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LATE PALEOCENE MAMMALS FROM NEAR DRAYTON VALLEY, ALBERTA

by

MICHAEL WILLIAM WEBB



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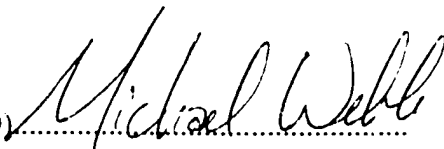
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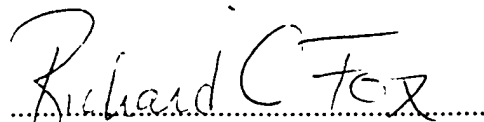
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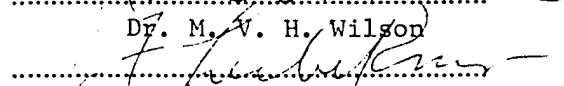
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The undersigned certify that they have read, and recommend to the Faculty of  
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## ABSTRACT

The Birchwood locality near Drayton Valley, Alberta bears sediments with fossil mammals of middle Tiffanian age. It is set within beds of the Paleocene Paskapoo Formation, which crop out along the banks of Modeste Creek. Mammalian fossils, mostly isolated teeth and rarer articulated dentulous dentary and maxillary fragments, were quarried at the site. The screen-washing of fossiliferous matrix was found to be relatively unproductive. The quarrying of the Birchwood locality undoubtedly led to the recovery of more nearly complete fossils than would have occurred through screen-washing. The Birchwood locality has yielded over 375 identified isolated teeth and incomplete jaws with teeth referable to 37 genera and 40 species in eight mammalian orders. These include multituberculates, lipotyphlans, "condylarths", and plesiadapiforms. Noteworthy members of the Birchwood Local Fauna include a new genus and species of arctocyonid condylarth, and new species of the plesiadapiform Saxonella, the pantolestid Bisonalveus, and the mixodectid Eudaemonema. Previously unrecorded teeth of Elpidophorus elegans, Protictis paralus, and Microcosmodon woodi are described. The Birchwood Local Fauna records the earliest known occurrences of the species Cyriacotherium sp., cf. C. argyreum and Neoplagiaulax sp., cf. N. hazeni. The latest occurrences of the genus Eudaemonema and the species Plesiolestes sp., cf. P. sirokyi, Chriacus sp., cf. C. pelvidens, Claenodon sp., cf. C. montanensis, Desmatoclaenus mearae, and Jepsenella sp., cf. J. praepropera are also recorded in the Birchwood Local Fauna. The strongest faunal resemblances of the Birchwood Local Fauna are with the temporally equivalent UADW-2 locality (Paskapoo Formation, Blindman River, Alberta). At over 53° North

latitude (approximately 5° further north in the Paleocene), the Birchwood locality is the most northerly middle Tiffanian, and the second most northerly Paleocene mammal locality in the world. The location of the site lends itself to extending the geographic ranges of many taxa, as well as to investigations regarding the distribution of Paleocene mammals.

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## I. INTRODUCTION

Fossil mammals from the Paskapoo Formation of Alberta have been studied by investigators for over 85 years. The famous fossil collector Barnum Brown is credited with collecting the first mammalian fossils from beds of the Paskapoo Formation along the Red Deer River in 1910 (Simpson, 1927; Fox, 1990a). More than 20 localities in the Paskapoo Formation, ranging in age from early to late Tiffanian, have yielded mammalian fossils (Fox, 1990a). This paper reports the results of my study of a new middle Tiffanian locality.

Discovered in 1990 by Danek Mozdzinski, an amateur paleontologist, the Birchwood locality was first worked by a UALVP field crew in the summer of 1991. During that first summer, G. P. Youzwysyn and K. L. Soehn collected fossils from four separate outcrops, subsequently dubbed the Pantocake, Rodeo, and Birchwood localities, and Danek's site. All of these quarries, within 500 m of each other, are located in cutbanks on Modeste Creek immediately downstream of its confluence with Bucklake Creek. Collecting efforts in 1993 by Youzwysyn and M. W. Webb focused on the Birchwood locality, which produced the most numerous well-preserved fossils. Except for isolated pantodont teeth and tooth fragments from the Rodeo and Pantocake localities, all fossils described and discussed here are from the Birchwood locality.



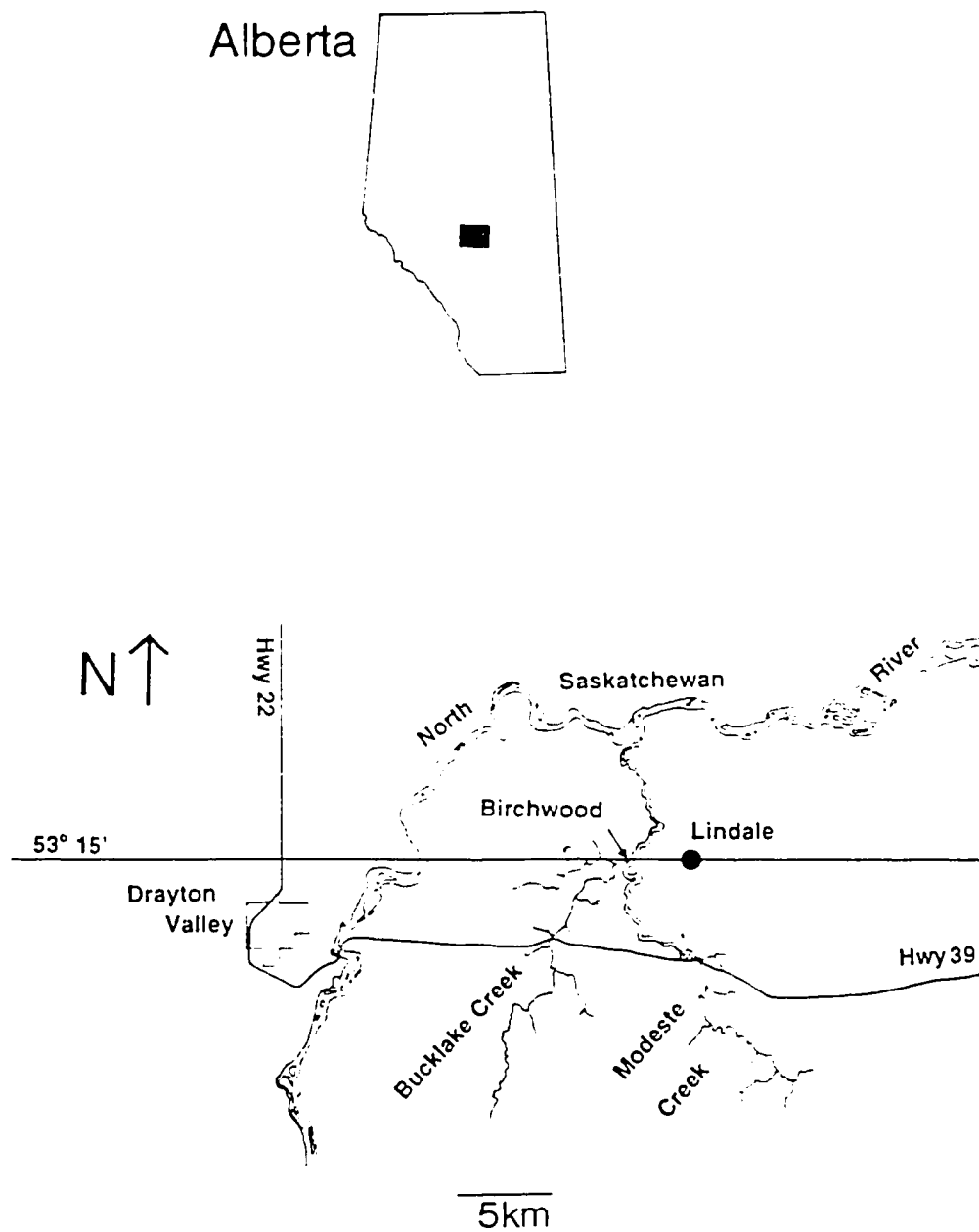
## II. GEOLOGICAL SETTING

### 1. LOCATION AND STRATIGRAPHY

The Paleocene Birchwood locality is located approximately 70 km southwest of Edmonton in central Alberta, Canada (see Text-fig. 1). It is located at NW¼ Sec.14, Tp.49, Rge.5 W5, in an outcrop of the Paskapoo Formation on the north side of Modeste Creek immediately downstream of its confluence with Bucklake Creek. At over 53° North latitude (approximately 5° further north in the Paleocene) the Birchwood locality is the second most northerly Paleocene mammal locality in the world.

The Paskapoo Series was described by J. B. Tyrrell (1887:135-138) as consisting of "...hard, light grey or yellowish, brown-weathering sandstone, usually thick-bedded, but often showing false bedding (crossbedding); also of light bluish-grey and olive sandy shales, often interstratified with bands of hard, lamellar ferruginous sandstone...". A recent diagnosis of the Paskapoo Formation notes its lithology as "interbedded hard to soft mudstone, siltstone and sandstone, with subordinate limestone, coal, pebble conglomerate and bentonite" (McLean, 1990). The Paskapoo was originally named after a series of outcrops along the Blindman and Red Deer river valleys. An exact type locality for the Paskapoo Formation was not recorded, and the type locality is thus a composite (Carrigy, 1970).

The Paskapoo Formation is situated within the Alberta Syncline, where it overlies the uppermost Cretaceous/lower Paleocene Scollard Formation, which is the



Text-fig. 1. Map showing the location of the Birchwood locality in Alberta. Upper outline of Alberta shows location of detailed map area (shaded).

uppermost unit of the Edmonton Group (Gibson, 1977). It has long been speculated that the Scollard/Paskapoo contact is unconformable (Allan and Sanderson, 1945), but this has only been proven in recent years. Lerbekmo et al. (1990, 1992, 1995) have shown the Scollard/Paskapoo contact to be unconformable at the Hand Hills and at several localities in the Red Deer River valley. The present erosional surface across most of the area of the Alberta Syncline is on the Paskapoo Formation; however, this unit is disconformably overlain at several isolated erosional remnants (such as the Hand Hills and Cypress Hills) by later Tertiary gravels (Soror, 1978; McLean, 1990). The Paskapoo Formation crops out along the eastern margin of the Rocky Mountain Foothills in central and southern Alberta. Its lateral equivalents include the Porcupine Hills and Ravenscrag formations in southwestern and southeastern Alberta, respectively.

Determining the stratigraphic position of the Birchwood locality has been facilitated by recent litho-, palyno-, bio-, and magnetostratigraphic zonations of the Paskapoo Formation. Although the Birchwood locality itself has not been included in these studies, its position can be inferred by correlation with other mammalian fossil localities of similar age and composition. Demchuk and Hills (1991) have proposed a threefold division of the Paskapoo Formation based solely on lithologic information retrieved from outcrops and drill cores. In ascending stratigraphical sequence these members are: a lower Haynes Member, an upper Lacombe Member and its partial lateral equivalent, the Dalehurst Member (Demchuk and Hills, 1991). The Birchwood locality, as well as other middle and late Tiffanian mammal localities in Alberta, is

located within the Lacombe Member, which is characterized by "interbedded siltstone, mudstone, shale and coal with subordinate sandstone and conglomerate" (Demchuk and Hills, 1991:275). The mammalian paleofaunas found within the Lacombe Member are middle (Ti3) to late (Ti4) Tiffanian in age, while those in the coarser-grained, sandstone-dominated Haynes Member suggest an early (Ti2) Tiffanian age; mammalian paleofaunas are unknown from the coal-bearing Dalehurst Member of the Alberta Foothills (Demchuk and Hills, 1991).

Demchuk (1987, 1990) has zoned the Paskapoo Formation into three formal biostratigraphic zones using lineages of Juglandaceous (walnut family) angiosperm pollens. Samples from the middle Tiffanian Joffre Bridge, Blindman, Burbank, and Delburne mammal localities contain pollens that define the Caryapollenites wodehousei Zone, equivalent to the P4 Zone of Nichols and Ott (1978). Correlating the Birchwood locality with the above middle Tiffanian mammal localities would also place it within the Caryapollenites wodehousei Zone. Due to faunal similarities between the Birchwood locality and the UADW-2 locality (Blindman River, Paskapoo Formation) (see below; Table 16) of Fox (1990a), I believe that they are nearly contemporaneous, and are within the lower portion of the P4 Zone (see Lerbekmo et al., 1992:fig. 8). The P4 Zone is contained within the lithological boundaries of the Lacombe Member of the Paskapoo Formation (Demchuk and Hills, 1991).

The biostratigraphical zonation of Paleocene sediments using fossil mammals has yielded intervals of finer resolution than those recognized using either litho- or palynostratigraphy. Generally following the plesiadapid primate zonations proposed by

Gingerich (1975, 1976), Krause (1978) and Fox (1990a) have been instrumental in zoning the Paleocene sediments of Alberta. Fox (1990a) has published the most recent review of mammal localities within the Paskapoo Formation, placing them in biochronological order and correlating them solely on the basis of their fossils. The Birchwood locality contains fossils of the plesiadapid primate Plesiadapis rex, which is the index fossil for the Plesiadapis rex - Plesiadapis churchilli lineage zone. This lineage zone defines the late Paleocene, middle Tiffanian (Ti3) North American Land Mammal Age (NALMA).

Lerbekmo et al. (1992) were the first to integrate magnetostratigraphic data with that provided by palyno- and biostratigraphy for Paleocene North American sediments. Strata bearing both pollens of the P4 Zone and mammals of the middle Tiffanian (Ti3) North American Land Mammal Age are within the 26r polarity chron (Lerbekmo et al., 1992:fig. 8). The results of Lerbekmo et al. (1992) accord well with integrations of bio- and magnetostratigraphic data from localities in New Mexico, Wyoming, and Montana conducted by Butler et al. (1987). It should be noted, however, that quarries bearing mammals of earliest and early Tiffanian age (Ti1 and Ti2, respectively) are also contained within the 26r polarity chron. As the Birchwood locality shows greatest faunal similarities with the UADW-2 locality (see below; Table 16), it is approximately the same age, and should also be within the upper portion of the 26r polarity chron.

In summary, indirect evidence suggests that the Birchwood locality is located within the Lacombe Member of the Paskapoo Formation, the Caryapollenites

wodehousei palynofloral zone, and the 26r polarity chron. The only direct source of information for the stratigraphic setting of the locality is its mammalian fauna; however, mammalian faunas have been used by many authors (see Archibald et al., 1987 and references within) to delimit various types of stratigraphic units with a high degree of accuracy. The presence of the plesiadapid primate Plesiadapis rex within the Birchwood Local Fauna, coupled with the above indirect evidence, strongly supports a middle Tiffanian (Ti3) age for the Birchwood locality.

## 2. SEDIMENTOLOGY

The fossil-bearing stratum at the Birchwood locality is approximately 30 cm thick and laterally discontinuous, bracketed by a greenish mudstone below and a shaly sandstone above. The fossiliferous layer is a blend of numerous lenses of poorly consolidated mudclast conglomerate, coarse and fine sandstone, and mudstone. Rounded mudclasts up to 3 cm in diameter comprise nearly 50 percent of the basal part of the unit; these mudclasts decrease in number and size upwards. In the upper portion of the unit, the isolated lenses merge and become more laterally continuous, and sand becomes more common. The unit grades upward into the overlying shaly sandstone. The fossiliferous layer is fully exposed, semi-prominent, and can be split by hand.

The upper contact of the fossiliferous unit is horizontal and gradational over a distance of 10 cm into an argillaceous, poorly consolidated sandstone with horizontal bands of iron oxide stains. This brownish-grey upper sandstone unit is approximately 5 m thick, and comprised of poorly sorted subangular to angular sand grains. Individual horizontal laminae, from 0.3 to 1.0 cm thick undulate mildly, and seem to be laterally continuous. Discontinuous thin coal layers are common in the sandstone, as are thin mud lenses. Coal layers range from 0.1 to 2 cm thick and up to 1 m in length, while clay lenses are up to 1 cm thick and 0.5 m long.

The fossiliferous unit rests upon a 1.5 m thick bed of brownish-grey mudstone, which weathers to a greenish-grey. This recessive unit is fully exposed. The upper contact of the mudstone is sharp, gently undulating, and generally

horizontal. The top 1.0 cm of mudstone is dark grey and saturated with groundwater.



### 3. GENERAL PALEONTOLOGY

Nonmammalian fossils include champsosaurian (Champsosaurus) centra and ribs; crocodilian (Leidyosuchus) scute fragments and teeth; turtle (Testudines, indet.) carapace fragments; neopterygian (Amia and Kindleia) denticles, teeth and bones; one lacertilian (Necrosauridae, indet.) maxillary; and Joffrea (a Cercidiphyllum-like angiosperm) fruits.

Mammalian fossils include teeth, tooth and jaw fragments, and disarticulated, mostly small, bones. See Table 16 for a complete mammalian faunal list.

There is little evidence of size-sorting in the Birchwood sample. Fossils show a wide range of size and degree of weathering, from nearly complete small dentaries with teeth, to heavily-weathered large bone fragments. The large: teeth and bones are most severely worn.

#### 4. NATURE OF THE DEPOSIT AND INFERRED MODE OF DEPOSITION

The Birchwood deposit is certainly fluvial in origin, as evidenced by the coarse clastic sediments and common fossils of nonmammalian freshwater species. The presence of these strictly (Amia and Kindleia) and highly (Champsosaurus and Leidyosuchus) aquatic species indicate an abundance and variety of permanent aquatic habitats near the Birchwood locality (Badgley et al., 1995). Mammalian paleobiological evidence in support of the channel or near-channel nature of the Birchwood deposit comes from the phenacodontid genus Ectocion. Thewissen (1990) noted that two contemporaneous (but geographically mutually exclusive) middle Tiffanian species, E. cedrus and E. mediotuber, are found in two distinct types of deposits, and proposed habitat specialization as an additional means of distinguishing between the two morphologically similar species. According to Thewissen (1990), the remains of E. cedrus are restricted to poorly-drained near-channel deposits, while those of E. mediotuber are restricted to well-drained floodplain deposits. It has been suggested (Badgley et al., 1995) that habitat preference or habitat-specific mortality could be likely causes of the differential abundances of these lineages. The presence of E. cedrus at the Birchwood deposit supports the hypothesis that this is a near-channel or channel deposit.

Taphonomic literature was surveyed in order to narrow down the type of fluvial channel deposit represented at the Birchwood locality. Fluvial systems are one of the most studied mechanical dispersal processes (Lyman, 1994), and are usually classified as allochthonous deposits in which animal remains have been transported

from the site of death and, perhaps, away from their original habitat. Voorhies (1969) divided mammalian skeletal elements into four groups, based on their susceptibility to fluvial transport. Isolated teeth and jaw fragments, the most common fossil elements in the Birchwood deposit, fall within Voorhies' Group III. Group III skeletal elements include skulls, mandibles and teeth, elements which are relatively resistant to movement in a stream and indicate a lag deposit. Behrensmeyer (1975, p. 490) claimed that "the proportions of different Voorhies Groups in fossil assemblages should provide evidence for the proximity of fossils to the original thanatocoenose and the habitats of the living animals". An abundance of Group III elements at the Birchwood deposit may indicate that the majority of these specimens did not travel far before being deposited. This conclusion is backed by the abundance of clay pebbles in the fossiliferous layer at Birchwood. Rigby (1987) determined that clay pebbles cannot survive extensive transport, and the fact that they are present at all indicates little transport. Lofgren (1995) adds that this holds true for any vertebrate remains derived from the same source. As well, the fluvial sequence containing the Birchwood deposit is diminutive in nature, again suggesting a nearby source for the fossils which comprise the Birchwood Local Fauna. The size of the region from which the fossils were derived remains unknown.

At the Birchwood deposit, the coarseness of the sediment and the high teeth-to-vertebrae ratio indicate a high-energy depositional environment and a deposit that has undergone significant winnowing (Behrensmeyer, 1975). However, fossils from a pure high energy depositional environment would not exhibit the excellent preservation

displayed by some fossil specimens from the Birchwood locality. Several gracile dentaries and dentary fragments with cuspidate teeth have been recovered from the Birchwood deposit. These would have presumably been destroyed during extensive transport in a fluvial environment. As well, the fossiliferous beds are composed of intermixed lenses of both coarse and fine-grained clastics, which would not be expected in a pure channel-lag deposit. In short, sedimentological and taphonomic evidence suggest that the deposit was formed in part by a channel bank collapse, rather than representing a simple channel-lag deposit.

## 5. AMOUNT OF TIME REPRESENTED BY THE BIRCHWOOD DEPOSIT

Determining the amount of time represented by the Birchwood deposit is attempted using sedimentation rates and faunal resolution. Vastly divergent sedimentation rates for fluvial deposits have been published by many authors (Behrensmeyer, 1975, 1982; Schwab, 1976; Schindel, 1980; Sadler, 1981; Anders et al., 1987). The only Alberta Paleocene sedimentation rate was published by Lerbekmo et al. (1992), who stated that sedimentation rates in the middle Paleocene Paskapoo Formation were about  $75 \text{ m}/10^6 \text{ y}$  or  $7.5 \text{ cm}/1000 \text{ y}$ . This would place the time required for the formation of the Birchwood deposit's 30 cm fossiliferous layer at approximately 4000 y. However, Schindel (1980), who recognized fluvial sedimentation rates ranging from  $0.06 \text{ m}/1000 \text{ y}$  to  $410 \text{ m}/1000 \text{ y}$ , noted that a deposit from 10 cm to 1 m thick can form in under 10 y. Behrensmeyer (1982:212) also concluded that "sedimentary units which we can see (in the sense of single, indivisible beds) represent very short periods of time, especially for fluvial systems, judging by modern rates of sedimentation".

The faunal temporal resolution of the Birchwood Local Fauna is also high, as almost all fossils from the deposit are consistent with a middle Tiffanian age. The Birchwood Local Fauna records the latest occurrences of the genus Eudaemonema and the species Plesiolestes sp., cf. P. sirokyi, Chriacus sp., cf. C. pelvidens, Claenodon sp., cf. C. montanensis, Desmatoclaenus mearae, and Jepsenella sp., cf. J. praepropera. As well, the earliest known occurrences of the species Cyriacotherium sp., cf. C. argyreum and Neoplagiaulax sp., cf. N. hazeni are recorded in the Birchwood Local

Fauna. Most of the above time range extensions are limited in extent, extending no further than one or two zones within the Tiffanian Land Mammal Age. Given our incomplete knowledge of the fossil record, the sedimentological nature of the Birchwood deposit, and the limited nature of most of the above geological range extensions, it can be concluded that the temporal resolution of the deposit is fairly high.

With the Birchwood deposit representing a combined channel-lag/bank-collapse deposit, it is likely that some fossils spent limited time in transit or in temporary storage (Behrensmeyer, 1982). However, any time extension in the formation of the Birchwood deposit over and above that of a channel-lag deposit is likely not significant, as evidenced by the high faunal temporal resolution. In fact, the deposit was undoubtedly formed in a geologically instantaneous period of time as a result of channel relocation during meandering. It is my conclusion that the Birchwood deposit was formed in a period which certainly represents less than 100 years, and possibly only a single season.

### III. ABBREVIATIONS, DEFINITIONS AND SYMBOLS

**Abbreviations** used in the text are as follows:

A) Institutions:

AMNH - American Museum of Natural History, New York.

CM - Carnegie Museum of Natural History, Pittsburgh.

MCZ - Museum of Comparative Zoology, Harvard University, Cambridge  
(Mass.).

PU - Museum of Natural History, Princeton University, Princeton. Specimens  
now housed in the Yale Peabody Museum, Yale University, New  
Haven, Connecticut (see Ostrom 1986 in Society of Vertebrate  
Paleontology News Bulletin).

ROM - Royal Ontario Museum, Toronto.

SMM - Science Museum of Minnesota, St. Paul.

UALVP - (=UA) University of Alberta, Laboratory for Vertebrate  
Paleontology, Edmonton.

UM - Museum of Paleontology, University of Michigan, Ann Arbor.

USNM - Smithsonian Institution, National Museum of Natural History,  
Washington.

B) Localities:

HHW-LL, Hand Hills West, lower level

HHW-UL - Hand Hills West, upper level.

UADW - University of Alberta, D. Wighton (discoverer).

C) Dentitions:

CF - cusp formula or cusp count

c, C - lower and upper canines, respectively

d, D - lower and upper deciduous teeth, respectively

i, I - lower and upper incisors, respectively

m, M - lower and upper molars, respectively

p, P - lower and upper premolars, respectively

D) Measurements:

AW - greatest width across anterior part of tooth

D - depth of tooth immediately below the crown, used for therian incisors

H - height of tallest part of tooth

L - greatest anteroposterior length

Lave - average length

PW - greatest width across posterior part of tooth

W - greatest transverse width

Wave - average width



\* - indicates an estimated measurement

#### E) Statistics:

CV - coefficient of variation

M - mean

N - sample size

OR - observed range

p - probability

SD - standard deviation

SE - standard error

#### **Definitions** of terms used in the text are as follows:

cf. - literally "compare (with)"; used to indicate the tentative identification of specimens.

Local Fauna - The terms "fauna" and "local fauna" have been used in various manners by different authors. Throughout this work, "local fauna" is used to apply to the mammals from the Birchwood locality. The term "local fauna" was defined by Tedford (1970) as an aggregate of fossil species collected from a restricted stratigraphic interval that is local in time and space. At the Birchwood locality, I interpret this geologically and geographically restricted interval as a channel-filling event.

#### IV. METHODS AND DENTAL TERMINOLOGY

Most of the specimens recovered from the Birchwood locality were obtained via hand quarrying. A small amount of the fossiliferous matrix was sacked and later screenwashed for fossils, but proved to be unproductive. Being that the matrix and the enclosed specimens were poorly consolidated, all but the most robust specimens were most likely destroyed in the washing process. Quarrying, on the other hand, yielded several delicate jaws that would not have survived screenwashing.

All measurements were made using a Wild M3 binocular microscope fitted with an ocular micrometer having both horizontal and vertical scales. In all cases, measurements were taken to the nearest tenth of a millimetre, the finest degree of accuracy that could be realistically reproduced. All specimens were measured by the author.

Multituberculate measurement techniques and nomenclature follow Simpson (1937), Jepsen (1940), Krause (1977, 1982), and Johnston and Fox (1984). Measurement techniques and nomenclature for therian dentitions follow Clemens (1966), Hershkovitz (1971), and Krishtalka (1976a). Phenacodontid condylarth measurements follow Thewissen (1990). Carnivoran nomenclature follows MacIntyre (1966), Gingerich and Winkler (1985), and Fox and Youzwyshyn (1994).

## V. SYSTEMATIC PALEONTOLOGY

Class MAMMALIA Linnaeus, 1758

Subclass ALLOTHERIA Marsh, 1880

Order MULTITUBERCULATA Cope, 1884

Suborder PTILODONTOIDEA Sloan and Van Valen, 1965

Family NEOPLAGIAULACIDAE Ameghino, 1890

MIMETODON Jepsen, 1940

MIMETODON SILBERLINGI (Simpson, 1935)

(Plate 1, figs. A, B)

**Holotype:** USNM 9798, left dentary fragment with i1, p4-m2.

**Type Locality:** Gidley Quarry, Lebo Formation, Sweetgrass County, Crazy Mountain Field, Montana.

**Known Age and Distribution:** Late Torrejonian (middle Paleocene) of Montana (type locality [Simpson, 1935d, 1937]) and Wyoming (Rock Bench Quarry, Polecat Bench Formation, Park County, Bighorn Basin [Jepsen, 1940]; earliest Tiffanian (late Paleocene) of Wyoming (Keefer Hill locality ["Shotgun local fauna"], Fort Union Formation, Wind River Basin [Sloan *in* D. E. Russell, 1967]) and Alberta (Cochrane 2 locality, Porcupine Hills Formation, Cochrane [Youzwysyn, 1988]);

early Tiffanian of Alberta (HHW-LL, Paskapoo Formation, Hand Hills [MacDonald, in prep.]) and Texas (localities 40147 and 41365, Black Peaks Formation, Big Bend National Park [Schiebout, 1974]); middle Tiffanian of Alberta (HHW-UL, Paskapoo Formation, Hand Hills [MacDonald, in prep.]; UADW-1 and UADW-2 localities, Paskapoo Formation, Blindman River [Fox, 1984a, 1990a]; Joffre Bridge locality, Paskapoo Formation, Red Deer River [Fox, 1990a]); late Tiffanian of Alberta (Police Point locality, Ravenscrag Formation [Krishtalka, 1973]; Swan Hills site 1, Paskapoo Formation, Swan Hills [Stonley, 1988]), Saskatchewan (Roche Percée local fauna, Ravenscrag Formation [Krause, 1977]), and Montana (Olive locality, Tongue River Formation, Powder River County [Sloan in D. E. Russell, 1967; Wolberg, 1979]).

**Referred Specimen:** UALVP 39122, p4.

**Description:** Represented at the Birchwood locality by a single specimen, this isolated p4 (L=3.9, W=1.3) shows several features diagnostic of Mimetodon silberlingi. The eleven serrations on the relatively low crown are preceded by two pseudoserrations. The third serration is the highest, with labial enamel ridges descending from the more distinct ultimate and penultimate serrations. The exodaenodont lobe is ventrally peaked. A strong interradicular crest descends approximately one quarter of the distance to the root tips. A more detailed description of this tooth and species has been provided by Krause (1977).

**Discussion:** A wide ranging species in geographical (Alberta to Texas) and geological (late Torrejonian to late Tiffanian) terms, M. silberlingi has also been reported from the late Tiffanian of North Dakota (Red Spring site, Sentinel Butte Formation, Mercer County [Kihm et al., 1993]).

NEOPLAGIAULAX Lemoine, 1882

NEOPLAGIAULAX sp., cf. N. HUNTERI (Simpson, 1936)

(Plate 2, figs. A-G)

**Holotype of Neoplagiaulax hunteri:** AMNH 33865, right dentary with i1-m2.

**Type Locality:** Scarritt Quarry, Melville Formation, Sweetgrass County, eastern Crazy Mountain Basin, Montana.

**Known Age and Distribution of Neoplagiaulax hunteri:** Earliest Tiffanian (late Paleocene) of Montana (Douglass Quarry, Melville Formation, Sweetgrass County, eastern Crazy Mountain Basin [Krause and Gingerich, 1983]); early Tiffanian of Montana (type locality [Simpson, 1936]); middle Tiffanian of North Dakota (Brisbane and Judson localities, Tongue River Formation, Grant and Morton Counties, respectively [Holtzman, 1978]) and Wyoming (Cedar Point Quarry, Polecat Bench Formation, Bighorn County, Bighorn Basin [Rose, 1981; Sloan, 1987]); late Tiffanian of Saskatchewan (Roche Percée local fauna, Ravenscrag Formation [Krause, 1977]), Montana (Circle locality, Tongue River Formation, McCone County [Wolberg, 1979]) and Alberta (Swan Hills local fauna, Paskapoo Formation, Swan Hills [Stonley, 1988]; Police Point locality, Ravenscrag Formation, Cypress Hills [Krishtalka, 1973]).

**Referred Specimens:** UALVP 39180, P3; UALVP 39128, M1; UALVP 39126, 39129, p4's.

**Description:** P3. In his 1977 work, Krause described the whole dentition of N. hunteri except for the upper and lower third premolars. UALVP 39180 is an isolated left upper third premolar tentatively assigned to N. sp., cf. N. hunteri based on comparative material held in the UALVP collections. UALVP 39180 (L=1.2, W=1.0) is subrectangular in occlusal outline and has a crown bearing four distinct cusps. The tooth bore two roots, the anterior being dominant and stout, while the posterior root is not preserved. The crown leans labially relative to the roots, with the labial cusps being less distinct than their lingual counterparts. The anterior margin of the crown overhangs the front root, and is generally transverse to the long axis of the tooth. Near the posterior edge of the front root, just posterior to the cusps, there is a posterior expansion of the crown that slopes down in order to interlock with the anterior lip of the P4.

M1. Cusp formula 8:11:7. UALVP 39128 (L=3.3, W=1.5) is an isolated, worn, left first upper molar. Except for one fewer cusp in the middle row, this tooth is virtually identical in size and morphology to an M1 adequately described by Krause (1977) and referred to N. hunteri, and will not be described further.

p4. UALVP 39129 is an anterior fragment of a right p4. It preserves the anteriormost six serrations and evidence of a minimum of ten ridges. It exhibits a convex labial side in end view, a character noted as diagnostic for N. hunteri by

Krause (1977). The preserved portion of the tooth indicates a trapezoidal outline, as opposed to the more arcuate outline of N. sp., cf. N. hazeni, the more common species of Neoplagiaulax in the Birchwood Local Fauna. UALVP 39126 is a posterior fragment of a right p4. It also exhibits a convex labial side in end view, as well as a straight, rather than convex posterior slope.

**Discussion:** A wide ranging species in both time (earliest to late Tiffanian) and space (Alberta to Wyoming), N. hunteri is most surely present at the Birchwood locality. The fragmentary nature of the specimens collected to date, however, necessitates a more cautious identification as N. sp., cf. N. hunteri.



NEOPLAGIAULAX sp., cf. N. HAZENI (Jepsen, 1940)

(Plate 1, figs. C-D)

**Holotype of Neoplagiaulax hazeni:** PU 14432, right maxillary fragment with incomplete P3 and P4-M2.

**Type Locality:** Princeton Quarry, "Silver Coulee beds", Polecat Bench Formation, Park County, Bighorn Basin, Wyoming.

**Known Age and Distribution of Neoplagiaulax hazeni:** Latest Tiffanian (late Paleocene) of Wyoming (type locality [Jepsen, 1940]).

**Referred Specimens:** UALVP 39124, 39125, 39132, 39134, p4's.

**Description:** p4. One of only two complete multituberculate p4's recovered from the Birchwood deposit is UALVP 39125, an isolated left p4 measuring 4.9 mm in length. The arcuate crown of UALVP 39125 has 13 serrations, the most posterior three bearing only weak ridges and having vertical crenulations of enamel beneath them. Wrinkling of enamel is strongest on the labial side of the tooth, but occurs on the lingual side as well. In end view, the labial side of the tooth is flat, precluding it from N. hunteri, which has p4's with convex labial sides (Krause, 1977). This tooth compares favorably in size and morphology with specimens of Neoplagiaulax sp., cf.

N. hazeni from the late Tiffanian Roche Percée local fauna of Saskatchewan (Krause, 1977).

**Discussion:** Originally named by Jepsen (1940) as a species of the genus Ectypodus, it has since been transferred to the genus Neopiagiaulax (Van Valen and Sloan, 1966:fig. 5). At present, over a half century since its discovery, the only published report of N. hazeni is from its type locality, Princeton Quarry, in the late Tiffanian Silver Coulee beds of Wyoming. However, other researchers have found similar specimens. Gazin (1956a) assigned a p4 from the Bison Basin, Wyoming to Ectypodus sp., cf. E. hazeni. Four years later, McKenna (1960) ascribed the same designation to an m1 from the Eocene Four Mile fauna of Colorado. Both Krause (1977) and Stonley (1988) assigned relatively large numbers of late Tiffanian specimens from Saskatchewan and Alberta, respectively, to Neoplagiaulax sp., cf. N. hazeni. More recently, N. sp., cf. N. hazeni has been reported from the late Tiffanian of North Dakota (Kihm et al., 1993).

## Family NEOPLAGIAULACIDAE Ameghino, 1890

## UNIDENTIFIED GENUS AND SPECIES

(Plate 1, figs. E-G)

**Referred Specimen:** UALVP 39123, P4.

**Description and Discussion:** UALVP 39123 (L=3.9, W=1.4) is a worn right upper fourth premolar. It has a cusp formula of 5:9:0, and superficially resembles specimens of Neoplagiaulax hazeni in the UALVP collection. It differs from Sloan's (1981) rediagnosis of the genus Neoplagiaulax in having more cusps in the external row (Sloan [1981:133] restricted the number of external cusps in Neoplagiaulax to a maximum of four) and much gentler anterior and posterior slopes, although the posterior slope of UALVP 39123 is almost certainly gentler due to wear. The anterolabial cusp row ends abruptly near the midlength of the tooth, bearing five cusps and one incipient cusp at the posterior end of the cusp row. Cusps in this row are largest near the middle of the row, and decrease in size both anteriorly and posteriorly. The middle row bears nine cusps, but wear is excessive on the posterior portion of this cusp row; therefore, this count is an estimate. Wear is most extensive on the posterolabial portion of the middle row, with wear facets obscuring the tooth morphology. The anterior and posterior margins of the tooth are transverse relative to the long axis of the tooth, and overlap the anterior and posterior roots, respectively.

The morphology of this tooth is unique among Birchwood specimens. It

certainly belongs to a neoplagiaulacid due to its Neoplagiaulax-like trenchant morphology, but does not belong to any of the neoplagiaulacid genera present at the Birchwood locality. Further specimens of this animal's dentition must be collected before its true affinities are revealed.

Family Ptilodontidae Gregory and Simpson, 1926

Ptilodus Cope, 1881

Ptilodus sp. T (see Krause, 1982)

(Plate 3, figs. A-F; Table 1)

**Holotype:** PU 14584, right dentary fragment with i1, p3-4, m1.

**Type Locality:** Douglass Quarry, Melville Formation, Sweetgrass County, eastern Crazy Mountain Basin, Montana.

**Known Age and Distribution:** Latest Torrejonian (middle Paleocene) of Montana (?Medicine Rocks site I, Tongue River Formation, Carter County, Powder River Basin [Krause, 1982]); earliest Tiffanian (late Paleocene) of Montana (type locality [Krause, 1982, 1987a; Krause and Gingerich, 1983]) and Alberta (Cochrane 2 locality, Porcupine Hills Formation, Cochrane [Youzwysyn, 1988]); early Tiffanian of Montana (Scarritt Quarry, Melville Formation, Sweetgrass County, eastern Crazy Mountain Basin [Krause and Maas, 1990]); middle Tiffanian of Alberta (Joffre Bridge Roadcut locality, lower level, Paskapoo Formation, Red Deer River [Fox, 1990a]).

**Referred Specimens:** UALVP 39147, P1; UALVP 39148, P2; UALVP 39139, 39140, P4's; UALVP 39145, 39146, M1's; UALVP 39141, 39142, p4's; UALVP 39143, 39144, m1's.

**Description:** While this species has been known for over a decade, it has yet to be thoroughly described in a published work. In his unpublished Ph.D. dissertation, Krause (1982) figured the intended holotype and an isolated P4, while providing only measurements for P3-4 and M1-2. Youzwyshyn (1988) figured P3-4, M1-2 and p4 in his unpublished M.Sc. thesis, and provided written descriptions for P3-4, M1-2, and p3-4, m1-2. Fox (1990a:fig. 7) figured an incomplete skull of Ptilodus sp. T showing left and right P1-4 and M1-2. Species designations of Birchwood specimens were made based on this and other comparative specimens in UALVP collections. Descriptions of Birchwood specimens will focus on those teeth not adequately described or figured in these works. Measurements for these and teeth of other positions are provided in Table 1.

P1. UALVP 39147 (L=3.2, W=2.5) is an isolated left upper first premolar of characteristic Ptilodus construction, bearing three cusps and having a triangular occlusal outline. All three cusps bear wrinkled enamel, forming vertical crenulations on their external, and to a degree, internal slopes. UALVP 39147 bears two roots, the posterior root stout and anteroposteriorly compressed, the anterior root smaller and circular in cross-section.

P2. UALVP 39148 (L=3.6, W=3.2) is an isolated left upper second premolar. Of typical Ptilodus construction, this tooth bears four cusps and has a rectangular occlusal outline. An anterolabial inflation does not bear any accessory cusps. The cusps of this tooth bear vertical crenulations of enamel, as on P1.

P4. Cusp formula (1-2)7-9:10-11:0. UALVP 39139 (L=6.1, W=2.6) is an

unworn, isolated left upper fourth premolar. It bears one or two more cusps in all rows than UALVP 39140 (L=5.8, W=2.6), which is slightly shorter. Variable cusp counts in ptilodontid P4's are common (Krause [1982:table 22] reports a variable cusp count of (0-2)6-7:9-10:0 for the P4's of Ptilodus sp. T from the earliest Tiffanian Douglass Quarry), and both of these teeth fall within the ranges of size and morphological variation for Ptilodus sp. T (Krause, 1982).

M1. Cusp formula 8-9:10:6. UALVP 39146 (L=6.7, W=2.9) is an isolated left upper first molar. Slightly longer than UALVP 39145 (L=6.6, W=2.9), UALVP 39146 bears an additional cusp in its external row. Both of these teeth fall within the ranges of size and morphological variation for Ptilodus sp. T (Krause, 1982). As noted by Krause (1982), Ptilodus sp. T bears more cusps in all rows than other species of Ptilodus.

p4. Only incomplete Ptilodus sp. T p4's have been recovered from the Birchwood deposit. Distinguished in part by their large size, UALVP 39141 and 39142 have substantial, ventrally rounded exodaenodont lobes. They bear a minimum of 11 ridges on a semi-elliptical crown, and have well-developed anterobasal concavities.

m1. Cusp formula 6:5-6. UALVP 39144 (L=4.5, W=2.1) is slightly longer and narrower than UALVP 39145 (L=4.4, W=2.2), bearing an additional cusp in the lingual row. Distinguished in part by their larger size, these m1's have elevated lingual cusp rows, deep grooves on the internal slopes of the lingual cusps, and fused ultimate and penultimate lingual cusps.

**Discussion:** Ptilodus sp. T and the congeneric Ptilodus sp. C are the most well-represented multituberculates, and some of the most common members of the Birchwood Local Fauna. The dentitions of these two species are primarily distinguished on the basis of size. The p4 morphology of these species is overall fairly similar to that of Prochetodon, and their similarity in size makes the assignment of isolated p4 fragments difficult. The p4's of Prochetodon have a reduced exodaenodont lobe and a lower profile in lateral outline, thus having lower angled ridges that near the horizontal.

Krause (1982) restricted Ptilodus sp. T to the earliest Tiffanian. However, the occurrence of this species at both the Birchwood locality and the middle Tiffanian Joffre Bridge Roadcut locality (Fox, 1990a) provide evidence for a geological range extension for this species. This finding also represents a geographic range extension for the species, northwards from central Alberta.



*PTILODUS* sp. C (see Krause, 1982)

(Plate 4, figs. A-I; Pl. 5, figs. A-J; Pl. 6, figs. A-D; Table 2)

**Holotype:** UM 63094, right dentary fragment with i1, p3-4.

**Type Locality:** Cedar Point Quarry, Polecat Bench Formation, Bighorn County, northern Bighorn Basin, Wyoming.

**Known Age and Distribution:** Earliest Tiffanian (late Paleocene) of Alberta (Cochrane 2 locality, Porcupine Hills Formation, Cochrane [Youzwysyn, 1988; Fox, 1990a]) and Montana (Douglass Quarry, Melville Formation, Sweetgrass County, eastern Crazy Mountain Basin [Krause and Maas, 1990]); early Tiffanian of Montana (Scarritt Quarry, Melville Formation, Sweetgrass County, eastern Crazy Mountain Basin [Simpson, 1936, 1937; Krause, 1982]) and Wyoming (Saddle locality, Fort Union Formation, Fremont County, Bison Basin [Gazin, 1956a; Krause, 1982]); middle Tiffanian of North Dakota (Judson and Brisbane localities, Tongue River Formation, Morton and Grant Counties, respectively [Holtzman, 1978; Krause, 1982]), Alberta (HHW-UL, Paskapoo Formation, Hand Hills [Fox, 1990a]; UADW-1 and UADW-2 localities, Paskapoo Formation, Blindman River [Fox, 1990a]) and Wyoming (Cedar Point Quarry, Polecat Bench Formation, Bighorn County, northern Bighorn Basin, Wyoming [Rose, 1981; Krause, 1982]; Type Chappo locality, Wasatch Formation, Lincoln County [Dorr and Gingerich, 1980; Krause, 1982; Gunnell, 1994]); late

Tiffanian of Alberta (Police Point locality, Ravenscrag Formation, Cypress Hills [Krishtalka, 1973; Krause, 1982]) and Montana (Circle locality, Tongue River Formation, McCone County [Wolberg, 1979]).

**Referred Specimens:** UALVP 39163, 39164, P1's; UALVP 39165-39173, 39176, P2's; UALVP 39174, 39175, 39177, P3's; UALVP 39157, 39158, P4's; UALVP 39162, M2; UALVP 39185, 39189, 39312, i1's; UALVP 39149-39156, p4's; UALVP 39159, 39160, m1's; UALVP 39161, m2.

**Description:** Ptilodus sp. C has never been adequately described in a published work. Krause (1982) figured the intended holotype as well as CM 18759, a left maxillary fragment with P<sub>1</sub>-4 from the Saddle Locality. Youzwyshyn (1988) figured a single m1 and provided written descriptions for p4, m1-2 and P3-4, M1-2. Descriptions of Birchwood specimens will focus on those teeth not adequately described or figured in these works. Measurements for these and teeth at other positions are provided in Table 2.

P1. UALVP 39163 (L=2.6, W=2.5) is an isolated left upper first premolar, the only complete P1 of this species recovered from the Birchwood deposit. Similar in morphology to the P1's of Ptilodus sp. T, UALVP 39163 has a triangular occlusal outline and wrinkled enamel, forming vertical crenulations on the external and, to a degree, internal slopes of the three cusps. UALVP 39163 has two roots, similar in morphology to those of the P1's of Ptilodus sp. T.

P2. Nine out of ten recovered P2's possess four cusps on their subrectangular crowns. The generally rectangular shape of the crowns is modified by convex anterior and posterior margins, and a variable anterolabial bulge. UALVP 39176 (L=2.8, W=2.4) bears a small accessory cusp on an anterolabial bulge. The cusps of all teeth bear vertical crenulations of enamel, most prominent on the exterior slopes of the cusps. The crowns are supported by two robust, anteroposteriorly compressed roots, which can be up to 5 mm in length.

P3. Cusp count for the P3's of Ptilodus sp. C is variable, with Birchwood specimens showing either six or seven cusps on their subrectangular crowns. Cusps show the familiar vertical enamel crenulations, and the crown may possess a posterolabial bulge. UALVP 39177 (L=3.5, W=2.4) possesses seven cusps, with an accessory cusp present on a small posterolabial bulge.

P4. Cusp formula (2)6:9:0. UALVP 39157 (L=5.8, W=2.7) is the only complete upper fourth premolar of this species collected from the Birchwood deposit. It is similar in morphology to the P4 of Ptilodus sp. T, but bears fewer cusps in all rows and is overall smaller in size.

M2. Cusp formula 1:3:4. UALVP 39162 (L=2.7, W=2.4) is the only upper second molar of Ptilodus sp. C recovered from the Birchwood deposit. This tooth is of typical Ptilodus configuration, with the anteriormost two lingual cusps partially fused.

i1. UALVP 39185 and 39189 are isolated fragments of left lower first incisors. The most nearly complete specimen is UALVP 39312, an isolated right lower first

incisor. These fragments are identified as Ptilodus sp. C based on comparison with an uncatalogued complete dentary of that species in the UALVP collections. Relatively long and narrow, UALVP 39312 curves gently along its length of 18.5 mm. At its mesiodistally compressed base, this fragment reaches a maximum diameter of 3.4 mm. Near its tip, the tooth has a minimum diameter of 0.7 mm. An external ridge runs posteroexternally from the near spatulate tip. Enamel is heaviest and most extensive on the ventral portion of the tooth. Overall, this tooth is of typical ptilodontid morphology.

p4. Referred specimens are anterior and posterior fragments only. The most nearly complete tooth (UALVP 39153) displays the 12 most posterior serrations and has a total length of 6.1 mm, approximately 75 percent of its estimated complete length. By overlapping anterior and posterior p4 fragments, it can be tentatively estimated that the Birchwood Ptilodus sp. C population had an average serration count between 14 and 15, and an average length near eight millimetres.

In profile view, the crown is a low, symmetrical arc. The height of the first serration is relatively high, between one-third and one-half the approximated standard length. The fourth serration is the highest above the standard length. The more posterior serrations are blunter and wider than the more anterior serrations. Ridges descending from the serrations are parallel and equidistant until the most posterior three or four serrations, which bear weak and irregular ridges. Labially, the ridges of the second serrations of two specimens (UALVP 39150 and 39156) descend and join the first serrations approximately one-third of the distance towards the anterobasal

concavity. The exodaenodont lobe is wide, extending up to one-half the standard length. At its ventral peak, the lobe is quite blunt, with the anterior margin being more oblique than the posterior margin.

m1. Cusp formula 7:5. UALVP 39159 (L=4.1, W=1.9) is the only complete lower first molar of this species collected from the Birchwood locality. It has a cusp formula and tooth dimensions entirely consistent with those m1's reported from the Cedar Point Quarry by Krause (1982).

m2. Cusp formula 4:2. UALVP 39161 (L=2.8, W=2.1) is a worn left second molar. It exhibits typical ptilodontid morphology, and is within the size range of those m2's collected from the Cedar Point Quarry, along with those from the UADW-2 locality (pers. obs.). The most posterolingual cusp appears to be partially divided into two parts, but following Krause's (1982) nomenclature, is here called a single cusp.

**Discussion:** A total of 31 isolated teeth at almost all tooth positions make Ptilodus sp. C the most common multituberculate at the Birchwood locality. These specimens represent a geographic range extension for the species, northwards from central Alberta.

Using Gingerich's (1975, 1976) stratophenetic approach, Krause (1982) sought to develop a biostratigraphic zonation of the North American Paleocene and early Eocene using members of the Ptilodontidae. He restricted Ptilodus sp. T to the earliest Tiffanian and Ptilodus sp. C to the early and middle Tiffanian (Krause, 1982:fig. 28, table 47). The presence of both Ptilodus sp. T and Ptilodus sp. C at the Birchwood

locality is the third piece of evidence (after Youzwysyn, 1988; Krause and Maas, 1990) for the contemporaneous occurrence (in both time and space) of these two species, and is the only middle Tiffanian record of this co-occurrence.

PROCHETODON Jepsen, 1940

PROCHETODON FOXI Krause, 1987

(Plate 6, figs. E, F)

**Holotype:** PU 21223, right dentary with base of i1 and p3-4.

**Type Locality:** Long Draw Quarry, Carbon County, Bighorn Basin, Montana.

**Known Age and Distribution:** Middle Tiffanian (late Paleocene) of North Dakota (Judson locality, Tongue River Formation, Morton County [Holtzman, 1978]); late Tiffanian of Alberta (Swan Hills site 1, Paskapoo Formation, Swan Hills [L. S. Russell, 1967; Stonley, 1988]), Saskatchewan (Roche Percée local fauna, Ravenscrag Formation [Krause, 1977]), Montana (type locality [Krause, 1987b]), and Wyoming (Divide Quarry, Polecat Bench Formation, Bighorn Basin [Gingerich, 1976]; Malcolm's locality, Fort Union Formation, Wind River Basin [Krishtalka et al., 1975]).

**Referred Specimens:** UALVP 39137, 39138, p4's.

**Description:** The most nearly complete specimen of Prochetodon from the Birchwood locality is UALVP 39138, an isolated posterior portion of a left lower fourth premolar. UALVP 39138 has a minimum length of 7.6 mm, preserving the posteriormost 12 serrations and 11 ridges. The broken anterior margin has a width of

2.5 mm. Although most of the blade is preserved, there is little or no evidence of any significant exodaenodont lobe, a generic character of Prochetodon (Krause, 1982).

Both UALVP 39137 and 39138 are referred to Prochetodon foxi on the basis of their size, reduced exodaenodont lobes, relatively low profile in lateral view, and low-angled serrations.

**Discussion:** The presence of this species along with Ptilodus sp. C and Ptilodus sp. T at the Birchwood locality demonstrates an abundance of medium- and large-sized ptilodontids. This may indicate either an abundance of available foodstuffs for these common omnivores, or preservation and/or collection biases towards the teeth of these mammals.



Suborder TAENIOLABIDOIDEA (Granger and Simpson, 1929)

Family EUCOSMODONTIDAE (Jepsen, 1940)

Subfamily MICROCOSMODONTINAE Holtzman and Wolberg, 1977

MICROCOSMODON Jepsen, 1930

MICROCOSMODON WOODI Holtzman and Wolberg, 1977

(Plate 7, figs. A-I)

**Holotype:** MCZ 19963, right ♂4.

**Type Locality:** New Anthill locality, anthill L, Shotgun Member, Fort Union Formation, Fremont County, Wyoming.

**Known Age and Distribution:** Earliest Tiffanian (late Paleocene) of Montana (Douglass Quarry, Melville Formation, Sweetgrass County, eastern Crazy Mountain Basin [Krause and Maas, 1990]); middle Tiffanian of Alberta (HHW-UL locality, Paskapoo Formation, Drumheller [Fox, 1990a]; UADW-2 locality, Paskapoo Formation, Blindman River [Fox, 1984a, 1990a]), North Dakota (Brisbane locality, Tongue River Formation, Grant County [Holtzman and Wolberg, 1977]), and Wyoming (type locality [Holtzman and Wolberg, 1977]); late Tiffanian of Montana (Circle locality, Tongue River Formation, McCone County [Holtzman and Wolberg, 1977; Wolberg, 1979]).

**Referred Specimens:** UALVP 39194, 39198, I2's; UALVP 39197, 39183, 39184, i1's; UALVP 39178, right dentary fragment with p3-4, m1; UALVP 39135, m1.

**Description:** To date, only the hypodigm of Microcosmodon woodi has been described and figured (see Holtzman and Wolberg, 1977). The hypodigm consists of teeth from the P4, M1, i1, and p4 positions. The discovery of UALVP 39178, a right dentary fragment with p3-4 and m1, is the first evidence of these teeth in association with each other. No upper cheek teeth belonging to this species have yet been recovered from the Birchwood locality.

I2. UALVP 39198 is an isolated upper second incisor (L=7.1, maximum diameter=1.8, minimum diameter=1.6), smaller than, but identical in morphology to those of Microcosmodon conus illustrated by Krause (1977). The bicuspid crown has been worn somewhat, to approximately the same level as that shown by UA 11712 (Krause, 1977:fig. 14). UALVP 39198 and 39194 are referred to M. woodi on the basis of their size and typical Microcosmodon morphology.

i1. UALVP 39184 is an isolated right lower first incisor. The crown and majority of the root is fractured but intact, with only the basal portion of the root missing. UALVP 39184 has a length of 10.6 mm and reaches a maximum diameter of 2.1 mm near its laterally compressed base. It is morphologically similar to i1's of other species of Microcosmodon, and compares well with the hypodigm specimens.

p3. UALVP 39178 exhibits a simple peg-like p3, nestled under the anterior

edge of the p4. Enamel covers only the small, slightly bulbous crown. The tooth is single-rooted, with the root nearly as wide as the crown. The p3 was not among the tooth positions included in the hypodigm of M. woodi by Holtzman and Wolberg (1977), and as far as is known to me, this is the first recorded p3 of this species.

p4. UALVP 39178 preserves the only p4 (L=3.0, W=1.7) of M. woodi known from the Birchwood locality. The tooth is worn and missing enamel on the anterolabial part of the low crown, but six serrations are clearly visible. The first serration is relatively low on the anterior margin of the crown. Serrations two and three, although distinct, are broken and not well preserved. The ultimate and penultimate serrations are cusp-like, as reported by Holtzman and Wolberg (1977), and the exodaenodont lobe is reduced.

m1. Cusp formula 5:4. The lower first molar preserved in UALVP 39178 (L=2.4, W=1.1) is one of two lower first molars of this species known from the Birchwood locality. The other, an isolated tooth (UALVP 39135 [L=2.5, W=1.3]), is slightly larger. Both teeth have a sub-rectangular occlusal outline with convex anterior and posterior margins, five sub-conical cusps in the labial row, and four rectangular cusps in the lingual row. The lingual rows of both specimens are elevated relative to the labial rows. The ultimate and penultimate labial cusps have strong vertical grooves on their internal surfaces. The posterior root of UALVP 39135 is longer and more robust than the anterior root.

**Discussion:** Several authors have independently questioned the relationships of

Microcosmodon woodi. Krause (1982:302) surmised that M. woodi (middle Tiffanian), M. conus (late Tiffanian), and M. rosei (Clarkforkian) should be included in the same phyletic lineage, characterized by "a progressive reduction in overall size, as well as a reduction in the relative size of p4". However, when Archibald (1982) erected the Puercan genus Acheronodon based on a single p4, he was first to note the similarities between the p4's of the genotype, A. garbani, and M. woodi. He hypothesized that the recovery of additional material may prove Acheronodon congeneric with Microcosmodon. Johnston and Fox (1984) argued the distinctness of M. woodi from the lineage involving M. arcuatus and M. conus. In his unpublished work, Youzwysyn (1988) pursued the hypothesis of a relationship between Acheronodon and M. woodi. He advocated the transfer of Microcosmodon woodi to Acheronodon. It would there join A. garbani Archibald, 1982 and A. vossae Youzwysyn, 1988 (unpublished) based on dental similarities. Youzwysyn (1988) suggested that the Acheronodon lineage (including M. woodi) shows a trend towards increasing p4 size, while the Microcosmodon lineage (M. arcuatus and M. conus) shows a trend towards reduction of p4 size and serration number with time.

I concur with Johnston and Fox (1984) and Youzwysyn (1988) regarding the distinctness of M. woodi from the Microcosmodon lineage. However, whether or not this species belongs within the Acheronodon lineage is beyond the scope of this work. Due to the unpublished nature of Youzwysyn's (1988) work, I will here retain M. woodi within the Microcosmodon lineage.

The discovery of M. woodi at the Birchwood locality represents a northerly

expansion of its known geographic range, northwards from central Alberta.

Subclass THERIA Parker and Haswell, 1897

Infraclass EUTHERIA Gill, 1872

Order LIPOTYPHILA (Haeckel, 1866)

Suborder ERINACEOMORPHA Gregory, 1910

Family ADAPISORICIDAE Schlosser, 1887

Subfamily LITOCHERINAE Gingerich, 1983

LITOCHERUS Gingerich, 1983

LITOCHERUS ZYGEUS Gingerich, 1983

(Plate 8, figs. A-F)

**Holotype:** UM 64508, right dentary with p3-4, m1-3.

**Type Locality:** Cedar Point Quarry, Polecat Bench Formation, Bighorn County, northern Bighorn Basin, Wyoming.

**Known Age and Distribution:** Middle Tiffanian (late Paleocene) of Wyoming (type locality [Gingerich, 1983]) and North Dakota (Brishane and Judson localities, Tongue River Formation, Grant and Morton Counties, respectively [Holtzman, 1978]).

**Referred Specimens:** UALVP 39287, P4; UALVP 39478, left dentary fragment with p4, m1; UALVP 39477, right dentary fragment with p4, m1-2; UALVP 39461, left dentary fragment with m1-2.

**Description:** The lower dentition of Litocherus zygeus has been adequately described and figured in the type description (Gingerich, 1983). The Birchwood specimens are consistent in size and morphology with the Cedar Point Quarry specimens, and will not be described here. The upper fourth premolar of Litocherus zygeus, previously unknown for this species, is described below.

P4. UALVP 39287 (L=2.1, W=3.0) is an isolated upper right fourth premolar bearing three roots. It is characterized by a large, blunt paracone and a strong protocone that is well separated from the paracone by a wide and shallow valley. The paracone leans gently posteriorly at an angle approaching 10 degrees from vertical. A distinct, papillate postparacrista descends posteriorly from the apex of the paracone, then curves anteriorly along the labial side of the tooth, terminating directly labially to the paracone. A deep invagination is associated with the postparacrista, separating its anterior margin from the posterior margin of the paracone. A small swelling, possibly an incipient metacone, occurs near the end of the postparacrista. Independent of and just labial to this swelling, is a small isolated cusp, possibly a metastyle. A distinct postcingulum is present, with a small swelling in the location of the hypocone. UALVP 39287 is broken along its anterior margin, just above the base of the crown. I believe that this damage has resulted in the loss of the precingulum and parastyle, and that they were once present, given that the majority of other adapisoricids possess both of these features.

UALVP 39287 most clearly resembles the type P4 of Litocherus notissimus figured by Simpson (1936:fig. 15) in general structure and, specifically, in possessing

a strong postprotocrista. UALVP 39287 (L=2.1, W=3.0) is of the same length, but considerably wider than the type P4 of Litocherus notissimus (L=2.1, W=2.2 [Simpson, 1936]). Gingerich (1983) reported the dentition of L. zygeus as about 22 percent larger than that of the type species; inflating the linear dimensions of the P4 of L. notissimus by this amount would yield a tooth of width similar to UALVP 39287.

**Discussion:** The four specimens of Litocherus zygeus from the Birchwood locality are the only evidence of this species in Alberta, and represent a northward geographical range extension for the species. Fox (1990a) reported Litocherus sp., cf. L. zygeus from the following middle Tiffanian Albertan localities within the Paskapoo Formation: HHW-UL, UADW-1, Joffre Bridge Roadcut upper and lower levels, and Joffre Bridge Mammal Site No. 1. Geologically younger members of this genus reported from Alberta include L. lacunatus and L. sp., cf. L. notissimus from the late Tiffanian Swan Hills locality (Stonley, 1988).



## Family ADAPISORICIDAE Schlosser, 1887

## UNIDENTIFIED GENUS AND SPECIES

(Plate 8, figs. G-I)

**Referred Specimen:** UALVP 39483, P4.

**Description and Discussion:** UALVP 39483 (L=2.2, W=1.9) is an isolated, right upper fourth premolar. The conical paracone dominates the crown and leans posteriorly, approaching 10 degrees from vertical. The paracone is flanked anteriorly by a small parastyle, and posteriorly by an incipient metacone and a small metastyle. The styler cusps are weak, little more than swellings on the labial corners of the pre- and postcingula. The metacone, located on the posterior slope of the paracone, is small but distinct, and conjoined with the paracone at its base. The metacone is approximately one-quarter the width of the paracone, but almost half its height. The protocone is strong, separated from the paracone by a wide and shallow valley. The protocone, although more robust, is approximately the same height as the metacone. Distinct pre- and postcingula border the anterior and posterior margins of the tooth. The bases of three well-developed roots are present, the root supporting the protocone the weakest.

The presence of a well-developed metacone and protocone indicate that this is a P4, rather than a P3. Members of the Litocherinae, such as Litocherus, have P4's "with the metacone on P4 usually small or absent" (Gingerich, 1983:228), thus

precluding UALVP 39483 from this subfamily. The upper premolars of other subfamilies of the Adapisoricidae are poorly known. The UALVP collections lack other examples of these teeth, and I have been unable to locate figures of any relevant specimens. The lack of comparative material may reflect the rarity of this specimen in Tiffanian faunas. Further collecting at the Birchwood and other middle Tiffanian localities in Alberta is necessary before the exact affinities of this creature will be revealed.

Suborder SORICOMORPHA Gregory, 1910

Family NYCTITHERIIDAE Simpson, 1928

LEPTACODON Matthew and Granger, 1921

LEPTACODON sp., cf. *L. TENER* Matthew and Granger, 1921

(Plate 9, figs. A-C)

**Holotype of *Leptacodon tener*:** AMNH 17179, crushed rostrum with complete upper left dentition, fragmentary right upper anterior dentition, and fragmentary lower jaws with left m1-3, right p3-p4, m1-m2, half of m3.

**Type Locality:** Mason Pocket, "Tiffany" beds, San Jose Formation, La Plata County, San Juan Basin, Colorado.

**Known Age and Distribution of *Leptacodon tener*:** Middle Tiffanian (late Paleocene) of Wyoming (Cedar Point Quarry, Polecat Bench Formation, Bighorn County, northern Bighorn Basin [Krishtalka, 1976b; Rose, 1981]) and North Dakota (Brisbane locality, Tongue River Formation, Grant County [Holtzman, 1978]); late Tiffanian of Colorado (type locality [Matthew and Granger, 1921; McKenna, 1968]), Montana (Olive locality, Tongue River Formation, Powder River County [Wolberg, 1979]) and Alberta (Police Point locality, Ravenscrag Formation, Cypress Hills [Krishtalka, 1973]; Swan Hills site 1, Paskapoo Formation, Swan Hills [Stonley, 1988]).

**Referred Specimen:** UALVP 39479, right dentary fragment with m1-3.

**Description:** The lower dentition of Leptacodon tener has been adequately described and figured by McKenna (1968) and Krishtalka (1976b). The Birchwood specimen does not differ significantly in size or morphology from these figured specimens, nor from specimens from the late Tiffanian Police Point locality of Alberta (Krishtalka, 1973). The lower molars of UALVP 39479 have more cusate paraconids and an elongate m3 talonid, features which distinguish it from L. munusculum (Krishtalka, 1976b). The lower molars are significantly smaller than those of specimens referred to L. packi (Jepsen, 1930b). Damage to the specimen has eliminated some diagnostic features from the trigonid crowns of the lower molars. For this reason, UALVP 39479 is more conservatively assigned to Leptacodon sp., cf. L. tener.

**Discussion:** Leptacodon sp., cf. L. tener has also been reported from the earliest Tiffanian Cochrane 2 locality of Alberta (Youzwysyn, 1988; Fox, 1990a) and the early Tiffanian Scarritt Quarry of Montana (Simpson, 1936; Rose, 1981).

LEPTACODON MUNUSCULUM Simpson, 1935

(Plate 9, figs. D-F)

**Holotype:** USNM 9819, left dentary fragment with m1 and m3.

**Type Locality:** Gidley Quarry, Lebo Formation, Sweetgrass County, Crazy Mountain Field, Montana.

**Known Age and Distribution:** Late Torrejonian (middle Paleocene) of Montana (type locality [Simpson, 1935d, 1937; Krishtalka, 1976b; Rose, 1981]); latest Torrejonian of Wyoming (Rock Bench Quarry, Polecat Bench Formation, Park County, Bighorn Basin [Rose, 1981]); earliest Tiffanian (late Paleocene) of Montana (Douglass Quarry, Melville Formation, Sweetgrass County, eastern Crazy Mountain Basin [Krause and Gingerich, 1983]; Bangtail locality, Fort Union Formation, Park County, western Crazy Mountain Basin [Gingerich et al., 1983]) and Alberta (Cochrane 2 locality, Porcupine Hills Formation, Cochrane [Youzwysyn, 1988; Fox, 1990a]); middle Tiffanian of Wyoming (Cedar Point Quarry, Polecat Bench Formation, Bighorn County, northern Bighorn Basin [Krishtalka, 1976b; Rose, 1981]).

**Referred Specimens:** UALVP 39480, right dentary fragment with m1-3; UALVP 39481, right dentary fragment with m2-3.

**Description and Discussion:** The lower dentition of Leptacodon munusculum has been adequately described and figured by Krishtalka (1976b) and Krause and Gingerich (1983). The Birchwood specimens fall within the morphological and size ranges of these samples, and accord well with specimens from the earliest Tiffanian Cochrane 2 locality of Alberta (Youzwyshyn, 1988).

Several authors (Krishtalka 1976b; Bown and Schankler, 1982; Youzwyshyn, 1988) have advocated the transfer of Leptacodon munusculum to the nyctitheriid genus Pontifactor due to shared features of the lower molars. Although the lower dentitions of Pontifactor and L. munusculum share some similarities, stronger evidence supporting this transfer may be present in the upper dentition of L. munusculum (Krishtalka, 1976b). Given that the upper dentition of L. munusculum has yet to be described, I here retain L. munusculum in the genus Leptacodon.

Order DERMOPTERA Illiger, 1811

Family PLAGIOMENIDAE Matthew, 1918

ELPIDOPHORUS Simpson, 1927

ELPIDOPHORUS ELEGANS Simpson, 1927

(Plate 10, figs. A-D, F-H; Pl. 11, figs. A-H; Tables 3, 4)

**Holotype:** AMNH 15541, right dentary fragment with m1-2.

**Type Locality:** Erickson's Landing, Paskapoo Formation, Red Deer River, Alberta.

**Known Age and Distribution:** Earliest Tiffanian (late Paleocene) of Montana (Douglass Quarry, Melville Formation, Sweetgrass County, eastern Crazy Mountain Basin [Krause and Maas, 1990]); early Tiffanian of Montana (Scarritt Quarry, Melville Formation, Sweetgrass County, eastern Crazy Mountain Basin [Szalay, 1969]) and Alberta (HHW-LL, Paskapoo Formation, Hand Hills [MacDonald, in prep.]); middle Tiffanian of Alberta (type locality [Simpson, 1927; Fox, 1990a]; UADW-1 and UADW-2 localities, Paskapoo Formation, Blindman River [Fox, 1990a]; Joffre Bridge Roadcut, lower level, and Joffre Bridge Mammal Site No. 1 localities, Paskapoo Formation, Red Deer River [Fox, 1990a]; HHW-UL, Paskapoo Formation, Hand Hills [Fox, 1990a]) and Wyoming (Cedar Point Quarry, Polecat Bench Formation, Bighorn County, northern Bighorn Basin [Rose and Simons, 1977]); late Tiffanian of Alberta

(Police Point locality, Ravenscrag Formation, Cypress Hills [Krishtalka, 1973]) and Montana (Circle locality, Tongue River Formation, McCone County [Wolberg, 1979]).

**Referred Specimens:** UALVP 39391, I1; UALVP 39392, maxillary fragment with P2-4, M1-2; UALVP 39393, P3; UALVP 39407, DP4; UALVP 39394, 39395, P4's; UALVP 39396, M2; UALVP 39400, dentary fragment with i1-2; UALVP 39401, 39412, i1's; UALVP 39402, p1; UALVP 39403, 39404, p3's; UALVP 39397, dentary fragment with p3-4, m1-3; UALVP 39398, dentary fragment with p4, m1-3; UALVP 39399, dentary fragment with p3-4, m1-2; UALVP 39405, dentary fragment with m2-3; UALVP 39406, m3.

**Description:** The majority of the dentition of Elpidophorus elegans is well known and has been adequately illustrated in the literature (Simpson, 1936; Szalay, 1969; Rose and Simons, 1977). However, as is common with many taxa of Paleocene mammals, the deciduous and anteriormost permanent teeth of E. elegans are poorly known. It is fortunate that the sample of E. elegans from the Birchwood locality contains i1-2 and I1 as well as DP4, as teeth from these positions have yet to be formally described. My description of the Birchwood specimens will focus on these tooth positions.

i1. UALVP 39400 is a right dentary fragment with i1-2. The i1 of UALVP 39400 (W=1.5, D=2.4), and isolated i1's UALVP 39401 (W=1.6, D=2.4) and 39412 (W=1.8, D=2.7) are right lower medial incisors that are assigned to Elpidophorus



elegans on the basis of uncatalogued, nearly complete lower dentitions in the UALVP collections. These comparative specimens are from the middle Tiffanian UADW-2 locality of Alberta, a quarry well known for its articulated mammalian dentitions (Archibald et al., 1987). The i1's from the Birchwood locality are laterally compressed, making them deep relative to their width. The teeth are spatulate with chisel-shaped tips. They bear posterior "margoconids", similar to but less pronounced than those of plesiadapids, but lack margocristids. Using UALVP 39400 and uncatalogued specimens from the middle Tiffanian UADW-2 locality, the orientation of i1 in the jaw can be determined. The tooth is procumbent and raised above the level of the molar row at approximately 45 degrees. The chisel-shaped tip of the tooth is oriented obliquely anterolingually-posterolabially.

i2. The i2 of UALVP 39400 (W=1.5, D=2.1) is similar to i1 in most respects. Minor differences between the two teeth include: i2 not as deep as i1; the occluding surface of the crown of i2 is slightly smaller than that of i1; and the chisel-shaped tip of i2 is less oblique to the long axis of the tooth row.

I1. UALVP 39391 (W=3.6, D=3.5) is an isolated left upper central incisor. It is most similar to AMNH 33857, a right upper central incisor from the early Tiffanian Scarritt Quarry referred to Elpidophorus elegans by Szalay (1969:plate 26, figs. 3-6). UALVP 39391 differs only slightly in size and morphology from a UALVP, uncatalogued right central incisor from the lower level of the middle Tiffanian Joffre Bridge Roadcut locality. UALVP 39391 also accords well with the description of AMNH 33857 given by Szalay (1969:221), but bears additional cuspules ("lobules" of

Szalay, 1969:221) along the lateral margin of the crown, giving the lateral margin of the tooth the appearance of a continuous papillate ridge.

DP4. UALVP 39407 (L=3.2, AW=3.8, PW=4.3) is a worn, right upper deciduous fourth premolar assigned to Elpidophorus elegans on the basis of its size, morphology, lack of roots, and wear characteristics. UALVP 39407 is approximately the same size as permanent fourth upper premolars of E. elegans from the Birchwood locality (Lave= 3.73, Wave=4.77). It is molariform with low cusps, strong conules, and a large metastylar lobe. The conical paracone and metacone are worn, but appear to have been equal in size. A deep crevasse-like trigon basin lies between the cones and conules. A distinct postmetacrista curves posterolabially from the apex of the metacone to a small metastyle on the metastylar lobe. The metaconule is prominent, conical, and lies approximately one-third the distance from the metacone to the hypocone. The paraconule and anterolingual slope of the paracone are extremely worn, producing a shallow basin bordered by the pre- and postparaconule cristae. The protocone is located slightly anterior of the tooth's midline, and is less worn than the para- and metacone. A distinct cingulum borders the tooth lingual to the para- and metacone. A small hypocone is present on this cingulum directly lingual of the metaconule. The enamel of the tooth is slightly wrinkled in several areas, as it is in permanent teeth of E. elegans. UALVP 39407 lacks roots and evidence for substantial roots. Poorly-developed or lacking roots are thought to be indicative of deciduous teeth (West, 1971). Wear is not evenly distributed across the tooth. Instead, it is focused on the paracone, paraconule, and parastylar areas. This uneven wear pattern,

which is attributed to an undeveloped dental arcade and likely an immature root system (Hillson, 1986; West, 1971), is characteristic of deciduous teeth.

**Discussion:** To my knowledge, none of the deciduous teeth of Elpidophorus elegans have been formally described. Stonley (1988) assigned six UALVP specimens to the DP4 position in his as yet unpublished description of a new species of Elpidophorus ("E. clivus") from the late Tiffanian Swan Hills locality of Alberta (see Plate 10, figs. D, E). Due to the small size (Lave=3.14, Wave=2.37 [Stonley, 1988:table 12]) and submolariform nature of the Swan Hills specimens, I reinterpret them as DP3's. There are three points of evidence which support the re-interpretation of Stonley's (1988) specimens as DP3's, and the DP4 assignment of UALVP 39407:

- 1) Since DP4's function as molars in the deciduous dentition (West, 1971), they must be molariform in structure. Stonley's (1988) "DP4's" are submolariform, while UALVP 39407 is fully molariform.
- 2) Stonley's (1988) "DP4's" are more equivalent in size (especially width) to the P3's of both E. elegans and "E. clivus", and not P4's. Stonley (1988) reported the dentition of "E. clivus" as about 15 percent smaller than that of E. elegans. See Stonley (1988:table 12) and Table 4 for measurements of the permanent premolars of "E. clivus" and Birchwood E. elegans, respectively.
- 3) Stonley's (1988) descriptions of the P3's and "DP4's" of "E. clivus" are very similar; teeth from both positions are three-rooted, longer than wide, and have triangular occlusal outlines. As mentioned above, deciduous fourth premolars function

as molars, and should be more fully molariform.

This finding of Elpidophorus elegans at the Birchwood locality represents a geographical range extension of this species northwards from central Alberta.

Order PRIMATES Linnaeus, 1758

Suborder PLESIADAPIFORMES Simons, 1972

Superfamily PAROMOMYOIDEA Simpson, 1940

Family PAROMOMYIDAE (Simpson, 1940)

PLESIOLESTES Jepsen, 1930

PLESIOLESTES sp., cf. P. SIROKYI Szalay, 1973

(Plate 12, figs. A, B)

**Holotype of Plesiolestes sirokyi:** AMNH 92135, right dentary fragment with m2-m3.

**Type Locality:** Saddle locality, Fort Union Formation, Fremont County, Bison Basin, Wyoming.

**Known Age and Distribution of Plesiolestes sirokyi:** Early Tiffanian (late Paleocene) of Wyoming (type locality [Szalay, 1973; Szalay and Delson, 1979]).

**Referred Specimen:** UALVP 39301, M1.

**Description:** UALVP 39301 (L=3.0, W=4.7) is an isolated right first upper molar with well-developed cristae and conules. The tooth is missing a small portion of enamel along the posterior part of the styler shelf, but is otherwise only slightly

worn and preserved in excellent condition. The nannopithec fold, or postprotocingulum ["distal cingulum" of Szalay (1973)], seems to connect at or near the apex of the protocone. UALVP 39301 is assigned to Plesiolestes sp., cf. P. sirokyi on the basis of its size and overall resemblance to an M2 in the P. sirokyi hypodigm, Amherst College Museum No. 4875 (Szalay, 1973:fig. 5B-E). UALVP 39301 differs from ACM 4875 (L=3.7, W=5.4) in being slightly smaller, a difference easily accounted for by their different tooth positions. UALVP 39301 is less similar morphologically to UALVP 28541, an M2 from the earliest Tiffanian Cochrane 2 locality assigned to Plesiolestes cf. P. sirokyi by Youzwysyn (1988). The Cochrane 2 specimen is wider relative to length and has a more transverse occlusal outline.

**Discussion:** The three known species of Plesiolestes, P. problematicus Jepsen 1930b, P. (=Torrejonina) wilsoni Gazin 1968, and P. sirokyi Szalay 1973, have so far been identified only from Wyoming in deposits restricted to the latest Torrejonian through early Tiffanian. Three isolated molars from the earliest Tiffanian Cochrane 2 locality of Alberta have been assigned to Plesiolestes cf. P. sirokyi by Youzwysyn (1988).

In describing the upper molars of P. sirokyi, Szalay (1973) offered only a single morphological difference between that species and P. problematicus, a higher attachment point of the distal cingulum (nannopithec fold or postprotocingulum) to the protocone in the latter. Quantitatively, the teeth of P. sirokyi are over 50 percent larger than those of P. problematicus. With its larger size and nannopithec fold

attaching on or near the apex of the protocone, UALVP 39301 seems to be intermediate in morphology between P. problematicus and the more progressive P. sirokyi.

The presence of Plesiolestes sp., cf. P. sirokyi at the Birchwood locality is the second occurrence of this lineage outside of Wyoming, after specimens described by Youzwyshyn (1988). Temporally, this occurrence extends the upper geological range of this species and genus from the early to middle Tiffanian.

IGNACIUS Matthew and Granger, 1921

IGNACIUS FRUGIVORUS Matthew and Granger, 1921

(Plate 12, figs. C, D)

**Holotype:** AMNH 1736<sup>2</sup>, left maxillary fragment with P2, P4, M1-2.

**Type Locality:** Mason Pocket, "Tiffany" beds, San Jose Formation, La Plata County, San Juan Basin, Colorado.

**Known Age and Distribution:** Earliest Tiffanian (late Paleocene) of Wyoming (Keefer Hill locality ["Shotgun local fauna"], Fort Union Formation, Fremont County, Wind River Basin [Gazin, 1971]); early Tiffanian of Montana (Scarritt Quarry, Melville Formation, Sweetgrass County, eastern Crazy Mountain Basin [Simpson, 1936]); middle Tiffanian of Alberta (UADW-2 locality, Paskapoo Formation, Blindman River [Fox, 1984a; 1990a]; Joffre Bridge Roadcut locality, lower level, Paskapoo Formation, Red Deer River [Fox, 1990a]; HHW-UL, Paskapoo Formation, Hand Hills [Fox, 1990a]), North Dakota (Brisbane and Judson localities, Tongue River Formation, Grant and Morton Counties, respectively [Holzman, 1978]) and Wyoming (Cedar Point Quarry, Polecat Bench Formation, Bighorn County, northern Bighorn Basin [Rose, 1981]; Type Chappo locality, Wasatch Formation, Lincoln County [Gunnell, 1994]); late Tiffanian of Alberta (Swan Hills site 1, Paskapoo Formation, Swan Hills [Stonley, 1988]; Police Point locality, Ravenscrag Formation, Cypress Hills



[Krishtalka, 1973; Krause, 1978]; Canyon Ski Quarry, Paskapoo Formation, Red Deer [Krause, 1978; Fox, 1990a]), Saskatchewan (Roche Percée local fauna, Ravenscrag Formation [Krause, 1978]), Wyoming (Locality V-77005, Fort Union Formation, Sweetwater County, eastern Rock Springs Uplift [Winterfeld, 1982]), Colorado (type locality [Simpson, 1935c]), Montana (Circle and Olive localities, Tongue River Formation, McCone and Powder River Counties, respectively [Wolberg, 1979]) and Texas (Joe's Bone Bed, Black Peaks Formation, Big Bend National Park [Schiebout, 1974]).

**Referred Specimen:** UALVP 39302, left maxillary fragment with M1-3.

**Description and Discussion:** UALVP 39302 is a left maxillary fragment preserving the upper molars which display several features diagnostic of *I. frugivorus*. A wide ranging species in both time (earliest to late Tiffanian) and space (Alberta to Texas), *Ignacius frugivorus* is a common member of most Tiffanian communities. More than adequately described and figured by Simpson (1955) and Krause (1978), this species will not be described further here.

Superfamily PLESIADAPOIDEA Trouessart, 1897

Family PLESIADAPIDAE Trouessart, 1897

PRONOTHODECTES Gidley, 1923

PRONOTHODECTES GAOI Fox, 1990

(Plate 12, figs. E-H; Table 5)

**Holotype:** UALVP 31238, incomplete left dentary containing p3-4, m1-2 and alveoli for i1-2, c, and p2.

**Type Locality:** UADW-2 locality, Paskapoo Formation, Blindman River, Alberta.

**Known Age and Distribution:** Middle Tiffanian (late Paleocene) of Alberta (UADW-1 and UADW-2 localities, Paskapoo Formation, Blindman River [Fox, 1990b]).

**Referred Specimens:** UALVP 39371, right dentary fragment with p4, m1-3 and alveoli for i1-2, c, and p2-3; UALVP 39372, left dentary fragment with i1, p3, and alveoli for i2, c, p2, p4, m1-3; UALVP 39373, left dentary fragment with m2 and alveoli for i1-2, c, p2-4, and m1.

**Description:** I refer to Pronothodectes gaoi only those specimens that exhibit a

primitive plesiadapid primate lower tooth formula of 2/1/3/3. UALVP 39372 best exhibits this lower tooth formula, clearly showing three alveoli between  $i_1$  and  $p_3$ . In all other respects, the referred dentaries and the teeth they bear differ in only minor details from those of Plesiadapis rex, the most common plesiadapid at the Birchwood locality.

**Discussion:** In his review of the Plesiadapidae, Gingerich (1976) placed Pronothodectes in a basal position within the family, and distinguished it from other plesiadapid genera by its small size and primitive plesiadapid dental formula of 2/2, 1/1, 3/3, 3/3. His plesiadapid phylogeny proposes Pronothodectes as ancestral to the genera Nannodectes, Plesiadapis, Chiromyoides, and Platychoerops, and restricts Pronothodectes to the late Torrejonian. Fox (1990b) discovered evidence of Pronothodectes in the middle Tiffanian sediments of Alberta, and named a new species, P. gaoi. Pronothodectes gaoi is larger than other species of Pronothodectes, its lower molars overlapping the lower end of the size range for Plesiadapis rex (Fox, 1990b, 1991a), while still retaining the primitive lower dental formula of 2/1/3/3.

Gingerich (1991) suggested that specimens which Fox (1990b) referred to Pronothodectes gaoi more accurately pertain to Plesiadapis anceps based upon their large size, expanded and fissured  $m_3$  hypoconulid lobe, and apparent loss of  $i_2$  in some specimens. Gingerich (1991) cited the above listed features as derived characteristics of Plesiadapis, carrying more weight than the primitive tooth formula suggestive of Pronothodectes. Concordant with this premise, he claimed that Fox

(1990b) provided no independent evidence for the age of the type locality, and suggested that the middle Tiffanian UADW-2 locality could easily be early Tiffanian (Ti2) in age.

Fox (1991a) responded to Gingerich's (1991) criticisms by restating independent bio- and palynostratigraphic evidence which indicates a middle Tiffanian (Ti3) age for the UADW-2 locality. He then questioned Gingerich's (1991) methods, which seemed to stress stratigraphic age rather than the morphology of the specimens, as a deciding factor of species determination. Fox (1990b) listed the following morphological features in which isolated teeth of Pronothodectes gaoi differ from those of Plesiadapis rex: overall smaller, although their size range overlaps that of Plesiadapis rex; p3-4 not as swollen; m3 hypoconulid lobe not so "squared"; upper molars are wider proportional to their lengths, have narrower styler shelves, and show less swelling of the cusps and coronal walls.

Despite the above morphological features which aid in separating Pronothodectes gaoi from Plesiadapis rex, Fox (1990b) acknowledged the difficulties in assigning isolated teeth from the Blindman and other Alberta localities (Fox, 1990a) to either taxon in question. Here, I assign to Pronothodectes gaoi only those specimens which exhibit the primitive plesiadapid lower dental formula of 2/1/3/3. Undoubtedly, I have assigned some isolated teeth of Pronothodectes gaoi to Plesiadapis rex, and until more is known about the size and morphological variation of the former species, these allocations should be considered suspect.

PLESIADAPIS Gervais, 1877

PLESIADAPIS REX (Gidley, 1923)

(Plate 13, figs. A-G; Table 6)

**Holotype:** USNM 9828, m2.

**Type Locality:** Locality 13, Fort Union Formation, Sweetgrass County, Crazy Mountain Basin, Montana.

**Known Age and Distribution:** Middle Tiffanian (late Paleocene) of Alberta, Montana, North Dakota, and Wyoming (numerous localities [see Gingerich, 1976; Fox, 1990a])

**Referred Specimens:** UALVP 39325-39334, I1's; UALVP 39359, maxillary fragment with P3-4, M1-3; UALVP 39341-39343, P4's; UALVP 39360-39362, M1's; UALVP 39363-39365, M2's; UALVP 39366, maxillary fragment with M2-3; UALVP 39367-39370, M3's; UALVP 39313, nearly complete dentary with i1, p4, m1-3; UALVP 39346, UALVP 39314-39319, 39321-39324, i1's; UALVP 39335, p3; UALVP 39346, dentary fragment with p3-4, m1-2; UALVP 39345, dentary fragment with p4, m1-3; UALVP 39336-39340, p4's; UALVP 39344, dentary fragment with m1-2; UALVP 39347, dentary fragment with m1-2; UALVP 39348-39350, 39374, m1's; UALVP 39351-39355, m2's; UALVP 39356, 39357, 39375, m3's.

**Description:** Adequately described and figured in past publications (Gingerich, 1976; Holtzman, 1978), this species will not be described further here. However, UALVP 39313, a nearly complete left dentary with i1, p4, and m1-3, is noteworthy due to its preservation of the mandibular processes. The dentary has experienced damage between the alveolus for p2 and i1, and on the lingual side of the mandibular condyle. The mandibular condyle, coronoid process and angular process are nearly complete. As noted by Gingerich (1976), the mandibular condyle is raised slightly above the level of the tooth row. The condylar process is subtriangular in shape and extends posterodorsally. The coronoid process is well developed, also extends posterodorsally, and leans labially relative to the long axis of the tooth row. The angle of the mandible extends posteroventrally, its blunt terminus recurved. A central ridge divides the angle of the mandible posteriorly. A large inferior dental foramen is present just beneath, and equidistant along a line between the mandibular condyle and the last molar. The area of the mandibular symphysis is slightly damaged, but relatively extensive along and below the root of the incisor. The relative completeness of UALVP 39313 places it among the best known material of Plesiadapis rex.

**Discussion:** Plesiadapis rex is an important index fossil for the middle Tiffanian (Ti3) Plesiadapis rex/P. churchilli lineage-zone (Gingerich, 1975, 1976; Archibald et al., 1987). See the above discussion of Pronothodectes gaoi regarding the assignment of isolated teeth to Plesiadapis rex.

The means of measurements for the various tooth loci of Birchwood

Plesiadapis rex generally fall within the size range of that species in Gingerich (1976). The measurements for the lower dentition more closely match Gingerich's (1976) than do those for the upper dentition. Size differences between the upper dentitions include: the lone P3 from the Birchwood locality is almost 20 percent smaller than the mean of those in Gingerich's sample; the Birchwood P4's are on average almost 20 percent narrower than those in Gingerich's sample; and, the upper molars in the Birchwood sample are slightly shorter and narrower than those in Gingerich's sample.

Despite these size differences, specimens from the Birchwood locality are morphologically indistinguishable from casts of Plesiadapis rex (PU 20058, left dentary; PU 21448, right maxillary) from Cedar Point Quarry, Wyoming.

Family CARPOLESTIDAE Simpson, 1935

ELPHIDOTARSIVUS Gidley, 1923

ELPHIDOTARSIVUS WIGHTONI Fox, 1984

(Plate 14, figs. A, B; Table 7)

**Holotype:** UA 21001, left dentary fragment with i1-2, c1, p4, m1-3, and alveolus for p3.

**Type Locality:** UADW-2 locality, Paskapoo Formation, Blindman River, Alberta.

**Known Age and Distribution:** Middle Tiffanian (late Paleocene) of Alberta (UADW-1 and UADW-2 localities, Paskapoo Formation, Blindman River [Fox, 1984c; 1990a]; HHW-UL, Paskapoo Formation, Hand Hills [Fox, 1990a]).

**Referred Specimens:** UALVP 39303, right dentary fragment with p4, m1-2; UALVP 39304, right dentary fragment with p4, m2; UALVP 39305, p4.

**Description:** The most nearly complete specimen, UALVP 39303, is a right dentary fragment preserving p4 and m1-2. These tooth positions and others have been well described and figured by Fox (1984c, 1993), and the Birchwood specimens are morphologically identical. Measurements of the Birchwood specimens fall within the



ranges of the hypodigm specimens published by Fox (1984c:table 1).

**Discussion:** The Birchwood locality is the fourth middle Tiffanian locality in Alberta to bear the remains of Elphidotarsius wightoni. This creature is presently unknown from sedimentary basins outside of Alberta. The Birchwood specimens extend the geographic range of the species and genus northwards from central Alberta.

CARPODAPTES Matthew and Granger, 1921

CARPODAPTES HAZELAE Simpson, 1936

(Plate 14, figs. C-E; Pl. 15, figs. A-E; Table 8)

**Holotype:** AMNH 33854, right dentary fragment with p4, m1-3.

**Type Locality:** Scarritt Quarry, Melville Formation, Sweetgrass County, eastern Crazy Mountain Basin, Montana.

**Known Age and Distribution:** Earliest Tiffanian (late Paleocene) of Wyoming (Keefer Hill locality ["Shotgun local fauna"], Fort Union Formation, Fremont County, Wind River Basin [Gazin, 1971]); early Tiffanian of Montana (type locality [Simpson, 1936; Rose, 1975a]); middle Tiffanian of Wyoming (Cedar Point Quarry, Polecat Bench Formation, Bighorn County, northern Bighorn Basin [Rose, 1975a; 1981]) and Alberta (UADW-1, UADW-2, and UADW-3 localities and Mel's Place, Paskapoo Formation, Blindman River [Fox, 1984c; 1990a]; Joffre Bridge Roadcut locality, lower level, Paskapoo Formation, Red Deer River [Fox, 1990a]; HHW-UL, Paskapoo Formation, Hand Hills [Fox, 1990a]); late Tiffanian of Montana (Circle locality, Tongue River Formation, McCone County [Wolberg, 1979]).

**Referred Specimens:** UALVP 39306, left maxillary fragment with P3-4, M1-2; UALVP 39310, i1; UALVP 39309, p4; UALVP 39307, left dentary fragment with p4,

m1-3; UALVP 39308, left dentary fragment with p4, m1.

**Description:** The cheek dentition of Carpodaptes hazelae is well known, and has been adequately figured and described in the literature (Simpson, 1936; Rose, 1975a; Fox, 1993). I will here describe only the lower medial incisor, which has received less attention than the cheek dentition.

i1. UALVP 39310 (W=1.2, D=1.8) is a worn lower right medial incisor. It is referred to C. hazelae on the basis of comparison with uncatalogued dentaries in the UALVP collections from the middle Tiffanian UADW-2 locality that preserve associated anterior and cheek dentitions. With a distinct margoconid and margocristid, this laterally-compressed tooth is less spatulate than those referred to other carpolestid genera (see Rose, 1975a:fig. 5). The crown and root of the tooth form a gentle labially convex arc. The tip of UALVP 39310 is slightly worn, producing a wear facet nearing a cross section of the tooth that is canted labially. Among the species of Carpodaptes, this tooth is deeper and wider than that of C. cygneus (Krause, 1978:fig. 2 D, E, table 1), and has a less elongate crown with only one margocristid (Krause cites two ridges on the medial incisor of C. cygneus). It is less spatulate than UW 6530, a medial incisor referred by Rose (1975a:fig. 5B) to ?Carpodaptes sp..

**Discussion:** The linear dimensions of the Birchwood sample of Carpodaptes hazelae are similar to those of the holotype (Simpson, 1936), and qualitatively, the Birchwood specimens are very similar to those figured in the literature. This

discovery represents a geographical range extension for the species, northwards from central Alberta.

## Family SAXONELLIDAE Russell, 1964

## SAXONELLA Russell, 1964

## SAXONELLA sp. nov. (unnamed)

(Plate 15, figs. F-H)

**Referred Specimen:** UALVP 39498, m2.

**Description:** UALVP 39498 (L=1.7, AW=1.5, PW=1.8) is an isolated lower second molar that is morphologically virtually identical to the m2 of Saxonella naylori (Fox, 1984a, 1991b). Two dentary fragments of S. naylori which bear m2's have been recovered from middle Tiffanian localities in Alberta; UALVP 29357 (not 29537, as in Fox, 1991b:340) from the UADW-2 (type) locality, and UALVP 29358 (not 29538, as in Fox, 1991b:340) from the HHW-UL locality. The anterior and posterior widths of the Birchwood specimen are 15 and 17 percent wider, respectively, than either the m2 of UALVP 29357 (L=1.7, AW=1.3, PW=1.5 [Fox, 1991b]) or UALVP 29358 (L=1.6, AW=1.3, PW=1.5 [Fox, 1991b]). The m2's of the genotype, S. crepaturae Russell, 1964 have not been described. Superficially similar to the m2's of carpolestids, UALVP 39498 differs from those of members of the Carpolestidae in having a talonid slightly wider than trigonid, shelf-like paracristid, and broad U-shaped talonid notch.

**Discussion:** The type locality of Saxonella is in the fissure deposits at Walbeck, near Magdeburg, Germany (Russell, 1964). Russell (1964) described the

genotype, S. crepaturae, on the basis of two dentary fragments and several isolated teeth. Two decades later, Fox (1984a) reported the first North American occurrence of Saxonella from the middle Tiffanian UADW-2 locality (Paskapoo Formation, Blindman River), making it one of several known genera of Euramerican Paleocene mammals (Fox, 1991b). This new North American species, S. naylori Fox, 1991, is similar in size to the genotype, and was interpreted by its author to be more primitive than the latter species. The size of UALVP 39498 precluding it from S. naylori, the Birchwood specimen likely represents a new and larger North American species of Saxonella. It is recognized here as a new species, but remains unnamed, as the material in hand prevents an adequate diagnosis.

Order CARNIVORA Bowdich, 1821

Family VIVERRAVIDAE Wortman and Matthew, 1899

PROTICTIS Matthew, 1937

PROTICTIS PARALUS Holtzman, 1978

(Plate 16, figs. A-F; Table 9)

**Holotype:** SMM P77.6.64, right dentary fragment with c, p4, m1-2, and alveoli for p1-3.

**Type Locality:** Judson locality, Tongue River Formation, Morton County, North Dakota.

**Known Age and Distribution:** Middle Tiffanian (late Paleocene) of Alberta (UADW-2 locality, Paskapoo Formation, Blindman River [Fox, 1990a]), North Dakota (type locality and Brisbane locality, Tongue River Formation, Grant County [Holtzman, 1978]), and Wyoming (Cedar Point Quarry, Polecat Bench Formation, Bighorn County, northern Bighorn Basin [Gingerich and Winkler, 1985]; Type Chappo locality, Wasatch Formation, Lincoln County [Gunnell, 1994]).

**Referred Specimens:** UALVP 39414, P4; UALVP 39415, p4; UALVP 39416, m1; UALVP 39417, m2.

**Description:** Protictis paralus is fairly well represented in middle Tiffanian deposits of Alberta, North Dakota, and Wyoming. Holtzman (1978) described and figured M1, p4, and m1-2 in his original description. Gingerich and Winkler (1985) refigured the same specimens, but provided no further description. The specimens of P. paralus from the Birchwood locality fall within the size ranges of those teeth reported from the Judson and Brisbane (Holtzman, 1978:table 31) and Cedar Point Quarry (Gingerich and Winkler, 1985:table 5) localities. The P4 of P. paralus is here described for the first time.

P4. UALVP 39414 (L=5.3, W=3.2) is an isolated left upper fourth premolar assigned to Protictis paralus on the basis of comparative material in the UALVP collections. UALVP 39414 accords well with an uncatalogued maxillary fragment of P. paralus containing P3-4 and M1; this specimen was mentioned, but not described by Fox and Youzwysyn (1994). The crown of UALVP 39414 is carnassiform and triangular in occlusal outline. The large central paracone is bordered anteriorly by a small conical parastyle, and posteriorly by a sharp metastylar blade. The paracone is larger than the other cusps, slightly compressed labiolingually, and leans posteriorly. A deep "carnassial notch" separates the paracone and metastylar blade, with the ventral apex opening into a "keyhole", as in most other Paleocene viverravids (Fox and Youzwysyn, 1994). The protocone is similar in size and shape to the parastyle, and lies on the anterolingually projecting slope of the paracone. The tooth is concave anteriorly, with a U-shaped depression formed between the projecting parastyle and protocone. A well-defined ridge descends from the apex of the paracone to the labial



side of the protocone. A labial cingulum extends dorsoposteriorly from the labial side of the parastyle to almost the end of the metastylar blade. Two faint bulges appear at the points of origination and termination of the labial cingulum. UALVP 39414 is three-rooted, with the anterior root nearly circular in cross section, and the dominant posterior root labiolingually compressed.

**Discussion:** Contrary to most authors, Stucky and McKenna (1993) place Protictis in the family Didymictidae Flynn and Galiano, 1982. Members of the genus Protictis are common in late Torrejonian and Tiffanian sediments ranging from New Mexico to Alberta (Gingerich and Winkler, 1985; Fox, 1990a). The most northerly occurrence of the genus is Protictis sp., cf. P. laytoni from the late Tiffanian Swan Hills locality (Stonley, 1988). The occurrence of Protictis paralus at the Birchwood locality represents a range extension for the species northwards from central Alberta.

RAPHICTIS Gingerich and Winkler, 1985

RAPHICTIS GAUSION Gingerich and Winkler, 1985

(Plate 16, figs. G-I)

**Holotype:** PU 21244, left dentary fragment with p3-4, m1-2.

**Type Locality:** Cedar Point Quarry, Polecat Bench Formation, Bighorn County, northern Bighorn Basin, Wyoming.

**Known Age and Distribution:** Middle Tiffanian (late Paleocene) of Wyoming (type locality [Gingerich and Winkler, 1985]).

**Referred Specimens:** UALVP 39418, 39419, m1's.

**Description:** UALVP 39418 (L=3.9, AW=2.2, PW=1.7) is an isolated right lower first molar virtually identical to that of the holotype (compared using UALVP 31198, an epoxy cast of PU 21244). The Birchwood specimen exhibits various generic features of Raphictis, including sharper cusps on m1 and an angled talonid (Gingerich and Winkler, 1985). UALVP 39418 and 39419 (AW=2.0) are morphologically similar to, but have slightly narrower trigonids than, the small sample (n=5) of Raphictis gausion reported from Cedar Point Quarry (AWave=2.48 [Gingerich and Winkler, 1985:table 10]). As these small samples from the Birchwood locality

and Cedar Point Quarry grow with additional collecting, it is quite likely that sample size will be positively correlated with wider observed ranges for all linear measurements.

**Discussion:** Fox (1990a) reported Raphictis sp., cf. R. gausion from the middle Tiffanian UADW-2 and HHW-UL localities of Alberta, and the late Tiffanian Roche Percée local fauna of Saskatchewan. The majority of these specimens are morphologically similar to R. gausion, but are smaller in size, possibly representing a new species. The discovery of Raphictis gausion at the Birchwood locality represents the first reported discovery of this species outside of the Wyoming type locality.

Order "CONDYLARTHRA" Cope, 1881

Family ARCTOCYONIDAE Giebel, 1855

Subfamily OXYCLAENINAE Scott, 1892

HOROLODECTES, gen. nov.

**Etymology:** horologion, Gr., "clock", "hourglass": dectes, Gr., "biter". In reference to the peculiar nature of the lower premolars which, in occlusal view, possess an "hourglass" shape.

**Type and Only Species:** Horolodectes albertensis, sp. nov.

**Known Distribution:** Late Paleocene, Alberta

**Diagnosis:** As for the type and only species.

HOROLODECTES ALBERTENSIS, sp. nov.

(Plate 17, figs. A-G; Pl. 18, figs. A-E; Table 10)

**Etymology:** albertensis, of Alberta. In reference to the type locality.

**Holotype:** UALVP 39201, right dentary with p2-4, m2-3, and alveoli for p1 and c.

**Type Locality:** Birchwood locality, outcrop on north side of Modeste Creek downstream of its confluence with Bucklake Creek, Paskapoo Formation, central Alberta (exact coordinates are available to qualified researchers through the University of Alberta Laboratory for Vertebrate Paleontology).

**Known Age and Distribution:** Middle Tiffanian (late Paleocene) of central Alberta (type locality and UADW-2 [Fox, 1990a; pers. obs.]).

**Hypodigm:** UALVP 39200, right dentary with p2-4, m1-3, and alveoli for p1, c, and i1-3; UALVP 39201, holotype, right dentary with p2-4, m2-3, and alveoli for p1 and c; UALVP 39292, p3; UALVP 39293, p4; UALVP 39291, m1; UALVP 39290, m2-3; UALVP 39463, right maxillary fragment with P3-4; UALVP 39464, 39465, P4's. All hypodigm specimens are from the Birchwood locality.

**Diagnosis:** Differs from all other members of the Oxycloeninae in possessing the following suite of features: smaller, length of lower molar row less than 8.5 mm; retaining p1-p4; p4 simple, with only incipient metaconid and hypoconulid and poorly developed cingula; trigonids and talonids subequal in height; paraconid smallest and lowest trigonid cusp, decreasing in size from m1 to m3; protoconid decreasing in size and height from m1 to m3; accessory cuspule ("entoconulid" of Hershkovitz, 1971) present on m3 directly anterior to the entoconid; P2 two-rooted; P3 and P4 three-

rooted, premolariform, bearing massive paracone and protocone; P2-4 leaning strongly posteriorly at about 30 degrees. Species diagnosis is as for the genus.

**Description:** The holotype of Horolodectes albertensis, UALVP 39201, is a nearly complete dentary with p2-4 and m2-3. As well as the preserved dentition, UALVP 39201 displays two large alveoli anterior to p2. The alveolus immediately anterior to p2 is large, slightly laterally compressed, and likely held a single-rooted p1. The most anterior alveolus is not well-preserved, but likely held a relatively large canine. There is little or no diastema present between p2 and the alveolus for p1, but a small (<1 mm) diastema exists between p2 and p3. The p4 is split and slightly separated transversely through its midlength. The crack is filled with sediment, but this does not obscure any tooth morphology. The majority of the mandibular symphysis scar and its associated ridge are intact. Most of the ventral margin of the dentary is absent due to breakage. The mandibular condyle and most of the ascending ramus are not preserved. Two mental foramina are present on the labial surface of the dentary, ventral to the midlength of p2, and the posterior root of p3, respectively. The teeth of the holotype and other specimens are described in detail below.

i1. The first lower incisor is represented only by its alveolus, displayed on UALVP 39200. This alveolus housed a large medial incisor that projected more mesially than dorsally, and ascended at a very slight angle (approx. 10 degrees) from horizontal. The alveolus for i1 is suboval in cross section, with the narrow ends of the oval oriented dorsolingually-ventrolabially at approximately 60 degrees.

i2. The first lower incisor is represented only by its alveolus, displayed on UALVP 39200. The alveolus for i2 suggests that the enclosed tooth projected more mesially than dorsally, and as in i1, ascended at a very slight angle from horizontal. The alveolus for i2 is subrectangular in shape, inclined in the same orientation as that for i1, but at a slightly shallower angle (approximately 50 degrees).

i3. The first lower incisor is represented only by its alveolus, displayed on UALVP 39200. The alveolus for i3 is much smaller than those for i1-2, circular in cross section, and ascends at a steeper angle, nearing a vertical orientation. The tooth housed in this alveolus was undoubtedly the smallest incisor and, unlike i1-2, it had a near vertical orientation.

c1. The lower canine is represented only by its alveolus, displayed on the holotype and UALVP 39200. The alveolus for the lower canine is large, semicircular in cross section, and oriented slightly mesially. Judging from the size of its alveolus, the canine may have been the tallest tooth in the tooth row. In occlusal view, the alveolus is positioned more toward the labial edge of the dentary.

p1. The first lower premolar is represented only by its alveolus, displayed on the holotype and UALVP 39200. The alveolus for p1 lies immediately anterior to p2. Semicircular in cross section and smaller than the alveolus for p2, this alveolus is near vertical in its orientation. The p1 likely resembled p2, but was smaller and single-rooted.

p2. The p2's of Horolodectes albertensis are two-rooted, with roots diverging strongly anteroposteriorly. The crown of a second lower premolar is simple and

laterally compressed, dominated by a protoconid that leans slightly towards the posterior. An incipient talonid is positioned slightly lingually rather than directly posteriorly, and no basin is present. The crown is inflated slightly above the root bases, producing a weak "hourglass" shape in occlusal view, with the posterior lobe being the larger. The lingual side of the crown is flat, while the labial side is weakly convex.

p3. The p3's of Horolodectes albertensis are two-rooted, with roots diverging weakly anteroposteriorly. The crown is as for p2, except slightly larger and taller. A weak ridge descends from the apex of the protoconid to an incipient metaconid located anterolingually; the ridge is also suggested on p2. The posterolingually placed unicuspid heel is stronger than that of p2, but still lacks a basin. Three ridges descend posteriorly from the apex of the protoconid; the first descends posterolingually to the single heel cusp, the hypoconulid; the second descends posterolabially, but does not reach the base of the crown; the third descends directly posteriorly and terminates on the heel just labial to the hypoconulid. The "hourglass" shape in occlusal view is better defined than that of p2, but proportions differ slightly. The posterior portion of p3 is significantly larger than that of its anterior counterpart. The lobes of the "hourglass" project more labially than lingually, while the lingual side of the crown remains nearly flat.

p4. The p4's of Horolodectes albertensis are the largest and tallest of the known teeth for this species. The p4's are two-rooted, with roots nearly parallel with one another. The protoconid is large and laterally compressed as in p2 and p3, but



taller and larger. A ridge descends anterolingually from the apex of the protoconid to the position of the incipient metaconid, as on p3. A cusp at the metaconid position, however, is not well-developed and the ridge continues posteriorly to approximately the midlength of the tooth. The posterolingually placed unicuspid heel stronger than that of p3, and a very small crevasse-like basin is present. As on p3, three ridges are present, descending posterolingually, posterolabially and directly posteriorly from the apex of the protoconid. The first of these ridges is strong but irregular, as the enamel forming this ridge is somewhat wrinkled. The second ridge travels straight and strong near the apex of the protoconid, but dissipates before it reaches the base of the crown. The third ridge is similar to the first in character. Wrinkled enamel is present, mostly posteriorly on the descending slope of the protoconid, but is also seen on the lingual crown surface. The "hourglass" shape present in p2-3 is retained in p4, but is more pronounced. The lobes are subequal in size, with the posterior one being the larger. The lobes of the "hourglass" project more labially than lingually, with the lingual side of the crown remaining nearly flat.

m1. The m1 of Horolodectes albertensis differs from m2 in having a trigonid relatively higher than the talonid. The paraconid on m1 is more distinct and further distanced from the metaconid, making the trigonid longer anteroposteriorly than on m2. The protocristid of m1 extends less transverse across the tooth's length, and the protoconid is larger and taller.

m2. The m2 of Horolodectes albertensis leans lingually relative to the premolars. The trigonid is higher and narrower than the larger talonid, and is

generally triangular in occlusal outline. The protoconid and metaconid are subequal in size and height, with the metaconid being slightly larger and higher. The paraconid is smaller and lower than the other trigonid cusps. The paraconid is low and triangular, positioned internally from the lingual margin of the trigonid. The paracristid rises gently and extends nearly transversely across the trigonid until it is directly anterior to the protoconid. It then rises sharply up the anterior face of the protoconid to its apex. The metaconid is conical and is positioned slightly posterior to the protoconid. The protocristid is oriented slightly posterolingually-antrolabially, with a wide, U-shaped notch equidistant between the protoconid and metaconid. The prevallid wall below the protocristid leans slightly anteriorly. The protoconid is conical and positioned posterior to the anterior margin of the trigonid. The talonid is wider than long, with straight margins producing an angular occlusal outline. The talonid basin is of moderate depth, its deepest axis extends almost directly posteriorly, terminating just labially of the hypoconulid. On both holotype and paratype, the hypoconulid is low and worn, oval in occlusal outline, appearing as a bulge on the labial slope of the larger entoconid. The entoconid and hypoconid are subequal in size. The entoconid is conical, positioned at the posterolingual corner of the talonid. A small entoconulid is present on the entocristid immediately anterior to the entoconid. The conical hypoconid is separate from the "twinned" entoconid and hypoconulid, positioned slightly anterior to the level of the entoconid, anterior to the posterior margin of the tooth. The postcristid is slightly worn, forming a deep notch about one third the distance from the hypoconulid to hypoconid. This notch corresponds with the most

posterior portion of the talonid basin's deepest axis. The cristid obliqua shows signs of wear, more so than the postcristid. A short but distinct precingulum is positioned anterolabially near the base of the protoconid. A short ectocingulid is also present posterior to the precingulum, at the base of the talonid notch. These cingulids may have originally been united, but later separated by labial wear near the base of the protoconid.

m3. The m3 of Horolodectes albertensis is similar to m2, but differs in having the trigonid and talonid subequal in height, with the talonid narrower and longer. The paraconid is much less distinct than that of m2, and is almost absent. The protoconid is reduced in size and height, while the protocristid extends transversely across the tooth's length. The precingulid continues along the labial tooth margin to join the ectocingulid. The hypoconulid is greatly enlarged, slightly taller than either entoconid or hypoconid, and protrudes posteriorly. The entoconid is much more distinct, although smaller than the entoconid and hypoconulid. The entoconid, along with the "twinning" entoconid and hypoconulid, form a "comb-like" structure that extends along the posterolabial portion of m3.

P3. The P3 of UALVP 39463 (L=2.7, W=2.5) is premolariform, three-rooted, and roughly triangular in occlusal outline. Two cusps form the crown of this tooth, the paracone the larger. A smaller protocone is lingual to the paracone, separated from the latter cusp by a narrow, shallow valley. The paracone is oval in occlusal outline, and slightly labiolingually compressed. Four distinct ridges descend from the apex of the paracone. Two of these ridges extend directly anteriorly and posteriorly,

respectively. The latter ridge descends the posterior face of the paracone, then extends labially just before its junction with the weak postcingulum. A small metastyle is present at the termination of this ridge. The third ridge descends posterolabially, while the fourth descends directly lingually, eventually ascending to the apex of the protocone. As set in the maxillary, the P3 of UALVP 39463 leans strongly posteriorly at approximately 30 degrees. The apices of the paracone and protocone, and the posterior portion of the crown are worn, evidenced by distinct wear facets. These wear facets intersect the plane of the maxillary at approximately 45 degrees. The anterior face of P3 is unworn.

P4. The P4 of UALVP 39463 (L=2.7, W=3.5) is slightly longer and narrower than UALVP 39464 (L=2.5, W=3.7) and UALVP 39465 (L=2.5, W=3.6). Each P4, like the P3, is three-rooted and bears two cusps on its crown. The paracone, small metastyle, and labial portion of the crowns are similar to the P3, but the lingual portions of the crowns are substantially extended lingually and anteroposteriorly. The P4 of UALVP 39463 leans strongly posteriorly, as does P3. The paracone of P4, similar in size and morphology to that of P3, bears four ridges as in the latter tooth, but the posterior and posterolabially extending ridges are more robust. The ridge which extends directly posteriorly is especially wide and robust, possibly indicating the development of a metacone. The protocone is expanded, relatively and absolutely higher than the protocone of P3, and is separated from the paracone by a narrow and shallow valley. A postprotocrista descends posterolabially from the apex of the protocone, where it joins the strong postcingulum. A small swelling and dorsal

fluctuation of the postcingulum occurs in the position of the hypocone, arguably indicating the development of such a cusp. A strong precingulum is present. Parallel with these of P3, strong wear facets mark the posterior half of the crown, especially the posterior faces of the paracone and protocone.

**Discussion:** Fox (1990a:61) reported "Arctocyonidae, new genus and species 1", "Arctocyonidae, new genus and species 2", and "Aphronorus sp." in his faunal list of the middle Tiffanian UADW-2 locality near Red Deer, central Alberta. Horolodectes albertensis is present among this undescribed material, represented by four incomplete dentaries and two maxillary fragments, only one of which displays any additional tooth positions. An uncatalogued maxillary with P2-4 exhibits a portion of the premolar dentition anterior to P3. The P2 (L=1.6, W=1.2) is two-rooted, oval in occlusal outline, and about one-half the size and height of P3. A single crista descends posteriorly from the apex of the paracone. A small lingual expansion, foreshadowing the protocone of P3-4, is present over the lingual edge of the large, anteroposteriorly compressed, posterior root. The anterior root is smaller than the former root, and circular in cross-section. There is a small (1.15 mm) diastema between P2 and P3. Overall, the specimens from the Birchwood and UADW-2 localities do not differ significantly in any manner. The upper and lower premolars from the Birchwood locality occlude with precision. Although both the Birchwood and UADW-2 collections contain unidentified therian upper molars, I have been unable to identify suitable specimens which occlude precisely with the lower molars.

Referral of Horolodectes albertensis in the Arctocyoniidae is based on its lack of dental specializations, which precludes placement in other families. Dental plesiomorphies (see Simpson, 1937; Matthew, 1937; Cifelli, 1983) include unspecialized molars, large canines, premolariform p4, and an unreduced number of premolars. These same dental plesiomorphies suggest that Horolodectes albertensis should be placed within the Subfamily Oxycloeninae, the basal group of all condylarths. Members of this subfamily include the smallest arctocyonids (Matthew, 1937). Other oxycloenines found at the Birchwood locality include Thryptacodon and Chriacus, taxa which cannot be confused with the new species due to its small size.

The presence of Horolodectes albertensis at the Birchwood and UADW-2 localities, and its apparent absence from more extensively sampled quarries in the northwestern United States may be indicative of a more northerly distribution for this species. This is consistent with the suggestion that quarries in the Paskapoo Formation record a terrestrial ecosystem significantly different from quarries further south in Montana and Wyoming (Fox, 1984b).

CHRIACUS Cope, 1883

CHRIACUS sp., cf. C. PELVIDENS (Cope, 1881)

(Plate 18, figs. F, G)

**Holotype of Chriacus pelvidens:** AMNH 3097, left dentary fragment with p4, m1-m3.

**Type Locality:** Torrejon locality, Nacimiento Formation, San Juan Basin, New Mexico.

**Known Age and Distribution of Chriacus pelvidens:** Late Torrejonian (middle Paleocene) of New Mexico (type locality [Matthew, 1937]) and Wyoming (Swain Quarry, Fort Union Formation, Carbon County, Washakie Basin [Rigby, 1980]); latest Torrejonian of Wyoming (Rock Springs locality V-77014, Fort Union Formation, Sweetwater County, eastern Rock Springs Uplift [Winterfield, 1982]); earliest Tiffanian (late Paleocene) of Alberta (Cochrane 2 locality, Porcupine Hills Formation, Cochrane [Youzwysyn, 1988]), Wyoming (Little Muddy Creek locality, Evanston Formation, Lincoln County [Gazin, 1969]) and Montana (Douglass Quarry, Melville Formation, Sweetgrass County, eastern Crazy Mountain Basin [Krause and Gingerich, 1983]); early Tiffanian of Wyoming (Saddle locality, Fort Union Formation, Fremont County, Bison Basin [Gazin, 1956a]).

**Referred Specimens:** UALVP 39222, M1.

**Description and Discussion:** UALVP 39222 (L=8.6, W=9.2) is a left upper first molar in relatively unworn condition. Morphologically, it differs only in subtleties from teeth assigned to C. pelvidens from the earliest Tiffanian Cochrane 2 locality (Youzwysyn, 1988). It also shows a close resemblance to PU23600, an LM1 of C. pelvidens from the earliest Tiffanian Douglass Quarry, figured in Krause and Gingerich (1983:fig. 21A). The protrusion of the styler areas give UALVP 39222 a subtriangular occlusal outline, and a concave posterior margin. It is slightly larger, especially longer, than the Cochrane 2 teeth (e.g., UALVP 24979, L=7.3, W=9.1), as well as the range of C. pelvidens M1 sizes from Swain Quarry (Rigby, 1980). It is also longer than the M1's from Little Muddy Creek (Gazin, 1969). However, most of the difference in length of these molars can be accounted for by the anterior extension of the parastylar area and, especially, the posterior extension of the metastylar area in UALVP 39222. The development of the para- and metastylar areas are undoubtedly a variable feature, and likely represent intraspecific variation.



THRYPTACODON Matthew, 1915

THRYPTACODON AUSTRALIS Simpson, 1935

(Plate 19, figs. A-H)

**Holotype:** AMNH 17384, associated lower jaws, nearly complete, with c-m3 both sides except Lp2. Left M2 and skeletal parts possibly associated.

**Type Locality:** Mason Pocket, "Tiffany" beds, San Jose Formation, La Plata County, San Juan Basin, Colorado.

**Known Age and Distribution:** Middle Tiffanian (late Paleocene) of Wyoming (Type Chappo locality, Wasatch Formation, Lincoln County [Gunnell, 1994]; Cedar Point Quarry, Polecat Bench Formation, Bighorn County, northern Bighorn Basin [Rose, 1981]) and North Dakota (Brisbane and Judson localities, Tongue River Formation, Grant and Morton Counties, respectively [Holtzman, 1978]); late Tiffanian of Colorado (type locality [Simpson, 1935c]) and Saskatchewan (Roche Percée local fauna, Ravenscrag Formation [Fox, 1990a]).

**Referred Specimens:** UALVP 39233, DP4; UALVP 39230, right dentary fragment with m1-2; UALVP 39231, m2; UALVP 39232, m3.

**Description:** DP4. UALVP 39233 is the lingual portion of a deciduous left

upper fourth premolar that has undergone significant wear. Due to breakage and wear, the present measurements of the tooth only moderately reflect its initial size. It has a minimum length of 4.8 mm and a minimum width of 5.2 mm, of which the width only is substantially underrated due to the absence of the stylar shelf. It differs from M1 in having a more curved anterolingual edge and a less protrusive hypocone. UALVP 39233 is most similar to UA 9643, an undescribed LDP4 from the late Tiffanian Roche Percée local fauna of Saskatchewan.

m1. UALVP 39230 is a right dentary fragment which preserves m1-2 in place in relatively unworn condition. The crowns of both teeth lean slightly lingually. The m1 (L=6.0, AW=3.4, PW=4.2) has a narrow triangular trigonid and a wider subrectangular talonid. The trigonid is much higher than the talonid. The paraconid is distinct, but lower than the other trigonid cusps, and leans anteriorly. An entoconulid is well developed anterior to the "twinning" entoconid and hypoconulid, quite similar to the m3 of Horolodectes albertensis. The massive hypoconid is the dominant talonid cusp.

m2. The m2 of UALVP 39230 (L=6.3, AW=4.5, PW=5.4) differs from m1 in being slightly longer and much wider. The trigonid and talonid are subequal in height, with the talonid slightly lower but much wider than trigonid. The paraconid is reduced, in a more median position, and still juts anteriorly as in m1. The entoconulid is weaker, while the ectocingulid is stronger. UALVP 39231 is an m2 talonid (PW=5.5) which corresponds closely to the m2 of UALVP 39230 in morphology and size.

m3. UALVP 39232 (L=6.0, AW=4.6, PW=4.0) is an isolated left third lower molar in unworn condition. It differs from m1 and m2 in having a talonid that is much longer and slightly lower than trigonid. The paraconid is little more than a median swelling on the paracristid. The entoconulid is absent, and the hypoconulid projects posteriorly.

**Discussion:** Undescribed UALVP specimens from the late Tiffanian Roche Percée local fauna, Saskatchewan are practically indistinguishable from the Birchwood specimens, which also closely match the holotype in size and morphology. This finding represents a geographical range extension northwards from North Dakota for both this genus and species.

Subfamily ARCTOCYONINAE Giebel, 1855

COLPOCLAENUS Patterson and McGrew, 1962

COLPOCLAENUS KEEFERI Patterson and McGrew, 1962

(Plate 20, figs. A-I; Pl. 21, figs. A-F; Table 11)

**Holotype:** MCZ 8355, left m3.

**Type Locality:** Keefer Hill locality ["Shotgun local fauna"], Fort Union Formation, Fremont County, Wind River Basin, Wyoming

**Known Age and Distribution:** Earliest Tiffanian (late Paleocene) of Wyoming (type locality [Patterson and McGrew, 1962]); middle Tiffanian of Alberta (UADW-1 and UADW-2 localities, Paskapoo Formation, Blindman River [Fox, 1990a]).

**Referred Specimens:** UALVP 39215, M3; UALVP 39216, 39217, p3's; UALVP 39218, 39286, p4's; UALVP 39203, right dentary fragment with m1-2; UALVP 39202, right dentary fragment with m2-3; UALVP 39204-39206, m1's; UALVP 39207-39213, m2's; UALVP 39214, m3.

**Description:** Patterson and McGrew (1962) first described this genus and species based on a collection of isolated teeth that included all of the molar dentition except for m1. This tooth, along with p3 and p4 will be described here.

p3. UALVP 39217 is an isolated left lower third premolar measuring 6.0 mm long and 3.5 mm wide near the beginning of the talonid, its widest point. The crown of the tooth is dominated by the protoconid, with accessory cusps both anterior and posterior. Anteriorly, a single serrated ridge descends the anterolabial face of the protoconid to a small but distinct metaconid. Posteriorly, a very strong serrated ridge descends the posterior face of the protoconid to the hypoconulid on the posterior lip of the bicuspid heel. An entoconid lies lingual to the hypoconulid. Both antero- and posterolabial corners of the crown are arcuate, while the lingual corners are rather angular. The enamel is slightly wrinkled on both lingual and labial surfaces.

p4. UALVP 39218 (L=7.9, AW=4.2, PW=4.5) is an isolated left lower fourth premolar in relatively unworn condition. It differs from p3 in being larger, and wider relative to its length. The p4 possesses a stronger metaconid, and the paraconid is a distinct cusp located on the posterolingual slope of the protoconid. A strong labial cingulid is present. The talonid heel remains bicuspid as on p3, but is longer and incipiently basined. The posterior slope of the protoconid bears multiple descending ridges with wrinkled enamel.

m1. UALVP 39203 is a right dentary fragment with m1-2. The m1 differs from the published accounts of m2 in being slightly shorter, but much narrower (L=8.5, AW=4.9, PW=6.2). The m1 trigonid is slightly higher relative to talonid, while also longer but narrower than its m2 counterpart, with a more curved anterior edge. The paraconid is further from the metaconid on m1.

**Discussion:** This sample of Colpoclaenus keeferi is very similar in linear measurements and morphology to that of the type specimen and hypodigm. The morphology of the Birchwood specimens is also essentially identical to specimens from the middle Tiffanian UADW-1 and UADW-2 localities.

This finding represents a geographical range extension for this species and genus, northwards from central Alberta.

Genus CLAENODON Scott, 1892

CLAENODON sp., cf. C. MONTANENSIS (Gidley, 1919)

(Plate 21, figs. G-I; Pl. 22, figs. A-H)

**Holotype of Claenodon montanensis:** USNM 8362, large portion of the skull and mandibles including most of the dentition, parts of fore and hind limbs, and other fragments.

**Type Locality:** Gidley Quarry, Lebo Formation, Sweetgrass County, Crazy Mountain Field, Montana.

**Known Age and Distribution of Claenodon montanensis:** Late Torrejonian (middle Paleocene) of Montana (type locality [Gidley, 1919; Simpson, 1937]) and Wyoming? (?Rock Bench Quarry, Polecat Bench Formation, Park County, Bighorn Basin [Van Valen, 1978; Rose, 1981]; ?Swain Quarry, Fort Union Formation, Carbon County, Washakie Basin [Rigby, 1980]); earliest Tiffanian (late Paleocene) of Montana (Douglass Quarry, Melville Formation, Sweetgrass County, eastern Crazy Mountain Basin [Krause and Gingerich, 1983]) and Alberta (Cochrane 2 locality, Porcupine Hills Formation, Cochrane [Youzwysbyn, 1988]); early Tiffanian of Wyoming (Saddle locality, Fort Union Formation, Fremont County, Bison Basin [Gazin, 1956a]) and Montana (Scarritt Quarry, Melville Formation, Sweetgrass County, eastern Crazy Mountain Basin [Krause and Mars, 1990]).

**Referred Specimens:** UALVP 39227, C1; UALVP 39223, M1; UALVP 39225, 39226, M3's; UALVP 39224, m2.

**Description:** C1. UALVP 39227 is a complete isolated left upper canine that measures 40.8 mm from end of the root to the crown apex. It is fairly robust, slightly curved, laterally compressed, and has a crown bearing a single row of serrations on both the anterior and posterior edges. The posterior serration row terminates 22.3 mm from the crown apex with a step-like descent that corresponds with the cessation of enamel. The anterior serration row is shorter, terminating along with the enamel 17.9 mm from the crown apex. The tooth reaches its maximum anteroposterior diameter of 8.5 mm, and maximum mediolateral diameter of 5.2 mm, just before the termination of the enamel. This canine is similar to those referred to Claenodon sp., cf. C. montanensis (UALVP 25023) by Youzwyshyn (1988) and Claenodon? sp. (UM 80825) by Krause and Gingerich (1983:fig. 19C). Following these authors, I refer this tooth to C. sp., cf. C. montanensis on the basis of its size and serrated posterior edge.

M1. UALVP 39223 (L=7.4, W=8.9) is a left upper first molar, heavily worn, and missing the labial portions of the paracone and metacone. It is referred to C. sp., cf. C. montanensis on the basis of its rectangular occlusal outline and its size, which is slightly smaller than the type of C. montanensis.

M3. UALVP 39225 (L=8.6, W=11.5) and 39226 (L=7.5, W=9.5) are left and right upper third molars, respectively. They are morphologically similar to each other



with the minor provision that UALVP 39226 has a narrower styler shelf and a weaker metaconid. Both specimens are larger than the holotype M3 (L=5.5, W=9.3) and those referred to Claenodon sp., cf. C. montanensis by Youzwyshyn (1988). Despite the size difference between the holotype and Birchwood specimens, these teeth are referred to Claenodon sp., cf. C. montanensis due to their similar morphology.

m2. UALVP 39224 (L=10.9, AW=8.2, PW=8.6) is a right lower second molar that has experienced post mortem loss of enamel along its lingual side and part of the lingual portion of the crown. It is slightly larger than that of the holotype (L=9.4, W=7.5), and differs in only minor details from m2's from the earliest Tiffanian Cochrane 2 locality.

**Discussion:** Although this sample and the holotype of Claenodon montanensis are very similar in morphology, their sizes differ by up to fifty percent. These size differences may not be specific in nature, but their extensive nature prompts me to acknowledge that they may, in fact, be taxonomically meaningful.

This finding represents a geographical (northwards from southern Alberta) and geological (early to middle Tiffanian) range extension for this species.

Family PHENACODONTIDAE Cope, 1881

DESMATOCCLAENUS Gazin, 1941

DESMATOCCLAENUS MEARAE Van Valen, 1978

(Plate 23, figs. A-I)

**Holotype:** UCMP 114308, right maxillary fragment with M1-2.

**Type Locality:** Saddle locality, Fort Union Formation, Fremont County, Bison Basin, Wyoming.

**Known Age and Distribution:** Early Tiffanian (late Paleocene) of Wyoming (type locality [Van Valen, 1978]) and Montana (Scarritt Quarry, Melville Formation, Sweetgrass County, eastern Crazy Mountain Basin [Simpson, 1936; Van Valen, 1978]).

**Referred Specimens:** UALVP 39249, DP4; UALVP 39235, P4; UALVP 39229, 39234, M2's; UALVP 39236, dp3.

**Description:** DP4. UALVP 39249 (L=6.8, W=6.9) is a deciduous left upper fourth premolar. This is a tooth locus that is not represented in the UALVP collections, nor do I know of its description elsewhere. UALVP 39249 is worn, has thin enamel, and is missing its parastylar region. It differs from P4 in being longer,

molariform and less cuspidate. It has a well developed hypocone and conules, and slightly wrinkled enamel.

P4. UALVP 39235 is an upper fourth premolar in relatively unworn condition. It differs little in morphology from specimens of Desmatoclaenus sp., cf. D. mearae from the earliest Tiffanian Cochrane 2 locality (Youzwysyn, 1988). UALVP 39235 (L=6.2, W=6.6) is slightly narrower transversely than similar teeth from the Cochrane 2 locality.

M2. UALVP 39234 (L=8.6, W=10.6) is an unworn left upper second molar. UALVP 39229 (L=8.0, W=10.9) is more worn, and from the right side. Both specimens accord favorably with samples of Desmatoclaenus sp., cf. D. mearae from the Cochrane 2 locality. They differ from the similar molars of Colpoclaenus keeferi figured by Patterson and McGrew (1962:fig. 1) in the following features: longer in relation to width, producing a squared occlusal outline; stronger, more centrally located hypocone; more posteriorly located protocone; and a more deeply invaginated ectoflexus.

dp3. UALVP 39236 is fragmentary, preserving only the posterior portion of the paraconid and talonid. It closely corresponds with teeth from the earliest Tiffanian Cochrane 2 locality assigned to Desmatoclaenus sp., cf. D. mearae, and displays typical primitive phenacodontid characteristics.

**Discussion:** Following Cifelli (1983), Thewissen (1990) did not include Desmatoclaenus in his revised Phenacodontidae (contra Simpson, 1945; West, 1976).

Thewissen excludes Desmatoclaenus from the Phenacodontidae due to the fragmentary nature of the known material, and because this genus shares only symplesiomorphies such as low bunodont crowns and partially molarized p4 with other phenacodontid genera. Due to dissension among more senior researchers, and the fact that Thewissen (1990) does not offer any convincing or constructive alternatives, I will follow here the more traditional view of Desmatoclaenus as a basal member of the Phenacodontidae.

This finding represents a geographic (northwards from Wyoming) and geological (early to middle Tiffanian) range extension for this species and genus.

ECTOCION Cope, 1882

ECTOCION CEDRUS Thewissen, 1990

(Plate 24, figs. A-K; Pl. 25, figs. A-L, Pl. 26, figs. A-I; Tables 12, 13)

**Holotype:** UM 82085, left dentary with p2-m3, and alveoli for c1 and p1.

**Type Locality:** Cedar Point Quarry, Polecat Bench Formation, Bighorn County, northern Bighorn Basin, Wyoming.

**Known Age and Distribution:** Middle and late Tiffanian (late Paleocene) of the Alberta Syncline and Williston, Bighorn, and Wind River Basins (numerous localities [see Thewissen, 1990]).

**Referred Specimens:** UALVP 39250-39252, P2's; UALVP 39253, 39254, DP3's; UALVP 39255, P3; UALVP 39256-39258, DP4; UALVP 39259-39261, P4; UALVP 39240, maxillary fragment with M1-2; UALVP 39241-39244, M2's; 39246-39248, M3's; UALVP 39274-39279, p3's; UALVP 39280, 39281, dp4's; UALVP 39262, dentary fragment with dp4, m1-2; UALVP 39265, m1; UALVP 39266-39270, m2's; UALVP 39271, 39272, m3's; UALVP 39263, dentary fragment with m2-3; UALVP 39264, dentary fragment with m2-3.

**Description:** Ectocion is a near ubiquitous member of Paleocene faunas in

North America, and has thus been described by numerous researchers. Ectocion cedrus has been adequately described and figured by Thewissen (1990) and will not be described further here.

**Discussion:** In his recent review of the Phenacodontidae, Thewissen (1990) based Ectocion cedrus on specimens assigned to ?Phenacodus and Ectocion wyomingensis (in part), stating that this species differs from all others in "its small overall size and several premolar characters" (p.29). He named one other middle Tiffanian species, E. mediotuber, distinguishing it from the contemporaneous E. cedrus using overall size and features of p3. Ectocion cedrus is the smaller of the two species, having premolars relatively smaller than molars and a p3 with a weak hypoconid and high paraconid (Thewissen, 1990:29). He did not cite molar characteristics which would aid in separating the two species in a combined sample. The Birchwood Ectocion sample falls within the size range of E. cedrus, but consists largely of isolated teeth with no association of p3's with molars. However, isolated p3's from the Birchwood locality fit within the morphological and quantitative boundaries of E. cedrus.

Thewissen (1990) proposed habitat specialization as an additional method of distinguishing between the contemporaneous E. cedrus and E. mediotuber. These two species have yet to be found in the same geographic location. Thewissen (1990) proposed that E. cedrus was restricted to poorly-drained near-channel environments, while E. mediotuber was restricted to well-drained floodplain environments. It has

been suggested (Badgley et al., 1995) that habitat preference or habitat-specific mortality could be likely causes of the differential abundances of these lineages. The discovery of the Birchwood specimens in a channel deposit supports the assignment of these specimens to E. cedrus.

PHENACODUS Cope, 1873

PHENACODUS sp.

(Plate 27, figs. A-C)

**Referred Specimens:** UALVP 39237, P4; UALVP 39238, M3.

**Description and Discussion:** UALVP 39237 (L=8.6) is an isolated and worn right upper fourth premolar and represents the most complete specimen of this taxon from the Birchwood locality. UALVP 39238 is a fragment of a left upper third molar which shows little distinctive morphology. While readily recognizable as Phenacodus due to their size and extreme bunodonty, the fragmentary nature of these specimens precludes a specific identification.



Family HYOPSODONTIDAE Trouessart, 1879

DORRALETES Gingerich, 1983

DORRALETES DIMINUTIVUS (Dorr, 1952)

(Plate 27, figs. D-F)

**Holotype:** UM 27231, left maxillary fragment with P4-M2.

**Type Locality:** Dell Creek Quarry, Hoback Formation, Sublette County, Hoback Basin, Wyoming.

**Known Age and Distribution:** Early Tiffanian (late Paleocene) of Alberta (HHW-LL, Paskapoo Formation, Hand Hills [MacDonald, in prep.]); middle Tiffanian of Alberta (HHW-UL, Paskapoo Formation, Hand Hills [MacDonald, in prep.]), North Dakota (Brisbane and Judson localities, Tongue River Formation, Grant and Morton Counties, respectively [Holtzman, 1978]) and Wyoming (Type Chappo locality, Wasatch Formation, Lincoln County [Gingerich, 1983; Gunnell, 1994]); late Tiffanian of Wyoming (type locality [Dorr, 1952]) and Montana (Olive locality, Tongue River Formation, Powder River County [Wolberg, 1979]).

**Referred Specimen:** UALVP 39484, M2.

**Description:** UALVP 39484 (L=2.2, W=3.0) is an unworn, isolated upper right

second molar. It exhibits the rounded cusps and basins, prominent conules, strong cingula, hypocone, and pericone diagnostic of Dorraletes (Gingerich, 1983). UALVP 39484 differs from the holotype of D. diminutivus (Dorr, 1952:fig. 7; Gingerich, 1983:fig. 7) in possessing a larger hypocone located posterior and slightly lingual of the protocone, and moderately well-developed para- and metastyles. I do not consider these differences to be taxonomically significant. Therefore, I conservatively refer UALVP 39484 to Dorraletes diminutivus.

**Discussion:** The discovery at the Birchwood locality of Dorraletes diminutivus, a species previously known only in North Dakota and Wyoming, significantly extends the geographical range of this genus and species to the north.

LITOMYLUS Simpson, 1935

LITOMYLUS sp.

(Plate 27, figs. G-I)

**Referred Specimen:** UALVP 39245, M1

**Description and Discussion:** UALVP 39245 is a heavily worn, left upper first molar. Although major morphological landmarks are visible, details are obscured by wear, and there is little or no enamel left on the crown. UALVP 39245 has a strong rectangular occlusal outline and sharp, angular corners. The major coronal features include a strong hypocone that "squares up" the crown and a very strong and wide postprotocone crista extending posterolabially from the protocone to the metacone. The metacone is larger than the paracone, and lies slightly labially to it.

Strong wear precludes a more precise identification for UALVP 39245, but the distinct, large and internal hypocone and general proportions of the crown in occlusal view readily identify it as pertaining to the genus Litomylus. Its size (L=5.4, W=6.9) places it within the range of Litomylus ishami Gazin, 1956b. This is the largest known species of Litomylus, present in the middle Tiffanian of Wyoming (Gazin, 1956b).

Family MESONYCHIDAE Cope, 1875

DISSACUS Cope, 1881

DISSACUS sp.

(Plate 28, figs. A-F)

**Referred Specimens:** UALVP 39221, px; UALVP 39220, mx.

**Description and Discussion:** UALVP 39220 and 39221 are lower cheek teeth from the left and right sides of the jaw, respectively. Due to the homogenous nature of mesonychid dentitions, these teeth are of uncertain position. Each tooth consists of a protoconid which dominates the tooth crown, an anterior small metaconid, and a posterior blade like hypoconulid. A deep carnassiform notch separates the posterior slope of the protoconid from the anterior slope of the hypoconulid. Neither tooth possesses cingula. UALVP 39221 (L=13.7, AW=6.0, PW=6.0) is the smaller of the two specimens and is likely a p4. UALVP 39220 (L=16.6, AW=6.5, PW=6.0) is the larger, has a paraconid developed lingual to the protoconid, and is likely an m1 or m2.

Order PANTODONTA Cope, 1873

Superfamily PANTOLAMBDOIDEA (Cope, 1883) Simons, 1960

Family TITANOIDEIDAE Simons, 1960

TITANOIDES Gidley, 1917

TITANOIDES PRIMAEVUS Gidley, 1917

**Holotype:** USNM 7934, right p3, m1-3; left m2; left and right parts of ventral region of symphysis. Presumed remainder of type, PU 16490, right I1-3, C, P1-4, M1-3, fragmentary left P2-4, M1-3, both petrosals and occipital condyles.

**Type Locality:** Witter locality, shale member, Sentinel Butte Formation, McKenzie County, North Dakota.

**Known Age and Distribution:** Middle Tiffanian (late Paleocene) of North Dakota (type locality [Gidley, 1917]; Riverdale and Judson localities, Tongue River Formation, McLean and Morton Counties, respectively [Holtzman, 1978]; Cross locality and White's River Basin Survey Site 3, Sentinel Butte Formation, McKenzie County [Hartman and Kihm, 1991]); latest Tiffanian of Wyoming ("Titanoides locality", Fort Union Formation, Fremont County, Bison Basin [Gazin, 1956a; Hartman and Kihm, 1991]; "Silver Coulee" beds, near Princeton Quarry, Polecat Bench Formation, Park County, Bighorn Basin [Simons, 1960; Hartman and Kihm, 1991]); earliest Clarkforkian (latest Paleocene) of Colorado (Plateau Valley local

fauna, Debeque ("Wasatch") Formation, Mesa County [Patterson, 1939; Gazin, 1956a; Simons, 1960; Hartman and Kihm, 1991]).

**Referred Specimens:** UALVP 39489, PX; UALVP 39486, 39487, M3's; UALVP 39488, 39490, MX's; UALVP 39491, mx.

**Description and Discussion:** The holotype of Titanoides primaevus (USNM 7934) was collected in 1913 (Gidley, 1917). Due to inaccurate field notes, the type locality was "lost" until 1951, when it was relocated by a field party from Princeton University (Simons, 1960). The presumed remainder of the holotype (PU 16490) was collected 38 years after the initial discovery of T. primaevus (Simons, 1960).

The dentition and most of the cranial and postcranial skeleton of Titanoides primaevus has been adequately described and figured by Gidley (1917), Patterson (1939), and Simons (1960). The Birchwood specimens accord well with these published descriptions.

Most of the teeth from the Birchwood locality referred here to Titanoides primaevus are fragmentary. The large size and strong dilambdodont nature of two nearly complete M3's support their referral to Titanoides. These two upper third molars, UALVP 39486 (L=18.8, AW=30.5, PW=23.0) and UALVP 39487 (L=20.0, AW=33.5, PW=21.5), fall within the size range of Titanoides primaevus (Simons, 1960:75-76), a common constituent of middle Tiffanian and younger deposits. Other species of Titanoides include the late Tiffanian T. gidleyi and the earliest to late

Tiffanian T. zeuxis (Simons, 1960). The upper M3 of T. gidleyi is shorter anteroposteriorly than those of the Birchwood specimens and the type of Titanoides primaevus (Simons, 1960). To my knowledge, the upper dentition of T. zeuxis is not known.

Family CYRIACOTHERIIDAE Rose and Krause, 1982

CYRIACOTHERIUM Rose and Krause, 1982

CYRIACOTHERIUM sp., cf. *C. ARGYREUM* Rose and Krause, 1982

(Plate 28, figs. G-H)

**Holotype of Cyriacotherium argyreum:** PU 18821, crushed snout with right P2-3, M2-3, labial part of left P1, left P2, associated tooth fragments; and alveoli for left and right I1-3, C, right P4-M1, and left P4.

**Type Locality:** Brice Canyon locality, "Silver Coulee beds", Polecat Bench Formation, Park County, Wyoming.

**Known Age and Distribution of Cyriacotherium argyreum:** Late Tiffanian (late Paleocene) of Wyoming (type locality [Rose and Krause, 1982]); latest Tiffanian of Wyoming (Rohrer and Low localities, Teton County, Purdy Basin [Rose and Krause, 1982]).

**Referred Specimen:** UALVP 39485, M1.

**Description:** UALVP 39485 is a slightly worn, isolated upper right first molar. The stylar shelf of UALVP 39485 has been broken off just labial to the apices of the paracone and metacone. Due to this damage, the full dimensions of this tooth cannot



be measured, but it has a minimum length and width of 6.5 mm and 10.2 mm, respectively. UALVP 39485 exhibits a strong W-shaped ectoloph, prominent conules, deep trigon basin, and wrinkled enamel. These features, along with the lack of a hypocone, are considered by Rose and Krause (1982) to be features characteristic of Cyriacotherium. Due to the fragmentary nature of the Birchwood specimen, I conservatively refer it to Cyriacotherium sp., cf. C. argyreum.

**Discussion:** Lucas (1982) argued against the pantodont affinities of Cyriacotherium. He proposed that Cyriacotherium was more closely related to the mixodectids and dermopterans (Lucas, 1982). Rose and Krause (1982) reviewed in detail the possible relationships of Cyriacotherium to many related and convergent mammals, including dermopterans and pantodonts. Rose and Krause (1982) argued strongly in support of the pantodont affinities of Cyriacotherium, and I concur with them here.

Rose and Krause (1982) also reported Cyriacotherium sp., cf. C. argyreum from the late Tiffanian Roche Percée local fauna of Saskatchewan and the late Tiffanian Sand Draw Anthill locality of Wyoming. Unfortunately, the small samples from these two localities do not contain upper molars. Fox (1990a) reported Cyriacotherium sp., cf. C. argyreum from the middle Tiffanian of Alberta. Undescribed and uncatalogued UALVP specimens from the UADW-2 locality include an upper first molar similar in both size and morphology to UALVP 39485.

The recovery of Cyriacotherium sp., cf. C. argyreum from the Birchwood

locality represents the fourth reported occurrence of Cyriacotherium, and the third from outside of the type locality in Wyoming. UALVP 39485 joins Fox's (1990a) specimens in confirming a more northerly distribution for this genus, and extending its range from the late to middle Tiffanian.

## Order UNCERTAIN

Family PALAEORYCTIDÆ (Winge, 1917)

PARARYCTES Van Valen, 1966

PARARYCTES PATTERSONI Van Valen, 1966

(Plate 29, figs. A-C; Table 14)

**Holotype:** UW 2002, left M1.**Type Locality:** Saddle locality, Fort Union Formation, Fremont County, Bison Basin, Wyoming.

**Known Age and Distribution:** Earliest Tiffanian (late Paleocene) of Alberta (Cochrane 2 locality, Porcupine Hills Formation, Cochrane [Van Valen, 1966; Youzwysyn, 1988]); early Tiffanian of Wyoming (type locality [Van Valen, 1966]) and Alberta (HHW-LL, Paskapoc Formation, Hand Hills [MacDonald, in prep.]); middle Tiffanian of Alberta (HHW-UL, Paskapoo Formation, Hand Hills [Fox, 1990a]; UADW-2 locality, Paskapoo Formation, Blindman River [pers. obs.]; Joffre Bridge Roadcut, lower level, Paskapoo Formation, Red Deer River [Fox, 1990a]) and North Dakota (Brisbane locality, Tongue River Formation, Grant County [Holtzman, 1978]); late Tiffanian of Alberta (Police Point locality, Ravenscrag Formation, Cypress Hills [Fox, 1990a]).

**Referred Specimens:** UALVP 39468, 39470, dentary fragments with p5, m1-3; UALVP 39471, dentary fragment with p5, m1; UALVP 39469, m1; UALVP 39472, dentary fragment with m2-3; UALVP 39473, m3.

**Description:** Pararyctes pattersoni, the sole species of Pararyctes, has been adequately described and figured by Van Valen (1966) and Holtzman (1978), and will not be described further here.

**Discussion:** The Palaeoryctidae has been assigned to various taxa by different authors. These include the Deltatheridia (Van Valen, 1966; Lillegraven, 1969; Rigby, 1980), Insectivora (Simpson, 1945; Clemens, 1973; Van Valen, 1978; Thewissen and Gingerich, 1989), Soricomorpha (Stuckey and McKenna, 1993), Proteutheria (Butler, 1972; Rose, 1981; Bown and Schankler, 1982) and Eutheria incertae sedis (Archibald, 1982; Johnston and Fox, 1984; Novacek, 1992). After nearly a century of studies, palaeoryctids are now thought to have given rise to basal members of the Creodonta, not the Carnivora (see Fox and Youzwyshyn (1994) and references therein). However, their own taxonomic position remains uncertain. The problem of palaeoryctid classification is largely due to their shared similarities with modern insectivores; it has long been a subject of debate among researchers whether these similarities are based on common ancestry or convergence.

The Birchwood specimens of Pararyctes pattersoni compare favorably with referred specimens of this species from the middle Tiffanian UADW-2 and HHW-UL

localities of Alberta. The size ranges of the Birchwood specimens are similar to those reported by Holtzman (1978:table 18) from the middle Tiffanian Brisbane locality.

The occurrence of *P. pattersoni* at the Birchwood locality represents a range extension for the genus and species northwards from the Blindman localities.

Family PENTACODONTIDAE Simpson, 1937

BISONALVEUS Gazin, 1956

BISONALVEUS GRACILIS, sp. nov.

(Plate 29, figs. D-F; Pl. 30, figs. A-D; Table 15)

**Etymology:** gracilis, L., "slender", "thin". In reference to the smaller and more slender teeth of this species in comparison to other members of Bisonalveus.

**Holotype:** UALVP 39432, left dentary fragment with p3-4, m1-3, and alveoli for p1-2.

**Type Locality:** Birchwood locality outcrop on north side of Modeste Creek downstream of its confluence with Bucklake Creek, Paskapoo Formation, central Alberta (exact coordinates are available to qualified researchers through the University of Alberta Laboratory for Vertebrate Paleontology).

**Known Age and Distribution:** Middle Tiffanian (late Paleocene) of central Alberta (type locality; UADW-1, UADW-2, and UADW-3, Paskapoo Formation, Blindman River [pers. obs.; Fox, 1990a]).

**Hypodigm:** UALVP 39420-39424, M2's; UALVP 39425, M3; UALVP 39443, p3; UALVP 39433, dentary fragment with p3-4; UALVP 39432, holotype, dentary

fragment with p3-4, m1-3, and alveoli for p1-2; UALVP 39427, 39435, dentary fragments with p4, m1; UALVP 39428, 39431, 39436, dentary fragments with p4, m1-2; UALVP 39434, dentary fragment with p4, m1-3; UALVP 39437, 39438, dentary fragments with m1-2; UALVP 39426, 39429, 39430, 39439, dentary fragments with m1-3; UALVP 39440-39442, 39453, dentary fragments with m2-3; UALVP 39444, 39452, m1's; UALVP 39445-39451, 39475, 39476, m2's. All hypodigm specimens are from the Birchwood locality.

**Diagnosis:** Smallest member of Bisonalveus in most linear measurements.

Readily distinguished from the middle Tiffanian B. holtzmani, the largest member of Bisonalveus, on the basis of size alone. Differs from B. browni in possessing narrower lower molars, especially m3, with more acute, less swollen cusps. Further differs from B. browni in possessing the following suite of features: paracone on M2 does not project labially to the same degree in B. browni, making the labial margin of the tooth more linear and less oblique to the long axis of the tooth row; the ranges of widths of M2 of B. gracilis and B. browni barely overlap, with B. gracilis narrower; single-rooted p2; p4 narrower, with more acute, less swollen cusps; m1 with shorter talonid than that of B. browni, the hypoconid positioned at the apex of a more acute angle formed by the cristid obliqua and the postcristid.

**Description:** Bisonalveus gracilis is morphologically nearly identical with the congeneric B. browni, differing mainly from the latter species in having a single-

rooted p2 and narrower lower molars with more acute, less swollen cusps. The sum of the differences between the two species are in the diagnosis, and will not be described further.

**Discussion:** In order to quantitatively separate members of Bisonalveus gracilis from B. browni, I compared a representative sample of specimens of B. browni from the earliest Tiffanian Cochrane 2 locality (UALVP specimens; Youzwysyn, 1988:table 42) and Douglass Quarry (cast of PU 14580; Krause and Gingerich, 1983:fig. 6, table 2) of Alberta and Montana, respectively, with the Birchwood sample. In order to supplement traditional measurements, I also measured the lower molars of the Birchwood and Cochrane 2 samples for talonid and trigonid length.

The M2's of Bisonalveus gracilis from the Birchwood locality are shorter and narrower than those of B. browni. This difference is most evident in the mean width of the M2's of these two species, with the mean of B. gracilis (3.53 mm) about six percent narrower than that of B. browni (3.75 mm). Although this difference is not statistically significant, the ranges of widths of the different samples are quite different. The width of the largest M2 of B. gracilis is 3.6 mm, compared with 4.1 mm and 4.0 mm, from samples of B. browni from Cochrane 2 and Douglass Quarry, respectively. The width of the smallest M2 of B. gracilis is 3.5 mm, compared with 3.6 mm and 3.5 mm from samples of B. browni from Cochrane 2 and Douglass Quarry, respectively. There is only a slight overlap in width between the largest specimen of B. gracilis and the smallest specimen of B. browni.



The length and width of the first and second lower molars of Bisonalveus gracilis from the Birchwood locality are only slightly smaller than those of B. browni from the Cochrane 2 locality, but average almost seven percent smaller than those from Douglass Quarry. The lower third molar of B. gracilis is only slightly smaller than the sample of B. browni from Cochrane 2, but averages about seven percent shorter and ten percent narrower than the single m3 of B. browni recovered from Douglass Quarry. When trigonid and talonid lengths of Cochrane 2 and Birchwood lower molars are compared, the only significant difference to appear is in the absolute length of the m1 talonids. The m1 talonids of B. gracilis are almost 20 percent shorter than those of B. browni from Cochrane 2.

Bisonalveus gracilis is also present at the middle Tiffanian UADW-1, UADW-2, and UADW-3 localities, Blindman River, central Alberta, where its presence was noted by Fox (1990a:61) as "Bisonalveus, new species". Uncatalogued dentaries from the UADW-2 locality possess p1 and p2, showing them to be simple, single-rooted teeth. In contrast, Krause and Gingerich (1983:166) reported the p2 of B. browni as double-rooted. UALVP 125, 28307, and 28346, specimens of B. browni from the earliest Tiffanian Cochrane 2 locality of Alberta, also demonstrate the double-rooted nature of p2 (pers. obs.). The UADW-2 p2 is about one-quarter the size of p3, bearing a small hypoconulid, a weak lingual cingulum, and anterior and posterior cristids. The p1 is slightly taller and larger in diameter than p2, bearing an anterior cristid and a lingual cingulum. There is a small (0.30 mm) diastema between p1 and p2, and a smaller (0.12 mm) diastema between p2 and p3. Although p1 and p2 are

unknown in specimens of B. gracilis from the Birchwood locality, certain dentary fragments (UALVP 39432 and 39433) have alveolar patterns that are consistent with the UADW-2 specimens. In UALVP 39432 and 39433, the alveolus for p2 is smaller than that for p1, and a relatively thick alveolar wall separates the alveoli for p1 and p2, as in the UADW-2 specimens.

The occurrence of B. gracilis at the Birchwood locality represents a range extension for the genus and species northwards from the Blindman localities.

Family PANTOLESTIDAE Cope, 1884

PROPALAEOSINOPA Simpson, 1927

PROPALAEOSINOPA SEPTENTRIONALIS (Russell, 1929)

(Plate 30, figs. E-I)

**Holotype:** UALVP 126, left dentary fragment with m3.

**Type Locality:** Cochrane site 1, Porcupine Hills Formation, Cochrane, southwestern Alberta.

**Known Age and Distribution:** Late Torrejonian (middle Paleocene) of Montana (Gidley Quarry, Lebo Formation, Sweetgrass County, Crazy Mountain Field [Simpson, 1935d, 1937]) and Wyoming (Swain Quarry, Fort Union Formation, Carbon County, Washakie Basin [Rigby, 1980]; localities V-82004, V-82006, V-82040, Polecat Bench Formation, southern Bighorn Basin [Hartman, 1986]); earliest Tiffanian (late Paleocene) of Alberta (type locality [Russell, 1929]; Cochrane 2 locality, Porcupine Hills Formation, Cochrane [Youzwysyn, 1988; Fox, 1990a]), Montana (Douglass Quarry, Melville Formation, Sweetgrass County, eastern Crazy Mountain Basin [Krause and Gingerich, 1983]), and Wyoming (Locality V-82015, Polecat Bench Formation, southern Bighorn Basin [Hartman, 1986]); early Tiffanian of Alberta (HHW-LL, Paskapoo Formation, Hand Hills [MacDonald, in prep.]) and Montana (Scarritt Quarry, Melville Formation, Sweetgrass County, eastern Crazy Mountain

Basin [Simpson, 1936]); middle Tiffanian of North Dakota (Brisbane and Judson localities, Tongue River Formation, Grant and Morton Counties, respectively [Holtzman, 1978]) and Alberta (HHW-UL, Paskapoo Formation, Hand Hills [Fox, 1990a]; UADW-2 and Burbank localities, Paskapoo Formation, Blindman River [Fox, 1984a, 1990a]; Joffre Bridge Roadcut, lower level, Paskapoo Formation, Red Deer River [Fox, 1990a]); late Tiffanian of Alberta (Police Point locality, Ravenscrag Formation, Cypress Hills [Krishtalka, 1973]).

**Referred Specimens:** UALVP 39454, P4; UALVP 39467, M1; UALVP 39455, p2; UALVP 39456, 39457, p4's; UALVP 39458, 39460, 39466, 39474, m2's; UALVP 39459, dentary fragment with m2-3.

**Description and Discussion:** Youzwyshyn (1988) noted that the holotype of Diacodon septentrionalis Russell, 1929 (UALVP 126, m3) was indistinguishable from teeth referred to the pantolestid Propalaeosinopa diliculi Simpson, 1935. Because the former specific name has priority over the latter, Youzwyshyn (1988) proposed the new combination of Propalaeosinopa septentrionalis (Russell, 1929). This new combination has been accepted by at least one author (Fox, 1990a), and I follow it here.

The dentition of Propalaeosinopa septentrionalis has been adequately described by Simpson in 1936 (as "Bessoecetor thomsoni") and 1937 (as "Bessoecetor diluculi"), and will not be described further here. The Birchwood sample does not differ

significantly from other specimens from the middle Tiffanian of Alberta, and compares favorably with specimens from the earliest Tiffanian Cochrane 2 locality. The Birchwood sample includes a larger, heavily worn left m2, UALVP 39460, that shows little detailed morphology. It may be referable to P. albertensis due to its larger size, but due to a lack of specific morphological features, I here conservatively refer UALVP 39460 to P. septentrionalis.

Propalacosinopa albertensis, the only other known member of the genus, is known from several Tiffanian localities in Alberta, including the northerly late Tiffanian Swan Hi's locality (Stonley, 1988). The occurrence of P. septentrionalis at the Birchwood locality thus represents a range extension for the species, northwards from central Alberta.

Family MIXODECTIDAE Cope, 1883

EUDAEMONEMA Simpson, 1935

EUDAEMONEMA ONKOTOS, sp. nov.

(Plate 31, figs. A-I)

**Etymology:** onkotos, Gr., "swollen", "rounded", "bulky". In reference to the overall larger size and relatively larger and swollen cusps of this species, in contrast with the smaller size and pointed cusps of the genotype, E. cuspidata.

**Holotype:** UALVP 39409, M1.

**Type Locality:** Birchwood locality, outcrop on north side of Modeste Creek downstream of its confluence with Bucklake Creek, Paskapoo Formation, central Alberta (exact coordinates are available to qualified researchers through the University of Alberta Laboratory for Vertebrate Paleontology).

**Known Age and Distribution:** Middle Tiffanian (late Paleocene) of central Alberta (type locality and UADW-2 [pers. obs.; Fox, 1990a]).

**Hypodigm:** UALVP 39409, holotype, M1; UALVP 39410, M2; UALVP 39411, M3, UALVP 39462, m2. All hypodigm specimens are from the Birchwood locality.

**Diagnosis:** Differs from the genotype and only previously known species

Eudaemonema cuspidata Simpson, 1935 in the following features: dentition larger in overall size, especially length; all cusps on upper molars, especially protocone, relatively larger and more swollen than those of E. cuspidata; hypocone of M1-2 does not project lingually to the same degree as in E. cuspidata. Further differs from referred molars of E. cuspidata from the late Torrejonian Gidley Quarry of Montana (Szalay, 1969:table 5) as follows: upper molars average 22.3 percent longer; posterior width of M3 averages 25 percent wider; m2 averages over 25 percent longer and 15 percent wider.

**Description:** M1. UALVP 39409 (L=4.1, AW=4.7, PW=4.8) is an isolated left upper first molar. This tooth is similar to the M1 of Eudaemonema cuspidata from the late Torrejonian Gidley Quarry of Montana (Simpson, 1937:fig. 26), but differs in the following features: larger size; labial margin biconcave and W-shaped rather than flat as in E. cuspidata, the three projecting points produced by the para-, meso-, and metastyles; broader parastyle and metastyle, further removed from, and with deeper invaginations separating them from the paracone and metacone, respectively; protocone relatively larger and swollen; and hypocone large, but does not project lingually to the same degree as in E. cuspidata.

M2. UALVP 39410 (L=4.1\*, PW=5.2) is an isolated right upper second molar with a damaged paracone and metacone, and lacking the parastylar area. It is similar to the M2 of Eudaemonema cuspidata from the late Torrejonian Gidley Quarry of

Montana (Simpson, 1937:fig. 26), but differs in the following features: larger size; hypocone large, but does not project lingually to the same degree as in E. cuspidata, leaving it much closer to the metaconule; and a small ridge descending from the apex of the hypocone extends anterolabially to the base of the metaconule.

M3. UALVP 39411 (L=3.9, AW=5.8, PW=4.8) is an isolated upper third molar which differs from that of Eudaemonema cuspidata from the late Torrejonian Gidley Quarry of Montana (Simpson, 1937:fig. 26) in the following features: larger, especially wider, than the homologous teeth of E. cuspidata; weaker conules (although the specimen is somewhat worn, it is apparent that the conules were never as prominent as those in E. cuspidata); and metacone leaning posteriorly, unlike that in E. cuspidata, which is erect.

m2. UALVP 39462 (L=4.5, AW=2.7, PW=3.2) is an isolated second lower molar with a worn trigonid, lacking the anterolingual ventral margin. This tooth resembles the m2 of Eudaemonema cuspidata from the late Torrejonian Gidley Quarry of Montana (Szalay, 1969:plate 25, table 5), but the former is larger in all linear measurements. UALVP 39462 is over 25 percent longer and averages 15 percent wider than the average measurements for E. cuspidata (ibid.). As in the m2 of the genotype, the metaconid of E. onkotos is the highest and largest trigonid cusp, slightly larger than the protoconid. The paraconid is reduced, to the extent that it resembles a bulge on an anterior, posterolingually sloping shelf. The cristid obliqua is strong, but there is no evidence of a "very prominent mesoconid" on UALVP 39462, as mentioned by Szalay (1969:226) for E. cuspidata. The entoconid is worn (a thin strip



of enamel has been worn away from the entoconid ventrally to near the base of the crown), but it is much larger than the unworn hypoconulid. The hypoconid is prominent but smaller than the entoconid. No precingulid is present on the undamaged portion of the anterior margin, nor is there a postcingulid. The talonid (or "lingual") notch is U-shaped as in E. cuspidata (Szalay, 1969:227).

**Discussion:** Rose (1975b) followed Simpson (1936) in proposing a common ancestry for the mixodectids and the plagiomenids. Rose and Simons (1977) analyzed the molar occlusion in plagiomenids and mixodectids (including Eudaemonema), and came to the same conclusion. Later authors (Stucky and McKenna, 1993) have agreed with this relationship, placing both the Plagiomenidae and the Mixodectidae in the Dermoptera.

There have been three reported occurrences of Eudaemonema in Alberta. In his unpublished thesis, Youzwyshyn (1988) assigned one lower and two upper molars from the earliest Tiffanian Cochrane 2 locality to Eudaemonema sp., cf. E. cuspidata. He observed that these specimens were "virtually identical to the homologous teeth of E. cuspidata, but differ primarily in being larger in all linear dimensions" (1988:265).

Youzwyshyn (1988) and Fox (1990a) also noted the presence of a new, undescribed species of Eudaemonema from the middle Tiffanian of Alberta, that being the subject of discussion here. Specimens of E. onkotos from the Birchwood locality accord well with uncatalogued specimens of from the middle Tiffanian UADW-2 locality of Alberta (Fox, 1990a), and I believe that the two samples represent the same

species. Youzwysyn (1988) speculated that his earliest Tiffanian Eudaemonema sp., cf. E. cuspidata is intermediate in morphology between E. cuspidata and E. onkotos. The species described by Youzwysyn (1988) is intermediate in size between E. cuspidata and E. onkotos, and I see no evidence preventing this hypothesis from being pursued. The occurrence of Eudaemonema onkotos at the middle Tiffanian Birchwood locality extends the Eudaemonema lineage in time and space from the late Torrejonian of Montana and the earliest Tiffanian of Alberta, to the middle Tiffanian of Alberta.

L. S. Russell (1967) assigned two specimens from the upper Tiffanian Swan Hills locality, ROM 5615 and 5614, to Eudaemonema sp., cf. E. cuspidata. Stonley (1988) noted these designations were in error, and reassigned ROM 5615 and 5614 to Elpidophorus and Propalaeosinopa, respectively. There are now no known mixodectids from the Swan Hills, and Eudaemonema cuspidata remains restricted to the type locality in Montana. Eudaemonema onkotos remains the only known middle Tiffanian species of Eudaemonema in Alberta.

Superfamily APATEMYOIDEA Saban, 1954

Family APATEMYIDAE Matthew, 1909

JEPSENELLA Simpson, 1940

JEPSENELLA sp., cf. J. PRAEPROPERA Simpson, 1940

(Plate 32, figs. A-H)

**Holotype of Jepsenella praepropera:** AMNH 35292, right dentary fragment with m1-3.

**Type Locality:** Gidley Quarry, Lebo Formation, Crazy Mountain Field, Sweetgrass County, Montana.

**Known Age and Distribution of Jepsenella praepropera:** Late Torrejonian (middle Paleocene) of Montana (type locality [Simpson, 1940; McKenna, 1963]) and Wyoming (Swain Quarry, Fort Union Formation, Carbon County, Washakie Basin [Szalay, 1968; Rigby, 1980]).

**Referred Specimens:** UALVP 39494, I1; UALVP 39493, M1; UALVP 39495, p2.

**Description:** I1. UALVP 39494 (L=3.5, W=1.9) is an isolated, right upper first incisor that is morphologically similar to the I1 of Labidolemur kayi (Gingerich

and Rose, 1982:fig. 1). UALVP 39494 is moderately worn, and missing the tip of the anterocone, which has been broken off. It is consistent with the I1 of L. kavi in possessing an enlarged crown, large simple anterocone, and small posterocone.

UALVP 39494 differs from the I1 of L. kavi (Lave=2.93, Wave=1.37 [Gingerich, 1982:table 1]) mainly in being larger. To my knowledge, the I1 of Jepsenella praepropera is not known.

M1. UALVP 39493 (L=2.4, W=3.1) is a worn, right upper first molar. The paracone is slightly higher and less worn than the metacone. Both cusps are cusate, equal in size, oval in cross section, and joined near their base. There are no conules. Small, ridge-like para- and metastyles are linked to the paracone and metacone by a distinct preparactista and postmetacrista, respectively. The styler shelf is broad near the bases of the para- and metacone, but narrows at midlength due to a prominent ectoflexus. The protocone is an apex at the junction of the pre- and postprotocrista, both cristae broadened by wear. The postprotocrista dips ventrally at midlength between the protocone and metacone, but wear has obscured any evidence of a hypocone. The part of the tooth lingual to the para- and metacone is canted anteriorly to a modest degree, creating a concave anterior margin. The posterior margin is convex and fairly linear. UALVP 39493 is shortest at midwidth, the portions labial and lingual to midwidth grow progressively longer. The labial portion of the tooth is noticeably longer than the lingual portion. In this respect, UALVP 39493 differs from the upper molars of Labidolemur kavi (and presumably those of L. soricoides), which are stouter and longer relative to their widths (Gingerich and Rose, 1982:fig. 1).

UALVP 39493 bears a worn precingulum and a more distinct postcingulum. The stout, laterally compressed lingual root is present. The two labial roots are absent, but their bases indicate that they were nearly circular in cross-section. UALVP 39493 most closely resembles AMNH 89513, a left M1 of Jepsenella praepropera from the late Torrejonian Swain Quarry of Wyoming (Szalay, 1968:fig. 1). AMNH 89513 and UALVP 39493 are similar in occlusal outline, both teeth possessing a distinct ectoflexus and rounded para- and metastylar lobes. UALVP 39493 differs from AMNH 89513 in being larger, having the paracone and metacone more nearly equal in size, and lacking a hypocone. As mentioned above, the lack of a hypocone on the Birchwood specimen may be an artifact of wear.

p2. UALVP 39495 (L=3.2, W=1.3) is an isolated right lower second premolar, readily identified as an apatemyid p2 by its "mittien-like" structure and single root. It resembles the p2 of L. kayi (Lave=2.05, Wave=1.00 [Gingerich, 1982:table 1]), but is larger in linear dimensions. UALVP 39495 differs from the p2 of L. kayi (Gingerich and Rose, 1982:fig. 2) in being more linear in nature, i.e., the long axes of the tooth crown and root are nearly continuous. The crown of UALVP 39495 does not project forwards, and would not overhang i1 to the same degree as in L. kayi. To my knowledge, the p2 of Jepsenella praepropera is not known. Youzwyshyn (1988) assigned one specimen, UALVP 28575 (L=2.9, W=1.4), to the p2 position of Jepsenella sp., cf. J. praepropera. This tooth differs from the Birchwood specimen in having a shorter crown and a root that curves labially.

**Discussion:** Members of the Apatemyidae are poorly known, being rare Paleocene faunal elements (Gingerich and Rose, 1982). Only two well-defined apatemyid species are recorded by Gingerich (1982:fig. 5) as present in middle Tiffanian North America faunas, Labidolemur soricoides Matthew and Granger, 1921, and Unuchinia dysmathes Holtzman, 1978. The Birchwood specimens differ substantially from these middle Tiffanian genera, as noted above. The genus Jepsenella has been restricted to the Torrejonian and earliest Tiffanian, the youngest species being Jepsenella praepropera (Gingerich, 1982). More conservatively, Archibald et al. (1987:34) constrained Jepsenella to the latest Torrejonian of the Swain, Rock Bench, and Gidley Quarries. Youzwysyn (1988) reported Jepsenella sp., cf. J. praepropera from the earliest Tiffanian Cochrane 2 locality of southern Alberta. An M1 from the Cochrane 2 locality (UALVP 28570) is most similar to AMNH 89513 (see above), and differs from the Birchwood specimen in the same respects. The occurrence of Jepsenella sp., cf. J. praepropera at the Birchwood locality extends the geographical and geological ranges of this genus and species.

The Birchwood specimens are referred to Jepsenella sp., cf. J. praepropera largely on the basis of UALVP 39493, an M1 most similar to those of Jepsenella praepropera. The incisors and anterior premolars of Jepsenella praepropera have not been described. Without UALVP 39493, it is unlikely that the other Birchwood specimens would be assigned to the same taxon. The possibility exists that more than one species of apatemyid existed at the Birchwood locality. However, Gingerich and Rose (1982:49) have noted that "few localities contain specimens representing more

than one or two individuals". In this case, it would be highly unlikely that the three Birchwood specimens represent more than one species.

## VI. CONCLUSIONS

### 1. AGE OF THE BIRCHWOOD FAUNA

The presence of the plesiadapid primate Plesiadapis rex places the Birchwood locality within the middle Tiffanian (Ti3) lineage zone (Gingerich, 1975, 1976; Archibald et al., 1987). The Birchwood Local Fauna includes three species and genera listed as Ti3 index fossils (Plesiadapis rex, Raphictis, and Saxonella), as well as at least 21 of the 38 genera listed by Archibald et al. (1987) as characteristic fossils for the Ti3 lineage zone. The exact location of the Birchwood locality within the middle Tiffanian is less certain. Sloan (1987) has subdivided the middle Tiffanian using the transition from Neoplagiaulax hunteri (Ti3a) to N. mckennai (Ti3b). The presence of N. sp., cf. N. hunteri at the Birchwood locality suggests that it joins the Brisbane, Judson, Cedar Point, and other localities within the Plesiadapis rex - Neoplagiaulax hunteri Ti3a composite range zone (Sloan, 1987). Middle Tiffanian Albertan localities belonging in the Ti3a composite range zone due to the presence of both P. rex and N. hunteri include the HHW-UL and UADW-2 localities (Fox, 1990a; MacDonald, in prep.). The Ti3 age of the UADW-2 locality has been supported by several lines of independent evidence, including palyno- and magnetostratigraphy.

However, palynostratigraphic work by Demchuk (1987) has contradicted the early Ti3 age suggested by Sloan's (1987) bi-fold division of the middle Tiffanian. Demchuk's evidence suggests the UADW-2 locality to be slightly younger than what is indicated by the mammalian paleofauna (Fox, 1991a), placing it in the late middle



Tiffanian. Due to faunal similarities of the Birchwood and UADW-2 localities (see below), I believe that they are approximately the same age. This would also place the Birchwood locality within the late middle Tiffanian.

Sloan's (1987) bi-fold division of the middle Tiffanian has not been accepted by many authors in the literature. Demchuk's (1987) palynofloral evidence integrates well with the Tiffanian zonation of Archibald and others (1987), which is often cited in Paleocene faunal studies. I am also tempted to assign Demchuk's (1987) palynofloral evidence greater weight, as it is based on rocks within the Paskapoo Formation. I therefore propose a late middle Tiffanian age for the Birchwood locality.

## 2. FAUNAL COMPARISONS

The Birchwood Local Fauna is most similar to that of the middle Tiffanian UADW-2 locality of Alberta, both in general composition and in possessing taxa unique to the two deposits. In the most recent faunal list (Fox, 1990a; pers. obs.), the UADW-2 locality has yielded 50 species referable to 43 genera. Twenty, or 40%, of the species from the UADW-2 locality occur in the Birchwood Local Fauna (Table 16). At the generic level, the Birchwood locality bears 25 genera in common with the UADW-2 locality, over 58% of the latter locality's genera. Differences in the type of sedimentary environments in which the two fossil deposits were formed are likely responsible for lowering the similarity between the two faunas. The Birchwood Local Fauna includes a variety of condylarths, a group which includes some of the larger Tiffanian mammals. The transport and deposition of these larger fossils was facilitated by the high energy fluvial environment in which the Birchwood deposit was formed. In contrast, the UADW-2 locality lacks many of these larger taxa, having been formed in a more passive depositional environment (interpreted as lacustrine by Fox [1984a]).

Further evidence for a high degree of similarity between the two localities comes from the presence of the relatively rare plesiadapiforms Saxonella and Pronothodectes gaoi, and the novel taxa Horolodectes albertensis, Bisonalveus gracilis, and Eudaemonema onkotos. As far as is known to me, only one other Albertan locality bears the genus Saxonella (HHW-UL), and no other localities have yielded the novel taxa described here.

Of the numerous middle Tiffanian mammalian faunas known from the northern United States, two are most similar to the Birchwood Local Fauna. The Judson/Brisbane localities in North Dakota and Cedar Point Quarry in Wyoming contain 14 and 13, respectively, of the 40 species found within the Birchwood Local Fauna (Table 16). A more southern fauna, Ray's Bone Bed and Annex in Big Bend National Park, Texas (Schiebout, 1974), contains only three of the genera and none of the species present in the Birchwood Local Fauna. The three genera common to the two localities, Ectocion, Phenacodus, and Titanoides, are ubiquitous in the North American Paleocene, and are thus only marginally useful in zoning sediments.

There is evidence that as latitude decreases, so does the faunal similarity with the Birchwood Local Fauna. Table 16 records the latitude of selected middle Tiffanian mammal localities, as well as their similarity to the Birchwood Local Fauna. As mentioned above, the nearby UADW-2 locality (at ~52°N) shares over 20 species with the Birchwood Local Fauna, while Ray's Bone Bed and the Birchwood Local Fauna share so few genera as to make their comparison questionable. The Judson/Brisbane localities (at ~47°N) and Cedar Point Quarry (at ~45°N) fall in the middle in descending order of similarity. Unfortunately, no well-documented middle Tiffanian mammal localities exist between Cedar Point Quarry and Big Bend.

### 3. BIOGEOGRAPHY

At over 55° North latitude, the most northerly known Paleocene mammal locality in the world is the late Tiffanian Swan Hills Site 1, which was studied by L. S. Russell (1967) and Stonley (1988). Both authors failed to address the significance of the latitude of this locality. Stonley (1988), although recognizing the latitudinal uniqueness of the Swan Hills locality, attached little or no significance to this fact. At over 53° North latitude, the Birchwood locality is the second most northerly Paleocene mammal locality and the most northerly middle Tiffanian locality in the world. In comparison with these Albertan localities, the most northerly Paleocene European mammalian locality is the middle Tiffanian Walbeck fissure deposit, near Magdeburg, Germany, at just over 52° North latitude. The most northerly Asian Paleocene mammalian fauna is the latest Tiffanian-Clarkforkian Gashato deposits in the Peoples Republic of Mongolia, at just over 44° North latitude. Due to its location in the northern part of the Western Interior, I believe the Birchwood locality has important biogeographical implications.

**Paleogeography.** During the late Paleocene, North America was connected to both Europe and Asia via the DeGeer/Thulean and Bering land bridges, respectively (Krause and Maas, 1990; Smith et al., 1994). The Euramerican coupling was facilitated by the DeGeer and Thulean bridges, located north and south of the Baltic Sea, respectively. The late Paleocene paleolatitude of the DeGeer bridge has been estimated at  $75.9^{\circ} \pm 3.5^{\circ}\text{N}$  (McKenna, 1983a), and that of the Thulean bridge at about  $65^{\circ}\text{N}$  (McKenna, 1983b). Both of these land bridges were flooding by the early

Eocene (Krause and Maas, 1990). A land bridge (or bridges) across the Bering Straits between North America and Asia was also present throughout the Paleocene (Krause and Maas, 1990; Smith et al., 1994). The late Paleocene paleolatitude of this area has been estimated at  $83^{\circ} \pm 9^{\circ}\text{N}$  (Hillhouse and Gromme, 1982). It has been suggested that the more northerly paleolatitude of the Bering Straits land bridge made crossing conditions less favorable (McKenna, 1983a; Krause and Maas, 1990), and that this is reflected in the high ratio of Euramerican genera to Asian-American genera during the Paleocene. The northern latitude of the Birchwood Local Fauna places it in relatively close proximity to these various land bridges, in a position to record potentially the intercontinental dispersal patterns of Paleocene mammals.

**Euramerican Genera.** Mammalian genera common to both Europe and North America include plesiadapiform primates, neoplagiaulacid multituberculates, mesonychid and arctocyonid condylarths, and proteutherians. Euramerican plesiadapiform genera include the plesiadapids Plesiadapis and Chiromyoides (Gingerich, 1976) and the saxonellid Saxonella (Fox, 1984a, 1991b). The neoplagiaulacids Neoplagiaulax and Parectypodus, the mesonychid Dissacus, the arctocyonid Arctocyon (Claenodon), and the proteutherian Propalaeosinopa (Russell, 1964; Vianey-Liaud, 1986; Archibald et al., 1987; Fox, 1991b) are also known Euramerican genera. Six of the above mentioned genera, Plesiadapis, Saxonella, Neoplagiaulax, Dissacus, Claenodon, and Propalaeosinopa, are recorded in the Birchwood Local Fauna. Two of these genera will not be discussed here; the problem of identifying isolated teeth of Dissacus to species level and the scant European

material of Propalaeosinopa exclude these genera. The location of the earliest occurrences of the remaining groups, and their subsequent relative progressiveness may indicate the direction or directions of travel across the DeGreer/ Thulean land bridge complex.

Throughout the Paleocene, European and North American species of the genus Plesiadapis are so similar that they have been considered "widely separated parts of a single continuous or nearly continuous pangeographic distribution evolving through the late Paleocene" (Gingerich, 1976:100). The fact that populations on either side of the Atlantic evolve in a similar fashion indicates that there was considerable interplay between the two groups. However, the oldest plesiadapiform primate, Purgatorius, is known from the earliest Paleocene of North America (Sloan and Van Valen, 1965; Johnston and Fox, 1984), suggesting a North American origin for the group.

Unlike all other Euramerican genera, Saxonella is known only from Alberta and Germany. The Birchwood locality is the third Albertan locality to yield gnathic material referable to Saxonella, and the first to show the existence of a North American species other than S. naylori. Although both are middle Tiffanian in age, the European species of Saxonella, S. crepaturae, is considered more advanced than S. naylori, the more completely known North American species (Fox, 1991b). The systematic position of Saxonella n. sp. (unnamed) from the Birchwood locality remains unknown.

There is support for both eastward (Gingerich, 1986; Fox, 1991b) and westward (Hooker, 1980; Gingerich, 1980) travel of mammals across the Atlantic land bridges.

Although evidence for the main direction of travel from Plesiadapis remains equivocal, the species of Saxonella suggest that the main direction of travel was from west to east. I consider it likely that saxonellids originated in North America, and at a time prior to the middle Tiffanian, the European S. crepaturae became distinct and advanced relative to the North American S. naylori. Saxonella n. sp. (unnamed) may represent a separate lineage which arose from the common ancestor of S. crepaturae and S. naylori, but lacking knowledge of the diagnostic lower premolars, this cannot be ascertained without speculation.

At least 10 and 5 species of the multituberculate genus Neoplagiaulax are known from deposits on the west and east sides of the Atlantic, respectively (Sloan, 1987; Vianey-Liaud, 1986). While the geologically oldest species of Neoplagiaulax include the Puercean N. kremnus Johnston and Fox, 1984 and N. macintyreii Sloan, 1981 from North America, all European species are Cernaysian or early Clarkforkian in age. This temporal distribution is additional evidence for eastward travel of Neoplagiaulax across the Atlantic land bridges at some time before the earliest Clarkforkian or latest Tiffanian. Vianey-Liaud (1986) believed that Euramerican exchanges of multituberculates were very selective, with migration occurring only from west to east. The North American ancestors of these Clarkforkian European genera likely inhabited the northern regions of North America, and may include species found at the middle Tiffanian Birchwood locality.

Van Valen (1978) proposed Claenodon as a junior synonym of Arctocyonides rather than of Arctocyon; he reports Arctocyon as restricted to Europe. Some authors

have concurred with this synonymy (Cifelli, 1983; Sloan, 1987), while others have followed Russell (1980) in considering Claenodon a junior synonym of Arctocyon (Archibald et al., 1987; Maas et al., 1995). Due to a lack of consensus on the systematics of the arctocyonids, throughout this paper I have used the generic name Claenodon as originally intended by Scott (1892), although I have little doubt that it is a junior synonym of Arctocyon, making that genus Euramerican in its distribution. Condylarths are considered to have originated in North America since the oldest known condylarth, Protungulatum, is known from the Lancian of Saskatchewan (Johnston and Fox, 1984) and Montana (Archibald, 1982). The record of North American species of Arctocyon begins in the Torrejonian (Sloan, 1987; Archibald et al., 1987), well before its middle Tiffanian Walbeck record (Russell, 1964). In addition, the European record of Arctocyon extends at least to the earliest Clarkforkian Berru deposits, after the genus is thought to have expired in North America. These recorded first and last appearances support west to east travel across the trans-Atlantic land bridges.

**Asian-American Genera.** By the earliest Clarkforkian, mammals including rodents, tillodonts, and coryphodontid pantodonts made their sudden appearance in North American faunas. Researchers in turn sought a North American, South American, and then an Asian origin for these new groups (Krause and Maas, 1990). It is now generally accepted that these groups emigrated from Asia to North America near the Tiffanian-Clarkforkian boundary (Gingerich, 1980; Sloan, 1987), with rodents being used as index fossils for the earliest Clarkforkian (Archibald et al., 1987).



Pantodonts were thought to have an exclusively holarctic distribution (Rose and Krause, 1982), until the discovery of pantodonts in South America (Marshall and de Muizon, 1988). Sloan (1987) cites Cyriacotherium as an example of an immigrant to North America from Asia. The hypodigm of the oldest species of Cyriacotherium, C. sp., cf. C. argyreum, includes specimens from the late Tiffanian (Ti4) deposits of Saskatchewan and Wyoming (Rose and Krause, 1982). Cyriacotherium sp., cf. C. argyreum has also been reported from the middle Tiffanian UADW-2 locality of Alberta by Fox (1990a) and from the Birchwood locality. These middle Tiffanian North American records of Cyriacotherium push back the date for the arrival of this genus from Asia via the Bering Straits land bridge.

**Summary.** The location and composition of the Birchwood Local Fauna has paleobiological implications regarding the intercontinental dispersal patterns of Paleocene mammals. The Birchwood Local Fauna provides additional evidence for eastward travel of various Euramerican and Asian-american genera across the trans-Atlantic and Bering Straits land bridges prior to the middle Tiffanian. The Birchwood Local Fauna has yielded the third middle Tiffanian record of Saxonella in North America and the first record of a new species of this genus. The middle Tiffanian record of Cyriacotherium in North America is strengthened by this second Alberta discovery, placing the immigration of this taxon from Asia prior to this time.

#### 4. IMPLICATIONS FOR FURTHER RESEARCH

The Birchwood Local Fauna has proven diverse, especially in light of the relatively small number of specimens collected. Simpson (1937:68) has suggested that "the best criterion of the adequacy of a collection as a sample of the preserved fossils is that of repetition". Within the Birchwood Local Fauna, several species are known only from single specimens, showing the weakness of the UALVP collection as an adequate sample of the regional mammalian community. As such, I believe that the potential of this site has not been fully realized, and I have little doubt that this locality will yield additional taxa with further sampling.

The northern position of the Birchwood locality places it geographically near the various land bridges that existed in the Paleocene. The mammals which comprise the Birchwood Local Fauna provide information regarding the timing and movements of Euramerican and Asia-american land mammals. In order to document better these movements and their chronology, more northerly mammal localities should be sought and investigated.

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## TABLES

Table 1. Measurements and descriptive statistics of the dentition of Ptilodus sp. T, Birchwood Local Fauna, Alberta.

Tooth	P	N	OR	M	SD	CV
p4	L	0	-	-	-	-
	W	2	3.3-3.5	3.40	0.14	4.1
m1	L	2	4.4-4.5	4.45	0.35	7.9
	W	2	2.1-2.2	2.15	0.35	16.3
P1	L	1	3.2	3.20	-	-
	W	1	2.5	2.50	-	-
P2	L	1	3.6	3.60	-	-
	W	1	3.2	3.20	-	-
P4	L	2	5.8-6.1	5.95	0.21	3.6
	W	2	2.6	2.60	0.00	0.0
M1	L	2	6.6-6.7	6.65	0.07	1.1
	W	2	2.9	2.90	0.00	0.0

Table 2. Measurements and descriptive statistics of the dentition of Ptilodus sp. C, Birchwood Local Fauna, Alberta.

Tooth	P	N	OR	M	SD	CV
p4	L	0	-	-	-	-
	W	8	2.1-3.0	2.50	0.33	13.2
m1	L	1	4.1	4.10	-	-
	W	2	1.9-2.0	1.95	0.07	3.6
m2	L	1	2.8	2.80	-	-
	W	1	2.1	2.10	-	-
P1	L	1	2.6	2.60	-	-
	W	2	2.4-2.5	2.45	0.07	2.9
P2	L	10	2.8-3.4	2.87	0.29	10.3
	W	10	2.4-3.0	2.60	0.18	7.0
P3	L	3	3.2-3.5	3.40	0.17	5.1
	W	3	2.2-2.5	2.37	0.15	6.5
P4	L	1	5.8	5.80	-	-
	W	1	2.7	2.70	-	-
M2	L	1	2.7	2.70	-	-
	W	1	2.4	2.40	-	-

Table 3. Measurements and descriptive statistics of the lower dentition of Elpidophorus elegans, Birchwood Local Fauna, Alberta.

Tooth	P	N	OR	M	SD	CV
i1	W	3	1.5-1.8	1.63	0.15	9.4
	D	3	2.4-2.7	2.50	0.17	6.9
i2	W	1	1.5	1.50	-	-
	D	1	2.1	2.10	-	-
p2	L	1	2.3	2.30	-	-
	W	1	1.7	1.70	-	-
p3	L	4	2.5-3.0	2.78	0.22	8.0
	W	4	2.2-2.5	2.35	0.13	5.5
p4	L	3	3.9-4.3	4.13	0.21	5.0
	W	3	2.8-3.1	2.93	0.15	5.2
m1	L	3	3.8-3.9	3.83	0.06	1.5
	AW	3	3.0-3.2	3.10	0.10	3.2
	PW	3	3.3-3.5	3.37	0.12	3.4
m2	L	3	4.1-4.3	4.17	0.12	2.8
	AW	3	3.2-3.6	3.37	0.21	6.2
	PW	4	3.5-3.8	3.60	0.14	3.9
m3	L	3	4.7-5.2	4.87	0.29	5.9
	AW	4	2.8-3.3	3.03	0.21	6.8
	PW	3	2.5-3.0	2.70	0.26	9.8

Table 4. Measurements and descriptive statistics of the upper dentition of Elpidophorus elegans, Birchwood Local Fauna, Alberta.

Tooth	P	N	OR	M	SD	CV
I1	W	1	3.6	3.60	-	-
	D	1	3.5	3.50	-	-
P2	L	1	2.6	2.60	-	-
	W	1	1.9	1.90	-	-
P3	L	2	3.6-3.9	3.75	0.21	5.7
	W	2	3.6-3.8	3.70	0.14	3.8
DP4	L	1	3.2	3.20	-	-
	AW	1	3.8	3.80	-	-
	PW	1	4.3	4.30	-	-
P4	L	3	3.5-3.9	3.73	0.21	5.6
	W	3	4.6-5.0	4.77	0.21	4.4
M1	L	1	4.1	4.10	-	-
	W	1	5.2	5.20	-	-
M2	L	2	3.9-4.1	4.00	0.14	3.5
	W	2	5.8-6.1	5.95	0.21	3.6

Table 5. Measurements and descriptive statistics of the lower dentition of *Pronothodectes gaoi*, Birchwood Local Fauna, Alberta.

Tooth	P	N	OR	M	SD	CV
i1	W	1	2.3	2.30	-	-
	D	1	3.9	3.90	-	-
p3	L	1	2.2	2.20	-	-
	W	1	1.8	1.80	-	-
p4	L	1	2.0	2.00	-	-
	W	1	2.2	2.20	-	-
m1	L	1	2.5	2.50	-	-
	AW	1	2.5	2.50	-	-
	PW	1	2.7	2.70	-	-
m2	L	2	3.1-3.5	3.30	0.28	8.6
	AW	2	2.8-2.9	2.85	0.07	2.5
	PW	2	3.0-3.1	3.05	0.07	2.3
m3	L	1	4.5	4.50	-	-
	AW	1	2.8	2.80	-	-
	PW	1	2.3	2.30	-	-

Table 6. Measurements and descriptive statistics of the dentition of Plesiadapis rex, Birchwood Local Fauna, Alberta.

Tooth	P	N	OR	M	SD	CV
i1	W	11	2.0-3.2	2.55	0.33	13.0
	D	11	3.1-4.4	3.88	0.37	9.4
p3	L	2	1.9-2.0	1.95	0.07	3.6
	W	2	1.7-1.8	1.75	0.07	4.0
p4	L	8	2.1-2.7	2.31	0.20	8.8
	W	8	1.9-2.4	2.10	0.15	7.2
m1	L	10	2.5-3.4	2.85	0.26	9.2
	AW	10	2.1-2.8	2.39	0.23	9.8
	PW	10	2.2-2.9	2.61	0.22	8.6
m2	L	9	2.8-3.4	3.07	0.20	6.5
	AW	10	2.5-3.2	2.77	0.22	7.9
	PW	9	2.7-3.3	2.94	0.23	7.8
m3	L	5	3.9-4.8	4.40	0.34	7.7
	AW	6	2.5-3.0	2.80	0.19	6.8
	PW	5	2.3-2.8	2.56	0.18	7.1
I1	W	10	2.3-2.8	2.60	0.16	6.3
	D	9	3.7-5.0	4.20	0.44	10.4
P3	L	1	1.9	1.90	-	-
	W	1	2.2	2.20	-	-
P4	L	4	2.1-2.4	2.23	0.13	5.6
	W	4	3.1-3.6	3.38	0.22	6.6
M1	L	3	2.7-2.8	2.77	0.06	2.1
	W	3	3.8-4.1	4.00	0.17	4.3
M2	L	4	3.0	3.00	0.00	0.0
	W	4	4.1-4.4	4.23	0.13	3.0
M3	L	5	2.7-3.0	2.94	0.13	4.6
	W	5	3.6-4.2	3.94	0.23	5.8

Table 7. Measurements and descriptive statistics of the lower dentition of Elphidotarsius wightoni, Birchwood Local Fauna, Alberta.

Tooth	P	N	OR	M	SD	CV
p4	L	3	1.8-2.0	1.90	0.10	5.3
	W	3	1.1-1.3	1.23	0.12	9.4
m1	L	1	1.3	1.30	-	-
	AW	1	1.0	1.00	-	-
	PW	1	1.0	1.00	-	-
m2	L	2	1.2-1.4	1.30	0.10	7.7
	AW	2	1.0-1.2	1.10	0.10	9.1
	PW	2	1.0-1.1	1.05	0.07	6.7



Table 8. Measurements and descriptive statistics of the dentition of Carpodactes hazelae, Birchwood Local Fauna, Alberta.

Tooth	P	N	OR	M	SD	CV
i1	D	1	1.8	1.80	-	-
	W	1	1.2	1.20	-	-
p4	L	3	2.4-2.7	2.53	0.13	4.9
	W	3	1.6-1.8	1.70	0.08	4.8
m1	L	2	1.5-1.9	1.70	0.20	11.8
	AW	2	1.2	1.20	0.00	0.0
	PW	2	1.2-1.3	1.25	0.05	4.0
m2	L	1	1.3	1.30	-	-
	AW	1	1.3	1.30	-	-
	PW	1	1.2	1.20	-	-
m3	L	1	1.9	1.90	-	-
	AW	1	1.1	1.10	-	-
	PW	1	1.2	1.20	-	-
P3	L	1	1.8*	1.80*	-	-
	W	1	2.1*	2.10*	-	-
P4	L	1	1.8*	1.80*	-	-
	W	1	2.6*	2.60*	-	-
M1	L	1	1.5	1.50	-	-
	W	1	2.1	2.10	-	-
M2	L	1	1.3	1.30	-	-
	W	1	2.1	2.10	-	-

Table 9. Measurements and descriptive statistics of the dentition of Protictis paralus, Birchwood Local Fauna, Alberta.

Tooth	P	N	OR	M	SD	CV
p4	L	1	4.2	4.20	-	-
	W	1	1.9	1.90	-	-
m1	L	0	-	-	-	-
	AW	1	2.7	2.70	-	-
m2	L	0	-	-	-	-
	AW	1	2.2	2.20	-	-
P4	L	1	5.3	5.30	-	-
	W	1	3.2	3.20	-	-

Table 10. Measurements and descriptive statistics of the dentition of Horolodectes albertensis, gen. and sp. nov., Birchwood Local Fauna, Alberta.

Tooth	P	N	OR	M	SD	CV
P3	L	1	2.7	2.70	-	-
	W	1	2.5	2.50	-	-
P4	L	3	2.5-2.7	2.57	0.12	4.5
	W	3	3.5-3.7	3.60	0.10	2.8
p2	L	2	2.1-2.4	2.25	0.21	9.4
	W	2	1.3	1.30	0.00	0.0
p3	L	3	2.4-2.6	2.47	0.12	4.7
	W	3	1.4-1.5	1.43	0.06	4.0
p4	L	3	3.1-3.3	3.17	0.12	3.6
	W	3	1.8-2.1	1.90	0.17	9.1
m1	L	2	2.5-2.7	2.60	0.14	5.4
	AW	2	1.7-1.8	1.75	0.07	4.0
	PW	2	1.9-2.1	2.00	0.14	7.1
m2	L	3	2.7-2.9	2.77	0.12	4.2
	AW	3	2.0-2.1	2.03	0.06	2.8
	PW	3	2.2-2.5	2.33	0.15	6.6
m3	L	3	2.8	2.80	0.00	0.0
	AW	3	1.9	1.90	0.00	0.0
	PW	3	1.9-2.1	2.00	0.14	7.1

Table 11. Measurements and descriptive statistics of the dentition of Colpoclaenus keeferi, Birchwood Local Fauna, Alberta.

Tooth	P	N	OR	M	SD	CV
p3	L	2	6.0	6.00	0.00	0.0
	W	2	3.1-3.5	3.30	0.28	8.6
p4	L	1	-	7.00	-	-
	AW	1	-	4.20	-	-
	PW	1	-	4.50	-	-
m1	L	3	7.7-8.5	8.13	0.40	5.0
	AW	4	4.9-6.0	5.45	0.20	3.7
	PW	3	5.9-6.9	6.33	0.51	8.1
m2	L	4	8.5-8.9	8.60	0.20	2.3
	AW	7	6.2-7.1	6.74	0.30	4.4
	PW	6	6.8-7.5	7.18	0.30	4.2
m3	L	1	-	11.50	-	-
	AW	1	-	7.20	-	-
	PW	1	-	4.90	-	-
M3	L	1	-	6.50	-	-
	W	1	-	7.80	-	-

Table 12. Measurements and descriptive statistics of the lower dentition of Ectocion cedrus, Birchwood Local Fauna, Alberta.

Tooth	P	N	OR	M	SD	CV
p3	L	4	4.5-5.2	4.85	0.25	5.2
	W	6	2.5-3.2	2.75	0.26	9.6
dp4	L	2	6.0-7.1	6.55	0.55	8.4
	W	2	3.7-4.3	4.00	0.30	7.5
p4	L	3	6.2-6.6	6.37	0.17	2.7
	W	3	3.8-4.3	4.03	0.21	5.1
m1	L	2	5.5-6.3	5.90	0.40	6.8
	AW	2	4.3-4.5	4.40	0.10	2.3
	PW	2	4.6-4.9	4.75	0.15	3.2
m2	L	7	6.0-6.8	6.36	0.23	3.7
	AW	7	4.5-5.2	4.77	0.27	5.7
	PW	8	4.6-5.2	4.83	0.24	4.9
m3	L	3	6.5-7.2	6.83	0.29	4.2
	AW	3	4.3-4.5	4.40	0.08	1.9
	PW	3	3.8-4.0	3.87	0.09	2.4

Table 13. Measurements and descriptive statistics of the upper dentition of Ectocion cedrus, Birchwood Local Fauna, Alberta.

Tooth	P	N	OR	M	SD	CV
P2	L	3	5.4-6.0	5.63	0.26	4.7
	W	3	4.6-5.2	4.90	0.25	5.0
DP3	L	2	6.0-6.2	6.10	0.10	1.6
	W	2	4.0	4.00	0.00	0.0
P3	L	1	6.6	6.60	-	-
	W	1	5.8	5.80	-	-
DP4	L	2	5.5-6.1	5.80	0.30	5.2
	W	2	5.9-6.3	6.10	0.20	3.28
P4	L	3	5.5-5.7	5.57	0.09	1.7
	W	3	6.2-6.8	6.53	0.25	3.8
M1	L	1	7.1	7.10	-	-
	W	1	7.8	7.80	-	-
M2	L	3	6.2-7.1	6.73	0.39	5.7
	W	3	7.2-8.8	8.07	0.66	8.2
M3	L	3	5.2-5.8	5.57	0.26	4.7
	W	2	5.8-6.3	6.05	0.25	4.1

Table 14. Measurements and descriptive statistics of the lower dentition of Pararyctes pattersoni, Birchwood Local Fauna, Alberta.

Tooth	P	N	OR	M	SD	CV
p5	L	3	1.5	1.50	0.00	0.0
	W	3	0.9-1.1	1.00	0.10	10.0
m1	L	3	1.8-2.0	1.87	0.12	6.2
	AW	3	1.4-1.5	1.47	0.06	3.9
	PW	3	1.0-1.2	1.10	0.10	9.1
m2	L	4	1.7-1.9	1.80	0.08	4.5
	AW	4	1.5-1.6	1.53	0.05	3.3
	PW	4	1.1-1.2	1.18	0.05	4.3
m3	L	4	1.9-2.4	2.08	0.22	10.7
	AW	4	1.4-1.5	1.48	0.05	3.4
	PW	4	0.8-1.2	0.98	0.17	17.5

Table 15. Measurements and descriptive statistics of the dentition of Bisonalveus gracilis, sp. nov., Birchwood Local Fauna, Alberta.

Tooth	P	N	OR	M	SD	CV
p3	L	3	1.6-1.8	1.73	0.12	6.7
	W	3	1.2-1.3	1.27	0.06	4.5
p4	L	8	1.9-2.3	2.08	0.13	6.2
	W	8	1.4-1.8	1.51	0.14	9.0
m1	L	13	2.1-2.4	2.22	0.08	3.7
	AW	12	1.5-1.9	1.68	0.13	7.5
	PW	13	1.5-1.9	1.69	0.14	8.5
m2	L	20	2.3-2.7	2.48	0.10	3.9
	AW	20	1.6-2.2	1.95	0.17	8.6
	PW	21	1.5-1.9	1.75	0.12	6.9
m3	L	8	2.3-2.6	2.41	0.11	4.7
	AW	9	1.5-1.9	1.62	0.12	7.4
	PW	6	1.3-1.5	1.40	0.09	6.4
M2	L	6	2.4-2.6	2.47	0.10	4.2
	W	3	3.5-3.6	3.53	0.06	1.6
M3	L	1	1.8	1.80	-	-
	W	1	2.8	2.80	-	-



Table 16. Comparisons of faunal composition of the Birchwood local fauna with selected middle Tiffanian mammal localities.

<u>Birchwood Taxa</u>	<u>UADW-2</u> <sup>1</sup> ~ 52°N	<u>I./B.</u> <sup>2</sup> ~ 47°N	<u>C.P.Q.</u> <sup>3</sup> ~ 45°N
Latitude →53°15'			
<u>Mimetodon silberlingi</u>	S <sup>4</sup>	-	-
<u>Neoplagiaulax</u> sp., cf. <u>N. hunteri</u>	S	?S	?S
<u>Neoplagiaulax</u> sp., cf. <u>N. hazeni</u>	S	G	G
<u>Neoplagiaulacidae</u> , unident. genus and species	-	-	-
<u>Ptilodus</u> sp. T	G	G	G
<u>Ptilodus</u> sp. C	S	S	S
<u>Prochetodon foxi</u>	G	S	-
<u>Microcosmodon woodi</u>	S	S	-
<u>Litocherus zygeus</u>	G	S	S
<u>Adapisoricidae</u> , unident. genus and species	-	-	-
<u>Leptacodon</u> sp., cf. <u>L. tener</u>	G	S	?S
<u>Leptacodon munusculum</u>	G	G	S
<u>Elpidophorus elegans</u>	S	-	S
<u>Plesiolestes</u> sp., cf. <u>P. sirokyi</u>	-	-	-
<u>Ignacius frugivorus</u>	S	S	S
<u>Pronothodectes gaoi</u>	S	-	-
<u>Plesiadapis rex</u>	?S	S	S
<u>Elphidotarsius wightoni</u>	S	-	-
<u>Carpodaptes hazelae</u>	S	G	S
<u>Saxonella</u> sp. nov. (unnamed)	G	-	-
<u>Protictis paralus</u>	S	S	S
<u>Raphictis gausion</u>	?S	-	S
<u>Horolodectes albertensis</u> , gen. and sp. nov.	S	-	-
<u>Chriacus</u> sp., cf. <u>C. pelvidens</u>	-	-	G
<u>Thryptacodon australis</u>	-	S	S
<u>Colpoclaenus keeferi</u>	S	-	-
<u>Claenodon</u> sp., cf. <u>C. montanensis</u>	G	G	G
<u>Desmatoclaenus mearae</u>	S	-	-
<u>Ectocion cedrus</u>	-	G	S
<u>Phenacodus</u> sp.	-	G	G
<u>Dorraletes diminutivus</u>	-	S	-
<u>Litomytus</u> sp.	-	-	G
<u>Dissacus</u> sp.	-	-	G
<u>Titanoides primaevus</u>	-	S	G
<u>Cyriacotherium</u> sp., cf. <u>C. argyreum</u>	S	-	-
<u>Pararyctes pattersoni</u>	G	S	-
<u>Bisonalveus gracilis</u> , sp. nov.	S	G	-
<u>Propalaeosinopa septentrionalis</u>	S	S	G
<u>Eudaemonema onkotos</u> , sp. nov.	S	-	-
<u>Jepsenella</u> sp., cf. <u>J. praepropera</u>	-	-	-
Total matches →	20S,8G,12-	14S,8G,18-	13S,9G,18-

<sup>1</sup> UADW-2 mammal locality, Paskapoo Fm., central Alberta (Fox, 1990a).<sup>2</sup> Judson and Brisbane mammal localities, Tongue River Fm, North Dakota (Holtzman, 1978).<sup>3</sup> Cedar Point Quarry, Polecat Bench Fm., Wyoming (Rose, 1981).<sup>4</sup> S = species match; G = genus match; - = no match at the species or generic level.

Plate 1.

Mimetodon silberlingi

A. Lp4, UALVP 39122, lingual view, about 13.8 x.

B. Same, labial view, about 13.8 x.

Neoplagiaulax sp., cf. N. hazeni

C. Lp4, UALVP 39125, lingual view, about 11.6 x.

D. Same, labial view, about 11.6 x.

Neoplagiaulacidae, unident. gen. and sp.

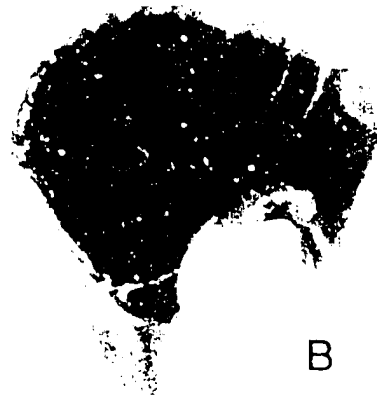
E. RP4, UALVP 39123, labial view, about 13.1 x.

F. Same, lingual view, about 13.1 x.

G. Same, occlusal view, about 13.1 x.



A



B



C



D



E



F



G

Plate 2.

Neoplagiaulax sp., cf. N. hunteri

- A. LM1, UALVP 39128, lingual view, about 13.6 x.
- B. Same, labial view, about 13.6 x.
- C. Same, occlusal view, about 13.6 x.
- D. LP3, UALVP 39180, lingual view, about 19.2 x.
- E. Same, occlusal view, about 25.8 x.
- F. Rp4, UALVP 39126, labial view, about 13.8 x.
- G. Same, lingual view, about 13.8 x.



A



B



C



D



E



F



G

Plate 3.

Ptilodus sp. T

- A. LP1, UALVP 39147, lingual view, about 12.2 x.
- B. Same, labial view, about 12.2 x.
- C. Same, occlusal view, about 12.2 x.
- D. LP2, UALVP 39148, occlusal view, about 13.1x.
- E. Rp4, UALVP 39142, lingual view, about 7.6 x.
- F. Same, labial view, about 7.6 x.



A



B



C



D



E



F

Plate 4.

Ptilodus sp. C

- A. LP1, UALVP 39163, lingual view, about 16.2 x.
- B. Same, labial view, about 16.2 x.
- C. Same, occlusal view, about 16.2 x.
- D. LP2, UALVP 39168, lingual view, about 13.0 x.
- E. Same, labial view, about 13.0 x.
- F. Same, occlusal view, about 13.0 x.
- G. RP3, UALVP 39175, lingual view, about 12.9 x.
- H. Same, labial view, about 12.9 x.
- I. Same, occlusal view, about 12.9 x.





A



B



C



D



E



F



G



H



I

Plate 5.

Ptilodus sp. C

- A. LP4, UALVP 39157, lingual view, about 10.2 x.
- B. Same, labial view, about 10.2 x.
- C. Same, occlusal view, about 8.6 x.
- D. RM2, UALVP 39162, lingual view, about 11.9 x.
- E. Same, labial view, about 11.9 x.
- F. Same, occlusal view, about 11.9 x.
- G. Li1, UALVP 39185, medial view, about 6.4 x.
- H. Same, labial view, about 6.4 x.
- I. Lp4, UALVP 39150, lingual view, about 6.8 x.
- J. Same, labial view, about 6.8 x.



A



B



C



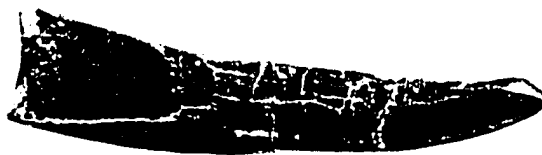
D



E



F



G



H



I



J

Plate 6.

Ptilodus sp. C

- A. Rm1, UALVP 39159, lingual view, about 12.9 x.
- B. Same, labial view, about 12.9 x.
- C. Same, occlusal view, about 10.7 x.
- D. Lm2, UALVP 39161, labial view, about 12.5 x.

Prochetodon foxi

- E. Lp4, UALVP 39137, lingual view, about 9.6 x.
- F. Same, labial view, about 10.4 x.



A



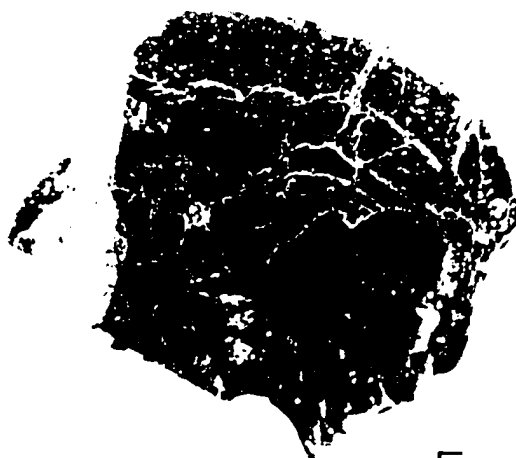
B



C



D



E



F

Plate 7.

Microcosmodon woodi

- A. Rm1, UALVP 39135, lingual view, about 12.5 x.
- B. Same, labial view, about 12.6 x.
- C. Same, occlusal view, about 12.6 x.
- D. LI2, UALVP 39198, labial view, about 10.1 x.
- E. Same, occlusal view, about 10.1 x.
- F. Ri1, UALVP 39184, medial view, about 9.0 x.
- G. Same, labial view, about 9.0 x.
- H. Right dentary fragment with p3-4 and m1, UALVP 39178, lingual view, about 11.0 x.
- I. Same, labial view, about 11.3 x.



A



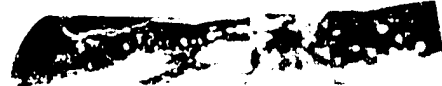
B



C



D



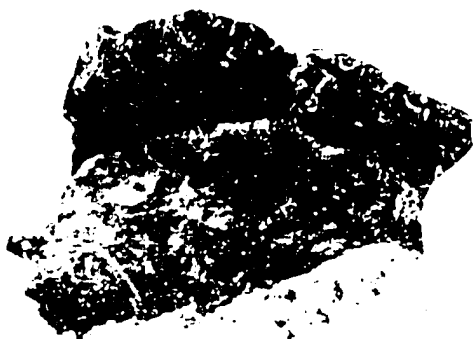
E



F



G



H



I

Plate 8.

Litocherus zygeus

- A. Right dentary fragment with p4 and m1-2, UALVP 39477, lingual view, about 6.4 x.
- B. Same, labial view, about 6.4 x.
- C. Same, occlusal view, about 12.7 x.
- D. RP4, UALVP 39287, anterior view, about 16.7 x.
- E. Same, labial view, about 15.0 x.
- F. Same, occlusal view, about 15.0 x.

Adapisoricinae, unident. gen. and sp.

- G. RP4, UALVP 39483, anterior view, about 15.0 x.
- H. Same, labial view, about 15.0 x.
- I. Same, occlusal view, about 15.0 x.





Plate 9.

Leptacodon sp., cf. L. tener

- A. Right dentary fragment with m1-3, UALVP 39479, lingual view, about 15.7 x.
- B. Same, labial view, about 15.7 x.
- C. Same, occlusal view, about 15.7 x.

Leptacodon munusculum

- D. Right dentary fragment with m1-3, UALVP 39480, lingual view, about 15.9 x.
- E. Same, labial view, about 15.9 x.
- F. Same, occlusal view, about 15.9 x.



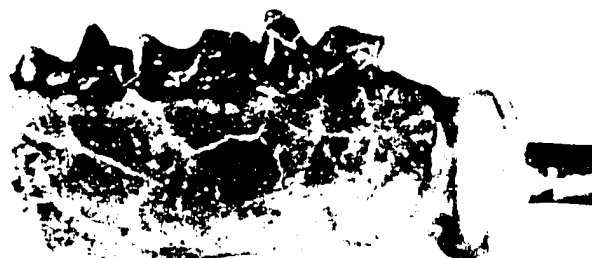
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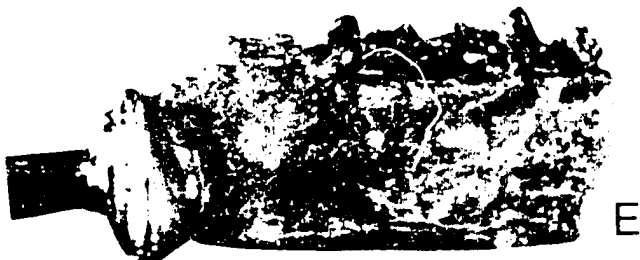
B



C



D



E



F

Plate 10.

Elpidophorus elegans

- A. Right maxillary fragment with P2-4 and M1-2, UALVP 39392, labial view, about 3.6 x.
- B. Same, occlusal view, about 3.6 x.
- C. RDP4, UALVP 39407, anterior view, about 10.5 x.
- D. Same, occlusal view, about 10.5 x.

Elpidophorus clivus (late Tiffanian Swan Hills Site 1, Stonley 1988, unpublished)

- E. "LDP4", UALVP 22491, occlusal view, about 12.1 x.

Elpidophorus elegans

- F. LI1, UALVP 39391, labial view, about 5.8 x.
- G. Same, occlusal view, about 8.9 x.
- H. Same, dorsal view, about 5.8 x.

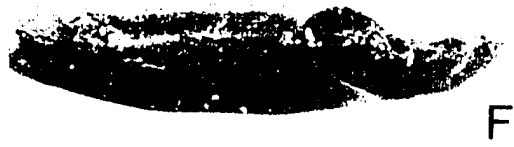


Plate 11.

Elpidophorus elegans

- A. Right dentary fragment with i1-2, UALVP 39400, medial view, about 8.7 x.
- B. Same, labial view, about 8.7 x.
- C. Same, occlusal view, about 8.7 x.
- D. Lp2, UALVP 39402, lingual view, about 11.5 x.
- E. Same, labial view, about 11.5 x.
- F. Same, occlusal view, about 11.5 x.
- G. Right dentary fragment with p3-4 and m1-3, UALVP 39397, labial view, about 3.7 x.
- H. Same, occlusal view, about 3.7 x.



A



B



C



D



E



F



G



H

Plate 12.

Plesiolestes sp., cf. P. sirokyi

A. RM1, UALVP 39301, anterior view, about 8.7 x.

B. Same, occlusal view, about 8.7 x.

Ignacius frugivorus

C. Left maxillary fragment with M1-3, UALVP 39302, labial view, about 11.7 x.

D. Same, occlusal view, about 11.7 x.

Pronothodectes gaoi

E. Left dentary fragment with i1, p3, and alveoli for i2, c, p2, p4, m1-3, UALVP 39372, anterolabial view, about 4.0 x.

F. Same, occlusal view, about 3.2 x.

G. Lp3 of UALVP 39372, labial view, about 11.4 x.

H. Same, occlusal view, about 11.4 x.





A



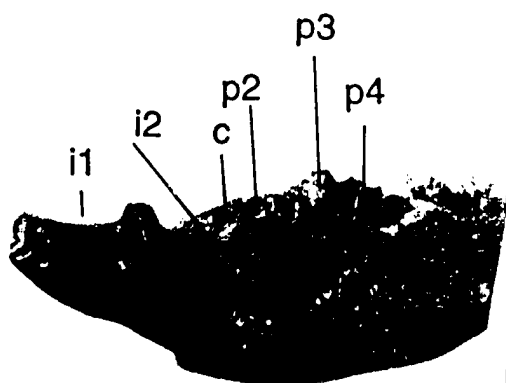
B



C



D



E



F



G



H

Plate 13.

Plesiadapis rex

- A. RI1, UALVP 39332, medial view, about 4.4 x.
- B. Same, labial view, about 4.4 x.
- C. Left dentary with i1, p4, and m1-3, UALVP 39313, lingual view, about 1.9 x.
- D. Same, labial view, about 2.7 x.
- E. Same, occlusal view, about 2.4 x.
- F. Right maxillary fragment with P3-4 and M1-3, UALVP 39359, labial view, about 4.0 x.
- G. Same, occlusal view, about 5.5 x.



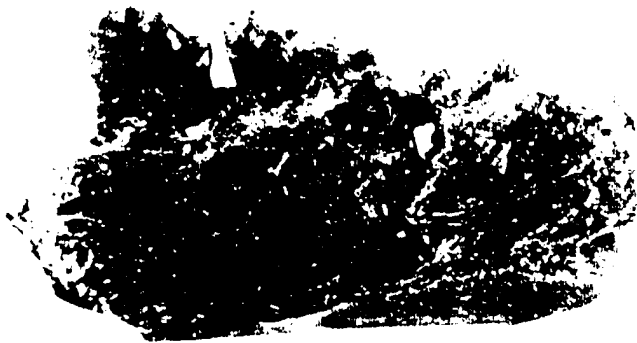
Plate 14.

Elphidotaraius wightoni

- A. Right dentary fragment with p4 and m1-2, UALVP 39303, lingual view, about 9.5 x.
- B. Same, labial view, about 9.5 x.

Carpodaptes hazelae

- C. Left dentary fragment with p4 and m1-3, UALVP 39307, lingual view, about 8.3 x.
- D. Same, labial view, about 8.3 x.
- E. Same, occlusal view, about 8.3 x.



A



B



C



D



E

Plate 15.

Carpodaptes hazelae

- A. Ri1, UALVP 39310, medial view, about 10.8 x.
- B. Same, labial view, about 10.8 x.
- C. Same, occlusal view, about 10.8 x.
- D. Left maxillary fragment with P3-4 and M1-2, UALVP 39306, labial view, about 10.0 x.
- E. Same, occlusal view, about 10.0 x.

Saxonella, sp. nov. (unnamed)

- F. Lm2, UALVP 39498, lingual view, about 18.0 x.
- G. Same, labial view, about 18.0 x.
- H. Same, occlusal view, about 18.0 x.

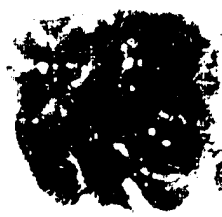
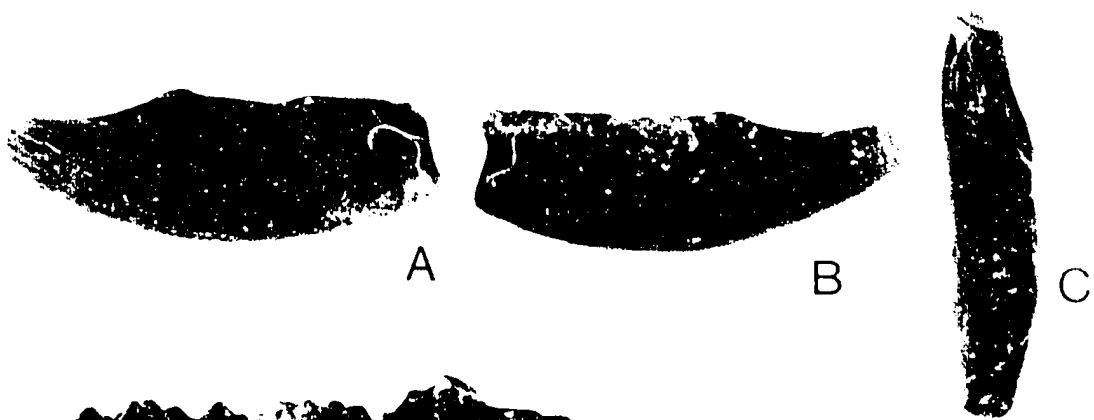


Plate 16.

Protictis paralus

- A. RP4, UALVP 39414, lingual view, about 10.8 x.
- B. Same, labial view, about 10.8 x.
- C. Same, occlusal view, about 10.8 x.
- D. Lp4, UALVP 39415, lingual view, about 11.0 x.
- E. Same, labial view, about 11.0 x.
- F. Same, occlusal view, about 11.0 x.

Raphictis gausson

- G. Rm1, UALVP 39418, lingual view, about 10.3 x.
- H. Same, labial view, about 10.3 x.
- I. Same, occlusal view, about 10.3 x.





A



B



C



D



E



F



G



H



I

Plate 17.

Horolodectes albertensis, gen. and sp. nov.

- A. Right dentary fragment with p2-4 and m2-3, holotype, UALVP 39201, lingual view, about 3.3 x.
- B. Same, labial view, about 3.3 x.
- C. Same, occlusal view, about 3.3 x.
- D. Right dentary fragment with p2-4, m1-3, and alveoli for i1-3, c, p1, lingual view, about 3.0 x.
- E. Same, labial view, about 3.0 x.
- F. Same, occlusal view, about 3.0 x.
- G. Same, anterolabial view, about 7.5 x.

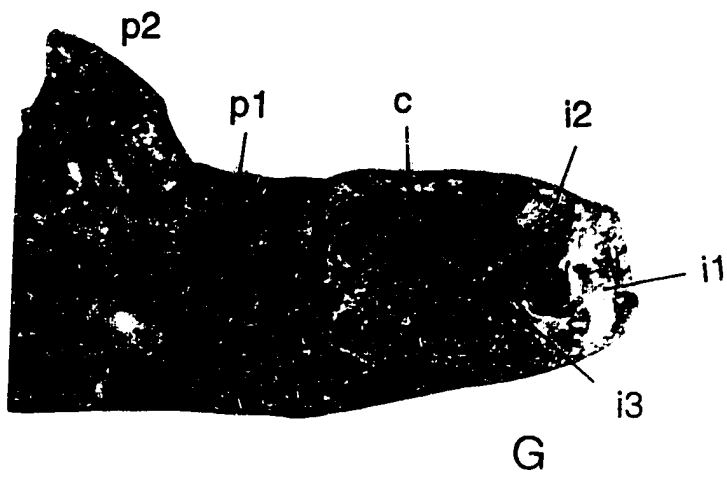
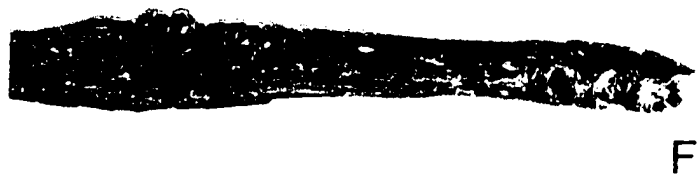


Plate 18.

Horolodectes albertensis, gen. and sp. nov.

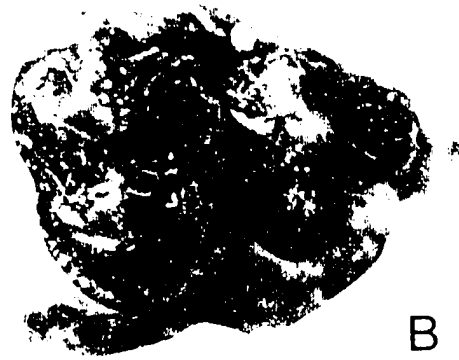
- A. Right maxillary fragment with P3-4, UALVP 39463, labial view, about 10.3 x.
- B. Same, occlusal view, about 10.3 x.
- C. RP4, UALVP 39465, anterior view, about 11.0 x.
- D. Same, posterior view, about 11.0 x.
- E. Same, occlusal view, about 11.0 x.

Chriacus sp., cf. C. pelvidens

- F. LM1, UALVP 39222, anterior view, about 6.3 x.
- G. Same, occlusal view, about 6.3 x.



A



B



C



D



E



F



G

Plate 19.

Thryptacodon australis

- A. LDP4, UALVP 39233, anterior view, about 8.1x.
- B. Same, occlusal view, about 8.1 x.
- C. Right dentary fragment with m1-2, UALVP 39230, lingual view, about 5.2 x.
- D. Same, labial view, about 5.2 x.
- E. Same, occlusal view, about 6.5 x.
- F. Lm3, UALVP 39232, lingual view, about 8.0 x.
- G. Same, labial view, about 8.0 x.
- H. Same, occlusal view, about 8.0 x.



A



B



C



D



E



F



G



H

Plate 20.

Colpoclaenus keeferi

- A. RM3, UALVP 39215, anterior view, about 6.5 x.
- B. Same, labial view, about 6.5 x.
- C. Same, occlusal view, about 6.5 x.
- D. Lp3, UALVP 39217, lingual view, about 7.8 x.
- E. Same, labial view, about 7.8 x.
- F. Same, occlusal view, about 7.8 x.
- G. Lp4, UALVP 39218, lingual view, about 6.6 x.
- H. Same, labial view, about 6.6 x.
- I. Same, occlusal view, about 6.6 x.



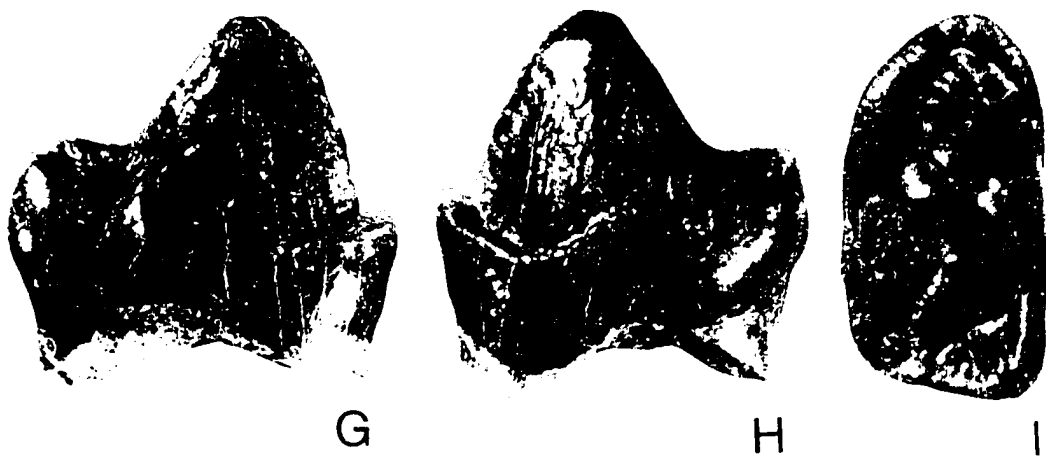
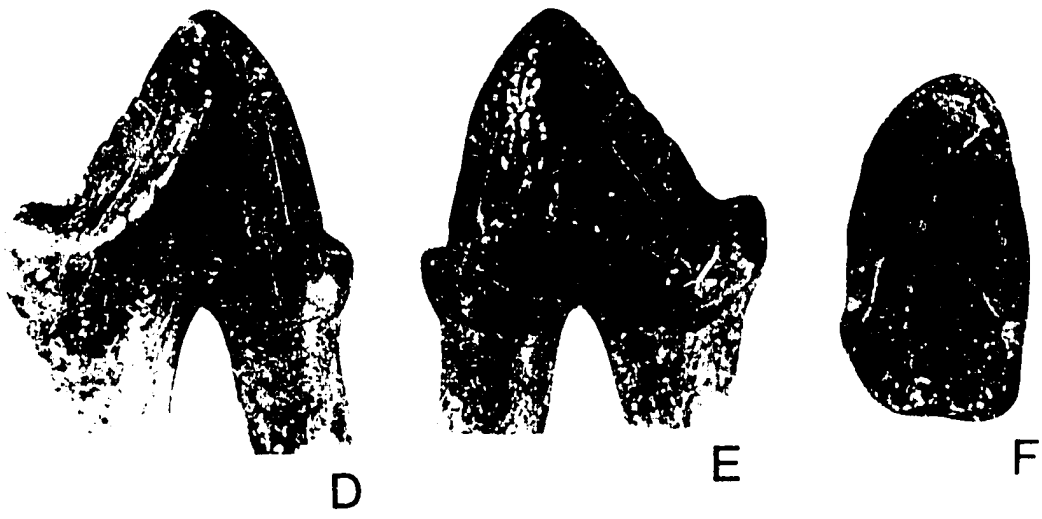
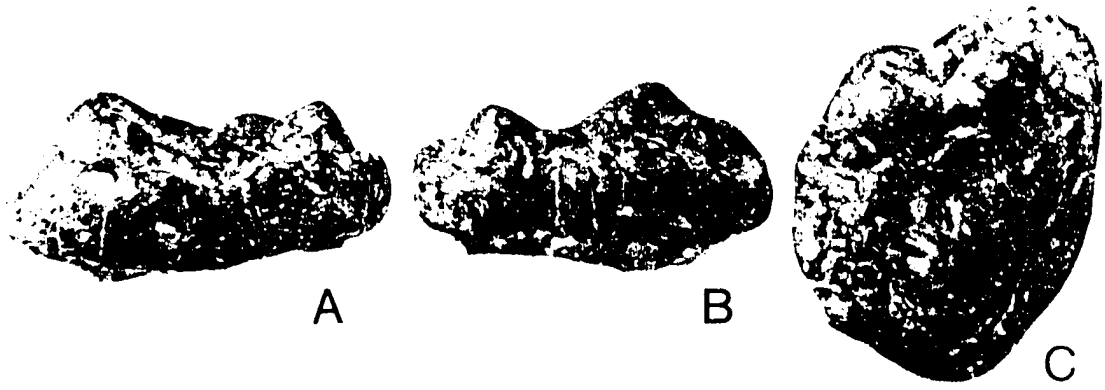


Plate 21.

Colpoclaenus keeferi

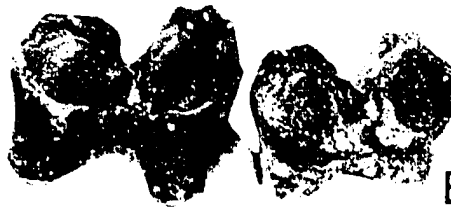
- A. Right dentary fragment with m1-2, UALVP 39203, lingual view, about 3.3 x.
- B. Same, labial view, about 3.3 x.
- C. Same, occlusal view, about 3.3 x.
- D. Right dentary fragment with m2-3, UALVP 39202, lingual view, about 3.6 x.
- E. Same, labial view, about 3.6 x.
- F. Same, occlusal view, about 3.6 x.

Claenodon sp., cf. C. montanensis

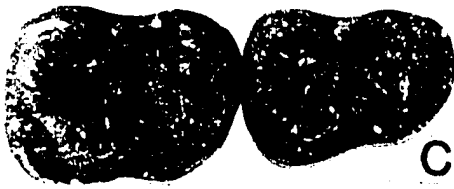
- G. LC1, UALVP 39227, medial view, about 3.5 x.
- H. Same, labial view, about 3.5 x.
- I. Same, occlusal view, about 3.5 x.



A



B



C



D



E



F



G



H



I

Plate 22.

Claenodon sp., cf. C. montanensis

- A. Rm2, UALVP 39224, labial view, about 5.3 x.
- B. Same, occlusal view, about 5.3 x.
- C. LM1, UALVP 39223, anterior view, about 5.2 x.
- D. Same, labial view, about 5.2 x.
- E. Same, occlusal view, about 5.2 x.
- F. LM3, UALVP 39225, anterior view, about 5.2 x.
- G. Same, labial view, about 5.2 x.
- H. Same, occlusal view, about 5.2 x.



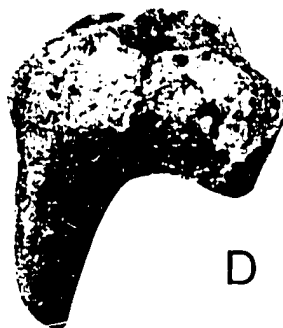
A



B



C



D



E



F



G



H

Plate 23.

Desmatoclaenus mearae

- A. LM2, UALVP 39234, anterior view, about 4.0 x.
- B. Same, labial view, about 4.0 x.
- C. Same, occlusal view, about 4.0 x.
- D. RP4, UALVP 39235, anterior view, about 7.6 x.
- E. Same, labial view, about 7.6 x.
- F. Same, occlusal view, about 7.6 x.
- G. LDP4, UALVP 39249, anterior view, about 7.2 x.
- H. Same, labial view, about 7.2 x.
- I. Same, occlusal view, about 7.2 x.



A



B



C



D



E



F



G



H



I

Plate 24.

Ectocion cedrus

- A. RDP3, UALVP 39254, anterior view, about 6.3 x.
- B. Same, labial view, about 6.3 x.
- C. Same, occlusal view, about 6.3 x.
- D. RDP4, UALVP 39257, anterior view, about 7.1 x.
- E. Same, labial view, about 7.1 x.
- F. Same, occlusal view, about 7.1 x.
- G. RP2, UALVP 39251, labial view, about 7.0 x.
- H. Same, occlusal view, about 7.0 x.
- I. LP3, UALVP 39255, anterior view, about 6.4 x.
- J. Same, labial view, about 6.4 x.
- K. Same, occlusal view, about 6.4 x.

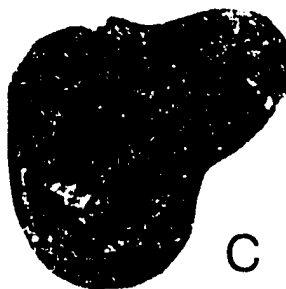




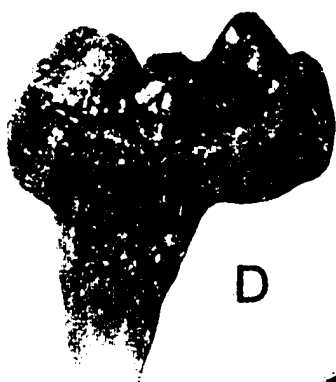
A



B



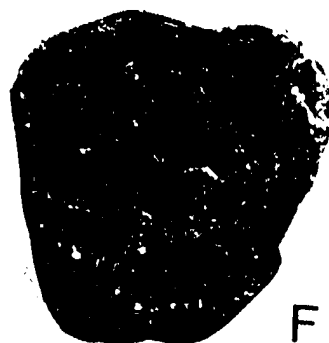
C



D



E



F



G



H



I



J

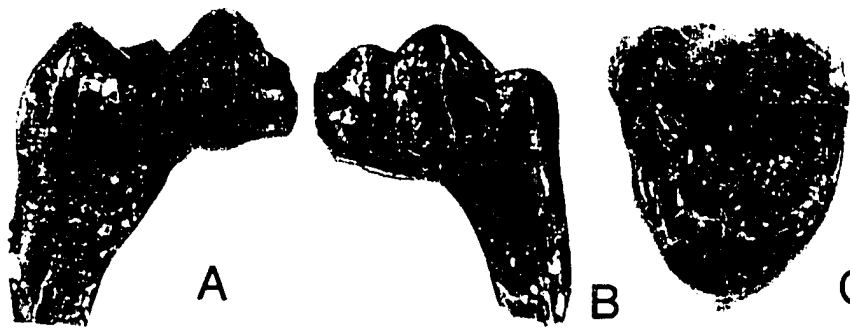


K

Plate 25.

Ectocion cedrus

- A. LP4, UALVP 39260, posterior view, about 5.9 x.
- B. Same, labial view, about 5.9 x.
- C. Same, occlusal view, about 5.9 x.
- D. LM2, UALVP 39242, anterior view, about 8.3 x.
- E. Same, labial view, about 6.9 x.
- F. Same, occlusal view, about 6.5 x.
- G. RM3, UALVP 39247, anterior view, about 9.2 x.
- H. Same, labial view, about 9.2 x.
- I. Same, occlusal view, about 9.2 x.
- J. Rp3, UALVP 39275, lingual view, about 7.7 x.
- K. Same, labial view, about 7.7 x.
- L. Same, occlusal view, about 7.7 x.



A

B



C



D



E



F



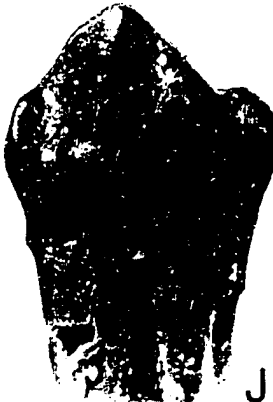
G



H



I



J



K



L

Plate 26.

Ectocion cedrus

- A. Lp4, UALVP 39282, lingual view, about 7.4 x.
- B. Same, labial view, about 7.4 x.
- C. Same, occlusal view, about 7.4 x.
- D. Rdp4, UALVP 39280, lingual view, about 7.7 x.
- E. Same, labial view, about 7.7 x.
- F. Same, occlusal view, about 7.7 x.
- G. Right dentary fragment with m2-3, UALVP 39263, lingual view, about 4.0 x.
- H. Same, occlusal view, about 4.0 x.
- I. Same, labial view, about 4.0 x.

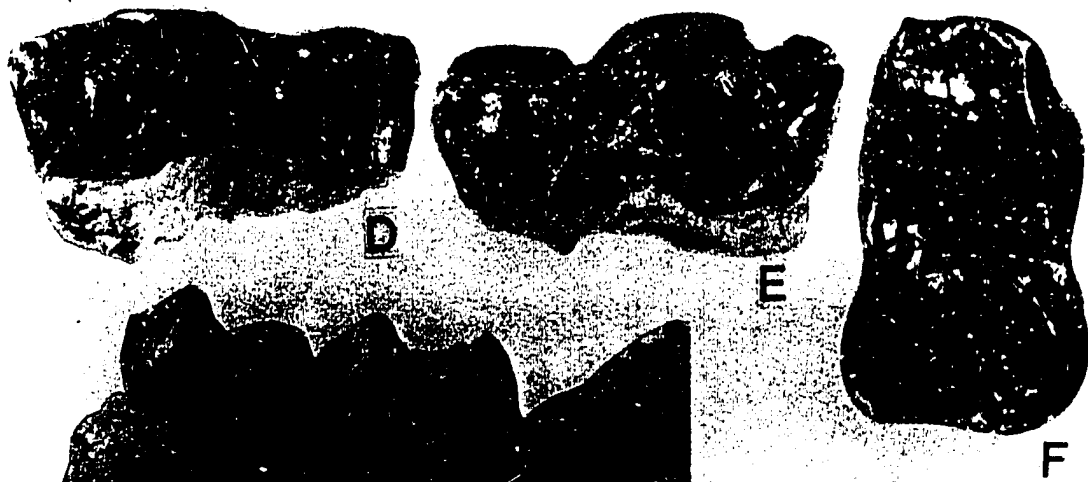
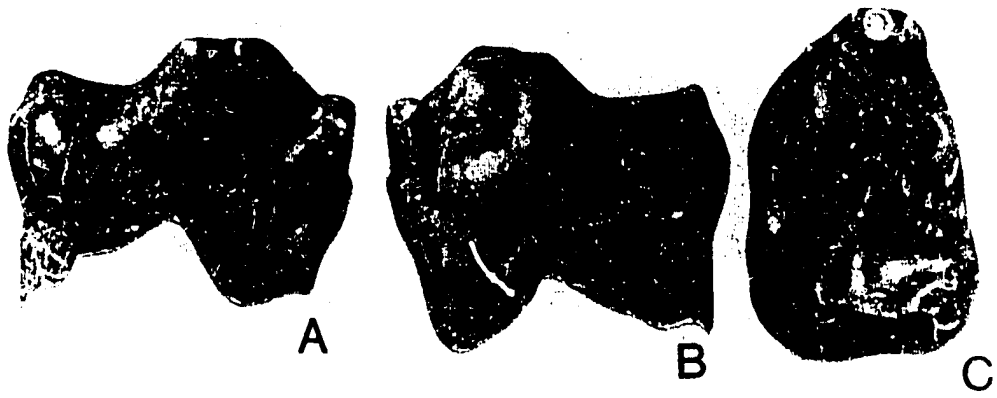


Plate 27.

Phenacodus sp.

- A. RP4, UALVP 39237, anterior view, about 6.7 x.
- B. Same, labial view, about 6.7 x.
- C. Same, occlusal view, about 6.7 x.

Dorraletes diminutivus

- D. RM2, UALVP 39484, anterior view, about 14.0 x.
- E. Same, labial view, about 14.0 x.
- F. Same, occlusal view, about 14.0 x.

Litomylus sp.

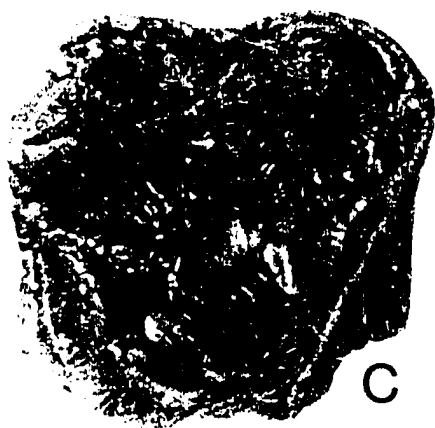
- G. LM1, UALVP 39245, anterior view, about 8.0 x.
- H. Same, labial view, about 8.0 x.
- I. Same, occlusal view, about 8.0 x.



A



B



C



D



E



F



G



H



I

Plate 28.

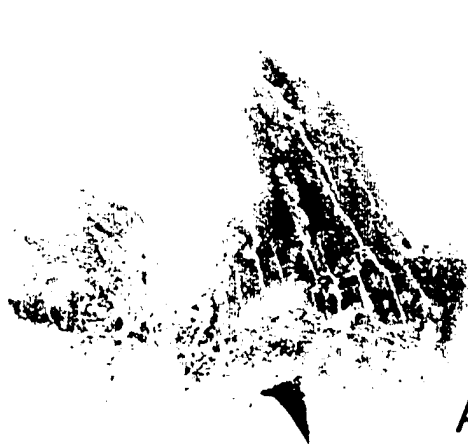
Dissacus sp.

- A. Lpx, UALVP 39221, lingual view, about 4.7 x.
- B. Same, labial view, about 4.7 x.
- C. Same, occlusal view, about 4.7 x.
- D. Lmx, UALVP 39220, lingual view, about 3.9 x.
- E. Same, labial view, about 3.9 x.
- F. Same, occlusal view, about 4.5 x.

Cyriacotherium sp., cf. C. argyreum

- G. RM1, UALVP 39485, anterior view, about 5.0 x.
- H. Same, occlusal view, about 5.0 x.





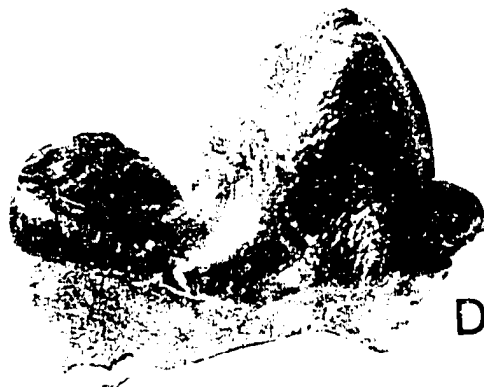
A



B



C



D



E



F



G



H

Plate 29.

Pararyctes pattersoni

- A. Right dentary fragment with p5 and m1-3, UALVP 39468, lingual view, about 10.0 x.
- B. Same, labial view, about 10.0 x.
- C. Same, occlusal view, about 10.0 x.

Bisonalveus gracilis, sp. nov.

- D. Left dentary fragment with p3-4, m1-3, and alveolus for p2, holotype, UALVP 39432, lingual view, about 6.0 x.
- E. Same, labial view, about 6.0 x.
- F. Same, occlusal view, about 6.0 x.



A



B



C



D



E



F

Plate 30.

Bisonalveus gracilis, sp. nov.

- A. LM2, UALVP 39422, anterior view, about 13.4 x.
- B. Same, occlusal view, about 13.4 x.
- C. RM3, UALVP 39425, anterior view, about 12.9 x.
- D. Same, occlusal view, about 12.9 x.

Propalaeosinopa septentrionalis

- E. LM1, UALVP 39467, anterior view, about 11.3 x.
- F. Same, occlusal view, about 11.3 x.
- G. Left dentary fragment with m2-3, UALVP 39459, lingual view, about 8.1 x.
- H. Same, labial view, about 8.1 x.
- I. Same, occlusal view, about 8.1 x.



A



B



C



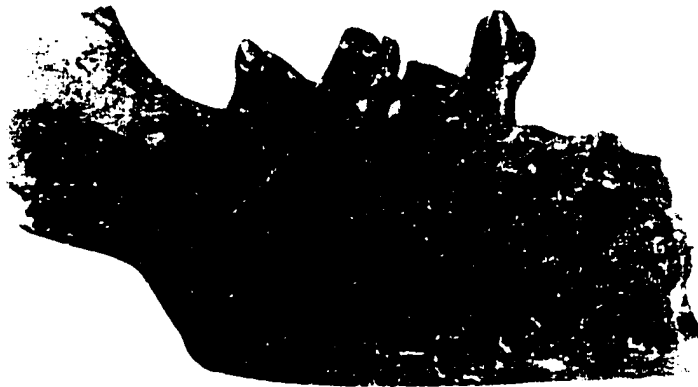
D



E



F



G



H



I

Plate 31.

Eudaemonema onkotos, sp. nov.

- A. LM1, holotype, UALVP 39409, anterior view, about 9.5 x.
- B. Same, occlusal view, about 9.5 x.
- C. RM2, UALVP 39410, anterior view, about 9.2 x.
- D. Same, occlusal view, about 9.2 x.
- E. RM3, UALVP 39411, anterior view, about 9.7 x.
- F. Same, occlusal view, about 9.7 x.
- G. Rm2, UALVP 39462, lingual view, about 9.1 x.
- H. Same, labial view, about 9.1 x.
- I. Same, occlusal view, about 9.1 x.

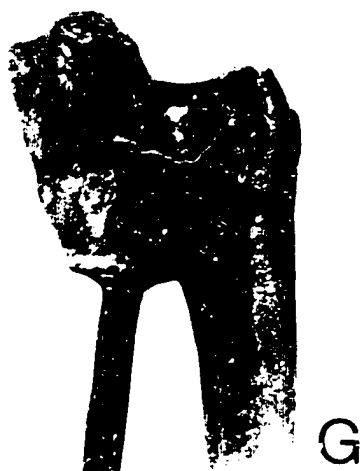
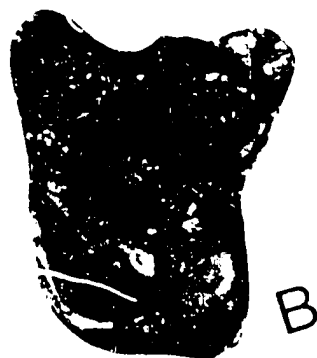


Plate 32.

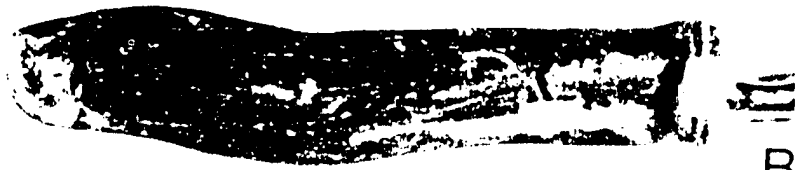
Jepsenella sp., cf. J. praepropera

- A. RI1, UALVP 39494, medial view, about 10.3 x.
- B. Same, occlusal view, about 10.3 x.
- C. RM1, UALVP 39493, anterior view, about 13.8 x.
- D. Same, posterior view, about 13.8 x.
- E. Same, occlusal view, about 13.8 x.
- F. Rp2, UALVP 39495, lingual view, about 13.1 x.
- G. Same, labial view, about 13.1 x.
- H. Same, occlusal view, about 13.1 x.

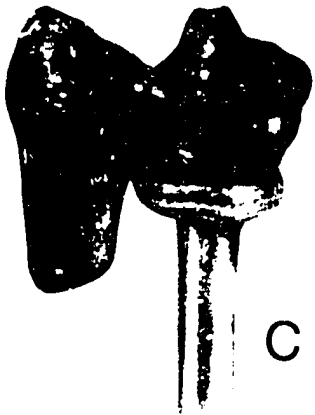




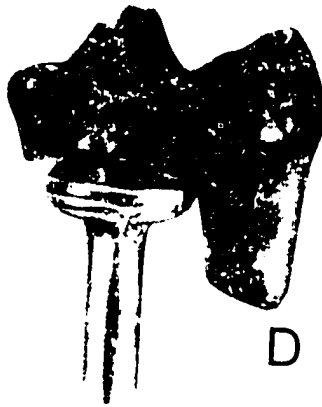
A



B



C



D



E



F



G



H