 except that the tooth is larger and was probably more transverse.

Discussion.—Although the specimens referred here represent a taxon that is clearly different from PU 23605, referred to Chriacus orthogonius? above, there are many similarities. The typodigm of Chriacus orthogonius consists of an isolated M² (UA 124) from Cochrane site II (Russell, 1929). As mentioned above, this is the only specimen that is unquestionably referrable to the species. PU 23598, the M² known from Douglass Quarry, is fragmentary but it is less transverse and much more tapered lingually than is the type specimen of C. orthogonius. The latter has nearly parallel anterior and posterior margins. If "Metachriacus" punitor is correctly syononymized with C. orthogonius, then additional differences are evident. AMNH 35665, a maxillary fragment of "M." punitor containing P⁴M¹⁻³ from Gidley Quarry, has much more transverse teeth than the Douglass Quarry form, as well as the presence of a metaconule on P⁴.

Measurements.—PU 23599: $P^4 = 4.1 \times 5.0$; PU 23594: $M^1 = 5.4 \times 6.0$; PU 23595: $M^1 = 5.6 \times 6.3$; PU 23598: $M^2 = 6.8$ mm wide.

Order CARNIVORA Bowdich, 1821
Family MIACIDAE Cope, 1880
Genus Protictis Matthew, 1937
Protictis sp.
Figure 22

Referred specimen.—PU 14642 (fragmentary RP⁴).

Description and discussion.—The only specimen of a true carnivore in the Douglass Quarry faunal sample is a broken right P⁴. It is most similar in crown length to Torrejonian specimens from Gidley and Silberling quarries that MacIntyre (1966) referred to Protictis (Bryanictis) microlestes, but differs in having a somewhat higher crown. The significance of this difference is not known. MacIntyre (1966, p. 189) reported P. (B.) microlestes from the earliest Tiffanian Keefer Hill locality in the Shotgun Member of the Fort Union Formation, central Wyoming, and this may well be the species represented at Douglass Quarry. In view of the fragmentary nature of the specimen at hand we are reluctant to attempt specific identification.

Measurements.—The only standard measurement that can be made accurately on PU 14642 is crown length, measured along the labial margin of the tooth. $P^4 = 4.9$ mm long.

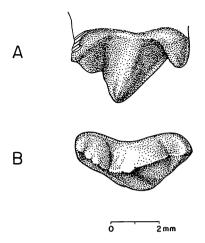


FIG. 22 — Protictis sp. (A) Labial and (B) occlusal views of PU 14642, fragmentary right P⁴.

Order PANTODONTA Cope, 1873 Family PANTOLAMBDIDAE Cope, 1883 *Titanoides* sp. Figure 23

Referred specimens.—PU 14617 (L dentary with P₁₋₂), PU 14618A (talonid of RM₃), and PU 14618B (L upper canine).

Description and discussion.—The best pantodont specimen from Douglass Quarry is PU 14617, a left dentary fragment preserving the posterior part of the canine alveolus and intact crowns of P_{1-2} . P_1 is single-rooted, with a high, narrow crown. The protoconid is a large, wedge-shaped cusp. A distinct paraconid cusp and a small metaconid crest are present as well. The talonid is very small and trenchant, with no distinct hypoconid. P_2 is a larger, double-rooted tooth with a relatively broader crown. The crown is trapezoidal in occlusal outline, with all cusps more strongly developed than on P_1 . A distinct paraconid lobe of the crown extends anteromedially, and the crown is widest at the base of the metaconid. The talonid on P_2 is small and trenchant, and there is a distinct hypoconid. An anterior mental foramen opens on the lingual surface of the mandible below P_1 . In addition, PU 14618A and B consist of the talonid of a right M_3 and partial crown of an upper canine (not associated). All of the Douglass Quarry pantodont specimens are similar in size, suggesting that a single species is represented.

The presence of a distinct paraconid and metaconid on P_1 and P_2 indicates a more advanced condition than is seen in *Pantolambda*. The coronal outline of P_1 and P_2 , the presence of a large notch anterior to the entoconid of M_3 , and the low crown height of all of the preserved cheek teeth indicate that these specimens are referable to *Titanoides*. The only primitive characteristic retained by the Douglass Quarry form that is lost in later *Titanoides* is the presence of a single-rooted P_1 . Simons (1960, pp. 36-37) questionably referred PU 14617 to *Titanoides zeuxis* but noted several differences. Until better specimens are recovered from Douglass Quarry, we prefer to not assign the known material to any particular species.

Measurements.—PU 14617: $P_1 = 12.1 \times 6.9$, $P_2 = 14.2 \times 10.3$. The talonid of M_3 in PU 14618A measures 11.8 mm in width.

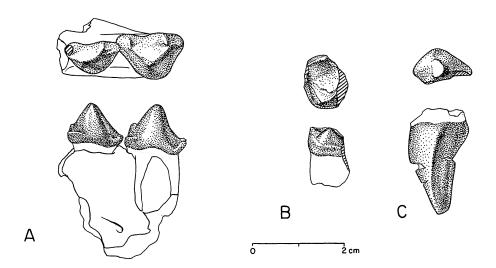


FIG. 23 — *Titanoides* sp. Occlusal views above and labial views below of (A) PU 14617, left dentary with P₁₋₂; (B) PU 14618A, talonid of right M₃; and (C) PU 14618B, left C¹.

AGE AND COMPOSITION OF THE DOUGLASS QUARRY LOCAL FAUNA

The Tiffanian Land-Mammal Age has been subdivided into a five-part sequence of lineage zones (abbreviated Ti₁ to Ti₅) based on the successive evolutionary stages of *Plesiadapis*. The Torrejonian (middle Paleocene) Land-Mammal Age consists of four zones (To₁ to To₄) based on the taxa Desmatoclaenus, Deltatherium, Pantolambda/Pronothodectes matthewi, and Pantolambda/ Pronothodectes jepi, respectively (Gingerich, 1976; Tomida and Butler, 1980; Lindsay et al., 1981). The composition of mammalian faunas of western North America during the Plesiadapis praecursor biochron, the earliest of the Tiffanian biochrons (Ti₁), is poorly known. Localities that have yielded mammalian faunas of probable earliest Tiffanian age include Cochrane sites I and II (L. S. Russell, 1929, 1932, 1958; D. E. Russell, 1967; Krause, 1978; Gingerich, 1982a), Keefer Hill (="Shotgun" fauna) (Keefer, 1961; McGrew and Patterson, 1962; Patterson and McGrew, 1962; Van Valen, 1966; D. E. Russell, 1967; Gazin, 1971; Holtzman and Wolberg, 1977), Little Muddy Creek (Gazin, 1969), and Bangtail (Gingerich et al., 1983). The faunas represented at these localities are either small (poorly sampled) or have been only partially described. Description of the mammalian fauna from Douglass Quarry is important because it provides additional characterization of a poorly known interval of Paleocene mammalian evolution.

The Douglass Quarry local fauna is assigned to Ti₁ because of the presence of *Plesiadapis* praecursor, Nannodectes intermedius, Ectocion collinus, and the new species of Ptilodus, all of which are restricted to that zone. In addition to forms restricted to zone Ti₁, the sample from Douglass Quarry provides the earliest records for several species that are known from later Tiffanian zones (Table 7). These include Neoplagiaulax hunteri, Bisonalveus browni, Paleotomus senior, and Phenacodus bisonensis. The remaining species charted in Table 7 (Anconodon cochranensis, Propalaeosinopa diluculi, Leptacodon munusculum, and Litomylus dissentaneus) are known from either before or after Ti₁.

TABLE 7 — The ranges of selected species from Douglass Quarry in the Torrejonian (To₁ to To₄) and Tiffanian (Ti₁ to Ti₅) Land-Mammal Ages of North America. Only species with definite identifications are included. Arctocyonids are excluded because their alpha taxonomy is in such disarray that meaningful ranges cannot be indicated.

| Species | Toı | To ₂ | To ₃ | To ₄ | Tiı | Ti ₂ | Ti ₃ | Ti ₄ | Ti ₅ |
|--------------------------------------|-----|-----------------|-----------------|-----------------|-----|-----------------|-----------------|-----------------|-----------------|
| Ptilodus, new species ¹ | | | | | x | | | | |
| Neoplagiaulax hunteri ^{1,2} | | | | | X | X | x | X | |
| Anconodon cochranensis³ | | | x | X | x | x | | | |
| Bisonalveus browni ¹ | | | | | x | x | | | |
| Propalaeosinopa diluculi | | | | x | x | x | x | | |
| Paleotomus senior ¹ | | | | | x | x | | | |
| Leptacodon munusculum ⁴ | | | x | x | x | | x | | |
| Nannodectes intermedius | | | | | x | | | | |
| Plesiadapis praecursor | | | | | x | | | | |
| Litomylus dissentaneus ¹ | | | X | X | x | X | X | | |
| Ectocion collinus | | | | | X | | | | |
| Phenacodus bisonensis¹ | | | | | X | X | X | | |

¹ Douglass Quarry record provides only reported occurrence from Ti₁.

Twenty-three species representing a minimum of 56 individuals have been recovered from Douglass Quarry. The phenacodontid condylarth *Ectocion collinus* is the most abundant mammal at Douglass Quarry (17.9% of individuals), followed by the new species of *Ptilodus* (12.5%). These are all medium to large-sized mammals for the Paleocene, a fact that may suggest a sampling bias against small mammals (all specimens have been recovered by quarrying) rather than actual relative abundances. This is also suggested by the high frequency of species that are represented by only five or fewer specimens (16 of 23 - see Table 1). Unfortunately, the resistant matrix at Douglass Quarry does not lend itself well to screen-washing and hence the smaller members of the fauna are not adequately represented, and possibly never will be.

At present, the Douglass Quarry fauna is much more similar in species richness to that of overlying Scarritt Quarry (16 species, 226 specimens; Rose, 1981a, inadvertently listed *Titanoides zeuxis* as coming from Scarritt Quarry, which is incorrect) than to that of underlying Gidley Quarry (57 species, 1027 specimens; Rose, 1981a). Rose (1981a, b) has hypothesized that the decreased species diversity and evenness of the middle Tiffanian mammalian fauna represented at Cedar Point Quarry was due to a period of gradual climatic cooling that extended from the late Torrejonian. If there was a gradual decline in species diversity owing to climatic change, then, based on the well-sampled late Torrejonian Gidley Quarry and Rock Bench Quarry (1,687 specimens, 57 species), and the middle Tiffanian Cedar Point Quarry (1,988)

² Possibly also from To₄ Swain Quarry (see Rigby, 1980).

³ Range includes probable junior synonym A. russelli. Ti₂ record from Saddle locality questionable (see Gazin, 1956).

⁴ To₄ record from Rock Bench Quarry questionable (see Rose, 1981a).

specimens, 38 species), one might expect intermediate diversities during the early Tiffanian, provided that the localities have been adequately sampled and are not strongly biased by other factors (e.g., markedly different depositional environments).

Douglass (Ti₁) and Scarritt (Ti₂) quarries have approximately half the species richness of Cedar Point Quarry (Ti₃). These low values are even more striking when compared with the much higher value represented at the middle Tiffanian (Ti₃) Brisbane locality (30 species represented by only 204 specimens, roughly the same number of specimens as at Douglass and Scarritt; see Holtzman, 1978). Douglass and Scarritt quarries may reflect a real decrease in faunal diversity during the early part of the Tiffanian, and hence a possible anomaly in relation to the general trend for climatic cooling, or the known samples from Douglass and Scarritt quarries may not accurately reflect true species diversities due to inadequate or biased sampling. It seems imperative, therefore, that larger collections of early Tiffanian mammals be obtained from Douglass Quarry, Scarritt Quarry, and elsewhere, to remove any inadequacies and biases of sampling. The result will be a clearer understanding of the evolution of faunal diversity across the Torrejonian-Tiffanian boundary.

ACKNOWLEDGEMENTS

We thank Dr. Donald Baird for loaning us the Princeton University collection of Douglass Quarry fossil mammals. Access to comparative material was provided by Drs. R. J. Emry (USNM), R. C. Fox (UA), and M. C. McKenna and M. J. Novacek (AMNH). Dr. Kenneth Rose, Johns Hopkins University, reviewed the manuscript and his comments have improved it greatly. We are indebted to Mr. and Mrs. William Donald Jr. and Mr. and Mrs. William Donald III of Melville, Montana, for access to Douglass Quarry. We are also very grateful to the Donalds, and to Mr. and Mrs. George Cremer and Mr. and Mrs. Lloyd Ford, also of Melville, for their hospitality during visits to the study area in 1978, 1980, and 1982. All of the illustrations in Figures 2 - 23 were drawn by Karen Klitz. William Ryan prepared the University of Michigan specimens, and George Junne assisted with photography. Support for this research was provided by the University Awards Program of the S.U.N.Y. Research Foundation, by EARTHWATCH and National Geographic Society grants to DWK and by National Science Foundation grant DEB 82-06242 to PDG.

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