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THE UNIVERSITY OF ALBERTA

# LATE PALEOCENE MAMMALS OF THE SWAN HILLS LOCAL FAUNA (PASKAPOO FORMATION), ALBERTA.

BY

GARY JOHN STONLEY

A THESIS
SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE OF
MASTER OF SCIENCE.

DEPARTMENT OF ZOOLOGY

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Late Paleocene mammals of the Swan Hills local fauna (Paskapoo Formation), Alberta.

submitted by

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in partial fulfilment of the requirements for the degree of

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# ABSTRACT

The mammalian fauna from two artificial exposures of the Paskapoo Formation in the Swan Hills is described. Swan Hills site 1 is a low-lying hillock at the back of a partially overgrown oil well-site; site 2 is a road cut approximately one kilometer northwest of site 1. The exposures are composed of lacustrine deposits of alternating layers of green and grey, friable, argillaceous shales. These shales are variably fossiliferous and have a high montmorillonite content. Thin beds of hard argillaceous and calcareous, fossiliferous shales are interbedded with the soft shales. Although several specimens were obtained by splitting the calcareous shales at site 2, the bulk of the sample was retrieved through screen-washing of the greenish-grey, argillaceous shales containing numerous gastropod shell fragments.

The description here of the first relatively large sample of Carpodaptes cygneus from the type locality raises several questions concerning the middle and late Tiffanian systematics of the Carpolestidae. A new species of Elpidophorus intermediate in size between E. minor and E. elegans suggests that species of Elpidophorus represent a specialized side branch of the Plagiomenidae not ancestral to younger plagiomenids. In addition to the first description of dentitions previously unknown for Elpidophorus and Limaconyssus, a new species of Mesodma and a new genus and species of erinaceid insectivoran are described.

The mammals present indicate a Late Tiffanian age for site 1 and correlate well with the largely undescribed Roche Percée local fauna (Late Tiffanian, Ravenscrag Formation), Saskatchewan. The age of site 2 is hard to determine based on the few specimens collected there; however, stratigraphic and elevational data suggest sites 1 and 2 may be approximately the same

age. The problematic *Plesiadapis* species present at si[illegible] is identified as *P. churchilli* and supports a late Tiffanian age (Ti4) for site 1.

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# INTRODUCTION

The Swan Hills are the remains of a plateau that stretched from the Athabasca River in the south to Lesser Slave Lake in the north (Allan, 1919; Russell, 1967). They extend for approximately 80 km along an east-west axis, forming the watershed for streams draining north and south into Lesser Slave Lake and Athabasca River, respectively (Jones, 1963; see fig. 1 and 2). The region is heavily forested and possesses extensive swamp and muskeg in the low-lying areas. With the discovery of oil in the Swan Hills in the 1950's numerous cutlines and access roads opened parts of the Swan Hills that were previously inaccessible.

The first geologic survey of the Swan Hills was conducted by pack train in 1918 by J. A. Allan (1919). At this time Allan demonstrated that the stratigraphic sequence consisted of the Upper Cretaceous Edmonton Formation, early Tertiary Paskapoo Formation, and late Tertiary gravels that may be comparable to those capping the Hand Hills and Cypress Hills in the more southern parts of Alberta (Allan, 1919). Due to the heavy forestation, Allan's survey of the area was restricted to examination of cut-banks along the many streams and small rivers, as well as scattered cliffs along the northern slopes of the Swan Hills.

An exposure of the Paskapoo Formation at the head of the east branch of Bruce Creek on Wallace Mountain (Fig. 2) yielded a rich concentration of fresh-water mollusks (Allan, 1919). The matrix containing the mollusks originated from two highly fossiliferous layers of hard, calcareous shale, each approximately 46 cm thick, interbedded with layers of soft, greenish, argillaceous shales that also contained bone fragments possibly belonging to a species of Champsosaurus (Allan, 1919; Russell, 1967). Unfortunately, this area still remains relatively inaccessable today.

L. S. Russell accompanied R. L. Rutherford on a traverse up Driftpile River in 1927; however, they "probably did not get stratigraphically above the Edmonton Formation" (Russell, 1967: p. 3). Russell returned to the Swan Hills in 1964 and again in 1965 (1967, p. 4), discovering invertebrate and vertebrate remains at thirteen localities. Only one of these localities, locality 1, approximately 10 km northwest of the town of Swan Hills, yielded mammalian remains (Locality 1 is equivalent to UAP-13 of Krishtalka [1973] and Swan Hills site 1 of the present study, Gingerich [1986], and Krause [1978]). Field parties from the University of Alberta worked site 1 in 1969, 1972, and 1976, bringing the total sample collected to approximately 200 specimens. With the undertaking of the current study, site 1 was worked again in 1985 and more extensively in 1986 and 1987, increasing the sample size to approximately 850 specimens, of which about 700 are identified and described here. The remaining localities of Russell (1967) were reprospected and found to be either overgrown with vegetation or reworked by bulldozers, save for locality 7, at which was collected a large carnosaur tooth and several fragmentary bones of an unidentified dinosaur.

Swan Hills site 1 is a low hillock, less than 1 m in height, produced by the removal of overburden during the construction of an oil well by the Home Oil Company in the late 1950's. Originally, the locality was visible from the road; however, at least a twenty-year growth of brush and trees has separated the locality from the still-producing well site, and it is necessary to traverse the brush and a low, wet area to reach the locality. Russell (1967) distinguished between an east and west portion to the site. These exposures are removed from the part of site 1 producing mammal fossils by approximately 60 m on either side and are quite close to, and visible from the road. Although the east and west localities were worked extensively, only fish scales and bone fragments were recovered.

Swan Hills site 2 is an approximately 21 m high, sloping road cut located about 1 km northwest of site 1. This locality was discovered in 1987 towards the end of the last field season and was not extensively worked. It is hoped that in the near future a much larger sample will be collected here.

## METHODS AND MATERIALS

The most productive area of site 1 proved to be at the extreme west end of the hillock, where a 45 to 50 cm thick layer of fossiliferous, soft, greenish-grey, argillaceous shale is overlain by approximately 12 cm of dark topsoil. Mollusk shells, especially gastropods, are abundant in the shale layer. Underlying this greenish-grey layer is a bed of a lighter greenish-yellow argillaceous shale devoid of mollusk shells. The depth of this layer is unknown.

The eastern part of site 1 has the layers described above overlain by a fossiliferous, hard, calcareous shale approximately 8-10 cm in thickness, which in turn is overlain by a thin layer of soft, grey, silty shale grading into topsoil. The calcareous layer was removed from the western portion of the site by bulldozers during construction of the well-site. Splitting this hard layer proved unproductive, and work at the locality consisted of splitting the soft argillaceous shale by hand and then bagging the matrix for screen-washing in the nearby Swan River (following methods outlined by Lillegraven, 1969), or in the laboratory at the University of Alberta.

Swan Hills site 2 is on a new road leading into several well sites and consists mainly of alternating layers of light grey and greenish, soft, argillaceous shales. At the base of the exposure is a hard layer of dark, carbonaceous, calcareous shale varying in thickness from 10 to 30 cm and possessing numerous mollusk shells and some bone fragments. It was from the splitting of this layer that the few best preserved specimens were collected. Approximately 4.5 m above the calcareous shale is a thin layer (varying from about 6 to 15 cm in thickness) of a soft, grey, argillaceous shale containing numerous shell fragments. Screen-washing of this matrix produced a number of edentulous dentary fragments and several teeth of small mammals. Preservation of the bone is such that occasionally bone fragments are preserved as a light blue in colour.

The Swan Hills has long been known for its wet summers and sudden flooding of the many small streams and rivers. During July, 1986, screen-washing was halted for a period after heavy rains the night before created high river conditions that resulted in the crib boxes being washed downstream. In order to continue the work, a frameless washing technique was improvised utilizing standard nylon window screen cut into squares with lengths of nylon chalk-line threaded around the periphery approximately 5 cm from the edge. With a shovel-sized portion of the argillaceous matrix placed in the center, the string pulled tight and tied with a slipknot, the resulting "teabag", as it came to be known, was hung from a bridge spanning the river. It was found that "teabags" hung directly in the current allowed free flow of water over the matrix and could produce a concentrate in an afternoon as compared to one or two days using boxes in the crib.

Although nylon screen is not as strong as the metal screen generally used in screen-boxes, the "teabags" were able to be utilized from seven to ten days before rips made them unusable, at which point new screen was cut and the nylon line was rethreaded using a leather working needle. This method is not only inexpensive, but can be used anywhere that flowing water is available (lacking a bridge or sturdy branch to tie them to, a rope tied across the water flow will suffice). It is appropriate for use where available space restricts transporting screen-boxes and cribs, where only a small sample of concentrate is desired from a particular locality as a test, and where large quantities of unprocessed matrix are difficult to handle (as when prospecting away from camp or a vehicle). Utilizing this method the following year it was found that with "teabags" we could process almost twice the amount of matrix in approximately the same time as we could with an equal number of boxes.

## ABBREVIATIONS

Abbreviations used in the text are as follows:

A) Institutions:

AMNH -- American Museum of Natural History.

CM -- Carnegie Museum of Natural History.

PU -- Princeton University.

ROM -- Royal Ontario Museum.

SMM -- Science Museum of Minnesota.

UALVP -- University of Alberta, Laboratory of Vertebrate Paleontology.

UM -- University of Michigan Museum of Paleontology.

USGS -- United States Geological Survey.

B) Localities:

UAP -- University of Alberta Paskapoo Formation.

UAR -- University of Alberta Ravenscrag Formation.

C) Dentitions:

c, C -- lower and upper canines, respectively.

d, D -- lower and upper deciduous dentitions, 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 -- Anterior width.

L -- Greatest anteroposterior length.

MND -- Minimum diameter.

MXD -- Maximum diameter.

PW -- Posterior width.

W -- Greatest transverse width.

E) Statistics:

CV -- Coefficient of variation.

M -- Mean.

N -- Sample size.

OR -- Observed range.

p -- Probability.

SD -- Standard deviation.

SE -- Standard error.

# DENTAL TERMINOLOGY AND MEASUREMENTS

Multituberculate dental terminology and techniques used for the production and superimposition of lateral profiles of multituberculate p4's follow Jepsen (1940) and Krause (1977). The measurements for multituberculate dentitions follow Krause (1977).

Eutherian dental terminology in part follows Van Valen (1966) and Szalay (1969). Terms used in reference to the morphology of P4/p4 follow Krishtalka (1976a). Terminology used in describing I1 of Carpodaptes cygneus follows Krause (1978). Width measurements for upper and lower incisors utilize the maximum lateral/mesial width of the crown, while the length is measured from the proximal base of the crown to the distal tip. Measurements for Elpidophorus follow Szalay (1969). The remaining measurements for eutherian dentitions follow Hartman (1986, p. 20).

All measurements were made using an occular micrometer disc inserted into the eyepiece of a Bausch & Lomb dissecting microscope and are expressed in millimeters. In all cases, measurements were taken to the nearest tenth of a millimeter.

Where used, the terms "lateral" and "mesial" refer to position in relation to the sagittal plane; "medial" refers to position in relation to the transverse axis of upper dentitions and the anteroposterior axis of lower dentitions.

# STRATIGRAPHIC SETTING

The "Paskapoo series" was proposed by J. B. Tyrrell (1887) for "Laramie rocks" overlying the "Edmonton series" in central Alberta. Although Tyrrell did not designate a type section, the word "Paskapoo" is an Indian word meaning "Blindman" and refers to the numerous sections of the Paskapoo Formation exposed in the area of the junction of the Blindman and Red Deer rivers northeast of the city of Red Deer. Tyrrell described a section at the junction of the two rivers and a second section on the Red Deer near the town of Ardley containing the contact between the "Edmonton series" and the overlying Paskapoo. Between these two sections, from 229 to 244 m of the Paskapoo Formation are exposed (Allan and Sanderson, 1945). The type section of the Paskapoo Formation, as noted by Carrigy (1970), is thus a composite.

The Paskapoo Formation represents sediments deposited by "broad drainage channels" cutting into an "extensive subsiding swampy plain" (Carrigy, 1971: p. 20), which filled a deep trough that existed just east of the present foothills and extended eastward as a "thinning apron of continental beds" (Allan and Sanderson, 1945: p. 95). Tyrrell (1887) measured a thickness of 1,737 m exposed along the banks of the Little Red Deer River, Carrigy gives a thickness of "3,000 feet [914 m] adjacent to the foothills belt" (1971, p. 15). Outcrops of the Paskapoo extend south from the Swan Hills to the Montana-Alberta border. In southeastern Alberta the Paskapoo may be equivalent to part of the Ravenscrag Formation of the Cypress Hills (Russell and Landes, 1940). The Paskapoo "has its greatest width, 96 miles, in the latitude of Ponoka in township 42" (Allan and Sanderson, 1945: p. 95). "The upper boundary of the formation is an erosional surface" (Carrigy, 1971: p.

15).

Many early authors considered the Edmonton-Paskapoo contact to be a disconformity (e.g., Allan and Sanderson [1945], Tozer [1956]). Ower (1960) and Carrigy (1970, 1971) argued that this was not the case: "The many minor disconformable contacts in these strata are typically associated with fluviatile continental sedimentation, in which channeling precedes deposition in an otherwise continuous succession, and the significance of these minor disconformities has been exaggerated" (Carrigy, 1971: p. 15). Irish (1970) elevated the Edmonton Formation to group status, placing the upper contact at the top of the Battle Formation, and defined the latest Cretaceous strata immediately above the Battle Formation as the "Scollard member", including it in the Paskapoo Formation. Gibson (1977) gave the "Scollard member" formational status and included it in the Edmonton Group, thus restricting the Paskapoo Formation to Tertiary strata.

The bulk composition of the Paskapoo Formation is described in detail by Carrigy (1971). In general the "Paskapoo consists chiefly of soft, grey, clayey sandstones, soft shales and clays slightly indurated. In the lower part of the formation there is a coarse, more or less uncemented sandstone weathering to buff colour and of uniform character over a large area" (Allan and Sanderson, 1945: p. 27). In the Swan Hills, the Paskapoo consists of relatively flat lying beds underlying the summit of the hills and resting on beds of the Edmonton Group:

> "The most continuous sections are exposed along the Driftpile, south of the eighteenth base-line, on the west slope of Wallace mountain, around the summit of House mountain, and approaching the summit of the upland in Deer mountain between the head-waters of the Swan and Saulteaux rivers. Upwards of 1,020 feet of beds have been placed in this formation. The beds are varied in character, but indurated and semi-indurated clays,

> clay shales, arenaceous shales, thin beds of hard and soft grey and ferruginous sandstones, and hard, scaly, highly calcareous shales predominate.The hard, calcareous shales form creamy coloured escarpments at various points around the summits of the upland, and are prominently exposed in House mountain and Deer mountain. Laminae of coal and thin layers of lignitic shale are common; also thin layers of dark shale enclosing carbonized and silicified fragments of wood and bark. Fragments of wood 0 to 3 feet in length, 1 foot in width, and compressed to one inch or less, occur about the middle of the formation. There are certain beds of clay shales which absorb water and become soft, greasy, greenish muds" (Allan, 1919: p. 10-11).

Subsurface data indicate that thick sandstones, equivalent to those at the base of the Paskapoo Formation elsewhere in the province, are also present in the Swan Hills (Jones, 1963).

The water-absorbing, greenish, clay shales described by Allan (1919) contain a high percentage of montmorillonite. Montmorillonite is an iron magnesium aluminosilicate clay mineral, greenish in colour, and formed by the fragmentation of volcanic glass (Carrigy, 1971). It readily absorbs water and expands greatly when wet. Characteristically, bentonite beds have a high montmorillonite content and are common throughout the formations in the Edmonton Group and in the Paskapoo Formation.

Swan Hills sites 1 and 2 are dominated by the montmorillonite-containing, soft, argillaceous shales. Interbedded with these shales are thin beds of silty clays and hard, calcareous shales. The predominance of the clay-sized clasts, abundance of complete fresh-water mollusks, and the quantities of small mammal remains lacking evidence of transport, suggest deposition in a low energy environment. The strong bias towards small size suggests remains of larger mammals were deposited elsewhere in a higher energy environment. Overall, the evidence seems to indicate the presence of a large inland lake in the Swan Hills area during the late Tiffanian.

The Swan Hills rise to over 610 m above Lesser Slave Lake. The relatively flat summit ranges in elevation between 1,190 and 1,280 m above sea level (Jones, 1963). Allan (1919, p. 11) estimated that there were approximately 200 m of Edmonton beds present and placed the Edmonton-Paskapoo contact at about 1,006 m above sea level on the Driftpile River. Strata belonging to the Paskapoo Formation total approximately 311 m and are generally flat lying, possessing "a slight dip of a few feet to the mile, towards the south and southwest" and "local rolls of minor importance" (Allan, 1919: p. 10).

Allan (1919, p. 12) describes a layer of "coarse gravel" overlying the Paskapoo Formation in the upland areas "which varies from a few inches up to 15 feet in thickness, and which consists almost entirely of water-worn pebbles of pure white quartzite up to 6 inches in diameter". Allan (1919) suggested these gravels may be correlated with the Miocene gravels capping the Hand Hills and Cypress Hills in southern Alberta. L. S. Russell (1958, p. 3) suggested that the possibly equivalent gravels in the Hand Hills were of a later Tertiary age, "probability favouring a late Pliocene age". Recent paleontological data, however, suggest that at least part of the Hand Hills conglomerate is of Miocene age (J. Burns, Provincial Museum of Alberta, pers. comm., 1988). Quarrying by road crews has produced numerous exposures of these gravels in the Swan Hills, but prospecting produced no specimens that could add to our knowledge of the age of the quartzite gravels.

Surrounding the edges of the uplands and scattered throughout the lower elevations, especially in the low lying area between the Swan Hills and Lesser Slave Lake, are morainal ridges of gravel and sand. These moraines are conspicuously missing on the flat upland areas. As well, in several places on the summit where bulldozers have removed overburden during well site construction, the quarzite gravels are seen to underlie the soils. This evidence suggests that the summit of the Swan Hills may not have been glaciated.

Swan Hills sites 1 and 2 are at about the same elevation, 1,050 m above sea level. Keeping in mind that the strata in the Swan Hills are relatively flat-lying (Allan, 1919), the examination of several exposures present between the two localities, suggests that the fossil bearing strata may be correlative. At a point 1.5 km up the main road from either locality is an exposure of the Upper Cretaceous strata cut through by the road leading down to the bridge spanning the Swan River. At the top of this exposure is a coal seam approximately 20 cm thick, which is overlain by a dark grey, almost black, carbonaceous shale of about 2.5 m in thickness. The elevation of this coal seam is estimated at about 1,006 m above sea level, and although an upper coal seam is not visible (due to an overburden of soil covering the exposure), this locality is similar to ones described by Allan (1919) on the Driftpile River and may represent the Cretaceous-Tertiary contact in this area. With the Cretaceous and Tertiary beds lying relatively horizontal, the difference in height between the possible contact above the Swan River and sites 1 and 2 is only 46 m. This suggests that, at least locally, late Paleocene strata are overlying Cretaceous strata.

# SYSTEMATIC PALEONTOLOGY

Class MAMMALIA
Subclass PROTOTHERIA
Infraclass ALLOTHERIA
Order MULTITUBERCULATA COPE, 1884a
Suborder PTILODONTOIDEA SLOAN AND VAN VALEN, 1965
Family PTILODONTIDAE GREGORY AND SIMPSON, 1926
Genus *Ptilodus* COPE, 1881a
*Ptilodus kummae* KRAUSE, 1977
(Fig. 8 J-M, 9 A-C)

*Referred specimens*. -- p4: UALVP 22751; m1: UALVP 22325; P4: UALVP 5645, 22324; M2: UALVP 11999.

*Locality*. -- Swan Hills site 1, Paskapoo Formation, Alberta.

## DESCRIPTION

p4. -- The single referred specimen, UALVP 22751 (Fig. 8 J-K), is the posterior half of a right p4. In lateral view the dorsal edge of the crown is a smooth arc. The serrations that are present become larger and more robust posteriorly, and the ridges that descend from them labially and lingually become further spaced apart. There is some wear on the fragment; however, it is evident that labially the antepenultimate serration and the one immediately anterior to it, do not have ridges that connect directly to them, but instead, have the ridges starting at a point ventral to them. Vertical crenulations are present labially above the posterobasal shelf, between the ridge for the antepenultimate serration and the region ventral to the ultimate serration. The antepenultimate through ultimate serrations do not possess ridges lingually; however, the serration anterior to the antepenultimate serration possesses a short ridge in addition to the primary ridge. This secondary ridge appears to begin at a point ventral to the serration, but close examination reveals a very faint trace of the ridge extending to the serration itself. The posterobasal shelf descends from the base of the ultimate cusp anteroventrally to a point at the base of the crown below the penultimate serration at an angle of approximately 45 ° from vertical.

m1. --The single referred specimen, UALVP 22325 (Fig. 9 C), is an anterior fragment of a right m1 preserving three lingual and three and one-half labial cusps. In occlusal view the anterior edge of the crown is straight and the two cusp rows show a slight divergence posteriorly. The first labial cusp is subconical and the smallest in size and height preserved on the fragment. The size and height of the labial cusps increases posteriorly to the fourth, which is incomplete posterior to its apex. The second and third labial cusps are four-sided, with the third cusp possessing concave anterior and posterior slopes and a shallow depression on its external face. Faint crenulations are present on the external slopes of the labial cusps. The cusps of the lingual row are taller and larger than the labial cusps. The height and size of the lingual cusps increases posteriorly to the third cusp, and all preserved lingual cusps possess crenulated, slightly convex lingual slopes and flattened valley-facing slopes with vertical grooves. The anteroventral base of the crown is shallowly concave.

P4. ---Cusp formula 6 : 9-10 : 0 (n=2). The crowns on the two specimens referred here, UALVP 5645 (L = 4.6, W = 2.3; Fig. 8 L, 9 A) and 22324 (L = 5.0, W = 2.4; Fig. 8 M), are complete. In occlusal view the anterior half of the tooth appears to be almost twice as wide as the posterior and the cusp rows are seen to be gently convex labially, the labial more so than the middle row. In lingual view the crown is low and runs roughly parallel to the base of the tooth. The subconical labial cusps increase in size and height posteriorly to the third and then decrease in size and height to the ultimate cusp. Slight lateral compression of the labial cusps emphasizes cristae extending up the anterior and posterior slopes and through the apices of the cusps. The cristae are not evident on the penultimate and ultimate cusps of the labial row on UALVP 22324, but this may be due to the presence of some wear on this tooth. External slopes of the labial cusps are crenulated. The well-developed anterolabial bulge of the crown is wrinkled on UALVP 22324, and papillate with a tiny cuspule developed labial to the valley between the penultimate and antepenultimate cusps on UALVP 5645. The labial row ends anteroexternally (UALVP 22324), or externally (UALVP 5645), to the penultimate cusp of the middle row. Cusps of the middle row are subconical, ridge-like in being joined almost to their apices, and are subequal in size and height posteriorly from the second cusp. On UALVP 22324, the ultimate cusp of the middle row is smaller than, and closely appressed to the penultimate cusp. On UALVP 5645, the lingual cusps have flattened internal slopes with traces of crenulations and vertical ribbing on the external slopes, giving each cusp a roughly triangular shape in occlusal view. Antereventrally the crown is shallowly concave. Roots are missing on both referred specimens.

M2. -- Cusp formula 1-: 3 : 4. The single referred specimen, UALVP

11999 (L = 2.4, W = 2.3; Fig. 9 B), is anteriorly concave in occlusal view and has the lingual and medial rows of cusps running approximately parallel to each other. The first cusps of each of the three rows are subequal in height. The single labial cusp is situated on the anterolabial corner of the crown and is continuous with a ridge running posterolingually and anterolingually, to the labial corners of the ultimate and first cusp, respectively, of the middle row. The first medial cusp is transversly elongate, closely appressed to, and half the height of the second medial cusp, which is pyramidal, the largest cusp on the crown, and subequal to the subcrescentic ultimate cusp in height. Lingual cusps are subcrescentic. The first cusp, the smallest cusp on the crown, is two-thirds the height of, and closely appressed to, the second lingual cusp. The second and third lingual cusps are slightly shorter than the second medial cusp and subequal to each other in size and height. The ultimate lingual cusp is two-thirds the height of the third (or penultimate) cusp. It is joined posterolabially to the ultimate cusp of the middle row by a low ridge.

## DISCUSSION

Ptilodus kummae was erected by Krause (1977) to include specimens collected from deposits of the Ravenscrag Formation near Roche Percée, Saskatchewan. At that time, the presence of P. kummae was also recognized in the Tongue River Formation, North Dakota (Riverdale locality; Holtzman, 1978), the Shotgun Member of the Fort Union Formation, Wyoming (Malcolm's locality; Krishtalka, et al., 1975), and, "questionably" in the Swan Hills local fauna. Recently Krause (1982) has identified P. kummae in a number of localities in the Bighorn Basin of Montana and Wyoming, as well as in the Piceance and San Juan basins of Colorado. Winterfeld (1982) has identified P. kummae in a late Tiffanian horizon of the Fort Union Formation in Wyoming (eastern Rock Springs Uplift).

A left P4 from Swan Hills site 1, UALVP 5645, was described by Krishtalka (1973) and referred to P. montanus Jepsen (1940) along with specimens from Police Point[1]. Krause (1977) referred this specimen tentatively to P. kummae along with a posterior fragment of a right M2 (UALVP 11999) collected by D. O'Brien in 1972 at Swan Hills site 1. Krause figured the M2 fragment (1977: pl. 2, fig. 6) and estimated the length and width to be 2.4 and 2.3, respectively. In 1985, the anterior fragment missing from UALVP 11999 was recovered at site 1 and the measurements calculated by Krause proved to be correct (see description above). For the present study I have felt it necessary to redescribe UALVP 5645 and the now complete UALVP 11999.

In the original diagnosis for P. kummae, Krause (1977) contrasted dentitions of P. kummae with those of "P." douglassi, excluding comparisons with other species of Ptilodus on the basis of size. "Ptilodus" douglassi has since been referred by Krause (1987) to a new ptilodontid genus, Baiotomeus, which is distinguished from species of Ptilodus in characters of P4/p4 and m1[2]. The fragmentary nature of the single specimens of p4 and m1 referred to P. kummae from the Swan Hills makes comparisons with the comparable tooth positions in Baiotomeus douglassi difficult; however, the two P4's from Swan Hills have well-developed anterolabial (=mesiobuccal) bulges as in species of Ptilodus, and not a "relatively poorly developed mesiobuccal bulge" as in species of Baiotomeus (Krause, 1987; p. 598). The morphology of P4, plus the known distribution of B. douglassi being restricted to the late

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[1] Contrary to Krause (1977, p. 12) UALVP 5645 was not figured by Krishtalka (1973).

[2] Sloan has referred "Ptilodus" douglassi to Mimetodon (Sloan, in Van Valen and Sloan, 1966), Neoplagiaulax (in a 1972 pers. comm. to Schiebout, 1974), back into Ptilodus (Sloan, 1981), and recently back into Neoplagiaulax (Sloan, 1987). Contrary to the referrals by Sloan, the referral by Krause (1987) of "Ptilodus" douglassi to Baiotomeus is here considered to be the most prudent.

Torrejonian of Montana and Wyoming (Krause, 1987), precludes the presence of *B. douglassi* in the Swan Hills local fauna.

Krause (unpublished PhD. dissertation, 1982) revised the diagnosis for *Ptilodus kummae* and contrasted the dentitions with those of *P. tsosiensis* Sloan (1981) and *P. fractus* Dorr (1952), excluding a comparison with other species of *Ptilodus* on the basis of size. *P. fractus* is approximately 20% shorter in length (Krause, 1982) and as a result relatively lower crowned than *P. kummae*. The posterior half of p4 from Swan Hills (UALVP 22751) is indistinguishable in size and morphology from three complete, undescribed p4's of *P. kummae* from Roche Percée (UALVP 22753-22755, collected in 1975 at UAR-2). *Ptilodus tsosiensis*, from the early Puercan of the San Juan Basin, has a wider P4, with a length/width ratio of 1.69 compared with 2.00 to 2.43 for *P. kummae* (Krause, 1982: p. 174). The specimens from Swan Hills, with length/width ratios of 2.00 (UALVP 5645) and 2.08 (UALVP 22324), clearly fall within the range for *P. kummae*.

### Genus *Prochetodon* JEPSEN, 1940

### *Prochetodon* sp. F KRAUSE, 1987

(Fig. 9 D-G)

*Referred specimens*. -- p4: UALVP 22414, 22752; P3: UALVP 22252; P4: UALVP 11997, 11998.

*Locality*. -- Swan Hills site 1, Paskapoo Formation, Alberta.

## DESCRIPTION

p4. -- The two referred specimens consist of anterodorsal fragments (Fig. 9 D-F). The anterior edge of the crown in lateral view is smoothly curved to the first serration, which is placed high and far posteriorly on the crown. The anterobasal concavity is peaked dorsally, and a shallow trough extends along the anterior face of the crown from the dorsal edge of the anterobasal concavity to a point ventral to the first serration. The first serration possesses one labial and lingual ridge, plus a third ridge descending from the serration along the midline of the anterior trough to a point dorsal to the anterobasal concavity. The ridges anteriorly are closely spaced dorsally, increase in spacing ventrally, and are oriented on the lateral slopes approximately 10 to 14 ° from horizontal.

P3. -- Cusp formula 5 : 4. The single referred specimen, UALVP 22252 (L = 3.8, W = 2.2; Fig. 9 G), consists of a crown lacking roots. In occlusal view the crown is roughly elliptical, convex labially, and slightly constricted at approximately midlength. The two cusp rows are approximately parallel to each other and are convex labially. The labial cusps are lenticular, taller and larger than the lingual cusps, and have cristae extending anteroposteriorly from their bases through their apices. The most anterior and posterior cusps are slightly smaller and shorter than the middle three subequal cusps of the labial row. The lingual cusps are triangular, subequal in size and height, and positioned lingual to the intercusp valleys of the labial row. Weak crenulations are present on the external and internal slopes of the labial and lingual cusps, respectively.

## DISCUSSION

Specimens from the Roche Percée local fauna, Ravenscrag Formation, Saskatchewan, and Swan Hills site 1 (UALVP 11997 and 11998) were referred to Prochetodon, cf. P. cavus, and Prochetodon sp., respectively, by Krause (1977)[3]. Krause (1982) proposed a new species of Prochetodon, present in middle and late Tiffanian horizons of the United States and Canada, to which he referred the specimens of Prochetodon, cf. P. cavus from Roche Percée (Prochetodon sp. F of Krause, 1987). At the same time he tentatively referred the Swan Hills specimens to Prochetodon sp. F. He stated that the "two fragments of P4 from Swan Hills site 1 show that the labial row of cusps was well developed and extended well past mid-length, as is characteristic of [Prochetodon sp. F]" (1982: p. 211). Definite referral of the Swan Hills specimens to his new species was deferred pending collection of a larger sample from Swan Hills.

The anterodorsal fragment of a left p4, UALVP 22414, is 6.0 mm in length and represents less than the anterior two-thirds of a complete specimen. Lower fourth premolars of the latest Tiffanian Prochetodon cavus have a length of 6.6 - 7.7 mm (Krause, 1982: pp. 218-219); thus, UALVP 22414 is greater than four-fifths the length of complete p4's of P. cavus. In size then, the p4's from the Swan Hills are larger than p4's of P. cavus and more like those of Prochetodon sp. F (particularly UALVP 22756, an undescribed p4 from Roche Percée here referred to Prochetodon sp. F) and another undescribed species listed by Krause, Prochetodon sp. T (1982, 1987) from the early to middle Clarkforkian of the Bighorn Basin, Wyoming. In addition, unlike

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[3] In the original description of Swan Hills site 1, Russell (1967) referred two specimens to Prochetodon sp. As noted elsewhere in the present study, these specimens were referred to Neoplagiaulax, cf. N. hazeni by Krause (1977).

*Prochetodon* sp. T, but like *Prochetodon* sp. F, the anterior profile of p4 on the Swan Hills specimens forms a smooth, circular arc.

A vertical line, 90 ° from the standard length, drawn from the ventral apex of the exodaenodont lobe labially, or from the base of the crown at the posterior edge of the anterior root lingually, consistently traverses at least one more ridge in *Prochetodon* sp. F than in *P. cavus* and possibly *Prochetodon* sp. T (pers. observ.). On examined specimens of *P. cavus* and the figured specimen of *Prochetodon* sp. T (Krause, 1982: fig. 27), the vertical line traverses eight or nine ridges labially and eight lingually, while on *Prochetodon* sp. F the line traverses nine to eleven labially and nine or ten ridges lingually. This reflects the apparently more anterior placement of the anteroventral termination points of the posterior ridges on *Prochetodon* sp. F than on either *P. cavus*, or possibly, on *Prochetodon* sp. T. A vertical line from the ventral apex of the exodaenodont lobe on UALVP 22752 would traverse eleven ridges and is therefore more like *Prochetodon* sp. F; however, before it can be determined whether this character is taxonomically significant, a much larger sample of p4's from the Swan Hills *Prochetodon* sp. F, and from *Prochetodon* sp. T, will need to be examined.

The labial cusp row on P3 of *Prochetodon cavus* is variably developed and may possess five cusps, whereas the labial cusp row seems to invariably possess five cusps in *Prochetodon* sp. F and on known specimens of P3 for *Prochetodon* sp. T (Krause, 1982). The number of labial cusps on P3 is then not a reliable taxonomic character, as noted by Krause (1982., p. 210). The length of the single referred P3 from Swan Hills falls just outside the range for P3's of *P. cavus* and within that for *Prochetodon* sp. F and the Clarkforkian *Prochetodon* sp. T (Jepsen, 1940; Krause, 1982).

Metrical and morphological data, as well as known temporal and range distributions, seem to more closely align the Swan Hills sample with

Prochetodon sp. F. In recognition of this, but because of the small sample size (N=5) and fragmentary nature of the referred specimens, the Swan Hills sample is tentatively referred to Prochetodon sp. F (following Krause, 1982) pending collection of a larger sample.

### Family NEOPLAGIAULACIDAE AMEGHINO, 1890

### Genus Neoplagiaulax LEMOINE, 1882

### Neoplagiaulax hunteri (SIMPSON, 1936)

(Fig. 10 I-N, 11 A-G; Table 1)

Referred specimens. -- p4: ROM 05602, 05605, UALVP 22201, 22205, 22207, 22427, 22428, 22594-22602, 22734-22736; m1: UALVP 22338, 22389, 22391, 22733; m2: UALVP 22209, 22616, 22618; P1: UALVP 22324, 22325, 22328, 22381, 22622, 22623; P2: UALVP 22220, 22334, 22335, 22624, 22626, 22737; P3: UALVP 22415; P4: ROM 05601, UALVP 22208, 22248, 22322, 22339, 22424-22426, 22603-22608, 22610; M1: UALVP 22394, 22611-22614; M2: UALVP 22252, 22319, 22345, 22385, 22619-22621.

Locality. -- Swan Hills sites 1 and 2, Paskapoo Formation, Alberta.

Known distribution. -- Swan Hills local fauna, Paskapoo Formation, Alberta; Roche Percée local fauna, Ravenscrag Formation, Saskatchewan (Krause, 1977); Scarritt Quarry, Melville Member, Fort Union Formation, Montana (Simpson, 1936); Circle local fauna, Tongue River Formation, Montana (Sloan, in D. E. Russell, 1967); Brisbane and Judson localities,

Table 1: Measurements and descriptive statistics of the dentition of Neoplagiaulax hunteri, Swan Hills local fauna, Alberta.

| Measurement | | N | OR | M±SE | SD | CV |
|---|---|---|---|---|---|---|
| m1 | L | 3 | 2.5-2.8 | 2.63 ± .09 | .153 | 5.8 |
| | W | 3 | 1.1-1.2 | 1.13 ± .03 | .058 | 5.1 |
| m2 | L | 3 | 1.4-1.7 | 1.53 ± .09 | .153 | 9.9 |
| | W | 3 | 1.2-1.3 | 1.27 ± .03 | .058 | 4.6 |
| P1 | L | 5 | 1.4 | - | - | - |
| | W | 5 | 1.1-1.2 | 1.12 ± .02 | .045 | 4.0 |
| P2 | L | 6 | 1.2-1.4 | 1.33 ± .03 | .082 | 6.1 |
| | W | 6 | 1.1-1.2 | 1.13 ± .02 | .052 | 4.6 |
| P3 | L | 1 | 1.5 | - | - | - |
| | W | 1 | 1.1 | - | - | - |
| P4 | L | 5 | 3.1-3.[illegible] | 3.22 ± .05 | .110 | 3.4 |
| | W | 7 | 1.1-1.4 | 1.27 ± .04 | .095 | 7.5 |
| M1 | L | 2 | 3.0 | - | - | - |
| | W | 3 | 1.3-1.4 | 1.37 ± .33 | .058 | 4.2 |
| M2 | L | 7 | 1.4-1.6 | 1.46 ± .03 | .079 | 5.4 |
| | W | 7 | 1.4-1.5 | 1.44 ± .02 | .053 | 3.7 |

Tongue River Formation, North Dakota (Holtzman, 1978); Police Point local fauna, Ravenscrag Formation, Alberta (Krishtalka, 1973); Douglass Quarry, Melville Member, Fort Union Formation, Montana (Krause and Gingerich, 1983); Cedar Point Quarry, Polecat Bench Formation, Wyoming (Sloan, 1987).

## DESCRIPTION

p4. -- Referred specimens are anterior and posterior fragments (Fig. 10 I-L); however, several specimens (e.g., UALVP 22595 and 22600, anterior and posterior fragments, respectively) are complete enough to give a good indication of p4 morphology. An approximation of serration count, achieved by careful overlap of alternating pairs of anterior and posterior fragments, gave a count of 14 or 15 serrations (standard length approximations were made using the same method). The height of the first serration is between one-third and one-half the approximated standard length. The edge of the crown curves relatively smoothly from the top of the anterobasal concavity to the second or third serration, from where it proceeds posteriorly parallel to the standard length and then descends sharply and relatively straight from the seventh or eighth serration to the ultimate serration.

The configuration of the anterior ridges descending labially and lingually from the first and second serrations is variable, but most of the specimens labially have a short ridge descending from the first serration that converges anteriorly with the ridge from the second serration. Lingually, the ridge from the second serration is deflected posteriorly to converge with the ridge descending from the third serration on about one-half of the specimens; on two specimens (UALVP 22596, 22735) both the first and second ridges converge on the third. Breakage of most of the assigned fragments perpendicular to the standard length allows the cross-sectional outline of p4 to be easily examined. Although the labial aspect is consistently convex, the lingual aspect was found to be variable, ranging from slightly concave to slightly convex, with approximately one-half of the assigned specimens possessing a flat lingual aspect.

The exodaenodont lobe is relatively large with a nearly straight anterior edge descending posteroventrally to a rounded ventral apex. The posterior edge of the lobe runs parallel to the posterior surface of the anterior root. The anterobasal concavity is deep with a dorsal edge that is nearly square. An interradicular ridge extends between the large anterior root and the smaller posterior root.

m1. -- One of the four referred specimens (UALVP 22338) has a cusp formula of 8 : 4 (Fig. 10 N); another of the referred specimens (UALVP 22391) has four lingual and nine labial cusps and may have a tenth small cusp anterior to the first identifiable one -- wear with slight breakage obscures this area. Although worn, UALVP 22733 possesses at least 11 cusps in the labial row, plus what may be interpreted as an incipiently developed fifth cusp anteriorly in the lingual row. The latter specimen is virtually indistinguishable in size and morphology from UALVP 9749, an m1 referred to Neoplagiaulax hunteri from the Roche Percée local fauna possessing a cusp formula of 11 : 5 (Krause, 1977). The labial cusps are the shorter and smaller of the two cusp rows, being pyramidal anteriorly and becoming increasingly crescentic posteriorly. Size and height increase posteriorly to a point about mid-length, after which they remain relatively equal. Shallow, vertical grooving, or dimpling, on the external walls of the labial cusps is variably developed. The size increases posteriorly from the first lingual cusp to the somewhat anteroposteriorly elongate ultimate cusp of the lingual row. The height of the first lingual cusp is slightly less than the remaining subequal lingual cusps. Valley-facing slopes of the lingual cusps possess shallow, vertical grooves, while lingually the cusps are rounded or convex. The crown, which overhangs the anterior root but not the larger posterior root, is notched anteriorly where it abuts against the p4.

m2. -- The cusp formula is 4 : 2 on UALVP 22209 (Fig. 10 M) and 22616, the latter possessing an incipient development of a fifth cusp on the anteroposteriorly elongate ultimate labial cusp. Another specimen, UALVP 22618, has a cusp formula of 6 : 2 and may possess a third lingual cusp posteriorly whose presence is obscured by wear. The labial cusps are equal in height, joined almost to their apices, and crescentic anterior to the ultimate cusp, which has one or two shallow, vertical grooves on its valley-facing slope. Anterolingually the ultimate labial cusp is joined to the ultimate cusp of the lingual row by a low ridge, which becomes obscured with wear. Lingual cusps, the more massive of the two cusp rows, are subequal in height, have rounded internal walls and flattened valley-facing slopes with one (anterior cusp) or two (posterior cusp) shallow, vertical grooves. The anterior lingual cusp is the less massive of the two and is crescentic posteriorly. The roots are subequal in size and there is only a slight overhang of the crown anteriorly and posteriorly.

P1. -- The referred P1's are three-cusped with a single, subconical, slightly laterally compressed posterolingual cusp, and two laterally compressed labial cusps joined to about two-thirds of their height (Fig. 11 A). The lateral compression of the labial cusps contributes to a crista through the apices of both cusps that is oriented anterolingually-posterolabially. The smaller anterior cusp contributes to the obliqueness of the crista by being positioned near to the midline of the crown. The lingual cusp is subequal to the posterior labial cusp in size and height. Anteriorly the crown does not overhang the anterior root as it does the more transverse posterior root. When viewed occlusally, the crown takes the shape of an equilateral triangle with extremely blunted corners. The sides of the cusps possess a slight wrinkling of the enamel. On the internal, posterior base of the crown an interdental wear facet is present, marking the position of articulation with P2.

P2. -- Upper second premolars are similar to P1 in morphology. They differ in having a single labial cusp that is taller and more laterally compressed than the single lingual cusp of P1, two lingual cusps with the anterior cusp being slightly taller and larger than the posterior cusp (a situation the reverse of the condition seen in the two labial cusps on P1), the crown overhanging the posterior and anterior roots, and an occlusal aspect that is more circular is shape. Interdental wear facets are present anteriorly and posteriorly on the internal bases of the crowns (Fig. 11 B).

P3. -- The single referred P3, UALVP 22415 (Fig. 11 C), has two pairs of subconical, laterally compressed cusps, and as in P1 and P2 the lateral compression contributes to the development of relatively strong cristae running through the apices of the two labial and two lingual cusps. The anterior lingual cusp is the shortest and smallest of the four cusps, the remaining three being sub-equal in height and size. The anterolabial cusp is connected to the anterolingual cusp by a low, weak ridge. The crown overhangs the anterior root and a posterior basal expansion is present.

Wrinkling of the enamel is present on the sides of the cusps.

P4. -- Cusp formula 1 : 9-10 : 0 (mode 1 : 9 : 0). Only one of the referred P4's, UALVP 22610, has a tenth cusp in the middle row. The crown of P4 is high and triangular in lingual profile, with a weakly convex anterior slope and a concave posterior slope (Fig. 11 D,E). Cusps of the middle row are subequal in size with the penultimate or ultimate cusp being the highest on the crown. The single labial cusp is the largest, most robust cusp on the crown, and is situated dorsal and labial to the third cusp of the middle row. Laterally, the crown overhangs the roots only slightly. Anteriorly, the crown forms a ledge over the anterior root that is convex ventrally when P4 is in position in the maxilla. This ledge overlaps the posterobasal expansion on P3. Where the crown overhangs the posterior root is an indistinct posterobasal cusp and a weak shelf that extends from the posterobasal cusp anteriorly around the base of the crown to a point dorsolingual from the posterior base of the ultimate cusp of the middle row. This character can be easily viewed on UALVP 22604, a posterior fragment of P4, but is obliterated with only a slight amount of wear. Although obscured by wear, specimens of P4 referred to *N. hunteri* from Roche Percée (Krause, 1977), and *N. kremnus* from the Ravenscrag Formation of Saskatchewan (Johnston and Fox, 1984), appear to have possessed this character.

M1. -- Cusp formula 7 : 11 : 6-7(N=2; Fig. 11 F). When viewed lingually the crown is strongly concave. This is produced by a rotation of the crown anterolingually-posterolabially about the anteroposterior axis, such that, the roots diverge from one another at an angle of approximately 30 °. The valley-facing slopes of all cusps possess distinct vertical grooves that become more prominent posteriorly. Labial cusps posterior to the second cusp are the largest, most robust cusps on the crown, have convex external and flattened internal slopes, and increase in size and height posteriorly. The first labial cusp is closely appressed to the subconical second cusp and appears somewhat ridge-like in being connected lingually to the first medial cusp. The medial cusps posterior to the first cusp are subequal in size and become increasingly crescentic and taller. The ultimate cusp is connected internally and externally to the ultimate lingual and labial cusps, respectively, by low ridges that define the curving posterior margin of the crown. The lingual cusp row begins internal to the fifth medial cusp and possesses cusps that are subconical, with somewhat flattened valley-facing slopes. They generally increase in height and size posteriorly. Unlike other referred specimens the ultimate cusp of the lingual row of UALVP 22613 is less than half the size and height of the penultimate cusp.

The anterior root is anteroposteriorly elongated, while the posterior root is strongly transverse. Anteriorly the crown overhangs the root negligibly.

M2. -- Cusp formula 1 : 4 : 4. Anteriorly the crown is shallowly concave (Fig. 11 G). The single labial cusp is situated at the anteroexternal corner of the crown and is incorporated into a ridge that extends posterointernally to the base of the ultimate cusp of the medial row. The cusps of the medial row are crescentic and increase in size and height posteriorly. The first medial cusp is closely appressed to the second. Shallow vertical grooves are variably developed on the valley-facing slopes of the medial and lingual rows of cusps. The lingual cusps are crescentic, subequal in size, decrease in height posteriorly, have convex internal slopes, flattened external slopes, and are ridge-like in being joined almost to their apices. The roots are subequal in size, the anterior being the larger and more transverse of the two.

# DISCUSSION

*Neoplagiaulax hunteri* was originally described by Simpson (1936) as a species of *Ectypodus*. Simpson noted the similarity of structure between the type and paratype, and specimens of *Ectypodus musculus*, citing the differences between *E. hunteri* and other species of *Ectypodus*, particularly *E. musculus*, lie in the possession of a greater number of serrations on p4, more "cuspules" on P4, and fewer cusps on M1/m1. Sloan (in Van Valen and Sloan, 1966) referred *E. hunteri* to *Neoplagiaulax* without explanation; however, *Neoplagiaulax* species have the penultimate or antepenultimate cusp of P4 higher above the base of the enamel than the ultimate cusp (thus, resembling species of *Ectypodus*), p4 possesses a less convex anterior profile with the fifth, sixth, or seventh serration highest above the standard length (as opposed to the fourth in species of *Ectypodus*), and p4/m1 length ratio is larger in *Neoplagiaulax* species than in *Ectypodus* (Sloan, 1981).

In the original description of the Swan Hills local fauna, Russell (1967) referred ROM 05602, an incomplete left p4, and ROM 05601, a right P4, to "*Ectypodus*" *cochranensis* (Sloan, in Van Valen and Sloan [1966] referred *E. cochranensis* to *Anconodon*). In addition, Russell (1967) also referred an anterior half of a left p4, ROM 05605, to *Anconodon* sp. These three specimens are indistinguishable from specimens referred to *Neoplagiaulax hunteri* from the Swan Hills local fauna and are here referred to that species. With the referral of the remaining specimen referred to *E. cochranensis* (ROM 05603) by Russell (1967) to *Neoplagiaulax*, cf. *N. hazeni* by Krause (1977), species of *Anconodon* are no longer identified in the Swan Hills local fauna.

An anterior half of a left p4 from Swan Hills site 2 (UALVP 22734) is virtually indistinguishable from specimens referred to *N. hunteri* at Swan Hills site 1. It differs only in having a relatively lower crown and a slightly shallower anterobasal concavity. Unless future sample size increases from Swan Hills site 2 invalidate this interpretation, the differences noted above are considered individual variation, and not taxonomically significant.

In size and general morphology, there is virtually no difference between specimens referred to N. hunteri from the Swan Hills and the sample from Scarritt Quarry. Swan Hills N. hunteri appears to be more conservative than the apparently "further advanced" N. hunteri of the Roche Percée local fauna (Krause, 1977: p. 20) in retaining a generally smaller size and lower m1 cusp formula. Further, Swan Hills N. hunteri differs from the Roche Percée sample in having a p4 that is narrower transversely, comparatively less arcuate and lower crowned with a more gracile exodaenodont lobe; fewer cusps on m2; and a P4 with a relatively larger, invariably present labial cusp (N=10), a straighter anterior slope, a slightly lower crown, and less transverse width.

### Neoplagiaulax, cf. N. hazeni (JEPSEN, 1940)

(Fig. 9 H-K, 10 A-H; Table 2)

Referred specimens. -- p4: ROM 05606-05608, UALVP 22200, 22202, 22206, 22215-22217, 22392, 22421, 22627-22630, 22739-22741; m1: ROM 05603, UALVP 22401, 22417, 22632-22634, 22744-22746; P1: UALVP 22218; P2: UALVP 22416, 22455, 22470; P1-P2: UALVP 22210; P3: UALVP 22750; P4: UALVP 22419, 22420, 22475, 22742, 22743; M1: UALVP 22203, 22204, 22387, 22418, 22615, 22631, 22747, 22748; M2: UALVP 22219, 22635-22638, 22749.

Table 2: Measurements and descriptive statistics of the dentition of _Neoplagiaulax_, cf. _N_. _hazeni_, Swan Hills local fauna, Alberta.

| Measurement | | N | OR | M±SE | SD | CV |
|---|---|---|---|---|---|---|
| m1 | L | 6 | 2.9-3.2 | 3.03 ± .04 | .103 | 3.4 |
| | W | 7 | 1.3-1.4 | 1.36 ± .02 | .053 | 3.9 |
| P1 | L | 2 | 1.6-1.7 | 1.65 ± .05 | .071 | 4.3 |
| | W | 2 | 1.3 | - | - | - |
| P2 | L | 4 | 1.6-1.7 | 1.65 ± .03 | .058 | 3.5 |
| | W | 4 | 1.3-1.4 | 1.35 ± .03 | .058 | 4.3 |
| P3 | L | 1 | 1.6 | - | - | - |
| | W | 1 | 1.4 | - | - | - |
| P4 | L | 1 | 3.6 | - | - | - |
| | W | 1 | 1.4 | - | - | - |
| M1 | L | 1 | 3.6 | - | - | - |
| | W | 2 | 1.7-1.8 | 1.75 ± .05 | .071 | 4.0 |
| M2 | L | 6 | 1.9-2.1 | 2.00 ± .04 | .089 | 4.5 |
| | W | 6 | 1.8 | - | - | - |

Locality. -- Swan Hills site 1, Paskapoo Formation, Alberta.

## DESCRIPTION

p4. -- All of the referred specimens are fragmentary; of these, approximately half are anterior and posterior fragments (Fig. 9 H-K). Through careful overlap of alternating pairs of anterior and posterior specimens, an approximate serration count of 15 to 16 serrations was obtained. Anteriorly the serrations are relatively small and closely spaced. The crown is relatively high and arcuate, gently curving dorsally from the nearly straight anterior edge to the fifth, sixth, or seventh serrations, from where it gradually descends posteriorly to the ultimate serration. Descending anteroventrally from the first serration are two anterolabial and one anterolingual ridge. UALVP 22206 bears no ridges on the ultimate and penultimate serrations; however, faint vertical crenulations are present on the labial and lingual walls below these cusps. On UALVP 22628 a weak ridge runs ventrolingually from the ultimate serration to a small swelling on the base of the crown below the ultimate serration. The anterobasal concavity is relatively deep and squared dorsally. The exodaenodont lobe is robust with a low, blunted ventral apex. The posterobasal shelf is worn on all referred specimens, but enough is preserved on UALVP 22206 to see that it was well-developed and extended initially as a ridge from the posteroventral edge of the ultimate cusp, anteroventrally around the labial base of the crown to a point ventrolabial to the antepenultimate cusp. A well-developed interradicular crest extended between the elongated, anterolingually-posterolabially oblique anterior root and the smaller, somewhat squared posterior root.

m1. -- Cusp formula 7-9 : 5 (mode 9 : 5). UALVP 22417, the only referred specimen with 7 labial cusps, is worn posteriorly and an eighth cusp may be present. Labial cusps are four-sided and increase in height from the small first cusp to the fourth, posterior to which the cusps remain subequal in size and height (Fig. 10 D). Anterior cusps are pyramidal and become increasingly crescentic posteriorly. On specimens exhibiting little wear, shallow dimples are present on the external face of the labial cusps. Lingual cusps are taller and larger than the labial cusps and although there is some variation they generally decrease in size and height anteriorly from the third; posteriorly they remain subequal in height while increasing in size to the ultimate cusp, which is the largest on the crown. The ultimate and penultimate cusps are joined to approximately two-thirds their height while the remaining lingual cusps are joined to approximately one-half their height. A low, weak ridge connects the ultimate cusp posterolabially to the ultimate cusp of the lingual row. The valley-facing slopes of the lingual cusps are flattened and have deep, vertical grooves, while the internal slopes are convex with variably developed dimpling of the enamel. Anteriorly the crown overhangs the four-sided, somewhat squared anterior root. The smaller posterior root is transversely elongated.

P1. -- The three-cusped P1's have a single, subconical, slightly laterally compressed posterolingual cusp and two lenticular, laterally compressed labial cusps oriented anterolingually-posterolabially on the crown (Fig. 10 E). All three cusps are subequal in size with the anterolabial cusp being slightly shorter in height than the other two cusps on the crown. The labial cusps are joined to about one-half of their height and possess cristae oriented anterolingually-posterolabially through their apices. The enamel of the crown is slightly crenulated on the external and internal surfaces of the labial and lingual cusps, respectively. In occlusal view the crown is roughly semi-circular in shape, being convex on the labial edge. Anteriorly the crown does not overhang the ovate, slightly anteroposteriorly compressed root. The posterior edge of the crown forms a short "shelf" over the posterior root, which is subequal to the anterior root in size and shape. Posterolingually on the edge of the crown is an interdental wear facet.

P2. -- The crown of P2 can be three-cusped (e.g., UALVP 22416) or four-cusped (e.g., UALVP 22470). The fourth cusp, when present on the crown, is tiny, laterally compressed, and situated anteriorly on the base of the single, subconical, slightly laterally compressed labial cusp. The latter, which tends to be the most robust cusp on the crown, is connected to the former by a crista running through the apices of the two cusps. The two lingual cusps are subconical (or lenticular) in shape, laterally compressed, joined to approximately half of their height and connected to one another by cristae running through their apices. The posterolingual cusp is situated slightly labial to the anterolingual cusp. The enamel is crenulated on the external and internal surface of the labial and lingual cusps, respectively. In occlusal view the crown is roughly circular with a well-defined bulge on the posterolingual corner that overhangs the posterior root. Both roots are subequal in size and anteroposteriorly compressed. Anteriorly the crown overhangs the root. Interdental wear facets are present on the anteroventral edge and posterodorsally on the posterolingual corner of the crown.

P3. -- The single referred specimen, UALVP 22750 (Fig. 10 F), possesses two labial and two lingual cusps. The labial cusps are more robust than the lingual cusps, lenticular, slightly laterally compressed, joined to approximately one-half of their height, and connected to one another by a crista running through their apices. The anterolabial cusp is somewhat smaller and shorter than the posterolabial cusp. The lenticular lingual cusps are slightly more laterally compressed than the labial cusps, the anterior cusp being approximately half the size and height of the posterior cusp, which is equal to the posterolabial cusp in height. The lingual cusps are connected by a crista through their apices. The two cusp rows are joined anteriorly by their cristae connecting to a low ridge situated transversely across the anterior edge of the crown between the cusp rows. The enamel is crenulated on the internal and external faces of the labial cusps, and on the internal face of the lingual cusps. The crown is ovate in occlusal view, overhangs the large anterior root, and forms a shelf posteriorly that overhangs the subequal posterior root only slightly. Faint interdental wear facets are visible on the anteroventral and posterodorsal edges of the crown.

P4. -- Cusp formula 2 : 8. Only one complete specimen is referred here, the rest are anterior fragments (Fig. 10 A-C). In occlusal view UALVP 22742 is roughly convex labially and concave lingually with a slight pinching of the crown at approximately midlength. In lateral profile the anterior slope is convex and the posterior slope strongly concave. The anterolabial cusp is tiny and situated dorsal and labial to the first cusp of the middle row, while the subconical, much larger second labial cusp is positioned dorsolabial to the second cusp of the middle row. The cusps of the middle row are subconical, subequal in size and increase in height posteriorly to the penultimate and antepenultimate cusps which are the highest on the crown (UALVP 22742 is worn and these features are better observed on assigned fragments). On specimens with little wear, vertical crenulations are present internally and externally on the slopes of at least the posterior five cusps of the middle row. The labial and lingual faces of the crown below the middle cusp row are concave. Anteriorly, the crown overhangs the root and is slightly exodaenodont over the posterolabial corner of the anterior root. The crown overhangs the posterior root only slightly and tends to be somewhat inflated posterolingually. The roots are subequal in size and on UALVP 22475 a trace of a posterobasal cusp is preserved.

M1. -- Cusp formula 6 : 11 : 4 or 5 (N=1). The single, complete speciemen referred here, UALVP 22203 (Fig. 10 G), is rotated anterolingually-posterolabially about the anteroposterior axis producing a concave crown in lateral profile. Labial cusps are the largest cusps on the crown; they appear to be subequal in size and height, have convex external slopes and flattened internal slopes with vertical grooves. A ridge connects the anterolabial cusp lingually to the first cusp of the middle row. Cusps of the middle row are four-sided, joined almost to their apices, become increasingly larger and crescentic posteriorly, and possess variably developed vertical grooves on both of their valley-facing slopes. The ultimate cusp of the lingual row is tiny compared to the penultimate cusp, but is a distinct and separate cusp. Anteriorly from the penultimate cusp, the size and height of the cusps decreases until they fuse anteriorly into a laterally compressed ridge, which fuses with the base of the crown lingual to the fifth cusp of the middle row. The valley-facing and internal slopes of the lingual row are flattened and convex, respectively. The anterior root is strongly compressed transversely, and the smaller posterior root is compressed anteroposteriorly.

M2. -- Cusp formula 1-6? : 4 : 5 (mode 1 : 4 : 5). The labial cusp row is essentially an anteroposteriorly elongate ridge connected anterolingually and posterolingually to the first and ultimate cusps of the middle row, respectively. On UALVP 22635 (Fig. 10 H), the labial "cusp"/"ridge" is papillate with as many as four identifiable small cuspules. One specimen possessing six relatively large cuspules labially, UALVP 22219, is considered to be an extreme variant. The first cusp of the middle row is smaller than, and closely appressed to the second cusp, which is subequal in size to the third and fourth cusps of the middle row. The cusps of the middle row become increasingly taller posteriorly and possess vertical grooves and ridges on both the internal and external slopes. The lingual cusps are ridge-like in appearence being subequal in size and joined almost to their apices. The cusps of the middle and lingual rows become increasingly crescentic posteriorly. The internal slopes of the lingual cusps are convex; labial slopes are flattened with vertical grooving present on the antepenultimate through ultimate cusps. The anterior root is anteroposteriorly compressed and larger than the almost circular posterior root.

## DISCUSSION

*Neoplagiaulax hazeni* was originally described by Jepsen (1940) as a species of *Ectypodus* (it was placed in *Neoplagiaulax* by Sloan, in Van Valen and Sloan, 1966: fig. 5). To date only the type locality, Princeton Quarry, Wyoming, has yielded specimens of this species. A fragmentary m1 from Eocene beds in Colorado was referred to *Ectypodus*, cf. *E. hazeni* by McKenna (1960). Gazin (1956) referred a p4 from Bison Basin, Wyoming to cf. *Ectypodus hazeni* (this specimen is referable to a small, new species of

*Ptilodus* present in the fauna from Cochrane locality 2, Alberta [G. P. Youzwyshyn, pers. comm., 1987]). A large sample of specimens from the Roche Percée local fauna of Saskatchewan has been referred to *Neoplagiaulax*, cf. *N. hazeni* by Krause (1977). Krause (1977) also referred to *Neoplagiaulax*, cf. *N. hazeni* specimens from the Swan Hills local fauna: ROM 05603 (a left m1), 05606 (an anterior fragment of a right p4), and 05607-05608 (anterior fragments of right p4's), specimens that were originally referred to *Ectypodus cochranensis*, *Anconodon* sp., and *Prochetodon* sp., respectively, by L. S. Russell (1967).

Anterior upper premolars of non-ptilodontid species of multituberculates in the Roche Percée local fauna were given a "type" letter designation and described by Krause (1977). He stated that types "D, E, and F are probably P1, P2, and P3, respectively, of *Neoplagiaulax*, cf. *hazeni* as they are the largest non-ptilodontid anterior premolars in the sample and are also the most common" (1977, p. 31). UALVP 22210, a left maxillary fragment from Swan Hills site 1, preserves P1 and P2 in position. Morphological and metrical data suggest these teeth belong to *Neoplagiaulax*, cf. *N. hazeni*; as well, these teeth are virtually indistinguishable from types D and E from the Roche Percée and lend verification to the association made by Krause.

The single P3 referred here from Swan Hills (UALVP 22750) does not tangibly differ from the fragment of P3 preserved in the type of *N. hazeni* (PU 14432), or from type F of Krause. An interdental wear facet anteriorly on this specimen matches the posterior interdental facet on the P2 of UALVP 22210. On the basis of these criteria UALVP 22750 is tentatively referred to *Neoplagiaulax*, cf. *N. hazeni*.

Jepsen (1940) identifies and gives a cusp formula of 8 : 6 for the m1 on PU 14323, a right lower jaw of *Neoplagiaulax hazeni* lacking only m2. This tooth is indistinguishable from ROM 05603, an m1 from Swan Hills site 1, which preserves a cusp formula of 8 : 5. Jepsen includes in his cusp count a slight dimpled area situated posterolingually on the ridge connecting the ultimate lingual cusp anterolabially to the ultimate cusp of the labial row -- a character also present on ROM 05603. Modern workers generally include these "cusps" as part of the connecting ridge and not as a separate cusp. The cusp formula for m1 on PU 14323 is here emended to 8 : 5.

Qualitatively and quantitatively, specimens from the Swan Hills local fauna referred to Neoplagiaulax, cf. N. hazeni are similar to both the sample of Neoplagiaulax, cf. N. hazeni from Roche Percée and the sample of N. hazeni from Princeton Quarry.The Swan Hills sample differs from both the Princeton and Roche Percée samples in having a p4 that is slightly lower crowned with serrations more closely spaced, and in having an M1 with a lower cusp formula. Measurements for the Swan Hills sample fall within or slightly below the range for the Roche Percée and Princeton samples; however, the low measurements for P4 and M1 are on single, and in the case of P4, worn specimens only, and fragments referred to these positions indicate the presence of larger specimens within the range of the Roche Percée sample for these tooth positions. The P4's of Neoplagiaulax, cf. N. hazeni from the Swan Hills differ from N. hazeni of Princeton Quarry and resemble Neoplagiaulax, cf. N. hazeni of Roche Percée in being lower crowned with a more arcuate anterior slope, having a more concave posterior slope, having the antepenultimate and penultimate cusps of the middle row highest above the base of the crown, and in possessing more concave lateral slopes of the crown below the cusps of the middle row.

Differences between the Swan Hills sample and that for Neoplagiaulax hazeni of Princeton Quarry, particularly for P4/p4, indicate that a new species close to N. hazeni may be present in the Swan Hills local fauna. However, description of this species is deferred pending the collection of a larger, and more nearly complete, sample.

### Neoplagiaulax, cf. N. nanophus HOLTZMAN, 1978
(Fig. 11 H-I)

Referred specimens. -- p4: UALVP 22410, 22422.

Locality. -- Swan Hills site 1, Paskapoo Formation, Alberta.

## DISCUSSION

The two specimens of p4 referred to Neoplagiaulax, cf. N. nanophus are both anterior fragments; however, one, UALVP 22410 (Fig. 11 H-I), is slightly more complete in preserving the exodaenodont lobe, anterior root, and all of the crown anterior to the seventh serration. Morphologically, the Swan Hills specimens very closely resemble N. nanophus from the middle Tiffanian Judson locality of North Dakota (Holtzman, 1978). Features shared in common with N. nanophus are: 1) a moderately deep, dorsally squared anterobasal concavity; 2) a nearly straight anterior edge of the crown in lateral profile; 3) the third or fourth serration is the highest above the line for measuring standard length; 4) the ridges anterolabially descend below the line for standard length and "terminate in a straight line that parallels and is close to the anterior margin of the exodaenodont lobe" (Holtzman, 1978: p. 27). As well as the above, the anterior root is similar in shape and angle of orientation to that of N. nanophus. Swan Hills Neoplagiaulax, cf. N. nanophus differs from *N. nanophus* in being slightly smaller (estimated length of p4 is 2.8-2.9 mm.), and in possessing a slightly less vertically inclined anterior edge of the crown.

Given the small sample size (N=2), the fragmentary nature of the referred specimens, and the albeit slight differences in size and morphology between the Swan Hills sample and the sample of *Neoplagiaulax nanophus*[4], the prudent choice is a tentative referral of the Swan Hills sample to *Neoplagiaulax*, cf. *N. nanophus*. Subsequent collection may indicate that the Swan Hills sample represents a younger, smaller morph of *N. nanophus*, or, based on the presence of synapomorphies, possibly a new species of *Neoplagiaulax* closely related to *N. nanophus*.

## Genus *Mesodma* JEPSEN, 1940

### *Mesodma pygmaea* SLOAN, 1987

(Fig. 11 J-K)

*Referred specimen*. -- isolated left p4: UALVP 23828.

*Locality*. -- Swan Hills site 2, Paskapoo Formation, Alberta.

*Known distribution*. -- Swan Hills site 2, Paskapoo Formation, Alberta; Medicine Rocks 1, Tongue River Formation, Montana (Sloan, 1987); Gidley Quarry, Lebo Formation, Crazy Mountain Basin, Montana (Sloan, 1987); Shotgun Quarry, Fort Union Formation, Wind River Basin, Wyoming (Sloan, 1987); Saddle locality, Fort Union Formation, Bison Basin, Wyoming (Sloan,

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[4] Krause (1977) referred specimens of p4 from the Roche Percée to *Ectypodus*, cf. *E. powelli*. After examination of the Roche Percée sample, I feel the referral of some of these specimens to *Neoplagiaulax nanophus* by Holtzman (1978) is justified.

1987); Locality V-77005, eastern Rock Springs Uplift, Fort Union Formation, Wyoming (Winterfeld, 1982); Brisbane locality, Tongue River Formation, North Dakota (Holtzman, 1978); Police Point local fauna, Ravenscrag Formation, Cypress Hills, Alberta (Krishtalka, 1973); UAR2a and UAR2g, Roche Percée, Ravenscrag Formation, Saskatchewan (Krause, 1977); Cochrane 2, Porcupine Hills Formation, Alberta (G. P. Youzwyshyn, in prep.).

## DISCUSSION

The p4's of Mesodma pygmaea have been adequately described by Krause (1977) and Holtzman (1978). The dorsal edge of the single, isolated p4 from Swan Hills site 2, UALVP 22766 (L = 2.4), is slightly damaged and probably possessed nine serrations. Morphologically it is almost identical to the type of M. pygmaea (AMNH 35298) from Gidley Quarry[5], and to specimens of p4 referred to M. pygmaea by Krause (1977). The Swan Hills specimen differs only in possessing a slightly more anteriorly placed first serration, producing a relatively straighter and more vertical anterior edge to the crown in lateral view. Lacking information to the contrary, this difference is not considered to be taxonomically important.

### Mesodma prolis, new species

(Fig. 3, 11 L-Q, 12 A-B; Table 3)

Etymology. -- From Latin, prolis (feminine) = offspring; in allusion to its possible descent from an earlier branch of the Mesodma pygmaea line.

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[5] Examination of a good cast of AMNH 35298 shows the type p4 to possess no more than 10 serrations, contrary to 12 as indicated by Sloan (1987: p. 193, table 5).

Table 3: Measurements and descriptive statistics of the dentition of _Mesodma p[illegible]lis,_ new species, Swan Hills local fauna, Alberta.

| Measurement | | N | OR | M±SE | SD | CV |
|---|---|---|---|---|---|---|
| p4 | L | 4 | 2.9-3.1 | 3.00 ± .04 | .082 | 2.7 |
| m1 | L | 9 | 1.8-2.1 | 1.92 ± .03 | .097 | 5.1 |
| | W | 9 | 0.8-1.0 | 0.86 ± .02 | .073 | 8.5 |
| m2 | L | 6 | 1.0-1.2 | 1.10 ± .04 | .089 | 8.1 |
| | W | 6 | 0.9-1.2 | 1.00 ± .05 | .110 | 10.9 |
| P4 | L | 3 | 1.8-2.0 | 1.90 ± .06 | .100 | 5.3 |
| | W | 3 | 0.7-0.8 | 0.73 ± .03 | .058 | 7.9 |
| M1 | L | 3 | 2.2-2.6 | 2.47 ± .13 | .231 | 9.4 |
| | W | 5 | 1.0-1.2 | 1.12 ± .04 | .084 | 7.5 |
| M2 | L | 6 | 1.0-1.1 | 1.05 ± .02 | .055 | 5.2 |
| | W | 6 | 1.0-1.2 | 1.10 ± .04 | .089 | 8.1 |

*Type specimen*. -- UALVP 22528, an isolated left p4.

*Type locality*. -- Swan Hills site 1, Paskapoo Formation, Alberta (exact co-ordinates are available to qualified researchers through the Laboratory for Vertebrate Paleontology, Department of Zoology, University of Alberta).

*Referred specimens*. -- p4: ROM 05604, UALVP 22193-22195, 22199, 22433-22439, 22529-22537, 22723, 22727, 23829-23834; m1: UALVP 22196, 22338, 22339, 22393, 22396, 22404, 22431, 22432, 22464, 22525, 22538, 22724, 22725; m2: UALVP 22334, 22382, 22405, 22429, 22513, 22521; P4: UALVP 22189-22191, 22380, 22395, 22406, 22440, 22609, 22728-22731; M1: UALVP 22335, 22383, 22384, 22388, 22397-22400, 22403, 22423, 22496, 22516, 22732, 23835-23837; M2: UALVP 22192, 22248, 22386, 22430, 22504, 22726.

*Locality*. -- Swan Hills site 1, Paskapoo Formation, Alberta.

*Known distribution*. -- Swan Hills local fauna, Paskapoo Formation, Alberta.

*Diagnosis*. -- A species of *Mesodma* having p4 significantly smaller than *M*. *senecta*, *M*. *thompsoni*, *M*. *garfieldensis*, and *M*. *ambigua*; differing from *M*. *pygmaea* in having p4 15 to 20% larger and relatively lower crowned with the apogee more anteriorly placed; differing from *M*. *hensleighi*, *M*. *formosa*, and *M*. *primaeva* in having p4 with modally one less serration (10), the third serration highest above the baseline instead of the fourth, fifth, or sixth, and in having the apogee of the crown more anteriorly placed; p4 further differing from M. hensleighi and M. formosa in being relatively higher crowned.

## DESCRIPTION

p4. -- In lateral profile the crown is a low, asymmetrical arc with 10 serrations (Fig. 11 L, N). The anterobasal concavity is relatively deep and squared dorsally. The anterior edge of the crown curves smoothly to the first serration, from which descend three relatively weak ridges, one anterolabially and two anterolingually. The height of the first serration is slightly less than, or approximately equal, to one-third the standard length of the crown. The crown curves gently posteroventrally from the third serration, which is highest above the base of the crown, and is nearly straight from the seventh through ultimate serrations. The serrations become more robust posteriorly. Labially the ultimate and penultimate serrations lack ridges; however, on unworn specimens, vertical crenulations are present above the posterodorsal shelf in their stead. The lingual ridges of the ultimate and penultimate serrations are variably developed and when present curve slightly posteroventrally. Variably developed, though usually very weak vertical crenulations of the enamel can be present lingually below these serrations as well. The anterior edge of the exodaenodont lobe is generally fairly straight and the lobe is relatively sharply peaked ventrally. The posterobasal shelf is well-developed and may extend as far anterior as a point ventral to the antepenultimate serration.

The anterior root is laterally flattened and positioned anterolingually-posterolabially to the anteroposterior axis of the crown. The much smaller posterior root is laterally flattened and tapers ventrally. Between the two roots is a well developed interradicular ridge.

m1. -- Cusp formula 7-8 : 4 (mode = 8 : 4). In occlusal view the two cusp rows are seen to diverge posteriorly (Fig. 11 M). The labial cusps increase in size and height posteriorly to the fourth, from where they remain subequal in size and height to the penultimate cusp. Posterior to the subconical, first two labial cusps the cusps are four-sid[illegible] become increasingly crescentic. The ultimate labial cusp is convex posteriorly, smaller than, and closely appressed to the penultimate cusp, and connected anterolingually to the ultimate cusp of the lingual row by a low ridge. Lingual cusps are taller and larger than the labial cusps; they increase in size posteriorly from the first and are subequal in height posteriorly from the second. The first lingual cusp is subconical and the rest become increasingly anteroposteriorly elongate. The internal slopes are convex and the flattened external slopes possess vertical grooves, which are deeper posteriorly. Roots are subequal in size, the anterior root being somewhat squared in cross-section, and the posterior root more rectangular. Anteriorly the crown overhangs the root slightly.

m2. -- Cusp formula 3-4 : 2 (mode = 3 : 2). The referred m2's differ only slightly from the m2 present on the type of <u>Mesodma pygmaea</u> (AMNH 35298) and from those referred to <u>M. pygmaea</u> by Krause (1977) in being slightly larger and in having a better differentiated fourth labial cusp when present (Fig. 11 O).

P4. -- Cusp formula 3-4 : 6 : 0 (mode = 3 : 6 : 0). In lateral view (Fig. 11 P-Q) the crown is triangular with the ultimate cusp of the middle row highest above the base (characters considered diagnostic for P4's of <u>Mesodma</u>: see Sloan, 1981). The three lenticular cusps of the labial row increase in size and height posteriorly, and are situated opposite the first through third cusps of the middle row, respectively. On seven specimens, a variably developed cuspule is located posterior to the third labial cusp, opposite and slightly dorsal to the fourth cusp of the middle row. On one specimen, UALVP 22395, this "cuspule" is developed as a true fourth labial cusp. The cusps of the middle row are lenticular and increase in size and height posteriorly from the first. When viewed laterally the anterior slope of the middle cusp row is straight and the posterior slope is straight to slightly concave. Although easily obscured by wear, a posterobasal depression and at least one posterobasal cuspule were present. On UALVP 22609 this cuspule, located immediately posterior and dorsal to the ultimate cusp of the middle row, is developed as a relatively large cusp. This specimen also possesses an anomalous, fairly large cuspule on the base of the crown, lingual and dorsal to the fifth cusp of the middle row. These conditions are considered to be examples of extreme variation.

The anteroventral edge of the crown is concave and overhangs the somewhat laterally flattened, anteroposteriorly elongate anterior root. The posterior root is slightly smaller in size and is squared in cross-section. The crown overhangs the posterior root only slightly.

M1. -- Cusp formula 7-8 : 9-10 : 5-8 (mode = 8 : 10 : 5 and 6). In lateral view the crown is slightly concave, being rotated anterolingually-posterolabially about the anteroposterior axis. In occlusal view the external edge of the crown is slightly concave, the internal edge is convex, the anterior edge is straight, and the labial and middle row of cusps diverge slightly posteriorly (Fig. 12 B). The cusps of the labial row are subcrescentic with convex external slopes and somewhat flattened internal slopes that become more flattened with wear. The first and ultimate cusps of the labial row are connected to the first and ultimate cusps, respectively, of the middle row by low ridges. The cusps of the middle row posterior to the small, subconical first cusp are four-sided, subequal in height, and become increasingly larger and crescentic to the ultimate cusp, which is slightly taller, though smaller in size than the penultimate cusp. Valley-facing slopes of the middle row may possess variably developed vertical grooves. The lingual cusp row begins opposite the third or fourth cusps of the middle row. Anteriorly the subconical lingual cusps may or may not be preceded by one or two small cuspules. Posteriorly they become increasingly taller, larger, and subcrescentic.

The roots are subequal in size. The anterior root is anteroposteriorly elongate and transversly flattened; conversely, the posterior root is transversly elongate and anteroposteriorly flattened.

M2. -- Cusp formula 1 : 3 : 3. In occlusal view M2 is as wide, or slightly wider than long (Fig. 12 A). The anterior edge of the crown is shallowly concave. The single labial cusp, located at the anteroexternal corner of the crown, is incorporated into a ridge connecting it to the anterior and ultimate cusps of the middle row. The anteroposteriorly flattened first middle cusp is closely appressed to, and joined in its entirety to about three-quarters the height of, the second cusp. It is connected to the first lingual cusp by a low, weak ridge. The second cusp of the middle row is crescentic, the tallest and largest cusp on the crown, and may possess a small, shallow depression on the external slope. The third, or, ultimate cusp of the middle row, is crescentic, slightly smaller and shorter than the second; and joined to the ultimate lingual cusp by a very weak, low ridge. Posterior to the first cusp, the lingual cusps are crescentic, joined to approximately two-thirds of their height, and decrease in size and height. The internal slopes are convex and the somewhat flattened external slopes become increasingly flattened with wear.

The crown overhangs the roots only slightly. The large anterior root is anteroposteriorly flattened and transversely elongate. The small posterior root is roughly circular in cross-section.

## DISCUSSION

Mesodma was erected by Jepsen (1940) with M. ambigua (Mantua lentil, Polecat Bench Formation, Wyoming) as the type species. To date there are eight recognized species of Mesodma: M. ambigua Jepsen (1940); M. senecta Fox (1971); M. hensleighi Lillegraven (1969); M. formosa (Marsh, 1889); M. thompsoni Clemens (1963); M. primaeva (Lambe, 1902); M. garfieldensis Archibald (1982); and M. pygmaea Sloan (1987). As in other ptilodontoids in general, species of Mesodma have been primarily diagnosed on the basis of characters of the fourth premolars. Lacking associated material in the Swan Hills sample of Mesodma, the specimens representing tooth positions other than p4 are tentatively referred to Mesodma prolis n. sp. and the diagnosis is based in its entirety on the lower fourth premolar.

Mesodma prolis represents one of the two smallest identified multituberculates in the Swan Hills local fauna. It is eclipsed in size only by the smaller, single specimen from Swan Hills site 2 referred to Mesodma pygmaea. In size Mesodma prolis approaches Mimetodon silberlingi (Simpson, 1935a). Morphologically, Mesodma prolis possesses characters that resemble not only Mesodma pygmaea, but also Mimetodon silberlingi. Krause (1977, p. 26) noted the difficulties in distinguishing lower fourth premolars of Mesodma pygmaea from Mimetodon silberlingi in the Roche Percée fauna. He differentiated the two on the basis of size, as well as the possession by Mesodma pygmaea of a lower first serration, a more horizontally inclined posterior slope, and the last two or three serrations being "without vertically oriented, anteriorly convex wrinkles on the lingual side"

(Krause, 1977: p. 26). In addition to these characters, the crown of *Mimetodon* tends to be higher and more nearly symmetrical, with the apogee less anteriorly positioned and the more robust exodaenodont lobe generally extends further ventrally (pers. observ.). *Mesodma prolis* p4's share these differences in common with *Mesodma pygmaea*; however, the crown of p4 is relatively lower and slightly more asymmetrical in *Mesodma prolis* as compared to *Mesodma pygmaea*. Several specimens of p4 referred to *Mimetodon silberlingi* by Krause (1977; UALVP 10222, 11609, 11617), are very similar in size and morphology to p4's of *Mesodma prolis* and may represent the presence of the latter in the Roche Percée sample. An examination of this hypothesis must await the collection of a larger sample of *Mesodma prolis* that would allow delineation of upper and lower limits of variation in this species.

Russell (1967) referred an anterior half of a left p4 from Swan Hills site 1 (ROM 05604) to *Ectypodus*, cf. *E. laytoni*. *Ectypodus laytoni* Jepsen (1940) has since been referred to *Parectypodus* by Sloan (1966). ROM 05604 is indistinguishable from other specimens of p4 referred to *Mesodma prolis*, n. sp. and is here referred to this species.

Three complete P4's referred to *Mesodma prolis* are very similar in size and morphology to P4's referred by Krause (1977) to *M. pygmaea*. They differ from the latter P4's in possessing a cuspule developed posterior to the third labial cusp. This character is consistent throughout the sample preserving this area of the crown, and, as noted in the description for P4, UALVP 22395 has this cuspule developed as a true cusp. The three complete P4's in the Swan Hills site 1 sample are approximately 63% the length of p4 and fall within the range observed for other species of *Mesodma*[6]. Fragments of P4's in the *M.*

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[6] In *Mesodma senecta* the P4 is approximately 59% the length of p4; it is 65% in *M. hensleighi*, 67% in *M. thompsoni* and *M. formosa*, and 71% in *M. garfieldensis* (pers. observ.).

prolis sample, from individuals larger than the referred complete specimens, indicate that this percentage will increase with further collection of better preserved material.

Molars referred to M. prolis bear striking resemblance to those referred to M. pygmaea by Krause (1977) and Krishtalka (1973). They differ from M. pygmaea in generally being larger and in modally having a slightly greater number of cusps on M1/m1. In his count of cusps for M1 of M. pygmaea, Krishtalka (1973) included as a separate cusp a slight raised area on the ridge connecting the ultimate labial cusp to the ultimate cusp of the middle row. He also counted incipiently developed cuspules on the papillate ridge anterior to the first lingual cusp as separate cusps. The cusp formula for specimens of M1 referred to M. pygmaea from Police Point is here considered to be 7-8 : 9-10 : 4-5 (mode 7 : 9 : 4). Krause (1977) did not include the M1 modal cusp number in his description of M. pygmaea. On examination of the referred specimens it was found to be 7 and 8 : 9 : 4.

The possibility does exist that a portion of the sample referred to Mesodma prolis, n. sp. is referable to M. pygmaea; however, current available data suggest that the material is indeed referred correctly, and similarities to M. pygmaea are due to descent from an earlier, possibly middle Tiffanian branch of the Mesodma pygmaea line. This interpretation may change when the sample of M. prolis from Swan Hills site 1 is increased.

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Percentages are based on mean lengths for P4/p4 obtained from Fox (1971), Clemens (1963), Lillegraven (1969), and Archibald (1982).

## Genus *Parectypodus* JEPSEN, 1930

### ?*Parectypodus* sp.

(Fig. 12 C-E)

*Referred specimen*. -- isolated left P4: UALVP 22412.

*Locality*. -- Swan Hills site 1, Paskapoo Formation, Alberta.

## DISCUSSION

This single, problematic P4, here referred to ?*Parectypodus* sp., is unworn and complete except for slight breakage to the apex of the ultimate cusp of the medial row. Morphologically, UALVP 22412 possesses characters that are similar to characters possessed by species of *Neoplagiaulax*, *Parectypodus*, and *Ectypodus*; however, overall the affinities seem to be with *Parectypodus*. The following discussion primarily uses generic diagnoses for the above three genera as redefined by Sloan (1981).

Despite the slight damage to the ultimate cusp of the medial cusp row it is evident the ultimate cusp on UALVP 22412 was slightly larger than, or at least equal to, the penultimate cusp in height. This character is reminiscent of *Ectypodus* species and not species of *Neoplagiaulax* or *Parectypodus* which have the penultimate or antepenultimate cusps highest above the base of the crown. On the poste[illegible]or slope of the medial cusp row, UALVP 22412 has what may be interpreted as an incipiently developed cusp. This "cusp" is confluent with the posterior slope and is only differentiated lingually by a very shallow, vertical groove between it and the ultimate cusp. Until a larger sample indicates otherwise, this character is not considered to be taxonomically significant.

A cusp formula of 7 : 10 : 0 is present on UALVP 22412. This number of cusps puts it well outside the range for *Ectypodus* (range = 0-3 : 6-7 : 0) as defined by Sloan (1981, p. 145). The presence of seven labial cusps on the Swan Hills P4 is outside the range given by Sloan for both *Neoplagiaulax* (range = 0-4 : 7-11 : 0; 1981, p. 133) and *Parectypodus* (range = 2-5 : 7-9 : 0; 1981, p. 134); however, Sloan does state that advanced species of *Parectypodus* possess additional cusps in the labial row (1981, p. 134). The middle cusp row on UALVP 22412 has one more cusp than the condition generally seen in *Parectypodus*[7] and falls within the range for species of *Neoplagiaulax*.

In lateral profile the crown is triangular and relatively high -- higher than the condition for the most part seen in *Parectypodus*, and approaching the height and shape seen in some species of *Ectypodus* and *Neoplagiaulax* (especially *N*. *hunteri*). The posterior slope is concave and relatively short and steep. The anterior slope is long and only weakly convex as compared to other *Parectypodus* species.

Sloan states that the posterobasal cusp in *Parectypodus* is "usually absent", "generally present" in *Neoplagiaulax*, and "usually weak or absent" in *Ectypodus* (1981: pp. 134, 133, and 145, respectively). UALVP 22412 lacks the posterobasal cusp, and, as in species of *Parectypodus* generally, the posterobasal depression is relatively well-developed (pers. observ.). Around the posterior border of the posterobasal depression on UALVP 22412 is a well defined, low ridge that extends a short distance anterodorsal from the internal edge of the posterobasal depression.

As stated above, the affinities of UALVP 22412 seem to lie with *Parectypodus*. It is united with species of *Parectypodus* in having on the

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[7] *Parectypodus armstrongi* Johnston and Fox, 1984, modally possesses 10 cusps in the middle row (pers. observ.).

middle cusp row a concave posterior slope and a convex, albeit a weakly convex, anterior slope, a large number of labial cusps, lacking a posterobasal cusp, and in having a well developed posterobasal depression. It differs from *Parectypodus* species in general in havi[illegible]ltimate cusp as the highest cusp above the base of the crown, and in possessing a triangular, relatively high crown in lingual view. UALVP 22412 further differs from *Parectypodus*, and from *Neoplagiaulax* and *Ectypodus*, in lacking an anterolabial bulge (currently it is not known whether this character is an individual variant, or is taxonomically significant).

In size, UALVP 22412 is larger (L = 3.8; W = 1.4) and has a greater number of cusps than P4's of *Parectypodus vanvaleni* Sloan (1981). P4's of *P. trovessartianus* (Cope, 1882) are unknown; however, with a modal length of 5.8 for p4's in *P. trovessartianus* (Sloan, 1987: p. 192), UALVP 22412 would appear to be too small to represent P4's of this species. In general appearance UALVP 22412 resembles P4's of *Parectypodus* sp. described from Puercan deposits near the village of Ravenscrag, Saskatchewan by Johnston and Fox (1984). It differs in being slightly larger, relatively higher crowned, lacking the anterolabial bulge, and in having a larger cusp formula. UALVP 22412 differs from *P. armstrongi* in being smaller, higher crowned, having a more weakly developed convex anterior slope, larger number of labial cusps, and in lacking an anterolabial bulge. Compared to all other described species of *Parectypodus*, UALVP 22412 is significantly larger.

Metrical and morphological data indicate that UALVP 22412 is a P4 of a new, hitherto unidentified species of Neoplagiaulacidae, probably belonging to the genus *Parectypodus*. The absence of referable specimens representing tooth positions other than this single specimen of P4 would indicate that ?*Parectypodus* sp. is a relatively rare element in the Swan Hills local fauna.

Although some workers would support the naming of a new species based on a single, relatively diagnostic specimen, the naming here of a new species is reserved pending collection of a larger sample that would allow a better understanding of the affinities of this interesting specimen.

Suborder TAENIOLABIDOIDEA GRANGER and SIMPSON, 1929

Family EUCOSMODONTIDAE (JEPSEN, 1940)

Subfamily MICROCOSMODONTINAE HOLTZMAN and WOLBERG, 1977

Genus _Microcosmodon_ JEPSEN, 1930

_Microcosmodon_ _conus_ JEPSEN, 1930

(Fig. 8 A-I; Table 4)

_Referred specimens_. -- i1: UALVP 22738; m1: UALVP 22467; ?DI2: UALVP 22408; I2: UALVP 22214, 22407; M1: UALVP 22390, 22413; M2: UALVP 22411.

_Locality_. -- Swan Hills site 1, Paskapoo Formation, Alberta.

_Known distribution_. -- Swan Hills local fauna, Paskapoo Formation, Alberta; Princeton Quarry, Polecat Bench Formation, Wyoming (Jepsen, 1930); Schaff Quarry, Polecat Bench Formation, Wyoming (Krause, 1977); Badwater Creek, Shotgun Member, Fort Union Formation, Wyoming (Krishtalka, _et al_., 1975); Roche Percée local fauna, Ravenscrag Formation, Saskatchewan (Krause, 1977); Sunday locality, Polecat Bench Formation, Wyoming (D. W. Krause, pers. comm. to Johnston and Fox, 1984); Jepsen Valley Quarry, Silver Coulee Beds, Polecat Bench Formation, Wyoming

Table 4: Measurements and descriptive statistics of the dentition of *Microcosmodon conus*, Swan Hills local fauna, Alberta.

| Measurement | | N | OR | M±SE | SD | CV |
|---|---|---|---|---|---|---|
| i 1 | MXD | 1 | 1.8 | - | - | - |
| | MND | 1 | 0.6 | - | - | - |
| m 1 | L | 1 | 2.5 | - | - | - |
| | W | 1 | 1.2 | - | - | - |
| DI2 | MXD | 1 | 1.3 | - | [illegible] | - |
| | MND | 1 | 0.8 | - | - | - |
| I 2 | MXD | 2 | 1.6-1.7 | 1.65 ± .05 | .071 | 4.3 |
| | MND | 2 | 0.9-1.0 | 0.95 ± .05 | .071 | 7.4 |
| M1 | L | 1 | 2.7 | - | - | - |
| | W | 2 | 1.4-1.6 | 1.50 ± .10 | .141 | 9.4 |
| M2 | L | 1 | 1.4 | - | - | - |
| | W | 1 | 1.3 | - | - | - |

(Schaff, 1980).

## DESCRIPTION

i1. -- The single referred specimen, UALVP 22738 (Fig. 8 A-B), is a fragment of a left incisor that is missing both the root and the tip of the crown. The strongly laterally compressed fragment tapers anteriorly and is gently curved dorsally. Enamel covers the ventral edge of the incisor and extends dorsally approximately two-thirds of the way up the lateral surface of the tooth and half-way up the mesial surface. This creates a dorsal strip on the incisor which lacks enamel. The mesial surface, between the ventral edge of the enameless dorsal strip and a raised rim on the enamel covered ventral margin of the incisor, is shallowly concave.

m1. -- Cusp formula 9 : 5. Wear partially obscures the very small, anteriormost cusps of the labial and lingual rows on this single referred specimen, UALVP 22467 (Fig. 8 E-F). A short, low, anterolabially directed ridge appears to have connected the anterolingual cusp to the anterolabial cusp. The cusps of the labial row decrease in height anteriorly and posteriorly from the fifth, which is the largest of the labial cusps. The cusps become progressively more crescentic from the second, which is subconical, to the ultimate cusp, which forms an anterolingually directed ridge joining the labial row to the posterolabial base of the ultimate lingual cusp. The ultimate labial cusp is closely adjoined to the penultimate and although the apex of the former is missing, it is evident they were joined almost to their apices. Posteriorly the crescentic lingual cusps become larger and more massive;

however, they decrease in height anteriorly and posteriorly from the third. This increase in height of cusps from either end of the crown towards the third lingual and fifth labial cusps emphasizes the crown's dorsal curvature. The intercusp grooves of both rows are deep. Vertical grooves on the valley-facing walls are present only on the lingual row of cusps.

The posterior root, though broken and largely missing, is clearly the larger of the two main roots. The anterior root is laterally compressed with a shallow, vertical groove extending down each of the anterior and posterior walls. Between these roots labially is a small, well-developed accessory root. Despite breakage between the main roots lingually, there are indications of at least one accessory root internally.

[illegible] ?DI2. -- The single specimen referred here, UALVP 22408 (Fig. 8 G), is approximately two-thirds the size of UALVP 22407, a left I2. The bicuspid, enamel-covered crown has an oblique wear facet on the posterior side of the larger anterior cusp. The slightly worn anterior edge of the longitudinal groove forms a narrow ridge joining the anterior cusp to the much smaller and little-worn posterodorsal cusp. The longitudinal groove narrows and becomes shallower proximally; in length, it is less than twice the maximum diameter of the tooth. When viewed from lateral or mesial aspects, the maximum diameter of the tooth is seen to progressively decrease proximally. This is in opposition to the slight proximal mesial flare observed when the tooth is viewed from the dorsal aspect. In the area of the mesial flare the enamel thins and ends. Proximally from this point, the edge of the enamel does not appear as a dorsal strip, as is seen in permanent upper incisors, but progressively moves up and over the dorsal edge of the tooth. Breakage obscures how far labially the edge of the enamel proceeds.

I2. -- UALVP 22407 represents the distal third of a bicuspid upper incisor that is crushed mesially and covered by premaxillary bone fragments laterally. UALVP 22214 (Fig. 8 C-D) is a more complete specimen possessing a worn crown and missing the root. Except for wear at the tip, the crown and lateral surface are enamel-covered. Mesially, just proximal to the wear surface of the crown, the enamel is present as a dorsal strip that is terminated proximally by breakage. On UALVP 22407 the large anterior and small posterodorsal cusps are unworn and covered with enamel. These two cusps are present on UALVP 22214 in a somewhat altered form due to wear. Both specimens possess a deep longitudinal groove on the lateral face. On UALVP 22214 this groove narrows slightly on the proximal portion of the incisor.

M1, -- Cusp formula 7 : 7 : 5. In occlusal view the anterior edge of the little-worn crown is slightly concave (Fig. 8 H). The labial and medial row of cusps run roughly parallel to each other and converge anteriorly only slightly. In lateral view, the crown is concave ventrally. The labial cusps, which decrease in size anteriorly and posteriorly from the fifth, are conical with flattened lingual walls that have a complex morphology, each with one or two deep, vertical grooves. The anteriormost cusp is closely adjoined to the second, being somewhat ridge-like in appearence and connecting the labial row with the first cusp of the medial row. The ultimate labial cusp is connected anterolingually and posterolingually to the ultimate cusp of the medial row by two low, relatively robust ridges. The former cusp has what may be interpreted as a small eighth cusp closely adjoined to it on the posterolingual ridge. A small, anomalous cuspule is present labially on the base of the crown between the fourth and antepenultimate cusps of the labial row on UALVP 22390. The second through sixth medial cusps are crescentic and increase in size posteriorly to the conical, ultimate medial cusp, which is the largest and tallest of the medial row. The first medial cusp has the second closely adjoined to it and is conical, with a deep vertical groove on the flattened external wall. The penultimate and antepenultimate cusps each possess a vertical groove on their internal wall. The lingual cusp row, which begins opposite the groove separating the third and fourth medial cusps, has five conical cusps and one or two indistinct anterior cuspules. The first and third cusps are very small and closely adjoined to the anterior bases of the second and fourth cusps respectively. A low ridge connects the ultimate cusp of the lingual row posterolabially to the ultimate cusp of the medial row.

The anterior root is roughly rectangular in shape with laterally flattened sides and shallow, vertical grooves on the anterior and posterior edges. The posterior root is broken away just below the base of the crown; however, it was clearly the larger of the two main roots. Two accessory roots are present lingually and one labially between the two main roots.

M2. -- Cusp formula 1 : 3 : 4. In occlusal view the crown on this single referred, unworn specimen, UALVP 22411 (Fig. 8 I), is longer anteroposteriorly than it is wide, the anterior edge is concave, and the medial and lingual rows of cusps are parallel to each other. The single external cusp is incorporated into a ridge that extends from the first medial cusp through the apex of the former and posterolingually to the base of the ultimate medial cusp. The first medial cusp is anteroposteriorly flattened, closely appressed to the second, and is subequal in height to the latter. The penultimate and ultimate cusps of the medial row are subequal in height, crescentic, and, like the medial cusp row of M 1/m1, are strongly recurved. Anteriorly from the ultimate cusp, the conical lingual cusps become progressively smaller and more closely adjoined, with the first and second cusps being confluent almost to their apices. The first and ultimate lingual cusps are joined by short, low ridges to the first and ultimate medial cusps respectively. The valley between these two rows of cusps consists of a complicated pattern of ridges and deep grooves. The roots below the crown are missing.

## DISCUSSION

The absence of identifiable p4's of *Microcosmodon* in the Swan Hills local fauna makes confident placement of isolated specimens difficult; however, UALVP 22467 (m1), 22407 (I2), and 22413 (M1) are virtually indistinguishable in size and morphology from specimens in the Roche Percée local fauna referred to *M. conus* by Krause (1977). Specimens of *M. conus* tend to be larger than the early and middle Clarkforkian *M. rosei* (Krause, 1980). As noted by Krause (1980), effective comparisons of *M. conus* and *M. rosei* are restricted by small sample sizes from all known localities, but when compared to the known data, specimens from the Swan Hills clearly fall within the size range for *M. conus*.

Upper dentitions of *Microcosmodon* are unknown in association with lower dentitions; however, size, frequency, and morphological data have allowed the tentative allocation of upper dentitions to *Microcosmodon* (Krishtalka, *et al.*, 1975; Krause, 1977, 1980)[8]. An isolated M2 (UALVP 22411) from Swan Hills site 1 is here tentatively referred to *M. conus*. In size this specimen is intermediate between the smaller M2 (CM 16168) tentatively

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[8] "*Microcosmodon*" *woodi* Holtzman and Wolberg, 1977, in keeping with Johnston and Fox (1984), is here not considered to be congeneric with *Microcosmodon*. G. P. Youzwyshyn (pers. comm., 1987) has pointed out similarities in p4 structure between "*M.*" *woodi* and *Acheronodon* Archibald, 1982. On the basis of these similarities "*M.*" *woodi* may better be placed in *Acheronodon* as the youngest known species.

referred to *M. conus* from Malcolm's locality, Wyoming (Krishtalka, *et al.*, 1975) and the larger M2 (UM 72702) tentatively referred to *M. rosei* from the Clarkforkian (Krause, 1980). Morphologically UALVP 22411 resembles both. Allocation of the Swan Hills M2 to *Microcosmodon conus* is thus primarily based on the absence of specimens referable to *M. rosei* in the Swan Hills local fauna and the similarity to the M2 referred to *M. conus* [illegible]y Krause (1980). With increases of sample sizes from known localities, future discoveries may necessitate a revision of the above interpretation.

A small, isolated eucosmodontid upper incisor (UALVP 22408) is allocated to *Microcosmodon conus* as a possible deciduous I2. Erupting and deciduous teeth have been previously described for multituberculates (e.g., Clemens, 1963; Hahn, 1969; Szalay, 1965; Vianey-Liaud, 1986); however, descriptions of deciduous incisors are limited to one of a fragmentary lower mandible from Swain Quarry possessing the root of a deciduous incisor of *Ptilodus mediaevus* (Szalay, 1965), and a description of two lower incisors of paulchoffatiids from the Lower Kimmeridgian of Portugal (Hahn, 1978). As far as is known to me, no previous descriptions of multituberculate deciduous upper incisors are to be found in the literature.

Morphologically, UALVP 22408 is very similar to permanent upper incisors of *M. conus* in having a bicuspid, enamel-covered crown, being completely covered in enamel laterally, and in having a deep, lateral longitudinal groove. It differs from the latter in having a much shorter longitudinal groove, being approximately 30 per-cent smaller, and in possessing a maximum diameter that decreases proximally in contast to the maximum diameter of the permanent upper incisors, which remains much the same throughout the length of the tooth. UALVP 22408 also lacks the well defined dorsal enamel band found on the mesial face of the permanent incisors.

An alternative hypothesis is that UALVP 22408 represents the upper permanent incisor of a small, hitherto unidentified eucosmodontid. Lacking evidence to the contrary, the former hypothesis is deemed to be the most parsimonious.

### Subclass THERIA
### Infraclass EUTHERIA
### Order LIPOTYPHLA HAECKEL, 1866
### Suborder ERINACEOMORPHA GREGORY, 1910
### Family ERINACEIDAE (FISCHER VON WALDHEIM, 1817)
### Genus _Hadrolestes_, new genus

_Etymology_. -- Grk. _hadros_: bulky or stout, and Grk. _lestes_: robber -- in allusion to the general morphology of the lower molars and P4/p4's, and in keeping with the suffix attached to other erinaceid genera.

_Type and only species_. -- _H_. _bounites_ new species.

_Diagnosis_. -- As for the species.

### _Hadrolestes bounites_, new species
(Fig. 12 F-L, 13 A-C; Table 5, 6)

_Etymology_. -- Grk. _bounites_: dweller in the hills -- in reference to its being present in the Swan Hills local fauna.

Table 5: Measurements and descriptive statistics of the lower dentition of *Hadrolestes bounites*, new genus and species, Swan Hills local fauna, Alberta.

| Measurement | | N | OR | M±SE | SD | CV |
|---|---|---|---|---|---|---|
| canine | L | 7 | 1.1-1.4 | 1.26 ± .04 | .098 | 7.8 |
| | W | 7 | 0.5 | - | - | - |
| p1 | L | 1 | 0.9 | - | - | - |
| | W | 1 | 0.4 | - | - | - |
| p2 | L | 9 | 0.9-1.0 | 0.93 ± .02 | .050 | 5.4 |
| | W | 9 | 0.4-0.6 | 0.50 ± .02 | .050 | 10.0 |
| p3 | L | 20 | 1.0-1.2 | 1.09 ± .01 | .049 | 4.5 |
| | W | 20 | 0.6-0.7 | 0.66 ± .01 | .051 | 7.8 |
| p4 | L | 24 | 1.3-1.6 | 1.48 ± .02 | .078 | 5.3 |
| | W | 24 | 0.8-1.1 | 1.00 ± .02 | .088 | 8.8 |
| m1 | L | 16 | 1.3-1.5 | 1.39 ± .01 | .057 | 4.1 |
| | AW | 19 | 0.9-1.1 | 1.00 ± .01 | .040 | 4.1 |
| | PW | 22 | 0.9-1.1 | 1.01 ± .01 | .049 | 4.8 |
| m2 | L | 14 | 1.1-1.2 | 1.16 ± .01 | .050 | 4.3 |
| | AW | 14 | 0.8-1.0 | 0.90 ± .02 | .055 | 6.2 |
| | PW | 17 | 0.8-1.0 | 0.91 ± .01 | .049 | 5.3 |
| m3 | L | 8 | 1.0-1.1 | 1.05 ± .02 | .053 | 5.1 |
| | AW | 8 | 0.7-0.8 | 0.74 ± .02 | .052 | 7.0 |
| | PW | 8 | 0.7-0.8 | 0.71 ± .01 | .035 | 5.0 |

Table 6: Measurements and descriptive statistics of the upper dentition of <u>Hadrolestes bounites</u> ,new genus and species, Swan Hills local fauna, Alberta.

| Measurement | | N | OR | M±SE | SD | CV |
|---|---|---|---|---|---|---|
| P3 | L | 1 | 1.3 | - | - | - |
| | W | 1 | 1.1 | - | - | - |
| DP4 | L | [illegible] | 1.4 | - | - | - |
| | W | 1 | 1.6 | - | - | - |
| P4 | L | [illegible] | 1.4-1.6 | 1.52 ± .04 | .084 | 5.5 |
| | W | 6 | 1.5-1.6 | 1.55 ± .02 | .055 | 3.5 |
| M1 | L | 6 | 1.2-1.4 | 1.30 ± .03 | .063 | 4.9 |
| | W | 7 | 1.6-1.8 | 1.74 ± .03 | .079 | 4.5 |
| M2 | L | 6 | 1.0-1.2 | 1.03 ± .03 | .082 | 7.9 |
| | W | 5 | 1.5-1.8 | 1.60 ± .06 | .122 | 7.7 |
| M3 | L | 2 | 0.7-0.8 | 0.75 ± .05 | .071 | 9.4 |
| | W | 2 | 1.2 | - | - | - |

*Type specimen.* -- UALVP 22348, a right dentary preserving p2-4, m1, roots for m2, and m3 (Fig. 12 F-H).

*Type locality.* -- Swan Hills site 1, Paskapoo Formation, Alberta (exact coordinates are available to qualified researchers through the Laboratory for Vertebrate Paleontology, Department of Zoology, University of Alberta).

Referred specimens. -- canine: UALVP 22326, 22515, 22522, 22708, 22709, 23865, 23866; p1: UALVP 22707; p3: UALVP 22223, 22225, 22246, 22696; p4: UALVP 22243, 22244, 22682, 22697-22699, 23869, 23870; m1: UALVP 22350, 22480, 22482, 22495, 22509, 22510, 22700, 23867, 23868, 23871; m2: UALVP 22222, 22228, 22229, 22347, 22349, 22493, 23872; m3: UALVP 22239, 22701, 22702; dentary fragment with p2-3: UALVP 22226, 22236, 22471, 22688, 23873, 23874; dentary fragment with p2-4: UALVP 23875; dentary fragment with p2-m1: UALVP 22689; dentary fragment with p3-p4: UALVP 22233, 22234, 22237, 22242, 22245, 23876, 23877; dentary fragment with p3-m1: UALVP 22235; dentary fragment with p4-m1: UALVP 22238, 22240, 22690, 22691; dentary fragment with p4-m2: UALVP 22692; dentary fragment with m1-2: UALVP 22232, 22241, 22693, 23878, 23879; dentary fragment with m1-3: UALVP 22694; dentary fragment with m2-3: UALVP 22231, 22463, 22695; P3: UALVP 23880; DP4: UALVP 22499, 23881; P4: UALVP 22322, 22329, 22344, 23882, 23883; M1: UALVP 22448, 22449, 22454, 22469, 22487, 22705, 22710, 23884, 23885; M2: UALVP 22342, 22441, 22500, 22704, 23898; M3: UALVP 22497; maxillary fragment with P4-M2: UALVP 23886; maxillary fragment with M1-2: UALVP 22474; maxillary fragment with M1-3: UALVP 22703.

Known distribution. -- Swan Hills site 1, Paskapoo Formation, Alberta; Roche Percée local fauna, Ravenscrag Formation, Saskatchewan (Krause and Fox, in prep.).

Diagnosis. -- A new species of erinaceid insectivoran differing from other primitive erinaceids (sensu Novacek, et al., 1985) in possessing where known a p3 that is relatively less reduced with a protoconid that is erect and inflated; in having a p4 with a more bulbous protoconid and a paraconid that is conical, lower on the crown, more nearly anterior to the protoconid, and separated from the protoconid by a narrow valley; p4 larger than m1; m3 with a small entoconulid; P4 with a very bulbous paracone; differing from most erinaceids and resembling Litolestes Jepsen (1930), and Entomolestes Matthew (1909), in possessing a premolariform p4 with a short talonid and a talonid basin that is less than one-third the width of the talonid; protoconid height on p4 differing from all but Entomolestes, Eolestes (Bown, 1979), and Dartonius Novacek, et al. (1985), in being as high or slightly higher than the m1 trigonid height; differing from Leipsanolestes Simpson (1928), and Entomolestes, in having a greater decrease in size of the molars posteriorly, and from Cedrocherus Gingerich (1983), in having less of a molar size decrease; m1 differing from m1 of Neomatronella Russell, et al. (1975), Leipsanolestes, Dartonius, and Eolestes in possessing a more inflated paraconid, and from the latter two plus Entomolestes in having less anteroposterior compression of the trigonid; lower molars differing from those of Eolestes, Entomolestes, Neomatronella, and Dartonius in having relatively lower entoconids and entocristids; hypoconulids differing from those of Dartonius, Cedrocherus, Entomolestes, and *Adapisorex* in being smaller, developed as in *Litolestes* and *Eolestes*; differing from *Cedrocherus* in having molars exhibiting a greater degree of labial exodaenodonty and more of an anterior cant to the trigonids, developed as in *Litolestes* and *Leipsanolestes*; differing from *Litolestes* in characters that differentiate *Hadrolestes* from other erinaceid genera, as well as in possessing relatively better developed cingulids labially on p4, a paraconid more closely appressed to the metaconid on m2, the cristid obliqua joining the posterior wall of the trigonid more labially on m2-3, possessing a metacone on P3-4, and in having smaller meta- and parastylar salients on M1-2; differing from *Adapisorex* Lemoine (1883), and *Neomatronella* in possessing upper molars that are less quadrate and more rectangular, and in lacking a hypocone on P4; differing from dormaaliids in those characters that differentiate early erinaceids from the Dormaaliidae.

## DESCRIPTION

c1. -- The canine is single-rooted and premolariform (Fig. 12 J). In occlusal view the outline of the crown is tear-drop shaped. The crown is dominated by a laterally compressed, anteriorly procumbent protoconid. The protoconid is convex labially and slightly concave lingually. Anteriorly in lateral profile the crown is somewhat spatulate. A cristid, positioned slightly labial to the anteroposterior midline of the crown, extends posteroventrally from the apex of the protoconid and turns slightly posterolingually at its base to a small, variably developed cusp on a short heel. Anteroventral to the protoconid apex the crown is strongly laterally compressed, forming a broad ridge that curves lingually. On one specimen, UALVP 23865, a tiny cuspule is located at the anterolingual base of this ridge. In cross-section the root is elliptical.

p1. -- The single referred p1 is single-rooted and very similar to the canine in morphology (Fig. 12 L). It differs from the canine in being much smaller, relatively less anteriorly elongate and procumbent, having the anterior edge of the crown curved lingually only slightly, and in having a wider heel. As on the canine, the root is elliptical in cross-section.

p2. -- p2 is double-rooted and more nearly elliptical in occlusal view than p1 (Fig. 12 F-H). As well, the laterally compressed protoconid is relatively taller, less anteriorly procumbent, and more erect than on p1. The heel is single-cusped, approximately one-quarter the crown length, and almost as wide as the posterior base of the protoconid. In oblique light, a weak cristid can be observed descending posteroventrally from the protoconid apex to the [illegible] weak cristid descends anteroventrally from the protoconid apex towards the anterior base of the crown. Before reaching the base, this cristid becomes better defined and turns sharply lingually. On several specimens (e.g., UALVP 22471) a tiny, incipiently developed paraconid can be identified at the anterolingual end of the cristid. The two roots are subequal in size and circular in cross-section.

p3. -- In occlusal view, p3 is pinched slightly between the two roots producing a subpyriform shape (Fig. 12 H). The crown is dominated by the low, bulbous protoconid. Unlike p2, the protoconid is fully erect. A weak cristid connects the protoconid anterolingually to a quite small, variably-developed paraconid on the base of the crown. Metaconids are generally lacking; however, on UALVP 22696 there is a distinct, small metaconid on the posterolingual base of the protoconid.

The incipiently developed talonid shows an unexpected degree of morphological variation. It can be between one-quarter and one-third of the total crown length and generally is the widest part of the crown. The posterior edge of the talonid, which can possess zero, one, or two small cusps, is formed as a low, transverse ridge with a shallow valley separating it from the protoconid. When a single cusp is present, it is positioned medially on the ridge. In cases where two small cusps are present (e.g., UALVP 22471), they are connected to the protoconid by a relatively well-developed cristid obliqua and entocristid. The cusp at the posterior terminus of the cristid obliqua is probably homologous to the hypoconid. The second cusp is located medially on the posterior ridge and is slightly larger than the hypoconid. Inasmuch as this cusp is situated medially on the posterior ridge and not on the posterolingual corner of the talonid, the homologies of this cusp are uncertain. It may represent the entoconid, however. The shallow talonid basin produced when both cristids are present is just over one-half the width of the talonid. Several specimens show indistinct anterolabial and/or lingual cingulids (e.g., UALVP 23875). The two roots are subequal in size and slightly anteroposteriorly flattened.

p4. -- p4 is premolariform and morphologically quite variable. In size it is as large as, or larger than m1 and is generally only slightly higher crowned (Fig. 12 F-H). The protoconid is low, bulbous, and massive. A small, conical paraconid, which may be equal to, or smaller than the metaconid in size, is usually positioned relatively low on the anterolingual corner of the crown. It is separated from the protoconid by a shallow valley. On several specimens (e.g., UALVP 22243) the paraconid is relatively high and only slightly lower than the metaconid in height. The metaconid is a small, conical cusp located on the posterolingual edge of the protoconid at about midheight. On some specimens a very weak cristid may be observed in reflected light on the anterior slope of the protoconid. This cristid does not connect the protoconid to the paraconid; however, the protoconid is invariably connected posterolingually to the metaconid by a short protocristid.

In general, the talonid of p4 is as wide as, or slightly wider than the posterior base of the protoconid and approximately one-quarter of the crown length. The posterior edge of the talonid is developed as a transverse ridge and may possess one or two indistinct cusps. A cristid obliqua is invariably present and may be terminated posteriorly by the transverse ridge or by a cusp on the ridge. The entocristid when present is generally weak and parallel to the cristid obliqua. It can be low [illegible] lingual edge of the talonid or as high and well-developed as the cristid [illegible]a. The shallow basin produced can be from one-quarter to one-third the width of the talonid. On a number of specimens (e.g., UALVP 22234) a short ridge can be found on the posterior wall of the protoconid above the talonid basin that roughly parallels the cristid obliqua and descends into the basin before fading. On several specimens (e.g., UALVP 22245, 23869) this ridge reaches the posterior edge of the talonid, thus, the cristid obliqua on these specimens appears twinned.

An anterolabial cingulid is developed that extends around the base of the crown from the paraconid to a point above the posterior edge of the anterior root. Posterolabially is another cingulid that is continuous with the posterior transverse ridge. On several specimens (e.g., UALVP 22234) these cingulids are continuous labially between the roots.

m1. -- The trigonid of m1 has a slight anterior cant. The protoconid and metaconid are low, bulbous cusps, the former being slightly larger and taller than the latter (Fig. 12 F-H). The paraconid is relatively large, cuspate, well-separated from, and slightly medial to the metaconid, and anteriorly salient. The paracristid descends anteroventrally from the apex of the protoconid towards its base before making an almost 90 ° turn to run lingually to the paraconid. The protocristid notch forms an acute angle of approximately 75 °. The trigonid basin is shallow and open lingually between the meta- and paraconid.

The talonid is as long anteroposteriorly as the trigonid and is as wide, or slightly wider. The hypoconid and entoconid are anteroposteriorly elongate with flattened basin-facing walls, producing a V-shaped talonid basin. The latter cusp is taller and somewhat more anteriorly positioned on the trigonid than the hypoconid. The hypconulid is a small, slightly anteroposteriorly compressed cusp situated on the postcristid just lingual to the anteroposterior midline of the crown. The posterior edge of the crown is almost straight, save for the slightly posteriorly projecting hypoconulid. The entocristid is of high relief, producing a relatively shallow talonid notch. The cristid obliqua joins the posterior wall of the trigonid below or slightly lingual to the protocristid notch, forming a moderately deep hypoflexid, A short cingulid is present on the base of the crown below the hypoflexid. This may be continuous anteriorly around the base of the trigonid with the narrow precingulid. Post- and lingual cingulids are absent.

m2. -- m2 is very similar to m1 in morphology and differs in the following characters: the crown of m2 is relatively smaller and lower crowned; the paraconid is further reduced, less cuspate, more closely appressed to the metaconid, and more shelf-like; the trigonid basin is closed lingually between the paraconid and metaconid; the protoconid and metaconid are subequal in size and height; the talonid is approximately equal to the trigonid in transverse width; the cristid obliqua joins the posterior wall of the trigonid slightly labial to the protocristid notch and thus forms a relativley shallower hypoflexid; the entoconid is directly lingual to the hypoconid producing a wider talonid notch in comparison to m1; a weak cingulid at the base of the hypoflexid is almost always continuous anterolabially with the narrow precingulid (Fig. 12 I).

m3. -- m3 is smaller than m2 and much smaller in comparison to m1 (Fig. 12 F-I). The trigonid of m3 resembles m2 and differs in having the paraconid more reduced, more anteriorly procumbent or shelf-like, and situated much lower on the anterior slope of the metaconid. On several specimens (e.g., UALVP 22348) a low enamel fold extends between the anterior bases of the metaconid and protoconid producing a small, shallow basin between it and the protocristid. The talonid is elongate due to the posteriorly projecting hypoconulid, which is nearer the size and height of the entoconid than seen on m1-2. On the entocristid is a small entoconulid situated just posterodorsal to the bottom of the talonid notch.

P3. -- In occlusal view the three-rooted P3 is roughly the shape of a scalene triangle, having sides slightly pinched between the paracone and protocone (Fig. 13 A). The paracone dominates the crown and is a relatively tall, conical cusp with a sharp crista descending posteroventrally to a small, transversely compressed and poorly differentiated metacone. The postmetacrista continues a short distance posteriorly to a small, slightly anteriorly recurved metastyle. Anteriorly, at the base of the paracone, is a small parastylar salient. A weak ectocingulum is present labially but is incomplete around the base of the paracone. The small protocone is conical and well-separated from the paracone lingually. Faint pre- and postprotocristae extend anterolabially and posterolabially, respectively, to the stylar cusps, forming cingula along the base of the crown.

DP4. -- Of the two referred specimens, only UALVP 22499 (Fig. 13 B) is complete. UALVP 23881 is a lingual half of a crown preserving the conules, protocone, and a portion of the hypocone. In occlusal view the crown is triangular. The conical paracone is the largest and tallest cusp on the crown. The metacone is slightly laterally compressed and approximately three-quarters the height, and one-half the size of the paracone. Both cusps are well separated from each other but connected via a centrocrista exhibiting some wear. Anterolabially the paracone is joined to a small parastylar salient by a worn preparacrista. The postmetacrista is tall, crestiform, and curves slightly posterolabially from the metacone to a small metastylar salient. Conules are well-developed, conical, and subequal in size and height. The protocone is subcrescentic with well-developed pre- and postprotocristae. The hypocone is small, conical, and is canted slightly posteriorly. It is situated on the posterolingual corner of the protocone and produces a noticeable posterolingual elongation of the crown.

A short, narrow precingulum is present on the base of the crown between the paraconule and protocone. The postcingulum is broad and relatively long, extending from the metaconule to the posterolingually positioned hypocone. A narrow ectocingulum is incomplete around the posterolabial base of the paracone. A metacingulum is terminated posterolabially by the crestiform postmetacrista. A paracingulum is continuous with the ectocingulum.

P4. -- P4 is roughly pyriform in occlusal view, with the labial edge representing the flattened, anteroposteriorly elongate base (Fig. 12 K). In size it is at least as large as M1. On UALVP 23886, a maxillary fragment preserving

P4-M2, P4 is longer anteroposteriorly than M1, but slightly smaller in transverse width. The conical paracone is a short, bulbous, very robust cusp. In labial view it appears strongly canted posteriorly. The metacone is poorly differentiated along the posterolabially curving, crestiform ridge extending between the paracone and metastyle. When viewed posterolingually the metacone exists as a small cuspule situated along the top of the ridge approximately midway between the apex of the paracone and the almost conical, strongly-developed metastyle. In labial view the metacone is differentiated by two vertical grooves, one on either side of the metacone, that separate it from the former two cusps. The parastyle is a small, yet strongly-developed conical cusp positioned directly anterior to the paracone. The protocone is subcrescentic and approximately one-half the height, and between one-quarter and one-third the size of the paracone. It is situated anterolingual to the apex of the paracone. The preprotocrista is continuous anteriorly with the paracingulum while the postprotocrista descends posteroventrally to a posterior cingulum. The enamel of the crown exhibits a slight degree of rugosity.

A poorly developed ectocingulum is present labially. A weak paracingulum is terminated anterolabially by the parastyle. A narrow cingulum is present along the posterior base of the crown, extending from the posterolingual base of the protocone to the base of the metastyle. A very short and narrow precingulum is developed on the anterior base of the protocone.

M1. -- In occlusal view, M1 is subrectangular and pinched slightly in the area of the conules (Fig. 13 C). The paracone is erect, the tallest cusp on the crown, and not quite conical, being slightly anteroposteriorly compressed. The metacone is approximately three-quarters the size of the paracone, slightly shorter, and is more nearly conical. Both the paracone and metacone have a variably developed vertical enamel fold on their labial slope, and are well separated by a strong centrocrista. A low, sharp preparacrista curves anterolabially onto a moderately-developed and rounded parastylar salient. The postmetacrista is crestiform and curves posterolabially quite abruptly to a small metastylar salient. The conules are strong and subequal in size and height. The paraconule is positioned further lingually than the metaconule. The postparaconule crista is continuous with a variably-developed enamel fold on the lingual face of the paracone. The protocone is the largest cusp on the crown, slightly shorter than the paracone, when unworn, and subcrescentic. The apex is positioned lingual to the paracone and becomes flat with wear. Pre- and postprotocristae are well-developed. The hypocone is a small, conical cusp situated posteriorly and slightly lingual to the protoconal apex. A small pericone is invariably present on the precingulum directly anterior to the hypocone. On UALVP 23884 the pericone is almost as large as the hypocone.

The ectocingulum is relatively well-developed with a shallow ectoflexus. The paracingulum curves labially onto the parastylar salient and is terminated by the preparacrista. The metacingulum curves posterolabially around the posterior base of the crestiform postmetacrista. The precingulum is relatively strong and extends along the anterior base of the crown from the paraconule to the pericone. The postcingulum is slightly wider than the precingulum and extends further labially to a point under the metaconule.

M2. -- Morphologically M2 is similar to M1 and differs in the following: the crown is smaller, relatively more transverse, and is positioned further labially in the maxillary than M1; the vertical enamel fold on the labial slope of the paracone and metacone, and on the lingual slope of the paracone, are more pronounced; the parastylar and metastylar salients are slightly more reduced; the ectoflexus is slightly deeper; the paraconule is more lingual in position; the hypocone is relatively larger and the pericone and precingulum smaller (Fig. 13 C).

M3. -- Compared to M2, M3 is significantly reduced in size. The posterolabial corner of the crown is reduced such that the metacone is less than one-quarter the size of the paracone. A metastylar salient is absent and the ectocingulum is incomplete around the posterolabial base of the metacone. A metaconule is present but reduced in size. A pericone and hypocone are absent from the reduced, narrow pre- and postcingula, respectively. The paracone retains a preparacrista extending onto a well-developed, anterolabially projecting parastylar salient. The centrocrista is present but reduced. Labially and lingually the slopes of the paracone retain vertical enamel folds, the latter being continuous with the postparaconule crista.

## DISCUSSION

Novacek, et al. (1985) provide a good working definition of the Erinaceidae based on Krishtalka (1976a, 1977) and Butler (1948). On the basis of this definition Hadrolestes bounites, new genus and species, is identified as an erinaceid. Hadrolestes differs from other primitive erinaceid genera in the characters outlined in the diagnosis above and shares the following: 1) a posterior reduction in the size of the lower molars from m1-3; 2) in occlusal view the lower molars are semirectangular; 3) lower molars show labial exodaenodonty; 4) the talonid basin on the lower molars is a V-shaped valley formed by the flat internal walls of the anteroposteriorly elongate hypoconid and entoconid; 5) m1 paraconid is cuspate and anteriorly salient; 6) hypoconulids on m1-2 are reduced and situated lingual to the midline of the crown; 7) M1-2 are semirectangular in occlusal view; and 8) M3 is markedly reduced and "oval" in outline.

The specimens from Swan Hills site 1 referred above as canines are virtually identical in morphology to the tooth immediately posterior to i3 in Litolestes ignotus (seen on PU 14333 and described by Schwartz and Krishtalka as a "premolariform canine" [1976: pp. 3 and 5, fig. 1-3]). An alternative interpretation was offered by Schwartz and Krishtalka that the "premolariform canine" of L. ignotus could "equally and more parsimoniously" be interpreted as p1 (1976, p. 2). In keeping with traditional views the above described specimens are considered to be canines; however, future discoveries could negate this interpretation.

The identification of the above teeth as premolariform canines of Hadrolestes is based on size and frequency data, their similarity to those of Litolestes ignotus, and data obtained from the examination of alveoli present in dentary fragments preserving this area of the jaw. Three dentary fragments preserving p2 and p3, UALVP 22226, 22236, and 22688, also preserve the alveoli for p1 and the canine. The canine alveolus is not vertical but descends into the dentary at a posteroventrally directed angle of approximately 60 ° from horizontal. The size of the alveolus indicates the canine was reduced in size and as large as, or slightly larger than p2. The roots preserved on the referred canines match the alveoli for size and when positioned in the dentary the crown would be anteriorly procumbent and oriented like that seen on PU 14333. The data thus seem to support the referral of these specimens to Hadrolestes as premolariform canines; however, pending collection of dentary fragments preserving the canine, the referral of the above teeth of necessity must remain tentative.

A single isolated specimen, UALVP 22707, is here tentatively referred to Hadrolestes as a left p1. The size of the root preserved on UALVP 22707 matches alveoli on numerous specimens of Hadrolestes preserving the alveolus for p1 (e.g., UALVP 22226). The preserved alveoli indicate p1 was single-rooted and smaller in size than either p2 or the canine. UALVP 22707 thus fills these criteria. Morphologically, UALVP 22707 resembles p2 but is more similar to the canine.

An isolated P3, UALVP 23880, is tentatively referred to Hadrolestes. In general morphology it resembles P3 of Litolestes; however, it differs in possessing a more lingually positioned protocone, a more posteriorly projecting metastylar salient, and a metacone. As on P4, the metacone is small and poorly differentiated from the crista extending posteriorly from the paracone. The posterolabial alveolus for P3 and a portion of the alveolus for the lingual root are preserved on UALVP 23886, a maxillary fragment of Hadrolestes preserving P4-M2. The spacing of the alveoli in the maxillary fragment could easily accomodate the roots preserved on UALVP 23880. The size of the roots on UALVP 23880 are slightly smaller than expected for the alveoli on UALVP 23886; however, given the relatively high degree of morphological variation observed in premolars of Hadrolestes, I do not feel a small size discrepancy to be a problem here. It is indeed possible that UALVP 23880 does not represent P3 of Hadrolestes, but given current data the referral is tenable.

Among primitive erinaceids upper dentitions were previously known only for Litolestes, Adapisorex, and Neomatronella. In general morphology, P4's of Hadrolestes are close to those of Litolestes and differ in being relatively much lower crowned, bulbous, and in possessing a poorly differentiated metacone. The metacone on the P4 of Neomatronella is poorly differentiated from the crest extending onto the metastylar salient from the paracone as in Hadrolestes. However, unlike in Hadrolestes, Litolestes, and Adapisorex, Neomatronella P4's possess hypocones, a character considered diagnostic for the Erinaceomorpha by Novacek, et al. (1985, p. 3). P4 of Hadrolestes has rugose enamel, thus resembling Adapisorex P4's in this character. In contrast to those of Hadrolestes, the metacone on P4 of Adapisorex is relatively well-developed and clearly differentiated on the paracone/metastylar crest.

Two isolated specimens, UALVP 22499 and 23881, are tentatively referred to Hadrolestes as deciduous P4's. The single complete specimen, UALVP 22499, is similar to the permanent M1 in size and the following characters: 1) the paracone is the tallest cusp on the crown; 2) the metacone is smaller in size and shorter than the paracone; 3) conules are strong and subequal in size and height; 4) parastylar salients are not greatly expanded; 5) the postmetacrista is crestiform and curves posterolabially onto a small metastylar salient; 6) the protocone is subcrescentic with well-developed pre- and postprotocristae; 7) hypocones are small and conical; 8) precingula are present; 9) a strong postcingulum is present and extends further lingually than the precingulum; and 10) strong para- and metacingula are developed. In occlusal view, the crown of UALVP 22499 appears very different from the crown of permanent M1's. The labial portion of the crown is greatly anteroposteriorly elongate and the hypocone is elongate posterolingually beyond the protocone. This produces a somewhat triangular occlusal outline in contrast to the semirectangular outline of the permanent M1. Deciduous P4's also differ from their permanent replacements in having a smaller metacone relative to the paracone, conules that are more nearly conical, ectocingula that are incomplete around the posterolabial base of the paracone, and paracingula continuous with the ectocingula.

Upper molars of *Hadrolestes* and *Litolestes* are very similar in morphology and differ in only a few characters as outlined in the diagnosis above. In both of these genera, the hypocones are smaller than other erinaceids. Contrary to the diagnosis of the Erinaceidae provided by Novacek, *et al*., the hypocones of these genera are smaller than all described dormaaliids and not "better developed on M1-2 than in dormaaliids" (1985, p. 10). In addition, although *Adapisorex* possesses relatively well-developed hypocones on M1-2, the hypocones of *Adapisorex* are not better developed than the condition observed on the dormaaliids *Macrocranion* or *Scenopagus*. As I understand it, for a character to be considered diagnostic it should clearly differentiate two closely related taxa from each other. As stated by Novacek, *et al*. (1985), the possession by erinaceids of a better developed hypocone on M1-2 than dormaaliids is incorrect and is here not considered a character that is diagnostic for erinaceids.

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The phylogenetic propinquity of *Hadrolestes* seems to be with *Litolestes*. The upper and lower molars possess a number of synapomorphic characters in common and differ in only a few characters as outlined above. As well, *Hadrolestes* also resembles *Litolestes* in the possession of a premolariform canine and p4. What clearly differentiates the two genera is the possession by *Hadrolestes* of characters of the premolars that are clearly apomorphic in comparison to *Litolestes*. In contrast to those of *Litolestes*, p2 and p3 are nearly erect in *Hadrolestes* and are much lower crowned with a more bulbous protoconid. The p4 protoconid of *Hadrolestes* is erect and much lower crowned and bulbous than in *Litolestes*, and the paraconid is positioned lower on the crown and clearly separated from the protoconid. The paracone of P4 is likewise much lower crowned and bulbous than what is observed on *Litolestes*. Unlike P4 of *Litolestes*, the enamel on the crown of P4 in

Hadrolestes is slightly rugose. These differences seem to point towards the development of more of an emphasis on crushing in Hadrolestes than is seen in Litolestes. Clearly, these differences warrant a generic separation of the two and suggest a divergence of the two lineages at least during the early Tiffanian.

Several specimens from a late Tiffanian horizon of the Ravenscrag Formation near the town of Roche Percée, Saskatchewan, are virtually identical to specimens from Swan Hills site 1 referred to Hadrolestes bounites (pers. observ.). These specimens are currently under study by D. W. Krause and R. C. Fox and will be described elsewhere.

ERINACEIDAE, unidentified genus and species

(Fig. 13 D-F; Table 7)

Referred specimens. -- p4: UALVP 22679-22681; m2: UALVP 22688, 23895, 23896; m3: UALVP 23897; dentary fragment with base of crown for p3, p4, talonid of m1, and m2: UALVP 22684; dentary fragment with talonid of m1, and m2: UALVP 22686, 23888; dentary fragment with m2-m3: ROM 05618.

Locality. -- Swan Hills site 1, Paskapoo Formation, Alberta.

## DESCRIPTION

p4. -- The p4's referred here are semimolariform and possess anteriorly canted trigonids (Fig. 13 D). The paraconid and metaconid are conical, relatively bulbous, and approximately equal in size. The paraconid is positioned slightly below the level of the metaconid on the anterolingual base

Table 7: Measurements and descriptive statistics of the dentition of Erinaceidae, unidentified genus and species, Swan Hills local fauna, Alberta.

| Measurement | | N | OR | M±SE | SD | CV |
|---|---|---|---|---|---|---|
| p4 | L | 3 | 1.3-1.4 | 1.33 ± .03 | .058 | 4.3 |
| | W | 3 | 0.8-0.9 | 0.87 ± .03 | .058 | 6.7 |
| m2 | L | 6 | 1.3-1.4 | 1.37 ± .02 | .052 | 3.8 |
| | W | 6 | 0.9-1.0 | 0.98 ± .02 | .041 | 4.2 |
| m3 | L | 2 | 1.3 | - | - | - |
| | W | 2 | 0.8 | - | - | - |

of the protoconid and is not as closely appressed to the protoconid as the metaconid. The apex of the metaconid is oriented lingual to the protoconid apex at approximately one-half of the way up the posterolingual edge of the protoconid. The two-cusped talonid is just under one-half of the crown length, and the talonid basin occupies slightly less than one-half of the transverse width of the talonid. The cristid obliqua and entocristid are roughly parallel to each other and are terminated posteriorly by a small hypoconid and entoconid, respectively. The hypoconid is slightly larger than the latter. The talonid of the p4 preserved on UALVP 22684 is incomplete posteriorly; however, length comparisons between it and what is preserved of m1 on UALVP 22684 indicates that p4 was smaller than m1. Comparisons between isolated p4's and UALVP 22686, a dentary fragment preserving m2 plus the talonid and base of the crown below the trigonid for m1, also indicates that p4 was smaller than m1.

m1. -- Trigonids of m1's are not preserved. Talonids possess V-shaped basins formed by the flattened internal walls of the hypoconid and entoconid (Fig. 13 F). Both cusps are somewhat anteroposteriorly elongate with the entoconid being the taller of the two. The hypoconulid is a small, though well-defined cusp located lingual to the anteroposterior midline of the crown. What is preserved of the entocristid shows it to have been relatively high. In occlusal view the posterior edge of the talonid is nearly straight.

m2. -- Comparisons of m2 to what is preserved of m1 shows m2 to have been smaller than m1 (Fig. 13 F). The low trigonid is dominated by the relatively bulbous protoconid and metaconid, which are subequal in size and height. The somewhat cuspate paraconid is small, relatively well-separated from the metaconid, positioned slightly medial to the centre of the metaconid, and incorporated into an anteroposteriorly compressed, anteriorly procumbent transverse ridge. The talonid is as wide and long as the trigonid. Morphologically, it is identical to the m1 talonid in structure, being only relatively smaller and lower crowned. As on m1, the hypoconid wears flat. The cristid obliqua joins the posterior wall of the trigonid below the ventral apex of the protocristid forming a moderately deep hypoflexid. The entocristid is relatively high, closing the talonid basin lingually. Anteriorly on the base of the crown below the paraconid is a narrow, though strong precingulid. A weak postcingulid extends a short distance ventrolabially from the base of the hypoconulid.

m3. -- m3 is the smallest of the lower molars (Fig. 13 E). The trigonid morphology is virtually identical to m2 and differs only in being smaller and possessing relatively less robust proto- and metaconids. The talonid is slightly narrower than the trigonid and elongate due to the lingually positioned, posteriorly projecting hypoconulid. The talonids of the two referred m3's (UALVP 23897 and ROM 05618) are extremely worn and wear obscures the structure of the entoconid, hypoconid, entocristid, and talonid basin. As on m2, the cristid obliqua joins the posterior trigonid wall below the ventral apex of the protocristid. A precingulid is present anteriorly and a very weak postcingulid is present between the hypoconid and hypoconulid.

## DISCUSSION

This unidentified erinaceid, which is approximately 8 to 10% smaller in size than Litolestes and Leipsanolestes and 10 to 15% larger than

Hadrolestes, new genus, may represent [illegible] new species closely related to Leipsanolestes. It is identified as an erinaceid (sensu Novacek, et al., 1985) on the basis of the following characters: a progressive reduction in size of molars posteriorly; the lower molars are semirectangular in occlusal view and exhibit a degree of labial exodaenodonty; the possession of a V-shaped talonid basin formed by flat internal walls of the entoconid and hypoconid; and the presence of reduced hypoconulids positioned lingual to the midline of the crown on the posterior wall of the talonid. The trigonid of m1 has not as yet been identified and it is unknown whether the paraconid was similar in form to other described erinaceids; however, judging from the development of the paraconids on m2 and m3, the paraconid on m1 was conceivably erinaceid in nature.

The p4 of this unidentified genus and species differs from p4's of Litolestes and resembles those of Leipsanolestes in being semimolariform rather than premolariform, in possessing a paraconid sitting lower than the metaconid on the anterolingual base of the crown, having a relatively longer talonid, a wider talonid basin, an entocristid that is approximately parallel to the cristid obliqua, and two talonid cusps. It differs from p4 of Leipsanolestes in having a slightly transversely narrower talonid basin. The p4's referred above differ from p4's of Adapisorex in having a much better developed paraconid, from Eolestes and Entomolestes in being higher crowned relative to m1 and m2, in having longer talonids, and from Dartonius in being higher crowned, in having a relatively shorter talonid, and in possessing a less anteriorly salient paraconid.

The decrease in size of the molars posteriorly is less than seen in Litolestes and other referred erinaceids (especially Cedrocherus), and more like the condition seen in Leipsanolestes. Compared to the type of Leipsanolestes, AMNH 22157 (illustrated in Novacek, et al., 1985: p. 14, fig.'s

8 and 9), the referred molars are very similar and differ in having a slightly larger and more lingually placed hypoconulid, and having a less posteriorly projecting hypoconulid on m3. In comparison to the condition seen on lower molars of ~~other~~ erinaceids, the hypoconulids are more lingually positioned than what is observed in Adapisorex, less lingual than in Eolestes, and much like the condition seen in Dartonius, Entomolestes, Litolestes, Hadrolestes, and Cedrocherus.

The structure of the above described p4's and the conservative decrease in molar size posteriorly seems to align this species more closely with Leipsanolestes than other known erinaceids. The differences in size and morphology separate it from Leipsanolestes siegfriedti, however. This suggests that the sample from Swan Hills site 1 may represent a new undescribed species of erinaceid. Unfortunately, although the samples of Hadrolestes bounites and Diacocherus, cf. D. meizon from the Swan Hills are relatively large, the sample referred here is small and precludes the proper formal identification and diagnosis of a new species. Until a larger sample can be procured and the affinities of this species better delineated, the referral to the Erinaceidae as an unidentified genus and species is considered the most prudent choice.

L. S. Russell (1967) tentatively referred ROM 05618, a dentary fragment from site 1 preserving m2-3, to Leptacodon tener. The talonids of these molars exhibit extreme wear; however, enough of the trigonid detail is preserved to refer this specimen along with others from site 1 to the above unidentified species. Another dentary fragment from site 1, preserving the talonid of m1 and a complete m2 (UALVP 23888) is virtually identical in size and general morphology to specimens referred above. It differs in possessing a slightly more anteriorly procumbent paraconid and the development of a small mesoconid on the cristid obliqua. Given the small sample size, it is unknown whether these differences are significant or represent individual variation within a single population. The collection of further specimens from Swan Hills site 1 will ultimately clarify its relationships. In the interim UALVP 23888 is tentatively referred with the above described sample.

ERINACEOMORPHA, _incertae sedis_

Genus _Litocherus_ GINGERICH, 1983

_Litocherus lacunatus_ (GAZIN, 1956)

(Fig. 13 G, 14 A)

_Referred specimens_. -- Left p3: UALVP 23850; labial fragment of left m2: UALVP 23849; talonid of right m3: UALVP 23848; left dentary fragment with m1-m2: ROM 05631.

_Locality_. -- Swan Hills site 1, Paskapoo Formation, Alberta.

_Known distribution_. -- Swan Hills site 1, Paskapoo Formation, Alberta; _Titanoides_ and West End localities, Fort Union Formation, Bighorn Basin, Wyoming (Gazin, 1956); localities V-77005 and V-77059, eastern Rock Springs Uplift, Fort Union Formation, Wyoming (Winterfeld, 1982); Battle Mountain, Hoback Formation, Wyoming (Gingerich, 1983); Type Chappo, "Wasatch" Formation, Wyoming (Gingerich, 1983); Brisbane and Judson localities, Tongue River Formation, North Dakota (Holtzman, 1978); Roche Percée local fauna, Ravenscrag Formation, Saskatchewan (Fox, in press); and questionably at locality V-82004, Bighorn Basin, Polecat Bench Formation, Wyoming (Hartman, 1986).

# DISCUSSION

The sample referred to Litocherus lacunatus from Swan Hills site 1 is extremely small (N=4) and does not significantly differ from samples described elsewhere; thus, description here is considered unnecessary. Descriptions of L. lacunatus can be found in Gazin (1956), Holtzman (1978), and Gingerich (1983).

Jepsen (1930) erected Litolestes with L. ignotus as the type and referred the genus with a query to the Insectivora. Simpson (1936) described "Litolestes" notissimus and referred the genus to the Condylarthra as an hyopsodontid, a move subsequently followed by Gazin (1956) with his description of "Litolestes" lacunatus. Van Valen (1967) placed the three species of Litolestes back in the Insectivora as creotarsine adapisoricids without explanation. Later, Krishtalka described Litolestes ignotus as an erinaceid, while stating "the affinities of L. notissimus and L. lacunatus are not as clear" (1976a, p. 28). He noted that the latter two "superficially resemble hyoposodontids [sic.]" (1976a, p. 29). Following suggestions made by D. E. Russell, et al. (1975), who retained Litolestes in the Adapisoricidae, Gingerich (1983) removed "L." notissimus and "L." lacunatus from Litolestes and placed them in a new genus, Litocherus, used as the type for a new subfamily of the Adapisoricidae. Included in the Litocherinae were his new genera Cedrocherus and Diacocherus ( including "Diacodon" minutus), plus Litolestes Jepsen, Mckennatherium Van Valen, and Leipsanolestes Simpson.

Recently, Novacek (1982) and Bown and Schankler (1982) have proposed the use of Dormaaliidae in place of Adapisoricidae (Adapisorex Lemoine, the type genus for the Adapisoricidae, is probably an erinaceid and therefore is unavailable). Novacek, *et al.* (1985) diagnosed the Dormaaliidae and emended the diagnosis for the Erinaceidae. Contrary to Gingerich (1983), Novacek, *et al.* (1985) considered *Litolestes*, *Leipsanolestes*, and *Cedrocherus* to be erinaceids and referred *Diacocherus*, *Mckennatherium* (as a junior synonym of *Adunator*), and *Litocherus* to the Erinaceomorpha, *incertae sedis*. The latter authors considered the erection of *Litocherus* to be warranted; however, they did not support the creation of the Litocherinae on the basis that "the definition of Litocherinae does not successfully account for its included taxa nor does it effectively eliminate more plausible alternate relationships...and that a special association between *Litocherus* and *Diacocherus* is unwarranted" (1985, p. 18).

*Litocherus* shares a number of features with members of the Erinaceidae as defined by Novacek, *et al.* (1985, p. 10), including: a reduction in size of lower molars from m1 to m3, semirectangular lower molars in occlusal view, a degree of labial exodaenodonty, a V-shaped talonid basin produced by flat internal hypoconid and entoconid walls, an m1 paraconid that is salient and anteriorly projecting, reduced hypoconulids positioned at or just lingual to the midline of the crown, and where known M1 and M2 are semirectangular in occlusal view.

Compared to known erinaceids, *Litocherus* differs in possessing more bulbous cusps on m1-3, and molar trigonids that are relatively lower in relation to the talonid height and more nearly vertical (less anterior cant to the postvallid). In addition, the paraconid on m1 is generally less anteriorly projecting and on m2-3 is more reduced and shelf-like (can be absent on m2 of *L. lacunatus*). The M3 in *Litocherus*, as compared to described erinaceid M3's, is not as markedly reduced, nor oval in outline, and the molar hypocones are not connected by a crest to the postprotocrista (although the latter character is variably developed in members of the Erinaceidae *sensu*

Novacek, et al. [1985] and certainly is absent on upper molars of Litolestes, Adapisorex, and Hadrolestes). In view of the differences noted above between the dentitions of Litocherus and described erinaceids, Litocherus is here considered to be better referred to the Erinaceomorpha, incertae sedis following Novacek, et al. (1985).

The single best preserved specimen of Litocherus lacunatus from Swan Hills site 1, ROM 05631, was originally described by L. S. Russell (1967) as an unidentified genus and species of ?Oxyclaeninae. Subsequently, ROM 05631 was made the type of a new species of hyopsodontid condylarth, Litomylus (?) alphamon, by Van Valen (1978). In his diagnosis Van Valen noted that the size ratio of m1 and m2 suggested "Adapisoricidae", but the crown morphology was "hyopsodontine" (1978, p. 60). Recently Gingerich (1986) examined a cast of ROM 05631 and correctly identified it as belonging to Litocherus lacunatus.

A relatively large, well-preserved sample from a late Tiffanian horizon of the Ravenscrag Formation near the town of Roche Percée, Saskatchewan, is referable to Litocherus lacunatus (pers. observ.; Fox, in press). These specimens are currently under study by D. W. Krause and R. C. Fox and will be described elsewhere.

### cf. Litocherus notissimus (SIMPSON, 1936)

(Fig. 13 H)

Referred specimen. -- M1: UALVP 23887.

Locality. -- Swan Hills site 1, Paskapoo Formation, Alberta.

# DISCUSSION

Litocherus notissimus was originally described from the early Tiffanian Scarritt Quarry (Crazy Mountain Basin, Montana) as a species of Litolestes by Simpson (1936), who considered it to be a hyopsodontid condylarth. It was subsequently put in the Insectivora as a creotarsine adapisoricid, as an erinaceid with unclear affinities, and again as an adapisoricid by various authors (see discussion for Litocherus lacunatus). Recently "Litolestes" notissimus was transferred by Gingerich (1983) to a new genus, Litocherus, as an "adapisoricid"; however, Novacek, et al. (1985) consider Litocherus to be better included in the Insectivora as Erinaceomorpha, incertae sedis, a view supported here (see discussion above). Complete descriptions of Litocherus notissimus may be found in Simpson (1936, 1937b).

The single specimen referred here from Swan Hills site 1 (UALVP 23887) is an isolated lingual half of a left M1. In size and morphology it is virtually indistinguishable from Scarritt Quarry specimens of M1 referred to Litocherus notissimus. UALVP 23887 possesses well-developed conules, a precingulum, and a strong postcingulum with a small hypocone positioned directly posterior to the protocone. This specimen is too small to represent M1 of L. lacunatus and is significantly larger than other erinaceomorphs present in the Swan Hills local fauna. Until further specimens are collected this referral remains tentative.

## Genus Diacocherus GINGERICH, 1983

### Diacocherus, cf. D. meizon GINGERICH, 1983

(Fig. 13 I, 14 B-K, 15 A; Table 8)

Referred specimens. -- p2: UALVP 23860; p3: UALVP 23856; p4: UALVP 22662-22664, 23854; m1: UALVP 22247, 22249, 22250, 22442, 22644, 22660, 22661, 23853, 23855; m2: ROM 05620, UALVP 22476, 22478, 22503, 22665, 23843-23845; m3: ROM 05616, 05617; UALVP 22323, 22666-22668, 23846, 23852; dentary fragment with p2-p3: UALVP 23859; dentary fragment with posterior half of p4 and m1: UALVP 22251; dentary fragment with talonid of m1 and m2: UALVP 22337; dentary fragment with m2-m3: UALVP 23847; P3: UALVP 23857; P4: UALVP 22328, 22333, 22336, 22341, 22655, 23858, 23861; M1: UALVP 22451-22453, 22456, 22457, 22459-22461, 22466, 22479, 22481, 22483-22486, 22490, 22656, 22657; M2: UALVP 22446, 22447, 22462, 22507, 22511, 22658, 22659; M3: UALVP 22458, 23851; maxillary fragment with M2-M3: UALVP 22331.

Locality. -- Swan Hills site 1 and 2, Paskapoo Formation, Alberta.

## DESCRIPTION

p2. -- The double-rooted p2 is premolariform with an anteriorly procumbent protoconid that is laterally compressed and overhangs the anterior root (Fig. 14 C). In occlusal view the crown is shaped like an elongate tear-drop with the single-cusped talonid at the base. A weak cristid extends posteriorly from the apex of the protoconid to the relatively large cusp on the heel. Anteriorly, a relatively broad cristid extends from the protoconid apex ventrolingually to a swelling at the anterolingual base of the protoconid. This

Table 8: Measurements and descriptive statistics of the dentition of Diacocherus, cf. D. meizon, Swan Hills local fauna, Alberta.

| Measurement | | N | OR | M±SE | SD | CV |
|---|---|---|---|---|---|---|
| p2 | L | 2 | 1.5 | - | - | - |
| | W | 2 | 0.6 | - | - | - |
| p3 | L | 2 | 1.8-1.9 | 1.85 ± .05 | .071 | 3.8 |
| | W | 2 | 0.8 | - | - | - |
| p4 | L | 2 | 1.5 | - | - | - |
| | W | 3 | 0.8-0.9 | 0.83 ± .03 | .058 | 6.9 |
| m1 | L | 4 | 1.7-1.8 | 1.78 ± .03 | .050 | 2.8 |
| | W | 7 | 1.2-1.3 | 1.23 ± .02 | .049 | 4.0 |
| m2 | L | 7 | 1.8-2.0 | 1.87 ± .03 | .076 | 4.0 |
| | W | 8 | 1.3-1.5 | 1.41 ± .02 | .064 | 4.5 |
| m3 | L | 5 | 1.7-1.8 | 1.76 ± .02 | .055 | 3.1 |
| | W | 6 | 1.1-1.3 | 1.20 ± .03 | .063 | 5.3 |
| P3 | L | 1 | 1.7 | - | - | - |
| | W | 1 | 1.2 | - | - | - |
| P4 | L | 3 | 1.6-1.7 | 1.67 ± .03 | .058 | 3.5 |
| | W | 4 | 1.8-2.0 | 1.88 ± .05 | .096 | 5.1 |
| M1 | L | 7 | 1.7-1.9 | 1.80 ± .02 | .058 | 3.2 |
| | W | 4 | 2.3-2.4 | 2.33 ± .03 | .050 | 2.2 |
| M2 | L | 1 | 1.8 | - | - | - |
| | W | 3 | 2.6-2.7 | 2.67 ± .03 | .058 | 2.2 |
| M3 | L | 2 | 1.3-1.4 | 1.35 ± .05 | .071 | 5.2 |
| | W | 2 | 1.9 | - | - | - |

region on the two referred specimens, UALVP 23860 (an isolated right p2) and UALVP 23859 (a left dentary fragment preserving p2-3), is worn and obscures the possible presence of a paraconid.

p3. -- The two referred specimens, one present on a dentary fragment with p2 (UALVP 23859; Fig. 14 C), are similar in morphology to p2. They differ in being larger, possessing a relatively better developed, single-cusped talonid, being less anteriorly procumbent, and in having a small, though well-developed paraconid on the anterolingual base of the protoconid.

p4. -- The trigonid of the semimolariform p4 has a slight anterior cant to it and is dominated by the large conical protoconid (Fig. 13 I, 14 B). The metaconid is well-developed, conical, approximately one-half the size of the protoconid, and situated posterolingually a little below the apex of the protoconid. The relatively large, conical paraconid is positioned well below the metaconid on the anterolingual base of the protoconid. The talonid is almost as wide and as long as the trigonid, and possesses three small, subconical cusps. The entoconid is the tallest cusp on the talonid. The hypoconulid is situated lingual to the midline of the tooth and may be weakly-developed (e.g., UALVP 22662, a dentary fragment showing p4 to be in the process of erupting) or relatively well-developed (e.g., UALVP 22663). The talonid basin is comparatively deep and the cristid obliqua joins the posterior wall of the trigonid below and slightly lingual to the protocristid notch, producing a fairly deep hypofexid. The beginnings of a small precingulid is present on the anterolabial base of the crown.

m1. -- The trigonid, as on p4 and m2-3, is canted slightly anteriorly (Fig.

14 E). The metaconid is slightly larger than, and subequal in height to the protoconid. The paraconid is a reduced cusp that is continuous with the paracristid and positioned anterior to, and closely appressed to the base of the metaconid. In essence it is lophid-like and fairly procumbent The talonid possesses an entoconid that is smaller and taller than the hypoconid, and a strong hypoconulid that is positioned slightly lingual to the middle of the crown. The moderately deep talonid basin is rounded and closed lingually by the entocristid and labially by the cristid obliqua, which joins the posterior trigonid wall below, or, below and slightly lingual to the ventral apex of the protocristid notch. The talonid is wider and longer than the trigonid. The precingulid is continuous with a weak labial cingulid that extends posterolabially around the base of the protoconid. A faint postcingulid is present posteriorly.

m2. -- m2 differs from m1 in being slightly larger, possessing a paraconid that is further reduced and shelf-like, more labially positioned, and located higher and more closely appressed to the metaconid; the metaconid is slightly larger in size relative to the protoconid; and the talonid is slightly smaller than, or approximately equal to the trigonid in width, and more elongate than on m1 (Fig. 14 D).

m3. -- The m3 is the smallest of the lower molars, but has the longest talonid relative to the length of the trigonid due to the enlarged, posteriorly projecting hypoconulid (Fig. 14 F). The paraconid is similar in development to m2. The size of the metaconid relative to the protoconid is more similar to the condition observed on m1. The m3 also differs from m1 and m2 in possessing a better developed labial cingulid around the base of the protoconid.

P3. -- The single referred P3, UALVP 23857 (Fig. 14 H), is damaged anterolabially around the base of the paracone; thus, a parastyle like that preserved on PU 14371, a left maxilla of D. minutus preserving P3-M3 (illustrated by Gingerich, 1983: p. 240, fig. 4), is not identifiable. A sharp centrocrista connects the large conical paracone posteriorly to a well-developed metacone. The apices of the latter two cusps are relatively quite sharp. The metacone is better separated from the paracone than on P4 and is approximately one-half the size and height of the paracone. The postmetacrista is sharp, crest-like, and curves slightly posterolabially to a strong metastylar salient. The protocone is small, conical, and positioned lingual to the paracone.

P4. -- P4's are semimolariform with three relatively large, conical cusps (Fig. 14 I). The paracone and metacone are closely appressed. The much smaller metacone is approximately two-thirds the height of the paracone. Between the apices of the paracone and metacone is a sharp centrocrista. In lateral view the protocone, which is opposite the paracone lingually, appears to be strongly canted labially. The protocone is a relatively robust cusp and two-thirds the height of the paracone. Anterior to the paracone is a small, conical parastyle. A well-defined postmetacrista extends posteriorly from the apex of the metacone to an incipiently developed metastyle. The ectocingulum is weak. A well-defined postcingulum continues labially around the base of the metacone and is terminated by the postmetacrista. Unlike the preprotocrista, which extends anterolabially towards the parastyle, the postprotocrista descends almost vertically along the posterolabial surface of the protocone to fade before reaching the postcingulum.

M1. -- In occlusal view M1 is somewhat transverse with the anterior and posterior margins slightly inflected in the area of the conules (Fig. 14 J). The parcone and metacone are subequal in size and height and are moderately tall. Whereas the centrocrista and postmetacrista are relatively well-developed, the preparacrista is absent. The postmetacrista extends anterolabially to a small metastylar salient. The parastylar salient is also small and positioned almost directly anterior to the paracone. The protocone is the most robust cusp on the crown, is subcrescentic, and approximately three-quarters the height of the paracone and metacone. A small, though well-defined, conical hypocone is present on the base of the protocone, anterior and slightly lingual to the protoconal apex, which leans labially in lateral profile. The hypocone is present on a strong postcingulum. Conules are well-developed with the paraconule being the slightly larger of the two and placed further lingually. The trigon basin is moderately deep. A narrow precingulum is present on the anterior base of the crown and extends from a point below the paraconule apex to a point below and just lingual to the protoconal apex. The paracingulum is continuous with the narrow ectocingulum and the metacingulum is interupted by the postmetacrista extending onto the metastylar salient. The labial edge of the crown possesses a shallow ectoflexus.

M2. -- M2 resembles M1 and differs primarily in being larger and more transverse (Fig. 14 K, 15 A). In addition, the hypocone is larger, the ectocingulum is relatively better developed, the metastylar area, already relatively small on M1, is further reduced, and the paracone possesses a weak preparacrista extending onto a slightly better developed parastylar salient.

M3. -- The posterolabial corner of M3 is greatly reduced with the metacone diminished to approximately one-third the size and height of the paracone. The ectocingulum is narrow and discontinuous around the posterolabial base of the metacone. A metastyle is absent. A metaconule is present but reduced. A hypocone and pre- and postcingula are absent.

## DISCUSSION

Diacocherus meizon, known from the middle Tiffanian Cedar Point Quarry of the Bighorn Basin, Wyoming, is based on a small sample of lower dentitions (Gingerich, 1983). Gingerich proposed Diacocherus with "Diacodon" minutus Jepsen (1930) as the type species and included the genus in a new subfamily, Litocherinae, within the Adapisoricidae (1983, p. 238). "Diacodon" minutus has had a checkered existence and its affinities are not well understood (for discussions see, for example, Krishtalka, 1976a; Winterfeld, 1982; Novacek, 1982; Novacek, et al., 1985; and others). For reasons alluded to in the above discussion for Litocherus, and discussed in depth by Novacek (1982) and Novacek, et al. (1985), the phylogenetic propinquity of Diacocherus (including "Diacodon" minutus) to other erinaceomorphs is currently problematic and Diacocherus is best left as Erinaceomorpha, incertae sedis.

In size and general morphology the sample of lower dentitions from the Swan Hills very favorably compares with Diacocherus meizon. The specimens from site 1 share with D. meizon a large suite of characters including the possession of an m2 that is equal or larger than the m1 in size, having a reduced, elevated paraconid appressed to the metaconid on m2 and m3, and in possessing a paraconid on p4 which is well below the level of the metaconid (Gingerich, 1983). *Diacocherus*, cf. *D. meizon* from Swan Hills differs from *D. meizon* in having the paraconid on p4 positioned more lingually and closer to the protoconid, the talonid on p4 possesses an hypoconulid, and the hypoflexid is relatively deeper due to a slightly more lingual joining of the cristid obliqua with the posterior trigonid wall. An examination of a good cast of the type for *D. meizon* (UM 82023) shows the paraconid on m1-m3 in *Diacocherus*, cf. *D. meizon* to be relatively more reduced and appressed to the metaconid, and the talonid on m3 to be relatively wider. The Swan Hills sample also differs in possessing weak labial cingulids around the base of the protoconid on m1-m3.

The above differences may be the result of biases due to the small sample size from Cedar Point Quarry and may not be significant. They may also be indicative of a slightly more primitive population of *Diacocherus meizon* being present in the Swan Hills during the late Tiffanian (as indicated by the p4 morphology; see Clemens [1973] for discussion), or alternatively, the presence of a new species of *Diacocherus* closely related to *D. meizon*. Until *D. meizon* from the type locality is better known, a more definite referral of the Swan Hills sample is deferred.

Two specimens from Swan Hills site 2, UALVP 23846, an isolated m3, and UALVP 23847, a left dentary fragment preserving m2-3, are virtually identical to specimens from site 1 referred to *Diacocherus*, cf. *D. meizon*. They differ in having the paraconid on m2 placed higher on the anterior wall of the metaconid, the talonid of m2 is slightly wider than the trigonid, the paraconid on m3 is slightly more labial in position, and the labial cingulid on m3 is stronger. Currently the significance of these differences is unknown and the above specimens are tentatively referred with the site 1 sample to *Diacocherus*, cf. *D. meizon*.

Upper dentitions of *Diacocherus meizon* are unknown. The sample of upper dentitions from Swan Hills site 1 are referred to *Diacocherus*, cf. *D. meizon* on the basis of size and frequency data, an examination of occlusal relationships with known lower dentitions, and similarities in general morphology to upper dentitions referred to *D. minutus* (e.g., Jepsen, 1930; Gingerich, 1983). As in *D. minutus*, the referred P3 and P4 of *Diacocherus*, cf. *D. meizon* possess a relatively large metacone, a diagnostic character which differentiates *Diacocherus* from other "litocherines" (Gingerich, 1983: p. 238). They differ from P3 and P4 of *D. minutus*, as do M1-M3, in being larger and relatively more robust. In addition, the Swan Hills sample differs from of *D. minutus* in having an M1 with the parastylar salient more reduced and lacking a preprotocrista, a slightly less transverse M2 with a shallower ectoflexus, and an M3 which is slightly less transverse and retains only a vestige of the small postcingulum seen on M3 of *D. minutus*.

Fox (in press) has recently identified *Diacocherus meizon* at the Canyon Ski Quarry near Red Deer, Alberta (late Tiffanian, Paskapoo Formation). In addition, a sample from a late Tiffanian horizon of the Ravenscrag Formation near the town of Roche Percée, Saskatchewan, is very similar to the sample from the Swan Hills local fauna here referred to *Diacocherus*, cf. *D. meizon* (pers. observ.; Fox, in press). These specimens are currently under study by D. W. Krause and R. C. Fox and will be described elsewhere.

L. S. Russell (1967) referred ROM 05620 to *Leptacodon tener* and ROM 05616 and 05617 to *Diacodon*, cf. *D. minutus*. These specimens are indistinguishable from specimens referred above to *Diacocherus*, cf. *D. meizon* and are here referred to the latter.

### Suborder SORICOMORPHA GREGORY, 1910

### Family NYCTITHERIIDAE SIMPSON, 1928

### Genus Nyctitherium MARSH, 1872

### Nyctitherium sp. 1

(Fig. 15 B)

Referred specimen. -- M1 or 2: UALVP 22468.

Locality. -- Swan Hills site 1, Paskapoo Formation, Alberta.

## DISCUSSION

The single referred specimen, UALVP 22468, is an isolated lingual half of an upper first or second molar. It is identified as a species of Nyctitherium by the presence of a well-developed hypoconal shelf and a hypocone, which, unlike the conical hypocone on M1-2 of Pontifactor West (1974), is slightly hooked or aquiline when viewed anterolingually. UALVP 22468 is approximately the size of M2 on N. serotinum (Marsh, 1872), slightly smaller than M1-2 of N. velox Marsh (1872), and much larger and less transverse than Limaconyssus sp. 1 from Swan Hills. It differs from both N. velox and N. serotinum in possessing a much narrower and shorter precingulum, a subconical metaconule, the hypocone is removed further posteriorly and not connected anterolingually to the base of the protocone (thus, resembling specimens of Saturninia Stehlin [1940], illustrated by Sigé [1976]), and the hypoconal shelf extends not as far labially. The protocone on UALVP 22468 resembles N. serotinum in being relatively lower crowned than N. velox. In comparison to the upper molars of Leptacodon tener Matthew and Granger

(1921), illustrated by McKenna (1968: p. 5, fig. 2), the hypoconal shelf on UALVP 22468 extends much further posteriorly, the precingulum is more reduced, the metaconule is more nearly conical and lacks a well-developed premetaconule crista, and the hypocone is larger, does not join with the posterolingual base of the protocone, and is aquiline is aspect.

The characters possessed by UALVP 22468 appear to be plesiomorphic relative to the condition observed on the upper molars of Eocene Nyctitherium. A structure like that observed on the upper molars of Nyctitherium can be obtained with an increase in the development of the hypoconal shelf, an increase in the size of the hypocone with a consequent joining of the hypocone to the base of the protocone, and an increase in the size of the precingulum. However, although UALVP 22468 probably represents a new species of Nyctitherium, further discussion of relationships must await the collection of a larger and more nearly complete sample from Swan Hills site 1.

### Nyctitherium sp. 2
(Fig. 15 C)

Referred specimen. -- M1 or 2: UALVP 22212.

Locality. -- Swan Hills site 1, Paskapoo Formation, Alberta.

## DISCUSSION

In general size of the crown and conules UALVP 22212, a lingual half of an M1 or M2, is similar to M1 of Nyctitherium velox. It differs from N. velox and N. serotinum in having a relatively taller protocone. As in Nyctitherium sp. 1 the hypocone is aquiline when viewed anterolingually, is not joined to the posterolingual edge of the protocone, and is removed slightly posteriorly from the base of the protocone. As well, the metaconule is more nearly conical than N. velox and N. serotinum and lacks a well-developed premetaconule crista. UALVP 22212 differs from the single specimen of Nyctitherium sp. 1 (UALVP 22468) in being slightly larger and much higher crowned, having a better-developed precingulum, and having a less expanded hypoconal shelf.

The possibility was entertained that UALVP 22212 and UALVP 22468 represent M1 and M2 of a single species; however, the disparity in hypoconal shelf development, height of the protocone, and precingulum development precludes such an interpretation. Another possibility is that UALVP 22468 may represent a molariform P4 of the same species as UALVP 22212. P4's of Saturninia have well-developed hypoconal shelves (Sigé, 1976); however, they are as large as, or slightly smaller than the shelves on M1 or 2 and not larger, as is the case above. Alternately, UALVP 22468 may represent a deciduous P4 of the same species as UALVP 22212. This would account for the morphological similarities to UALVP 22212 (particularly in the metaconule development), the less transverse appearence of UALVP 22468, the overall smaller size, and anteroposterior elongation of the hypoconal shelf. These interpretations must, however, await collection of a larger sample. In the interim both specimens are here described as belonging to two separate, but possibly related species.

## Genus *Leptacodon* MATTHEW AND GRANGER, 1921

### *Leptacodon* sp.

(Fig. 15 D-F)

*Referred specimens.* -- Left dentary fragment with p3-4: UALVP 22227; right dentary fragment with talonid for p4 and m1: UALVP 22685.

*Locality.* -- Swan Hills site 1, Paskapoo Formation, Alberta.

### DESCRIPTION

p3. -- The single referred p3 (L = 1.0, W = 0.5) is present on a dentary fragment with p4, UALVP 22227 (Fig. 15 D-E). The protoconid on the double-rooted crown is tall, trenchant, and is slightly recurved posteriorly. Although the tip of the protoconid is missing on both p3 and p4, it is evident p3 was only slightly shorter in height than p4. Anteriorly on the base of the crown is a small, weakly-developed paraconid. The incipiently-developed talonid is approximately one-quarter of the crown length and possesses the rudiments of a short cristid obliqua and shallow basin. Wear on the talonid obscures the possible presence of a cusp on the posterior margin of the talonid. Labially below the shallow hypoflexid the crown exhibits a degree of exodaenodonty.

p4. -- The tip of the p4 crown on UALVP 22227 (L = 1.3, W = 0.8) is broken dorsal to the metaconid; however, it appears to have been recurved and relatively tall and trenchant. The conical paraconid is situated low on the base of the protoconid. It is relatively closely appressed to the protoconid and positioned slightly lingual to a point anterior to the protoconid apex. The metaconid is conical, subequal to the paraconid in size, and is positioned approximately three-quarters of the way up the posterolingual edge of the protoconid. The talonid is one-third the length of the crown and possesses three small cusps. On UALVP 22685, a dentary fragment with an unworn p4 talonid and a complete m1, the cusps of the p4 talonid are slightly larger and better differentiated than on UALVP 22227. The shallow talonid basin is approximately two-thirds the width of the talonid and bordered labially and lingually by a slightly labially concave cristid obliqua and a low entocristid, respectively. The hypoflexid is relatively deep. Labially at the base of the hypoflexid, the crown is exodaenodont. An anterolabial cingulid is very weakly-developed below the paraconid.

m1. -- The single referred m1 (L = 1.3, AW = 0.8, PW = 0.8), preserved on UALVP 22685 (Fig. 15 F), is unworn and missing the metaconid. What remains of the base of the metaconid indicates it was at least as large as the protoconid. The trigonid leans lingually and the postvallid is slightly canted anteriorly. The protoconid is relatively tall and trenchant. The paraconid is cuspate, although reduced, and at the lingual end of a relatively high, crestiform paracristid. It is slightly anteriorly salient and well-separated from the metaconid, producing a lingually open trigonid basin. The talonid is as long as, and slightly wider than, the trigonid. The talonid basin is closed on all sides and moderately deep and rounded ventrally. The hypoconid and entoconid are subequal in height, the former being subcrescentic and larger than the latter, which is more nearly conical. The hypoconulid is subconical, shorter and smaller than the entoconid and is positioned lingual to the midline of the crown. The posterior edge of the talonid is curved posteriorly. The cristid obliqua is very slightly convex labially and is confluent with the posterolabial edge of the metaconid, which projects slightly further posteriorly than the posterior wall of the protoconid. The hypoflexid is moderately deep and at its base the enamel of the crown is slightly exodaenodont. Anteriorly is a narrow but strong precingulid. A postcingulid is absent.

## DISCUSSION

The specimens provisionally referred here are united with species of Leptacodon Matthew and Granger (1921) through the possession of the following characters: a relatively large, double-rooted p3 with a recurved, tall and trenchant protoconid; the p4 protoconid is tall, recurved, and trenchant, and the paraconid is strong and located anteriorly low on the base of the protoconid; the p4 talonid is well-developed and the cristid obliqua is slightly concave labially; the hypoflexid is relatively deep on p4 and the crown shows a degree of exodaenodonty below it; m1 has a cuspate paraconid, a tall and trenchant protoconid, a trigonid that leans lingually, a strong precingulid, subequal entoconid and hypoconid, strong hypoconulid lingual to the midline of the crown, and cristid obliqua that is slightly convex labially.

The p3 of Leptacodon sp. is larger than that of Saturninia and unlike the p3 of Amphidozotherium Filhol (1877) and Plagioctenoides Bown (1979) is double-rooted. Compared to p3 of Plagioctenodon Bown (1979), the crown of the p3 in Leptacodon sp. is much higher and less reduced in size relative to p4, the talonid is shorter, and the paraconid is smaller. Plagioctenodon has a p4 with a higher paraconid that is less nearly conical and not as closely appressed to the protoconid as it is in Leptacodon sp. In addition, the p4 of Leptacodon sp. differs from Plagioctenodon in having a talonid that is shorter with more reduced cusps, and a shallower talonid basin. The m1 of Leptacodon sp. differs from that of Plagioctenodon in having a deeper trigonid basin, a paraconid that is taller and leans more anteriorly, and a trigonid that has more of a lingual cant. In contrast to p4 of Pontifactor sp. (Krishtalka, 1976b), p4 of Leptacodon sp. has a narrower talonid with three cusps and the paraconid is lower on the crown and more anteriorly positioned. The m1 of Leptacodon sp. lacks the mesoconid present on m1 of Pontifactor sp. and further, the paraconid is less inflated, the hypoconulid is more lingual, the trigonid is less anteroposteriorly compressed, the cristid obliqua is convex labially, and a postcingulid is lacking. Unlike p4 in species of Nyctitherium, the paraconid of p4 in Leptacodon sp. is more nearly conical, lower on the crown, and anterior in position. As well, the p4 talonid cusps are much lower than in Nyctitherium p4's, and p4 and m1 lack the development of cingulids seen labially on p4 and m1 in Nyctitherium.

Swan Hills Leptacodon sp. is L. tener-sized; however, it differs from L. tener in not having a distinct, shelf-like precingulid on p4, the paraconid on m1 is slightly less inflated, and in comparison to the right lower jaw of the type specimen (AMNH 17179, illustrated in McKenna [1968: p. 9, fig. 4]), the p3 and p4 are slightly taller and more trenchant, thus resembling L. packi Jepsen (1930) in this character. The development of the talonid on p4 is virtually indistinguishable from L. rosei Gingerich (1987), but the referred specimens are higher crowned, p3 is larger relative to p4, the p4 paraconid is lower and more anteriorly positioned, and the hypoconulid on m1 is closer to the entoconid than observed on m1 of L. rosei. The p4 of Leptacodon sp. resembles p4 of L. packi in the development of the talonid and paraconid, and in having a "conspicuous labioinferior depression of the enamel beneath the p4 hypoflexid" (Bown and Schankler, 1982). Unlike L. packi, Leptacodon sp. has a less inflated m1 paraconid which leans slightly anteriorly.

In comparison to dentitions of Leptacodon catulus Krishtalka (1976b), Swan Hills Leptacodon sp. has a better developed paraconid on p4 and m1, the p4 talonid has three cusps (compared to 2 on p4 of *L. catulus*), the hypoflexid on m1 is shallower due to a more labial joining of the cristid obliqua with the trigonid, and a postcingulid is absent on m1. Compared to AMNH 35942, a left dentary fragment preserving p3-m3 of "*L.*" *munusculum* Simpson (1935a) (figured by Krishtalka, 1976b: p. 12, fig. 2), *Leptacodon* sp. has a p3 that is less compressed laterally and has a shorter talonid, p4 lacks a deep anterolabial "shelf" below the paraconid and does not have the cristid obliqua and entocristid parallel and straight, and the paraconid of m1 is less inflated.

*Leptacodon* sp. may represent a new species of *Leptacodon* present in the Swan Hills local fauna; however, until a larger and more nearly complete sample can be collected from site 1 and compared with samples already described, its affinities will remain uncertain.

L. S. Russell referred three specimens to *Leptacodon tener* with a query stating "reference of these specimens to *Leptacodon tener* is based mainly on the similarity in size" (1967, p. 18). ROM 05618 is a dentary fragment with a well worn m2 and m3. Despite wear, the molars on ROM 05618 were undoubtedly lower crowned than those of nyctitheres, the posterior edge of the talonid of m2 is virtually straight, and the metaconid and protoconid were somewhat inflated. These characters are more in keeping with erinaceomorphs, and ROM 05618 is referred above with other specimens to the Erinaceidae as an unidentified genus and species. ROM 05620, a trigonid of a left m2, is referred above to *Diacocherus*, cf. *D. meizon*. ROM 05619, a right dentary fragment with an incomplete m2 and an unworn m3, is the only specimen referable to the Nyctitheriidae and is discussed below.

### Genus Limaconyssus GINGERICH, 1987

### Limaconyssus sp. 1

(Fig. 4, 15 G-J)

Referred specimens. -- m2: UALVP 22230, 22520; M1 or 2: UALVP 22501.

Locality. -- Swan Hills site 1, Paskapoo Formation, Alberta.

## DESCRIPTION

m2. -- UALVP 22230 is an isolated trigonid which is indistinguishable from the trigonid on UALVP 22520 (Fig. 15 G-I), a right dentary fragment preserving m2 (L = 1.0; W = 0.7; trigonid height = 1.3) and alveoli for m1 and m3. The trigonid of UALVP 22520 leans strongly lingually and is quite tall with a trenchant protoconid and metaconid, the latter being slightly shorter in height than the former. The paraconid is half the height of the metaconid, anteroposteriorly compressed, at the lingual end of a relatively high, trenchant paracristid, and is slightly anteriorly procumbent. In occlusal view the paracristid and protocristid form an acute angle and the protoconid appears slightly "pinched" anteroposteriorly. The paraconid is well separated from the metaconid, opening the trigon basin lingually.

The talonid is approximately equal to the trigonid in width and slightly shorter in length. The talonid basin is moderately deep and rounded. The subconical entoconid and hypoconulid are subequal in size and height. The hypoconid is slightly higher than the former two cusps and appears quite "pinched" in occlusal view. The hypoconulid is slightly lingual to the midline of the crown. The cristid obliqua drops relatively steeply from the apex of the hypoconid and becomes confluent with the metaconid, producing a "crease" up the posterior wall of the metaconid to its apex. In occlusal view the cristid obliqua is slightly concave labially. The base of the crown below the relatively deep hypoflexid is moderately exodaenodont. A narrow but strong precingulid is present anteriorly. A weak, short postcingulid is present posteriorly.

M1 or 2. -- UALVP 22501 (L = 1.0, W = 1.5; Fig. 15 J) is an isolated left upper first or second molar in a maxillary fragment. It is unworn and complete except for the dorsal half of the paracone. In occlusal view the crown is quite transverse, the protocone and metacone are crescentic, and the protocone appears anteroposteriorly "pinched". Viewed posteriorly the metacone, protocone, and paraconule are relatively tall, trenchant, and aquiline in aspect. What remains of the paracone suggests it was slightly larger than the metacone and at least as tall. The preparacrista extends almost directly labially to a well-developed, anterolabially projecting parastylar salient. The premetacrista is situated on the extreme anterolabial edge of the metacone and in combination with the crestiform, posterolabially curving postmetacrista, which extends onto a small but distinct metastylar salient, makes the labial slope of the metacone appear concave. A moderately wide ectocingulum with a gently curving, shallow ectoflexus is present labially.

The paraconule is subconical and almost "twinned" with the protocone. The preparaconule crista is well-developed and crestiform. In combination with the strong, sharp postparaconule crista, a distinct basin is formed between the cristae. This basin is continuous with a narrow paracingulum extending onto the parastylar salient. In contrast to the paraconule the metaconule is very reduced and exists as a faint "bump" on the postprotocrista quite far removed from the base of the metacone. The premetaconule crista is low and indistinct. The postmetaconule crista is low and forms the posterior border of a narrow metacingulum extending partway onto the metastylar salient.

The protocone is subequal to the metacone in height. The pre- and postprotocristae are short and sharp, the former being much shorter than the latter. The trigon basin is deep and quite narrow transversely. Posterolingual to the protoconal apex is a small, subconical hypocone, which sits at the posterolingual corner of an expanded hypoconal shelf. The hypoconal shelf does not extend labially past a point below the apex of the metaconule. Anteriorly is the vestige of a precingulum positioned on the base of the crown between the apices of the protocone and paraconule.

## DISCUSSION

*Limaconyssus habrus* was recently described by Gingerich (1987) from an early Eocene locality in the Willwood Formation of the Clark's Fork Basin, Wyoming. The m2 on UALVP 22520 is very similar in morphology to the m2 on UM 86724, the type and only known specimen of *L. habrus* (illustrated in Gingerich, 1987: p. 305, fig. 20). It differs from m2 of *L. habrus* in being approximately fifteen percent smaller, and in having a metaconid that is slightly shorter than the protoconid in height, the hypoconulid subequal to the entoconid in size, and the paraconid slightly less inflated. Size alone indicates that the Swan Hills sample of *Limaconyssus* may belong to a new species; however, the small sample size from both localities precludes the possibility of a good comparison of the samples. Despite the small sample size, the characters of UALVP 22520, as outlined in the description above, clearly unites it with *Limaconyssus* and thus extends the range of the genus back into the late Tiffanian of Alberta.

The three specimens referred to Limaconyssus from site 1 belong to the smallest identified eutherian in the Swan Hills local fauna; however, it is not size alone that unites the single specimen referred here as an upper molar, UALVP 22501, with the two referred m2's. Both upper and lower teeth are gracile with relatively tall, trenchant cusps. The protocone of UALVP 22501 is very anteroposteriorly compressed and is ideal for occlusion in the anteroposteriorly short talonid basin of m2. In addition, the well-developed and subconical paraconule on UALVP 22501, being close to the protocone and positioned slightly further anterior than the protocone, would be in an ideal position to slide along the oblique "crease" on the posterior wall of the metaconid as the teeth moved into centric occlusion.

Gingerich (1987) classified Limaconyssus as a nyctitheriid, although he recognized characters possessed by the type were clearly distinctive compared to known nyctitheres. He felt it was "easier to expand the concept of Nyctitheriidae than to erect a new monotypic family for this genus and species" (1987, p. 305). If correctly identified, the referral of UALVP 22501 to Limaconyssus as an M1 or M2 would be the first description of an upper tooth for this genus and would also provide support for Gingerich's referral of the genus to the Nyctitheriidae.

The resemblance between UALVP 22501 and upper molars of Nyctitherium is strong, particularly in the development of the hypoconal shelf. It differs from Nyctitherium in being much more transverse, having relatively taller and sharper cusps and cristae, in having a more reduced metaconule, in virtually lacking a precingulum, having the hypocone removed further posteriorly from the base of the protocone, and in having a less expanded hypoconal shelf. The above differences clearly demarcate upper molars of Limaconyssus and Nyctitherium; however, they are reminiscent of characters of upper molars found in some species of the European genera Saturnina and Amphidozotherium (Sigé, 1976).

Several specimens of lower dentitions from Cochrane 2 and from UADW-2, Alberta, are very similar to Limaconyssus habrus and Limaconyssus sp. 1 (pers. observ.; Youzwyshyn, pers. comm.). These specimens are currently understudy by G. P. Youzwyshyn and R. C. Fox, respectively, and will be described elsewhere.

### Limaconyssus sp. 2
(Fig. 15 K)

Referred specimen. -- Right dentary fragment preserving m1-2: UALVP 23922.

Locality. -- Swan Hills site 1, Paskapoo Formation, Alberta.

## DISCUSSION

The two lower molars preserved on the single dentary fragment referred here (UALVP 23922) are identified as belonging to Limaconyssus on the basis of characters possessed in common with Limaconyssus sp. 1 and Limaconyssus habrus Gingerich (1987). These characters include: acute-angled trigonid crests; tall and trenchant protoconids; the cristid obliqua "runs up the back of the metaconid, creasing it to the apex" (Gingerich, 1987: p. 305); the presence of pre- and postcingulids; and the hypoconid and protoconid appear "pinched" and "pillarlike" (Gingerich, 1987: p. 305).

Although m1-2 on UALVP 23922 are worn, the above characters are easily identified on the specimen.

UALVP 23922 (m1: L = 1.5, AW = 1.0, PW = 0.[illegible]; m2: L = [illegible], AW = 1.0, PW = 0.8) differs from Limaconyssus sp. 1 in being approximately 20% larger and from L. habrus in being only slightly larger. It further differs from the latter two in possessing narrow cingulids labially around the base of the hypoconids.

## NYCTITHERIIDAE, unidentified genus and species

(Fig. 15 L)

Referred specimens. -- Dentary fragment with incomplete m2 and unworn m3: ROM 05619.

Locality. -- Swan Hills site 1, Paskapoo Formation, Alberta.

## DISCUSSION

ROM 05619 was originally referred to Leptacodon tener by L. S. Russell (1967). Although ROM 05619 shares characters in common with other nyctitheres, several characters possessed by ROM 05619 exclude it as a member of the genus Leptacodon. Characters shared in common with nyctitheres include: sharp, subconical to subcrescentic cusps; angular trigonids and talonids; an unreduced hypoconulid that is lingual in position; an entoconid and hypoconulid that are subequal in height, or the latter slightly higher than the former; a cuspate paraconid not appressed to the metaconid; a deep hypoflexid; and a trigonid that leans lingually (Krishtalka, 1976b; Rose and Gingerich, 1987). Characters which exclude it from the genus Leptacodon are a cristid obliqua that is slightly concave labially on m2 and straight on m3, and a paraconid on m3 which is less cuspate, taller, and more nearly erect and lophid-like than seen in species of Leptacodon.

Unlike Nyctitherium, ROM 05619 lacks labial cingulids and the crowns do not lean as strongly lingually. In comparison to m2 talonids and m3's of Plagioctenodon, ROM 05619 has much shallower talonid basins, the entoconids and hypoconids are more nearly conical, the entoconid is shorter and subequal to the hypoconid, and the m3 paraconid is taller and more erect (a difference which also separates ROM 05619 from Plagioctenoides). Unlike Pontifactor, ROM 05619 lacks a deeply basined talonid and a mesoconid on the cristid obliqua, and although the paraconid on Pontifactor resembles ROM 05619 in being "lophid-like", the paraconid on m3 of ROM 05619 is more erect and not anteriorly salient.

As in other nyctitheriid taxa found in the Swan Hills local fauna the sample referred here is very small (N=1), and although certain characters identify ROM 05619 as a nyctitheriid, other characters remove it from close association with known nyctitheres. Apparently, nyctitheres present in the Swan Hills local fauna possess suites of characters that separate them from related taxa found in the depositional basins of the western United States. Until further material is collected from Swan Hills sites 1 and 2, the affinities of the Swan Hills nyctitheres to described species elsewhere will remain an enigma.

Order PRIMATES LINNAEUS, 1758

Infraorder PLESIADAPIFORMES SIMONS, 1972

Superfamily PLESIADAPOIDEA TROUESSART, 1897

Family PLESIADAPIDAE TROUESSART, 1897

Genus Plesiadapis GERVAIS, 1877

Plesiadapis churchilli GINGERICH, 1975

(Fig. 15 M, 16 A-B)

Referred specimens. -- i1: ROM 05626, UALVP 22359; I1: ROM 05625; P3: UALVP 11737; M2: UALVP 22221; M3: UALVP 22617.

Locality. -- Swan Hills site 1, Paskapoo Formation, Alberta.

Known distribution. -- Swan Hills site 1, Paskapoo Formation, Alberta; Long Draw Quarry, Croc. Tooth Quarry, Divide Quarry, Lower Sand Draw and Airport localities, Polecat Bench Formation, Big Horn Basin, Wyoming (Gingerich, 1975, 1976); Malcolm's locality, Fort Union Formation, Badwater Creek, Wyoming (Krishtalka, et al., 1975); numerous localities near the town of Roche Percée, Ravenscrag Formation, Saskatchewan (Krause, 1978); "probably" present at V-77005-77008 and V-77061, Fort Union Formation, eastern Rock Springs Uplift, Wyoming (Winterfeld, 1982).

## DESCRIPTION

M2. -- UALVP 22221 is an anterolabial fragment of a relatively large, slightly worn, right M2 preserving the paracone, parastyle, mesostyle, paraconule, and anterolabial half of the protocone (Fig. 16 A). The posterior half of the tooth including hypocone, metaconule, and metacone is missing.

The paracone is conical and relatively large with strong pre- and postparacristae. The preparacrista extends directly anterior from the apex of the paracone to a low, bulbous parastyle on the anterolabial end of a well-developed paracingulum. The paraconule is low, stoutly subconical, and separated slightly from the paracone, being positioned more on the anterolabial base of the protocone. The apex of the protocone is missing; however, the protocone was as tall as, or slightly taller than the paracone. The mesostyle is quite strong and the centrocrista leading onto it is oriented posterolabially away from the paracone. What remains of the precingulum shows it to have been sizeable. The ectocingulum is inflected internally between the mesostyle and paracone, and discontinuous around the labial base of the paracone. Enamel on the crown is unmistakably crenulated, but not strongly so.

M3. -- The single referred specimen, UALVP 22617 (L = 3.0, W = 4.4), is slightly worn and complete, except for a small piece of the mesostyle and a small wedge of the crown missing in the region of the paraconule (Fig. 16 B). The posterolabial corner of the crown is reduced. The trigon basin is relatively deep. The basin on the expanded talon is well-developed and approximately one-half the size of the trigon basin. The protocone is the tallest, most robust cusp on the crown and located anterior to the transverse midline of the crown. The preprotocrista is better developed than the postprotocrista and extends anterolabially to what remains of the small paraconule. The metaconule is quite small and sits lingual to the reduced, conical metacone. The paracone is about three times the size and height of the metacone, and, unlike the metacone, has pre- and postcristae. The ectocingulum, mesostyle, and hypocone are all reduced but still easily identifiable. A parastyle is virtually absent. The precingulum and nannopithex fold are relatively well-developed. Crenulations of the enamel are present and pronounced, especially on all slopes of the protocone.

## DISCUSSION

L. S. Russell (1967) collected a right upper incisor (ROM 05625) and a left lower incisor (ROM 05626) at Swan Hills site 1, which he referred to "Plesiadapis," cf. "P." gidleyi. He hesitated referring them directly to "P." gidleyi (Matthew, 1917) because of the presence in the literature of two Plesiadapis species of approximately the same size -- P. dubius (Matthew, 1915), for which no upper incisors were known at that time, and P. fodinatus Jepsen, 1930. Russell felt that when cheek teeth were recognized from site 1, it would "probably be clear that the Swan Hills representative is either P. gidleyi or a new species very similar to it" (1967, p. 22)[9]. Gingerich (1975, 1976) transferred "P." gidleyi to his genus Nannodectes, which differs from Plesiadapis in having "much narrower central incisors and cheek teeth...and lacking a centroconule on I1" (1975, p. 138). Krause (1978), noting the robust nature of the Swan Hills incisors and the presence of a centroconule on ROM 05625, referred the Swan Hills specimens to Plesiadapis sp., along with a P3 (UALVP 11737; Fig. 15 M) collected by D. O'Brien in 1972 at site 1. Unlike P3's of Nannodectes, Krause (1978) noted UALVP 11737 possessed a well-developed paraconule. He deferred specific allocation of the specimens pending collection of a larger sample, stating the "teeth of Plesiadapis from Swan Hills are similar in size to P. rex, P. churchilli, and P. fodinatus" (1978, p.

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[9] It is interesting to note that with inclusion of the specimens described above, the upper and lower incisors from Swan Hills would eventually be referred to P. churchilli, a species erected by Gingerich eight years after Russell's original description.

1268).

In size UALVP 11737 is in the uppermost part of the range for P3's of *Plesiadapis rex*, *P. fodinatus*, and *P. churchilli*. *Plesiadapis fodinatus* usually lacks a paraconule and the metacone varies in development from being absent to "distinctly" developed (Gingerich, 1976: p. 29). Despite being water worn, UALVP 11737 has both a well-developed metacone and a very robust paraconule, and in comparison to the P3 on PU 13306 and PU 13393, maxillary fragments of *P. fodinatus*, UALVP 11737 is much more transverse. In comparison to the P3 on UMMP 27230, the type for *P. farisi* (referred to *P. fodinatus* by Gingerich [1976]), UALVP 11737 is only slightly more transverse (length/width ratios of 0.743 and 0.735, respectively). A good cast of PU 21448, a right maxilla of *P. rex* from [illegible]dar Point Quarry, and the [illegible]strated maxillary of *P. rex* (PU 20703) in Gingerich (1976: p. 124; pl. 4, fig. H), show the metacone, paraconule, and parastyle to be not as well developed as on the Swan Hills P3. Among the P3's of *P. churchilli* from Roche Percée (Krause, 1978), there is a great degree of variation (pers. observ.). UALVP 11737 falls well within the range of variation here, and comes very close to several specimens in size and morphology (e.g., UALVP 9504).

The fragment of M2 (UALVP 22221) has a very strong mesostyle that is larger than observed mesostyles on *P. fodinatus* and especially *P. rex*. The enamel shows crenulations that are comparable to the condition observed on M2's of *P. rex*, but comes no where near the "highly crenulated" enamel observed on *P. fodinatus* (Gingerich, 1976: p. 29). In size and morphology UALVP 22221 is indistinguishable from numerous M2's of *P. churchilli* in the large sample (N=40) from Roche Percée (Krause, 1978).

Except for a very slight amount of wear, a tiny wedge of enamel missing from the crown at the paraconule, and a missing piece of the mesostyle, the single referred M3 (UALVP 22617) is exceptionally preserved. This specimen was recovered in three pieces and unfortunately one of the fracture lines extended through the posterolabial corner of the crown, resulting in a loss of a posterodorsal piece of the mesostyle. Despite this loss, it was evident that the mesostyle was well-developed and larger than generally seen on M3's of P. rex. Enamel on the crown is prominently crenulated but not as pronounced as on M3's of P. fodinatus. In size UALVP 22617 is slightly smaller than the smallest M3 in the Roche Percée sample of P. churchilli, but again, like M2 it has numerous specimens in the Roche Percée sample that are virtually indistinguishable from it.

Although the sample size of Plesiadapis churchilli from Swan Hills site 1 is still small (N=6), the recent collection of an M2 and M3 from site 1 finally allows, after more than twenty years, an identification of the species of Plesiadapis present in the Swan Hills local fauna. The collection of further specimens will of course strengthen the referral; however, I feel there can be little doubt as to the identification of P. churchilli in the Swan Hills.

### Family PAROMOMYIDAE SIMPSON, 1940
### Genus Ignacius MATTHEW AND GRANGER, 1921
### Ignacius frugivorus MATTHEW AND GRANGER, 1921
(Fig. 16 C)

Referred specimen. -- UALVP 22360, an isolated left m3.

Locality. -- Swan Hills site 1, Paskapoo Formation, Alberta.

Known distribution. -- Swan Hills site 1, Paskapoo Formation, Alberta;

Mason Pocket, Tiffany Formation, Colorado (Matthew and Granger, 1921); Scarritt Quarry, Melville Formation, Montana (Simpson, 1936); Joe's Bone Bed, Black Peaks Formation, Texas (Schiebout, 1974); Brisbane and Judson localities, Tongue River Formation, North Dakota (Holtzman, 1978); Cedar Point Quarry, Polecat Bench Formation, Wyoming (Rose, 1981); Roche Percée local fauna, Ravenscrag Formation, Saskatchewan (Krause, 1978); Locality V-77005, eastern Rock Springs Uplift, Fort Union Formation, Wyoming (Winterfeld, 1982); Badwater Creek, Shotgun Member, Fort Union Formation, Wyoming (Krishtalka, et. al., 1975); Canyon Ski Quarry, Joffre Bridge Road Cut lower level, and UADW-2, Paskapoo Formation, Red Deer, Alberta (Fox, in prep.); Hand Hills west (upper level), Paskapoo Formation, Hand Hills, Alberta (Fox, in prep.).

## DISCUSSION

Descriptions of the dentition of Ignacius frugivorus are to be found in a number of references, including Matthew and Granger (1921), Simpson (1935, 1936), Krause (1978), and Holtzman (1978). The single referred specimen from Swan Hills site 1 (UALVP 22360) is heavily abraded and most of the enamel is missing; however, the lack of cingulids, the presence of an expanded third lobe, the paraconid closely appressed to the metaconid, and the presence of a relatively shallow talonid basin, identify this specimen as an m3 of Ignacius (after the emended diagnosis for Ignacius by Bown and Rose, 1976). UALVP 22360 (L = 2.8; W = 1.5) is larger than m3's of I. mcgrewi (Robinson, 1968) and I. fremontensis (Gazin, 1971), and smaller than m3's of I. graybullensis Bown and Rose, 1976. In size and morphology, UALVP 22360 does not differ significantly from m3's referred to I. frugivorus from Scarritt Quarry (Simpson, 1936), Roche Percée (Krause, 1978), and Brisbane and

Judson localities (Holtzman, 1978).

### Family CARPOLESTIDAE SIMPSON, 1935b
### Genus *Carpodaptes* MATTHEW AND GRANGER, 1921
### *Carpodaptes cygneus* (RUSSELL, 1967)
(Fig. 5, 16 D-H, 17 A-E; Table 9, 10)

*Referred specimens*. -- p4: ROM 05622, 05623, UALVP 11717, 22198, 22213, 22351, 22352, 22639, 22640; m1: UALVP 22354; m2 UALVP 11722, 22356, 22358, 22645; m3: UALVP 11723, 22355, 22643; dentary fragments with p4-m1: UALVP 11718, 22353; dentary fragment with incomplete p4, and m1-3: UALVP 22257; dentary fragments with m2-m3: UALVP 22641, 22642; I1: UALVP 11724, 22357, 22402, 22524, 22654; I2: UALVP 22211; P2: UALVP 22652, 22653; P3: ROM 05624, UALVP 11719, 22646; M1: UALVP 22648; M2: UALVP 22649, 22650; M3: UALVP 22498, 22651; maxillary fragments with P2-P3: UALVP 11720, 11721, 22197; maxillary fragment with P4-M2: UALVP 22647.

*Locality*. -- Swan Hills site 1, Paskapoo Formation, Alberta.

*Known distribution*. -- Swan Hills site 1, Paskapoo Formation, Alberta; Canyon Ski Quarry, Paskapoo Formation, Red Deer, Alberta (Krause, 1978); Roche Percée local fauna, Ravenscrag Formation, Saskatchewan (Krause, 1978); Brisbane and Judson localities, Tongue River Formation, North Dakota (Holtzman, 1978); Olive locality, Tongue River Formation, Montana (Rose, 1975a); UADW-1, Paskapoo Formation, near Red Deer, Alberta (Fox, in

Table 9: Measurements and descriptive statistics of the lower dentition of *Carpodaptes cygneus*, Swan Hills local fauna, Alberta.

| Measurement | | N | CR | M±SE | SD | CV |
|---|---|---|---|---|---|---|
| p4 | L | 10 | 1.9-2.3 | 2.08 ± .04 | .123 | 5.9 |
| | W | 9 | 1.0-1.3 | 1.20 ± .03 | .087 | 7.2 |
| m1 | L | 3 | 1.4 | - | - | - |
| | W | 3 | 1.1-1.3 | 1.20 ± .06 | .100 | 8.3 |
| m2 | L | 7 | 1[illegible]-1.3 | 1.21 ± .03 | .069 | 5.7 |
| | W | 7 | 1.1-1.2 | 1.16 ± .02 | .053 | 4.6 |
| m3 | L | 4 | 1.6-1.8 | 1.73 ± .05 | .096 | 5.6 |
| | W | 4 | 1.1 | - | - | - |

Table 10: Measurements and descriptive statistics of the upper dentition of *Carpodaptes cygneus*, Swan Hills local fauna, Alberta.

| Measurement | | N | OR | M±SE | SD | CV |
|---|---|---|---|---|---|---|
| I1 | L | 2 | 1.4-1.5 | 1.45 ± .05 | .071 | 4.9 |
| | W | 2 | 0.8-0.9 | 0.85 ± .05 | .071 | 8.3 |
| I2 | L | 1 | 0.9 | - | - | - |
| | W | 1 | 0.5 | - | - | - |
| P2 | L | 4 | 0.6-0.7 | 0.68 ± .03 | .050 | 7.4 |
| | W | 4 | 0.5-0.6 | 0.53 ± .03 | .050 | 9.5 |
| P3 | L | 6 | 1.5-1.7 | 1.60 ± .03 | .063 | 4.0 |
| | W | 6 | 1.6-1.8 | 1.70 ± .04 | .089 | 5.3 |
| P4 | L | 1 | 1.6 | - | - | - |
| | W | 1 | 1.8 | - | - | - |
| M1 | L | 2 | 1.2 | - | - | - |
| | W | 2 | 1.6-1.7 | 1.65 ± .05 | .071 | 4.3 |
| M2 | L | 3 | 1.1-1.2 | 1.17 ± .03 | .058 | 4.9 |
| | W | 3 | 1.8 | - | - | - |
| M3 | L | 2 | 1.1 | - | - | - |
| | W | 2 | 1.5-1.7 | 1.60 ± .10 | .141 | 8.8 |

press).

## DESCRIPTION

p4. -- In occlusal view the crown is shaped roughly like a robust Fig. eight with a very wide waist and the medial edge indented more lingually than labially (Fig. 16 D). The cusps of the crown are joined by cristids running through their apices and do not form a straight line, but rather, a gentle curve that is convex labially or slightly S-shaped, dependent on the positioning of the anterior two apical cusps. On specimens preserving the crown (N=9) the apical cusp number is invariably five plus a single talonid cusp. No specimen exhibits, nor does one show a tendency towards producing a sixth apical cusp on the anterior edge of the crown like that seen in <u>Carpodaptes cygneus</u> from Roche Percée (Krause, 1977). The apical cusps are subconical and become increasingly lenticular posteriorly. The second, third, and fourth apical cusps are approximately equidistant from one another. The talonid cusp is anteroposteriorly compressed and continuous with ridges running ventrolabially and ventrolingually from it. The third apical cusp is the tallest cusp above the base of the crown. The second and fourth apical cusp are subequal in height. The first cusp is intermediate in height between the fourth and fifth apical cusps. The fifth apical cusp is situated on the cristid joining the talonid to the fourth apical cusp at a point approximately half way, or, a little over half way to the fourth apical cusp.

When viewed labially the anterior edge of the crown is variably curved to the first cusp, and the posterior edge forms a sinusoidal curve from the posterior base of the crown to the talonid cusp. Ridges from the apical cusps labially are variably developed, but generally weak. A ventrally directed, shallow, vertical groove is present between the fifth apical and talonid cusps. The ridge, or crest, descending from the talonid cusp is short and becomes continuous with the posterior edge of the crown.

Lingually the ridges from the apical cusps can be well-developed (e.g., ROM 05623 or UALVP 11718) or can be reduced (e.g., UALVP 22353) and approach the condition seen in C. hobackensis. Unlike the majority of the specimens from Swan Hills, UALVP 22353 has a weakly developed ridge descending from a reduced fifth apical cusp. This produces a relatively well-developed posterolingual depression which appears as well developed as, or better developed than, specimens of C. hobackensis illustrated in Holtzman (1978: fig. 9.3, p. 76). The ridge descending ventrolingually from the talonid cusp curves anteriorly about midpoint between the cusp and the base of crown before fading.

Exodaenodonty of the base of the crown is present lingually and labially over each of the anterior and posterior roots producing a bilobed appearence. This is especially well-developed over the labial roots of carpolestids in general. The posterolabial lobe as a rule extends further ventrally than the anterolabial lobe.

m1. -- The cusps of the trigonid form an obtuse angle (approximately 105 °) that is a rough posterior continuation of the blade-like p4 (Fig. 16 D). The paraconid is the smallest of the subconical trigonid cusps, is intermediate in height between the meta- and protoconid, and is positioned anterolingually to the protoconid, which is the largest and tallest of the trigonid cusps. The paracristid forms an angle of approximately 125 ° by first extending directly anterior from the protoconid to the bottom of the valley separating the proto- and paraconid, and then veering sharply to the paraconid. The labial slope of the paraconid, which may be continuous with what was once a very robust and anteroposteriorly wide precingulum, is separated from the labial slope of the protoconid by a relatively deep, vertical groove that extends almost to the ventral edge of the crown (Fig. 16 E). The metaconid is intermediate in size between the para- and protoconid and set off slightly from the rest of the trigonid by being positioned very low on the posterolingual corner of the trigonid. This separation is emphasized by the metaconid being continuous with a wide cristid obliqua that splits the postvallid into anterodorsal and posteroventral segments, producing a dorsolingually-ventrolabially oblique "step".

The hypoconid and entoconid are well-developed, the entoconid being the larger of the two. The hypoconulid is reduced to a barely noticeable swelling on the postcristid close to the entoconid. The talonid is relatively deep and open lingually due to a deep talonid notch. The hypoflexid is relatively well-developed and deep. A weakly developed postcingulum is present on the posterior wall of the hypoconid.

Labially the exodaenodont base of the crown on m1 appears almost squared with rounded anterior and posterior corners, and a flattened, relatively straight ventral edge.

m2. -- The trigonid is anteroposteriorly compressed, leans slightly anterolingually, and the three cusps form an acute angle of approximately 34 ° (Fig. 16 G). The trigonid basin is shallow. The protoconid is situated relatively low on the labial portion of the crown and is intermediate in height between the hypoconid and metaconid. The metaconid is the tallest cusp on the crown and subequal to the protoconid in size. The paraconid is well-developed, conical and is slightly smaller and shorter than the metaconid. The para- and protocristids are distinct.

The talonid possesses a well-developed hypoconid and entoconid that are slightly lower in height relative to the m1 hypoconid and entoconid. In contrast to m1's the hypoconulid is better developed, a mesoconid is variably developed on the cristid obliqua, and the cristid obliqua does not become confluent with the metaconid, but terminates on the posterior wall of the trigonid. The talonid basin is open lingually at the deep talonid notch and is relatively wider and deeper than on m1. Anteroposteriorly, m2 possesses a much longer talonid than m1.

The precingulid is variably developed and may reach dorsolingually to the paracristid (e.g., UALVP 22642). Ventrally the precingulid may proceed around the base of the protoconid to produce an anterodorsally-posteroventrally oblique "shelf" (e.g., UALVP 22356). A low, variably developed postcingulid is present on the posterobasal wall of the hypoconid.

m3. -- The trigonid of m3 differs from m2 in being slightly more anteroposteriorly compressed and shorter in height relative to the height of the talonid (Fig. 16 G). The talonid continues trends established in m1 and m2 by having a generally better developed mesoconid on the cristid obliqua, a lower height measured from the base of the crown, a deeper basin, and a greater transverse width. The entoconid is anteroposteriorly elongate. The hypoconulid lobe is bilobed and centered slightly lingual to the midline of the crown.

I1. -- The upper medial incisors of Carpodaptes cygneus from Swan Hills site 1 are virtually identical in all respects to the sample referred to C. cygneus from Roche Percée, Saskatchewan (Krause, 1978). For continuity of description, the terminology used by Krause (1978) to describe the cusps of the upper incisors of the Roche Percée sample is used here.

The crown possesses a large, almost conical, mesioapical cusp that is placed labially to a smaller distoapical cusp (Fig. 16 H). The two apical cusps have three ridges joining their apices: one ridge on each of the labial and lingual edges of the cusps, and a third running medially between them. A circular interdental wear facet on UALVP 22654 marks the position of articulation with the complimentary medial incisor. A relatively large, conical distobasal cusp is joined mesiolingually to a smaller, conical mesiobasal cusp, by a dorsally curving crista on the lingual base of the crown. Cristae on the lateral edges of the crown join the distobasal and mesiobasal cusps anteroventrally to the distoapical and mesioapical cusps, respectively. A variably developed cuspule is present just anteriorly/labially to the mesiobasal cusp on the crista joining the latter to the mesioapical cusp. A "basin" is present between the base of the common trunk of the apical cusps, the lateral cristae, and the basal cusps. A ridge is present on the lingual face of the common apical trunk, that roughly parallels, and is close to, the distolateral crista. This ridge extends between the "basin" and the lateral base of the distoapical cusp. As well, on this ridge is a small, teardrop-shaped wear facet located approximately at the base of the common apical trunk. A larger, lenticular wear facet is located mesially to the latter on the mesiolateral crista. The root is straight and laterally compressed.

I2. -- The single specimen referred here, UALVP 22211 (Fig. 17 B), is present in a premaxillary fragment possessing the posterior half of the alveolus for I1, and the alveolus for I3. The tooth is single-rooted with one major cusp, and is much reduced in size compared to I1. An accessory cusp is present posteriorly. A smaller accessory cusp anteriorly is incorporated into a well-developed lingual basal cingulum extending posteriorly to the posterior accessory cusp. A cingulum is absent labially. The major cusp is conical, joined to the posterior accessory cusp by a relatively well-defined crista, and is positioned well anterior on the crown. In lateral view the crown appears to be anteriorly procumbent.

Lingual and dorsal to the tooth row, the premaxillary fragment has a rugose area of bone. This rugosity marks the sutural contact with the maxillary, and is comparable to the condition illustrated by Rose for UM 71002, a right premaxillary and maxillary fragment of <u>Carpolestes</u> <u>nigridens</u> (1981: p. 62, fig. 27 E-F).

P2. -- The small, single-rooted P2 possesses a single conical cusp, and is almost circular in occlusal outline, being only slightly laterally compressed (Fig. 17 C). Weak cristae extend up the anterior and posterior slopes to the apex of the cusp. A relatively strong basal cingulum is present on all but the labial portion of the crown.

P3. -- The outline of the crown in occlusal view is pyriform (Fig. 17 C). The four labial cusps are aligned anteroposteriorly on the crown and form a serrate crest. The conical anterolabial cusp is well separated from, and two-thirds the height of the second cusp. Depending on the extent of posterior inflection of the anterior edge of the crown and cingulum, the anterolabial cusp can extend anteriorly only slightly (e.g., UALVP 22646), or can form a well-developed anterior extension of the crown (e.g., UALVP 11719). The remaining three subconical cusps of the labial row are subequal in height. They are joined to approximately three-quarters of their height, decrease in size posteriorly, and are slightly laterally compressed with relatively sharp cristae developed on their anterior and posterior slopes and through their apices. A subconical cusp, subequal to, or slightly shorter than the anterolabial cusp, is situated internal to the valley between the anterolabial and second labial cusp. This more medial cusp is incorporated into a ridge that extends posteriorly approximately parallel to the labial cusp row before turning posterolabially to end at the posterolingual base of the ultimate labial cusp. A well-developed crista joins the medial cusp anterolabially to the anterolabial cusp[10].

A posterior cingulum, extending lingually from the posterior edge of the medial ridge, is deflected anteriorly and forms an elongate, laterally compressed "cusp", or ridge, approximately parallel to the medial ridge. This "cusp"/ridge may be very cusp-like when reduced and extending anteriorly but a short distance (e.g., UALVP 22646), or can be very ridge-like when well-developed and extending anteriorly to a point lingual to the valley between the second and third labial cusps. These two character states are equally divided between the referred specimens.

Lingually, the protocone and hypocone are joined by a sharp, distinct crista possibly the homologue of the nannopithex fold. The hypocone, is half the size and height of the protocone, and can be situated at the posterolingual corner of the crown (e.g., UALVP 22197), or, a point slightly anterior to it (e.g., ROM 05624). The trigon and talon basins combine in P3 to produce one large, variably developed basin, which is generally deeper labial to the hypocone.

Labial cingula are variably developed and range from being absent (e.g., UALVP 22197), to present but reduced (e.g., UALVP 11720). The anterior

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[10] The homologies of the cusps in the labial and medial rows are uncertain; however, a paper currently being prepared by Krause, Maas, and Youzwyshyn, on the upper dentition of *Elphidotarsius russelli*, may shed some light on this area.

cingulum can be continuous with the crista of the protocone (the probable homologue of the preprotocrista) and the ectocingulum. It can be terminated at the anterior base of the anterolabial cusp and thus not continuous with the ectocingulum, or, it can be bisected at a point on the anterior edge of the crown between the lingual and medial cusps.

On unworn specimens the enamel is crenulated on all but the very bottom of the trigon-talon basin, and the basal edges of the crown.

P4/-- The single specimen of P4 in the Swan Hills sample is present on a left maxillary fragment also bearing M1 and M2 (UALVP 22647: Fig. 17 D). The tooth exhibits some wear and is damaged anterolabially and labially, obscuring characters of the crown anterior and labial to the penultimate cusp of the labial cusp row, and anterior to the central median cusp. In occlusal aspect the crown is pyriform. The crest extending posteriorly from the median cusp has the incipient development of another cusp that is positioned lingual to what is left of the penultimate labial cusp. As on P3 the posterior cingulum is deflected anteriorly, lingual to the posterior crest from the median cusp, forming a short ridge. Anteriorly the cingulum is deflected posteriorly to produce the same kind of character; however, on UALVP 22647 this character is more cusp-like and less ridge-like. The combination of the large central protocone, the well-developed pericone and hypocone (both nearly as tall as the protocone) being situated anterolingually and posterolingually, respectively, to the protocone, and the tall, relatively sharp cristae extending labially from the pericone and hypocone, produces two relatively deep basins anterior and posterior to the protocone. The central transverse crest joining the protocone to the median cusp is reduced. The slopes of the cusps show a varying degree of crenulation of the enamel.

M1. -- The two referred specimens show post-mortem abrasion that partially obscures the ectocingulum. The paracone is broken on UALVP 22648, but UALVP 22647 (Fig. 17 D) shows the paracone on M1 to be slightly taller and larger than the metacone. The meta- and paracrista are well-developed, and the paracingulum and metacingulum are continuous with the ectocingulum. The paraconule and metaconule are relatively large, with the paraconule being the taller and larger of the two. Except for the absence of a premetaconule crista, the conule cristae are prominent. The protocone is slightly taller than the paracone and has the apex situated a little anterior to a transverse line through the middle of the crown. The preprotocrista is short and not as sharp as the longer postprotocrista. The trigon basin is relatively deep. A precingulum extends lingually from a point dorsal to the internal edge of the paracone, to a well-developed pericone on the anterior base of the protocone. The postcingulum becomes quite broad lingual to the fairly large, conical hypocone, producing a shallow but sizeable talon basin. The nannopithex fold is prominent.

M2. -- M2 is similar to M1 and differs in the following characters: the crown is slightly shorter anteroposteriorly and more transverse; the difference in height and size between the paracone and metacone is more pronounced; the metacingulum is not continuous with the ectocingulum; the pre- and postprotocristae are longer (related to the slightly greater transverse width); the pericone and hypocone are more reduced (the pericone can be absent); the apex of the protocone is situated slightly more anteriorly; the nannopithex fold is better developed; the talon basin is relatively larger.

M3. -- The posterolabial corner of the crown is reduced producing a more anterolabially-posterolingually oblique external edge to the crown than is seen on M2 (Fig. 17 E). Relative to the condition seen on M2, both the metacone and metaconule are smaller, lower, and positioned more lingually than the paracone and paraconule, respectively. The metaconule is more conical than on M2 and the apex of the protocone is situated more anteriorly relative to the transverse midline of the crown. The hypocone is reduced to a mere inflated area on the postcingulum. The talon basin remains shallow and anteroposteriorly broad. The precingulum is as well-developed as, or slightly smaller than the precingulum of M2. A pericone is absent. The ectocingulum is reduced, does not extend posteriorly beyond the anterolabial base of the metacone, and is terminated anteriorly by a very small parastyle situated slightly labial to the anterior base of the paracone. The preparacrista extends to the parastyle, forming a small paracingulum.

## DISCUSSION

In 1967, L. S. Russell erected a new species, *Carpolestes cygneus*, to include specimens of a small carpolestid he collected in 1965 from his locality 1 in the Swan Hills (= site1). At this time Russell's sample consisted of three teeth: right and left mandibular fragments containing p4's (the holotype, ROM 05622, plus ROM 05623), and a left maxillary fragment with P3 (ROM 05624). Including P4, these dentitions are considered to be the most diagnostic (Rose, 1975a; Krause, 1978) and subsequent comparisons were based on collation with this extremely small sample size.

Krishtalka (1973) described specimens of a carpolestid from the Police Point local fauna, Cypress Hills, Alberta, which he referred to *Carpodaptes*, cf. *C. hazelae*, and transferred "*Carpolestes*" *cygneus* to *Carpodaptes*. Rose (1975a) emended the diagnosis for *Carpodaptes cygneus* on the basis of specimens from Roche Percée, Saskatchewan (under study by D. Krause at that time), and referred the Police Point carpolestid to *Carpodaptes*, cf. *C*. *cygneus*. Krause described the Roche Percée sample of *C*. *cygneus*, limiting the description to the upper and lower medial incisors and "delineation of the variablility in the premolars" (1978, p. 1253). At this time Krause also referred to *C*. *cygneus* eight more specimens collected at the type locality by University of Alberta field parties, as well as a small sample from Canyon Ski Quarry near Red Deer, Alberta. Holtzman (1978) described *C*. *cygneus* and *C*. *hobackensis* Dorr, 1952 (to which Russell [1967] made no comparisons), from the Brisbane and Judson localities, respectively, of the Tongue River Formation, North Dakota. He described upper dentitions of *C*. *hobackensis* for the first time, basing his referrals on comparisons with *C*. *cygneus* as redefined by Rose (1975a) and described by Krause (1978). Winterfeld (1982) briefly described a single P3, and one each of M3 and m3, from a late Tiffanian horizon on the east-central flank of the Rock Springs Uplift (Fort Union Formation) that he referred to *Carpodaptes* sp. He stated "the referred P3 most closely resembles those of *C*. *cygneus*" (1982, p. 93); however, he did not illustrate these specimens and their affinities are not discussed here. A single, water worn M3 from a middle Tiffanian locality, UADW-1, near Red Deer, Alberta, is virtually identical to M3's of *C*. *cygneus* from Swan Hills and may be referable to that species (pers. observ.; Fox, pers. comm.).

A larger and more complete sample of *C*. *cygneus* has been collected at the type locality by field parties from the University of Alberta during 1985, 1986, and 1987..These specimens, described above, raise several questions about the relationship of *C*. *cygneus* *sensu* Krause (1978), Rose (1975a), and Holtzman (1978) to *C*. *cygneus* from the Swan Hills.

Although the sample referred to *C*. *cygneus* from Roche Percée is still much larger than the Swan Hills sample, the new, albeit relatively small, sample size from Swan Hills site 1 gives the first picture of the degree of variability present in *C. cygneus* from the type locality. As stated above, all referred p4's from the type locality preserving the crown (N=9) possess five apical cusps, in contrast to those from Roche Percée:

> "The modal number of cusps along the apical crest (excluding the talonid cusp) is six (18 specimens). In four of these specimens the anterior most cusp is only incipiently developed. Two p4's have seven cusps and one, lacking the anterior most cusp, has only five" (Krause, 1978: p. 1253).

In *C. cygneus* from Swan Hills the highest cusp above the base of the crown is the third apical cusp. The addition of apical cusps to the crown of p4 in the Roche Percée sample creates a condition where the fourth or fifth apical cusp is the highest. In measurements of length and width for p4 the Swan Hills sample overlaps the bottom of the range for the Roche Percée sample, and no significant difference appears to be present. However, the Roche Percée p4's are generally much higher crowned (see Fig. 5) and a significant difference is noted (Student's *t*-test) when measurements of labial height ($.0005 < p < .005$) and lingual height ($p < .0005$) for the two samples are compared[11]. When a Roche Percée p4 approaches a Swan Hills p4 in size and crown height, the Roche Percée specimen invariably possesses six apical cusps. In addition to the above, p4 of *C. cygneus* from Roche Percée tends to have a greater degree of labial exodaenodonty than the Swan Hills specimens.

Further differences in the Roche Percée sample, relative to the Swan

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[11] Statistics for the two samples are as follows: a) *Carpodaptes cygneus* from Roche Percée -- labial height: N=29, M=2.39, SD=0.198; lingual height: N=29, M=1.82, SD=0.142; b) *C. cygneus* from Swan Hills -- labial height: N=8, M=2.15, SD=0.120; lingual height: N=9, M=1.63, SD=0.071. The unpaired t-values for labial and lingual height are 5.757 and 3.289, respectively.

Hills sample of *C. cygneus*, are noted in tooth positions other than p4, and are as follows: 1) mean size for all tooth positions generally slightly larger; 2) paraconid slightly more anteriorly positioned on m1's, producing a more obtuse angle between the meta-, para-, and protoconid (approximately one hundred and twenty degrees) as compared to the Swan Hills m1's (angle approximately one hundred and five degrees); 3) the height of the trigonid relative to the talonid on m1's is slightly greater; 4) m2's on the average have a less anteroposteriorly compressed trigonid; 5) the labial base of the crown on m2 appears more squared and extends further anteriorly; 6) the widths of talonids on lower molars is relatively greater; 7) posterior upper premolars and molars are relatively more transverse; 8) P3 and P4 possess a greater degree of crenulation of the enamel on cusp slopes; 9) in the maxillary fragments of *C. cygneus* from Roche Percée (UALVP 8799 and 8800), M2 is as long as, or longer than, but less transverse than M1. This is the opposite of the situation seen in the single maxillary fragment of *C. cygneus* from Swan Hills (UALVP 22647) in which M2 is shorter and more transverse than M1.

Although the preceeding list seems to effectively separate the two samples, it must be noted that there is a great deal of variation within each sample and overlap of all characters occurs between the two samples. Intuitively I am inclined to separate them; however, both samples also share numerous characters in common and the sample size from the type locality is still relatively small. I feel that the removal of the Roche Percée sample from *C. cygneus* would at this time be premature and in the interim the Roche Percée sample is here considered to be a variant of *C. cygneus*

Rose (1975a) and Krause (1978) noted the following differences between *Carpodaptes cygneus* and *C. hobackensis*: p4 of *C. hobackensis* has less pronounced vertical ribs lingually, a less developed posterior apical cusp, and a deeper posterolingual depression. Further, *C. hobackensis* has a "weak cingulum that descends down the lingual face of the paraconid on m1" (Krause, 1978: p. 1256). The increase in the sample size from Swan Hills and a comparison of this new sample to a good cast of the type for *C. hobackensis* (UMMP 27233) and to UMMP 27253, an incomplete p4 in a dentary fragment referred by Dorr (1952), allows for the addition of several more characters to this list. The p4 of *C. hobackensis* is sharper peaked than in *C. cygneus* and possesses a flat or even slightly concave labial face compared to the convex labial face on p4 of *C. cygneus*. In addition, the paraconid on m1 of *C. hobackensis* is directly anterior to the protoconid and not anterolingually positioned as in the Swan Hills specimens (an indication that *C. cygneus* may be slightly more primitive in morphology and hence older than *C. hobackensis*). These differences serve to augment the interpretation that *C. cygneus* is indeed a valid species and not a junior synonym of *C. hobackensis*, contrary to the interpretation of Szalay and Delson (1979, p. 98).

Holtzman's (1978) conceptualization of *C. cygneus* may have been different if he had access to the larger sample now available from the type locality. In general, the characters used by Holtzman (1978) to differentiate between *C. hobackensis* and *C. cygneus* from the Brisbane and Judson localities, are the characters that appear to differentiate the Swan Hills sample from the Roche Percée sample of *C. cygneus*. UALVP 22353, a right dentary fragment with p4-m1, has a p4 with reduced internal vertical ribs and posterior apical cusp, and a relatively well-developed posterointernal depression. It is very similar to SMM P77.6.62, a left mandible with p4-m3 of *C. hobackensis* illustrated in Holtzman (1978: p. 76, fig. 9.1-3). As well, the paraconid on m1 of SMM P77.6.62 is anterolingual to the protoconid and not anteriorly positioned as in *C. hobackensis*.

According to Holtzman, p4 of *C. cygneus* relative to *C. hobackensis* "has steeper anterior and posterior slopes, a higher penultimate cusp with a stronger internal ridge, no posterointernal concavity, and more distinct talonid cusp and crests" (1978, p. 51). The p4's of C. cygneus from Roche Percée have steeper anterior and posterior slopes than seen on p4's of C. cygneus from Swan Hills. This is correlated with the higher p4 crown in the Roche Percée sample. The p4's in the Swan Hills sample are relatively lower crowned, like the known p4's of C. hobackensis. The development of the talonid cusp and crests, and the position of the penultimate cusp and the development of the internal ridge from it, are variable characters in both the Swan Hills and Roche Percée samples, and as stated in the description above, some p4's in the sample from the type locality for C. cygneus are very similar to the p4's illustrated for C. hobackensis by Holtzman. Holtzman (1978, p. 51) stated that p4's of C. cygneus lacked a posterointernal concavity. This is certainly in error, for again, this character is seen to be variably developed on p4's in the Canadian samples, although not as well-developed as on p4 of C. hobackensis. In addition, the p4 of C. cygneus from the Brisbane locality illustrated by Holtzman (1978: p. 76, fig. 9.7) appears to show the presence of a relatively well-developed posterointernal depression.

The upper dentition of C. hobackensis was first described by Holtzman based on a single maxillary fragment (SMM P77.7.133) from the Judson locality possessing P2-M2 (1978: p. 76, fig. 9.4). The P3 on this specimen is virtually indistinguishable from UALVP 11719 and 22197 from the Swan Hills. The anterior projection of the anteroexternal cusp on P3 is a variable character on the Swan Hills sample and is well-developed on UALVP 11719. This character, which was used by Holtzman to distinguish his C. cygneus from C. hobackensis , is thus not a character distinguishing C. hobackensis from C. cygneus, but rather, a character which serves to further unite the

Judson C. hobackensis with the Swan Hills C. cygneus. The placement of the posterointernal cusp on P3 is another character used to differentiate the two North Dakota samples. Holtzman sees the posterointernal cusp as occupying a "more forward postion" in C. cygneus and being located on the posterointernal corner of the crown in C. hobackensis (1978, p. 51). Both of these character states are observed in the Swan Hills sample.

A maxillary fragment of C. cygneus from Swan Hills possessing P4-M2 (UALVP 22647) is virtually indistinguishable from the P4-M2 on SMM P77.7.133. The P4 on UALVP 22647 is only slightly less anteriorly inflected than the P4 on SMM P77.7.133. In the Roche Percée sample this character is seen to be quite variable and thus is not considered here to be of significant taxonomic value. UALVP 22647 also possesses relatively deep anterointernal and posterointernal basins on P4 that are at least as deep as those described and illustrated for C. hobackensis by Holtzman (1978: p. 76, fig. 9.4; this character is also seen to be quite variable in the Roche Percée sample). Holtzman states that for C. cygneus the "upper molars are also more transverse and have better developed pre- and postcingula and hypocones" (1978, p.51). This is not true for the Swan HIlls sample of C. cygneus, but does appear to hold for C. cygneus from Roche Percée.

The specimens referred to Carpodaptes cygneus and illustrated by Holtzman (1978: p. 76, fig. 9.5-15) have counterparts in the sample of C. cygneus from Roche Percée, but not in the sample from Swan Hills. Alternatively, the specimens referred to C. hobackensis by Holtzman have counterparts in the Swan Hills specimens of C. cygneus but not in the sample from Roche Percée. It would seem then, that Holtzman may be correct in identifying two suites of carpolestid specimens, one from the Brisbane locality and one from the Judson locality; however, whether the Brisbane suite belongs to C. cygneus and the Judson suite to C. hobackensis now seems contentious, and a careful comparison between the North Dakota samples and the larger suite of specimens from the type locality of *C. cygneus* will have to be made. Not having viewed the North Dakota samples firsthand, I am currently in no position to make an unqualified statement.

It thus appears that the picture of carpolestid diversity during the middle and late Tiffanian is may be more complicated than previously envisioned (a point discussed by Fox [1984] in relation to *Elphidotarsi*[illegible]. What remains to be done, then, is the collection of further specimens from the type locality of *C. cygneus* and a careful comparison between these and the samples referred to *C. cygneus* from the Roche Percée and Brisbane localities, and the sample referred to *C. hobackensis* by Holtzman (1978). I do feel; however, that the samples from Roche Percée and Brisbane may ultimately be referable to a new species of *Carpodaptes* and the Judson sample may be found to represent *C. cygneus* and not *C. hobackensis*.

Order DERMOPTERA ILLIGER, 1811

Family PLAGIOMENIDAE MATTHEW, 1918

Genus *Elpidophorus* SIMPSON, 1927

*Elpidophorus clivus*, new species

(Fig. 6, 7, 17 F-L, 18 A-L, 19 A-C; Table 11, 12)

*Etymology*. -- Latin: *clivus* = hill; in reference to the Swan Hills.

*Type specimen*. -- UALVP 22317, a right dentary with p4, m1-3.

*Type locality*. -- Swan Hills site 1, Paskapoo Formation, Swan Hills,

Table 11: Measurements and descriptive statistics of the lower dentition of Elpidophorus clivus, new species, Swan Hills local fauna, Alberta.

| Measurement | | N | OR | M±SE | SD | CV |
|---|---|---|---|---|---|---|
| i1 | L | 1 | 4.6 | - | - | - |
| | MXD | 1 | [illegible] | [illegible] | - | - |
| | MND | 1 | 1.5 | - | - | - |
| ?i3 | L | 1 | 3.8 | - | - | - |
| | MXD | 1 | 2.0 | - | - | - |
| | MND | 1 | 1.3 | - | - | - |
| p1 | L | 2 | 1.5-1.7 | 1.60 ± .10 | .141 | 8.8 |
| | W | 2 | 1.2-1.3 | 1.25 ± .05 | .071 | 5.7 |
| p2 | L | 1 | 2.1 | - | - | - |
| | W | 1 | 1.6 | - | - | - |
| dp3 | L | 2 | 2.2-2.3 | 2.25 ± .05 | .071 | 3.1 |
| | W | 2 | 1.4-1.5 | 1.45 ± .05 | .071 | 4.9 |
| p3 | L | 3 | 2.2-2.5 | 2.30 ± .10 | .173 | 7.5 |
| | W | 4 | 1.7-1.8 | 1.73 ± .03 | .058 | 3.3 |
| dp4 | L | 2 | 3.2 | - | - | - |
| | AW | 2 | 1.8-2.0 | 1.90 ± .10 | .141 | 7.4 |
| | PW | 2 | 2.1-2.3 | 2.20 ± .10 | .141 | 6.4 |
| p4 | L | 4 | 3.2-3.4 | 3.30 ± .06 | .115 | 3.5 |
| | AW | 5 | 2.3-2.4 | 2.36 ± .02 | .055 | 2.3 |
| | PW | 8 | 2.2-2.7 | 2.45 ± .07 | .193 | 7.9 |
| m1 | L | 3 | 3.1-3.2 | 3.17 ± .03 | .058 | 1.8 |
| | AW | 4 | 2.5-2.6 | 2.55 ± .03 | .058 | 2.3 |
| | PW | 3 | 2.6-2.7 | 2.63 ± .03 | .058 | 2.2 |
| m2 | L | 5 | 3.0-3.5 | 3.26 ± .10 | .230 | 7.1 |
| | AW | 6 | 2.3-2,7 | 2.48 ± .05 | .133 | 5.4 |
| | Pw | 6 | 2.6-2.9 | 2.77 ± .04 | .103 | 3.7 |
| m3 | L | 3 | 3.9-4.1 | 4.00 ± .06 | .100 | 2.5 |
| | AW | 4 | 2.3-2.7 | 2.48 ± .09 | .171 | 6.9 |
| | PW | 6 | 2.2-2.5 | 2.33 ± .04 | .103 | 4.4 |

Table 12: Measurements and descriptive statistics of the upper dentition of Elpidophorus clivus, new species, Swan Hills local fauna, Alberta.

| Measurement | | N | OR | M±SE | SD | CV |
|---|---|---|---|---|---|---|
| P1 | L | 2 | 1.8-1.9 | 1.85 ± .05 | .071 | 3.8 |
| | W | 2 | 1.3-1.4 | 1.35 ± .05 | .071 | 5.2 |
| P2 | L | 2 | 1.9 | - | - | - |
| | W | 2 | 1.3-1.4 | 1.35 ± .05 | .071 | 5.2 |
| P3 | L | 3 | 3.1-3.2 | 3.13 ± .03 | .058 | 1.8 |
| | W | 2 | 2.9-3.1 | 3.00 ± .10 | .141 | 4.7 |
| DP4 | L | 4 | 3.1-3.2 | 3.14 ± .03 | .058 | 1.8 |
| | W | 3 | 2.3-2.5 | 2.37 ± .07 | .115 | 4.9 |
| P4 | L | 5 | 3.4-3.5 | 3.44 ± .02 | .055 | 1.6 |
| | AW | 3 | 4.0-4.3 | 4.13 ± .09 | .153 | 3.7 |
| | PW | 4 | 3.9-4.3 | 4.05 ± .10 | .191 | 4.7 |
| M1 | L | 9 | 3.1-3.4 | 3.28 ± .04 | .109 | 3.3 |
| | AW | 6 | 3.9-4.7 | 4.50 ± .12 | .303 | 6.7 |
| | PW | 8 | 4.0-4.6 | 4.41 ± .07 | .196 | 4.4 |
| M2 | L | 7 | 3.1-3.4 | 3.27 ± .04 | .095 | 2.9 |
| | AW | 7 | 4.8-4.9 | 4.83 ± .02 | .049 | 1.0 |
| | PW | 7 | 4.3-4.6 | 4.44 ± .04 | .098 | 2.2 |
| M3 | L | 3 | 2.7-2.8 | 2.77 ± .03 | .058 | 2.1 |
| | AW | 3 | 4.1-4.4 | 4.23 ± .09 | .153 | 3.6 |
| | PW | 3 | 3.2-3.6 | 3.40 ± .12 | .200 | 5.9 |

Alberta (exact coordinates are available to qualified researchers through the Laboratory for Vertebrate Paleontology, Department of Zoology, University of Alberta).

*Referred Specimens*. -- i1: UALVP 22378, 22379; ?i3: UALVP 23839; p1: UALVP 22712, 22717; p2: UALVP 22258; dp3: UALVP 23862-23864; p3: UALVP 22330, 22345, 22346; dp4: UALVP 22465, 22502, 22593, 22714; p4: ROM 05621, 05627, UALVP 22[illegible], 22284-22289, 22316; m1: UALVP 22282, 22283, 22375, 22376, 22588, 22716, 22718; m2: UALVP 22279, 22281, 22589, 22590; m3: ROM 05613, UALVP 22275-22277, 22373, 22591, 22592, 22715, 22719; fragment of left dentary with m1-m2: UALVP 22318; fragment of left dentary with m2-m3: ROM 05612; I1: UALVP 22472, 22492, 22527; P1: UALVP 22625, 23842; P2: UALVP 22409, 22711; P3: UALVP 22263, 22264, 22556; DP4: ROM 05615, UALVP 22327, 22473, 22491, 22562, 22678; P4: ROM 05610, UALVP 22259-22262, 22361, 22362, 22488, 22557-22561, 22563-22565, 22713, 22720; M1: UALVP 5783, 22265-22268, 22363-22371, 22488, 22489, 22514, 22566-22573, 22721, 23841; M2: ROM 05609, UALVP 22269-22273, 22372, 22518, 22574-22581, 22722, 23838, 23840; M3: ROM 05611, UALVP 22274, 22278, 22374, 22582-22587; fragment of right maxillary with P4-M1: UALVP 22377.

*Localities*. -- Swan Hills sites 1 and 2, Paskapoo Formation, Alberta.

*Diagnosis*. -- A species of *Elpidophorus* approximately 10-15% smaller than *E. elegans*, and 10-15% larger than *E. minor*; differing from *E. elegans* and *E. minor* in having a p4 that is more fully molariform with the trigonid closed more anterolingually as the result of a relatively greater posterolingual placement of the paraconid, and the talonid extending further labially relative to the trigonid; differing from E. elegans in having the hypoconulid on m1-2 much reduced, the mesoconid on m1-3 relatively less developed, a more fully molariform P4 with a well-developed mesostyle effectively separating the subequal paracone and metacone, and a well developed hypocone on M1-3 (particularily on M2).

## DESCRIPTION

i1. -- The crowns of the two referred specimens (UALVP 22378 and 22379) are bilobed with the lateral lobe being the smaller of the two and positioned lower on the crown than the mesial lobe. The mesial edge of UALVP 22379 (Fig. 17 F,G) is relatively straight and flattened where it articulates with the central incisor in the opposite half of the lower jaw, creating a sharp, angular edge leading onto the lingual face. On the lateral edge of UALVP 22379, below the lobe, there is a concave facet into which the mesial edge of the i2 fits. This helps create a ridge extending down the tooth along the lateral edge of the lingual face. A low, medial ridge extends down the lingual slope of UALVP 22379 from near the tip of the mesial lobe towards the base where it is truncated by a missing portion of the specimen. This ridge produces two shallow, concave regions that divide the posterior slope of the incisor into subequal halves.

?i3. -- The single specimen tentatively referred here (UALVP 23839: Fig. 17 H,I) has the lateral tip of the crown damaged; however, a small mesial cusp is present indicating the crown was at least bilobed. A shallow depression is present on the dorsolingual slope of the incisor that separates the mesial cusp from the lateral portion of the crown tip. An interdental wear facet is present on the mesial edge of the mesial cusp. Below this facet, the edge of the crown becomes concave and appears to be canted mesially when viewed lingually. Approximately one-third of the way up the lateral edge of the crown is what appears to be a tiny, incipiently developed cusp. The root is strongly mesiolaterally compressed.

p1. -- The single-rooted p1 is longer anteroposteriorly than wide (Fig. 17 J). A sharp cristid runs the anteroposterior length of the tooth from the posterior base of the protoconid, through the apex, to the anterior base where it makes a sharp turn lingually to end at an incipiently developed paraconid. The protoconid is relatively tall and leans anterolingually. The shape of the cristid makes it appear that the protoconid is slightly concave lingually.

The talonid is small with a well developed hypoconid. An incipient postcristid extends lingually from the hypoconid to the posterolingual corner of the talonid.

p2. -- The single referred p2 (UALVP 22258: Fig. 17 K,L) is double-rooted and intermediate in size and morphology between p1 and p3. Both the paraconid and metaconid are small, only incipiently developed. The talonid possesses a well-developed hypoconid and an incipiently developed entoconid. The cristid obliqua becomes confluent with a sharp cristid running the anteroposterior length of the tooth. In length and transverse width, the talonid on p2 is shorter and narrower, respectively, than the talonid observed on p3. On the labial base of the hypoconid is a small, conical cuspule.

dp3. -- The trigonid of the double-rooted dp3 is four-cusped and leans strongly anterolingually (Fig. 18 A-C). The paracristid extends anterolabially from the apex of the protoconid to a small, conical paraconid situated on the base of the crown slightly anterolabial to the protocone apex. The relatively sharp protocristid descends posterolingually to a metaconid that is little more than a swelling on the protocristid. The metaconid is at approximately the same level on the crown as the paraconid. A cristid on the posterolabial slope of the protoconid connects the apex of the protoconid to an accessory cusp as large as the paraconid on the posterolabial side of the protoconid. This accessory cusp is situated on the crown at a level slightly higher than the paraconid and metaconid. The talonid of dp3 occupies approximately one-quarter the length of the crown. The moderately deep basin is just under half the width of the talonid. The variably developed cristid obliqua and short entocristid are roughly parallel to each other and enclose the basin labially and lingually, respecively. On UALVP 23862 the talonid possesses an incipient hypoconulid flanked by a tiny entoconid and hypoconid. Cingulids are present anterolabially below the paraconid and on UALVP 23862 on the base of the crown below the hypoflexid. The enamel is weakly crenulated.

p3. -- p3 is almost as wide transversely as long (Fig. 18 D). As on p1 and p2 there is a sharp cristid running the anteroposterior length of the tooth that turns lingually at the anterior base of the protoconid and merges into a variably developed paraconid. On UALVP 22345 and 22330, the paraconid is incipiently developed, but on UALVP 22346 it is developed as a relatively large cusp. The protoconid leans anterolingually. At the posterolingual base of the protoconid on UALVP 22330 there is an incipiently developed metaconid. This region is worn on UALVP 22345 and the metaconid is absent.

One quarter the total length of the tooth is composed of the incipiently basined talonid, which is nearly as wide transversely as the trigonid and possesses three cusps, a well developed hypoconid, and small hypoconulid and entoconid. Wear and breakage on UALVP 22345 partly obscures the hypoconid and hypoconulid. Extending anterolingual from the hypoconid is a short cristid obliqua that is continuous with the cristid that runs the length of the tooth. Entocristids can be weakly developed or absent.

On UALVP 22330 and 22345 there is an elongate cuspule developed just above the base of the crown on the anterolabially-facing wall of the hypoflexid. This cuspule is well-developed on UALVP 22330 and, although smaller on UALVP 22345, it is still easily identified. UALVP 22345 also possesses a second tiny cuspule at the same level, posterior to the first. These cuspules seem to foreshadow the labial cingulids present on p4-m3.

dp4. -- In occlusal view the crowns of the three most nearly complete referred specimens (UALVP 22465, 22502, and 22593) increase progressively in width posteriorly (Fig. 18 E). The trigonids lean strongly anterolingually and are subquadrate, possessing a cusp in each of the four corners. The metaconid, the largest and tallest cusp on the trigonid, is nearly triangular in occlusal view with a flattened lingual surface and a relatively flat posterior wall characterized by a series of vertical excavations and enamel ridges. The metaconid is connected to the smaller labial protoconid by a weak protocristid. The posterior wall of the protoconid is smooth, lacking the ridges and excavations present on the metaconid. A low, V-shaped cristid connects the protoconid anteriorly to a well-developed, conical accessory cusp approximately one-half of its height. The crown anterior to the metaconid and protoconid on UALVP 22502 is missing, and on UALVP 22465 and 22593, the anterolingual corner of the crown is slightly damaged, obscuring some of the structure of the paraconid; however, the paraconid appears to have been slightly taller and larger than the anterior accessory cusp, flattened anteroposteriorly, and connected to the accessory cusp by a high, strong, ridge-like cristid.

The talonid is wider transversely than the trigonid and is approximately one-third the anteroposterior length of the crown. The entoconid is nearly conical in shape, leans slightly lingually, and is the tallest cusp on the talonid. The hypoconid is the largest cusp on the talonid, leans lingually, and is subcrescentic. On UALVP 22465, 22502, and 22714, there is evidence of an incipiently developed mesoconid on the cristid obliqua. The hypoconulid is positioned high on the posterolingual base of the entoconid, is roughly conical in shape, and connected to the hypoconid by the postcristid. On UALVP 22714, the hypoconulid is separated from the entoconid by a narrow, V-shaped notch. The talonid basin is relatively deep and the talonid notch possesses a sharp ventral apex.

A shelf-like postcingulid descends ventrolabially from the posterolabial base of the hypoconulid to a point on the posterior base of the hypoconid immediately below the apex of the cusp. An incomplete, cuspate labial cingulid extends along the base of the protoconid to the posterolabial base of the anterior accessory cusp on UALVP 22465 and 22593. On UALVP 22465, part of a horizontal, shelf-like precingulid is present below the anterior accessory cusp. This is truncated by anterolingual breakage of the crown.

The tooth is two-rooted with the posterior root being longer anteroposteriorly and wider transversely than the anterior root.

p4. -- p4 is almost fully molariform, the main difference between it and the lower molars being in the positioning and size of the paraconid, which is cuspate and less shelf-like, larger, and placed more anterolabially (Fig. 18 F). The paraconid is flattened anteroposteriorly, creating a somewhat elongated oval in occlusal view. The paraconid, situated anterolabial to the metaconid, is the smallest and shortest cusp on the trigonid. The metaconid is both the tallest cusp and has the widest base of the trigonid cusps. A shallow, concave depression on the posterior wall of the [illegible]onid produces a low, vertical, posterolabial ridge extending from below the tip of the metaconid to a point above the level of the talonid notch. The protoconid is intermediate between the metaconid and paraconid in the width of its base and cusp height. A deep, vertical excavation in the posterior wall of the protoconid begins at approximately the level of the ventral apex of the protocristid and ends at a level just below the point where the cristid obliqua meets the trigonid. Below the protocristid notch and between the excavations on the posterior walls of the metaconid and protoconid are two ridges. One extends ventrolabially across the base of the protoconid to become confluent with the cristid obliqua. The second ridge extends ventrolingually across the base of the metaconid to fade before it reaches the floor of the talonid basin. The protoconid is placed slightly more anterior on the trigonid than the metaconid. The trigonid leans anterolingually.

The talonid is almost as long anteroposteriorly as the trigonid and is wider transversely. The entoconid is the tallest cusp on the talonid and is roughly conical in shape. A ridge descends down the labial slope of the entoconid from the tip of the entoconid to a point just dorsal to the bottom of the basin. The hypoconid is the largest cusp on the talonid and is subcrescentic. Hypoconulids on the referred specimens (N=9) show variation in development from relatively well-developed (e.g., UALVP 22285) to virtually absent (e.g., UALVP 22287). The mesoconid on most referred specimens is little more than a slight bulge on the cristid obliqua. On UALVP 22280 and 22289 it is a recognizable, though small, cusp. On several specimens (e.g., UALVP 22286) there is a small cuspule on the postcristid between the hypoconid and hypoconulid.

On unworn specimens, a papillate precingulid passes posterolabially around the protoconid to merge with a papillate labial cingulid. The labial cingulid does not proceed past the anterolabial edge of the hypoconid. A postcingulid extends from the posterolabial base of the hypoconid dorsolingually to a point below the small cuspule on the postcristid. Lingual cingulids are absent.

m1. -- The trigonid leans strongly anterolingually. The paraconid, considerably compressed anteroposteriorly, is reduced to a low, broad lophid slightly anterolabial to the metaconid (Fig. 18 F). The crest of this lophid is approximately one-half the height of the metaconid. The tallest and strongest cusp on the trigonid is the metaconid. A relatively robust protocristid connects the metaconid to the protoconid, which is approximately two-thirds the height of the metaconid. An enamel ridge runs vertically down the posterolingual corner of the metaconid from just below the apex of the cusp to the V-shaped talonid notch. The posterior wall of the trigonid is characterized by deep, roughly vertical excavations, and three or four short, rugose enamel ridges. The size, shape, and positions of these excavations and ridges varies among the referred specimens. When the teeth are heavily worn these become obliterated.

The talonid is much wider transversely and longer anteroposteriorly than the trigonid. The talonid basin is deep, sloped steeply and closed off on all sides. The entoconid is the tallest cusp on the talonid and more nearly conical than the larger, subcrescentic hypocone. A variably developed mesoconid is present on the cristid obliqua. On UALVP 22588, this cusp is small but easily identified, whereas on UALVP 22317 and 22283, two specimens with little wear, the mesoconid is barely identifiable. The anterolabial wall of the hypoconid is shallowly excavated by two depressions separated by a short, low enamel ridge on UALVP 22317, 22282, and 22283. These depressions are located below the cristid obliqua between the apex of the hypoconid and mesoconid. The posterior wall of the hypoconid is rugose. From the hypoconid, the postcristid runs relatively straight towards the entoconid to an incipiently developed cuspule. The postcristid then veers sharply posterolingually to the posterolabial base of a very small, almost incipiently developed hypoconulid situated on the posterolabial base of the entoconid. The postcristid continues as a short, well-developed ridge running from the hypoconulid up the posterolabial wall of the entoconid to a point just ventral to the apex of the entoconid. An enamel ridge extends ventrally towards the talonid basin on the labial wall of the entoconid. This ridge fades before reaching the bottom of the talonid basin, and together with the postcristid and hypoconulid, creates a subquadrate depression open anterolabially.

A papillate precingulid extends posterolabially around the base of the protoconid to join with a papillate labial cingulid, which in all referred specimens (N=7) is incomplete around the labial base of the hypoconid. A relatively wide, shelf-like postcingulid runs ventrolabially from the posterior base of the hypoconulid to the posterolabial corner of the hypoconid. Lingual cingulids are absent.

m2. -- In many respects m2 is essentially identical to m1 (Fig. 18 F); however, it is slightly larger than m1 and can be differentiated by the following: the paraconid is less lophid-like and more procumbent and shelf-like than on m1; the metaconid appears much taller on m2 when viewed lingually, owing to a more ventral placement of the procumbent paraconid; the trigonid is longer anteroposteriorly relative to the talonid than on m1; the mesoconid is relatively larger on m2; the cuspule on the postcristid between the hypoconid and hypoconulid is larger and the postcristid does not veer sharply posterolingually from the cuspule as on m1; the hypoconulid is equal to, or smaller than the hypoconulid on m1, and is placed more anteriorly on the base of the entoconid; an enamel ridge runs a short distance anterolingually into the talonid basin from the cuspule on the postcristid, and ends before intersecting the enamel ridge extending down the labial face of the entoconid.

m3. -- The trigonid leans strongly anterolingually as on m1 and m2. m3 is similar to m2 in possessing a procumbent and shelf-like paraconid placed slightly anterolingual to the metaconid, the metaconid being the largest and tallest cusp on the trigonid, and the protoconid positioned directly labial to, and one-half the height of the metaconid. The protocristid is strong, U-shaped and on the type, UALVP 22317 (Fig. 18 F), has an incipiently developed cuspule approximately one-half way down the posterolabial corner of the metaconid. A vertical enamel ridge runs down the posterolingual corner of the metaconid from near the apex of the cusp to the V-shaped talonid notch. The posterior walls of the metaconid and protoconid are deeply excavated with a series of rugose enamel ridges present between the excavations and below the protocristid notch. One of these enamel ridges on the posterior wall of the trigonid becomes confluent with the cristid obliqua.

The talonid is narrower transversely than the trigonid. The talonid basin is deep, the walls are steeply sloped, and the basin is closed on all sides. On the cristid obliqua is a small mesoconid approximately the same size as the m2 mesoconid. The hypoconid has the largest base of the talonid cusps, is subcrescentic, and has a rugose anterolabial wall. On UALVP 22317 and ROM 05612, the anterolabial wall of the hypoconid is deeply excavated. The tallest trigonid cusp is the conical entoconid, which is placed directly lingual to the hypoconid. The cuspule present on the postcristid of m1 and m2 is larger and better developed on m3. However, with the posterior movement of the hypoconulid, the cuspule is now positioned just posterolabial to the base of the entoconid, between the latter and the hypoconid. The strong postcristid connecting the hypoconid to the cuspule does not extend lingually beyond the cuspule. Directly posterior to the cuspule is a large, conical hypoconulid. The hypoconulid may be equal, or subequal to the entoconid in size and height. On some referred specimens (e.g., UALVP 22276) a short, robust cristid connects the hypoconulid anteriorly to the cuspule. This cristid may be homologous to the section of the postcristid extending from the cuspule to the hypoconulid on m1 and m2. A short, vertical enamel ridge on the labial wall of the entoconid curves posterolabially at the base of the entoconid towards the postcristid cuspule. This ridge fades before reaching the base of the cuspule.

As on p4-m2, a papillate precingulid is continuous with a labial cingulid. The labial cingulid is incomplete around the base of the hypoconid and a short postcingulid extends from the anterolabial corner of the hypoconulid to the posterior base of the hypoconid. A lingual cingulid is absent.

I1. -- The three tentatively referred specimens are fragments of enlarged central incisors. The most complete specimen, UALVP 22492 (Fig. 6), consists of the dorsal base of a crown resting on the ventral portion of the root. A relatively large posterolateral cusp is connected by a crista to a smaller mesiodorsal cusp. A mesially curving crista connects the posterolateral cusp posterodorsally to an incipiently developed cuspule. The posterolateral cusp is connected to the missing portion of the crown by an anteroventrally directed crista. The portion of the crown anterior to the posteromesial cusp is gently curving anteroventrally to where it is truncated by the missing ventral portion of the crown. Mesially, laterally, and posteriorly the crown overhangs the root slightly.

P1. -- The two referred specimens, UALVP 22625 and 23842, are single rooted and resemble P2 in general crown morphology (Fig. 18 G,H). A weak crista extends along the anteroposterior length of the crown from a weak, shelf-like area posteriorly that possesses an incipient metacone, through the apex of the conical paracone, to a very small, incipiently developed parastyle anteriorly. The paracone is relatively tall, positioned slightly anterior to the middle of the crown, and appears slightly anteriorly procumbent. The root is almost circular in cross-section.

P2. -- The single referred specimen, UALVP 22711 (Fig. 18 I), is double-rooted and somewhat oval in occlusal view. The paracone is relatively tall and possesses a sharp crest posteriorly that extends from the tip of the cusp to the base of the paracone, where a very small metacone is located. Anteriorly, the crest is greatly reduced and ends at an incipiently developed parastyle. In cross-section the anterior root is almost circular and the larger posterior root is oval.

P3. -- P3 is semimolariform, three-rooted, and is as long, or slightly longer anteroposteriorly as wide. In occlusal view the crown appears to take the shape of an equilateral triangle (Fig. 18 K). The enamel on the crown is crenulated. The protocone is small, conical and placed directly lingual to the paracone. The paracone and metacone are connate and joined to approximately five-eighths of their height. The apices are joined by short, sharp postparacrista and premetacrista. The metacone is approximately two-thirds the height of the paracone. Hypocones are absent on the two referred specimens that retain the lingual half of the crown. Directly anterior to the apex of the paracone, the preparacrista connects the paracone to a relatively large, conical parastyle. The postmetacrista connects the metacone posteriorly to a small metastyle.

Development of the conules is variable. UALVP 22263 lacks both conules; however, one of the tiny cuspules on the cuspidate preprotocrista may be an incipiently developed paraconule. UALVP 22264 lacks a paraconule but possesses a small, though readily identifiable, metaconule. The paraconule on UALVP 22556 is relatively large; however, breakage obscures the presence or absence of a metaconule.

Precingula can be incipiently developed or absent. Postcingula on UALVP 22263 and 22264 are well-developed. A narrow, papillate ectocingulum, which can be reduced at the labial base of the paracone, is present on all referred specimens.

DP4. -- Deciduous P4's are three-rooted, roughly triangular in outline when viewed occlusally, and are longer anteroposteriorly than they are wide (Fig. 18 J). They are essentially molariform in possessing the three main cusps (paracone, metacone, and protocone), para- and metaconules, mesostyles, and para- and metastyles; however, they lack hypocones and are slightly shorter anteroposteriorly and one-half the transverse width of M1. They thus appear very different from M1.

The paracone is the largest and tallest cusp on the crown and is conical when viewed occlusally. The metacone varies from two-thirds to three-quarters the height of the paracone, and owing to the labial curving of the strong pre- and postmetacristae, appears to have a slightly concave labial face. The conical protocone is shorter than the metacone, leans slightly labially and to a small extent is displaced anterior to a point equidistant between the apices of the paracone and metacone. The postparacrista and premetacrista curve labially to meet at a variably developed mesostyle on the ectocingulum. On UALVP 22491 the mesostyle is a small cuspule, whereas on UALVP 22473 it is a relatively large cusp despite the presence of some wear. The preparacrista connects the paracone anteriorly to a large, conical parastyle. The metastyle is located at the posterolabial corner of the crown atop the relatively tall, ridge-like postmetacrista. Generally, the metaconule is larger than the paraconule, except for UALVP 22327 on which the paraconule is small and the metaconule is only incipiently developed. The enamel on the crown is lightly crenulated.

Paracingula and metacingula are present and relatively strong. Precingula are absent or small. Postcingula are variably developed and range from incipient to well-developed. The papillate ectocingulum is best developed around the base of the metacone and is reduced around the base of the paracone.

P4. -- P4 is molariform, three-rooted, and has crenulated enamel. Paracone and metacone are equal in height and well separated by a strong mesostyle. In occlusal view the paracone is more conical than the metacone, which appears slightly concave labially due to the labial curvature of the well developed and sharp pre- and postmetacristae (Fig. 18 L). An enamel fold extends down the labial face of the metaconid onto the narrow stylar shelf. The postmetacrista is relatively high, ridge-like and connects the metacone to the metastyle at the posterolabial corner of the crown. The preparacrista does not curve labially, but connects the paracone directly anterior to the conical, sizeable parastyle. Conules are large and possess prominent cristae. On four of the referred specimens (e.g., UALVP 22720), the postparaconule crista is incipiently developed. The protocone, positioned directly lingual to the paracone, is intermediate in height between the conules and the paracone/metacone, being approximately three-quarters the height of the paracone/metacone. A small cuspule is developed on the postprotocrista where the latter meets the anterolingual base of the metaconule. Hypocones are invariably present and vary in size from small to relatively large; however, in no case do they reach the size or development seen on M1.

The ectocingulum is papillate, reasonably well developed around the labial base of the metacone, and may be reduced at the base of the paracone. The narrow, though pronounced, postcingulum extends from the posterolingual corner of the protocone to the posterolabial base of the metastyle. On one specimen, UALVP 22559, the postmetaconule crista intersects and terminates the postcingulum, the former continuing posterolabially as a metacingulum. The precingulum, slightly narrower than to as wide as the postcingulum, runs from the anterolingual base of the protocone towards the parastyle where it can be terminated by an intersecting preparaconule crista before reaching the base of the parastyle.

M1. -- The tallest cusps on the somewhat transversely elongate, relatively low crowned tooth are the paracone and metacone, which are equal in height and possess large enamel folds running down their labial faces onto a relatively wide stylar shelf (Fig. 19 A). The paracone is more nearly conical in shape when viewed occlusally than the subcrescentic metacone. The pre- and postparacone and metacone cristae make abrupt turns labially. The postparacrista and premetacrista remain well separated and run roughly parallel to each other before joining to produce a V-shaped centrocrista on the large mesostylar lobe. The preparacrista extends labially onto a well-developed parastylar lobe, the most lingually positioned of the stylar lobes, while the postmetacrista extends onto an equally well-developed metastylar lobe. The mesostylar lobe is on the posterior half of the tooth, positioned slightly anterolingual to the metastylar lobe. The protocone is the broadest based cusp on the crown, leans anterolabially, is subequal in height to the paracone/metacone, and positioned directly lingual to the paracone. A small, though well defined, cuspule, is present on the postprotocrista at the lingual base of the metaconule. Posterolingual to the protocone is the relatively large, well-developed hypocone, which tends to be somewhat anteroposteriorly elongate. Thus, when viewed occlusally the lingual portion of the crown appears almost square.

The conules are subcrescentic, large and bulbous, with distinct conule cristae. The metaconule is larger and taller than the paraconule, being approximately two-thirds the height of the paracone/metacone, while the paraconule is approximately one-half the height of the paracone/metacone. On several specimens (e.g., UALVP 22267 and 22567) the preparaconule crista possesses a small cuspule. The anteroposteriorly narrow trigon basin is relatively deep with steep slopes that can be quite crenulated (e.g., UALVP 22567). The transverse elongation of the trigon basin is enhanced by the labial placement of the mesostylar lobe and the wide separation of the postparacrista and premetacrista at the U-shaped mesostylar lobe. Where unworn the enamel of the crown generally possesses prominent crenulations.

The ectocingulum is papillate and discontinuous. The relatively broad and well-developed precingulum extends from the anterior base of the protocone to the anterolingual base of the paracone, where it is terminated by the preparaconule crista. The equally developed postcingulum is likewise terminated by meeting the postmetaconule crista at the posterolingual base of the metacone. Both conule cristae are continuous with the paracingulum and metacingulum, respectively. On UALVP 22364 and 22368 an incipiently developed pericone is present on the precingulum.

M2. -- M2 resembles M1 in having a low, subcrescentic metacone equal to the paracone in height, strong stylar lobes, a U-shaped centrocrista on the mesostylar lobe, a discontinuous, papillate ectocingulum, well-developed, bulbous conules with the metaconule larger than the paraconule, an anterolabially inclined protocone placed lingual to the paracone, broad, well developed cingula, strongly crenulated enamel, and a relatively deep, anteroposteriorly narrow, transversely elongate trigon basin (Fig. 19 C). M2 is slightly larger and more quadrate in occlusal view than M1. The stylar shelf is wider and the parastylar lobe placed further labially. In contrast to M1, the mesostylar lobe is generally the most labially placed of the stylar lobes. The metaconule is more nearly conical and a well-developed cuspule is present on the preparaconule crista of all specimens lacking wear. The hypocone is exceptionally well-developed and more nearly conical on M2, while the enamel between the hypocone and the cuspule on the postprotocrista is often sculptured with small enamel ridges and excavations. On some specimens (e.g., ROM 05609 and UALVP 22269) accessory cuspules are developed anterolingually on the base of the hypocone. Small pericones are variably developed on the precingulae of M2.

M3. -- Posterolabially, the crown of M3 is rounded and much reduced (Fig. 19 B). The ectocingulum, stylar shelf, and metastyle are lacking, and the metacone is two-thirds the height of, and more nearly conical than the paracone. The paracone, parastylar lobe, mesostylar lobe, and U-shaped centrocrista remain relatively large and well-developed. Conules are subequal in size, the metaconule being the shorter and more nearly conical of the two. The cuspule anterolabial to the paraconule on the preparaconule crista is present and variably developed. The protocone remains relatively large and broad based, but is more medial to the midline of the tooth and leans less anterolabially than on the more anterior molars. The preprotocrista ends lingual to the paraconule and the postprotocrista extends to a variably developed cuspule at the anterolingual base of the metaconule. Cingula remain relatively well-developed, although the postcingulum and metacingulum are somewhat reduced. Hypocones are variably developed and can be relatively [illegible] conical (e.g., UALVP 22278). On UALVP 22374, a lingual [illegible] a right M3, the lingual base of the protocone is papillate. Two specimens, UALVP 22278 and 22587, have a well-developed, conical cuspule on the lingual base of the protocone.

## DISCUSSION

Elpidophorus elegans was erected by Simpson (1927) as a new genus and species to include specimens collected in 1910 by Barnum Brown from exposures of the Paskapoo Formation near the town of Red Deer, Alberta ("Erickson's Landing"). At that time, he questionably referred Elpidophorus to the Oxyclaenidae. Later, Simpson described Elpidophorus patratus from Scarritt Quarry and referred both E. patratus and E. elegans to the Mixodectidae, while noting "Elpidophorus makes a definite approach toward the Plagiomenidae" (1936, p.16). He rejected a relationship between Elpidophorus and the Plagiomenidae on the grounds that Elpidophorus at the time was thought to be contemporaneous with the oldest known plagiomenid, Planetetherium. Still, Simpson suggested that similarities between the Mixodectidae (including Elpidophorus) and the Plagiomenidae might be due to descent from a common ancestor (ibid.).

Elpidophorus minor, known only from the type material (PU 14201), was described by Simpson (1937a) from the late Torrejonian Silberling Quarry, Crazy Mountain Basin, Montana. It has been proposed as the ancestor of later species of Elpidophorus by several authors (e.g., Szalay, 1969; Rose, 1975b), and present data, albeit based solely on the type of E. minor, does not refute such an interpretation. As well as the description of E. minor, Simpson (1937a) also listed characters that suggested a relationship between mixodectids and plagiomenids, basing his comparisons with mixodectids primarily on Elpidophorus. He concluded that a "relationship cannot be very close, if it exists at all" (1937a, p. 131), and provided a second list of criteria that distinguished the two families from each other. As noted by Rose (1975b), this latter list did indeed separate mixodectids from plagiomenids, but it did not effectively separate Elpidophorus from the latter.

Szalay (1969) synonymized E. patratus with E. elegans, and referred a small species of "Elpidophorus", "E." minutulus (erected by Dorr, 1958), to the genus Leptacodon, reducing the number of species in Elpidophorus to two[12]. Like most authors subsequent to Simpson (1937a), and before Rose (1975b), Szalay considered Elpidophorus a mixodectid and did not consider the available evidence enough to warrant "any special affinity" between mixodectids ("Elpidophorus in particular") and the Plagiomenidae (1969, p. 244). McKenna (1960) referred Elpidophorus to ?Plesiadapidae, incertae sedis, believing it possessed enlarged anterior incisors; however, as noted by Rose (1975b), at that time incisors belonging to Elpidophorus had not been

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[12] "E". minutulus has since been referred to Diacocherus minutus by Gingerich (1983, p. 239).

identified, and known dentaries did not preserve the anterior alveoli. Later, McKenna (1967) removed *Elpidophorus* from the Plesiadapidae.

*Elpidophorus* was referred to the Plagiomenidae, "the earliest probable representative of the order Dermoptera", by Rose (1975b, p. 676). Rose provided a list of characters and stated that "[virtually] all the features in which *Elpidophorus* differs from mixodectids are characters shared with plagiomenids, particularly with *Plagiomene*" (1975b, p. 678). Further support for the referral by Rose was provided by Rose and Simons (1977), who examined the molar wear patterns of *Elpidophorus elegans* and compared them to other members of the Plagiomenidae (in particular *Plagiomene*), and to the extant dermopteran *Cynocephalus*. They concluded that the "molar wear patterns and dental structure of *Elpidophorus* are so similar to those of *Plagiomene* that its allocation to the Plagiomenidae can hardly be doubted" (1977, p. 233). An examination of wear patterns on the molars of *Elpidophorus clivus* n. sp. (a late Tiffanian species closer in age to the younger members of the Plagiomenidae than *E. elegans*) raises questions concerning trends in the evolution of characters within species of *Elpidophorus*, and the affinity of *Elpidophorus* to other plagiomenids.

Excluding the problematic *Thylacaelurus montanus* Russell (1954), which possesses a small hypocone that may not be homologous with the hypocone found in *Elpidophorus* (Rose and Simons, 1977), members of the Plagiomenidae other than *Elpidophorus* do not possess a hypocone. This led Rose and Simons (1977, p. 222) to consider the presence of a hypocone in the upper molars of *Elpidophorus* a plesiomorphic character for plagiomenids. *Elpidophorus clivus* is probably directly descended from *E. elegans* and possesses well-developed hypocones on all upper molars. Occlusion of the hypocone of the upper molars with the trigonid and the posterior margin of the preceeding tooth in the lower molars produces wear facets in *E. clivus* not generally seen in E. elegans (Fig. 7).

Wear facets 1-8 are produced during the crushing/shearing, or Phase I portion of the chewing cycle (Kay and Hiiemae, 1974; approximates the "buccal phase" of Mills [1955] and Butler [1973]). Rose and Simons (1977), using nomenclature introduced by Crompton (1971) and augmented by Kay and Hiiemae (1974), identified a small wear facet 7 on the paraconid in a single specimen of M3 of Elpidophorus elegans (AMNH 33857). As in some species of primates with reduced paraconids (Kay and Hiiemae, 1974), facet 7 on E. clivus is well-developed and located on the anterolabial face of the metaconid. Facets on the paraconid in m2 and m3 of E. clivus that are in an homologous position to that observed on AMNH 33857 are produced by attrition with the dorsolabial surface of the well-developed hypocone of the upper molars. These facets are considered to be analogous to, and lingual extensions of facet, 10 seen on the lower molars of some primates (Kay and Hiimae, 1974). Facet 7 is generally absent on the metaconid of m1 due to the reduced nature of the hypocone on P4. On the upper molars, facet 7 is present on the posterolingual edge of the hypocone. On M3, facet 7 is produced not by occlusion with a metaconid, instead, it is owing to occlusion with the expanded hypoconulid lobe.

Facet 8, extending along portions of the postcingulid and posterior edges of the hypoconulid and entoconid on m1 and m2 of E. clivus, was identified on specimens of E. elegans and Plagiomene by Rose and Simons (1977). They considered this facet to be "formed by occlusion with the metacone or metaconule rather than the hypocone" (1972, p. 227). A complementary facet 8 is present on the talon basin side of the hypocone of M1 and M2 in E. clivus, and the facet on the lower molars is undoubtedly primarily produced by occlusion with the hypocone. However, a close examination of the occlusal relationships between these teeth indicates that the metacone and metaconule also contribute to the production of facet 8 on the lower molars of E. clivus.

Wear facets 9 and 10 (L1 and L2, respectively, of Gingerich, 1974) are produced during the grinding, or Phase II portion of the chewing cycle (Kay and Hiiemae, 1974; approximates the "lingual phase" of Mills [1955] and Butler [1973]). Facet 10 on upper molars of E. clivus is restricted to a narrow strip extending from the apex of the hypocone labially along the posterodorsal edge of the postcingulum. On lower molars, facet 10 is present along the dorsal edge of the paracristid[13](e.g., ROM 05613 and UALVP 22281) and does not seem to extend onto the lingual face of the protoconid (apical wear on heavily worn specimens possibly may be obscuring parts of facet 10 in this position). In heavily worn specimens, facet 10 on the upper and lower molars [illegible] confluent with facet 2.

In general, the remaining wear facets are seen to be better developed in E. clivus than the degree indicated for E. elegans by Rose and Simons (1977: pp. 225-226, fig.'s 3 and 4). Facets 1,2,5, and 6 on the lower molars of E. clivus are expanded beyond what is illustrated for E. elegans and in some cases goes beyond that illustrated for Plagiomene (Rose and Simons, 1977). The upper molars of E. clivus have well-developed parastylar and mesostylar lobes, which in occlusion with the protoconid and hypoconid of the lower molars, respectively, form relatively deep furrows that effectively extend the areas of the associated wear facets illustrated by Rose and Simons for both E. elegans and Plagiomene (1977; p. 226, fig. 4). Occlusion of the entoconid with the upper molars produces a very distinct and relatively deep furrow in the

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[13] The paraconid on lower molars of E. clivus is relatively more procumbent than on lower molars of E. elegans, and much more so than what is observed on Plagiomene. This may serve to increase the area of the trigonid available for crushing and grinding.

position of wear facet 6 on the upper molars of E. clivus. This, too, is well beyond what has been illustrated for E. elegans and Plagiomene. Facet 9 on the upper molars covers a larger surface of the labial face of the protocone than on E. elegans or Plagiomene, and often extends relatively deep into the trigon basin.

Elpidophorus has been proposed as a possible ancestor to younger members of the Plagiomenidae (Sloan, 1969: fig. 6; Rose, 1973; Rose and Simons, 1977). With the addition of E. clivus to the Elpidophorus line, it would seem that characters present in Elpidophorus are moving members of the genus away from the younger plagiomenids and not towards them. These characters include a relatively wider ectocingulum and greater development of the parastylar and mesostylar lobes in E. clivus over what is observed in E. elegans (Plagiomene, Worlandia, and Planetetherium have the stylar cusps developed at the expence of the stylar lobes), the presence in E. clivus of well-developed hypocones on all upper molars that have a much greater development over what is observed in E. elegans (the hypocone is small or absent on M3 of E. elegans, and excluding Thylacaelurus is lacking in other members of the Plagiomenidae), and more of an emphasis on both the crushing/shearing and grinding components of the chewing cycle as evidenced by the development of the wear facets on molars of E. clivus. The above suggests that the presence of a hypocone in Elpidophorus may not be plesiomorphic for plagiomenids, as interpreted by Rose and Simons (1977), but rather, a synapomorphy for species of Elpidophorus. Thus, Elpidophorus may represent at least a specialized side branch of the Plagiomenidae (a possibility indicated by Rose, 1975b).

Given the evidence currently available, I believe that it is not appropriate to remove Elpidophorus from the Plagiomenidae; however, I feel it should be included as a specialized lineage possibly arising from an early common ancestor and not in an ancestor/descendant relationship with the younger members of the Plagiomenidae.

L. S. Russell (1967) originally referred the specimens he collected at Swan Hills site 1 to *Elpidophorus elegans* with reservations. He noted differences between his sample and those of *E. elegans* and *E. "patratus"* (synonymized with *E. elegans* by Szalay, 1969), and although he recognized that the Swan Hills *Elpidophorus* might belong to a new species he felt the material available to him was too incomplete to effectively designate a new species. Of the specimens Russell referred to *E. elegans* (ROM 05609-05613), two of them were misidentified (not surprising given the condition and size of the sample available to him). RO[illegible] described as a "left upper molar, probably M1" (Russell, 1967: p. 15) [illegible] actually an M2, and ROM 05611, described as an "incomplete left P4" (Russell, 1967: p. 15), is an incomplete M3.

In the same paper Russell referred elsewhere specimens referable to *E. clivus* n. sp. ROM 0561[illegible] described as a left M3 of *Eudaemonema*, cf. *E. cuspidata* (1967, p. 16), is an incomplete right deciduous P4 of *E. clivus*[14]. ROM 05621, "probably [an] m1", referred to Pantolestidae?, genus and species undetermined (1967, p. 19), is the trigonid of a left p4 of *E. clivus*. ROM 05627, described as an "incomplete trigonid of a left lower molar" of *Didymictis*? sp. (Russell, 1967: p. 22), is an incomplete trigonid of a left p4 belonging to *E. clivus* and is virtually indistinguishable from ROM 05621, a point apparently missed by Russell.

The anteromost lower dentition of a plagiomenid was first described for *Plagiomene* and then for *Worlandia* by Rose (1973 and 1982, respectively)

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[14] The only other specimen referred to *Eudaemonema*, cf. *E. cuspidata* by Russell (1967) is referable to *Propalaeosinopa* and is discussed below. The reassignment of specimens Russell (1967) referred to *Eudaemonema* eliminates mixodectids from the Swan Hills local fauna.

and is unknown for *Elpidophorus* anterior to p2. The identification of UALVP 22378 and 22379 as anterior medial incisors of *E. clivus* is based on comparisons with uncatalogued and undescribed material referable to *E. elegans* from the University of Alberta Joffre Bridge Mammal Site number 1, near the town of Red Deer, Alberta (Fox, pers. comm.; Fox, in press)[15]. The Joffre sample includes two partial dentaries: one specimen preserving i1, the base of i2, roots of i3 and the canine, and p1-p3; the second preserves i1-i2, the root of i3, the canine, and p1-p4. Wear is present on the apex of both Joffre Bridge i1's; however, one specimen preserves what remains of a small lateral lobe on the apex of the crown. The Swan Hills specimens differ only in having a relatively better developed lateral lobe on the crown, and UALVP 22379 is slighlty larger in size than the two Joffre i1's. The bilobed nature of the medial incisors on *Elpidophorus* is reminiscent of the condition seen on PU 14552, a left dentary of *Plagiomene* preserving the entire dentition (Rose, 1973: pp. 3-4, fig.'s 1 and 2), and UM 73788, a left dentary of *Worlandia* also preserving the entire dentition (Rose, 1982: p. 180, fig. 1A and B). As discussed above, *Elpidophorus* is not considered to be in an ancestral position to other plagiomenids, and thus the bilobed medial incisor is either a plesiomorphic character for the Plagiomenidae, or has arisen in parallel with *Plagiomene* and *Worlandia*.

A specimen from Swan Hills site 2 is questionably referred as an i3 of *E. clivus*. UALVP 23839 very much resembles ~~in form~~ the i2 of *Litolestes ignotus*

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[15] Recently, in a personal communication to Fox (1988), L. S. Russell has indicated that "Erickson's Landing" is located where Joffre Bridge stands today. In support of this I have found a reference to "Erickson's Landing" in Allan and Sanderson (1945, p. 99) who state that Brown discovered his specimens in a block of sandstone along the Red Deer River near "Brookseley" bridge. The pilings for the old "Brookseley" bridge are alongside those of the present day Joffre Bridge. Thus, the University of Alberta Joffre Bridge Mammal site number 1 is probably equivalent to "Erickson's Landing". This information serves to pinpoint the type locality of *Elpidophorus elegans* and *Propalaeosinopa albertensis*.

described and figured by Schwartz and Krishtalka (1976: p. 5, fig. 3). The Swan Hills specimen is distinctly much larger, however. The roots of i3 preserved in the dentaries from the Joffre Bridge sample show the root to have been laterally compressed. The orientation of the root in the Joffre dentaries is such that in order for i3 to produce a relatively tight fit with i2, the crown of i3 would have to be canted mesially, much as it is on UALVP 23839. The possibility exists that UALVP 23839 may be an incisor of a large insectivore, possibly *Litocherus lacunatus* which is also present in the Swan Hills local fauna; however, available data currently supports the former interpretation.

Both partial dentaries from Joffre Bridge Mammal Site number 1 preserve p1. The two specimens of *E. clivus* referred as p1's (UALVP 22712 and 22717) are identical to the p1's preserved in the Joffre specimens, and differ only in being slightly smaller in size.

The specimens referred here as dp3's (UALVP 23862-23864) resemble permanent p3's in their shape and size of the talonid, but differ in being smaller and slightly more anteroposteriorly elongate. As on dp4, described above, they have an accessory cusp on the trigonid; however, this extra cusp is positioned much differently than on dp4. Unlike permanent p3's, but like p4's, dp3's have small paraconids and metaconids, a relatively well-developed talonid basin, and a strong entocristid.

Krishtalka (1973) referred a specimen, consisting of a trigonid possessing four cusps and an incomplete talonid, to *E. elegans* as a possible deciduous p4 (UALVP 5792, from Police Point, Alberta). The four specimens from Swan Hills referred to *E. clivus* as dp4 differ from the Police Point specimens only in being smaller. In addition to the similarities between the Police Point dp4 and permanent lower molars of *E. elegans* noted by Krishtalka (1973, p. 26), dp4 of *E. clivus* resembles the permanent lower molars in possessing a papillate labial cingulid, a well-developed postcingulid, and a small hypoconulid situated on the posterolabial base of the entoconid.

In addition to the lower deciduous p3's and p4's, six specimens from Swan Hills site 1 have been identified as upper deciduous fourth premolars of *E. clivus* (ROM 05610, UALVP 22327, 22473, 22491, 22562, 22678). These resemble the permanent M1's in possessing crenulated enamel, a well-developed parastylar lobe, a sharp ridge-like postmetacrista extending onto a relatively strong metastylar area, a sharp, well-defined centrocrista, pre- and postcingula, and a mesostyle that can be quite large and shaped like an inverted U. They differ in being very anteroposteriorly elongate and transversely narrow, much reduced in size, having the parastylar lobe oriented directly anterior to the paracone, the three major cusps being more conical, lacking a hypocone, possessing much reduced conules (the metaconule is virtually absent from UALVP 22327), and in lacking well-defined meta- and mesostylar lobes.

The fragments of upper medial incisors referred to *E. clivus* (Fig. 6) resemble the incisor from Scarritt Quarry tentatively referred to *E. elegans* by Szalay (1969: p. 221, plate 26, fig. 3-6) and two complete incisors probably referable to *E. elegans* from the Joffre Bridge Road Cut lower level and DW-1 (Fox, pers. comm.). In a personal communication to Fox in 1985, D. Krause indicated that he had further specimens of upper incisors from Scarritt Quarry similar to the Joffre Bridge specimens and probably referable to *Elpidophorus*. The specimens from Swan Hills differ from the above specimens in possessing a small cusp situated mesially and dorsally (described above as a mesiodorsal cusp) from the posterodistal cusp (described by Szalay as the "lateral" and "most dorsally situated on the crown"[1969, p.221]). In the position of the mesiodorsal cusp of the Swan Hills specimens, the base of the crown on the former incisors possesses a swollen ~~or~~ bulbous area. If the upper incisors from Swan Hills do represent incisors of E. clivus, the presence of the mesiodorsal cusp would most certainly represent an advancement over the condition seen in the presumed upper medial incisors of E. elegans.

In addition to the descriptions of i1, ?i3, p1, dp3, and DP4, P1 is here described in Elpidophorus for the first time. The alveolus for P1 preserved on AMNH 35963 (illustrated by Szalay, 1969: plate 27, fig.'s 7 and 8), and on two uncatalogued and undescribed specimens from UADW-2 and Joffre Bridge Mammal Site number 1 that preserve this area of the maxilla, indicates that P1 was a relatively large and single rooted tooth. The P1's referred to E. clivus (UALVP 22625 and 23842) are almost as large as P2 and differ only in having a single root and the characters slightly less developed. The close morphological similarity of UALVP 22625 and 23842 to P2's of E. clivus leaves little doubt as to their allocation as P1's.

Order CARNIVORA BOWDICH, 1821

Family VIVERRAVIDAE WORTMAN AND MATTHEW, 1899

Genus Protictis MATTHEW, 1937

"Protictis", cf. "P." dellensis (DORR, 1952)

(Fig. 19 D,F)

Referred specimens. -- DP3: UALVP 23910.

Locality. -- Swan Hills site 2, Paskapoo Formation, Alberta.

# DESCRIPTION

DP3. -- The single isolated specimen referred here, UALVP 23910, is three-rooted and in occlusal view is Y-shaped with the "protoconal" area making up the short "stem" or arm of the letter. The upper arms of the letter "Y" are composed of the parastyle and metastyle. They are symmetrical and widely separated forming a very obtuse angle. The subconical paracone is tall and trenchant, leans slightly posteriorly, and is somewhat laterally compressed with sharp anterior and posterior cristae. It is situated in the axis for the three arms of the "Y". The preparacrista connects the paracone anteriorly and slightly labially to a low, relatively strong parastyle. The postparacrista connects the paracone posteriorly to the blade-like metastyle, which is approximately two-thirds the height of the paracone. A well-developed carnassial notch is present immediately posterior to the paracone where the postparacrista meets the metastylar blade. Directly lingual to the paracone is an extension of the crown (the "stem" of the "Y"), which appears to have lacked a protocone. There is a very slight amount of wear and damage in this area; however, the amount is miniscule and it appears unlikely it was enough to obliterate even a small protocone if one was present. A weakly papillate, narrow cingulum extends from the posterolingual edge of the lingual extension of the crown, to the posterolingual base of the metastylar blade. The labial edge of the crown is gently concave and a very narrow ectocingulum is incomplete labially around the base of the paracone. The roots below the lingual extension and the parastyle are almost circular in cross-section and relatively long and slender. The root below the metastylar blade is strongly transversely compressed and anteroposteriorly elongate. The distal three-quarters of this root are missing; however, it appears to have tapered sharply.

## DISCUSSION

There are no described viverravid deciduous P3's to which UALVP 23910 can be compared; however, the comparative collection of the Laboratory for Vertebrate Paleontology, University of Alberta, has in it a good cast of an undescribed specimen of a maxillary fragment from the Willwood Formation, Bighorn Basin, Wyoming, that has both deciduous P3 and P4 plus a permanent M1 (USGS 1452, referable to *Didymictis* sp.; pers. observ.). The positioning of the cusps and the relative proportions of the "arms" of the crown are virtually identical to those of UALVP 23910. USGS 1452 differs from UALVP 23910 only in being slightly larger and more robust, having a more anteroposteriorly elongate paracone, and in possessing a very small protocone on the lingual extension of the crown.

UALVP 23910 (L = 8.1; W = 5.0) is much too large to be a deciduous P3 of *Protictis laytoni* Gingerich and Winkler (1985) or *P. schaffi* Gingerich and Winkler (1985). It is slightly larger than what would be expected for "*P.*" *agastor* Gingerich and Winkler (1985)[16]; however, it is well within the size range for "*P.*" *dellensis* from the latest Tiffanian Dell Creek Quarry, Hoback Formation, Wyoming (Dorr, 1952). Compared to specimens of P4's from the Roche Percée local fauna (currently under study by D. W. Krause and R. C. Fox), which are referable to "*P.*" *dellensis* (pers. observ.), UALVP 23910 differs in being relatively more anteroposteriorly elongate, slightly smaller in size, much more gracile in general appearence with more slender roots and cusps, lacking a protocone, and having the "protoconal" lobe of the crown medially positioned and directly lingual to the paracone (in contrast to the

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[16] Youzwyshyn (in preparation) has erected a new genus to contain "*P.*" *agastor* and "*P.*" *dellensis*, plus a new species of viverravid from Cochrane 2, Porcupine Hills Formation, Alberta.

anterolingually projecting protoconal lobe of the permanent P4).

The absence of specimens that can be positively referred to "P." dellensis from either Swan Hills site 1 or 2 necessitates a tentative referral. Further collecting may require a revision of the above interpretation.

### VIVERRAVIDAE, unidentified genus and species

(Fig. 19 E,G)

Referred specimens. -- Isolated trigonid fragment of a left m1: UALVP 22319; isolated trigonid of a right m2: UALVP 23911.

Locality. -- Swan Hills site 1, Paskapoo Formation, Alberta.

## DESCRIPTION

m1. -- UALVP 22319 consists of most of the protoconid and a small labial piece of the paraconid base, including the carnassial notch. The protoconid is tall and trenchant, and has the trigonid basin-facing slope oriented anterolingually. The carnassial notch is slightly worn but still relatively strong.

m2. -- The trigonid referred here, UALVP 23911, is very low crowned with somewhat bulbous cusps that exhibit some wear. The metaconid and protoconid are subconical and subequal in size and height. The paraconid is a small though well-developed conical cusp positioned just lingual to the midline of the crown and leaning slightly anteriorly. The trigon basin is very shallow and open lingually. Anteriorly is a short, narrow precingulum. The existence of a carnassiform notch is not evident due to the presence of wear. The anterior remains of the cristid obliqua join the posterior wall of the trigonid very slightly labial to the ventral apex of the protocristid.

## DISCUSSION

The two specimens referred here could conceivably belong to either Raphictis gausion Gingerich and Winkler (1985), or Protictis laytoni Gingerich and Winkler (1985). Both species are very close to one another in size (P. laytoni being the smallest species of Proticits), and both UALVP 23911 and 22319 could easily be accomodated in either species based on size alone. Compared to the type of Raphictis gausion (PU 21244), UALVP 22319 is virtually identical; however, given the fragmentary nature of UALVP 22319 it can just as easily belong to Protictis laytoni. As well, the isolated m2 trigonid, UALVP 23911, is virtually indistinguishable from the m2 preserved on the type of R. gausion. It differs in having a more nearly conical paraconid that is slightly less anteriorly salient. The m2 has not been described for P. laytoni and as a result UALVP 23911 cannot be compared to this species. Consequently, a more definite referral cannot be made and must await the collection of better preserved and more nearly complete material.

### Order CONDYLARTHRA COPE, 1881b
### Family PHENACODONTIDAE COPE, 1881b
### Genus Ectocion COPE, 1882
### Ectocion osbornianum COPE, 1882

(Fig. 20 A-D, Table 13)

Table 13: Measurements of the dentition of *Ectocion osbornianum*, Swan Hills local fauna, Alberta.

| Specimen no. | Element | L | W | AW | PW |
|---|---|---|---|---|---|
| UA 22340 | p2 | 3.1 | 1.8 | | |
| UA 23913 | p3 | 4.5 | 2.3 | | |
| UA 23914 | dp4 | 5.9 | 3.6 | | |
| UA 23915 | m3 | 6.3 | | 3.8 | 3.7 |
| UA 22505 | " | - | | 4.1 | - |
| UA 23917 | DP3 | 5.2 | 3.8 | | |
| UA 23918 | M1 or 2 | *5.6 | *7.2 | | |

*Approximate measurement.

Referred specimens. -- p2: UALVP 22340; p3: UALVP 23913; dp4: UALVP 23914; m1 or 2: UALVP 22494, 22512, 23916; m3: UALVP 22505, 23915; DP3: UALVP 23917; M1 or 2: UALVP 23918-23921, 22343.

Locality. -- Swan Hills site 1, Paskapoo Formation, Alberta.

Known distribution. -- Swan Hills local fauna, Paskapoo Formation, Alberta; Polecat Bench (several levels), Fort Union Formation, Wyoming (West, 1976); Shotgun Butte, Fort Union Formation, Wyoming (D. E. Russell, 1967); Malcolm's locality, Fort Union Formation, Wyoming (Krishtalka, et al., 1975); Police Point local fauna, Ravenscrag Formation, Alberta (Krishtalka, 1973); Buckman Hollow local fauna, Almy Formation, Wyoming (Gazin, 1956); Four Mile Fauna, Wasatch Formation, Colorado (McKenna, 1960); "Graybull Beds", Willwood Formation, Bighorn Basin, Wyoming (Cope, 1882; Granger, 1915); Powder River, Wasatch Formation, Wyoming (Delson, 1971); Plateau Valley local fauna, De Beque Formation, Colorado (Patterson, B., 1936 unpublished material: cited in West [1976]); Princeton Quarry, Fort Union Formation, Wyoming (West, 1976); numerous late Tiffanian through early Wasatchian localities of Clark's Fork Basin, Willwood and Polecat Bench Formations, Wyoming (Rose, 1981); Roche Percée local fauna, Ravenscrag Formation, Saskatchewan (Fox, in press; Krause and Fox, in prep.).

## DISCUSSION

The specimens from Swan Hills site 1 referred to Ectocion osbornianum are fragmentary save for the single specimens referred as p2, p3, dp4, and DP3, plus UALVP 23915 (a left m3). In size and morphology the above specimens are virtually identical to specimens of E. osbornianum described elsewhere (e.g., Granger, 1915; West, 1971, 1976; Krishtalka, et al., 1975) and thus description here is considered unneccessary. In addition, the small sample from Swan Hills is indistinguishable from specimens in a much larger and better preserved sample of E. osbornianum from the Roche Percée local fauna (late Tiffanian, Ravenscrag Formation) in south eastern Saskatchewan (Fox, in press; Krause and Fox, in prep.).

### Family ARCTOCYONIDAE GIEBEL, 1855
### Genus Claenodon SCOTT, 1892
### Claenodon sp.
(Fig. 20 E-H)

Referred specimens. -- ?m1: ROM 05630; P3: UALVP 23923; P4: UALVP 23924; ?M1: UALVP 22526.

Locality. -- Swan Hills site 1, Paskapoo Formation, Alberta.

## DESCRIPTION

?m1. -- ROM 05630 is the worn and slightly damaged talonid of a left lower molar. L. S. Russell considered this specimen to represent "probably m2" (1967, p. 23). Based on the transverse width (PW = 9.2) it is here questionably referred as an m1. In occlusal view the talonid is subquadrate with rounded corners. The talonid basin is relatively shallow. The hypoconid is a low, bunodont cusp. The entoconid is damaged and contrary to the interpretation of Russell (1967, p. 24) does not appear to have been as large as the hypoconid. The hypoconulid is quite reduced and medial in position. The cristid obliqua extends almost directly anterior. A narrow, papillate cingulid is present around the talonid save for the labial base of the hypoconid and a small area posteroventral to the hypoconulid where an interdental wear facet is located. Unworn enamel surfaces are rugose.

P3. -- In occlusal view UALVP 23923, a right P3 (L = 9.0, W = 9.5), is roughly an equilateral triangle. The crown of this three-rooted specimen is heavily worn and the apex of the paracone and a portion of the preparacrista are damaged. The paracone is the tallest and most robust cusp on the crown and appears to have been subconical and relatively low. It is located medially along the anteroposterior axis of the crown. A metacone is lacking. The protocone is positioned directly lingual to the paracone and is a robust, relatively low cusp, shorter and smaller than the paracone. A small parastyle and metastyle are located anterolabially and posteriorly to the paracone, respectively. The anterior and posterior margins of the crown appear to have possessed papillate cingula. A remnant of the anterior cingulum is present on the anterolingual base of the protocone. A hint of a papillate ectocingulum is present labially between the paracone and metastyle. Wherever the crown is unworn, the enamel is rugose.

P4. -- UALVP 23924 consists of a metastyle and a portion of the posterolabial base of the metacone belonging to a left P4. It is well-developed and posterolabially salient. Wear obscures the postparacrista; however, the metastyle is relatively tall and crestiform and was apparently continuous with the former. A well-developed, papillate cingulum surrounds the metastyle. Enamel surfaces where unworn are rugose.

?M1. -- UALVP 22526 is worn virtually flat and tentatively referred as a left M1 based on size (L = 10.4, W = 12.7) and crown shape (on M2's of Claenodon the hypocone extends the posterolingual corner of the crown further posteriorly [pers. observ.]). The only identifiable characters present are the anterior two-thirds of a narrow but strong papillate ectocingulum and a small portion of the labial bases of the paracone and metacone, which show the enamel to be distinctly rugose.

## DISCUSSION

In referring ROM 05630 to Claenodon, L. S. Russell noted:

> "In spite of its incomplete and worn condition it may be referred to Claenodon with some confidence. Such broad, low-cusped teeth have been found among Paleocene mammals only in the arctocyonids and the phenacodonts, such as Tetraclaenodon. From the latter the present specimen may be distinguished by the orientation of the anterior crest of the hypoconid, which extends almost directly forward, and not obliquely inward and forward. The various pits and grooves on the triturating surface also suggest Claenodon; they result from wear of an originally wrinkled surface" (1967, p. 24).

In addition to the specimens referred above, there are numerous fragments of large teeth that are probably referable to Claenodon; however, the fragmentary nature of the material precludes their being identified as belonging here. In fact, UALVP 22526 (M1) was recovered in numerous fragments and it was only after the fortuitous recovery and piecing together of all the fragments that it was recognized as belonging to Claenodon.

The above refefred specimens are within the known size range for Claenodon ferox (Cope, 1883) and C. acrogenius Gazin (1956). Without a more nearly complete and larger sample from Swan Hills site 1, the specific allocation of these specimens is virtually impossible; however, they compare very closely to specimens referred to ~~Claenodon,~~ cf. C. ferox from the middle Tiffanian UADW-2 locality, Alberta (Fox, in press; Fox, in prep.). This indicates that the Swan Hills sample may be tentatively referable to C. ferox, but notwithstanding, given the present size and condition of the sample it would be premature to proceed with such a referral.

### Order PANTODONTA COPE, 1873

### Family PANTOLAMBDIDAE COPE, 1883

### Genus Titanoides GIDLEY, 1917

### Titanoides sp.

(Fig. 20 I, J)

Referred specimens. -- isolated fragmentary left M1 or 2: UALVP 22444; isolated fragmentary left M2 or 3: UALVP 22332.

Locality. -- Swan Hills site 1, Paskapoo Formation, Alberta.

## DESCRIPTION

M1 or 2. -- UALVP 22444 consists of the worn and partially damaged posterolabial corner of the crown for a left first or second upper molar. The metastylar area is well-developed, being low, quite robust, and posterolabially salient. What remains of the metacone shows it to have been a relatively low, robust cusp. The premetacrista extends anterolabially onto the remains of a strong mesostyle. A very narrow cingulum is present posteriorly along the base of the crown. Wear and damage obscures the presence of a labial cingulum. The enamel is strongly rugose where unworn.

M2 or 3. -- UALVP 22332 preserves the lingual half of a left M2 or 3. The metacone is lacking save for an extremely small portion of the base. What remains of the paracone shows it to have been a robust cusp positioned slightly further lingually than the metacone. The protocone is low, somewhat anteroposteriorly broad, and does not extend very far lingually from the paracone. There is no evidence of a metaconule; however, a very reduced paraconule is present on the preprotocrista at the anterolingual base of the paracone. Narrow, papillate anterior and posterior cingula are discontinuous around the lingual base of the protocone. An hypocone is lacking. The enamel is strongly rugose where unworn.

## DISCUSSION

The size, development of the metastyle and mesostyle, the unmistakable dilambdodont nature of the crown, protocone and conule morphology, lack of an hypocone, structure of the cingula, and the rugosity of the enamel clearly identify these specimens as belonging to Titanoides. Although these specimens are incomplete, size approximations show them to be larger than Titanoides simpsoni Simons (1960) and T. zeuxis Simpson (1937b), smaller than I. majus Simons (1960), and within the size range for I. primaevus Gidley (1917) and I. gidleyi Jepsen (1930). However, the fragmentary nature of this extremely small sample size precludes a specific identification.

### EUTHERIA, incertae sedis
### Family LEPTICTIDAE GILL, 1872
### Genus Prodiacodon MATTHEW, 1929
### Prodiacodon sp.
(Fig. 21 A, B)

Referred specimens. -- M1 or 2: UALVP 22683, 23912.

Locality. -- Swan Hills site 1, Paskapoo Formation, Alberta.

## DISCUSSION

Both referred specimens preserve the crown lingual to the paracone and metacone. The characters which unite UALVP 22683 and 23912 with upper molars of Prodiacodon are the possession of lingually positioned conules (particularly the transversely elongate paraconule), an anteroposteriorly compressed protocone that is relatively tall and sectorial, a well-developed postcingulum, a strong hypocone which is "short relative to the protocone", and a long precingulum which extends almost to the anterolingual corner of the crown (Novacek, 1977: p. 23). In size the Swan Hills specimens are close to Prodiacodon concordiarcensis Simpson (1935a) and thus are smaller than other species of Prodiacodon. However, they differ from P. concordiarcensis in having a larger hypocone with better developed pre- and postcingula, the precingulum extends further lingually, and lingually the crown is relatively lower. Morphologically UALVP 22683 and 23912 appear to be closest to the upper molars of P. tauricinerei from the early Eocene Willwood Formation (as compared to a good cast of the type, PU 13104).

The specimens referred above probably represent a new species of Prodiacodon; however, the small sample size and poor preservation of the specimens precludes a proper comparison with known leptictids.

### Family PALAEORYCTIDAE (WINGE, 1917)

### Genus Palaeoryctes MATTHEW, 1913

### Cf. Palaeoryctes sp.

(Fig. 21 C-F)

Referred specimens. -- m3: UALVP 22434; P4: UALVP 22477.

Locality. -- Swan Hills site 1, Paskapoo Formation, Alberta.

## DESCRIPTION

m3. -- The trigonid on this isolated left m3 is anteroposteriorly compressed and extremely tall and trenchant. The protoconid is larger and taller than the metaconid. The slopes of the metaconid and protoconid adjacent to the trigon basin face anterolabially and anterolingually, respectively. A small carnassiform notch, partially obscured by wear, is present at the ventral apex of the protocristid notch. The paraconid is not a distinct cusp but is continuous with the low, shelf-like paracristid. The trigon basin is open lingually. The short, transversely narrow talonid appears to curve posterolabially in occlusal view. The hypoconid is worn below ~~the~~ level of the hypoconulid; however, it appears to have been approximately the size of the hypoconulid. The entoconid and hypoconulid are subconical, the former being much smaller and shorter than the latter, which is somewhat anteroposteriorly compressed. The cristid obliqua is labially concave and joins the posterior wall of the trigonid lingual to the protocristid notch producing a deep hypoflexid. An entocristid is absent and the shallow, rounded talonid basin is open lingually. A very short but strong precingulid is present relatively high on the anterior edge of the crown.

P4. -- The single, isolated right P4 referred here (UALVP 22477) is missing the portion of the crown lingual to the paracone. The paracone is almost lenticular in occlusal view, being slightly transversely compressed. It is a tall, trenchant cusp that leans slightly posteriorly and is positioned medially on the anteroposterior axis of the labial edge of the crown. The small, subconical, slightly transversely compressed metacone is closely appressed to the paracone. A preparacrista connects the paracone anteriorly and slightly labially to a small but distinct and sharp parastyle. Immediately posterior to the metacone, a small carnassiform notch separates the metacone from the crestiform metastyle. The metastyle is a little larger than the parastyle and projects slightly further labially. A very narrow ectocingulum is present and the labial edge of the crown is shallowly concave. A paracingulum extends labially around the base of the paracone onto the parastyle.

## DISCUSSION

The m3 referred here, UALVP 22434 (L = 1.8, AW =1.5, PW = 1.0, protoconid height = 2.6), differs from *Palaeoryctes puercensis* Matthew (1913) in being approximately 30% larger, in having the trigonid slightly shorter in height relative to the talonid, the hypoconulid placed closer to the hypoconid, the precingulid placed relatively higher on the crown, and the talonid extending further posterolabially. The talonid for m3 was not identified in the sample for "*Paleoryctes* [sic.], cf. *P. punctatus*" from the Brisbane and Judson localities of North Dakota (Holtzman, 1978); however, the talonids of m1 and m2 in the North Dakota sample possessed mesoconids and entoconulids, cusps not identified on the talonid of UALVP 22434. Further, P4 of cf. *Palaeoryctes* sp. from Swan Hills (UALVP 22477; L = 2.0), differs from the P4's in the North Dakota sample of *Palaeoryctes*, cf. *P. punctatus* in having a shallowly concave labial margin and lacking a mesostyle and an accessory cuspule on the paracingulum. As near as can be determined, UALVP 22434 differs from the type of *P. punctatus* Van Valen (1966), AMNH 15850, in being only slightly larger.

In size and morphology UALVP 22434 and 22477 are virtually indistinguishable from undescribed specimens from Princeton Quarry referred to cf. *Palaeoryctes* sp. by Rose (1981, p. 36). Compared to a good cast of PU 17806, UALVP 22434 differs only in having a very slightly narrower talonid. UALVP 22477 differs from P4 preserved on PU 17804 and PU 14122 only in having a slightly taller metastyle. These differences are not thought of as taxonomically significant and the Swan Hills sample is considered to be conspecific with the Princeton Quarry cf. *Palaeoryctes* sp.

## "Palaeoryctoid", unidentified genus and species

(Fig. 21 G)

Referred specimen. -- Talonid of an isolated m1 or 2: UALVP 23909.

Locality. -- Swan Hills site 1, Paskapoo Formation, Alberta.

### DISCUSSION

This problematic specimen, UALVP 23909 (L = 1.3, PW = 1.7), is unique in its morphology but seems to have its closest affinities with palaeoryctids. The talonid is relatively short and appears to have been slightly narrower than the trigonid. Although there is some wear to the hypoconid, all three major talonid cusps were subequal in height. The small entoconid is conical and sharp. The hypoconulid is positioned close to the subcrescentic hypoconid and is subconical and slightly posteriorly projecting. The cristid obliqua possesses a swelling in front of the hypoconid that might represent an incipient mesoconid. Before reaching the posterior wall of the trigonid the cristid obliqua drops to what appears to be the remains of a small carnassiform notch, then it climbs a short distance to meet the postvallid. In this feature UALVP 23909 resembles Acmeodon Matthew and Granger (1921), which bears a "slit" on the most ventral portion of the cristid obliqua (Van Valen, 1966; Hartman, 1986). The postcristid possesses a small, though well-defined accessory cuspule between the hypoconulid and entoconid. The lowest point of the small valley between the cuspule and entoconid is developed as a sharp carnassiform notch. The talonid basin is relatively deep and steeply sloped with a small, transverse "trough" at the bottom. An entocristid is lacking, and thus the basin is open lingually; however, the posterolingual and anterolingual edges of the metaconid and entoconid, respectively, are slightly transversely "pinched" at the bottom of the talonid notch and form a structure which looks very much like a carnassiform notch.

Unlike Acmeodon, but like Thelysia Gingerich (1982a), Leptonysson Van Valen (1967), and Palaeoryctes Matthew (1913), UALVP 23909 lacks an entocristid, leaving the talonid basin open lingually. When viewed labially the hypoconid resembles the condition described for Thelysia by being "a massive, pillar-like cusp" (Gingerich, 1982a: p. 45). UALVP 23909 also resembles specimens referred to "Paleoryctes [sic.], cf. P. punctatus" from the Brisbane and Judson localities, North Dakota (Holtzman, 1978), in possessing an incipient mesoconid; however, unlike the latter specimens UALVP 23909 does not possess an entoconulid. In addition, UALVP 23909 differs from all described palaeoryctids in possessing an accessory cuspule on the postcristid.

It is not known whether this specimen does indeed represent a palaeoryctid, but the close proximity of the well-developed hypoconulid to the hypoconid, the apparently short talonid, the lack of an entocristid, the development of almost vertical wear facets on the anterior and posterior faces of the hypoconid, and the proliferation of "carnassiform"-like notches seems to suggest a propinquity to the Palaeoryctidae. If further collecting shows UALVP 23909 to be a palaeoryctid, it will undoubtedly represent a new genus.

### Family PANTOLESTIDAE COPE, 1884b

### Genus Propalaeosinopa SIMPSON, 1927

### Propalaeosinopa albertensis Simpson, 1927

(Fig. 21 H-N, 22 A-C; Table 14)

Referred specimens. -- p2: UALVP 23891; p3: UALVP 22519, 23892-23894; p4: UALVP 22523, 22677, 22687, 22706, 23899-23901; m1: ROM 05614, UALVP 22320, 23902, 23907; m2: UALVP 23905; m3: UALVP 22321, 22674, 22675; talonid fragments of m1 or m2: UALVP 22676, 23904, 23906; P4: UALVP 22508; M1: UALVP 22256, 22450, 22670; M2: UALVP 22224, 22253-22255, 22669, 22671; M3: UALVP 22443, 22445, 22506, 22672, 22673; maxillary fragment with M1-2: UALVP 23908.

Locality. -- Swan Hills site 1, Paskapoo Formation, Alberta.

## DESCRIPTION

p2. -- The single referred specimen, UALVP 23891, is heavily water worn and preserved in a dentary fragment with the alveolus for a single-rooted p1 and an alveolus with a fragment of root from an enlarged canine. p2 is double-rooted and appears to have been trenchant and slightly recurved. Posteriorly there appears to have been a short heel.

p3. -- p3 is double-rooted and the crown is dominated by the relatively tall, trenchant, and slightly recurved protoconid. A poorly defined cristid extends anteriorly from the protoconid apex to the base of the crown where it

Table 14: Measurements and descriptive statistics of the dentition of *Propalaeosinopa albertensis*, Swan Hills local fauna, Alberta.

| Measurement | | N | OR | M±SE | SD | CV |
|---|---|---|---|---|---|---|
| p2 | L | 1 | 2.0 | - | - | - |
| | W | 1 | 1.0 | - | - | - |
| p3 | L | 4 | 2.3-2.7 | 2.45 ± .10 | .191 | 7.8 |
| | W | 4 | 1.1-1.4 | 1.23 ± .06 | .126 | 10.3 |
| p4 | L | 5 | 3.0-3.3 | 3.22 ± .06 | .130 | 4.0 |
| | W | 7 | 1.5-1.8 | 1.64 ± .05 | .127 | 7.7 |
| m1 | L | 2 | 2.8-3.0 | 2.90 ± .10 | .141 | 4.9 |
| | AW | 4 | 1.8-1.9 | 1.88 ± .03 | .050 | 2.7 |
| | PW | 2 | 2.0-2.1 | 2.05 ± .05 | .071 | 3.4 |
| m2 | L | - | - | - | - | - |
| | AW | 2 | 2.1 | - | - | - |
| | PW | - | - | - | - | - |
| m3 | L | 1 | 3.6 | - | - | - |
| | AW | 2 | 2.1-2.3 | 2.20 ± .10 | .141 | 6.4 |
| | PW | 2 | 1.9-2.0 | 1.95 ± .05 | .071 | 3.6 |
| P4 | L | 1 | 3.1 | - | - | - |
| | W | - | - | - | - | - |
| M1 | L | 1 | 2.8 | - | - | - |
| | W | 1 | 3.6 | - | - | - |
| M2 | L | 1 | 3.2 | - | - | - |
| | W | 1 | 4.3 | - | - | - |

curves slightly lingually to a very small paraconid. A metaconid is absent. A sharp cristid extends posteriorly from the protoconid apex to become confluent with a short cristid obliqua. Shallow vertical troughs are present on either side of the posterior cristid. The cristid obliqua is terminated posteriorly by a small, conical, relatively sharp hypoconid. A variably developed entocristid can be weakly developed (e.g., UALVP 23894) or relatively strong, resulting in a shallow talonid basin that is just under one-half the width of the short talonid (e.g., UALVP 23893 and 22519). On UALVP 22519 the remnants of a very small entoconid are present on the posterior margin of the talonid. Labially is a very shallow hypoflexid below which the crown exhibits a slight degree of exodaenodonty.

p4. -- p4 resembles p3 in morphology by being double-rooted, having a tall, slightly recurved and trenchant protoconid, and vertical troughs present on either side of the posterior cristid. p4 differs from p3 in having a much stronger paraconid on the anterolingual base of the crown, a better developed, slightly more elongate talonid with a deeper basin, well-defined entocristid and entoconid, and a deeper hypoflexid. The talonid basin is slightly over one-half the width of the talonid and on most referred specimens (e.g., UALVP 23900) possesses a tiny cuspule in the bottom of the basin. Several specimens possess a slight bulge of enamel on the posterolingual edge of the protoconid at a level a little higher than the paraconid. This may represent the incipient development of a metaconid.

m1. -- The trigonid of m1 is relatively tall and little anteroposteriorly compressed. The protoconid is subequal to the metaconid in height and is more nearly trenchant than the latter. The metaconid converges on the condition seen in some erinaceomorphs (e.g., Litocherus) by being more inflated than the protoconid and appearing almost "bulbous" in occlusal view. The subconical paraconid is small and positioned slightly medial to the metaconid at the end of a low paracristid. When worn the paraconid and paracristid are very "shelf"-like. On UALVP 22320 and 23903, a small, conical accessory cuspule is present anterolingually on the crown just below the paraconid. Wear partially obscures a carnassiform notch on the protocristid of UALVP 23902.

The talonid is as long as, and slightly wider than, the trigonid. The hypoconid is subcrescentic and shorter in height than the somewhat laterally compressed, subcrescentic entoconid. The hypoconulid is preserved only on UALVP 23902. It is strong and shorter in height than the entoconid and owing to wear on the anterior face appears to be anteroposteriorly compressed. It is positioned lingual to the midline of the crown. The talonid basin is rounded and enclosed by the entocristid and cristid obliqua. The latter joins the posterior wall of the trigonid below the ventral apex of the protocristid. The talonid notch is relatively deep and acutely V-shaped. Anteriorly the very short precingulid carries a small, sharp, anteriorly projecting cuspule. Labial, lingual, and posterior cingulids are absent.

m2. -- m2 is represented by a single isolated left trigonid, UALVP 23905 (several talonid fragments are identified; however, it is unknown whether these pertain to m1 or m2). In morphology the trigonid is similar to m1 and differs in being more anteroposteriorly compressed, having the paraconid slightly more lingually positioned and more closely appressed to the metaconid, in lacking the anterolingual accessory cuspule below the paraconid, in being slightly larger with a relatively taller metaconid and protoconid, and having a less inflated metaconid relative to the protoconid. A carnassiform notch on the protocristid is largely obscured by wear. Below the anterior edge of the paraconid is a very well-developed interdental wear facet for articulation with the posterior edge of the strong hypoconulid on m1.

m3. -- The trigonid of m3 is essentially identical to m2. The metaconid and protoconid are trenchant, subequal in height, and the former is slightly more inflated than the latter. The paraconid is a relatively low cusp closely appressed to, and slightly medial to the metaconid. The precingulid is short, lacks the cuspule development observed on m1, and at the lingual end flares slightly anteriorly. On UALVP 22674 the paracristid and protocristid possess a small carnassiform notch. The talonid is narrower than the trigonid and is more elongate than on m1-2. Although worn, the entoconid appears to have been slightly larger and taller than the hypoconulid, which projects posteriorly and is positioned lingual to the midline of the crown. The cristid obliqua joins the posterior wall of the trigonid below the ventral apex protocristid. The entocristid is lower and more obtuse than on m1 and the talonid basin is rounded and relatively shallower.

P4. -- UALVP 22508 is the single, isolated specimen tentatively referred above as a left P4. Due to breakage it lacks the protocone. The conical paracone is tall, trenchant, and slightly recurved posteriorly. A metacone is lacking. Anteriorly is a small parastyle at the base of the paracone. Posteriorly a low, somewhat crestiform crista extends from the paraconal apex to a metastylar salient that is approximately twice the size of the parastyle. A narrow ectocingulum is incomplete around the anterolabial base of the paracone.

M1. -- The only complete M1 is present on a maxillary fragment (UALVP 23908) also preserving M2. In occlusal view the crown is "pinched" in the area of the conules. The metacone and paracone are conical, relatively tall and trenchant, subequal in height, and the former is slightly larger in size than the latter. A well-developed centrocrista connects the two cusps. A weak preparacrista connects the paracone anteriorly to a very small, rounded parastylar salient. The postmetacrista is well-developed, crestiform, and curves posterolabially to connect the metacone to a relatively small, posterolabially projecting metastylar salient. The narrow ectocingulum possesses a shallow ectoflexus. Conules are small. The paraconule is positioned further lingually than the metaconule and lacks a postparaconule crista giving it a conical appearance. A narrow precingulum extends around the anterolabial base of the paracone to the parastylar salient. The metaconule is better developed than the paraconule and subcrescentic. The premetaconule crista curves anterolabially around the base of the metacone. The postmetaconule crista forms a narrow metacingulum around the posterolingual base of the metacone. The protocone is three-quarters the height of the paracone/metacone, subcrescentic, the largest cusp on the crown, and possesses relatively strong protocristae. The conical hypocone is large and positioned posterolingual to the base of the protocone. An enamel fold connects the hypocone to the base of the protocone. The postcingulum is well-developed and extends from a point on the base of the crown just anterior to the metaconule to the hypocone. The precingulum is short and narrow. The trigon basin is moderately deep.

M2. -- M2 is similar to M1 in morphology and differs in the following: the crown is larger, more transverse, and the labial margin is relatively more anteroposteriorly elongate; parastylar and metastylar salients are larger and positioned further labially producing a relatively deeper ectoflexus; pre- and postcingulae are slightly better developed; the protocone is more anteroposteriorly compressed and taller; and the hypocone extends slightly further lingually.

M3. -- All referred specimens are lingual fragments or are incomplete. The most complete specimen, UALVP 22443, lacks the parastylar salient and the paracone above its base. The metacone is small and conical. A metastyle is lacking and the ectocingulum around the labial base of the metacone is incomplete. The metaconule is reduced and subconical to pyramidal. On no specimen is the reduced paraconule clearly differentiated from the preprotocrista. The lingual half of the crown is much more anteroposteriorly compressed than on M1-2. The precingulum is narrower than on M2; however, on several specimens (e.g., UALVP 22673) it extends almost to the lingual base of the protocone. The postcingulum is reduced and relatively narrow. On a number of specimens (e.g., UALVP 22673) a small hypocone is present.

## DISCUSSION

Propalaeosinopa albertensis was erected by Simpson (1927) to contain a left dentary preserving alveoli for p3, m1-3, and a badly worn p4 from "Erickson's Landing" (Paskapoo Formation, near Red Deer, Alberta). Unfortunately the exact location of "Erickson's Landing" was unknown and no further specimens positively identified[17]. This has led to some confusion in

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[17] As noted elsewhere above, "Erickson's Landing" may be equivalent to the University of

the literature as to whether or not P. albertensis is the senior synonym of P. "diluculi" as proposed by Van Valen (1967, p. 226). Dorr (1977) and Holtzman (1978), the latter referring specimens from localities in North Dakota to P. albertensis, followed the synonymy of Van Valen. Rose (1981, p. 150) suggested the "synonymy requires further documentation" and kept P. albertensis and P. "diluculi" as separate taxa, a move subsequently followed by later authors (e.g., Gingerich, 1980; Krause and Gingerich, 1983; Hartman, 1986)[18].

Fox (pers. comm.; in press) has identified two morphs in the sample of Propalaeosinopa from UADW-2. One of the morphs is clearly referable to P. "diluculi" and the other morph may represent P. albertensis (pers. observ.; Fox, in press). The latter morph differs from P. "diluculi" in being slightly larger and in having more inflated cusps on the lower molars (particularly the metaconid). In these characters it very much resembles specimens from Police Point local fauna, Cypress Hills, Alberta, referred to P. "diluculi" by Krishtalka (1973) and to the sample from Swan Hills site 1. However, the upper molars from Swan Hills differ from those in the Police Point sample in being less transverse and having the labial edge of M1-2 more anteroposteriorly elongate with a much shallower ectoflexus.

In comparison to the dentitions of Propalaeosinopa "diluculi" the specimens of P. albertensis in the Swan Hills sample are fifteen to twenty percent larger, have a relatively better developed talonid on p4, the molar

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Alberta Joffre Bridge Mammal site 1; this would make Joffre Bridge Mammal site 1 the type locality of Propalaeosinopa albertensis .

[18] G. P. Youzwyshyn (pers. comm., 1987) has recently pointed out, and I concur, that the type of Diacodon septentrionalis Russell (1929) is actually an m3 of Propalaeosinopa "diluculi" (Simpson, 1935). Following the rules of nomenclature P. "diluculi" would become the junior synonym of P. septentrionalis. This synonymy is discussed more fully by Youzwyshyn (in prep.).

cusps are more inflated (particularly the metaconid), the hypoconulid on m3 is nearer the height of, and positioned slightly closer to the entoconid, M1-2 is less transverse and the stylar salients are less labially positioned, producing a more anteroposteriorly elongate labial edge and a shallower ectoflexus (particularly on M2). If the Police Point sample of Propalaeosinopa is indeed referable to P. albertensis, a possibility indicated by Fox (in press), then the Swan Hills sample may represent, based on differences in the upper molars, a new species of Propalaeosinopa. Whether the UADW-2 sample is closer to the Swan Hills or the Police Point samples is dependent on the morphology of the upper molars, which have yet to be identified. In light of the differences between the Swan Hills sample and P. "diluculi", the similarities in the lower dentitions to those from Police Point and UADW-2, and until upper dentitions are identified from UADW-2 the Swan Hills sample is provisionally referred to P. albertensis.

L. S. Russell (1967) referred a lingual half of an upper molar from site 1 to Eudaemonema, cf. E. cuspidata (ROM 05614). This specimen is clearly referable to Propalaeosinopa and is referred above to P. albertensis as a right M1. A single isolated trigonid of a left lower molar (ROM 05621) was referred by Russell (1967) questionably to the Pantolestidae as an undetermined genus and species. This specimen has been identified and referred above as a trigonid of a left p4 belonging to Elpidophorus clivus, n. sp.

## Family APATEMYIDAE MATTHEW, 1909

### Genus Labidolemur MATTHEW AND GRANGER, 1921

### Labidolemur, cf. L. soricoides MATTHEW AND GRANGER, 1921

(Fig. 22 D-G)

Referred specimens. -- i1: UALVP 23889; p2: UALVP 23890.

Locality. -- Swan Hills site 1, Paskapoo Formation, Alberta.

## DESCRIPTION

i1. -- UALVP 23889 is an isolated right i1 lacking the root and showing slight damage and wear to the crown. In lateral view the crown curves dorsally in a gently arc. The crown is somewhat spatulate and is enamel covered save for a V-shaped wedge above the breakage for the root on the mesial side of the crown, and a smaller area roughly U-shaped on the lateral edge. The mesial face possesses an interdental wear facet on the proximal three-quarters of the crown. The somewhat flattened mesial slope is separated from the gently convex dorsal face by a low ridge of enamel. Between this ridge and the convex dorsal face the crown is shallowly concave. The lateral slope is also separated from the dorsal face by a ridge. This ridge is much better developed than the dorsomesial ridge and although worn it exhibits the remains of small serrations extending from near the tip to a point above the base of the crown where damage obscures the proximal extent of the serrations. Small serrations may also have been present on the mesiodorsal ridge. A narrow strip of the crown lying between the convex dorsal face and dorsolateral ridge is shallowly concave.

p2. - UALVP 23890 is a slightly water-worn crown of a right p2 lacking the root. The crown is elongate, strongly laterally compressed, and in lateral view is roughly "mitten" shaped. The labial surface of the crown is gently convex and lingually there is a shallow, narrow basin extending down the crowns posterolingual slope to the base of a large, conical cusp on the posterior edge of the crown. A sharp cristid begins at the anterolabial base of the posterior cusp and extends anteriorly the length of the crown. This cristid divides the crown into unequal labial and lingual halves.

## DISCUSSION

The single referred i1 from Swan Hills site 1, UALVP 23889, is indistinguishable morphologically from Labidolemur soricoides of the late Tiffanian Mason Pocket, Colorado, in possessing an elongate, spatulate crown with serrations extending the length of the dorsolateral ridge (McKenna, 1963: p. 20). The lower central incisor of the middle Clarkforkian L. kayi (Simpson, 1929) differs from L. soricoides in lacking serrations on the dorsolateral ridge and in their stead possessing "two faint cuspules near the base of the crown" (Gingerich and Rose, 1982: p. 50). i1 of L. serus Gingerich (1982), from the early Eocene Willwood Formation of the Clark's Fork Basin, is not illustrated or described by Gingerich; however, he does state that "the lower dentition of [L. serus] is generally similar to that of L. kayi" (1982b, p. 63). It is therefore assumed that morphologically i1 of L. serus does not siginificantly differ from L. kayi. In size UALVP 23889 (L = 7.5, W = 2.0) is larger than i1 of L. kayi and only slightly larger than L. soricoides and L. serus.

The p2 of Labidolemur soricoides and L. serus has not been identified. Morphologically UALVP 23890 is virtually indistinguishable from the p2 of L.

*kayi* illustrated by Gingerich and Rose (1982: p. 53, fig. 2). It differs only in having a larger, more nearly conical and erect posterior cusp. In size UALVP 23890 (L = 1.9, W = 0.7) is smaller than p2 of *L. kayi*. This is contrary to what would be predicted since i1's of *L. kayi* are smaller than *L. soricoides* and UALVP 23889. This is suggestive of two species of apatemyids being present in the Swan Hills fauna. However, an examination of the alveoli for p2 of *L. soricoides* preserved on PU 20614 (illustrated in West, 1973: p. 35, fig. 1B) suggests that p2 may have been smaller in size relative to i1 than in *Jepsenella praepropera* (West, 1973: p. 35, fig. 1A) and *L. kayi* (Gingerich and Rose, 1982: p. 53, fig. 2).

Apatemyids are "rare faunal elements and few localities contain specimens representing more than one or two individuals" (Gingerich and Rose, 1982: p. 49). If the two referred specimens from Swan Hills were to represent two separate apatemyid species from a single locality this would be, as I understand it, unprecedented. Rather, I would consider it more parsimonious to accept the data for alveolar size and hypothesize a smaller p2 relative to i1 in *Labidolemur soricoides* and *L.*, cf. *L. soricoides* than to consider, based on size alone, the presence of two species of apatemyids in the Swan Hills local fauna. Thus, I invoke the principle "*Species non sunt multiplicanda praeter necessitatem*" as used by Van Valen (1967, p. 226) and refer UALVP 23890 to *Labidolemur*, cf. *L. soricoides*.

# AGE OF THE SWAN HILLS LOCAL FAUNA

The first Paleocene mammals in Alberta were found in the Paskapoo Formation by Barnum Brown in 1910 while prospecting the Red Deer River valley for dinosaurian remains (Brown, 1914; Simpson, 1927). They were discovered in an isolated block of sandstone that had originated in the canyon wall above the Red Deer River near a place called "Erickson's Landing". In the original description of the fauna Brown considered the sample to have a Lance component in the multituberculates, but the placental component appeared to belong to the Paleocene (1914, p. 362). In the same volume W. D. Matthew agreed with Brown stating:

> "The mammals, according to Mr. Brown's identifications, checked by the present writer, are unmistakably those of the Lance fauna in part, but include an element which has not been found in the Lance and appears to belong to the Paleocene group of mammals, although none of its representatives compare at all closely with any Puerco or Torrejon genera. I suspect that it will be found to compare more nearly with the Fort Union Fauna" (1914, p. 388).

Subsequently, in a more detailed description of the fauna, Simpson (1927) revealed that specimens from the Hell Creek Formation of Montana were mistakenly included with the Paskapoo sample. He identified "the age of at least part of the Paskapoo as probably post-Torrejon...that is, as equivalent to the Tiffany-Clark Fork-Cernaysian" (1927, p. 10).

The first mammal specimens from the Swan Hills Paskapoo were collected at site 1 by L. S. Russell in 1964 and 1965. In the initial description of the fauna, Russell correctly identified them to be of "late but not latest Paleocene time" (1967, p. 26). To date, Swan Hills site 1 and 2 represent the most northerly Paleocene localities in the world yielding fossil mammals.

Rose alluded to an early or early middle Tiffanian age for site 1 based on the evolutionary grade of Carpodaptes cygneus (1977: p. 537, text-fig. 1). He considered C. cygneus to be the least structurally advanced species of Carpodaptes due to its small size and its structure relative to C. hobackensis (1977, p. 538). Based on the inclusion of specimens referred to C. cygneus from Roche Percée, Krause (1978) considered C. cygneus to be structurally more advanced than did Rose. Krause felt that C. cygneus "probably occurs late in the Tiffanian", citing its relationship to the further advanced C. hobackensis (latest Tiffanian, Dell Creek Quarry) and the common occurence of Plesiadapis churchilli at Roche Percée (1978, p. 1256). Although I agree that C. cygneus is structurally more primitive than C. hobackensis (Krause, 1978; Rose, 1977; Gingerich, 1986) and that together they probably represent a separate lineage of small Carpodaptes (Krause, 1978), based on information covered in detail in the discussion for C. cygneus above, I must question the utility of using C. cygneus as a biostratigraphic indicator. Until the taxonomic problems are worked out I feel it necessary to omit C. cygneus in the discussion of the age for site 1.

As noted by Gingerich, the fauna "associated with Carpodaptes cygneus at Swan Hills Site-1 [is] generally too fragmentary to permit precise correlation with better known faunas elsewhere, too long ranging to be of use in correlation, or too poorly known systematically to have biostratigraphic importance" (1986, pp. 1135-1136). This still remains true in part despite the much larger sample that has since been collected at site 1. However, based on this new sample a much better approximation of the age of Swan Hills site 1 is now able to be determined.

Swan Hills site 2 is geographically very close to site 1 (approximately 1 km) and has no specimens associated with it that can be used to assist in dating the locality: the long ranging Mesodma pygmaea (latest Torrejonian to late Tiffanian) is tentatively identified by a single specimen from site 2 and is unknown from site 1; UALVP 23910, DP3 of "Protictis", cf. "P." dellensis, is unlike anything identified at site 1; the specimen referred to Diacocherus, cf. D. meizon from site 2 differs slightly from site 1 specimens referred to the same taxon; and the fragmentary p4 referred to Neoplagiaulax hunteri and the ?i3 referred to Elpidophorus clivus, n. sp., suggest affinities with site 1 specimens but are not enough to provide age information. Elevational and stratigraphic data, however, suggest that site 1 and 2 may be correlative and thus are here tentatively considered to be of approximately the same age.

Elpidophorus elegans is well known from early and middle Tiffanian horizons of the United States and Canada. Elpidophorus clivus, new species, from the Swan Hills local fauna, possesses characters more advanced than those observed in its progenitor E. elegans (better developed para- and mesostylar lobes and hypocone for instance; see discussion above), and thus, the evolutionary grade of E. clivus suggests an age younger than that for the primarily middle Tiffanian E. elegans. In addition, the evolutionary grade of Mesodma prolis, new species, as compared to Mesodma pygmaea suggests an age younger than middle Tiffanian for Swan Hills site 1. There is little doubt that M. prolis evolved from M. pygmaea and the morphological differences observed between Swan Hills M. prolis and M. pygmaea from Roche Percée suggests that Swan Hills site 1 may postdate the Roche Percée local fauna in time.

Gingerich (1975, 1976) uses Plesiadapis churchilli as an index fossil in his plesiadapid biostratigraphic zonation of North America, citing its presence at a number of late Tiffanian localities in the United States. Krause identified the Swan Hills plesiadapid as falling "somewhere within the P. rex-P.

churchilli-P. fodinatus complex, which spans the middle and late Tiffanian" (1978, p. 1268). With the recovery of dentitions from site 1 referable to Plesiadapis churchilli, the fauna at site 1 can be assigned a late Tiffanian age.

Litocherus lacunatus is known from middle and late Tiffanian localities that range from the upper part of the middle Tiffanian Plesiadapis rex Zone into the latest Tiffanian Plesiadapis simonsi Zone (Gingerich, 1976, 1983, 1986). As noted by Gingerich (1986, pp. 1136-1137) the more primitive species in the Litocherus lineage, Litocherus zygeus, occurs at Cedar Point Quarry (middle Tiffanian) and thus Swan Hills site 1 probably post-dates Cedar Point in age. This is discussed in detail by Gingerich (1986). In addition, a relatively large sample of L. lacunatus is present in the Roche Percee local fauna, which has been accorded a late Tiffanian age by Krause (1978) largely based on the presence of Plesiadapis churchilli and other primate evidence. Morphologically the specimens of L. lacunatus from Swan Hills site 1 are indistinguishable from this sample.

The Swan Hills local fauna appears taxonomically most similar to the Roche Percée local fauna (largely undescribed; Krause and Fox, in progress). Of the 34 species from Swan Hills and 30 species so far identified from Roche Percée (Krause and Fox, in progress; Fox, in press), 17 species appear to be shared in common, although 4 species may not be conspecific with those in the complementary fauna (table 15). Compared to other known late Paleocene localities, the Swan HIlls local fauna possesses much less in common. For instance, compared to the fauna of the Badwater Creek area, central Wyoming (Krishtalka, et al., 1975), there are only 5 species in common: Microcosmodon conus, Mesodma pygmaea, Plesiadapis churchilli, Ignacius frugivorus, and Ectocion osbornianum; and compared to the fauna known from the Mason Pocket, Colorado (Simpson, 1935c; Matthew and

Granger, 1921), there is only 1 species in common: *Ignacius frugivorus* (table 15), although, *Labidolemur*, cf. *L. soricoides* identified in the Swan Hills local fauna is probably conspecific with *Labidolemur soricoides* from Mason Pocket. Other late Tiffanian localities are either too poorly known or are undescribed.

When comparisons are made between the taxa present in the Swan Hills local fauna and middle and latest Tiffanian localities, there is decidedly more similarity between the Swan Hills local fauna and sites producing a later middle Tiffanian fauna. For example, Cedar Point Quarry possesses *Litocherus zygeus* (Gingerich, 1983), and therefore, using the scheme of Gingerich (1983, 1986), it is probably earlier in the middle Tiffanian than the North Dakota Brisbane and Judson localities, which possess *Litocherus lacunatus*. There are only 2 taxa present at Cedar Point Quarry which are present in the Swan Hills local fauna: *Neoplagiaulax hunteri*, and *Ignacius frugivorus* (again, the Cedar Point *Labidolemur soricoides* is probably conspecific with the Swan Hills specimens). Including *Carpodaptes cygneus*, there are seven taxa present in the Brisbane and Judson local faunas that are also present in the Swan Hills: *Prochetodon* sp. F, *Mesodma pygmaea*, *Neoplagiaulax hunteri*, *Litocherus lacunatus*, *Propalaeosinopa albertensis*, and *Ignacius frugivorus*. If further sampling at the Swan Hills localities shows the pantodont present to be *Titanoides primaevus* and the few specimens tentatively referred to *Neoplagiaulax*, cf. *N. nanophus* to be *Neoplagiaulax nanophus*, then, there will be 8 and 9 taxa found in common between the Swan Hills localities and Brisbane and Judson. Of the 37 taxa identified at Princeton Quarry (latest Tiffanian; Rose, 1981) 3 are also found in the Swan Hills local fauna: *Microcosmodon conus*, cf. *Palaeoryctes* sp., and *Ectocion osbornianum* (table 15).

The same holds true in comparisons between the Swan Hills local fauna

Table 15: Comparison of the mammalian fauna present in the Swan Hills local fauna with selected Tiffanian localities.*

| Swan Hills | Cedar Point | Brisbane and Judson | Roche Percée | Badwater Creek | Mason Pocket | Princeton Quarry |
|---|---|---|---|---|---|---|
| *Ptilodus kummae* | | | x | | | |
| *Prochetodon* sp. F | | x | x | | | |
| *Mesodma pygmaea* | | ~ | ~ | ~ | | |
| *Mesodma prolis* | | | | | | |
| *Neoplagiaulax hunteri* | x | x | ~ | | | |
| *Neoplagiaulax*, cf. *N. hazeni* | | | ~ | | | |
| *Neoplagiaulax*, cf. *N. nanophus* | | ? | ? | | | |
| ?*Parectypodus* sp. | | | | | | |
| *Microcosmodon conus* | | | x | x | | x |
| *Hadrolestes bounites* | | | x | | | |
| Erinaceidae, unident. | | | | | | |
| *Litocherus lacunatus* | | x | x | | | |
| cf. *Litocherus notissimus* | | | | | | |
| *Diacocherus*, cf. *D. meizon* | | | x | | | |
| *Nyctitherium* sp. 1 | | | | | | |
| *Nyctitherium* sp. 2 | | | | | | |
| *Leptacodon* sp. | | | | | | |
| *Limaconyssus* sp. 1 | | | | | | |
| *Limaconyssus* sp. 2 | | | | | | |
| Nyctitheriidae, unident. | | | | | | |
| *Plesiadapis churchilli* | | | x | x | | |
| *Ignacius frugivorus* | x | x | x | x | x | |
| *Carpodaptes cygneus* | | x | ~ | | | |
| *Elpidophorus clivus* | | | | | | |
| "*Protictis*", cf. "*P.*" *dellensis* | | | x | | | |
| Viverravidae, unident. | | | | | | |
| *Ectocion osbornianum* | | | x | x | | x |
| *Claenodon* sp. | | | | | | |
| *Titanoides* sp. | | ? | x | | | |
| *Prodiacodon* sp. | | | | | | |
| cf. *Palaeoryctes* sp. | | | | | | x |
| "Palaeoryctoid" | | | | | | |
| *Propalaeosinopa albertensis* | | x | ? | | | |
| *Labidolemur*, cf. *L. soricoides* | ? | | | | ? | |

* After Matthew and Granger (1921), Simpson (1935c), Krishtalka, *et al.* (1975), Krause (1977, 1978), Holtzman (1981), Fox (in press), Krause and Fox (in preparation).

x Species found in common.

~ May not be conspecific with complementary species.

? Swan Hills species possibly conspecific with closely related species in this fauna.

and other Tiffanian localities in Alberta. Taxonomic similarity is greatest between the Swan Hills local fauna and the late middle or early late Tiffanian Police Point local fauna (Krishtalka, 1973; Krause, 1978; Fox, in press) and late Tiffanian Canyon Ski Quarry (Krause, 1978; Fox, in preparation; Fox, in press) than between the early middle Tiffanian localities found in the area of Red Deer, Alberta (e.g., DW-2 and Joffre Bridge Road Cut, lower level [Fox, pers. comm.; Fox, in preparation; Fox, in press]).

Overall, taxonomic comparisons, the evolutionary grade of _Elpidophorus clivus_, n. sp., and _Mesodma prolis_, n. sp., and the presence of _Plesiadapis churchilli_ and _Litocherus lacunatus_ suggest for the Swan Hills local fauna an age slightly younger than the Roche Percée local fauna, perhaps the latter part of the early late or middle late Tiffanian.

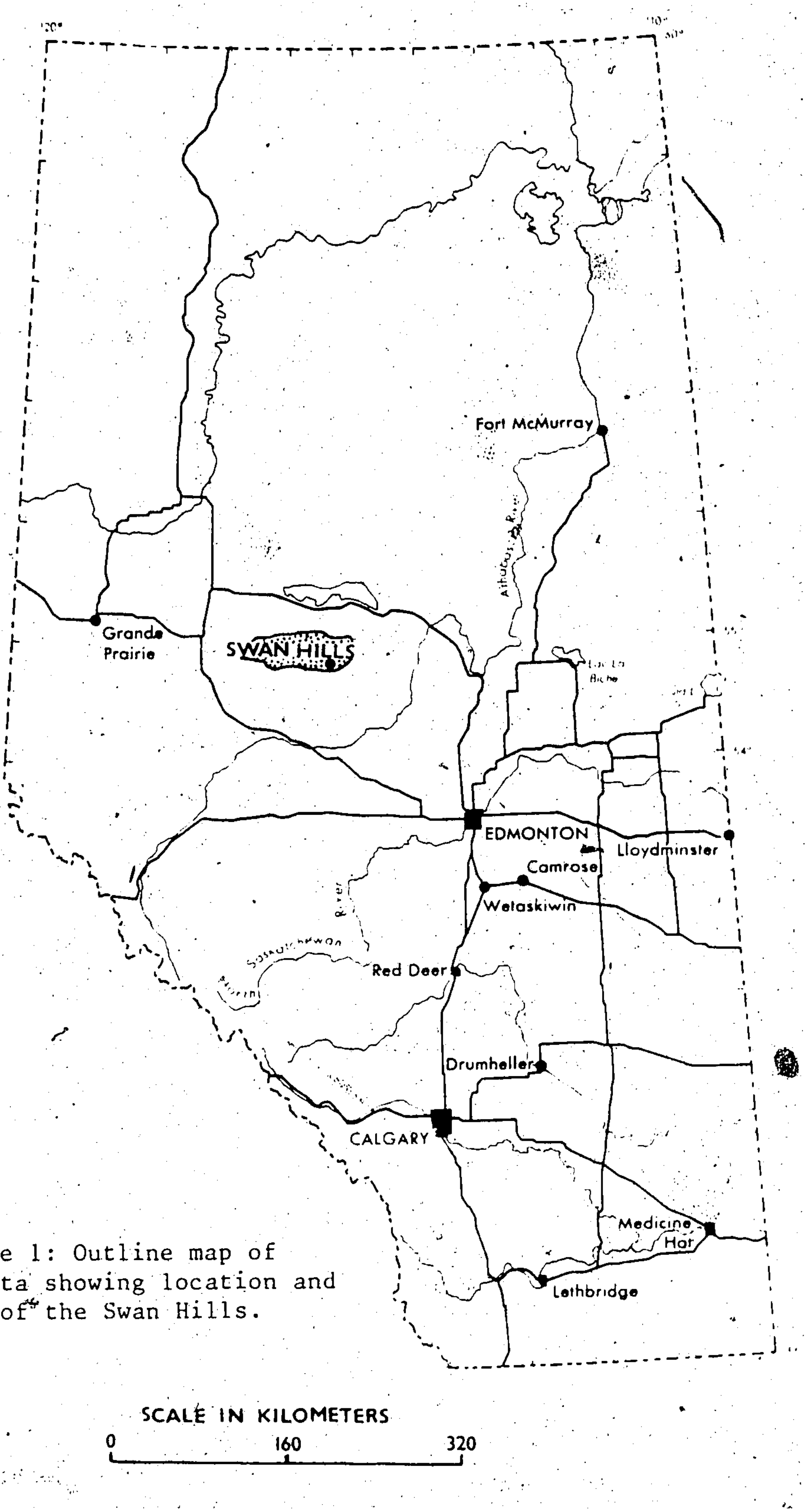


Figure 1: Outline map of Alberta showing location and area of the Swan Hills.

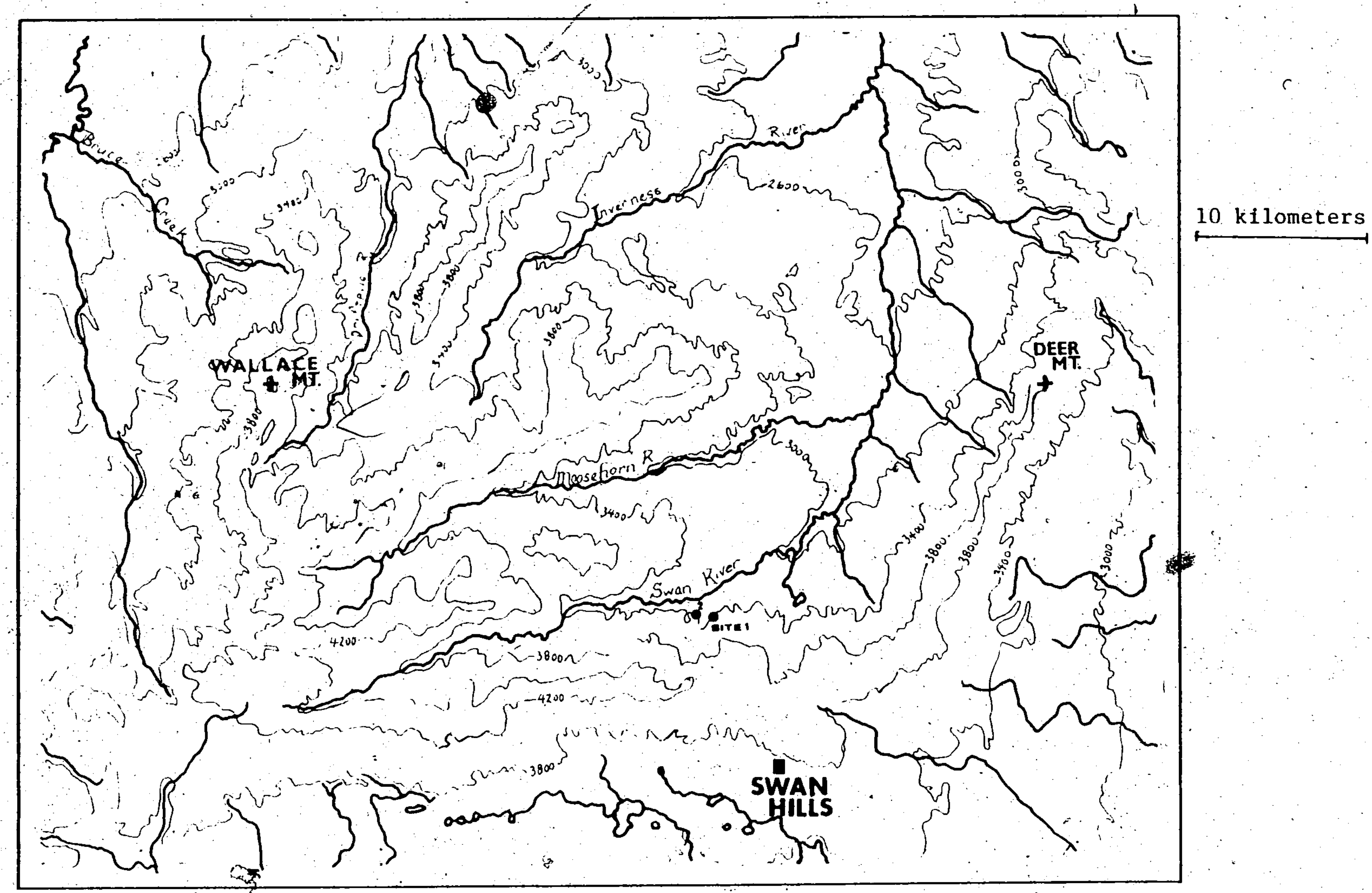


Figure 2: Detailed map of the Swan Hills showing the location of Swan Hills site 1 and 2.

Figure 3. Superimposed outlines of the labial profiles of (a) *Mesodma prolis*, n. sp. and (b) Roche Percee *Mesodma pygmaea*. The horizontal line is drawn through the peak of the anterobasal concavity and the interserrational notch between the ultimate and penultimate serrations.

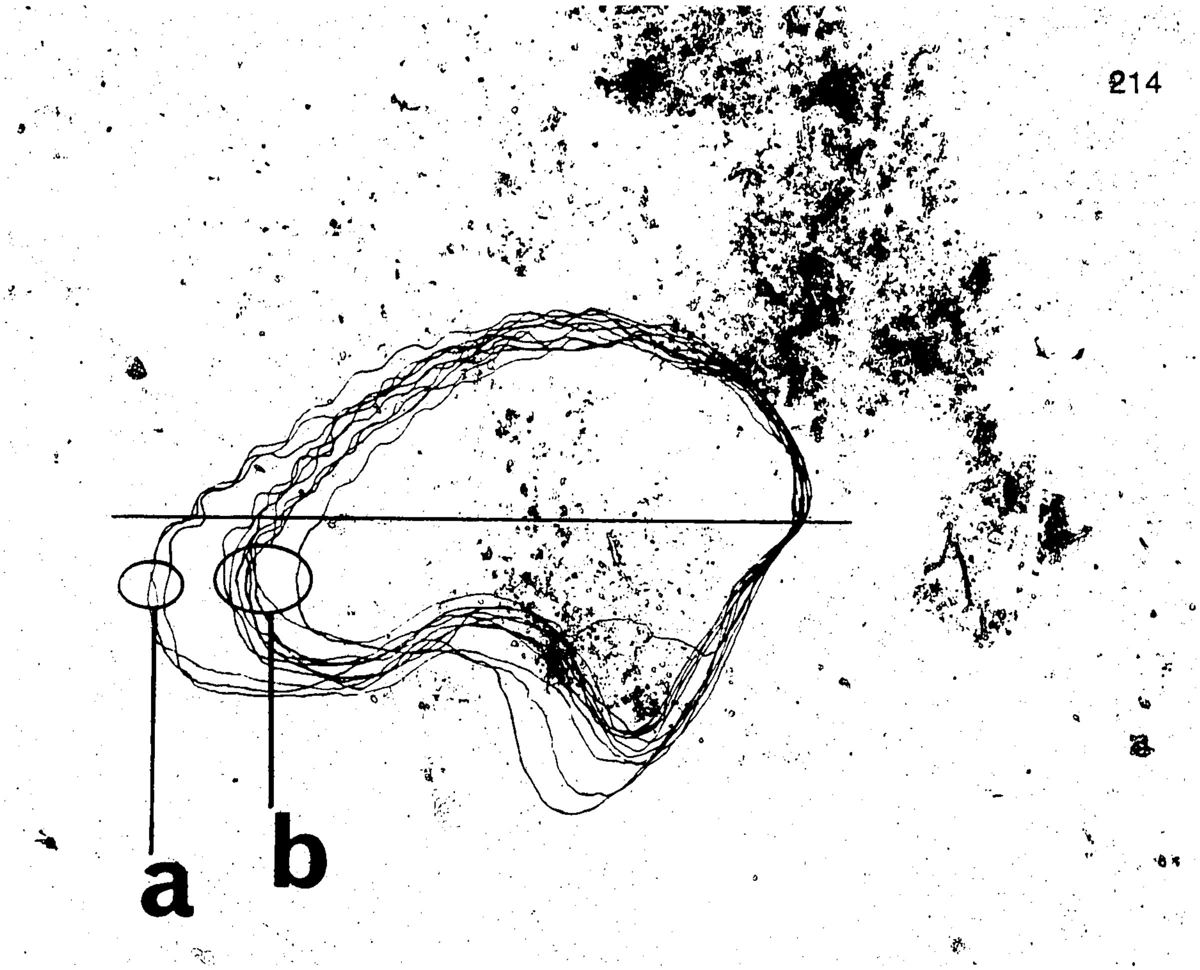

214
a
a
b

Figure 4. Camera lucida drawing of (a) the occlusal aspect and (b) the posterior aspect of UALVP 22501, M1 or 2 of *Limaconyssus* sp. 1, Swan Hills local fauna, Alberta.

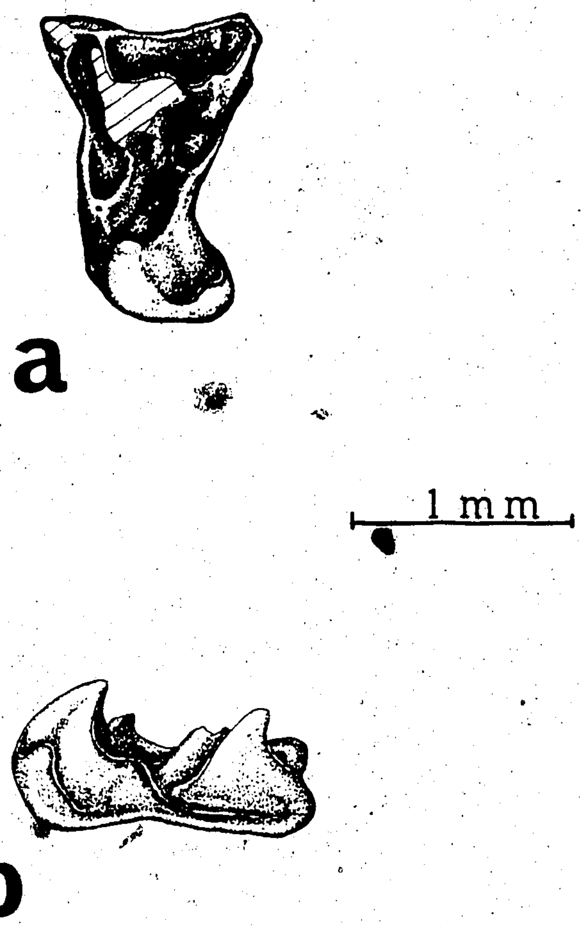

a
1 mm
b

Figure 5. Superimposed outlines of right p4 labial profiles of *Carpodaptes cygneus* from Swan Hills and Roche Percee showing the range of variation of the two samples. The solid lines represent specimens from the Swan Hills local fauna (ROM 5622, UALVP nos. 11718, 22351, 22353, 22639); the dashed lines represent specimens from the Roche Percee local fauna (UALVP nos. 8736, 8742, 8744, 8829, 9200, 11031). Orientation as in Krause (1978).

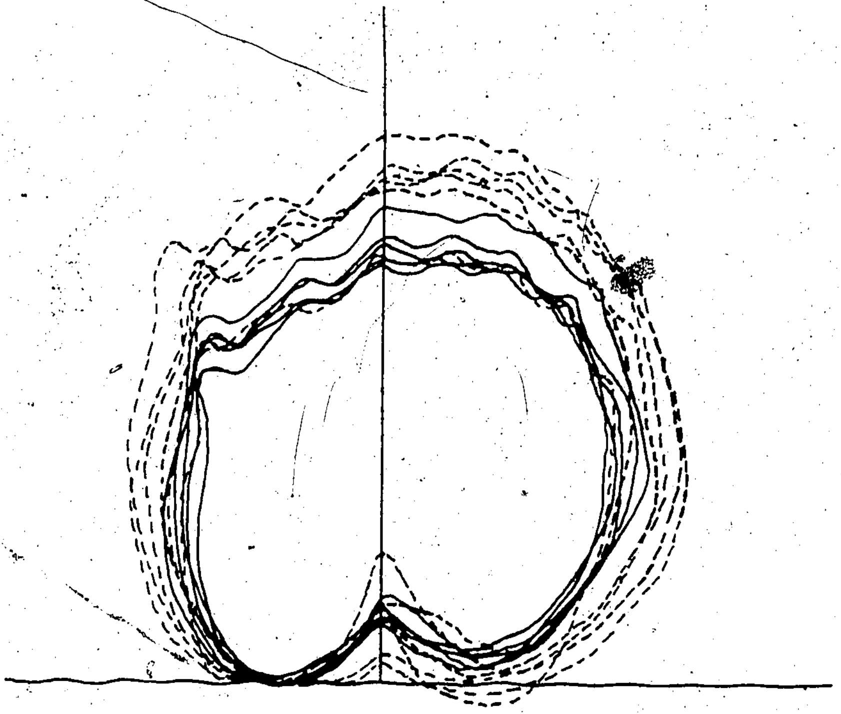
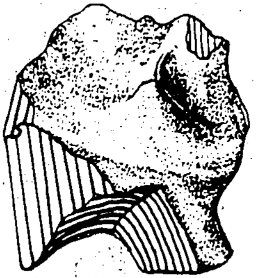
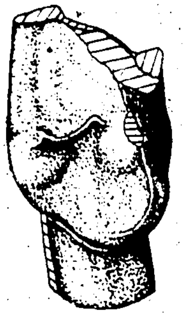


Figure 6. Camera lucida drawings of (a) the mesial aspect and (b) occlusal aspect of UALVP 22492, I1 of Elpidophorus clivus, n. sp., Swan Hills local fauna, Alberta.



**a**



**b**

Figure 7. Outline drawings of upper and lower molars of Elpidophorus clivus, n. sp. showing wear facets.

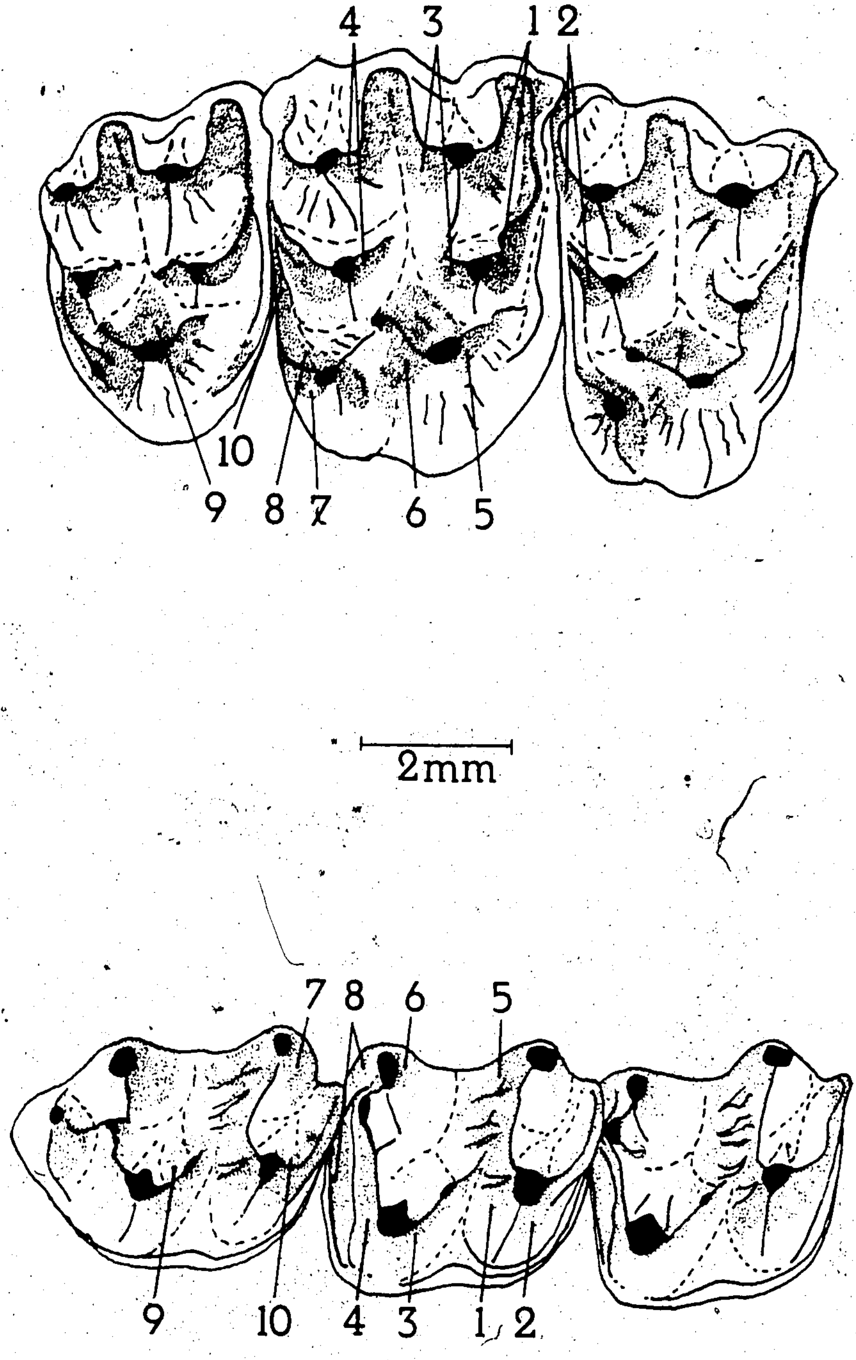

4
3
1
2
10
9
8
7
6
5
2mm
7
8
6
5
9
10
4
3
1
2

Figure 8. Dentitions of Microcosmodon conus, Swan Hills local fauna: (A) lateral, and (B) mesial view, UALVP 22738, left i1, about X9; (C) lateral, and (D) mesial view, UALVP 22214, right I2, about X9; (E) occlusal, and (F) lingual view, UALVP 22467, right m1, about X9; (G) lateral view, UALVP 22408, left DI2, about X9; (H) occlusal view, UALVP 22413, right M1, about X9; (I) occlusal view, UALVP 22411, left M2, about X10.

Dentitions of Ptilodus kummae, Swan Hills local fauna: (J) labial, and (K) lingual view, UALVP 22751, right p4, about X8.5; (L) lingual view, UALVP 5645, left P4, about X8.5; (M) occlusal view, UALVP 22324, right P4, about X8.5.

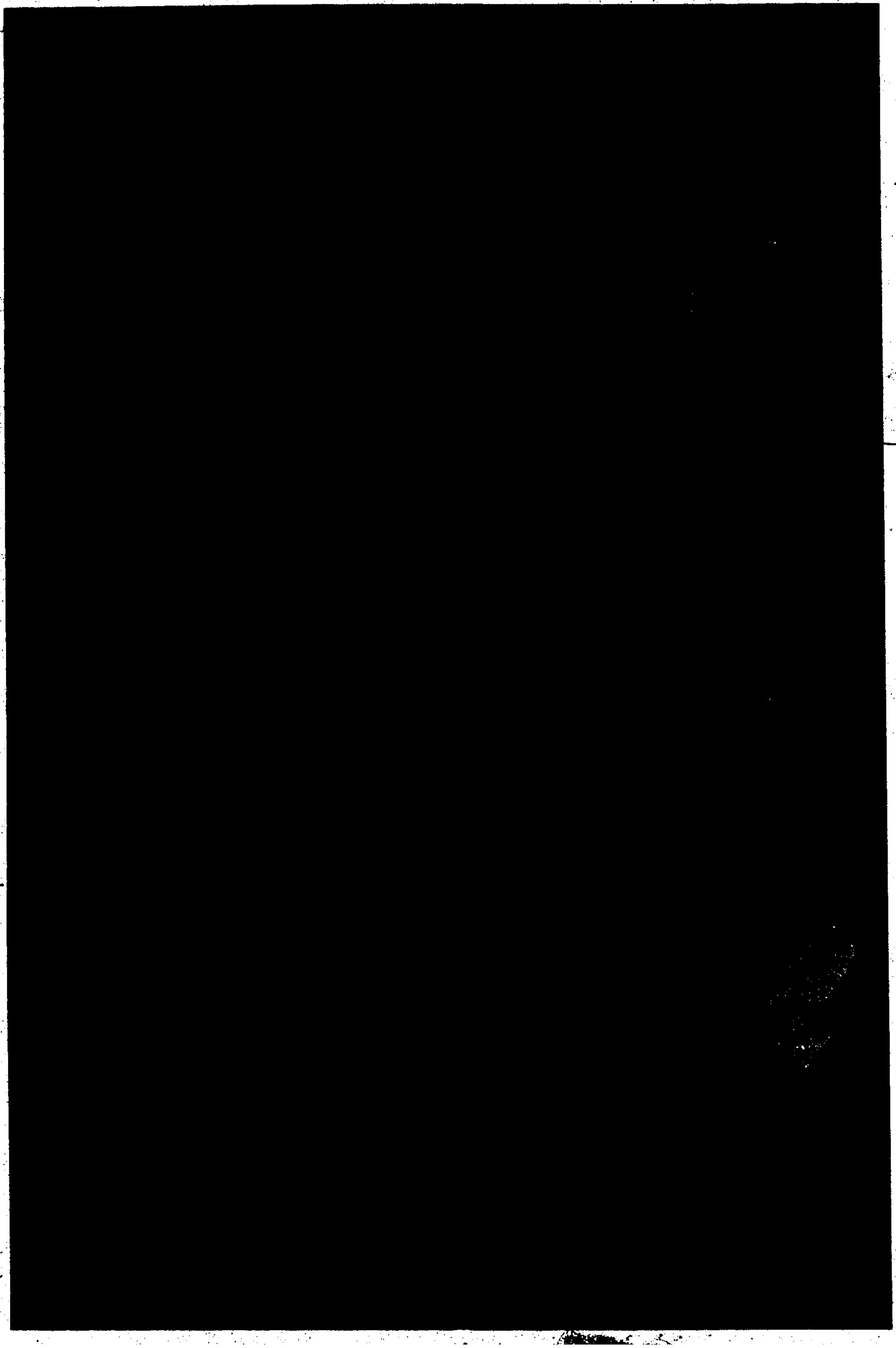


Figure 9. Dentitions of *Ptilodus kummae*, Swan Hills local fauna: (A) occlusal view, UALVP 5645, left P4, about X8.5; (B) occlusal view, UALVP 11999, right M2, about X8.5; (C) occlusal view, UALVP 22325, right m1, about X8.5.

Dentitions of *Prochetodon* sp. F, Swan Hills local fauna: (D) labial, and (E) lingual view, UALVP 22752, right p4, about X8.5; (F) lingual view, UALVP 22414, left p4, about X8.5; (G) occlusal view, UALVP 22252, left P3, about X8.5.

Dentitions of *Neoplagiaulax*, cf. *N. hazeni*, Swan Hills local fauna: (H) labial, and (I) lingual view, ROM 05607, right p4, about X8.5; (J) labial, and (K) lingual view, UALVP 22628, right p4, about X8.5.

Figure 10. Dentitions of Neoplagiaulax, cf. N. hazeni, Swan Hills local fauna: (A) lingual view, UALVP 22475, right P4, about X9; (B) occlusal, and (C) labial view, UALVP 22742, left P4, about X8.5; (D) occlusal view, ROM 05603, left m1, about X8.5; (E) occlusal view, UALVP 22210, left maxillary fragment with P1-2, about X10; (F) occlusal view, UALVP 22750, left P3, about X 8.5; (G) occlusal view, UALVP 22203, right M1, about X8.5; (H) occlusal view, UALVP 22635, right M2, about X8.5.

Dentitions of Neoplagiaulax hunteri, Swan Hills local fauna: (I) labial, and (J) lingual view, UALVP 22735, left p4, about X8.5; (K) labial, and (L) lingual view, UALVP 22600, right p4, about X8.5; (M) occlusal view, UALVP 22209, left m2, about 8.5; (N) occlusal view, UALVP 22338, left m1, about X8.5.

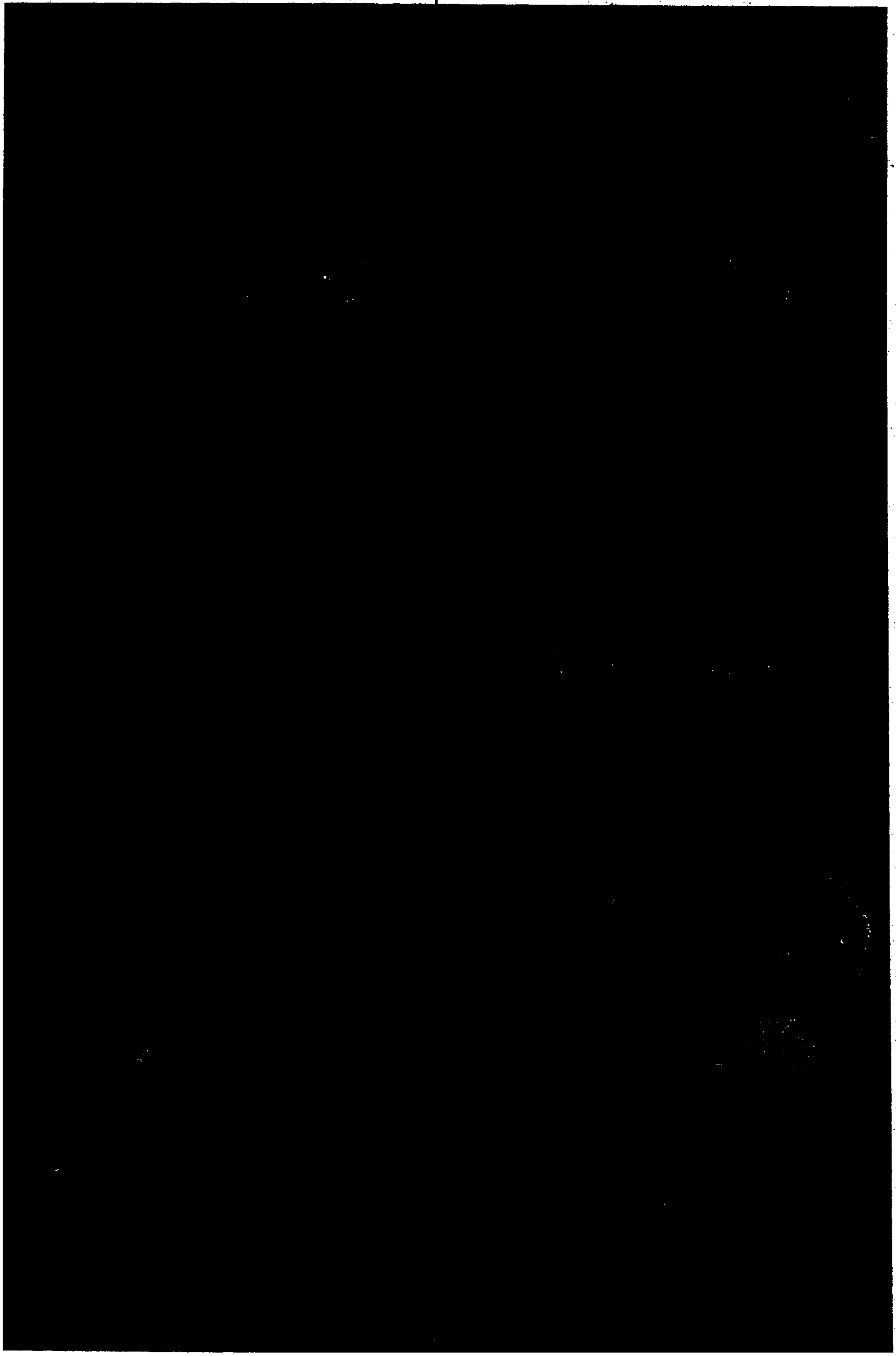


Figure 11. Dentitions of *Neoplagiaulax hunteri*, Swan Hills local fauna: (A) occlusal view, UALVP 22622, right P1, about X8.5; (B) occlusal view, UALVP 22334, right P2, about X9; (C) occlusal view, UALVP 22415, left P3, about X 8.5; (D) labial, and (E) lingual view, UALVP 22208, left P4, about X8.5; (F) occlusal view, UALVP 22613, left M1, about X8.5; (G) occlusal view, UALVP 22619, left M2, about X8.5.

Specimen referred to *Neoplagiaulax*, cf. *N. nanophus*, Swan Hills local fauna: (H) labial, and (I) lingual view, UALVP 22410, right p4, about X10.

Specimen referred to *Mesodma pygmaea*, Swan Hills local fauna: (J) labial, and (K) lingual view, UALVP 23828, left p4, about X10.

Dentitions of *Mesodma prolis*, n. sp., Swan Hills local fauna: (L) labial view, UALVP 22194, right p4, about X10; (M) occlusal view, UALVP 22432, right m1, about X10; (N) lingual view, UALVP 22194, right p4, about X10; (O) occlusal view, UALVP 22429, right m2, about X10; (P) labial, and (Q) lingual view, UALVP 22189, left P4, about X10.

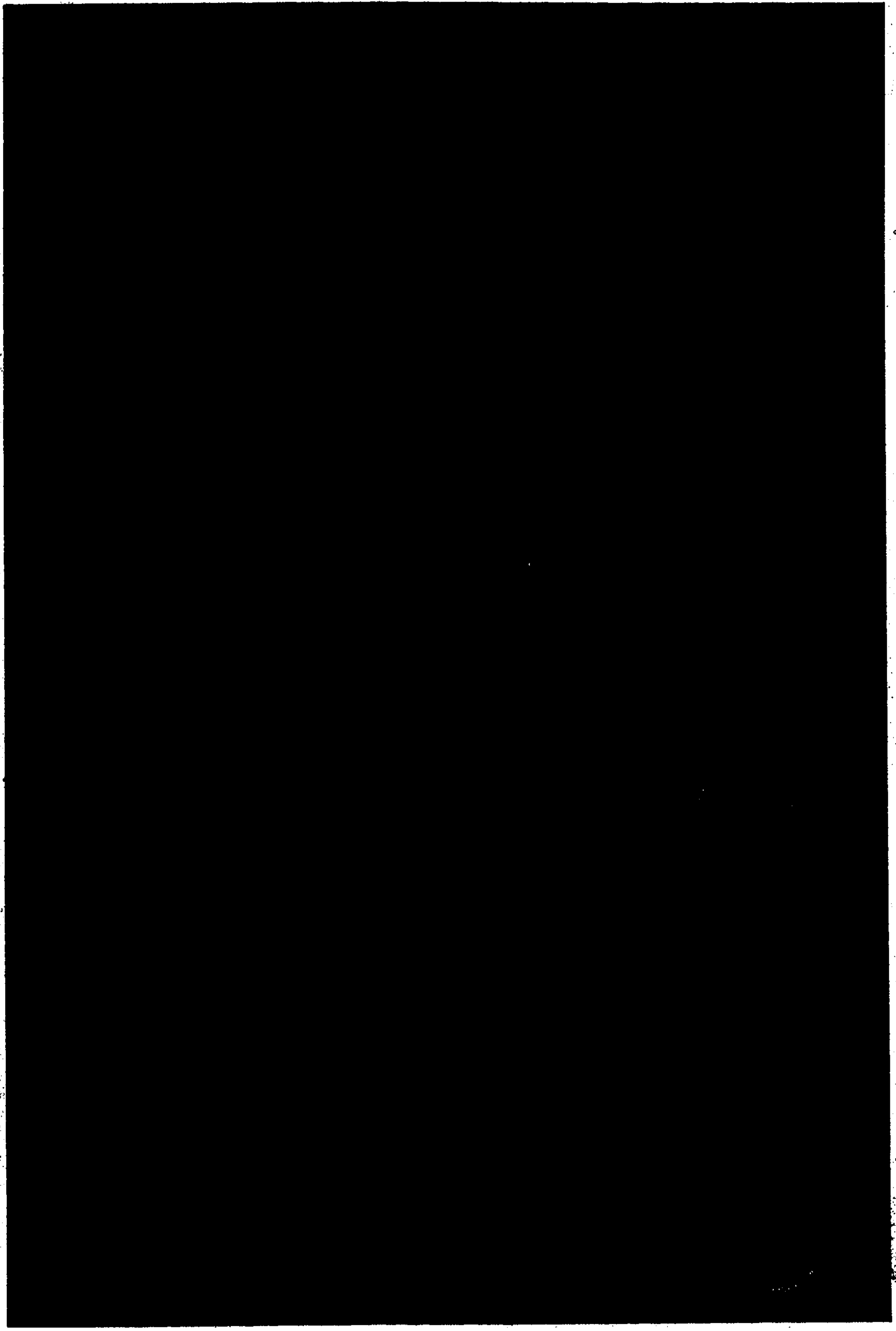


Figure 12. Dentitions of Mesodma prolis, n. sp., Swan Hills local fauna: (A) occlusal view, UALVP 22504, left M2, about X10; (B) occlusal view, UALVP 23835, left M1, about X10.

Specimen referred to ?Parectypodus sp., Swan Hills local fauna: (C) occlusal, (D) labial, and (E) lingual view, UALVP 22412, left P4; (C) about X10, (D) and (E) about X9.

Dentitions of Hadrolestes bounites, n. gen. and sp., Swan Hills local fauna: (F) labial, (G) lingual, and (H) occlusal view, UALVP 22348 (holotype), right dentary with p2-4, m1, m3, about X8; (I) occlusal view, UALVP 22231, right dentary fragment with m2-3, about X9; (J) lingual view, UALVP 22515, left canine, about X9; (K) occlusal view, UALVP 23882, right P4, about X8.5; (L) lingual view, UALVP 22707, left p1, about X9.

Figure 13. Dentitions of *Hadrolestes bounites*, n. gen. and sp., Swan Hills local fauna: (A) occlusal view, UALVP 23880, left P3, about X9; (B) occlusal view, UALVP 22499, left DP4, about X10; (C) occlusal view, UALVP 22703, right maxillary fragment with M1-3, about X9. Dentitions of Erinaceidae, unidentified gen. et sp., Swan Hills local fuana: (D) occlusal view, UALVP 22679, left p4, about X10; (E) occlusal view, ROM 05618, right dentary fragment with m2-3, about X10; (F) occlusal view, UALVP 22686, left dentary fragment with talonid of m1 plus m2, about X10.

Dentitions of *Litocherus lacunatus*, Swan Hills local fauna: (G) occlusal view, ROM 05631, left dentary fragment with m1-2, about X7.5.

Specimen referred to Cf. *Litocherus notissimus*, Swan Hills local fauna: (H) occlusal view, UALVP 23887, left M1, about X10.

Specimen referred to *Diacocherus*, cf. *D. meizon*, Swan Hills local fauna: (I) occlusal view; UALVP 22662, right p4, about X11.

Figure 14. Specimen referred to Litocherus lacunatus, Swan Hills local fauna: (A) labial view, UALVP 23850, left p3, about X7.5.

Dentitions of Diacocherus, cf. D. meizon, Swan Hills local fauna: (B) labial view, UALVP 22662, right p4, about X10; (C) labial view, UALVP 23859, right dentary fragment with p2-3, about X10; (D) occlusal view, UALVP 22337, left dentary fragment with incomplete m1, plus m2, about X 9.5; (E) occlusal view, UALVP 22644, right m1, about X10; (F) occlusal view, ROM 05616, left m3, about X10; (G) occlusal view, UALVP 23847, left dentary fragment with m2-3 from site 2, about X10; (H) occlusal view, UALVP 23857, left P3, about X8.5; (I) occlusal view, UALVP 22333, left P4, about X10; (J) occlusal view, UALVP 22481, right M1, about X10; (K) occlusal view, UALVP 22507, left M2, about X10.

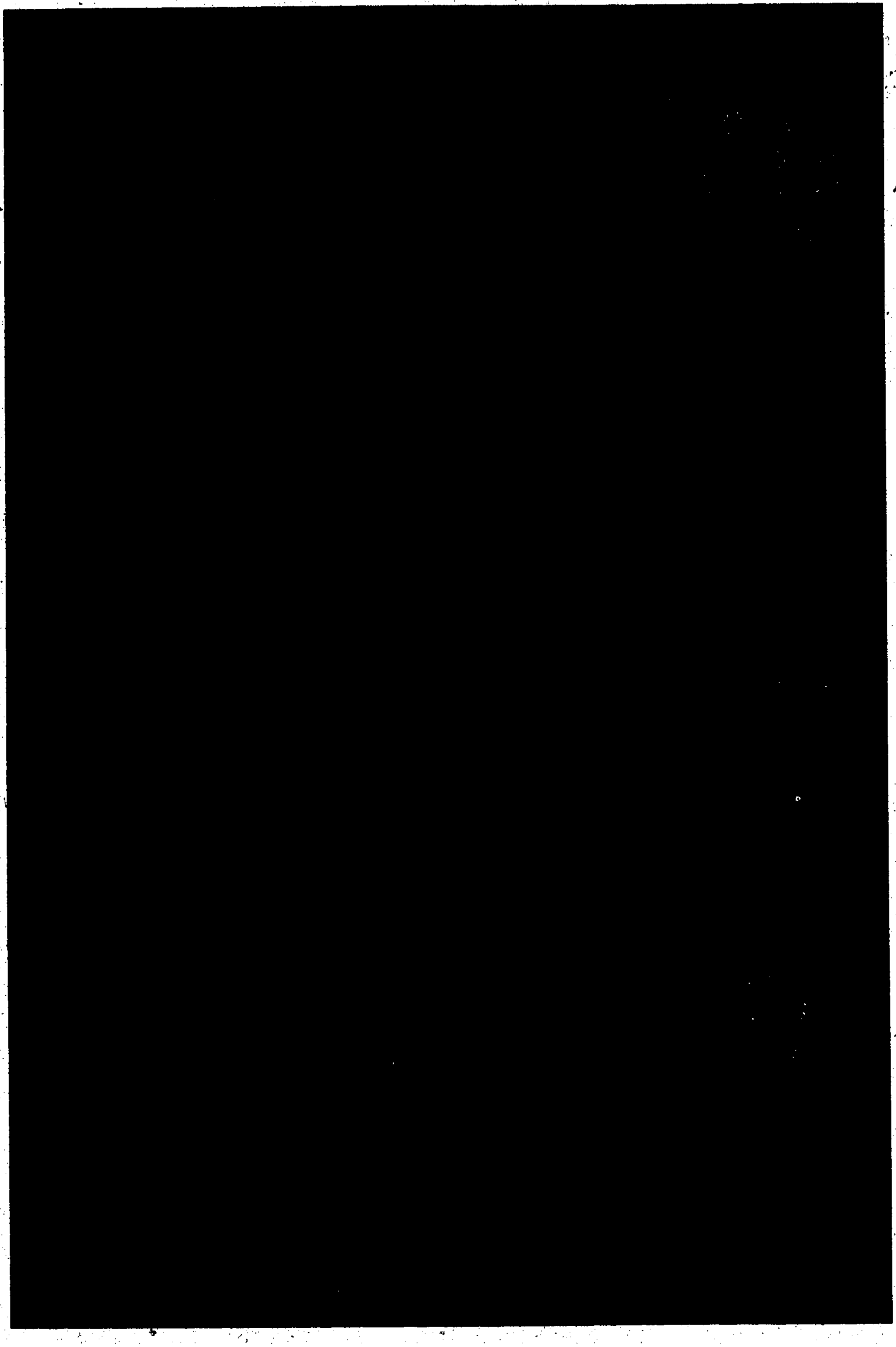


Figure 15. Dentitions of *Diacocherus*, cf. *D. meizon*, Swan Hills local fauna: (A) occlusal view, UALVP 22331, left maxillary fragment with incomplete M2, plus M3, about X10.

Specimen referred to *Nyctitherium* sp. 1, Swan Hills local fauna: (B) occlusal view, UALVP 22468, left M1 or 2, about X10.

Specimen referred to *Nyctitherium* sp. 2, Swan Hills local fauna: (C) occlusal view, UALVP 22212, left M1 or 2, about X10.

Dentitions of *Leptacodon* sp., Swan Hills local fauna: (D) labial and (E) occlusal view, UALVP 22227, left dentary fragment with p3-4, about X10; (F) occlusal view, UALVP 22685, right dentary fragment with incomplete p4, plus m1, about X10.

Dentitions of *Limaconyssus* sp. 1, Swan Hills local fauna: (G) occlusal, (H) labial, and (I) lingual view, UALVP 22520, right dentary fragment with m2, about X11; (J) occlusal view, UALVP 22501, left M1 or 2, about X11.

Dentitions of *Limaconyssus* sp. 2, Swan Hills local fauna: (K) occlusal view, UALVP 23922, right dentary fragment with m1-2, about X11.

Dentitions of Nyctitheriidae, unidentified gen. et sp., Swan Hills local fauna: (L) occlusal view, ROM 05619, right dentary fragment with incomplete m2, plus m3, about X11.

Specimen referred to *Plesiadapis churchilli*, Swan Hills local fauna: (M) occlusal view, UALVP 11737, right P3, about X9.

Figure 16. Dentitions of *Plesiadapis churchilli*, Swan Hills local fauna: (A) occlusal view, UALVP 22221, right M2, about X9; (B) occlusal view, UALVP 22617, right M3, about X9.

Specimen referred to *Ignacius frugivorus*, Swan Hills local fauna: (C) occlusal view, UALVP 22360, right m3, about X9.5.

Dentitions of *Carpodaptes cygneus*, Swan Hills local fauna: (D) occlusal, (E) labial, and (F) lingual view, UALVP 22353, right dentary fragment with p4-m1, about X10; (G) occlusal view, UALVP 22642, left dentary fragment with m2-3, about X 11; (H) occlusal view, UALVP 22654, right I1, about X10.

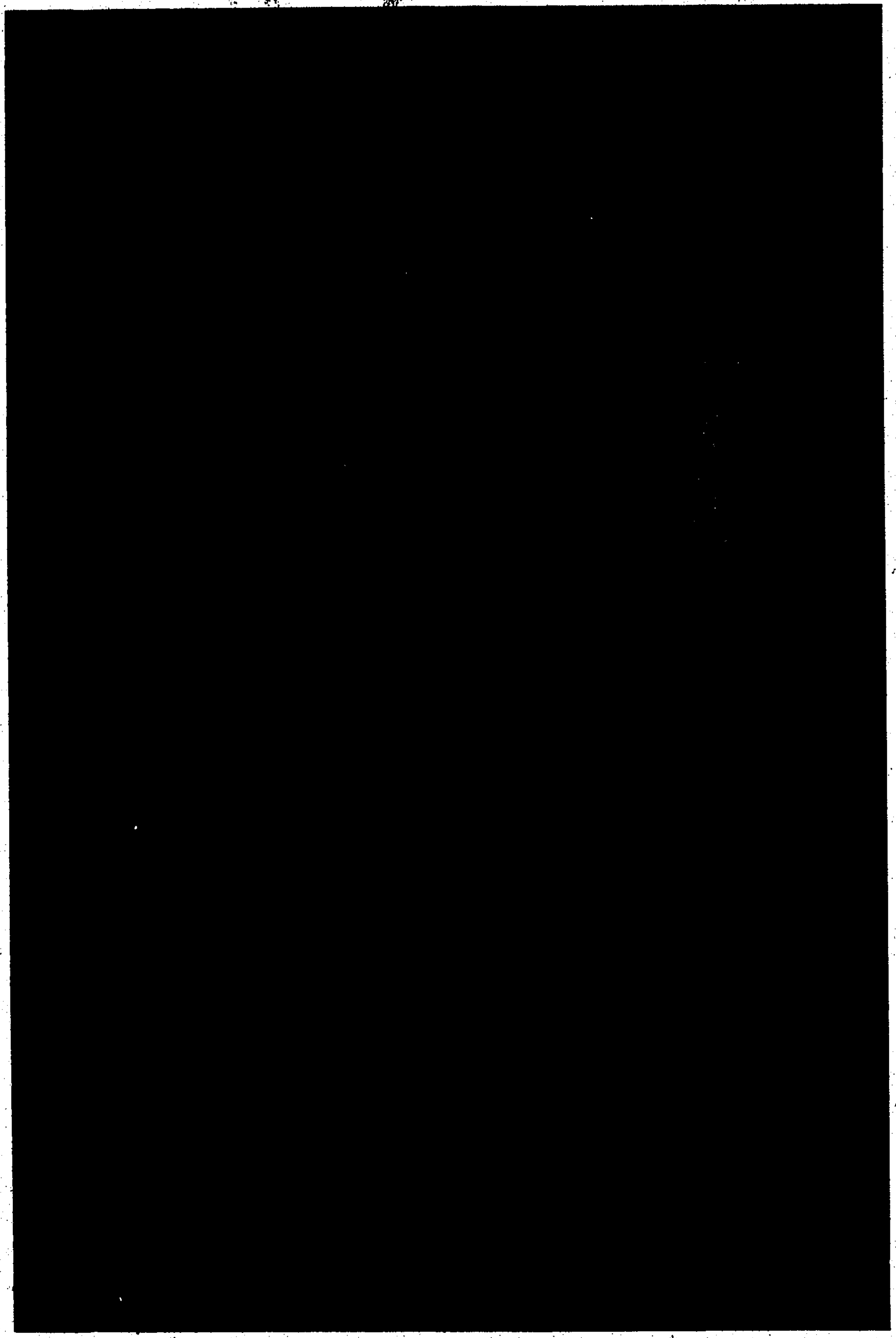


Figure 17. Dentitions of Carpodaptes cygneus, Swan Hills local fauna: (A) labial view, UALVP 22257, right dentary fragment with incomplete p4, plus m1-3, about X10; (B) occlusal view, UALVP 22211, left I2, about X10; (C) occlusal view, UALVP 11720, right maxillary fragment with P2-3, about X10; (D) occlusal view, UALVP 22647, left maxillary fragment with P4, M1-2, about X10; (E) occlusal view, UALVP 22498, right M3, about X10.

Dentitions of Elpidophorus clivus, n. sp., Swan Hills local fauna: (F) lingual and (G) lateral view, UALVP 22379, left i1, about X8; (H) lingual and (I) mesial view, UALVP 23839, left ?i3, about X8; (J) occlusal view, UALVP 22712, right p1, about X10; (K) occlusal and (L) lingual view, UALVP 22258, right p2, about X9.

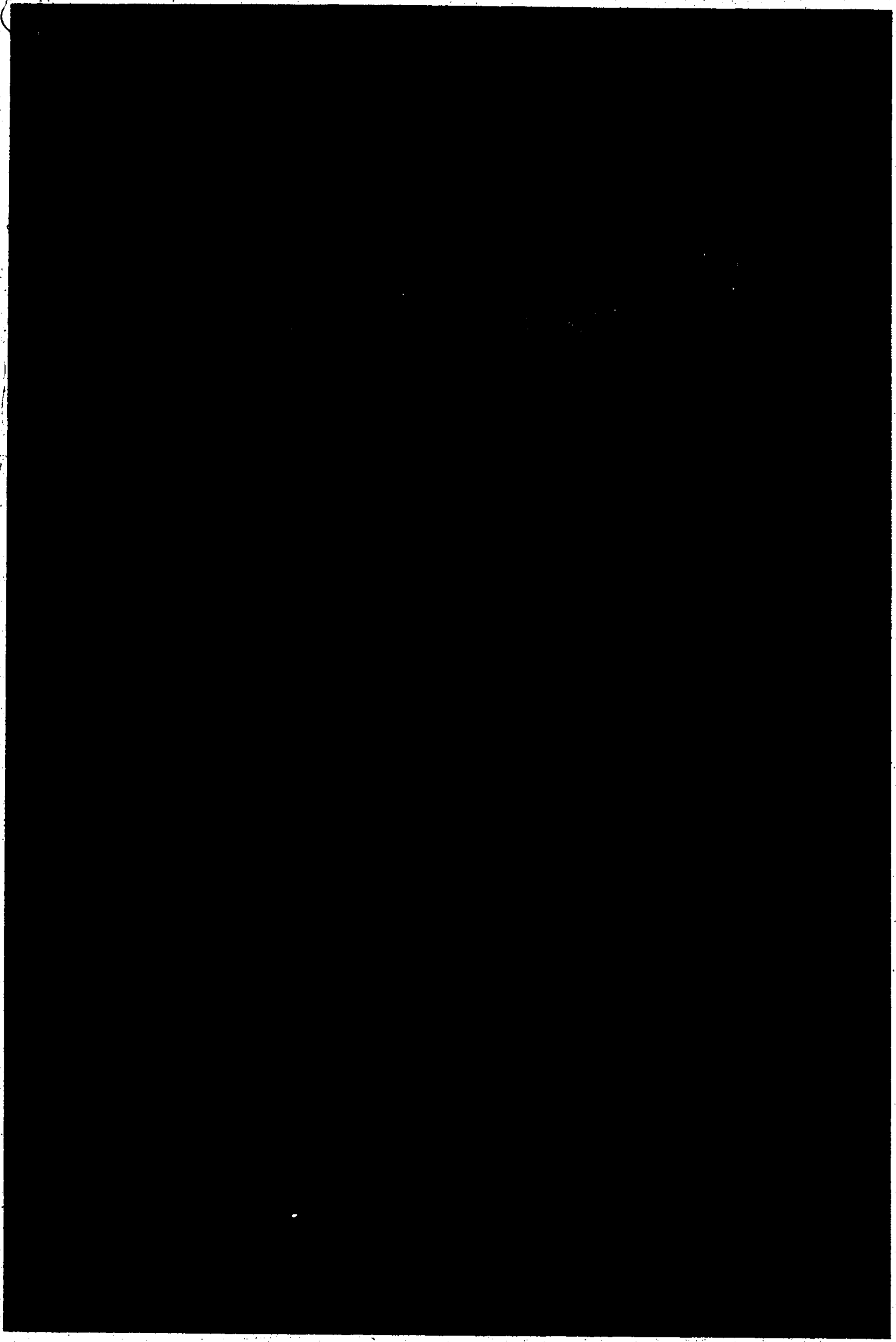


Figure 18. Dentitions of Elpidophorus clivus, n. sp., Swan Hills local fauna: (A) labial, (B) occlusal, and (C) lingual view, UALVP 23864, left dp3, about X8; (D) occlusal view, UALVP 22330, right p3, about X9.5; (E) occlusal view, UALVP 22593, right dp4, about X9; (F) occlusal view, UALVP 22317 (holotype), right dentary fragment with p4, m1-3, about X5; (G) labial and (H) lingual view, UALVP 22625, right P1, about X10; (I) labial view, UALVP 22711, right P2, about X10; (J) occlusal view, UALVP 22327, right DP4, about X9; (K) occlusal view, UALVP 22264, left P3, about X9; (L) occlusal view, UALVP 22362, left P4, about X9.

Figure 19. Dentitions of Elpidophorus clivus, n. sp., Swan Hills local fauna: (A) occlusal view, UALVP 22364, right M1, about 9.5; (B) occlusal view, UALVP 22584, right M3, about 9.5; (C) occlusal view, UALVP 22269, right M2, about 9.5.

Specimen referred to "Protictis", cf. "P." dellensis, Swan Hills local fauna: (D) occlusal and (F) lingual view, UALVP 23910, right DP3, about X6.

Dentitions of Viverravidae, unidentified gen. and sp., Swan Hills local fauna: (E) labial view, UALVP 22319, incomplete left m1, about X10.5; (G) occlusal view, UALVP 23911, incomplete right m2, about X11.

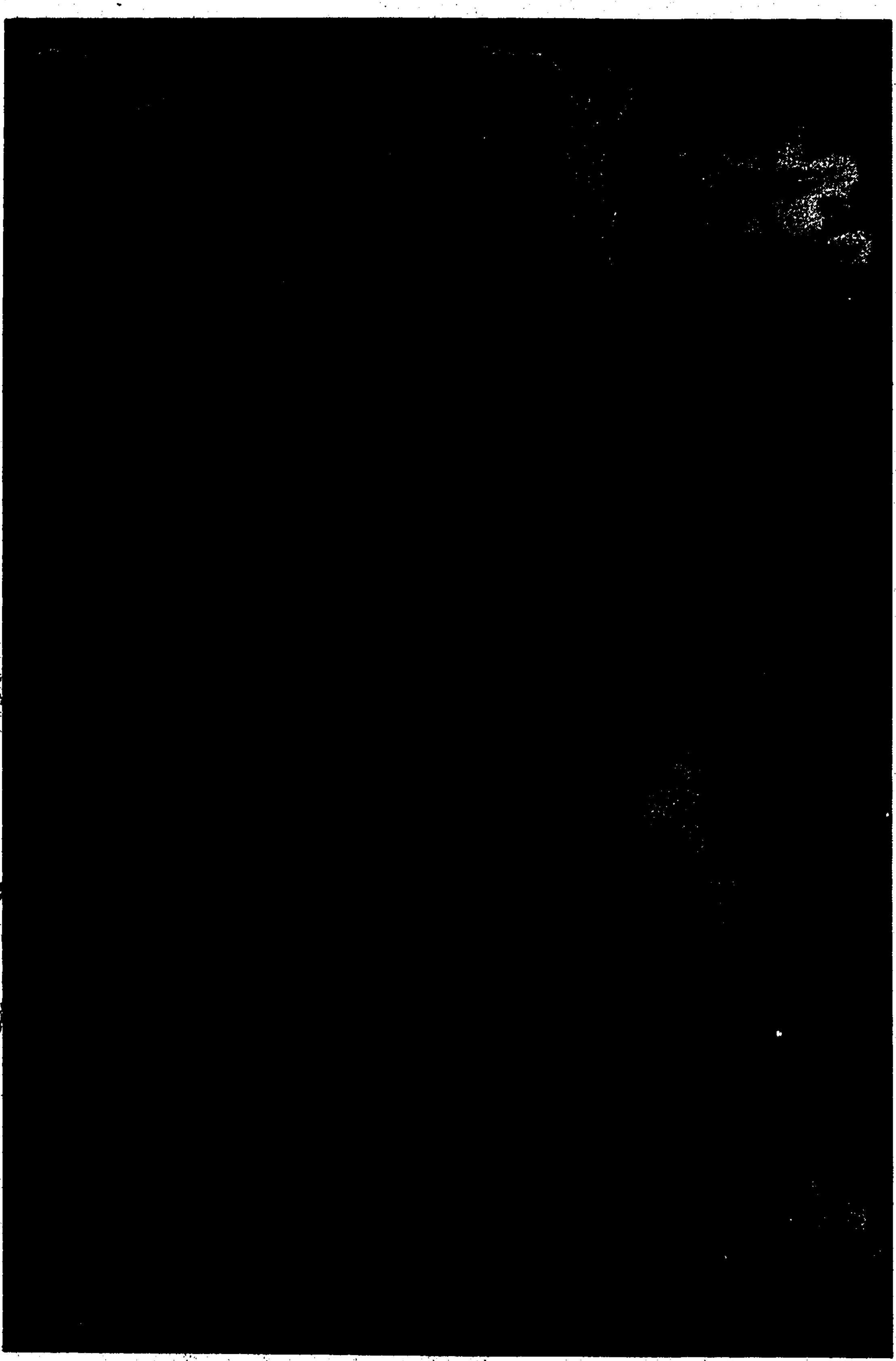


Figure 20. Dentitions of *Ectocion osbornianum*, Swan Hills local fauna: (A) occlusal view, UALVP 23913, left p3, about X6.5; (B) occlusal view, UALVP 23914, right dp4, about X6.5; (C) occlusal view, UALVP 23915, left m3, about X6.5; (D) occlusal view, UALVP 23917, right DP3, about X6.5.

Dentitions of *Claenodon* sp., Swan Hills local fauna: (E) occlusal view, UALVP 23923, right P3, about X4; (F) occlusal view, ROM 05630, talonid of a left ?m1, about X4; (G) occlusal view, UALVP 23924, fragment of a left P4, about X4.5; (H) occlusal view, UALVP 22526, left M1, about X 3.5.

Dentitions of *Titanoides* sp., Swan Hills local fauna: (I) occlusal view, UALVP 22332, incomplete left M2 or 3, about X2.3; (J) occlusal view, UALVP 22444, fragment of a left M1 or 2, about X2.3.

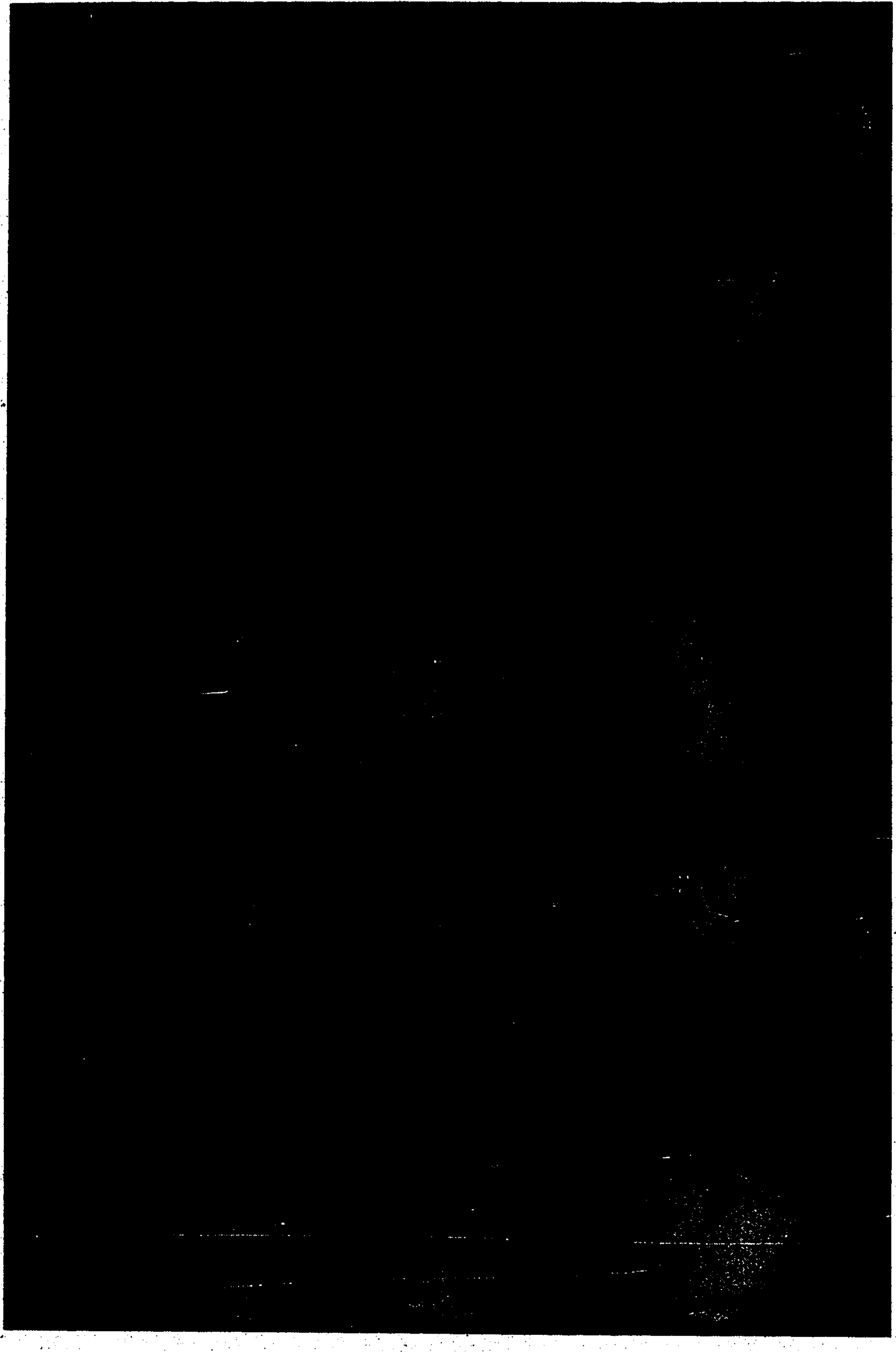


Figure 21. Dentitions of *Prodiacodon* sp., Swan Hills local fauna: (A) occlusal view, UALVP 23912, incomplete left M1 or 2, about X10; (B) occlusal view, UALVP 22683, incomplete left M1 or 2, about X10. Dentitions of cf. *Palaeoryctes* sp., Swan Hills local fauna: (C) labial, (D) occlusal, and (E) lingual view, UALVP 22434, right m3, (C) about X10 and (D) and (E) about X8.5; (F) occlusal view, UALVP 22477, incomplete right P4, about X10.

Specimen referred to "Palaeoryctoid", unidentified gen. and sp., Swan Hills local fauna: (G) occlusal view, UALVP 23909, talonid of a right m1 or 2.

Dentitions of *Propalaeosinopa albertensis*, Swan Hills local fauna: (H) lingual view, UALVP 23893, right p3, about X8; (I) occlusal and (J) labial, UALVP 23900, left p4, (I) about X10 and (J) about X8; (K) occlusal view, UALVP 23902, left m1, about X8; (L) labial, (M) lingual, and (N) occlusal view, UALVP 22321, right m3, (L) and (N) about X8.5 and (M) about X8.

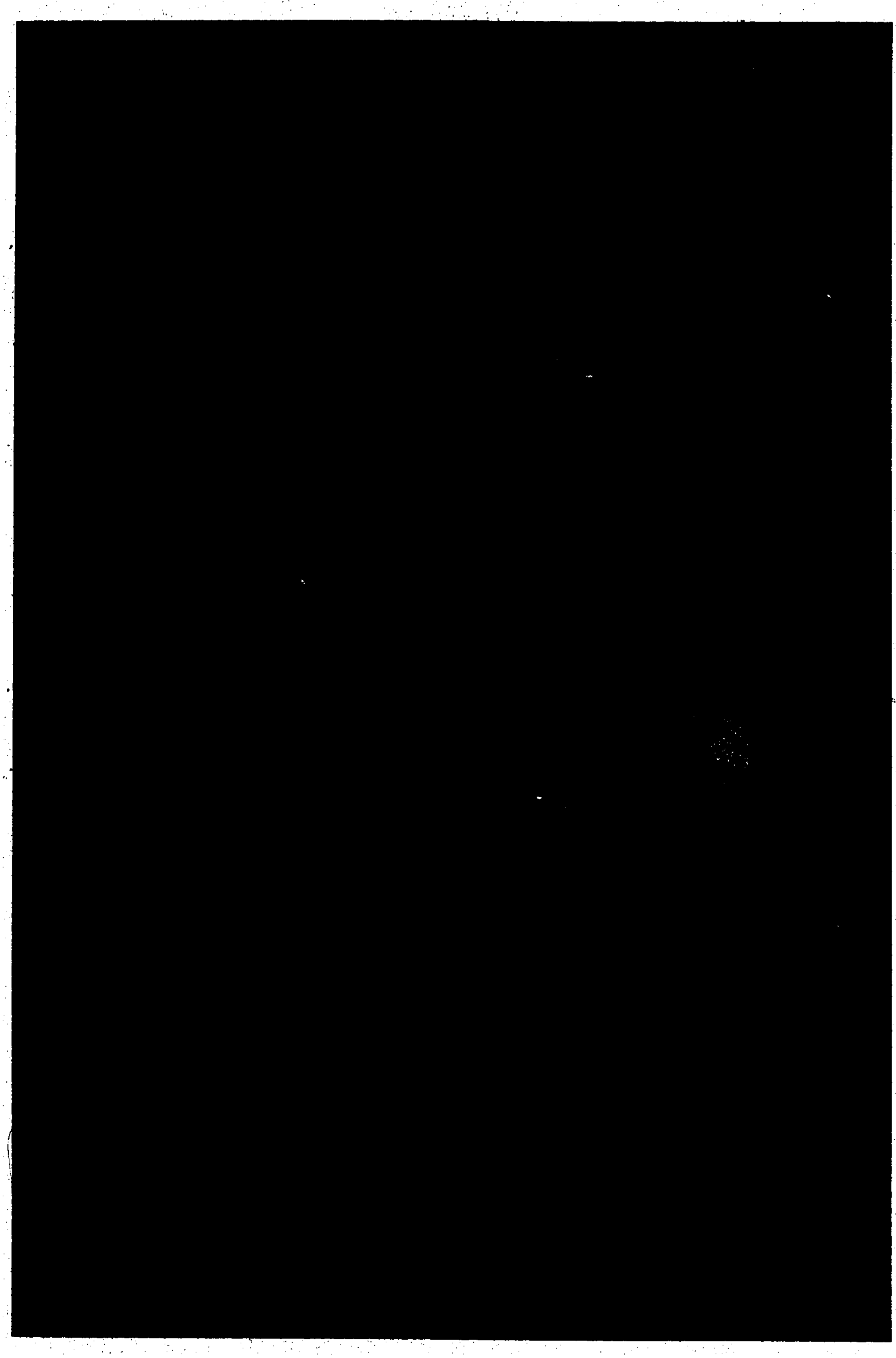


Figure 22. Dentitions of _Propalaeosinopa albertensis_, Swan Hills local fauna: (A) occlusal view, UALVP 23908, right maxillary fragment with M1-2, about X9; (B) labial view, UALVP 22508, left P4, about X8; (C) occlusal view, UALVP 22443, right M3, about X 9.5.

Dentitions of _Labidolemur_, cf. _L_. _soricoides_, Swan Hills local fauna: (D) mesial and (E) lingual view, UALVP 23889, right i1, about X7; (F) labial and (G) lingual, UALVP 23890, right p2, about X10.

# REFERENCES CITED

ALLAN, J. A. (1919): Geology of the Swan Hills in Lesser Slave Lake district, Alberta. - Geol. Surv. Can. Summ. Rept. 1918, **C**: 7-13.

ALLAN, J. A. & SANDERSON, J. O. G. (1945): Geology of the Red Deer and Rosebud sheet, Alberta. - Res. Counc. Alta., Rept. **13**: 1-115.

AMEGHINO, F. (1890): Los Plagiaulacidos Argentinos, y sus Relaciones Zoológicas, Geológicas, y Geográphicas. - Bol. Inst. Geogr. Argent., **11**: 143-201.

ARCHIBALD, J. D. (1982): A study of Mammalia and geology across the Cretaceous-Tertiary boundary in Garfield County, Montana. - Univ. Calif. Publ. Geol. Sci., **122**: 11-286.

BOWDICH, T. E. (1821): Analysis of the natural classification of Mammalia for the use of students and travellers. - J. Smith, Paris: 1-115.

BOWN, T. M. (1979): Geology and mammalian Paleontology of the Sand Creek Facies, Lower Willwood Formation (Lower Eocene), Washakie County, Wyoming. - Geol. Sur. Wyoming, Memoirs, 2: 1-151.

BOWN, T. M. & ROSE, K. D. (1976): New early Tertiary primates and a reappraisal of some Plesiadapiformes. - Folia Primatologica, **26**: 109-138.

BOWN, T. M. & SCHANKLER, D. (1982): A review of the Proteutheria and Insectivora of the Willwood Formation (lower Eocene) Bighorn Basin, Wyoming. - U. S. Geol. Surv. Bull., **1523**: 1-79.

BROWN, B. (1914): Cretaceous Eocene correlation in New Mexico, Wyoming, Montana, Alberta. - Bull. Geol. Soc. Amer., **25**: 355-380.

BUTLER, P. M. (1948): On the evolution of the skull and teeth in the Erinaceidae, with special reference to the material in the British Museum. - Proc. Zool. Soc., London, **118**: 446-500.

_, _ (1973): Molar wear facets of early Tertary North American Primates. - Symp. IVth Int. Congr. Primat., **3**: 1-27.

CARRIGY, M. A. (1970): Proposed revision of the boundaries of the Paskapoo Formation in the Alberta Plains. - Bull. Can. Petr. Geol., **18**: 156-165.

_ , _ (1971): Lithostratigraphy of the uppermost Cretaceous (Lance) and Paleocene strata of the Alberta Plains. - Res. Counc. Alta., Bull., **27**: 1-161.

CLEMENS, W. A. (1963): Fossil mammals of the type Lance Formation, Wyoming: Part 1. Introduction and Multituberculata. - Univ. Calif, Publ. Geol. Sci., **48**: 1-105.

_ , _ (1973): Fossil mammals of the type Lance Formation, Wyoming, Part III. Eutheria and summary. - Univ. Calif. Publ. Geol. Sci., **94**: 1-102.

COPE, E. D. (1873): On the short footed *Ungulata* of the Eocene of Wyoming. - Proc. Amer. Philos. Soc., **13**: 38-74.

_ , _ (1881 a): Eocene Plagiaulacidae. - Amer. Nat., **15**: 921-922.

_ , _ (1881 b): On some Mammalia of the lowest Eocene beds of New Mexico. - Amer. Philos. Soc. Proc., **19**: 484-495.

_ , _ (1882): Notes on Eocene Mammalia. - Amer. Nat., **16**: 522.

_ , _ (1883): First addition to the fauna of the Puerco Eocene. - Proc. Amer. Philo. Soc., **20**: 545-563.

_ , _ (1884 a): The Tertiary Marsupialia. - Amer. Nat., **18**: 686-697.

_ , _ (1884 b): Second addition to the knowledge of the Puerco epoch. - Proc. Amer. Philos. Soc., **21**: 309-324.

CROMPTON, A. W. (1971): The origin of the tribosphenic molar. - In KERMACK, D. M. & KERMACK, K. A. (eds.): Early Mammals. - Zool. J. Linn. Soc., **50**: 65-87.

DELSON, E. (1971): Fossil mammals of the early Wasatchian Powder River local fauna, Eocene of northeast Wyoming. - Bull. Amer. Mus. Nat. Hist., **146**: 305-364.

DORR, J. A., JR. (1952): Early Cenozoic stratigraphy and vertebrate paleontology of the Hoback Basin, Wyoming. - Bull. Geol. Soc. Amer., **63**: 59-94.

_ , _ (1958): Early Cenozoic vertebrate paleontology, sedimentation, and orogeny in central western Wyoming. - Bull. Geol. Soc. Amer., **69**: 1217-1244.

_ , _ (1977): Partial skull of *Palaeosinopa simpsoni* (Mammalia, Insectivora), latest Paleocene Hoback Formation, central western Wyoming, with some general remarks on the family Pantolestidae. - Contr. Mus. Paleont. Univ. Mich., **24**: 281-307.

FILHOL, H. (1877): Consideration sur la decouverte de quelques mammiferes fossiles appartenant a l'Eocene superieur. - Soc. Philo. Paris Bull., **1**: 51-54.

FISCHER VON WALDHEIM, G. F. (1817): Adversaria Zoologica. Part 2. De systemata mammalium. - Mem. Soc. Imperiale Naturalistes, Mosquae, **5**: 368-391.

FOX, R. C. (1971): Early Campanian multituberculates (Mammalia: Allotheria) from the Upper Milk River Formation, Alberta. - Can. J. Earth Sci., **8**: 916-938.

_ , _ (in press): The succession of Paleocene mammals in western Canada. - In BOWN, T. M. & ROSE, K. D. (eds.): Dawn of the Age of mammals in the northern Rocky Mountain region. - Geol. Soc. Amer., Spec. Paper.

GAZIN, C. L. (1956): Paleocene mammalian faunas of the Bison Basin in south-central Wyoming. - Smith. Misc. Coll., **131**: 1-57.

GAZIN, C. L. (1971): Paleocene primates from the Shotgun Member of the Fort Union Formation in the Wind River Basin, Wyoming. - Biol. Soc. Washington, Proc., **84**: 13-38.

GERVAIS, P. (1877): Enumération de quelques ossements d'animaux vertébrés recueillis aux environs de Reims par M. Lemoine. - J. Zool., **6**: 74-79.

GIBSON, D. W. (1977): Upper Cretaceous and Tertiary coal-bearing strata in the Drumheller-Ardley region, Red Deer River valley, Alberta. - Geol. Surv. Can. Pap., **76-35**: 1-41.

GIDLEY, J. M. (1917): Notice of a new Paleocene mammal, a possible relative of the titanotheres. - Proc. U. S. Nat. Mus., **52**: 431-435.

GIEBEL, C. G. (1855): Die Saugetiere in zoologischer, anatomischer und palaeontologischer Beziehung umfassend dargestellt. - 1108 pp. Leipzig (A. Abel).

GILL, T. (1872): Arrangement of the families of mammals and synoptical tables of characters of subdivisions of mammals. Smithson. Misc. Coll., **230**: 1-98.

GINGERICH, P. D. (1974): Dental function in the Paleocene primate Plesiadapis. - In MARTIN, R. D., DOYLE, G. A. & WALKER, A. C. (eds.): Prosimian Biology. - Duckworth, London: 531-541.

_ , _ (1975): New North American Plesiadapidae (Mammalia, Primates) and a biostratigraphic zonation of the middle and upper Paleocene. - Cont. Mus. Paleont. Univ. Mich., **24**: 135-148.

_ , _ (1976): Cranial anatomy and evolution of early Tertiary Plesiadapidae (Mammalia, Primates). - Mus. Paleo. Univ. Mich., Papers on Paleont., **15**: 1-139.

_ , _ (1980): A new species of Palaeosinopa (Insectivora: Pantolestidae) from the late Paleocene of western North America. - J. Mamm., **61**: 449-454.

_ , _ (1982 a): Aaptoryctes (Palaeoryctidae) and Thelysia (Palaeoryctidae?): New insectivorous mammals from the late Paleocene and early Eocene of western North America. - Contr. Mus. Paleont. Univ. Mich., **26**: 37-47.

_ , _ (1982 b): Labidolemur and Apatemys from the early Wasatchian of the Clark's Fork Basin, Wyoming. - Contr. Mus. Paleont. Univ. Mich., **26**: 57-69.

_ , _ (1983): New Adapisoricidae, Pentacodontidae, and Hyopsodontidae (Mammalia, Insectivora and Condylarthra) from the late Paleocene of Wyoming and Colorado. - Contr. Mus. Paleont., Univ. Mich., **26**: 227-255.

_ , _ (1986): Systematic position of Litomylus(?) alphamon VAN VALEN (Mammalia: Insectivora): Further evidence for the Late Paleocene age of Swan Hills site-1 in the Paskapoo Formation of Alberta. - J. Paleo., **60**: 1135-1137.

_ , _ (1987): Early Eocene bats (Mammalia, Chiroptera) and other vertebrates in freshwater limestones of the Willwood Formation, Clark's Fork Basin, Wyoming. - Contr. Mus. Paleont. Univ. Mich., **27**: 275-320.

GINGERICH, P. D. & ROSE, K. D. (1982): Dentition of Clarkforkian Labidolemur kayi. - Contr. Mus. Paleont. Univ. Mich., **26**: 49-55.

GINGERICH, P. D. & WINKLER, D. A. (1985): Systematics of Paleocene Viverravidae (Mammalia, Carnivora) in the Bighorn Basin and Clark's Fork Basin, Wyoming. - Contr. Mus. Paleont. Univ. Mich., **27**: 87-128.

GRANGER, W. D. (1915): Part III - Order Condylarthra. Families

Phenacodontidae and Meniscotheriidae. - In MATTHEW, W. D. & GRANGER, W. D.: A revision of the lower Eocene Wasatch and Wind River faunas. - Bull. Amer. Mus. Nat. Hist., **34**: 329-361.

GRANGER, [illegible] & SIMPSON, G. G. (1929): A revision of the Tertiary Multituberculata. - Bull. Amer. Mus. Nat. Hist., **56**: 601-676.

GREGORY, W. [illegible]910): The orders of mammals. - Bull. Amer. Mus. Nat. Hist., **27**: 1-524.

GREGORY, W. K. & SIMPSON, G. G. (1926): Cretaceous mammal skulls from Mongolia. - Amer. Mus. Novit., **225**: 1-20.

HAEKEL, E. (1866): Systematische Einleitung in die allgemeine Entwidklungsgeschichte. - Generelle Morphologie der Organismen, Georg Reimer, Berlin, **2**: 27-160.

HAHN, G. (1969): Beitrage Zur Fauna der Grube Guimarota Nr. 3. Die Multituberculata. - Palaeontographica (A), **133**: 1-10.

_ , _ (1978): Milch-bezahnungen von Paulchoffatiidae (Multituberculata; Ober-Jura). - Neues Jahrb. Geol. Palaontol., **1**: 25-34.

HARTMAN, J. E. (1986): Paleontology and biostratigraphy of lower part of Polecat Bench Formation, southern Bighorn Basin, Wyoming. - Contr. Geol. Univ. Wyo., **24**: 11-63.

HOLTZMAN, R. C. (1978): Late Paleocene mammals of the Tongue River Formation, western North Dakota. - Rept. of Invest. 65, North Dakota Geol. Sur., p. 1-88.

HOLTZMAN, R. C. & WOLBERG, D. L. (1977): The Microcosmodontinae and <u>Microcosmodon</u> <u>woodi</u>, new multituberculate taxa (Mammalia) from the late Paleocene of North America. - Sci. Pub. Sci. Mus. Minnesota, **4**: 1-13.

ILLIGER, J. C. W. (1811): Prodromus Systematics Mammalium et Avium additis terminis zoographicis utriudque classis. - C. Salfeld, Berlin: 1-301.

IRISH, E. J. W. (1970): The Edmonton Group of south-central Alberta. - Bull. Can. Petr. Geol., **18**: 125-155.

JEPSEN, G. L. (1930): Stratigraphy and paleontology of the Paleocene of northeastern Park County, Wyoming. - Proc. Amer. Phil. Soc., **69**: 463-528.

_ , _ (1940): Paleocene faunas of the Polecat Bench Formation, Park County, Wyoming. - Proc. Amer. Phil. Soc., **83**: 217-340.

JOHNSTON, P. A. & FOX, R. C. (1984): Paleocene and Late Cretaceous mammals from Saskatchewan, Canada. - Palaeontographica (A), **186**: 163-222.

JONES, J. F. (1963): Reconnaissance goundwater study Swan Hills and adjacent areas, Alberta. - Res. Counc. Alta., Prelim. R[illegible]t., **62-5**: 1-43.

KAY, R. F. & HIIEMAE, K. M. (1974): Jaw movement and to[illegible]use in Recent and fossil primates. - Am. J. Phys. Anthrop., **40**: 227-256.

KRAUSE, D. W. (1977): Paleocene Multituberculates (Mammalia) of the Roche Percée Local Fauna, Ravenscrag Formation, Saskatchewan, Canada. - Palaeontographica (A), **159**: 1-36.

_ , _ (1978): Paleocene primates from western Canada. - Can. J. Earth Sci., **15**: 1250-1271.

_ , _ (1980): Multituberculates from the Clarkforkian Land-mammal age, late Paleocene-early Eocene, of western North America. - J. Paleont., **54**: 1163-1183.

_ , _ (1982): Evolutionary history and paleobiology of Early Cenozoic Multituberculata (Mammalia), with emphasis on the Family Ptilodontidae. (Volumes I and II). - Unpublished Ph.D. dissertation, University of Michigan, Ann Arbor, Michigan: 1-575.

_ , _ (1987): *Baiotomeus*, a new ptilodontid multituberculate (Mammalia) from the Middle Paleocene of western North America. - J. Paleont., **61**: 595-603.

KRAUSE, D. W. & GINGERICH, P. D. (1983): Mammalian fauna from Douglass Quarry, earliest Tiffanian (late Paleocene) of the eastern Crazy Mountain Basin, Montana. - Univ. Mich., Contr. Mus. Paleont., **26**: 157-196.

KRISHTALKA, L. (1973): Late Paleocene mammals from the Cypress Hills, Alberta. - Spec. Publ. Mus. Texas Tech. Univ., **2**: 1-77.

_ , _ (1976 a): Early Tertiary Adapisoricidae and Erinaceidae (Mammalia: Insectivora) of North America. - Bull. Carnegie Mus. Nat. Hist., **1**: 1-40.

_ , _ (1976 b): North American Nyctitheriidae (Mammalia: Insectivora). - Ann. Carnegie Mus. Nat. Hist., **46**: 7-28.

_ , _ (1977): Early Eocene Euramerican Insectivora., GeoBios, Mem. Spec., **1**: 135-139.

KRISHTALKA, L., BLACK, C. C., & RIEDEL, D. W. (1975): Paleontology and geology of the Badwater Creek area, central Wyoming. Part 10. A late Paleocene mammal fauna from the Shotgun Member of the Fort Union Formation. - Ann. Carnegie Mus., **45**: 179-212.

LAMBE, L. (1902): On Vertebrata of the Mid-Cretaceous of the northwestern Territory. 2: New genera and species from the Belly River series (Mid-Cretaceous). - Geol. Surv. Canada, Contr. Can. Paleont., **3**: 25-81.

LEMOINE, V. (1882): Sur deux Plagiaulax tertiares recueillis aux environs de Reims. - C. R. Ac. Sci. Paris, **95**: 1009-1011.

_ , _ (1883): Etude sur le Neoplagiaulax de la faune éocène inférieure des environs de Reims. - Bull. Soc. Geol. France, (3), **11**: 249-271.

LILLEGRAVEN, J. A. (1969): Latest Cretaceous mammals of upper part of Edmonton Formation of Alberta, Canada, and review of marsupial-placental dichotomy in mammalian evolution. - Paleont. Contr. Univ. Kansas, **50**: 1-122.

LINNAEUS, C. (1758): Systema naturae per regna tria naturae, secundum classes, ordines, genera, species cum characteribus, differentiis, synonymis, locis. - Edito decima, reformata. Laurentii Salvii, Stockholm, **1**: 1-824.

MCKENNA, M. C. (1960): Fossil Mammalia from the early Wasatchian Four Mile fauna, Eocene of northwest Colorado. - Univ. Calif. Publ. Geol. Sci., **37**: 1-130.

_ , _ (1963): Primitive Paleocene and Eocene Apatemyidae (Mammalia, Insectivora) and the primate-insectivore boundary. - Amer. Mus. Novit., **2160**: 1-39.

_ , _ (1967): Classification, range, and deployment of the prosimian primates. - Coll. Internat. C. N. R. S., **163**: 603-610.

_ , _ (1968): Leptacodon, an American Paleocene nyctithere (Mammalia, Insectivora). - Amer. Mus. Novit., **2317**: 1-17.

MARSH, O. C. (1872): Preliminary description of new Tertiary mammals. - Amer. J. Sci., **4**: 122-128, 202-224.

_ , _ (1889): Discovery of Cretaceous Mammalia, part ii. - Amer. J. Sci., **38**:

177-180.

MATTHEW, W. D. (1909): The Carnivora and Insectivora of the Bridger Basin. - Mem. Amer. Mus. Nat. Hist., **9**: 289-567.

_ , _ (1913): A zalambdodont insectivore from the basal Eocene. - Bull. Amer. Mus. Nat. Hist., **32**: 307-314.

_ ,_ (1914): Evidence of the Paleocene vertebrate fauna on the Cretaceous-Tertiary problem. - Bull. Geol. Soc. Amer., **25**: 381-402.

_ , _ (1915): A revision of the lower Eocene Wasatch and Wind River faunas. Part IV. Entelonychia, Primates, Insectivora (part). - Bull. Amer. Mus. Nat. Hist., **34**: 429-483.

_ , _ (1917): The dentition of Nothodectes. - Bull. Amer. Mus. Nat. Hist., **37**: 831-839.

_ , _ (1918): Part V - Insectivora (continued, Glires, Edentata). - In MATTHEW, W. D. & GRANGER, W.: A revision of the lower Eocene Wasatch and Wind River faunas. - Bull. Amer. Mus. Nat. Hist., **38**: 565-657.

_ , _ (1929): Preoccupied names. - J. Mamm., **10**: 171.

_ , _ (1937): Paleocene faunas of the San Juan Basin, New Mexico. - Trans. Amer. Philos. Soc., **30**: 1-510.

MATTHEW, W. D. & GRANGER, W. (1921): New genera of Paleocene mammals. - Amer. Mus. Novit., **13**: 1-7.

MILLS, J. R. E. (1955): Ideal dental occlusion in the primates. - Dent. Pract., **6**: 47-61.

NOVACEK, M. J. (1977): A review of Paleocene and Eocene Leptictidae (Eutheria: Mammalia) from North America. - PaleoBios, **24**: 1-42.

_ , _ (1982): Diacodon alticuspis, an erinaceomorph insectivore from the early Eocene of northern New Mexico. - Contr. Geol. Univ. Wyo., **20**: 135-149.

NOVACEK, M. J., BOWN, T. M. & SCHANKLER, D. (1985): On the classification of the Early Tertiary Erinaceomorpha (Insectivora, Mammalia). - Amer. Mus. Novit., **2813**: 1-22.

OWER, J. R. (1960): The Edmonton Formation. - J. Alta. Soc. Petr. Geol., **8**: 309-323.

ROBINSON, P. (1968): The paleontology and geology of the Badwater Creek area, central Wyoming. Part 4: Late Eocene primates from Badwater, Wyoming, with a discussion of material from Utah. - Ann. Carnegie Mus., **39**: 307-326.

ROSE, K. D. (1973): The mandibular dentition of Plagiomene (Dermoptera, Plagiomenidae). - Breviora, **411**: 1-17.

_ , _ (1975 a): The Carpolestidae, Early Tertiary primates from North America. - Mus. Comp. Zool. Harvard Bull., **147**: 1-74.

_ , _ (1975 b): Elpidophorus, the earliest dermopteran (Dermoptera, Plagiomenidae). - J. Mamm., **56**: 676-679.

_ , _ (1977): Evolution of carpolestid primates and chronology of the North American middle and late Paleocene. - J. Paleo., **51**: 536-542.

_ , _ (1981): The Clarkforkian land-mammal age and mammalian faunal composition across the Paleocene-Eocene boundary. - Pap. Paleont. Mus. Paleont. Univ. Mich., **26**: 1-197.

_ , _ (1982): Anterio[illegible] the early Eocene plagiomenid dermopteran Worlandia. - J. Ma[illegible]79-183.

ROSE, K. D. & GING[illegible] (1987): A new insectivore from the Clarkforkian (earl[illegible]cene) of Wyoming. - J. Mamm., **68**: 17-27.

ROSE, K. D. & SIMONS, E. L. (1977): Dental function in the Plagiomenidae: origin and relationships of the mammalian order Dermoptera. - Contr. Mus. Paleont. Univ. Mich., **24**: 221-236.

RUSSELL, D. E. (1967): Le Paléocène continental d'Amérique du Nord. - Mem. Mus. Natl. Hist. Nat., (C), **16**: 1-99.

RUSSELL, D. E., LOUIS, P. & SAVAGE, D. E. (1975): Les Adapisoricidae de L'Éocène inférieur de France: Réévaluation des formes considérées affines. - Bull. Mus. Natl. Hist. Nat., **327**: 129-193.

RUSSELL, L. S. (1929): Paleocene vertebrates from Alberta. - Amer. J. Sci., **217**: 162-178.

_ , _ (1954): Mammalian fauna of the Kishenehn Formation, southeastern British Columbia. - Ann. Rep. Nat. Mus. Canada, **132**: 92-111.

_ , _ (1958): A horse astragalus from the Hand Hills Conglomerate of Alberta. - Nat. Mus. Can. Natur. Hist. Pap., **1**: 1-3.

_ , _ (1967): Palaeontology of the Swan Hills area, north-central Alberta. - Roy. Ont. Mus. Life Sci. Contri., **71**: 1-31.

RUSSELL, L. S. & LANDES, R. W. (1940): Geology of the southern Alberta plains. - Mem. Geol. Surv. Canada, **221**: 1-223.

SCHAFF, C. R. (1980): Paleocene mammals from the Beartooth region of Wyoming and Montana. - National Geographic Society Research Reports: 1979 Projects: 589-595.

SCHIEBOUT, J. A. (1974): Vertebrate paleontology and paleoecology of Paleocene Black Peaks Formation, Big Bend National Park, Texas. - Bull. Texas Mem. Mus., **24**: 1-88.

SCHWARTZ, J. H. & KRISHTALKA, L. (1976): The lower antemolar teeth of <u>Litolestes ignotus</u>, a late Paleocene erinaceid (Mammalia, Insectivora). Ann. Carnegie Mus., **46**: 1-6.

SCOTT, W. B. (1892): A revision of the North American Creodonta, with notes on some genera which have been referred to that group. - Proc. Acad. Nat. Sci. Philadelphia, **44**: 291-323.

SIGÉ, B. (1976): Insectivores primitifs de l'Éocène supérieur et Oligocène inférieur d'Europe occidentale. Nyctithériidés. - Mém. Mus. Natl. Hist. Nat., (C), **34**: 1-140.

SIMONS, E. L. (1960): The Paleocene Pantodonta. - Trans. Amer. Philos. Soc., **50**: 1-99.

_ , _ (1972): Primate evolution: An introduction to Man's place in nature. Macmillan, New York: 1-322.

SIMPSON, G. G. (1927): Mammalian fauna and correlation of the Paskapoo Formation of Alberta. - Amer. Mus. Novit., **268**: 1-10.

_ , _ (1928): A new mammalian fauna from the Fort Union of southern Montana. - Amer. Mus. Novit., **297**: 1-15.

_ , _ (1935 a): New Paleocene mammals from the Fort Union of Montana. - Pro. U. S. Nat. Mus., **83**: 221-244.

_ , _ (1935 b): The Tiffany fauna, upper Paleocene. 3. Primates, Carnivora, Condylarthra and Amblypoda. - Amer. Mus. Novit., **817**: 1-28.

_ , _ (1935 c): The Tiffany fauna, upper Paleocene. 1. Multituberculata, Marsupialia, Insectivora, and ?Chiroptera. - Amer. Mus. Novit., **795**: 1-19.

_ , _ (1936): A new fauna from the Fort Union of Montana. Amer. Mus. Novit., **873**: 1-27.

_, _ (1937 a): The Fort Union of the Crazy Mountain Field, Montana, and its mammalian faunas. - Bull. U. S. Nat. Mus., 169: 1-287.

_, _ (1937 b): Additions to the upper Paleocene fauna of the Crazy Mountain field. - Amer. Mus. Novit., **940**: 1-15.

_, _ (1940): Studies on the earliest primates. - Bull. Amer. Mus. Nat. Hist., **77**: 185-212.

SLOAN, R. E. (1966): Paleontology and geology of the Badwater Creek area, Central Wyoming: Part 2. The Badwater Multituberculata. - Carnegie Mus. Nat. Hist. Annals, **38**: 309-315.

_, _ (1969): Cretaceous and Paleocene terrestrial communities of western North America. - Proc. N. Amer. Paleont. Conv., (E): 427-453.

_, _ (1981): Systematics of Paleocene multituberculates from the San Juan Basin, New Mexico. In LUCAN, S., RIGBY, K., JR. & KUES, B. (eds.): Advances in San Juan Basin Paleontology. - Univ. New Mexico Press, Albuquerque: 127-160.

_, _ (1987): Paleocene and latest Cretaceous mammal ages, biozones, magnetozones, rates of sedimentation, and evolution. In FASSETT, J. E. & RIGBY, J. K. (eds.): The Cretaceous-Tertiary Boundary in the San Juan and Raton Basins, New Mexico and Colorado. - Geol. Soc. Amer. Spec. Pap., **209**: 165-200.

SLOAN, R. E. & VAN VALEN, L. (1965): Cretaceous mammals from Montana. - Science, **148**: 220-227.

STEHLIN, H. G. (1940): Zur Stammesgeschichte der Soriciden. - Eclog. Geol. Helvetiae, **33**: 298-306.

SZALAY, F. S. (1965): First evidence of tooth replacement in the subclass Allotheria (Multituberculata). - Amer. Mus. Novit., **2226**: 1-12.

_, _ (1969): Mixodectidae, Microsyopidae, and the insectivore-primate transition. - Bull. Amer. Mus. Nat. Hist., **140**: 193-330.

SZALAY, F. S. & DELSON, E. (1979): Evolutionary history of the primates. - Academic Press, New York-London-Toronto-Sydney-San Francisco: 1-580.

TOZER, E. T. (1956): Uppermost Cretaceous and Paleocene non-marine molluscan faunas of Western Alberta. - Geol. Surv. Can. Mem., **280**: 1-

125.

TROUESSART, E. L. (1897): Catalogus Mammalium tam Viventium quam Fossilium, Vol. 1, R. Friedländer und Sohn, Berlin: 1-664.

TYRRELL, J. B. (1887): Report on part of northern Alberta and portions of adjacent districts of Assiniboia and Saskatchewan embracing the country lying south of the North Saskatchewan River and north of Lat. 51° 6' between Long. 110° and 115° 15' west. - Geol. Nat. Hist. Surv. Ann. Rept.. 1886, **2E**: 1-176.

VAN VALEN, L. (1966): Deltatheridia, a new order of mammals. - Bull. Amer. Mus. Nat. Hist., **132**: 1-126.

_ , _ (1967): New Paleocene insectivores and insectivore classification. - Bull. Amer. Mus. Nat. Hist., **135**: 217-284.

_ , _ (1978): The beginning of the age of mammals. - Evol. Theory, **4**: 45-80.

VAN VALEN, L. & SLOAN, R. E. (1966): The extinction of the multituberculates. - Sys. Zool., **15**: 261-278.

VIANEY-LIAUD, M. (1986): Les Multituberculés Thanetiens de France, et leurs rapports avec les Multituberculés Nord-Américains. - Palaeontographica (A), **191**: 85-171.

WEST, R. M. (1971): Deciduous dentition of the early Tertiary Phenacodontidae (Condylarthra, Mammalia). - Amer. Mus. Novit., **2461**: 1-37.

_ , _ (1973): Review of the North American Eocene and Oligocene Apatemyidae (Mammalia, Insectivora). - Spec. Publ. Mus. Tex. Tech. Univ., **3**: 1-42.

_ , _ (1974): New North American middle Eocene nyctitheres (Mammalia, Insectivora). - J. Paleont., **48**: 983-987.

_ , _ (1976): The North American Phenacodontidae (Mammalia, Condylarthra). - Milwaukee Publ. Mus. Contr. Biol. Geol., **6**: 1-78.

WINGE, H. (1917): Udsigt over Insektaedernes indbyrdes Slaegtskab. - Vidensk. Meddel. Dansk Naturh. Foren., **68**: 83-203.

WINTERFELD, G. F. (1982): Mammalian paleontology of the Fort Union Formation (Paleocene), eastern Rock Springs Uplift, Sweetwater County, Wyoming. - Contr. Geol. Univ. Wyo., **21**: 73-112.

WORTMAN, J. L. & MATTHEW, W. D. (1899): The ancestry of certain members of the Canidae, Viverravidae, and Procyonidae. - Bull. Amer. Mus. Nat. Hist., **12**: 109-138.