University of Alberta

Early late Paleocene mammals from the Roche Percée local fauna, southeastern Saskatchewan, Canada

by

Brian Daniel Rankin

A thesis submitted to the Faculty of Graduate Studies and Research
in partial fulfillment of the requirements for the degree of

Master of Science
in
Systematics and Evolution

Department of Biological Sciences

©Brian Daniel Rankin

Fall, 2009
Edmonton, Alberta

Permission is hereby granted to the University of Alberta Libraries to reproduce single copies of this thesis and to lend or sell such copies for private, scholarly or scientific research purposes only. Where the thesis is converted to, or otherwise made available in digital form, the University of Alberta will advise potential users of the thesis of these terms.

The author reserves all other publication and other rights in association with the copyright in the thesis and, except as herein before provided, neither the thesis nor any substantial portion thereof may be printed or otherwise reproduced in any material form whatsoever without the author's prior written permission.

Examining Committee

Dr. Richard C. Fox, Biological Sciences, University of Alberta

Dr. Mark V. H. Wilson, Biological Sciences, University of Alberta

Dr. Alison M. Murray, Biological Sciences, University of Alberta

Dr. Pamela R. Willoughby, Anthropology, University of Alberta

For all my friends and family —
who still think I research dinosaurs.

ABSTRACT

The occurrence of vertebrate fossils from the Ravenscrag Formation near Roche Percée, southeastern Saskatchewan, Canada, documents the presence of a large and diverse assemblage of early late Paleocene (approx. 58 million years) mammals. Previous studies of the Roche Percée localities have examined only a small portion of the fauna, with the vast majority of taxa remaining undescribed. The current research centers on the identification, description and, where appropriate, evolutionary relationships of these undescribed mammals. Significant discoveries, to date, include two new species of the rare viverravid carnivoran Raphictis, a new species of the phenacodontid condylarth Ectocion, a large collection of a probable new species of the semi-aquatic pantolestid Palaeosinopa, and only the second known occurrence of the predominantly European lipotyphlan Adapisorex in North America. This research provides an improved understanding of mammalian diversity and evolution in the northern part of the Western Interior during this important time interval.

ACKNOWLEDGMENTS

My most sincere thanks are owed to Dr. Richard C. Fox for his co-supervision during my thesis research and for the opportunity to study the mammalian remains from the Roche Percée local fauna, one of the largest and most diverse assemblages in the University of Alberta Laboratory for Vertebrate Paleontology collections. Because of the influence and guidance of Dr. Fox, I have gained much experience and a broad knowledge of early Tertiary mammals. The co-supervision and mentoring of Dr. Mark V. H. Wilson was also paramount to the success of this study and to my development as an academic, and I thank him for all the unexpected (but much appreciated) support. I additionally thank Dr. Ruth A. Stockey for her suggestion and encouragement to continue with academics after graduating with my Bachelor's of Science, and the other members of my examining committee, Drs. Pam R. Willoughby and Alison M. Murray, for their advice and comments on my thesis research.

Dr. Craig S. Scott is owed an enormous debt of gratitude for his guidance during my undergraduate and graduate studies, and for sharing his thoughts on the evolutionary history of several early Tertiary mammals. For reading an earlier version of this thesis and providing many helpful comments during the course of my studies, I thank Dr. Eric Snively. Thanks are also extended to Dr. Michael G. Newbrey for advice on photographic techniques and Dr. Michael W. Caldwell for use of photographic equipment.

For their friendship, support, and insight, I owe many thanks to my peers and colleagues at the University of Alberta Laboratory for Vertebrate Paleontology: Victoria Arbour, Braden Barr, Phil Bell, Stephanie Blais, Lisa Buckley, Michael Burns, Todd Cook, Jessica Hawthorn, Michael James, Dr. Takuya Konishi, Derek Larson, Aaron LeBlanc, Lindsay MacKenzie, Dr. Erin E. Maxwell, Scott Persons, Miriam Reichel, Bradley Scott, Robin Sissons, and Andrew Wendruff. In addition, I am fortunate to have met many other graduate students from the Department of Biological Sciences at the University of Alberta (past and present) who were helpful and perceptive. In particular, I thank Steve Karafit, Linnea Mowat, Dustin Raab, Christine Robichaud, Barry Robinson, Jeremy Wideman and Drs. Stefan A. Little, Randal A. Mindell and Selena Y. Smith.

My friends and family (Dad, Mom, Lorelle, Nigel, Moya, Rankin, Donna, and Brad) have been a constant source of support and a relaxing break from academic life. Their continued patience, encouragement, and general interest with regards to my education is no small reason for the completion of this study - I hope that you are all proud. Finally, I thank Tara Jamison. Without her love and support this project would not have come to fruition.

Funding for this project was provided to me by Graduate Teaching Assistantships from the Department of Biological Sciences and minor awards granted to me from several faculties at the University of Alberta.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF ABBREVIATIONS AND NOMENCLATURE

Institutional abbreviations

AMNH	American Museum of Natural History, New York, New York
SMM	Science Museum of Minnesota, St. Paul, Minnesota
UALVP	Laboratory for Vertebrate Paleontology, University of Alberta, Edmonton, Alberta
UM	The University of Michigan Museum of Paleontology, Ann Arbor, Michigan
USNM	United States National Museum of Natural History, Smithsonian Institution, Washington, D. C.
UW	University of Wyoming, Laramie, Wyoming
YPM-PU	Princeton University collections accessioned at the Peabody Museum of Natural History, Yale University, New Haven, Connecticut

Anatomical abbreviations

c	lower canine
C	upper canine
d	lower deciduous tooth
D	upper deciduous tooth
i	lower incisor
I	upper incisor
m	lower molar
M	upper molars
p	lower premolars
P	upper premolars
x	lower tooth unidentifiable to position
X	upper tooth unidentifiable to position

Measurements and statistical abbreviations

cf	confer; used to indicate a tentative identification of a specimen/taxa
CV	coefficient of variation
D	maximum dorsoventral height of tooth crown
L	maximum anteroposterior length of the tooth crown
M	mean
N	sample size
OR	observed range
P	parameter
SD	standard deviation
TaW	maximum labiolingual width of the talonid
TrW	maximum labiolingual width of the trigonid
W	maximum labiolingual width of the tooth crown

North American Land Mammal Ages

Br	Bridgerian
Cf	Clarkforkian
Pu	Puercan
Ti	Tiffanian
To	Torrejonian
Wa	Wasatchian

Taxonomic nomenclature

Higher-level taxonomy and taxonomic organization generally follows McKenna and Bell (1997).

INTRODUCTION

THE CRETACEOUS-PALEOGENE (K/Pg) transition (approximately 65 million years ago) has historically been recognized as a critical phase in the evolution of mammals (e.g., Matthew, 1914, 1921a; Simpson, 1937a; Sloan and Van Valen, 1965; Van Valen, 1978; Archibald, 1982; Lofgren, 1995; Foote et al., 1999). It was relatively soon after the catastrophic events that marked the K/Pg boundary that marsupial and, particularly, placental mammals underwent a dramatic adaptive radiation (Archibald, 1983; Lillegraven and Eberle, 1999; Clemens, 2002) and a remarkable increase in body size (Alroy, 1998). It is also during the Paleocene (comprising roughly the first 10 million years of time following the K/Pg boundary) that many extant orders of placental mammals first appear in the fossil record [e.g., Primates (Van Valen and Sloan, 1965), Carnivora (Fox and Youzwhyshyn, 1994; Fox, Scott, and Rankin, in prep.), etc.], although some molecular clock-based analyses suggest that at least some, if not all, of these originations occurred earlier, within the Mesozoic (Springer, 1997; Kumar and Hedges, 1998; Springer et al., 2003).

The available record of Paleocene mammalian faunas, representing direct evidence of this adaptive radiation, is geographically concentrated in continental deposits in the Western Interior of North America (Lofgren et al., 2004). In the present research, work centered on a large assemblage of early late Paleocene (late middle Tiffanian, Ti4) mammalian remains from the Ravenscrag Formation, near the hamlet of Roche Percée, southeastern Saskatchewan, Canada (Krause, 1977) (see Figure 1). The Roche Percée localities occur within artificial and natural exposures of an abandoned lignite coal mine and were first discovered in 1971 by Roxanne Young, a young girl from Winnipeg, Manitoba (Krause, 1977). Subsequent fieldwork during the summers of 1972-1974 by parties from the University of Alberta, led by D. W. Krause, collected over 5000 specimens. The collection consists mainly of isolated mammal teeth and incomplete dentitions in jaw fragments, and is accessioned within the University of Alberta Laboratory for Vertebrate Paleontology (UALVP). Fragmentary remains of non-mammalian vertebrates from the localities include those of fishes (e.g., Wilson, 1980), turtles, salamanders (e.g., Naylor and Krause, 1981; Naylor, 1987), frogs, lizards, champsosaurs, crocodilians, and birds.

Previous studies of the mammals from the Roche Percée localities have examined the multituberculates (e.g., Krause, 1977, 1987; Jenkins and Krause, 1983; Krause and Jenkins, 1983), plesiadapiform primates (Krause, 1978; Fox, 2002), specimens of the pantolambdoid pantodont Cyriacotherium cf. C. argyreum (Rose and Krause, 1982), and the erinaceid lipotyphlan Oncocherus krishtalkai (Scott, 2006). The bulk of the material from the Roche Percée local fauna [“an aggregate of fossil vertebrates species that have a limited distribution in time from a number of closely grouped localities in a limited geographic area” (Woodburne, 2004a, p. xiii)] remains, however, undescribed. On that account and because of the remarkable size of the fauna, the primary objective of the current research is to identify and provide thorough taxonomic descriptions of the mammalian taxa from the Roche Percée local fauna, excluding those previously described. With a comprehensive taxonomic description of all the mammals within the Roche Percée assemblage, a more detailed correlation with faunas elsewhere in North America will be conducted, and its overall evolutionary significance will be assessed. This research will provide an improved understanding of mammalian diversity and evolution in the northern part of the Western Interior during the early late Paleocene.

REGIONAL GEOLOGICAL SETTING AND LOCATION

The Williston Basin is a large intracratonic sedimentary basin that is centered in northwestern North Dakota and extends outward into regions of Saskatchewan, Alberta, Manitoba, South Dakota and Montana (Mossop and Shetsen, 1994; Whittaker et al., 2004). Following the advent of the Laramide Orogeny in the Late Cretaceous and the associated long-term eustatic regression, thick successions of lacustrine, paludal, and fluvial rocks were deposited throughout the basin during parts of the latest Cretaceous and Tertiary (Kent and Christopher, 1994). These sediments are extensively exposed across the southern Saskatchewan plains and form much of the present day erosional surface in this region.

The Roche Percée local fauna occurs in the Ravenscrag Formation, a widespread unit of strata deposited in the Williston Basin during the Paleocene (McLearn, in Fraser et al., 1935; Lerbekmo, 1985). The unit overlies the Maastrichtian Frenchman Formation, with the Ferris (No. 1) coal seam intervening between these two units and locally marking the K/Pg boundary (Russell, 1974; Lerbekmo, 1985), and is overlain unconformably in the southwest by gravels and conglomerates of the Eocene-Miocene Cypress Hills Formation (Storer, 1975, 1993, 1996; Skwara, 1988). The Ravenscrag Formation consists principally of fine-grained buff to gray sandstones, siltstones, clays, and shales, “with much interbedding and lateral change” (Russell, 1950, p. 31); economically important coal deposits occur throughout the formation. These interbedded strata, along with the abundant remains of aquatic and semi-aquatic vertebrates, suggest that deposition likely occurred in a low-energy fluvial/alluvial plain (McLearn, in Fraser et al., 1935; Lerbekmo, 1985), dominated by meandering streams, ponds, swamps, and lowland forests (McIver and Basinger, 1993). Based on several floral studies (McIver and Basinger, 1993; Postnikoff, 2009), the paleoclimate was likely mesothermal (Köppen, in Köppen and Geiger, 1936), with mild, humid conditions, and no dry seasons.

Correlates of the Ravenscrag Formation include the Paskapoo Formation and upper part of the Scollard Formation of southcentral Alberta, the Fort Union Group of southern Montana, and the Fort Union Formation (=Polecat Bench Formation) of northern Wyoming (Mossop and Shetsen, 1994).

TECHNIQUES OF STUDY

Methods

Most of the fossils from the Roche Percée localities were collected by underwater screening, with rock matrix from the productive layers returned to the laboratory and broken down using the underwater screen washing method of D. W. Krause (see Johnson et al. 1994). A small number of specimens [e.g., UALVP 9001, a well-preserved postcranial skeleton of the ptilodontid multituberculate Ptilodus kummae (see Krause, 1977; Jenkins and Krause, 1983; Krause and Jenkins, 1983)] were, however, collected by quarrying. Although fossils were recovered from a total of 13 localities, the majority of specimens were collected from two sites, UAR2 and UAR2a, which were both discovered in overburden from the coal mine (Krause, 1977, 1978).

Measuring techniques

Techniques for dental measurements follow Clemens (1966), with measurements of the length and width representing the maximum anteroposterior and labiolingual dimensions of the crown, respectively; depth is also taken as the maximum dorsoventral dimension of the tooth crown. Dental measurements for small specimens were made using a Wild M7A Zoom binocular microscope with 10X oculars that had been fitted with a micrometer. For larger specimens, dental measurements were taken directly with digital calipers. To ensure the finest degree of reproducible accuracy, measurements are given to the nearest tenth of a millimeter. All measurements were taken by the author.

Dental nomenclature

The dental terminology employed in this thesis generally follows that of Van Valen (1966) and Szalay (1969) with several exceptions. Incisor nomenclature is adapted from Gingerich (1976). Stylar cusp terminology used by Clemens (1966) for the upper molars of marsupials is adopted here (i.e., stylar cusps A-E). For the carnivoran P4 and M1, cusp terminology follows MacIntyre

(1966), while for the p4 follows Flynn and Galiano (1982) in recognizing a first and second posterior accessory cusp; however, consistent with the nomenclature of MacIntyre (1966), Gingerich and Winkler (1985), and Scott (2008), the “anterior accessory cusp” of p4 is considered a paraconid (contra Flynn and Galiano, 1982).

SYSTEMATIC PALEONTOLOGY

Class MAMMALIA Linnaeus, 1758
Subclass THERIIFORMES Rowe, 1988
Infraclass HOLOTHERIA Wible, Rougier, Novacek, McKenna,
and Dashzeveg, 1995
Supercohort THERIA Parker and Haswell, 1897
Cohort MARSUPIALIA Illiger, 1811
Order DIDELPHIMORPHIA Gill, 1872
Family PERADECTIDAE Crochet, 1979
Genus PERADECTES Matthew and Granger, 1921

Peradectes MATTHEW and GRANGER, 1921, p. 2.

Type species.—Peradectes elegans Matthew and Granger, 1921.

Included species.—Peradectes pusillus Matthew and Granger, 1921; P. californicus (Stock, 1936); P. chesteri Gazin, 1952; P. pauli Gazin, 1956; P. protinnominatus McKenna, 1960; ?P. austrinum (Sigé, 1971); P. minor Clemens, 2006.

PERADECTES CF. P. PROTINNOMINATUS McKenna, 1960

Figure 2.1-2.5

Material examined.—UALVP 51528, M1 (L=1.6; W=1.6); UALVP 9435, mx (L=1.6; TrW=0.9; TaW=1.0).

Age and occurrence.—Peradectes protinnominatus is known from the latest Paleocene (earliest Clarkforkian, Cf1, Rodentia/Plesiadapis cookei Interval Subzone of the P. gingerichi/P. cookei Lineage Zone of Lofgren et al., 2004) to the earliest Eocene (early Wasatchian, Wa3, Homogalax protapirinus/Hyracotherium aemulor Interval Zone of Gingerich, 2001) of the Western Interior of North America.

Discussion.—Towards the end of the Cretaceous and during the earliest parts of the Paleogene, the taxonomic diversity and relative abundance of marsupials in North America was dramatically reduced (see, e.g., Clemens, 1966; Lillegraven, 1969; Archibald, 1982; Fox, 1987; Lofgren, 1995). In fact, only three genera are known from North American Paleocene deposits: Peradectes Matthew and Granger, 1921 [including Thylacodon Matthew and Granger, 1921 (see Clemens, 2006; but also see Korth, 2008 for a different opinion about this synonymy)], Swaindelphys Johanson, 1996, and a third unpublished, new genus and species from the middle Tiffanian of Alberta (Scott, 2008). Among these taxa, Peradectes is the longest ranging stratigraphically, spanning the earliest Paleocene (Puercan) to the early Oligocene (at least to the Orellan) (e.g., Matthew and Granger, 1921; Setoguchi, 1978; Archibald, 1982; Storer, 1996; Clemens, 2006), and widest distributed geographically, ranging from western California to central Alberta (e.g., Gazin, 1956; Fox, 1990; Lofgren et al., 1999; Scott, 2008). Additional, albeit tentative, identifications of Peradectes have been made in the Paleocene of South America (e.g., Sigé, 1971; Marshall and Muizon, 1988; Sigé et al., 2004) and the Eocene of Europe (e.g., Crochet, 1977a, 1977b, 1979), suggesting that this group may have been even more widely spread than previously thought.

The latest Paleocene and earliest Eocene Peradectes protinnominatus is known from the central parts of the Western Interior and has been described by McKenna (1960), Rose (1981), Krishtalka and Stucky (1983), and Bloch (2001). The referred specimens from the Roche Percée local fauna most closely resemble homologous teeth of P. protinnominatus from the type locality (Alheit Pocket) in Colorado (McKenna, 1960): stylar cusps A, B, C, and D are well developed, while stylar cusp E is virtually absent, the centrocrista is straight (i.e., not deflected labially), the protocone is more anteroposteriorly compressed than that in P. elegans and P. pauli and more anteriorly positioned, the conules are weakly developed, and the hypoconulid and entoconid are subequal in size, with the hypoconulid projecting slightly posteriorly. Specimens of Peradectes cf. P. protinnominatus from Saskatchewan differ, however, from those of P.

protinnominatus from Colorado principally in the greater width of the M1 crown and in having a shorter preparacrista.

Although a more confident identification of the two referred specimens from the Roche Percée local fauna is impossible at this time, the presence of a P. protinnominatus-like marsupial in the late middle Tiffanian (Ti4) is interesting because of the proposed ancestor-descendent relationship of the early to middle Tiffanian (Ti1-Ti4) P. pauli and early Clarkforkian to Wasatchian (Cf1-Wa3) P. protinnominatus (see Krishtalka and Stucky, 1983). A larger collection of this marsupial is needed, however, to more thoroughly assess its evolutionary relationships to other peradectid marsupials.

Cohort PLACENTALIA Owen, 1837
Superorder LEPTICTIDA McKenna, 1975
Family LEPTICTIDAE Gill, 1872
Genus PRODIACODON Matthew, 1929

Diacodon MATTHEW, 1918, p. 571 (in part).

Type species.—Diacodon puercensis Matthew, 1918.

Included species.—Prodiacodon tauricinerei (Jepsen, 1930); P. concordiarcensis Simpson, 1935a; P. furor Novacek, 1977; P. crustulum Novacek, 1977; P. paucus Secord, 2008.

PRODIACODON CF. P. CONCORDIARCENSIS Simpson, 1935a

Figure 3.1-3.4; Table 1

Material examined.—UALVP 9407-9409 (total:3), M2.

Age and occurrence.—Prodiacodon concordiarcensis is known from the early to late Paleocene (middle Torrejonian, To2, Protoselene opisthacus/Mixodectes pungens Interval Zone to the late early Tiffanian, Ti2, Plesiadapis anceps/P. rex Lineage Zone of Lofgren et al., 2004) of the Western Interior of North America.

Description and Discussion.—Leptictidae are an enigmatic clade of dentally primitive, insectivorous mammals that have traditionally been aligned with lipotyphlans (e.g., Gregory, 1910; Butler, 1956), although this relationship has recently proven more tenuous (Butler, 1988; McKenna and Bell, 1997; Rose, 1999; Asher et al., 2003; see Rose, 2006 for a more recent review). The referred upper molars from Saskatchewan most closely resemble the M2 of the early Paleocene to early Eocene leptictid Prodiacodon and differ from that of the contemporaneous Palaeictops Matthew, 1899, in having taller, more acute cusps, more lingually positioned conules, and a longer precingulum (see Novacek, 1977; Eberle and McKenna, 2002). The Roche Percée specimens, however, are considerably smaller than those of most species of Prodiacodon, and differ in having a deeper ectoflexus and a wider metastylar lobe. These teeth potentially pertain to the smallest species of Prodiacodon, P. concordiarcensis [=Diacodon pearcei Gazin, 1956 (Novacek, 1977; see Secord, 2008 for a contrasting opinion)], but the only referred elements of the upper dentition of this species were not described or figured by Rigby (1980). Therefore, a more confident assignment of these leptictid specimens from the Roche Percée local fauna must await a closer comparison with the upper molars of this latter species.

Grandorder LIPOTYPHLA Haeckel, 1866
Order ERINACEOMORPHA Gregory, 1910
Family uncertain
Genus DIACOCHERUS Gingerich, 1983

Diacodon COPE, 1875: JEPSEN, 1930, p. 511 (in part).
Diacocherus GINGERICH, 1983, p. 238.

Type species.—Diacodon minutus Jepsen, 1930.

Other species.—Diacocherus meizon Gingerich, 1983.

DIACOCHERUS CF. D. MEIZON Gingerich, 1983

Figure 4.1-4.22; Table 2-3

Material examined.—UALVP 9432, P3; UALVP 9438, 9439, 9440, 9441, 9442, 9443, 9444, 9445, 9447, 51765 (total: 10), P4; UALVP 9244, 9254, 9255, 9256, 9257, 9413, 9414, 9415, 9417, 9418, 9420, 9429, 9430, 10868 (total:14), M1; UALVP 9242, 9243, 9250, 9253, 9258, 9419, 9423, 9424, 9427, 9446, 10882, 10899, 51766 (total:13), M2; UALVP 9265, 9269, 9271, 9326, 9327, 10859 (total: 6), M3; UALVP 9182, incomplete right dentary with p4, m1-3 and alveoli for p3; UALVP 51767, incomplete right dentary with m2-3 and talonid of m1; UALVP 51768, incomplete left dentary with m2-3; UALVP 9359, incomplete right dentary with m2 and alveoli for m3; UALVP 51769, incomplete left dentary with m2 and alveoli for m3; UALVP 9312, 51770-51775 (total: 7), p4; UALVP 9282, 9289, 9290, 9330, 9339, 9366, 9369, 9395, 9336, 9337, 9338, 9349, 9373, 9385, 9389, 9391, 9401, 9404 (total: 18), m1; UALVP 9275, 9281, 9284, 9293, 9294, 9329, 9331, 9333, 9334, 9335, 9356, 9357, 9362, 9363, 9370, 9372, 9377, 9380, 9381, 9394, 9400, 51776 (total: 22) m2; UALVP 9280, 9283, 9288, 9340, 9360, 9368, 9374, 9375, 9376, 9378, 9386, 9388, 9390, 9396, 9398, 51777-51781 (total: 20), m3.

Age and occurrence.—Diacocherus meizon is known from the late Paleocene (early middle Tiffanian, Ti3, Plesiadapis rex /P. churchilli Lineage Zone of Lofgren et al., 2004) of the northern part of the Western Interior of North America.

Description and discussion.—Specimens of the late Paleocene erinaceomorph lipotyphlan Diacocherus have been recovered throughout most of the northern part of the Western Interior of North America (see Rose, 1981; Gingerich, 1983; Fox, 1990; Secord, 2008). The referred specimens from the Roche Percée local fauna bear their closest similarities to homologous teeth of D. meizon from its type locality (Cedar Point Quarry) in the Bighorn Basin of northern Wyoming (Gingerich, 1983; Secord, 2008): the paraconid is elevated high on the anterior surface of the metaconid on m2 and m3, and the m2 is larger than m1. The Saskatchewan specimens differ, however, from those of D. meizon in having a taller p4 paraconid relative to the height of the metaconid, a smaller, less anteriorly projecting paraconid on m1, and a more lingually positioned hypoconulid on m3. These differences are likely taxonomically important and are currently under study by R. C. Fox (in prep.), in context with other specimens of Diacocherus from western Canada and the taxonomic problems commonly associated with the genus (see Secord, 2008 for the most recent review).

Genus “XYNOLESTES” Scott, 2008

Type species.—“Xynolestes denommei” Scott, 2008, by monotypy.

“XYNOLESTES DENOMMEI” Scott, 2008

Figure 4.23-4.31; Table 4

Holotype.—UALVP 46886, incomplete right dentary with p1-4, m1-3 and alveoli for i2-3, c. DW-2 locality, Paskapoo Formation of Alberta, early late Paleocene (early middle Tiffanian, Ti3, Plesiadapis rex/P. churchilli Lineage Zone of Lofgren et al., 2004).

Material examined.—UALVP 10872, incomplete right dentary with p2, p4, m1-3, and alveoli for c, p1, p3; UALVP 10909, incomplete left dentary with p4, m1, and alveoli for p2, p3, m2; UALVP 51782, incomplete right dentary with p4, and alveoli for p3, m1; UALVP 51783, incomplete left dentary with p4, and alveoli for p3, m1; UALVP 51784, incomplete right dentary with m1-3; UALVP 9309, incomplete left dentary with m1-2, and alveoli for m3; UALVP 9272, incomplete left dentary with m2-3.

Age and occurrence.—“Xynolestes denommei” is known from the late Paleocene (earliest Tiffanian, Ti1, Plesiadapis praecursor/P. anceps to late middle Tiffanian, Ti4, P. churchilli/P. simonsi Lineage Zone of Lofgren et al., 2004) of the northern parts of the Western Interior of North America.

Description.—Lower dentition: Scott (2008) described the lower dentition of "Xynolestes denommei" in detail. The lower premolars of "X. denommei" from Saskatchewan are virtually identical to those from Alberta. The p2 is procumbent and supports a large sectorial protoconid, and a small anterior cusp and talonid cuspule. The tall and narrow p4 consists of an enlarged, bilaterally compressed protoconid, a lower, anteriorly positioned paraconid, a weak to moderately developed metaconid (positioned halfway up the posterolingual shoulder of the protoconid), and a small, shallow talonid that bears two to three cusps. The hypoflexid of the p4 is deep and enamel overhangs the labial surface of the posterior root.

The lower molars of "X. denommei" decrease in size from m1 to m3, although, as reported by Scott (2008), this reduction is not as dramatic as that in most erinaceids. The trigonids of the lower molars lean anteriorly and are comprised principally of a tall protoconid, a lower metaconid, and an even lower, crestiform paraconid; deep notches are developed in the sharp paracristids and protocristids. The deep talonid basins are V-shaped, with the flat, opposing walls of the hypoconid and entoconid meeting at the midline axis of the crown; the hypoconulid is smaller then these other talonid cusps and positioned lingual to the midline of the crown, closer to but not appressed to the entoconid. As with the p4, the hypoflexids of the lower molars are deep.

Discussion.—The referred specimens represent the youngest occurrence of an unpublished, new genus and species, "Xynolestes denommei" (see Scott, 2008), previously only known from central Alberta. As noted by Scott (2008), the dentition of "X. denommei" reveals a number of traits that closely resemble those of primitive soricomorphs (e.g., the nyctitheriid Leptacodon Matthew and Granger, 1921), such as tall, sharp cusps and a distinct, blade-like molar paraconid. Despite these similarities, Scott (2008) placed this new taxon in the order Erinaceomorpha, with familial status uncertain, based principally on the results of his phylogenetic analysis and the larger number of resemblances the taxon shares with several primitive erinaceomorphs (e.g., Dartonius Novacek, Bown, and Schankler, 1985), including a relatively weak metaconid on p4, a decrease in size from m1-3, and a tall molar entoconid. Unfortunately, other than extending the geographic and stratigraphic record of this taxon, specimens of "X. denommei" from the Roche Percée local fauna add little to the evolutionary knowledge of this enigmatic lipotyphlan.

Genus LITOCHERUS Gingerich, 1983

Litolestes JEPSEN, 1930, p. 513 (in part).
Litocherus GINGERICH, 1983, p. 232.

Type species.—Litocherus zygeus Gingerich, 1983.

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

LITOCHERUS LACUNATUS (Gazin, 1956)

Figure 5.1-5.25; Table 5-6

Litolestes lacunatus GAZIN, 1956, p. 41, original description; WINTERFELD, 1982, p. 86.
Haplaletes cf. H. disceptatrix DORR, 1958, p. 1224.
?Litomylus alphamon VAN VALEN, 1978, p. 60.
Litocherus lacunatus GINGERICH, 1983, p. 234, new combination.

Holotype.—USNM 21016, incomplete left dentary with p4 and m1 (see Gazin, 1956, p. 41). Titanoides locality, Fort Union Formation of Wyoming, early late Paleocene (early late Tiffanian, Ti5, Plesiadapis simonsi/P. gingerichi Lineage Zone of Lofgren et al., 2004).

Material examined.—UALVP 9448-9449, 51785-51795 (total: 13), P4; UALVP 9231, 9236, 9238, 9450, 9715, 11755-11756, 51523, 51796-51804 (total:17), M1; UALVP 9233-9235, 9237, 9706, 9711, 9713, 51805-51813 (total: 16), M2; UALVP 8746, 9263, 9267-9268, 9270, 51814-51817 (total: 9), M3;

UALVP 9183, incomplete left dentary with p2-p4, m1 and alveolus for p1; UALVP 51818, incomplete left dentary with p3-4, m1-3; UALVP 51819, incomplete left dentary with p4, m1-2, and trigonid of m3; UALVP 51825, incomplete left dentary with p4, m1 and alveoli for p3; UALVP 9622, 51820, incomplete right dentary with m1-3; UALVP 9623, incomplete left dentary with m1-3 and posterior alveoli for p4; UALVP 9638, incomplete left dentary with m1-3; UALVP 51821-51822, incomplete right dentary with m1-2; UALVP 9665, incomplete left dentary with m1-2, and alveoli for m3; UALVP 9611, 51823, incomplete left dentary with m2-3; UALVP 51824, incomplete left dentary with m2, and alveoli for m1, m3; UALVP 9620, 9669, incomplete right dentary with m2, and alveoli for m3; UALVP 11017, p3; UALVP 51826-51835, (total: 10), p4; UALVP 9633-9634, 9661, 9672, 51836-51838 (total: 7), m1; UALVP 9614, 9616-9619, 9622, 9654-9657, 9659, 9663, 9667-9668, 9670-9671, 9676, 51839-51841 (total: 20), m2; UALVP 9353, 9615, 9627-9628, 9630, 9631, 9635, 9666, 9674-9675, 51842-51845 (total: 14), m3.

Age and occurrence.—Early late Paleocene (early middle Tiffanian, Ti3, Plesiadapis rex/P. churchilli Lineage Zone to the early late Tiffanian, Ti5, P. simonsi/P. gingerichi Lineage Zone of Lofgren et al., 2004) of the Western Interior of North America.

Description.—Upper dentition, P4: The P4 of L. lacunatus broadly resembles that of L. notissimus (Simpson, 1936; Scott, 2008): the metastylar lobe is swollen but not expanded posteriorly, and both the paracone and protocone are inflated, with the paracone being considerably larger and leaning more posteriorly. Immediately anterior to the paracone, a robust, subconical parastyle is developed on the parastylar lobe; generally a preparacrista is not developed, although a short crest can be present between the apex of the parastyle and the anterior base of the paracone. Posteriorly, a short, thick, and posterolabially curving postparacrista is developed and a small swelling (?metacone) commonly occurs along this crest. In contrast to the strong protoconal cristae of L. notissimus, the preprotocrista and postprotocrista of L. lacunatus are only short and low crests that terminate before joining with the cingulum or, more often, are wholly undeveloped. Neither a paraconule nor a metaconule is developed. The precingulum and postcingulum are robust but discontinuous lingually, while the ectocingulum is weaker and usually only faintly continuous across the labial margin of the crown.

M1: The crown of M1 is subquadrate in occlusal outline, narrowing only slightly lingually from the level of the conules. The slightly anterolabially projecting parastylar lobe and more smoothly rounded metastylar lobes are inflated, and a shallow ectoflexus is developed midway along the labial margin of the crown between these lobes; the ectocingulum is generally low but rises slightly as it wraps around the anterolabial corner of the crown. The inflated principal cusps are subconical, with blunted apices; the protocone and paracone are subequal in height and size, while the metacone is slightly shorter and smaller than both. The preparacrista is moderately developed, and the centrocrista and postmetacrista are slightly stronger; the postmetacrista extends directly posteriorly from the apex of the metacone but curves posterolabially as it descends to become confluent with the ectocingulum. Both conules are well developed but the metaconule is larger, lower and is positioned further labially than the paraconule, close to the base of the metacone. The conular crests are strong; the preparaconule crista terminates prior to joining the paracingulum, while the postmetaconule crista runs continuous with the metacingulum before ending posterior to the metacone. The precingulum is confluent labially with the paracingulum but the postcingulum is abruptly terminated by the postmetaconule crest+metacingulum; the precingulum commonly terminates lingually at a small pericone, and the postcingulum ends at a slightly larger hypocone.

M2: The crown of M2 is anteroposteriorly shorter and labiolingually wider than that of M1 but otherwise similar. The parastylar lobe is usually expanded farther labially, the ectoflexus is deeper, a pericone is less commonly developed, and the hypocone is smaller.

M3: The paracone and protocone of M3 are subequal in both height and size, and larger and taller than the metacone. The parastylar lobe is swollen and expanded labially, while the metastylar lobe is virtually undeveloped; the ectocingulum is undeveloped posterolabial to the metacone but becomes increasingly prominent from this point as it continues anteriorly to the parastylar lobe. The protoconal cristae are thick and confluent labially with the external conular cristae; these crests join with the para- and metacingulum, and continue to the labial corners of the crown. The conules can be wholly indistinct from these elongate crests or form robust swellings along their lengths. The pre- and postcingulum are shorter than those on either M1 or M2, and neither a pericone nor a hypocone is developed.

Lower dentition, p3: The crown is swollen and dominated principally by an enlarged protoconid and considerably shortened talonid. Only a faint paracristid descends the anterior face of the protoconid and neither a metaconid nor a paraconid is developed; an equally faint crest descends the posterior surface of the protoconid but does not continue on to the talonid. The talonid appears to support a single cusp, although wear might distort this interpretation, and only the posterior talonid rim is prominent. The narrow postcingulid forms the posterior border of the deep hypoflexid.

p4: The p4 is considerably taller and wider than the p3, and closely resembles that of L. zygeus (Gingerich, 1983) and L. notissimus (Simpson, 1936; Scott, 2008). As on p3, the protoconid dominates the crown and the paracristid is faint. A small but distinct paraconid can be developed in some specimens (e.g., UALVP 51832) at the base of the paracristid, near its confluence with the narrow precingulid; however, more often the paraconid is only a small swelling or completely indistinct (e.g., UALVP 8923). A weak to moderately developed metaconid is developed approximately midway up the posterolingual shoulder of the protoconid; a short crest connects the apices of the protoconid and metaconid. The narrow talonid is better defined than that of p3 and supports a hypoconid and an entoconid; narrow crests extend between these cusps and from these cusps to the postvallid surface, enclosing the talonid basin on all sides. As on p3, the hypoflexid is deep and bordered posteriorly by the postcingulid.

m1: The talonid of the m1 is slightly wider than the trigonid, conveying a pyriform (pear-shaped) outline to the crown in occlusal view. The protoconid and metaconid are both swollen and subequal in height, although the base of the metaconid is slightly larger than that of the protoconid; the internal walls of these cusps are convex and can form a small cleft anterior to the V-shaped protocristid notch. The paraconid is much smaller than these other trigonid cusps, ranging from a small, bulbous cusp to a weak swelling at the anterolingual end of the short, arcuate paracristid. The talonid is only slightly lower than the trigonid and the talonid cusps are swollen, with the hypoconid being the largest, followed closely by the taller entoconid, and the much smaller and lower hypoconulid; the talonid basin is deep and smoothly rounded, rather than V-shaped. The thick cristid obliqua is high and contacts the postvallid surface ventral and slightly labial to the protocristid notch, while the entocristid is also high and thick, and extends to the postvallid surface. In most specimens, the ectocingulid is complete but narrows across the hypoflexid.

m2: The m2 very closely resembles the m1 but is shorter, wider, and more rectangular in occlusal outline, with the trigonid slightly wider than or subequal in width to the talonid. The protoconid and metaconid are less labiolingually compressed than on m1, and the metaconid is less posterior to the level of the protoconid. The paraconid on m2 is even more reduced than that on the m1 and is commonly indistinct from the faintly shelf-like paracristid. The talonids of the two molars are virtually identical, except that the hypoconulid is more vertically oriented on m2, rather than leaning slightly posteriorly as on m1. The development of the ectocingulid is variable but is often similar to the condition on m1.

m3: The m3 is the smallest tooth in the lower molar series. The trigonid is wider than the talonid and the crown is subrectangular in occlusal outline. The protoconid and metaconid dominate the trigonid, while the paraconid is much smaller and can be a discrete cusp or completely indistinct from the paracristid. The talonid is proportionally longer than on m1 and m2, and the hypoconulid is better developed and more closely appressed to the entoconid than on these other molars. The ectocingulid is continuous along the anterior half of the labial margin of the crown but commonly fades posterior to the hypoflexid.

Discussion.—The phylogenetic relationships of Litocherus have remained problematic since its initial discovery and description. Generally, Litocherus is classified as an erinaceomorph lipotyphlan, with varying familial assignments (Van Valen, 1967; Krishtalka, 1976a; McKenna and Bell, 1997; Gingerich, 1983; Scott, 2008), although some members of the genus have been thought to bear close affinities with the "condylarth" hyopsodontids (Simpson, 1936; Van Valen, 1978). Gingerich (1983) noted, however, that the teeth of Litocherus differ from those of hyopsodontids in having a well-developed preparacrista and, particularly, postmetacrista on the upper molars, a weak or undeveloped ectocingulid on the lower molars, a more distinct molar paraconid, and a decrease in size between m1 and m2. More definitive evidence for the assignment of Litocherus to Lipotyphla was recently revealed by studies on the postcranial skeleton of L. notissimus (Scott and Boyer, 2006, in prep.; Scott, 2008), specimens of which were recovered from the early middle Tiffanian (Ti3) of central Alberta.

The referred specimens from the Roche Percée local fauna are virtually identical to comparable teeth of L. lacunatus from the type locality (Titanoides locality) in Wyoming (Gazin, 1956), differing only slightly in having lower, more inflated cusps, and a more robust ectocingulid on the lower molars. As noted above, Gingerich (1983) wrote that the ectocingulid of Litocherus was absent or poorly developed. However, the sample at hand shows that this feature is well developed on the lower molars of L. lacunatus and, hence, is not as useful in distinguishing Litocherus from hyopsodontid condylarths as previously proposed. L. lacunatus is well represented within the Roche Percée local fauna and the present sample documents the largest single collection of this taxon.

LITOCHERUS CF. L. ZYGEUS Gingerich, 1983

Figures 5.26-5.31; Table 7

Material examined.— UALVP 51846, incomplete left dentary with p4 and m1; UALVP 8924, incomplete right dentary with p4, and alveoli for p3, m1; UALVP 8923, incomplete left dentary with p4, and alveoli for p3, m1; UALVP

9637, incomplete left dentary with m1-3; UALVP 51847, incomplete left dentary with m1-3; UALVP 10853, incomplete right dentary with m2-3; UALVP 9613, incomplete left dentary with m2-3; UALVP 10852, incomplete right dentary with m2, talonid of p4, m1, and roots of p3, m3; UALVP 9636, incomplete left dentary with m2, and alveoli for p3-4, m1; UALVP 51848, p4; UALVP 9112, m1; UALVP 9662, m2; UALVP 9621, 51849, m3.

Age and occurrence.—Litocherus zygeus is known from the early late Paleocene (early middle Tiffanian, Ti3, Plesiadapis rex/P. churchilli Lineage Zone to the late middle Tiffanian, Ti4, P. churchilli/P. simonsi Lineage Zone of Lofgren et al., 2004) of the Western Interior of North America.

Description and discussion.—Specimens referred to Litocherus cf. L. zygeus differ principally from those of L. lacunatus in being smaller and narrower, having less inflated cusps, and in tending to have a larger metaconid on p4, more distinct paraconid on m1, and more shelf-like paracristid/paraconid on m2. There is, however, considerable overlap, both in size and morphology, between specimens of Litocherus cf. L. zygeus and small specimens of L. lacunatus from the Roche Percée local fauna, and the accuracy of some of these assigned identifications could be questioned; more detailed comparison of small specimens of Litocherus from the Roche Percée localities with a larger collection of L. zygeus might help clear this confusion. Gingerich (1983, 1986) suggested that the species included within Litocherus are members of a single evolutionary lineage ranging from the latest Torrejonian (To3) to the early late Tiffanian (Ti5), and the specimens referred here to Litocherus cf. L. zygeus could potentially represent transitional forms between the two latest occurring species, L. zygeus and L. lacunatus.

Family ADAPISORICIDAE Schlosser, 1887

Genus ADAPISOREX Lemoine, 1883

Type species.—Adapisorex gaudryi Lemoine, 1883.

Included species.—Adapisorex abundans Russell, 1964.

ADAPISOREX SP.

Figure 6.1-6.5; Table 8

Material examined.—UALVP 51850, M1; UALVP 51851, 51852, m1.

Age and occurrence.—Adapisorex is known from the late Paleocene (?Selandian to Thanetian) of Europe and the early late Paleocene (late middle Tiffanian, Ti4, Plesiadapis churchilli /P. simonsi Lineage Zone of Lofgren et al., 2004) of the Western Interior of North America.

Description.—Upper dentition, M1: The crown of M1 is subquadrate in outline and the bunodont principal cusps and slightly lower hypocone are quadritubercular in their arrangement. The stylar shelf is narrow and only a shallow ectoflexus interrupts the otherwise straight labial margin of the crown. The paracone is slightly taller than the metacone; the preparacrista and centrocrista are poorly developed, while the stronger postmetacrista curves posterolabially from the apex of the metacone. A distinct parastyle is not present but the ectocingulum is conspicuously raised as it wraps around the anterolabial corner of the crown. The conules are inflated and low, with the paraconule slightly more labially positioned than the metaconule; the conular cristae are short and weakly developed. The protocone is positioned lingual and slightly posterior to the level of the paracone, rather than directly lingual to this principal cusp as it is in other species of Adapisorex. The precingulum is narrow and likely terminated lingually at a small pericone, although this feature is worn on the one specimen at hand; posteriorly, the postcingulum is equally narrow and ends lingually at the hypocone.

Lower dentition, m1: The crown is weakly pyriform in outline, with the talonid wider than the trigonid. The trigonid is dominated by a massive protoconid and metaconid that are connected by a deeply notched protocristid; the opposing walls of these two cusps are strongly swollen and meet in the trigonid basin, forming a deep, narrow cleft anterior to the protocristid. A well-defined paracristid extends anteriorly from the protoconid apex before bending lingually to join the low, robust paraconid. The opposing walls of the hypoconid and the taller but less inflated entoconid form a shallow, faintly V-shaped talonid basin; the hypoconulid is the smallest talonid cusp and is just lingual to the midline of the crown. The low cristid obliqua and deeply notched entocristid contact the postvallid surface of the trigonid; an extension of the cristid obliqua persists on to the postvallid wall, continuing towards the protocristid notch. Conspicuous cingulids are developed along the anterior and posterior surfaces of the crown, but neither of these continues on to the labial margin.

Discussion.—The specimens described here bear their closest similarities to teeth of the adapisoricid lipotyphlan Adapisorex: subquadrate M1 with swollen, bunodont cusps, trigonids of the lower molars dominated by a considerably enlarged protoconid and metaconid but with a distinct paraconid, and lower molars with a shallow talonid basin. Prior to its discovery in the late middle Tiffanian (Ti4) of central Alberta (Fox and Scott, personal commun., 2009), Adapisorex was known only from the late Paleocene of France and Germany (Lemoine, 1983; Russell, 1964), thus joining the plesiadapiform primate Saxonella (Fox, 1984, 1991) as another late Paleocene Euramerican genus restricted only to western Canada on the North American continent. The recovery of Adapisorex in the Tiffanian of southeastern Saskatchewan represents an even wider geographic distribution of this taxon in North America then previously recognized and will be discussed in more detail by Fox and Scott (in prep.).

Family ERINACEIDAE Fischer de Waldheim, 1817

Genus LITOLESTES Jepsen, 1930

Type species.—Litolestes ignotus Jepsen, 1930, by monotypy.

LITOLESTES CF. L. IGNOTUS Jepsen, 1930

Figure 6.6-6.7

Material examined.—UALVP 10885, M1 (L = 1.9; W = 2.4).

Age and occurrence.—Litolestes ignotus is known from the early late Paleocene (early middle Tiffanian, Ti3, Plesiadapis rex/P. churchilli to early late Tiffanian, Ti5, P. simonsi/P. gingerichi Lineage Zone of Lofgren et al., 2004) of the Western Interior of North America.

Discussion.—The upper dentition of Litolestes ignotus has been thoroughly described by Krishtalka (1976a) and figured by Gingerich (1983) and Secord (2008). The single referred upper molar recovered from the Roche Percée localities compares closely with the M1 of L. ignotus but differs principally in being slightly larger, in having better developed, more acutely pointed stylar lobes (i.e., less smoothly rounded), a less anteroposteriorly compressed protocone, and in lacking a distinct hypocone on the postcingulum. The upper molars of Oncocherus krishtalkai Scott, 2006 are morphologically close to those of L. ignotus and it is possible that this tooth pertains to this genus; however, the specimen differs from the M1 of O. krishtalkai in many of the same ways that it differs from that of L. ignotus, and also in having apically sharper cusps and in lacking a pericone. A larger collection is needed for a more complete evaluation of this specimen's taxonomic affinities and a more precise assignment is deferred until then.

Order SORICOMORPHA Gregory, 1910

Family NYCTITHERIIDAE Simpson, 1928

Genus NYCTITHERIUM Marsh, 1872

Type species.—Nyctitherium velox Marsh, 1872.

Included species.—Nyctitherium serotinum (Marsh, 1872); N. christopheri Krishtalka and Setoguchi, 1977.

NYCTITHERIUM SP.

Figure 6.8-6.9

Material examined.—UALVP 51853, M2 (L = 1.2; W = 1.9).

Age and occurrence.—Nyctitherium is known from the early to middle Eocene (near the Wasatchian-Bridgerian boundary to the early Duchesnean of Robinson et al., 2004) of the Western Interior of North America.

Description.—Upper dentition, M1: The crown of this upper molar supports tall, sharp cusps with equally sharp associated crests. A weak ectoflexus divides the labial margin of the crown into well-defined stylar lobes: the parastylar lobe projects slightly anteriorly and narrows to short, hook-like structure, while the metastylar lobe is expanded more labially and narrows to a point. The ectocingulum is faintly developed along the ectoflexus. The paracone and metacone are spire-like, and the metacone is lower and slightly more labiolingually compressed than the paracone. The preparacrista descends directly anterolabially to the base of the parastyle and the tall, blade-like postmetacrista curves posterolabially to the posterolabial corner of the crown. The paraconule is more labially positioned than the metaconule and slightly anterior to the level of the paracone; the preparaconule crista extends to the anterolabial corner of the crown and forms a narrow shelf anterior to the base of the paracone, while the postparaconule crista terminates at the lingual base of the principal cusp. The postmetaconule crista forms a narrow shelf posterior to the metacone and ends at the posterolabial base of the metacone. The protocone leans anteriorly and is anteroposteriorly compressed. Beginning from the level of the metaconule to the posterolingual surface of protocone, the postcingulum is expanded posteriorly and forms a relatively wide shelf; a small hypocone is developed at the posterolingual-most extension of this cingulum. A much shorter and narrower precingulum is developed anteriorly.

Discussion.—Nyctitheriid soricomorphs are common, conspicuous members of most Paleocene to Oligocene local faunas in North America, Europe and Asia (see e.g., Sigé, 1976; Krishtalka, 1976b; Bown and Schankler, 1982; Russell and Dashzeveg, 1986; Smith 1996; Hooker, 2001; Scott, 2003; Missiaen and Smith, 2005; Rose, 2006). The referred specimen from Saskatchewan is nearest in size and morphology to the M2 of Nyctitherium velox but differs in being slightly shorter anteroposteriorly, in having less anteroposteriorly compressed paracone and metacone, a shorter and narrower precingulum, and a smaller hypocone that is more distinct from the protocone (i.e., only a moderately developed crest extends from the hypocone to the posterolingual base of the protocone). UALVP 51853 also bears some similarities to the M2 of several species of Leptacodon [e.g., L. rosei (see Gingerich, 1987), and L. dormaalensis (see Smith, 1996)], yet differs principally in having a wider stylar shelf, smaller protocone, weaker precingulid, and a better-developed postcingulum shelf.

The oldest definitive record of Nyctitherium is from the early Eocene (near the Wasatchian-Bridgerian boundary) of Colorado (Robinson, 1966; Krishtalka, 1976b; Robinson et al., 2004). More ambiguously, Krishtalka (1973) referred a single specimen from the late Paleocene of the Cypress Hills of southern Alberta to cf. Nyctitherium and numerous other unpublished descriptions of Nyctitherium-like specimens have been previously made from late Paleocene localities in western Canada (see e.g., Youzwyshyn, 1988; Stonley, 1988; MacDonald, 1996). Notably, many of the features that distinguish UALVP 51853 from the upper molars of Nyctitherium are similar to features of uppers of other Nyctitherium-like specimens from western Canada. Youzwyshyn (1988) and later Stonley (1988) suggested that these characters are plesiomorphic relative to those of early Eocene Nyctitherium and hypothesized that specimens from western Canada may represent structural precursors to Nyctitherium and other later nyctitheriids (excluding Leptacodon and Pontifactor West, 1974). The referred M2 from Saskatchewan adds further support to this claim; however, a more thorough discussion and analysis must await the collection of a larger, more complete sample and detailed comparisons with derived forms of Leptacodon.

Grandorder FERAE Linnaeus, 1758
Order CIMOLESTA McKenna, 1975
Family uncertain
Genus PARARYCTES Van Valen, 1966

Pararyctes VAN VALEN, 1966, p. 57.

Type species.—*Pararyctes pattersoni* Van Valen, 1966.

Other included species.—*Pararyctes rutherfordi* Scott, Fox, and Youzwyshyn, 2002.

PARARYCTES PATTERSONI Van Valen, 1966

Figure 7.1-7.10; Table 9

Pararyctes pattersoni Van Valen, 1966, p. 57.

Holotype.—UW 2002, upper left M1. Saddle locality, Fort Union Formation of Wyoming, early late Paleocene (early Tiffanian, Ti2, *Plesiadapis anceps*/*P*. *rex* Lineage Zone of Lofgren et al., 2004).

Material examined.—UALVP 9059, 9057, 51756-51758 (total: 5), M2; UALVP 9307, 9316, 10898 (total:3), m1; UALVP 9305, m3.

Age and occurrence.—Early late Paleocene (late early Tiffanian, Ti2, *Plesiadapis anceps*/*P*. *rex* Lineage Zone to late middle Tiffanian, Ti4, *P*. *churchilli*/*P*. *simonsi* Lineage Zone of Lofgren et al., 2004) of the Western Interior of North America.

Discussion.—The phylogenetic relationships of this poorly known cimolestid have remained uncertain since its formal naming, with some authors placing *Pararyctes* within the Palaeoryctidae (Van Valen, 1966, 1967; Asher et al., 2002; Bloch et al., 2004a; Gunnell et al., 2008) and others classifying the genus close to but outside the palaeoryctid clade (Kellner and McKenna, 1996; McKenna and Bell, 1997). A clear consensus on this issue has yet to be reached and I provisionally follow the classification of McKenna and Bell (1997), recognizing *Pararyctes* as a cimolestid with uncertain familial relationships. The referred specimens from the Roche Percée local fauna are virtually identical to specimens of *P*. *pattersoni* from early middle Tiffanian (Ti3) localities in central Alberta (Scott, 2008) differing only slightly in their smaller size. As noted by Scott (2008), specimens of *P*. *pattersoni* from Alberta (and now Saskatchewan) differ from those of the type Saddle locality from Wyoming (Van Valen, 1966) in having an anteroposteriorly longer pre- and postcingulum on the upper molars, a feature that could prove to be taxonomically important in future studies.

Suborder DIDELPHODONTA McKenna, 1975
Family CIMOLESTIDAE Marsh, 1889
Genus PALEOTOMUS Van Valen, 1967

Palaeosinopa MATTHEW, 1901, p. 22 (in part).
Niphredil VAN VALEN, 1978, p. 66.

Type species.—Palaeosinopa senior Simpson, 1937c.

Included species.—Paleotomus radagasti (Van Valen, 1978); P. milleri Rigby, 1980; P. carbonensis Secord, 1998; P. junior Scott, Fox, and Youzwyshyn, 2002.

PALEOTOMUS CF. P. JUNIOR Scott, Fox, and Youzwyshyn, 2002
Figure 8.1-8.3

Material examined.—UALVP 8875, m1 (L=3.6; TrW=2.1; TaW=1.9).

Age and occurrence.—Paleotomus junior is known from the early to late Paleocene (middle Torrejonian, To2, Protoselene opisthacus/Mixodectes pungens Lineage Zone to the early middle Tiffanian, Ti3, Plesiadapis rex/P. churchilli Lineage Zone of Lofgren et al., 2004) of the northern part of the Western Interior of North America.

Description and discussion.—Thorough descriptions of Paleotomus junior are provided by Scott et al. (2002) and Scott (2003, 2008). The referred specimen most closely resembles the m1 of P. junior from the early middle Tiffanian (Ti3) DW-2 locality in central Alberta (Scott, 2008), but differs in several notable ways. Specifically, the lower molar from Saskatchewan is longer and narrower, the talonid is proportionally longer, and the cristid obliqua is lower and weaker (a wide, U-shaped notch is developed between the posterior wall of the trigonid and the hypoconid). If confirmed as P. junior, the single specimen would represent the youngest occurrence of this taxon yet known and the first recovery of this species outside of Alberta.

CF. PALEOTOMUS SP. 1

Figure 8.4-8.20; Table 10

Material examined.—UALVP 51592, M3; UALVP 51593, p2; UALVP 8776, 8777, 51594 (total:3), p4; UALVP 8871, m1; UALVP 8780, m2; UALVP 8778, m3.

Age and occurrence.—Paleotomus is known from the early to late Paleocene (middle Torrejonian, To2, Protoselene opisthacus/Mixodectes pungens Lineage Zone to the early late Tiffanian, Ti5, Plesiadapis simonsi/P. gingerichi Lineage Zone of Lofgren et al., 2004) of the Western Interior of North America.

Description.—Upper dentition, M3: UALVP 51592 is extensively damaged and many of the features of the labial half of the crown are broken and missing, including most of the paracone and metacone. The metastylar lobe is undeveloped, while the parastylar lobe was likely expanded anterolabially. The paracone and metacone arise from a common base, and the paracone was the larger of the two cusps. The paraconule is better developed than the minute metaconule and more lingually positioned; the preparaconule crista terminates anterior to the paracone and the postmetaconule crista ends posterior to the metacone. A short postparaconule crista is developed. The sharp protocone leans slightly anteriorly and is anteroposteriorly compressed; the protoconal cristae extend to the lingual bases of the conules. The pre- and postcingulum are well developed and form narrow anterior and posterior shelves along the lingual half of the crown, respectively; these cingula do not meet lingually. A hypocone is not developed.

Lower dentition, p2: The elongate crown is blade-like, with a tall, bilaterally compressed and slightly recurved protoconid, and a low talonid cusp that is also bilaterally compressed. The well-developed paracristid is subarcuate in lateral profile and terminates at the anterior base of the crown; a paraconid is not developed. A second, straighter crest descends posteriorly from apex of the protoconid and meets a short crest originating from the hypoconid; a shallow notch can be developed at the juncture of these crests. A faint cingulid extends anterolingually from the hypoconid to the level of the protoconid, forming the ventral border to a shallow sulcus on the posterolingual surface of the protoconid; a shorter cingulid also descends anterolabially from the hypoconid.

p4: Like that in p2, the p4 crown is elongate, blade-like, and supports a tall protoconid that is bilaterally compressed and slightly recurved. The paracristid is straighter in profile than that on p2 and descends from the apex of the protoconid into a shallow carnassial notch before connecting to the apex of a small, robust paraconid; the apex of the paraconid is somewhat set off anterolingually from the base of the protoconid. Weak cingulids are developed anterolabially and anterolingually. The crest descending posteriorly from the protoconid apex is more robust than that on p2 and joins with the short crest extending anteriorly from the hypoconid; a wide notch is developed at the juncture of these crests. In one of the three specimens at hand (UALVP 8871), a swollen but heavily worn metaconid occurs approximately midway down the posterior surface of the protoconid and directly on the posteriorly extending crest. The weak posterolingual cingulid descends anterolingually from the hypoconid and encloses the talonid basin lingually; a faint extension of this cingulid in UALVP 8871 and 8776 curves anterodorsally from the anteriormost level of the talonid basin and ascends the posterolingual surface of the protoconid. A small, subconical entoconid can be developed adjacent to the hypoconid (e.g., UALVP 8871).

Lower molars: Other than the difference in size (e.g., length, m1 = 4.7 mm versus m2 = 5.5 mm), the m1 and m2 are virtually identical. The trigonid is elevated high above the talonid, and the trigonid cusps are apically sharp and form a nearly equilateral triangle in occlusal view. The protoconid is the tallest trigonid cusp, followed by the metaconid and the lower, anteroposteriorly compressed paraconid. The paracristid and protocristid are both well developed and interrupted at their deepest parts by weak carnassial notches. The talonid is considerably narrower than the trigonid, and the basin is shallow and slopes steeply anterolingually. The subconical talonid cusps are closely spaced and subequal in height; the hypoconid is slightly larger than the other cusps. The cristid obliqua contacts the postvallid surface ventral to the protocristid notch and lingual to the midline of the crown; an entocristid is not present and the talonid notch is wide. A prominent shelf-like precingulid is developed along the labial half of the anterior surface and a large interdental facet is formed between the cingulid and the anterolingual surface of the paraconid. The m3 is longer than either the m1 or the m2, the trigonid is wider and more anteroposteriorly compressed, the talonid is proportionally longer and narrower than that in the other molars, the hypoconulid is more posteriorly positioned, and the posterior root is slightly bilaterally compressed and more anterodorsally-posteroventrally directed.

Discussion.—The Roche Percée specimens are most similar to homologous teeth of early Tertiary North American pantolestine pantolestids [e.g., Palaeosinopa Matthew, 1901, Thelysia Gingerich, 1982a, and Leptonysson Van Valen, 1967 (the latter of these recognized as a pantolestid by Secord, 2008)], and the enigmatic cimolestid didelphodontan Paleotomus [classified, at times, within the Pantolestinae, (see Gingerich, 1980; Gunnell et al., 2008)]. The sectorial premolars, high and broad molar trigonids, undeveloped entocristid, and prominent precingulid appear to more closely align these referred specimens to Paleotomus (compare with P. senior; see Krause and Gingerich, 1983); yet, the narrow molar talonid and the closely spaced talonid cusps precludes reference of these specimens to Paleotomus or to any other genus of pantolestine pantolestids. It seems likely that these specimens document the presence of new, previously undescribed genus that is closest in dental morphology to Paleotomus; however, the formal naming and presentation of a diagnosis of this taxon is deferred until more detailed comparisons with other early Tertiary cimolestids (and pantolestids) can be conducted.

CF. PALEOTOMUS SP. 2

Figure 8.21-8.23

Material examined.—UALVP 51595, p2 (L= 4.73; W=2.53).

Description and discussion.—The referred specimen is virtually identical to the p2 of cf. Paleotomus sp. 1 (see description above) differing, however, in its considerably larger size, longer paracristid, and more prominent posterolingual cingulid. Although only a single specimen is thus far known for this taxon, it is sufficient to document the presence of a second species of this previously unknown genus.

Suborder APATOTHERIA Scott and Jepsen, 1936

Family APATEMYIDAE Matthew, 1909

Genus UNUCHINIA Simpson, 1937b

Apator SIMPSON, 1936, p. 16.
Unuchinia SIMPSON, 1937b, p. 78.

Type species.—Apator asaphes Simpson, 1936.

Included species.—Unuchinia dysmathes Holtzman, 1978; U. diaphanes Gunnell, 1988.

UNUCHINIA CF. U. DYSMATHES Holtzman, 1978

Figure 9.1-9.36; Table 11-12

Referred material.—UALVP 51530-51536, 51750 (total: 8), I1;UALVP 10848, 51537-51541 (total: 5), I2; UALVP 51542, P4; UALVP 51543, M1; UALVP 51544, M2; UALVP 51545, i2; UALVP 51546-51547, p2; UALVP 51548, 51550-51552 (total: 4), m1; UALVP 51549, 51553-51554, 51751-51752 (total: 5), m2; UALVP 51753-51754, m3.

Age and occurrence.—Unuchinia dysmathes is known from the late Paleocene (early middle Tiffanian, Ti3, Plesiadapis rex/P. churchilli Lineage Zone to the late middle Tiffanian, Ti4, P. churchilli/P. simonsi Lineage Zone of Lofgren et al., 2004) of the Western Interior of North America.

Description.—Upper dentition, I1: The robust I1 is mediolaterally compressed and hook-like in lateral profile, similar to the I1 in U. dysmathes (Scott, 2008) and other apatemyids [e.g., Labidolemur Matthew and Granger, 1921 (see Gingerich, 1982b), and Apatemys Marsh, 1872 (see Gingerich, 1982b; Gingerich and Rose, 1982)]. The anterocone is the dominant coronal cusp; it is stout and abruptly bent ventrally along its length. Two crests arise from the apex of the anterocone: a tall, slender crest that runs along the lateral margin of the ventral surface to the small posterocone and a second, shorter crest that extends posterodorsally onto the medial surface. The lateral surface of the crown is nearly flat, whereas the medial surface is convex; the enamel is thicker and extends farther posteriorly on the lateral surface than on the medial surface. The elongate root is robust and mediolaterally compressed.

I2: I2 of Unuchinia cf. U. dysmathes closely resembles I2 of U. dysmathes, as described by Scott (2008): large ventrally hooked anterocone dominating the crown and a small posterocone developed posterior and slightly medial to this main cusp. As in I2 of U. dysmathes, the outline of the anterior surface of the crown resembles a dorsoventrally elongate scalene triangle; however, owing to the taller anterocone, this triangle is taller in Unuchinia cf. U. dysmathes than U. dysmathes. The anterior surface is shallowly depressed and bordered on all sides by sharp crests; the lateral crest is the longest, followed by the medial crest and finally the short, faintly cuspate ventral crest. Both the lateral and medial crests originate at the apex of the anterocone and become increasingly robust as they descend the anterior surface, ultimately terminating dorsally in conspicuous accessory cusps; the lateral accessory cusp is larger and more conical than the small, slightly compressed medial accessory cusp. The lateral surface of the crown is flat and the enamel on this surface is thicker and extends farther dorsally than it does on the slightly concave medial surface. The root is short and stout, progressively narrowing mediolaterally near its base.

P4: The subtriangular crown of P4 consists primarily of a tall, enlarged paracone and shorter, much smaller protocone. A small parastylar cuspule is developed directly anterior to the paracone on the paracingulum, and only a weak preparacrista extends between the two cusps; posteriorly, a high, sweeping postparacrista descends from the apex of the paracone to the posterolabial corner of the crown. A metacone is not developed. The ectocingulum is weakly developed across the posterior half of the labial margin. Neither conules nor conular crests are developed. The preprotocrista descends anteriorly from the apex of the protocone and joins the precingulum; this elongate crest is confluent with the paracingulum and continues towards the anterolabial corner of the crown. A postprotocrista was likely developed but the posterior surface of the protocone is heavily worn on the single specimen at hand (UALVP 51542); the postcingulum, beginning at the base of this wear facet, is truncated labially by the postparacrista and a small swelling occurs at the junction between these crests.

M1: The labial margin of the M1 crown is considerably longer than the lingual margin, imparting a subtriangular outline to the crown, and the principal cusps are well developed and apically rounded. The centrocrista is strong on both the paracone and the slightly lower metacone, and forms a deep, V-shaped notch between these two cusps; the paracone leans anteriorly while the metacone is erect. The parastylar lobe projects anteriorly and bears a small parastyle at its anteriormost tip; the slender preparacrista descends anteriorly from the apex of the paracone, but curves labially near the base of the cusp and extends to the ectocingulum. As in the M1 of U. dysmathes (see Scott, 2008), a transverse facet is developed between the base of the paracone and parastylar lobe, corresponding to contact with the protoconid on m1. The metastylar lobe is swollen and expanded posterolabially; the high postmetacrista extends from the apex of the metacone to the posterolabial corner of the crown. The ectoflexus is shallow and the stylar shelf is narrow across most of the labial margin but widens posterior to the metacone and around the metastylar lobe. A faint ectocingulum is developed across the anterior half of the labial margin and a small cuspule is developed on the cingulum at the contact between the preparacrista and ectocingulum. Lingual to the paracone and metacone, the crown narrows and a shallow embayment occurs midway along the posterior margin between the metacone and posteriorly expanded postcingulum, further constricting the crown. The apex of the protocone leans anteriorly and is positioned directly lingual to the apex of the paracone; the cusp is subequal in height to the metacone. The preprotocrista is continuous with the paracingulum and forms an elongate crest that terminates labially at the parastylar lobe; a narrow shelf is developed anterior to the base of the paracone by this crest. Similar to this, the postprotocrista joins with the metacingulum and forms a narrow shelf posterolingually to the base of the metacone; however, this crest terminates posterior to the metacone and does not reach the metastylar lobe. No conules are developed, although a faint swelling occurs on the base of the postprotocrista near the base of the metacone. A small conical hypocone is developed on the posterolingual corner of the postcingulum; anteriorly, only a short precingulum is developed.

M2: The M2 resembles M1 but differs mainly in being wider, and in having both the parastylar and metastylar lobes extending far labially and separated by a deep ectoflexus. The parastylar lobe is anteroposteriorly shorter than the metastylar lobe and projects farther labially. The ectocingulum is irregularly developed across the labial margin and faintly cuspate. The preparacrista descends from the apex of the paracone and splits into two separate crests near the base of the cusp: the more prominent crest extends directly labially towards the ectocingulum, while the other, fainter crest runs towards the anterolabial corner of the crown. As with M1, the tall paracone and slightly smaller protocone lean anteriorly, while the metacone is more nearly vertical. Distinct conules are undeveloped but, as seen in M1, a small swelling occurs on the postprotocrista near the base of the metacone. The elongate crest formed by the preprotocrista and paracingulum is much straighter than that on M1, and the narrow shelf this crest produces at the anterior base of the paracone in M1 is not developed in M2. The postcingulum is larger and more lingually projecting than that on M1 and the hypocone is taller.

Lower dentition, i2: The i2 of Unuchinia has been previously described for U. diaphanes Gunnell, 1988, and U. dysmathes, as presented by Scott (2008). Similar to these forms, the procumbent i2 of Unuchinia cf. U. dysmathes is elongate and mediolaterally compressed, with the crown strongly recurved dorsally. A prominent crest that extends from the crown apex to its base borders the concave occlusal surface of the crown laterally; a stout, conical cusp is developed on this crest slightly anterior to the base of the crown. As noted by Scott (2008), in the i2 of U. dysmathes the tip of the incisor is splayed laterally at the level of the medial interdental facet and a short crest runs posteromedially from the tip to the anteriormost extension of this facet. The root is strongly compressed mediolaterally and a shallow, longitudinal depression occurs across the medial surface, continuing a short distance onto the crown. The enamel on the medial surface extends along the ventral and dorsal sides of this weak depression and eventually joins anteriorly at the interdental facet; laterally, the enamel covers most of the crown.

p2: The strongly procumbent, blade-like crown of p2 is dominated by a tall, bilaterally compressed protoconid and a small but robust cusp developed on the posterolabial margin of the crown. A sharp, anterolingually arcuate paracristid descends from the apex of the protoconid to the short, prominent lingual cingulid at the base of the crown; this cingulid is slightly more anteriorly bulging than that in U. diaphanes Gunnell, 1988, and U. dysmathes, as illustrated by Scott (2008). A second crest originating at the protoconid apex extends posterolabially to the smaller posterolabial cusp, forming a sharp edge along the labial margin of the occlusal surface. Both the labial and lingual surfaces are faintly convex; the enamel extends considerably farther ventrally on the labial surface than on the lingual surface. The single, bilaterally compressed root tapers quickly from below the crown of the tooth to its base.

m1: The m1 of Unuchinia cf. U. dysmathes is virtually identical in coronal morphology to the m1 of U. dysmathes (see Holtzman, 1978; Scott, 2008). The trigonid is elevated above the talonid, and the trigonid cusps are arranged roughly in an equilaterally triangular pattern. The low paraconid is anteroposteriorly compressed, leans anteriorly, and is further inset from the lingual margin than that on m2 and m3. The paracristid is low and runs posterolabially from the paraconid apex to a notch between the paraconid and protoconid, then turns posteriorly to ascend the anterior surface of the protoconid. The protoconid and metaconid are much taller than the paraconid and subequal in height; the metaconid is slightly more robust at its base and positioned posterolingual to the protoconid. The protocristid is strongly developed and, in longitudinal view, forms a deep, V-shaped notch between the metaconid and protoconid. A short crest can descend posteriorly from the paraconid to the base of the metaconid (e.g., UALVP 51550). The hypoconid is the tallest and largest talonid cusp, and the shallow talonid basin slopes steeply anterolingually from the apex of this cusp. The cristid obliqua is low and contacts the postvallid surface ventral to the protocristid notch. The hypoconulid is displaced posteriorly and is slightly taller than the entoconid; the postcristid and entocristid are low but form an elongated, arcuate crest that encloses the wide talonid basin lingually. A short, shelf-like cingulid is developed on the anterolabial corner of the trigonid.

m2: As in U. dysmathes (see Holtzman, 1978; Scott, 2008), the m2 of Unuchinia cf. U. dysmathes closely resembles the m1 but differs as follows: slightly larger size, the trigonid is more anteroposteriorly compressed, the paraconid leans further anteriorly and is more lingually positioned, and the hypoconid is taller, while the hypoconulid and, in some specimens, the entoconid are more reduced. In addition to these differences, the m2 paracristid is lower and longer then that on m1, as it is on the m2 of U. dysmathes; however, unlike in U. dysmathes, the paracristid runs almost directly labially from the paraconid apex to the notch between the paraconid and protoconid before turning sharply posteriorly to ascend the protoconid. As a result, the anterolabial corner of the trigonid is more squarish than that in other species of Unuchinia.

m3: Due in large part to the narrow, posteriorly expanded talonid and finger-like hypoconulid, m3 is the longest lower molar. The trigonid is more anteroposteriorly compressed than that of either m1 or m2 but slightly wider, with the metaconid and protoconid farther apart and the protocristid more widely notched. In comparison to m2, the paraconid is more nearly vertical and farther inset from the lingual margin; the paracristid descends labially and only slightly posteriorly from the apex of the paraconid, then turns directly posteriorly to ascend the protoconid. The hypoconulid is the tallest talonid cusp, followed closely by the hypoconid and the much-reduced entoconid. The elongate crest formed by the postcristid and entocristid extends from the hypoconulid to the postvallid surface. The cristid obliqua is robust and contacts the postvallid surface ventral to the protocristid notch; a small mesoconid is developed on this crest in one specimen (UALVP 51754).

Discussion.—The Apatemyidae are an unusual family of purported arboreal eutherian mammals that range from the early Paleocene to the early Oligocene of North America and Europe (see, e.g., Marsh, 1872; Matthew 1921b; Matthew and Granger, 1921; Jepsen, 1934; Simpson, 1940; Clemens, 1964; West, 1973a; Gingerich, 1982b; Gingerich and Rose, 1982; Gunnell, 1988; von Koenigswald, 1987a, 1990; von Koenigswald et al., 2005a, 2005b; Scott, 2003, 2008; and see McKenna, 1963, for a historical review). The group is mainly characterized by dental and skeletal specializations that were likely for extracting wood-boring insect larvae from trees, including enlarged upper and lower incisors that could gouge dead wood or remove bark and, where known, elongate digits that may have acted as probes (e.g., von Koenigswald, 1987a, 1990; von Koenigswald and Schierning, 1987; Bloch and Boyer, 2001; Bloch et al., 2004b; Koenigswald et al., 2005a, 2005b).

Apatemyids were more traditionally thought to bear close affinities to primates (including plesiadapiform primates), based mainly on the possession of enlarged incisors and general features of the molars (e.g., Scott and Jepsen, 1936; Simpson, 1940; Gingerich, 1989). Some authors, however, strongly questioned this relationship and alternatively suggested the placement of the family within the “Insectivora” (e.g., Jepsen, 1934; McKenna, 1963) or closely related to the Palaeoryctidae (e.g., Szalay, 1968). More recent classifications have recognized the group as part of the Cimolesta (McKenna and Bell, 1997; Rose, 2006), a likely polyphyletic assemblage of eutherians considered by some to be related to carnivorans, creodonts, and pholidotans. Intriguingly, the results of the first phylogenetic analysis for the family do not support any of these hypotheses (Silcox et al., 2007); instead, these findings recognize the Apatemyidae as a basal member of the laurasiatherian clade (which includes lipotyphlans, chiropterans, carnivorans, pholidotans, perissodactyls, and cetartiodactyls).

Unuchinia is a relatively poorly known apatemyid, distinct from all other members of the family in possessing two, and not one, lower incisors (Holtzman, 1978; Gunnell, 1988; Scott, 2008). Simpson (1936) was the first to describe a specimen that would later be assigned to the genus, a single incomplete dentary from the early Tiffanian (Ti2) Scarritt Quarry in Montana that was originally assigned to “Apator” asaphes [the generic name was later found to be preoccupied and emended by Simpson (1937b) to Unuchinia]. Initially, Simpson (1936, 1937b) did not recognize the apatemyid affinities of the single specimen and referred it to the Insectivora with question; however, McKenna (1963), reviewing Paleocene and Eocene apatemyids in North America, re-described the single specimen and placed the genus within the Apatemyidae. Holtzman (1978) described a second species of Unuchinia, U. dysmathes, from the middle Tiffanian (Ti3-Ti4) Judson and Brisbane localities of North Dakota that was distinct from U. asaphes in being slightly larger and in possessing a double-rooted, rather than single-rooted, p4. A third species, U. diaphanes, was later described by Gunnell (1988) from the middle Torrejonian (To2) Rock Bench Quarry in Wyoming; this species differs from U. asaphes in having a double-rooted p4 and in lacking a diastema between p3 and p4, and differs from U. dysmathes in being smaller.

The specimens of Unuchinia cf. U. dysmathes from Saskatchewan compare most favorably to those of U. dysmathes from North Dakota (Holtzman, 1978) and central Alberta (Scott, 2008) but differ in several ways. Perhaps most notably, the paracristid on the m2 and m3 of Unuchinia cf. U. dysmathes is longer than that on homologous teeth of U. dysmathes and the anterolabial corner of the trigonid is more squarish. This condition is not seen in any other species of Unuchinia and is somewhat reminiscent of that seen in several apatemyines [e.g., Jepsenella Simpson, 1940 (see McKenna, 1963), and Labidolemur (see Gingerich, 1982b)], although, the paracristid does not extend nearly as far anteriorly as it does in these forms, nor is a fourth trigonid cusp developed anywhere on this crest (see McKenna, 1963). The lower molars of Unuchinia cf. U. dysmathes from Saskatchewan are also considerably narrower than those of the holotype of U. dysmathes (SMM P77.6.31) (e.g., mean width, m1 = 1.75 mm, Unuchinia cf. U. dysmathes from Saskatchewan, versus mean width, m1 = 2.35 mm, SMM P77.6.31), yet similar in width to specimens of U. dysmathes from Alberta (Scott, 2008). Secord (2008) described lower molars from the early late Tiffanian (Ti5) of Wyoming that he assigned to Unuchinia cf. U. dysmathes and that are also narrower than those in SMM P77.6.31; however, in comparison to these, the lower molars of Unuchinia cf. U. dysmathes from Saskatchewan are still more narrow (although the width of the talonid is slightly greater).

At present, only two reports have described elements of the upper dentition of Unuchinia: Secord (2008) questionably referred an insolated I1 and an isolated I2 to Unuchinia sp., while Scott (2008) described the complete upper dentition of U. dysmathes, including the remarkably preserved UALVP 47818 (an incomplete premaxilla with Il, and alveolus for I2, and an associated incomplete maxilla with P3-P4, and M1-M3, and alveoli for P2). The referred elements of the upper dentition of Unuchinia cf. U. dysmathes closely resemble the comparable teeth described for U. dysmathes by Scott (2008) but with several differences. Specifically, the upper molars of Unuchinia cf. U. dysmathes are wider than those of U. dysmathes, with the stylar lobes slightly better developed; this is most apparent in M1, in which the metastylar lobe projects further posteriorly. In addition to these differences, the molar protocone is less anteroposteriorly compressed than that in U. dysmathes and the constriction lingual to the paracone and metacone is less pronounced.

The occurrence of Unuchinia cf. U. dysmathes at Roche Percée documents the first record of an apatemyid in the Paleocene of Saskatchewan. The specimens referred here likely represent a new, undescribed species of Unuchinia; however, the formal naming and presentation of a diagnosis are deferred until a larger collection is made.

Genus LABIDOLEMUR Matthew and Granger, 1921

Type species.—Labidolemur soricoides Matthew and Granger, 1921.

Included species.—Labidolemur kayi Simpson, 1929a; L. serus Gingerich, 1982b.

LABIDOLEMUR SORICOIDES Matthew and Granger, 1921

Figure 9.37-9.39

Holotype.—AMNH 17400, associated, incomplete left and right dentaries, with i1 and m1 (see Matthew and Granger, 1921, p. 4). Mason Pocket locality, Animas Formation of Colorado, late Paleocene (late middle Tiffanian, Ti4, Plesiadapis churchilli/P. simonsi Lineage Zone of Lofgren et al., 2004).

Referred material.—UALVP 51755, m1 (L= 2.0; TrW= 1.2; TaW= 1.3).

Age and occurrence.—Early late Paleocene (early middle Tiffanian, Ti3, Plesiadapis rex/P. churchilli Lineage Zone to the late middle Tiffanian, Ti5, P. simonsi/P. gingerichi Lineage Zone of Lofgren et al., 2004) of the Western Interior of North America.

Description and discussion.—The dentition of the middle to late Tiffanian apatemyid Labidolemur soricoides has been thoroughly described and figured by Matthew and Granger (1921), McKenna (1963), West (1973a), and Secord (2008). The single referred lower molar is virtually identical in morphology to the m1s in the holotype (AMNH 17400) from the Mason Pocket locality in Colorado (Matthew and Granger, 1921): the trigonid is low and subquadrate in occlusal outline, with an accessory cusp developed at its anterolabial corner, the protoconid and metaconid are connected by a narrow, V-shaped protocristid, the talonid basin is shallow and wide, and the rim of the talonid forms a nearly complete, level crest around the entire basin. Although documented only by a single specimen, the occurrence of L. soricoides represents the second record of an apatemyid in the Paleocene of Saskatchewan and the first known report of the genus in Canada.

Suborder PANTODONTA Cope, 1873a
Superfamily PANTOLAMBDOIDEA Cope, 1883a
Family TITANOIDEIDAE Patterson, 1934
Genus TITANOIDES Gidley, 1917

Sparactolambda PATTERSON, 1939, p. 352.

Type species.—Titanoides primaevus Gidley, 1917.

Included species.—Titanoides gidleyi Jepsen, 1930; T. zeuxis Simpson, 1937c; T. looki (Patterson, 1939); T. major (Simons, 1960); T. nanus Gingerich, 1996.

TITANOIDES CF. T. PRIMAEVUS Gidley, 1917
Figure 10.1-10.10

Material examined.—UALVP 8765, right incomplete maxilla with M2-M3; UALVP 8768, M3; UALVP 8772, 8873, MX; UALVP 8770, 51529, mx.

Age and occurrence.—Titanoides primaevus is known from the late Paleocene (early middle Tiffanian, Ti3, Plesiadapis rex/P. churchilli Lineage Zone to the earliest Clarkforkian, Cf1, Rodentia/P. cookei Interval Subzone of the P. gingerichi/P. cookei Lineage Zone of Lofgren et al., 2004) of the Western Interior of North America.

Description and Discussion.—Although never particularly abundant, heavily built, omnivorous to herbivorous pantodonts are relatively common as discoveries in Paleocene and Eocene mammalian faunas of North America, Europe, and Asia (see, e.g., Matthew, 1937; Simons, 1960; Lucas, 1993, 1998;

Rose, 2006). Traditionally, this enigmatic clade was classified with ungulates or ungulate-like groups (see, e.g., Cope, 1875; Gregory, 1910; Simpson, 1945; Simons, 1960); however, with the emergence of comprehensive cladistic-based classifications, the group was placed in the Grandorder Ferae, closely related to the didelphodontines (McKenna, 1975; Lucas, 1993, 1998). Current consensus generally favors this latter hypothesis and in their classification scheme McKenna and Bell (1997) place the group within the order Cimolesta (but see Scott, 2008 for a different opinion).

Most of the specimens from the Roche Percée localities referred here to the Pantodonta are isolated and fragmentary teeth, and are distinguished from the teeth of other mammals at the localities based on their large size and prominent dilambdodont (i.e., W-shaped ectoloph) outline visible in the upper molars. Based on the few traits that can be assessed, specimens from Saskatchewan appear to most closely resemble those of Titanoides primaevus (Gidley, 1917; Simons, 1960; Hartman and Kihm, 1991): M2 appears to have been larger than M3 [although the isolated M3 (UALVP 8768) appears to be larger than the M3 in the maxillary fragment (UALVP 8765), particularly in the length of the lingual half], the conules are weak (UALVP 8768) to absent (UALVP 8765), the metacingulum ("posterior cingulum" of Simons, 1960) of the M3 is narrow and does not form a large shelf, and the trigonids of the lower molars are open. More recent treatments of T. primaevus (e.g., Gingerich, 1996; Secord, 2008) have noted the close similarities that this species shares with T. looki (previously synonymized under T. primaevus by Gazin, 1956 and Simons, 1960, but re-validated by Gingerich, 1996), T. gidleyi, and T. zeuxis, and it seems likely that some (if not all) of these species represent junior synonyms of T. primaevus. Pending a revision of Titanoides and, more broadly, the Pantodonta, I tentatively assign the referred specimens from Saskatchewan to T. primaevus.

Suborder PANTOLESTA McKenna, 1975

Family PANTOLESTIDAE Cope, 1884a

Genus BESSOECETOR Simpson, 1936

Palaeictops MATTHEW, 1899 (in part): VAN VALEN, 1967, p. 232.
Palaeosinopa MATTHEW, 1901 (in part): SIMPSON, 1935a, p. 230.
Thylacodon MATTHEW and GRANGER, 1921 (in part): RUSSELL in RUTHERFORD, 1927, p. 41.
Propalaeosinopa SIMPSON, 1927, p. 2.
Bessoecetor SIMPSON, 1936, p. 9.

Type species.—Bessoecetor thomsoni Simpson, 1936.

Included species.—Bessoecetor septentrionalis (Russell, 1929); B. pilodontus Secord, 2008; B. krausei new species.

BESSOECETOR PILODONTUS Secord, 2008

Figure 11.1-11.22; Table 13

Bessoecetor pilodontus SECORD, 2008, p. 56.

Holotype.—UM 91332, incomplete right dentary containing p4, m1-3 and alveoli for i3, p2-3. Divide Quarry, northern Bighorn Basin of Wyoming, early late Paleocene (late middle Tiffanian, Ti4, Plesiadapis churchilli/P. simonsi Lineage Zone of Lofgren et al., 2004).

Material examined.—UALVP 9723, 51030, 51455, P4; UALVP 51031-51037 (total:7), M1; UALVP 51038-51042 (total:5), M2; UALVP 51043, incomplete right dentary containing p4, m1 and alveoli for p2-3, m2; UALVP 51044, incomplete right dentary containing m2 and alveoli for p2-4, m1, m3; UALVP 9632, 9652, 9673, 10867, 51045-51046 (total:6), m1; UALVP 51047-51050 (total:4), m2.

Age and occurrence.—Early late Paleocene (late middle Tiffanian, Ti4, Plesiadapis churchilli/P. simonsi Lineage Zone of Lofgren et al., 2004) of the Western Interior of North America.

Description.—Upper dentition: Secord's (2008) tentative assignment of an isolated M1 to B. pilodontus has been the only tooth of the upper dentition known for the species. Included among the specimens from the Roche Percée localities are isolated P4, M1 and M2 referable to B. pilodontus, thereby broadening knowledge of the upper dentition of this species.

P4: The P4 of B. pilodontus closely resembles that of B. thomsoni Simpson, 1936, (see Scott, 2008) and B. septentrionalis (see Scott et al., 2002; Scott, 2008): the enlarged paracone is the dominant cusp, the postparacrista extends posterolabially from the paraconal apex to the metastylar lobe, and the low protocone is positioned directly lingual to the paracone. A robust ectocingulum is developed along the posterior half of the labial margin of the crown. No metacone is developed. A minute parastylar cuspule arises on the anterolabial corner of the crown, and a short preparacrista extends from the apex of the cuspule on to the paracone. The preprotocrista joins with the paracingulum, which continues to the base of the parastyle, while the postprotocrista joins with the metacingulum but is terminated labially by the postparacrista. A faint lingual cingulum can be developed along the base of the protocone.

M1: The crown of M1 is subtriangular in occlusal outline, with the metastylar lobe expanded posterolabially and the parastylar lobe swollen but more smoothly rounded than the metastylar lobe; a shallow ectoflexus indents the labial margin of the crown between these lobes. The stylar shelf is narrow and bordered labially by a weak ectocingulum. The paracone and more labially positioned metacone are subconical and subequal in height; the centrocrista becomes increasingly pronounced as it extends towards the base of these cusps and forms a relatively shallow, V-shaped notch between them. The faint preparacrista descends anterolabially from the paracone and continues to the anterolabial corner of the crown and on to the small parastyle, while the more pronounced and much sharper postmetacrista curves posterolabially from the apex of the metacone to the posterolabial corner of the crown. As in other species of Bessoecetor (Simpson, 1936, 1937d; Scott, 2008), both conules are strongly developed, with the paraconule more lingually positioned than the metaconule. The postparaconule crista is characteristically undeveloped, although in one unworn specimen (UALVP 51037) the crest is sharp and higher above the floor of the trigon basin than the short premetaconule crista. The preparaconule crista is steep and continuous with the paracingulum; this crest forms a shelf anterior to the base of the paracone and terminates labially at the parastylar lobe. A similar shelf is formed posterior to the base of the metacone by the postmetaconule crista and metacingulum; this crest terminates posterolingual to the metacone and does not reach the posterolabial corner of the crown. The protocone is subequal in height to the paracone and metacone, but more massive at its base; the apex of this cusp leans slightly anteriorly and is nearly lingually opposite to that of the paracone. The protoconal cristae extend from the apex of the protocone directly to the lingual bases of the conules. The robust hypocone is developed on the posterolingual corner of the long and expanded postcingulum; a shorter and less pronounced precingulum is developed anteriorly.

M2: The M2 is wider relative to its length than M1, with the finger-like metastylar lobe flared more labially and the postcingulum projecting farther posterolingually. The parastylar lobe is more swollen than on M1 but narrows anteriorly to a short hook-like process; the parastyle is positioned at the anteriormost apex of this lobe and is more acute and better developed than that on M1. A shallow ectoflexus is developed. The metacone is labial to the level of the paracone and slightly compressed labiolingually. The low preparacrista originates from the apex of the paracone and continues towards the anterolabial corner of the crown, but does not ascend the parastyle as on M1; instead, it terminates at the base of this cusp. Posteriorly, the elongate postmetacrista curves from the apex of the metacone to the posterolabial corner of the crown. As with the M1, both conules are strongly developed and the paraconule is more lingually positioned than the metaconule. The base of the protocone is more anteroposteriorly compressed than in M1, but the apex of the cusp remains transversely opposite to the apex of the paracone. The preprotocrista is straight and extends directly from the protoconal apex to the lingual base of the paraconule, while the postprotocrista is longer and curves posterolingually from the protoconal apex to the lingual base of the metaconule. The hypocone is more robust and the precingulum is more pronounced than on M1.

Dentary and lower dentition, Dentary: Two incomplete dentaries of B. pilodontus have been recovered from the Roche Percée localities. As in other species of Bessoecetor (e.g., Simpson, 1936; Scott, 2008; Secord, 2008), the mandibular ramus of these specimens is long and relatively shallow, with the ventral margin faintly convex in lateral view. Two mental foramina are developed along the labial surface: the smaller anterior foramen is positioned either ventral to the intersection between the posterior alveolus of p2 and anterior alveolus of p3 (UALVP 51043) or between the anterior and posterior alveoli of p3 (UALVP 51044), while the larger, more posterior foramen is beneath m2. The anterior mental foramen in both specimens from Saskatchewan is more rostrally positioned than in the holotype of B. pilodontus (UM 91332), in which the foramen is beneath the posterior alveolus of p3 (Secord, 2008), and more closely corresponds to that in other species of Bessoecetor. The masseteric fossa of B. pilodontus is deeply excavated and bordered anteriorly by the robust anterior rim of the coronoid process. The surface of the temporalis fossa is nearly flat and, as described for B. thomsoni and B. septentrionalis (see Scott, 2008) and other pantolestids [e.g., Pantolestes Cope, 1872 (see Matthew, 1909) and Palaeosinopa Matthew, 1901 (see Rose and von Koenigswald, 2005)], a bony protuberance is developed at the anteriormost extent of this fossa, posteromedial to m3. As pointed out by Scott (2008), this protuberance likely represents the point of insertion for the anterior tendinous parts of the deep temporalis musculature (see Turnbull, 1970).

p4: As noted by Secord (2008), the p4 of B. pilodontus is more robust than that of either B. thomsoni or B. septentrionalis, with the base of the enlarged protoconid considerably swollen. Also, the paraconid is less separated from the base of the protoconid than in these other species of Bessoecetor; a faint, deeply notched paracristid extends between the apices of these cusps. A second low crest descends directly posteriorly from the apex of the protoconid to the hypoconid.

An anterolingually arcuate crest extending from the apex of the hypoconid to the posterolingual base of the protoconid encloses the small talonid basin.

m1: Unlike the condition in B. thomsoni and B. septentrionalis, the m1 trigonid of B. pilodontus is narrower than the talonid (Secord, 2008). The low paraconid is anteroposteriorly compressed and inset from the lingual margin of the crown, positioned directly on the medial axis of the crown. The protoconid and metaconid are subconical, subequal in height, and their opposing walls are swollen. A short, strongly flexed paracristid extends between the paraconid and protoconid, while a sharp, V-shaped protocristid is developed between the protoconid and metaconid. The hypoconulid is smaller and positioned posterior to the level of the robust entoconid and hypoconid, which are transversely opposite each other; the apex of the hypoconulid is slightly lingual to the anteroposterior axis of the crown. The cristid obliqua contacts the postvallid surface ventral to deepest part of the protocristid. The entocristid extends from the apex of the entoconid to the posterolingual base of the metaconid and encloses the broad talonid basin lingually. Only a short precingulid is developed across the anterior surface of the trigonid.

m2: The m2 closely resembles m1 but differs as follows: the trigonid is subequal to or wider than the talonid, the protoconid and metaconid are further apart and the protocristid notch is wider, the paraconid is slightly lingual to the medial axis of the crown, the paracristid is longer, and the hypoconulid is displaced further lingually and closer to the entoconid. A wear facet is deeply incised between the hypoconid and hypoconulid in some specimens (e.g., UALVP 51044).

Discussion.—Members of the Pantolestidae are known from the early Paleocene to the late Oligocene of North America, Europe, Asia, and possibly Africa (see, e.g., Matthew, 1909; Simpson, 1936, 1937d; Dorr, 1977; Bown and Simons, 1987; Gheerbrant, 1991; McKenna and Bell, 1997; Scott et al., 2002; Scott, 2003, 2008; Rose and von Koenigswald, 2005; Rose, 2006). In most conventional classifications, three subfamilies are recognized in the group: Pantolestinae, Pentacodontinae, and Dyspterninae (e.g., McKenna and Bell, 1997). The semi-aquatic habits of the pantolestines were first inferred by Matthew (1909), based largely on the close resemblances of specimens of *Pantolestes* from the middle Eocene of Wyoming to modern lutrines (otters). More recent studies on several exceptionally well-preserved and nearly complete skeletons of *Buxolestes* from Germany (von Koenigswald, 1980, 1987b; Pfretzschner, 1993) and *Palaeosinopa* from Wyoming (Rose and von Koenigswald, 2005) have corroborated these similarities and interpretations.

Among the oldest and most poorly known pantolestine pantolestids is the early to late Paleocene *Bessoecetor*, known only from dental and gnathic remains. The first specimens attributed to the genus were described by Simpson (1936) and assigned to *B*. *thomsoni*. Van Valen (1967) and Dorr (1977), however, considered *B*. *thomsoni* and a similar form from the middle Torrejonian (To2) Silberling and Gidley quarries of Montana, *B*. “*diliculi*” Simpson 1935a, as junior synonyms of “*Propalaeosinopa* *albertensis*” Simpson, 1927. Following the suggestions of several other authors (e.g., Rose, 1981; Krause and Gingerich, 1983), Scott et al. (2002) regarded “*Propalaeosinopa*” as a nomen dubium because of the poor preservation of AMNH 15543B, the type specimen for “*P*. *albertensis*”; Scott et al. (2002) then synonymized *B*. *thomsoni* and *B*. “*diliculi*” with *Diacodon* *septentrionalis* Russell, 1929, and transferred this species to *Bessoecetor*. Later, based on new specimens from the early middle Tiffanian (Ti3) of central Alberta, Scott (2008) re-validated *B*. *thomsoni*, citing many of the characters originally listed by Simpson (1936) as taxonomically significant. I provisionally follow the revisions suggested by Scott (2008) here.

Bessoecetor *pilodontus* and a very similar form, *Bessoecetor* cf. *B*. *pilodontus*, were recently described by Secord (2008) based on specimens from several late middle Tiffanian (Ti4) localities in the Bighorn Basin of northwestern Wyoming. Secord (2008) distinguished these two forms from *B*. *septentrionalis* and *B*. *thomsoni* (then the only other species in the genus, but see descriptions of *B*. *krausei* n. sp. below) in being larger in all dimensions, in having a wider, more inflated p4 with a less distinct paraconid and a shorter talonid, and an m1 trigonid that is narrower than the talonid. In these regards, the referred specimens from the Roche Percée localities are virtually identical to homologous teeth in B. pilodontus and Bessoecetor cf. B. pilodontus, although slightly longer and narrower.

To distinguish B. pilodontus from Bessoecetor cf. B. pilodontus, Secord (2008) cited the slightly smaller size and somewhat narrower molars of Bessoecetor cf. B. pilodontus as potential taxonomically significant differences, but wrote that these could be, and more likely were, examples of intraspecific variation. I favor the latter of these opinions and identify the referred specimens from the Roche Percée localities as belonging to B. pilodontus. This identification extends the known geographic range of this taxon from the type locality in northwestern Wyoming to southeastern Saskatchewan.

BESSOECETOR KRAUSEI new species

Figure 12.1-12.6; Table 14

Diagnosis.—Differs from other species of Bessoecetor in being much smaller (length of the m1 of B. krausei approximately 20% shorter than m1 of B. thomsoni and B. septentrionalis), and in being less robustly constructed in all known parts. Differs further from B. thomsoni and B. septentrionalis in having the trigonid of the lower first molar narrower than the talonid.

Description.—Dentary and lower dentition, Dentary: The elongate mandibular ramus is shallow, slender (even more so than that in other species of Bessoecetor), and bears two mental foramina. The smaller of the two mental foramina opens ventral to the p2 and its subcircular aperture faces anteroventrally, while the larger foramen opens beneath the m1, its aperture also facing anteroventrally but being more ovate. The symphyseal surface extends posteriorly to the level of the anterior root of p2; a sharp crest borders the superior margin of the symphyseal surface anteriorly but quickly fades away posteriorly. As in all other species of Bessoecetor, the masseteric fossa is deeply excavated, while the surface of the temporalis fossa appears to have been flat and terminates anteriorly at a bony protuberance.

Lower incisors: The precise number of lower incisors in B. krausei is uncertain. The only preserved incisor crown in the holotype (UALVP 9300) is identified here as i1; the placement of this incisor at the anteriormost extent of the dentary makes it certain that no other tooth was anterior to it. This tooth is strongly procumbent and projects nearly horizontally from the dentary. The spatulate crown is anteroposteriorly compressed and heavily worn across the apical margin. The concave occlusal surface is bordered laterally and medially by sharp crests, with only the lateral crest becoming increasingly pronounced towards the base of the crown. Between i1 and the alveolus for the lower canine, I tentatively identify two alveoli. The more posteriorly positioned alveolus, lying immediately anterior to the canine alveolus, is the better defined of these two, with most of the walls of the alveolus preserved and the incomplete aperture being subovate in outline. The other, more tentatively identified alveolus is wedged between the i1 and the more posterior alveolus; the walls of this alveolus are almost all broken and missing, with a partition of bone not present between this alveolus and that of i1. I provisionally interpret these two alveoli as housing i2 and i3.

Lower canine: The lower canine alveolus is shallow and directed anterodorsally-posteroventrally; the aperture is anteroposteriorly elongate. The alveolus for p1 is immediately posterior to the alveolus of the lower canine.

p1: The alveolus for p1 is shallow and much smaller than that for the lower canine, but is similarly oriented in the horizontal ramus. The aperture is subovate in outline.

p2: The trenchant crown of p2 consists primarily of a tall, laterally compressed protoconid that is slightly recurved and a short talonid heel that bears a single, small cusp. Two crests descend from the apex of the protoconid: the more pronounced of the two crests arcs anterolingually down the cusp then turns posteriorly as a short anterolingual cingulid, while the second, longer crest extends directly posteriorly to meet the small talonid cusp. Short cingulids are developed along the posterolingual and posterolabial corners of the crown.

p3: The p3 is known only from its alveoli. The anterior alveolar aperture is subcircular, while the posterior alveolar aperture is more ovate and slightly larger. Both alveoli are shallow and directed vertically.

p4: The crown of p4 of B. krausei is unknown, but its alveoli are preserved in the holotype (UALVP 9300). These alveoli are similar in morphology to those of p3 but are slightly larger, indicating that the crown of this tooth was probably larger than that of p3.

m1: The m1 trigonid is taller than the talonid and slightly narrower, as in B. pilodontus (Secord, 2008). The medially positioned paraconid is anteroposteriorly compressed, slightly anteriorly projecting, and lower than the other trigonid cusps; the paracristid extends labially from the paraconid apex to a shallow notch between the paraconid and protoconid before turning abruptly posteriorly to ascend the protoconid. The tall, slender protoconid and metaconid are subequal in height and size; in cross section, these cusps are subtriangular, with flattened internal walls. Extending between the acute apices of these cusps is a deep, V-shaped protocristid. The hypoconid and entoconid are subequal in both height and size, while the hypoconulid is smaller, anteroposteriorly compressed, and more posteriorly positioned than these other talonid cusps. The low cristid obliqua contacts the postvallid surface ventral to the protocristid notch and continues a short distance dorsally on this surface; the broadly notched entocristid encloses the wide talonid basin lingually. The shelf-like precingulid is developed across the anterior surface of the trigonid.

m2: The m2 is very much like the m1 but with the following differences: m2 is slightly larger, with the trigonid anteroposteriorly compressed but slightly wider than the talonid. The paraconid is closely appressed to the anterolabial base of the metaconid and projects less anteriorly than in m1; the paracristid is also longer and more deeply notched. The protoconid and metaconid are further apart, and the protocristid notch is deeper and wider; the internal walls of these cusps are slightly broader than in m1. The hypoconulid is displaced more lingually and positioned closer to the entoconid; the cristid obliqua is even lower than on m1 and contacts the postvallid surface ventral and slightly labial to the protocristid notch. The shelf-like precingulid fits snugly against the labial surface of the hypoconulid of m1 and the two structures form an elongate shearing crest.

m3: The m3 is the longest tooth in the molar series, owing in large part to the posteriorly expanded talonid and finger-like hypoconulid. The trigonid is wider than the talonid and anteroposteriorly compressed, even more so than in m2, with the paraconid closely appressed to the base of the metaconid and only slightly projecting anteriorly. The morphology of the protoconid and metaconid is similar to that in m2. The notch developed along the paracristid is deeper than it is in the other lower molars. The subconical hypoconulid is slightly taller than the hypoconid and entoconid.

Etymology.—Named in honor of David W. Krause for his tremendous contributions to mammalian paleontology of western Canada.

Holotype.—UALVP 9300, an incomplete right dentary containing i1, p2, m1-3, and alveoli for ?i2-3, p3-4 (Figs. 12.1-12.3). Roche Percée local fauna, Ravenscrag Formation of Saskatchewan, early late Paleocene [late Tiffanian, Ti4 (see Krause, 1978; Fox, 1990) Plesiadapis churchilli/P. simonsi Lineage Zone of Lofgren et al., 2004].

Other material examined.—From Roche Percée: UALVP 10908, m3.

From DW-2: UALVP 47817, m1.

Age and occurrence.—Early late Paleocene (early middle Tiffanian, Ti3, Plesiadapis rex/P. churchilli Lineage Zone to late middle Tiffanian, Ti4, P. churchilli/P. simonsi Lineage Zone of Lofgren et al., 2004) of the northern part of the Western Interior of North America.

Discussion.—Aside from its much smaller size, little distinguishes the dentition of Bessoecetor krausei from that of B. thomsoni or B. septentrionalis. The m1 trigonid is slightly narrower than the talonid (as in B. pilodontus), the trigonid cusps are slightly less swollen, and the m3 paraconid is less separated from the anterolingual base of the metaconid. Also, unlike that in B. septentrionalis (Scott, 2008), the ultimate incisor is large and directly anterior, rather than laterally positioned, to the lower canine (inferred from the position and dimensions of the alveolus in UALVP 9300). An isolated lower m1 from early middle Tiffanian (Ti3) DW-2 locality in central Alberta is also assigned to this new species and extends the temporal and geographic ranges of this taxon.

In addition to documenting a previously unknown species of Bessoecetor, specimens from Saskatchewan preserve for the first time details of the anteriormost, lower dentition of the genus. Unfortunately, a precise dental count cannot be made owing to damage to the horizontal ramus lateral to the posterior incisor(s); however, there is at least some evidence that there are three lower incisors (see description above). In this context, the dental formula of B. krausei is reconstructed as 3.1.4.3, in common with many primitive eutherians and resembling that of other pantolestids [e.g., Palaeosinopa (see Rose and von Koenigswald, 2005)].

Genus PALAEOSINOPA Matthew, 1901

Type species.—Palaeosinopa veterrima Matthew, 1901.

Included species.—Palaeosinopa didelphoides (Cope, 1881a); P. osborni (Lemoine, 1891); P. lutreola Matthew, 1918; P. incerta Bown and Schankler, 1982; P. dorri Gingerich, 1980; P. russelli Smith, 1997; P. nunavutensis Eberle and McKenna, 2002.

PALAEOSINOPA SP.

Figure 13.1-13.22; Table 15-16

Material examined.—UALVP 9721, 9724-9725, 51051-51054, 51760-51763 (total: 11), P4; UALVP 51055-51063, 51577-51590 (total: 23), M1; UALVP 10856, 51064-51079, 51575-51576, 51591 (total: 20), M2; UALVP 9072, 51080-51087 (total: 9), M3; UALVP 34129, incomplete left dentary containing p2-4, and m1-3; UALVP 51088, incomplete right dentary containing p2, p4, and m1-3; UALVP 51089, incomplete left dentary containing p4 and m1-3; UALVP 51090, incomplete right dentary containing p4 and m2-3; UALVP 51091, incomplete left dentary containing p4 and m2-3; UALVP 51092-51094 (total:3), incomplete right dentary containing m2-3; UALVP 10854, 51095-51096 (total:3), incomplete left dentary containing m2-3; UALVP 10855, 51097, incomplete right dentary containing m2; UALVP 51098, incomplete right dentary containing m3; UALVP 51099-51100, incomplete left dentary containing m3; UALVP 51101, incomplete, edentulous right dentary containing alveoli for lower canine, p1-4, and m1; UALVP 51102, incomplete, edentulous left dentary containing alveoli for p2-4 and m1-3; UALVP 10900, 51103-51107 (total:6), p2; UALVP 51108-51109, p3; UALVP 51110-51118 (total:9), p4; UALVP 51119-51127 (total:9), m1; UALVP 51128-51142 (total:15), m2; UALVP 51143-51155 (total:13), m3.

Age and occurrence.—Palaeosinopa is known from the early late Paleocene (late early Tiffanian, Ti2, Plesiadapis anceps/P. rex Lineage Zone of Lofgren et al., 2004) to the late early Eocene (late Bridgerian, Br3, Twinbuttean Subage faunas of Robinson et al., 2004) of the Western Interior of North America.

Description.—Upper dentition, P4: The swollen crown of P4 is dominated by a tall, inflated paracone and shorter, smaller protocone. A small parastylar cuspule is developed directly anterior to the paracone on the paracingulum and only a weak preparacrista extends between the two cusps. Posteriorly, a high, curving postparacrista descends from the apex of the paracone to the posterolabial corner of the crown; in one specimen a large swelling (?metacone) occurs midway along this crest. The ectocingulum is strongly developed along the posterior half of the labial margin of the crown. The preprotocrista is virtually undeveloped, while the postprotocrista joins with the metacingulum and is truncated labially by the postparacrista. A weak, short postcingulum and even shorter precingulum are developed in some specimens.

M1: The referred M1s are virtually identical to the M1 of P. dorri (Dorr, 1977; Gingerich, 1980) differing, however, in being smaller, in having a shallower (or completely absent) ectoflexus, and a slightly more posterolingually positioned hypocone (although this cusp is still less lingual than that in Paleotomus Van Valen, 1967).

M2: As in other species of Palaeosinopa (Matthew, 1901; Bown and Schankler, 1982), the M2 very closely resembles the M1 but differs as follows: the crown is wider, both stylar lobes are more expanded, the parastylar lobe narrows anteriorly to a short hook, the parastyle is better developed, the protocone is more anteroposteriorly compressed, the precingulum is longer, the postcingulum is more lingually expanded, and the hypocone is more robust.

M3: The parastylar lobe in M3 is much more expanded labially than that in either M1 or M2, while the metastylar lobe is virtually undeveloped. The paracone is roughly twice the size and height of the metacone, and the well-developed centrocrista extending between these cusps is shallowly notched. The preparacrista extends anterolabially from the paraconal apex to the anterolabial corner of the crown, while, posteriorly, the postmetacrista is undeveloped. A parastyle is not present on any of the specimens at hand. The protocone is slightly lower than the paracone and even more anteroposteriorly compressed than in M2. The paraconule is not a distinct cusp but a large swelling on the elongate crest formed by confluence of the preprotocrista and the preparaconule crista; this crest continues to the anterolabial corner of the crown. The metaconule is more distinct than the paraconule and positioned at the lingual base of the metacone. The postprotocrista is longer than the preprotocrista and terminates at the lingual base of the metaconule. The sharp premetaconule crista descends anterolabially from the metaconule and joins with a crest that extends to the apex of the metacone; the postmetaconule crista fades posterior to the metacone. The postcingulum is not posterolingually expanded as it is in M1 or M2, but forms only a narrow shelf along the lingual half of the posterior margin; the precingulum is similar to the postcingulum and the two cingula can join lingually.

Dentary and lower dentition, Dentary: The dentary of Palaeosinopa sp. is known from a large number of fragmentary specimens from the Roche Percée localities and is virtually identical to that described for other species of Palaeosinopa (Matthew, 1901, 1918; Rose and von Koenigswald, 2005). The body of the horizontal ramus is robustly constructed and, as described for Palaeosinopa sp. from the Eocene of Wyoming (see Rose and von Koenigswald, 2005), has a shallow groove along the lateral surface below the molars and near the ventral margin. As in all other species of Palaeosinopa, the symphyseal surface ends beneath the p2 and a thick crest delimits the superior margin of the surface anteriorly. UALVP 51088 preserves parts of the coronoid and angular processes, as well as the entire condyle, which was recently thoroughly described for Palaeosinopa sp. from Wyoming (see Rose and von Koenigswald, 2005). Similar to the dentary in this other form, the angular process of Palaeosinopa sp. from Saskatchewan is short, hook-like, and bears a robust, shelf-like crest ventromedially, the coronoid process has a long, steep anterior margin that borders the masseteric fossa, and the subcyclindrical condyle is medially sloping and wider than long (extending further laterally than medially). The subcircular aperture of the mandibular foramen opens posteriorly and medially, and is positioned anteroventral to the condylar process.

p1: The aperture of the p1 alveolus is subovate (i.e., longer than wide) and the alveolus is canted slightly anteroventrally-posterodorsally. Based on its proximity to the canine alveolus, a diastema was undeveloped between the p1 and the lower canine.

p2: p2 is two-rooted and the crown is dominated by a tall, bilaterally compressed protoconid that is apically acute and slightly recurved. Two crests originate from the apex of the protoconid: a sharp anterolingually curving paracristid that bends posteriorly along the base of the protoconid as a short lingual cingulid, and a much lower, posteriorly directed crest that extends to the apex of the small, subconical hypoconid. A short and weakly developed crest curves anterolingually from the hypoconid and partially encloses a shallow talonid basin posteriorly and lingually.

p3: The p3 is larger and more robust than p2. The paracristid is less conspicuous than that on p2 and straighter (i.e., less lingually curving). At the position of the paraconid, on the anterolingual corner of the crown, the lingual cingulid widens to form a short, weak shelf, but no distinct cusp or cuspule is developed. The hypoconid is slightly larger than the hypoconid on p2, and the crest curling anterolingually from its apex is more distinct and more nearly encloses the talonid basin.

p4: The crown is wide and robust, and the paraconid although distinct is appressed closely to the protoconid. The paracristid descends almost directly anteriorly from the sharp, recurved protoconid apex into a deep notch between the protoconid and paraconid, then turns anterolingually to ascend the paraconid. A short crest descends posteriorly from the apex of the paraconid to the anterolingual base of the protoconid and encloses the small trigonid basin lingually. The hypoconid is swollen and connected to the postvallid surface by a high, blade-like cristid obliqua; an extension of this crest continues towards the apex of the protoconid in most specimens. Small cuspules can be developed adjacent to the hypoconid and in some specimens a well-developed cusp (?entoconid) is present on the posterolingual corner of the crown (e.g., UALVP 34129, 51111). The talonid basin is better developed than in the other premolars and in most specimens is completely enclosed by the crest extending lingually and anteriorly from the hypoconid to the posterolingual base of the protoconid.

m1: The crown of m1 is subrectangular in occlusal outline, with the trigonid elevated above and slightly narrower than the talonid. The paraconid is much lower than the other trigonid cusps and more anteroposteriorly compressed; the apex of this cusp can be on the medial axis of the crown or slightly lingual to the axis. The paracristid extends anteriorly from the apex of the protoconid to a shallow notch between the protoconid and paraconid; from this point, the crest turns lingually to join the paraconid. A short extension of the paracristid continues lingually from the paraconid apex and fades low on the anterolingual corner of the trigonid. A small accessory cusp can be developed on the paracristid just labial to the paraconid. The protoconid and metaconid are subconical with sharp apices and swollen internal walls; these cusps are subequal in height, but the base of the metaconid is slightly wider than that of the protoconid. The protocristid is well developed on both of these cusps, and the protocristid notch is narrower than in m2 and m3. The hypoconid and slightly smaller entoconid are subequal in height; the internal walls of these cusps are flattened and form the lateral and medial sides of a deep, broad talonid basin. The hypoconulid is anteroposteriorly compressed and positioned slightly posterior to the other talonid cusps. The cristid obliqua meets the postvallid surface ventral and slightly labial to the protocristid notch, while the entocristid descends directly anteriorly from the apex of the entoconid but terminates just before reaching the postvallid surface. The strong, shelf-like precingulid is developed ventral to the paraconid and paracristid.

m2: The m2 resembles m1, but the trigonid is wider than the talonid and the trigonid cusps are even more swollen. The paraconid is positioned directly on the midline axis of the crown. The paracristid is longer and the notch developed between the protoconid and paraconid is deeper; labial to the paraconid an accessory cusp is sometimes present, but is smaller and less swollen than that on m1; the extension of the paracristid lingual to the additional cusp is more robust than it is on m1 and shelf-like. The hypoconid is slightly larger than the entoconid, while the smaller hypoconulid is anteroposteriorly compressed and slightly more lingual than in m1. The entocristid descends directly anteriorly from the apex of the entoconid but terminates just before reaching the postvallid surface, leaving the talonid open lingually.

m3: The trigonid of m3 is virtually identical to that seen in m2, yet with the paraconid positioned just lingual to the anteroposterior axis of the crown and a longer and more deeply notched paracristid. Also, the accessory cusp labial to the paraconid, seen on m1 and m2, is undeveloped on m3 and only a short extension of the paracristid, not connected to the apex of the paraconid, is present low on the lingual half of the anterior surface. The talonid is longer and narrower than the trigonid. The subconical hypoconulid is slightly taller than the other talonid cusps, but subequal in size to the entoconid (both slightly smaller than the hypoconid); the entoconid and hypoconulid are more closely appressed to one another than in the other molars. As in m1 and m2, the entocristid does not reach the postvallid surface and the talonid basin is left open lingually.

Discussion.—Specimens of the semi-aquatic pantolestid Palaeosinopa are relatively common from latest Paleocene and earliest Eocene (Clarkforkian through Bridgerian) faunas of North America and Europe (e.g., Dorr, 1977; Bown and Schankler, 1982; Eberle and McKenna, 2002; Rose and von Koenigswald, 2005); however, reports of the pantolestid from early late Paleocene faunas remain relatively sparse (Secord, 2008). In fact, only one species of the genus (P. simpsoni) and only a small handful of specimens are known from the Tiffanian of North America (Dorr, 1977; Gingerich, 1980; Secord, 2008). The sample of Palaeosinopa sp. from the Roche Percée local fauna represents the single largest Tiffanian collection of specimens pertaining to the genus yet known; additionally, the referred specimens from Saskatchewan can be distinguished from those of P. simpsoni by their smaller size and more robust construction. It seems likely that the specimens referred here represent a new, undescribed species of Palaeosinopa; however, the formal naming and presentation of a diagnosis are deferred until more detailed comparisons can be made with specimens of younger species of the genus.

Order CARNIVORA Bowdich, 1821

Family VIVERRAVIDAE Wortman and Matthew, 1899

Genus DIDYMICTIS Cope, 1875

Limnocyon MARSH, 1872, p. 126-127 (in part).
Didymictis COPE, 1875, p. 5.

Type species.—Limnocyon protenus Cope, 1874.

Included species.—Didymictis leptomylus Cope, 1880; D. altidens Cope, 1880; D. proteus Simpson, 1937e; D. dellensis Dorr, 1952; D. vancleveae Robinson, 1966.

DIDYMICTIS DELLENSIS Dorr, 1952

Figure 14, 15.1-15.6

Didymictis proteus SIMPSON, 1937e: POLLY, 1997, p. 34 (in part).

Didymictis dellensis DORR, 1952, p. 85.
Protictis dellensis GINGERICH and WINKLER, 1985, p. 117.

Holotype.—UM 27232, incomplete right dentary with c, p1, p3-4, m1-2, and alveoli for p2 (Dorr, 1952, p. 85). Dell Creek Quarry, Hoback Formation of Wyoming, early late Paleocene (early late Tiffanian, Ti5, Plesiadapis simonsi/P. gingerichi Lineage Zone of Lofgren et al., 2004).

Material examined.—UALVP 8779, 51555, P4; UALVP 8781, m1.

Age and occurrence.—Late Paleocene (early middle Tiffanian, Ti3, Plesiadapis rex/P. churchilli Lineage Zone to the latest Tiffanian, Ti6, P. gingerichi/Rodentia Interval Subzone of the P. gingerichi/P. cookei Lineage Zone of Lofgren et al., 2004) of the Western Interior of North America.

Description.—Upper dentition, P4: The P4 of D. dellensis is subtriangular in occlusal outline, with a deep embayment between the parastyle and protocone. The enlarged and centrally positioned paracone dominates the crown; the cusp is tall, nearly conical, and leans posteriorly. The parastyle is robust but low and conical. The preparacrista and parastylar crest are prominent, but are abruptly interrupted by a notch between the paracone and parastyle, and are not continuous. The protocone is larger and slightly taller than the parastyle; it is positioned anterolingual to the paracone and opposite the parastyle. A distinct crest descends from the protoconal apex into the notch between the protocone and paracone, and continues briefly onto the anterolingual surface of the paracone. From the apex of the paracone, a strong postparacrista descends posteriorly and slightly lingually into a deep carnassial notch (i.e., an inverted keyhole-like notch; Matthew, 1909; MacIntyre, 1966), separating the paracone from the metastylar blade. This blade is short and massive, and is nearly in line with the paracone. In labial and lingual views, the metastylar blade is subarcuate. A small but distinct swelling at the posterior margin of the metastylar blade could represent a metastyle; however, a clear separation between this swelling and the metacone is not evident. A faint anterior cingulum extends between the apices of the parastyle and protocone; wear facets damage the cingulum near the base of the protocone.

Cingula are well developed on the labial and posterior margin of the crown, with the posterior cingulum being slightly more prominent than the ectocingulum. Near the posterolingual base of the protocone, a short ridge of enamel extends towards the protoconal apex from the posterior cingulum. A small part of the anterior surface of the parastyle is broken and missing, preventing precise measurements; however, the remaining crown is approximately 8.5 mm in length and 7.0 mm in width.

Lower dentition, m1: An isolated trigonid of m1 (UALVP 8781) is referred here to D. dellensis. The trigonid is tall and subtriangular in occlusal outline. The cusps are acute and subtriangular in cross section, with the internal walls flattened; the protoconid is the tallest, while the paraconid is only slightly taller than the metaconid. The paraconid is slightly displaced internally from the lingual margin. Deep carnassial notches are developed in the paracristid and protocristid. On the postvallid surface, a deep wear facet extends ventrally and slightly labially from the base of the protocristid notch. At the base of the postvallid surface, there is a short but conspicuous remnant of the cristid obliqua. A strong, shelf-like precingulid is developed on the anterolabial margin of the trigonid.

Discussion.—Despite being relatively well studied, the systematics of Didymictis dellensis have remained somewhat uncertain. Dorr (1952) initially described D. dellensis based on specimens from the early late Tiffanian (Ti5) Dell Creek Quarry in western Wyoming. Later, Gingerich and Winkler (1985), referring additional specimens from Tiffanian localities in Wyoming to this species, cited features of the upper and lower molars that they considered uncharacteristic of Didymictis and transferred Dorr’s species to Protictis. More recently, based on a stratocladistic analysis, Polly (1997) considered “P.” dellensis to be conspecific with D. proteus, suggesting that the two forms are part of a single anagenetic evolutionary lineage ranging from the early late Paleocene (middle Tiffanian, Ti3) to the earliest Eocene (earliest Wasatchian, Wa0).

Although sharing some general similarities with Protictis, “P.” dellensis is distinct and best separated from Protictis by its lower paraconid on p4, which is clearly separated from the protoconid, the notable absence of a carnassial notch between the paraconid and protoconid on p4, and the relatively taller trigonid and wider talonid on m2 (Scott, 2008). Additionally, while agreeing with Polly (1997) that "P." dellensis should be re-assigned to Didymictis, the synonymy of this species with D. proteus is not followed here. In D. proteus [UM 68432, illustrated in Polly (1997, p. 35, fig. 13)], the first posterior accessory cusp on p4 is considerably larger than in D. dellensis, the molar crowns are lower, the trigonid cusps of the molars are lower and more robust, and the talonid on m2 is wider. For these reasons, I regard D. dellensis as a distinct and valid taxon.

In an important study examining patterns of variation in the dentition of the extant non-sexually dimorphic red fox (Vulpes vulpes Linnaeus, 1758), Gingerich and Winkler (1979) observed that the upper and lower first molars have a range of variation in linear dimensions of approximately 0.2 units on a natural logarithm scale. Gingerich and Winkler (1979), and later Pengilly (1984), suggested that this value of 0.2 units could be applied as a standard for the range of variation in a non-sexually dimorphic carnivoran species. Hence, for these authors, if the range of variation in linear dimensions of the upper or lower first molars of two carnivoran specimens is below 0.2 units on a natural logarithm scale, then the specimens are likely members of a sexually nondimorphic species; alternatively, if the range of variation is beyond 0.2 units, the specimens are either members of a single, sexually dimorphic species or represent two separate species.

Gingerich and Winkler (1985), applying these principles to samples of Paleocene viverravids from Wyoming and Montana, demonstrated that the range of variation in the linear dimension of lower first molars identified as Didymictis dellensis was just beyond 0.2 units on a natural logarithm scale, and interpreted this variation as evidence that D. dellensis was a sexually dimorphic species. Consequently, UM 27232, the holotype of D. dellensis, and YPM-PU 13937, an incomplete dentary from the Princeton Quarry in northern Wyoming, were interpreted as male and female, respectively, of the same species. Within the Roche Percée local fauna, both "male" and "female" morphs are present;

however, combining these two forms into a single, sexually dimorphic species conceals several potentially important taxonomic differences.

Besides the considerable differences in size (e.g., length of m1, UM 27232 = 8.5 mm, and length of m1, YPM-PU 13937 = 7.5 mm) (also see Figure 14), YPM-PU 13937 differs from UM 27232 as follows: two mental foramen are present in YPM-PU 13937, in contrast to four in UM 27232, the p4 paraconid is directly anterior to the protoconid, not displaced labially, and the first posterior accessory cusp is shorter. Furthermore, the m1 talonid is narrower and less "squarish" in occlusal outline on YPM-PU 13937 than that on UM 27232, and the m2 entoconid is more reduced, and the labial cingulid is shorter and does not extend posteriorly beyond the hypoflexid. Therefore, in an effort to take these differences into account, specimens of the large morph are referred here to D. dellensis, whereas specimens of the small morph are referred to Didymictis cf. D. dellensis (see description and discussion of Didymictis cf. D. dellensis below).

The referred m1 trigonid most closely resembles that in the holotype of D. dellensis (UM 27232), and the referred P4 can be confidently placed in this taxon based on its overall size and in having a parastyle that is smaller than the protocone, as seen in YPM-PU 14319. The occurrence of D. dellensis at the Roche Percée localities is the first known of this taxon in Saskatchewan.

DIDYMICTIS CF. D. DELLENSIS Dorr, 1952

Figure 14, 15.7-15.12; Table 17

Material examined.—UALVP 8774, incomplete left dentary containing p2, p4, m1, and alveoli for p1, p3, m2; UALVP 10918, 10920, 51556 m2.

Description.—Dentary and lower dentition, Dentary: UALVP 8774 is a fragmentary left dentary that includes only minor parts of the coronoid and angular processes. Because of the poor condition of the specimen, the horizontal ramus is largely uninformative; however, two mental foramen are clearly present, one ventral the p1 and the other beneath the posterior alveolus of p3. The coronoid process is steeply angled relative to the horizontal ramus; the lateral margin of the anterior portion of the process forms a ridge that borders the deep masseteric fossa, while the surface of the temporalis fossa is flat. The angular process, forming the ventral border of the masseteric fossa, is slender and likely would have been short.

Lower canine: The lower canine is missing in UALVP 8774, but the damage to the medial margin of the dentary reveals that the canine alveolus extends posteriorly to beneath p3.

p1: The alveolar aperture of p1 in UALVP 8774 is teardrop-shaped in occlusal outline, narrowing anteriorly. The alveolus is directed anteroventrally, rather than directly vertically.

p2: The elongate crown of p2 is slender and dominated by a tall, acute, and slightly recurved protoconid. A faint paracristid descends anteroventrally from the protoconid apex towards the anterior base of the crown. A single, reduced talonid cusp is developed at the posteriormost extremity of the crown, and a small, worn cristid extends anteriorly from its apex to the posterior base of the protoconid. No cingulids are present.

p3: The p3 alveoli are vertical and shallow; the apertures are subovate and labiolingually narrow, with the posterior alveolus larger than the anterior alveolus.

p4: The crown is dominated by a tall, vertically oriented, trenchant protoconid and two well-developed, massive posterior accessory cusps. The subconical paraconid, although stout, is low and closely appressed to the base of the protoconid; the apex of this cusp leans slightly lingually. A weak paracristid extends between the apices of the paraconid and protoconid but, as in other species of Didymictis (Dorr, 1952), no carnassial notch is developed between them. The first posterior accessory cusp is conical and developed high on the posterolabial shoulder of the protoconid, whereas the second posterior accessory is more blade-like and positioned posterolingual to the first posterior accessory cusp. Carnassial notches are well developed between the protoconid and the first posterior accessory cusp, and between the first and second posterior accessory cusps. A broad posterolabial cingulid extends from the apex of the second posterior accessory cusp to beneath the first posterior accessory cusp and, combined with the inflated base of the second posterior accessory cusp, considerably expands the width of the crown posteriorly.

m1: The m1 bears a tall, open trigonid that is wider than the talonid, and generally triangular in occlusal outline. The trigonid cusps are subtriangular in cross section and their apices are pointed; the protoconid is the tallest cusp, and it is slightly recurved posteriorly. The paraconid, inset from the lingual margin, is only slightly taller than the metaconid. Well-developed carnassial notches are present in the paracristid and protocristid. The talonid is short and dominated by a large, robust hypoconid; a strong cristid obliqua descends anterolingually from the apex of the hypoconid and contacts the base of the postvallid surface ventral to the protocristid notch. The hypoconulid is well developed and separated from the hypoconid by a small carnassial notch. The entoconid and entocristid are reduced. A short but distinct cingulid is developed on the anterolabial margin of the talonid and faintly continues labially around the base of the protoconid. A deep wear facet is developed on the hypoflexid; the presence of a cingulid in this region cannot be determined.

m2: The m2 of Didymictis cf. D. dellensis is known from its alveoli in UALVP 8774 and several isolated teeth (UALVP 10918, 10920, and 51556). The crown is anteroposteriorly elongate and teardrop-shaped in occlusal outline, narrowing towards the hypoconulid. The trigonid is low and wider than the talonid. The cusps of the trigonid are low and inflated; the protoconid is the tallest, and the metaconid is taller than the paraconid. The paracristid is anteriorly convex and a shallow, narrow slit can be developed in the deepest part of this crest; a similar slit can also be present in the protocristid. The basin of the talonid is shallow and slopes posterolabially-anterolingually. The hypoconulid, positioned on the posterior extremity of the talonid, is relatively tall and pointed; it is separated from the low, massive hypoconid by a shallow notch. A prominent cristid obliqua extends from the apex of the hypoconid to the base of the postvallid surface, ventral to the protocristid slit, and continues a short distance onto the post-vallid. The entoconid is reduced, relative to the other talonid cusps, and the entocristid is short. The anterolabial cingulid is robust and continuous around the labial base of the protoconid and across the hypoflexid; however, unlike that on the m2 of D. dellensis, the cingulid does not extend around the base of the hypoconid and there is no evidence of a posterolabial cingulid (Gingerich and Winkler, 1985).

Discussion.—The referred specimens are nearly identical to corresponding teeth in PU 13937, collected from the early late Tiffanian (Ti5) Princeton Quarry in northern Wyoming, differing only in their slightly smaller size. Gingerich and Winkler (1985) interpreted YPM-PU 13937 to represent a “female” morph of Didymictis dellensis but differences between YPM-PU 13937 and UM 27232, the holotype and “male” morph of D. dellensis, suggest that these specimens likely represent separate species (see discussion above). The formal naming and diagnosis of this new species, however, are deferred until a larger collection of this previously undescribed taxon can be made.

Genus PROTICTIS Matthew, 1937

Didymictis COPE, 1882a, p. 464 (in part); COPE, 1884a, p. 306 (in part); MATTHEW, 1897, p. 287: SIMPSON, 1935a, p. 238: SIMPSON, 1937d, p. 209.
Viverravus MATTHEW, 1899, p. 29 (in part): WORTMAN, 1901, p. 145 (in part).
Didymictis (Protictis) MATTHEW, 1937, p. 101.
Protictis MATTHEW, 1937, p. 101: MACINTYRE, 1966, p. 148 (in part): GINGERICH AND WINKLER, 1985, p. 103 (in part).

Type species.—Didymictis haydenianus Simpson, 1935a

Included species.—Protictis agastor Gingerich and Winkler, 1985; P. paralus Holtzman, 1978; P. simpsoni Meehan and Wilson, 2002; P. minor Meehan and Wilson, 2002.

PROTICTIS CF. P. PARALUS Holtzman, 1978

Figure 15.13-15.18; Table 18

Material examined.—UALVP 8867, 9067, 51557, p4.

Age and occurrence.—Protictis paralus is known from the late Paleocene (early middle Tiffanian, Ti3, Plesiadapis rex/P. churchilli Lineage Zone to the late middle Tiffanian, Ti4, P. churchilli/P. simonsi Lineage Zone of Lofgren et al., 2004) of the Western Interior of North America.

Description.—Lower dentition, p4: The highly sectorial p4 of Protictis cf. P. paralus is labiolingually compressed and bears sharp cusps and high, trenchant crests. The crown is somewhat C-shaped in occlusal outline, with the labial margin convex and the lingual margin concave. The paraconid is subconical, relatively tall, approximately one-third the height of the protoconid, and displaced from the protoconid. A prominent paracristid extends between the apices of the paraconid and protoconid, but is interrupted at its deepest part by a carnassial notch, similar to that on the p4 of Protictis and Bryanictis. The protoconid is subconical and recurved. A well-developed crest descends posteriorly from its apex into a deep carnassial notch that separates the protoconid and first posterior accessory cusp. The first posterior accessory cusp is positioned high on the posterolabial shoulder of the protoconid and can be conical (e.g., UALVP 8867 and 9067) to more blade-like (e.g., UALVP 51557). The second posterior accessory cusp, developed posterolingual to the first posterior accessory cusp, is tall and blade-like. A small, narrow slit can be present in the crest between the first and second posterior accessory cusps. A strong posterolabial cingulid extends from the apex of the second posterior accessory cusp to beneath the first posterior accessory cusp, and a short, faint posterolingual cingulid is developed beneath the weak basin.

Discussion.—The referred specimens most closely resemble the p4 of the middle Tiffanian (Ti3-Ti4) viverravid carnivoran Protictis paralus: the cusps are laterally compressed, the paraconid is tall, the paracristid is high and blade-like, and the labial cingulid is well developed. Specimens of Protictis cf. P. paralus from Saskatchewan differ, however, from those of P. paralus in having a labially convex crown and a slightly higher paracristid, and in this regard are similar to the p4 of Bryanictis described from the middle to late Torrejonian (To2 and To3) (Simpson, 1937d; MacIntyre, 1966; Meehan and Wilson, 2002). Holtzman

(1978) previously recognized the similarities between P. paralus and B. microlestes (then the only known species of Bryanictis), and suggested that P. paralus is generally characterized by a greater shearing capacity, exemplified on the p4 by a more trenchant posterior heel. In Protictis cf. P. paralus, the posterior heel of p4 is trenchant but variations in the first posterior accessory cusp (i.e., conical to more blade-like), and in the development of a carnassial notch between the first and second posterior accessory cusps emphasize potentially important taxonomic differences.

Genus RAPHICTIS Gingerich and Winkler, 1985

Raphictis GINGERICH and WINKLER, 1985, p. 122.

Type species.—Raphictis gausion Gingerich and Winkler, 1985.

Included species.—Raphictis "iota" Scott, 2008; R. machaera, new species; R. nanoptexis, new species.

RAPHICTIS "IOTA" Scott, 2008

Figure 14, 16.1-16.9; Table 19

Raphictis cf. R. gausion FOX, 1990, p. 66.
Raphictis "iota" SCOTT, 2008, p. 742.

Material examined.—UALVP 51558, P4; UALVP 9062, incomplete right dentary with p4 and m1 and alveoli for p3; UALVP 9063, 51559, m1.

Age and occurrence.—Early late Paleocene (early middle Tiffanian, Ti3, Plesiadapis rex/P. churchilli Lineage Zone to the late middle Tiffanian, Ti4, P. churchilli/P. simonsi Lineage Zone of Lofgren et al., 2004) of the northern part of the Western Interior of North America.

Description.—Because the teeth of this viverravid carnivoran have already been thoroughly described (see Scott, 2008), only a brief description is provided here. The P4 is subtriangular in outline, with the enlarged, centrally placed paracone dominating the crown. The parastyle is sharp and positioned anterior to the paracone, while the slightly larger protocone is positioned anterolingual to the paracone and just posterior to the level of the parastyle. The metastylar blade is tall and oriented oblique to the paracone; a deep carnassial slit separates these two cusps. Cingula are well developed around most of the crown.

The small, damaged fragment of the dentary is slender and deep, and a partial depression, likely for the posterior mental foramen, is preserved on the lateral surface beneath the p3. The p4 is similar to that of R. gausion: the crown is anteroposteriorly elongate and dominated by a large pointed protoconid, a small paraconid is positioned directly anterior to the protoconid and a carnassial notch is not developed between these cusps, the first and second posterior accessory cusps are well developed, and a shallow carnassial slit is present between the protoconid and the first posterior accessory cusp. The m1 trigonid is high and consists principally of a tall protoconid, a smaller metaconid, and an even lower paraconid; carnassial notches are developed in the deepest parts of the paracristid and protocristid. The talonid basin is shallow and steeply inclined posterolabially-anterolingually. The hypoconid is the largest talonid cusp, followed by the hypoconulid, while the entoconid is only a small swelling on the posterior rim of the talonid.

Discussion.—In his unpublished doctoral dissertation, Scott (2008) described a new species of Raphictis, R. “iota”, from the middle Tiffanian (Ti3 and Ti4) of central Alberta. As reported by Scott (2008), this new species differs from R. gausion (then the only other known species within the genus, but see descriptions of R. nanoptexis n. sp. and R. machaera n. sp.), in being smaller, in having a relatively larger paraconid and first posterior accessory cusp on p4, and a more posteriorly positioned paraconid and shorter talonid on m1. The referred specimens of R. “iota” from the Roche Percée local fauna document the first occurrence of this new carnivoran outside of Alberta. A more extensive treatment of this species will be presented elsewhere (Rankin and Scott, in prep.), in context with other middle Tiffanian viverravid carnivorans from western Canada.

RAPHICTIS MACHAERA new species

Figure 14, 16.10-16.25; Table 20-21

Raphictis, new species 2 FOX, 1990, p. 66.

Diagnosis.—Largest known species of Raphictis (length m1 approximately 30% larger than length m1, R. gausion). Differs additionally from all other species of Raphictis in having a shorter and more massive metastylar blade on P4, a less transverse M1 than in R. nanoptexis, with a more rounded metastylar lobe and a deeper ectoflexus, an anterobasal lobe and first and second posterior accessory cusps developed on p3, and in having cusps and crown that are considerably more inflated. It also differs from R. "iota" in having a shorter, more robust metastylar blade on P4 that is less oblique to the anteroposterior axis of the crown.

Description.—Upper dentition, P4: The crown is labiolingually compressed and subtriangular in occlusal outline, with a deep embayment anteriorly between the parastyle and protocone. The enlarged paracone is tall and leans strongly posteriorly. The parastyle is small, pointed, and positioned anteriorly to the paracone, but well separated from it by a V-shaped notch. The preparacrista is prominent and extends anterolabially from near the apex of the paracone into this notch, where it can meet the parastylar crest. As on the P4 of other species of Raphictis (see Scott, 2008; descriptions above), the protocone is positioned anterolingual to the paracone, and opposite and slightly posterior to the level of the parastyle; it is taller and larger than the parastyle, and slightly recurved. A V-shaped notch separates the paracone and protocone, but no crests extend into this notch. The postparacrista is sharp and descends posterolingually from the apex of the paracone into a deep, narrow carnassial slit. The metastylar blade is sharp and high; it is oriented oblique to the paracone and can be straight to weakly arcuate in labial and lingual views. A faint anterior cingulum extends between the apices of the parastyle and protocone. The pattern and development of the ectocingulum is variable but commonly it is prominent below the metastylar blade and weakly developed between the parastyle and paracone; the cingulum is usually discontinuous around the base of the paracone. The posterior cingulum is well developed and extends from the base of the protocone to the posterolingual margin of the crown.

M1: The crown is anteroposteriorly compressed and asymmetrically triangular in occlusal outline. The parastylar lobe is expanded anterolabially and narrows anteriorly into a hook; the development of a parastyle on this lobe is variable but this feature is never strongly developed. The metastylar lobe is expanded but is not as large as the parastylar lobe; as a result, the stylar shelf is broad anteriorly but narrows quickly posteriorly. The ectoflexus is deeper than on the M1 of R. nanoptexis. The ectocingulum is low although it rises around the anterolabial corner of the parastylar lobe. The tall paracone and metacone are sharp and share a common base; the metacone is approximately two-thirds the height of the paracone, and the two cusps are joined for slightly more than half of the total height of the metacone. The paracone is subconical and leans anteriorly; the labial slope of this cusp is steep. The preparacrista is poorly developed near the apex of the paracone but becomes increasingly robust near its base; from here, the elevated, blade-like crest continues labially and slightly anteriorly to the ectocingulum. A small swelling at the contact between the preparacrista and the ectocingulum in one specimen (UALVP 9230) could represent the remnants of a stylocone, but this feature is absent in all other observed specimens. The metacone is subconical and leans posteriorly; the postmetacrista is poorly developed but extends to the posterolabial corner of the crown. The centrocrista is well developed on the paracone and metacone, and, in labial view, forms a V-shaped notch between the two cusps. The paraconule is distinct and positioned approximately halfway up the anterolabial face of the protocone; the preprotocrista is short and separated from the paraconule by a shallow carnassial notch. The preparaconule crista is steep and confluent with the paracingulum; this elongate crest continues to the parastylar lobe and forms a narrow shelf anterior to the base of the paracone. The postparaconule crista is not developed. A metaconule is not developed, but the postmetaconule crista is strong and forms a long, uninterrupted crest with the postprotocrista; posterolabially, this crest becomes confluent with the metacingulum. The sharp protocone is compressed anteroposteriorly, steep lingually, leans anteriorly, and is only slightly lower than the paracone. The trigon basin is shallow and slopes steeply anterolabially-posterolingually. The broad precingulum and postcingulum do not continue lingually around the base of the protocone, and terminate labially before becoming confluent with the paracingulum and metacingulum, respectively.

M2: The crown is labiolingually elongate and asymmetrically triangular in occlusal outline, with the parastylar lobe is expanded anterolabially and the metastylar lobe virtually undeveloped. The parastylar lobe narrows only slightly anteriorly, and a small swelling (?parastyle) is present on the anterolabial corner of the crown. The stylar shelf is wide anteriorly, owing to the expansion of the parastylar lobe, but narrows quickly posteriorly. An ectoflexus is not developed. As on M1, the paracone and metacone arise from a common, swollen base; the paracone is only slightly taller the metacone, and the two cusps are joined for most of the height of the metacone. Both cusps are stout and subcircular in cross section; the paracone leans slightly anteriorly, while the metacone is more erect. The preparacrista becomes increasingly robust as it descends the paracone and continues to the anterolabial corner of the crown; a distinct stylocone is not developed. The centrocrista is high and well developed on both the paracone and metacone, and forms a broad, V-shaped notch between these cusps. The postmetacrista is faint and curves from the apex of the metacone to the posterolabial corner of the crown. The paraconule is distinct but low; a shallow slit separates the preprotocrista and paraconule. The preparaconule crista is confluent with the paracingulum and continues labially to the parastylar lobe; as on M1, this crest forms a shelf anterior to the base of the paracone. The metaconule, if present, is only a small swelling at the posterolingual base of the protocone (e.g., UALVP 9066). The postprotocrista is confluent with the postmetaconule crista; this crest joins the metacingulum and terminates posterior to the base of the metacone. The internal conular cristae are not developed. The protocone is conical, slightly compressed labiolingually, leans anteriorly, and is equal in height to the paracone. The trigon basin is shallow and less steeply sloped than that on M1. The precingulum is longer and more prominent than the postcingulum; these cingula are discontinuous lingually. The meta- and paracingulum are not continuous labially with the low ectocingulum.

Dentary and lower dentition, Dentary: UALVP 8775 preserves a badly damaged fragment of the left dentary with p4 and m1, roots for the lower canine and p3, and alveoli for p2 and m2. In anterior view, the horizontal ramus of this specimen is nearly flat on is medial surface but more convex laterally. A circular mental foramen is present on the lateral surface, beneath the posterior alveolus of p3.

Lower canine: Only a small fragment of the lower canine root, still within its alveolus, is preserved on UALVP 8775; it is mainly exposed along the anterior break in the dentary. The root is compressed bilaterally and can be seen, through a medial break in the dentary, to extend at least as far posterior as beneath the anterior root of p3.

p2: The p2 of R. machaera is known only from its alveoli preserved on UALVP 8775. In this specimen, the broken anterior alveolus is vertical and penetrates only a short depth into the dentary, while the posterior alveolus is complete, shallow and directed anteroventrally, rather than vertically. The aperture of the posterior alveolus is subovate and laterally compressed.

p3: A nearly complete, isolated p3 (UALVP 9060) can be referred to this species. The crown is elongate and moderately compressed, becoming slightly wider posteriorly. The sharp protoconid is tall and nearly conical; the posterior slope is steeply inclined and the cusp is slightly recurved. A paraconid is not developed but the crown is slightly expanded anterior to the base of the protoconid and a short ledge is formed. The paracristid is poorly developed, extending anteriorly from near the apex of the protoconid to its base. The first posterior accessory cusp arises low on the posterolabial shoulder of the protoconid, and is long and blade-like, with somewhat inflated labial and lingual surfaces. A carnassial notch separates the protoconid and the first posterior accessory cusp. The second posterior accessory cusp is conical and positioned posterolingually to the first posterior accessory cusp. A short cingulum is developed on the posterolabial margin of the crown.

p4: The crown of p4 is elongate, labiolingually compressed, and dominated by a tall, acute protoconid and a sectorial posterior heel, which bears two accessory cusps. The protoconid is massive and subconical, with both the labial and lingual sides slightly inflated. The anterior and posterior margins of the protoconid are steep and the cusp is nearly vertical, rather than recurved. The conical paraconid is low and inflated, with a pointed apex; it is set off anteriorly from the base of the protoconid and is distinctly canted lingually. A weak paracristid connects the apices of the paraconid and protoconid, although no carnassial notch is developed between these cusps. The first posterior accessory cusp is a stout blade with swollen labial and lingual sides, and in most specimens is positioned relatively low on the posterior margin of the protoconid. The second posterior accessory cusp varies from a subconical, pointed cusp in some specimens to a swollen, blade-like cusp in others; it is positioned posterolingually to the first posterior accessory cusp. Small carnassial notches are developed between the protoconid and the first accessory cusp, and between the first and second posterior accessory cusps (e.g., UALVP 8775). A moderate posterolabial cingulid is developed.

m1: The m1 bears a tall trigonid with sharp cusps and a talonid that is slightly skewed labially. The trigonid cusps are subtriangular in cross section; the protoconid is the tallest cusp, while the metaconid is slightly lower than the paraconid. The paraconid leans only slightly anteriorly and is displaced internally from the lingual margin, giving the trigonid an open appearance. Narrow carnassial notches are developed in the deepest parts of the paracristid and protocristid. The talonid basin is shallow and slopes steeply posterolabially-anterolingually. The hypoconid is the largest of the talonid cusps, while the hypoconulid is smaller but nearly equal to it in height. Unlike the m1 of other known species of <u>Raphictis</u> (see Gingerich and Winkler, 1985; Scott, 2008), a distinct, subconical entoconid can be developed lingually and slightly anterior to the hypoconulid (e.g., UALVP 8775). The entocristid is poorly developed and forms a low crest across the talonid notch. A short, moderately developed cingulid is present on the anterolabial margin of the trigonid. In some specimens (e.g., UALVP 8775), deep wear facets are seen along the hypoflexid, cristid obliqua, and in the deepest part of the talonid basin from contact with the paracone, paraconule, protocone, and associated crests of M1.

m2: The crown of m2 is anteroposteriorly elongate and subovate in occlusal outline. The trigonid is low, but taller and wider than the talonid. The cusps of the trigonid are relatively tall and sharp; the protoconid is the tallest cusp, and the metaconid is taller than the paraconid. The apex of the paraconid is positioned internally from the lingual margin and projects anteriorly; the trigonid is open between the paraconid and metaconid. Small carnassial notches can be developed in the paracristid and protocristid (e.g., UALVP 51574). The elongate talonid is only slightly angled posterolabially. The basin of the talonid is shallow and slopes steeply posterolabially-anterolingually. The hypoconulid is tall and pointed, whereas the hypoconid is low and inflated. The cristid obliqua is robust and extends onto the postvallid surface, nearly reaching the carnassial notch in the protocristid on UALVP 9065. The entoconid and entocristid are reduced. A short but distinct anterolabial cingulid is developed.

Etymology.— From machaera, Latin, a bent sword, in reference to the labially skewed talonid seen in members of the genus.

Holotype.— UALVP 8775, incomplete left dentary with p4, m1, roots for the c, p3, and alveoli for p2, m2 (Figs. 16.17-16.19). Roche Percée local fauna, Ravenscrag Formation of Saskatchewan, early late Paleocene [late middle Tiffanian, Ti4, Plesiadapis churchilli/P. simonsi Lineage Zone of Lofgren et al., 2004 (see Krause, 1978; Fox 1990)].

Other material examined.—From the Roche Percée local fauna: UALVP 8861, 8863, 10917, 51563 (total:4), P4; UALVP 9064, 9069, 9230, 51564, 51565 (total:5), M1; UALVP 9066, 51566, M2; UALVP 9060, p3; UALVP 51567-51569 (total:3), p4; UALVP 8862, 8864, 8866, 8868, 8870, 8874, 9068, 51570-51572 (total:10), m1; UALVP 8865, 9065, 51573-51574 (total:4), m2.

From DW-2: UALVP 47810, incomplete right maxilla with P4 and alveoli for P2-3.

Age and occurrence.—Early late Paleocene (early middle Tiffanian, Ti3, Plesiadapis rex/P. churchilli Lineage Zone to the late middle Tiffanian, Ti4, P. churchilli/P. simonsi Lineage Zone) of the northern part of the Western Interior of North America.

Discussion.—Raphictis machaera is most similar to R. gausion in the parts that can be compared and is consistent with Gingerich and Winkler's (1985) diagnosis for the genus: narrow crowns, cusps that are tall and sharp, and the molar talonid is skewed labially. The referred specimens of R. machaera differ, however, from their homologues in R. gausion and other species of Raphictis principally in their larger size (e.g., mean length m1, R. machaera = 4.75 mm versus mean length m1, R. gausion = 3.70 mm) and in having a small anterobasal lobe and a well developed first and second posterior accessory cusp on p3, as well as a more robust paraconid on p4 that leans strongly lingually. In addition, a distinct entoconid can be developed on m1 of R. machaera, the first time this feature has been observed in any member of the genus.

Based on specimens from several middle Tiffanian (Ti3-Ti4) localities in central Alberta, Scott (2008) recently described the first elements of the upper dentition for Raphictis. The upper dentition of the genus reveals an unusual combination of primitive and derived traits (Scott, 2008). For example, the protocone of P4 is only slightly anterior to the level of the paracone as it is in most primitive viverravids (e.g., Pristinictis Fox and Youzwyshyn, 1994, and Protictis), while the metastylar blade is long and less transversely oriented like that in more derived viverravids (e.g., Viverravus Marsh, 1872). Additionally, the M1 is relatively broad, the protocone is anteroposteriorly compressed and the pre- and postcingulum are weak, similar to the condition of the M1 of Ravenictis Fox and Youzwyshyn, 1994, the geologically oldest carnivoran. The closely appressed paracone and metacone on M1 is a feature that Scott (2008) suggested might help resolve the phylogenetic relationships of Raphictis but further studies are needed to test this hypothesis; interestingly, this condition is now known to be present in M2, a tooth that was previously unknown for the genus.

RAPHICTIS NANOPTEXIS new species

Figure 14, 16.26-16.36; Table 22

Raphictis, new species 1 FOX, 1990, p. 66.

Diagnosis.—Smallest known species of Raphictis (length of the m1 approximately 25% shorter than m1, R. “iota” and 35% shorter than m1, R. gausion, and 50% shorter than m1, R. machaera). Differs farther from other species of Raphictis in having a smaller parastyle on P4, a shorter first posterior accessory cusp on p4, and a more reduced hypoconid on m1. Differs farther from R. machaera in having M1 wider relative to it length, with a shallower ectoflexus.

Description.—Upper dentition, P4: Resembling that in most other viverravids, the P4 of R. nanoptexis is Y-shaped in occlusal outline, with a deep embayment anteriorly between the parastyle and protocone. The crown is dominated by an enlarged, centrally positioned paracone that is tall, slightly compressed labiolingually, and strongly canted posteriorly. The preparacrista is prominent but low throughout its length. The parastyle, positioned directly anterior to but well separated from the paracone, is small and subconical. A distinct parastylar crest is not developed but the crown is inflated between the paracone and parastyle. The protocone is slightly taller and larger than the parastyle, but otherwise similar; it is positioned anterolingual to the paracone and slightly posterior to the level of the parastyle. A U-shaped notch separates the paracone and protocone. A faint preprotocrista descends from the apex of the protocone to the base of the cusp but does not extend across the notch to the paracone. From the apex of the paracone, the postparacrista descends posteriorly and slightly lingually into a deep, narrow slit that separates the paracone from the metastylar blade; the slit is damaged at its deepest part and the development of a carnassial notch cannot be determined. The metastylar blade is high and sharp, and oriented oblique to the paracone; in labial and lingual views, it is subarcuate. A strong anterior cingulum is developed between the apices of the parastyle and protocone, but contact with the protoconid of the p4 has slightly worn the cingulum near the base of the protocone. The ectocingulum is well developed and extends from the apex of the parastyle posteriorly to the posterolabial margin of the metastylar blade. Similarly, on the lingual margin, a prominent posterior cingulum continues from the protoconal apex to the posterolingual margin of the metastylar blade.

M1: The crown of M1 is anteroposteriorly compressed and subtriangular in occlusal outline, with the labial margin considerably longer than the lingual margin. The parastylar lobe is expanded anterolabially, and hooks lingually at its anteriormost tip; a small, low parastyle is developed on the anterolabial corner of this lobe. The metastylar lobe is reduced relative to the parastylar lobe. The stylar shelf is broad anteriorly but narrows at the ectoflexus and around the metastylar lobe; the ectocingulum is low and continuous with the para- and metacingulum. The sharp paracone and metacone arise from a common base; the metacone is approximately half the height of the paracone and joined with the paracone for nearly two-thirds of its total height. The paracone is circular in cross section and leans anteriorly; a distinct but low preparacrista connects the apices of the paracone and parastyle. The metacone is more compressed labiolingually than the paracone and leans slightly posteriorly. The centrocrista is strong on both the paracone and metacone, and forms a V-shaped notch between the two cusps. The postmetacrista descends from the apex of the metacone to the base of the crown and becomes confluent with the metacingulum. A prominent paraconule is developed high on the protocone; the preprotocrista is short and separated from the paraconule by a shallow slit. The preparaconule crista is steep and continuous with the paracingulum; this crest forms a moderate shelf anterior to the base of the paracone that terminates labially at the parastylar lobe. A metaconule is not developed, but the postmetaconule crista is strong and forms a long, uninterrupted crest with the postprotocrista; labially, this crest becomes confluent with the metacingulum. Internal conular cristae are not developed. The protocone is acute, slightly compressed anteroposteriorly, and leans slightly anteriorly; the slope of the lingual surface is steep. The trigon basin is shallow and slopes steeply anterolabially-posterolingually. The broad precingulum and postcingulum are not continuous lingually and terminate labially before joining the paracingulum and metacingulum, respectively.

Lower dentition, p4: The p4 is elongate and labiolingually compressed, with only a slight labiolingual expansion posteriorly. The crown is dominated by a tall, slightly recurved protoconid that is relatively flat labially and more convex lingually. The paraconid is small, low, and displaced anteriorly from the base of the protoconid; the apex leans slightly posteriorly. A faint paracristid connects the apices of the paraconid and protoconid; as in the p4 of R. gausion, a carnassial notch is not developed between these cusps (Gingerich and Winkler, 1985). The first posterior accessory cusp, which arises low on the posterolabial shoulder of the protoconid, and the second posterior accessory cusp, positioned posterolingual to the first posterior accessory cusp, are blade-like. Shallow slits are developed between the protoconid and first posterior accessory cusp, and between the first and second posterior accessory cusps. Posterolabial and posterolingual cingulids descend from the apex of the secondary posterior cusp.

m1: The m1 has a high trigonid with tall, sharp cusps and a talonid that is angled obliquely to the long axis of dentary, similar to m1 of Raphictis (Gingerich and Winkler, 1985; Scott, 2008). The trigonid cusps are subtriangular in cross section; the protoconid is the tallest cusp, and the metaconid and paraconid are nearly equal in height. The paraconid leans anteriorly and is inset slightly from the lingual margin, giving the trigonid an open appearance. Narrow carnassial notches are present in the deepest parts of the paracristid and protocristid. The talonid is short and the shallow talonid basin slopes steeply posterolabially-anterolingually. The hypoconid is the largest talonid cusp and was likely taller than the hypoconulid, although minor apical wear to the hypoconid makes the original height of this cusp impossible to determine. The cristid obliqua is steeply angled, contacting the base of the postvallid surface ventral to the protocristid notch, and is less robust than in other species of Raphictis. The entoconid is only a small swelling near the apex of the hypoconulid. The entocristid descends steeply from the entoconid and forms a low crest along the talonid notch. Only a short anterolabial cingulid is developed. The hypoflexid and cristid obliqua are heavily worn, and there is a circular groove worn into the lowest part of the talonid basin.

Etymology.—From nanos, Greek, dwarf, in reference to the small size of R. nanoptexis relative to all other viverravids, and ptexis, Greek, terror.

Holotype.—UALVP 8876, an isolated left m1 (Figs. 16.34-16.36). Roche Percée local fauna, Ravenscrag Formation of Saskatchewan, early late Paleocene [late Tiffanian, Ti4 (see Krause, 1978; Fox, 1990) Plesiadapis churchilli/P. simonsi Lineage Zone of Lofgren et al., 2004].

Other material examined.—UALVP 51560, P4; UALVP 51561, M1; UALVP 9070, p4; UALVP 9061, m1.

Age and occurrence.—Early late Paleocene (late middle Tiffanian, Ti4, Plesiadapis churchilli/P. simonsi Lineage Zone of Lofgren et al., 2004) of Saskatchewan.

Discussion.—With the exception of their much smaller size, specimens of Raphictis nanoptexis are virtually identical to comparable teeth of R. gausion. Less conspicuous differences between these taxa include the shorter first posterior accessory cusp and the lower second posterior accessory cusp on p4, and the less inflated m1 hypoconid of R. nanoptexis. Also, similar to the condition in R. “iota” and R. machaera, but unlike that in R. gausion, the p4 is longer than the m1 (i.e., in R. gausion the p4 is shorter than the m1). Raphictis nanoptexis is among the smallest viverravid carnivorans known from the Paleocene and its occurrence documents the presence of a third species of Raphictis at the Roche Percée localities (Rankin and Fox, 2008).

Grandorder UNGULATA Linnaeus, 1766

Order PROCREODI Matthew, 1915

Family OXYCLAENIDAE Scott, 1892

Genus CHRIACUS Cope, 1883b

Lipodectes COPE, 1881c, p. 1019 (in part).
Deltatherium Cope, 1881c: COPE, 1882a, p. 463 (in part).
Chriacus COPE, 1883b, p. 80 (in part).
Tricentes COPE, 1884a, p. 314 (in part).
Pelycodus COPE, 1875: COPE, 1884b, p. 255 (in part).
Epichriacus SCOTT, 1892, p. 296.
Metachriacus SIMPSON, 1935a, p. 235.
?Spanoxyodon SIMPSON, 1935a, p. 236.

Type species.—Lipodectes pelvidens (Cope, 1881c).

Included species.—Chriacus baldwini (Cope, 1882a); C. gallinae Matthew, 1915; C. calenancus Van Valen, 1978; C. katrinae Van Valen, 1978; C. metacometi Van Valen, 1978; C. oconostotae Van Valen, 1978; C. badgleyi Gingerich, 1989.

CHRIACUS CF. C. BALDWINI (Cope, 1882a)

Figure 17.1-17.2; Table 23

Material examined.—UALVP 9643, 51451, M1.

Age and occurrence.—Chriacus baldwini is known from the early to late Paleocene (earliest Torrejonian, To1, Periptychus carinidens /Protoselene opisthacus Interval Zone to early late Tiffanian, Ti5, Plesiadapis simonsi/P. gingerichi Lineage Zone of Lofgren et al. 2004) of the Western Interior of North America.

Description.—M1: Of the two referred specimens, UALVP 9643 is the more nearly complete, although even on this specimen many of the coronal features are appreciably worn. The crown is subrectangular in occlusal outline. The parastylar lobe is slightly expanded anteriorly and narrows to a short hook-like process, while the metastylar lobe is more smoothly rounded. The stylar shelf is narrow and a faint ectoflexus occurs midway along labial margin of the crown.

From the dimensions of their bases, the principal cusps were swollen; the base of the protocone is larger than those of the other principal cusps and is positioned almost directly lingual to the paracone. Both the paraconule and metaconule bases are inflated, but the base of the metaconule is slightly larger than that of the paraconule. The postcingulum is expanded posterolingually and supports an inflated hypocone; the posterolingual corner of the crown is distinctly “squarish”, while the anterolingual corner is more rounded. The pre- and postcingulum are continuous lingually around the base of the protocone.

Discussion.—Van Valen (1978) revised the taxonomy of Chriacus baldwini and considered Tricentes crasicollidens Cope, 1884a, Chriacus truncatus Cope, 1884a, C. schlosserianus Cope, 1888, Metachriacus provocator Simpson, 1935a, and Spanoxyodon latrunculus Simpson, 1935a, as subjective junior synonyms of C. baldwini. Van Valen’s (1978) revisions permit an exceedingly large diagnostic variability, both in terms of size and morphology, for C. baldwini and emendments are likely required [see Scott (2008) and Secord (2008) for a similar opinion]. Therefore, although the specimens are virtually identical to the M1 of C. baldwini, I agree with the course taken by Scott (2008) and Secord (2008), and defer the assignment of these specimens to C. baldwini pending more thorough evaluation of the taxonomy of the genus.

CHRIACUS CF. C. OCONOSTOTAE Van Valen, 1978

Figure 17.3-17.5

Material examined.—UALVP 51452, m2 (TaL = 4.5; TaW = 5.5).

Age and occurrence.—Chriacus oconostotae is known from the early late Paleocene (late middle Tiffanian, Ti3, Plesiadapis rex/P. churchilli Lineage Zone of Lofgren et al. 2004) of the Western Interior of North America.

Description and discussion.—UALVP 51452 compares closely with the talonid of the m2 of Chriacus oconostotae from the early middle Tiffanian (Ti3) of central Alberta (Scott, 2008), particularly in having tall, acute cusps, a deep talonid basin, and a hypoconulid that is supported on a broad postcingulid. This referred specimen differs, however, in being slightly smaller and in having a taller hypoconulid that is more nearly excluded from the talonid rim by the hypocristid and postcristid. Other than the sample from central Alberta, C. oconostotae is known only from early middle Tiffanian localities in Wyoming (Van Valen, 1978; Gunnell, 1994) and, if confirmed as C. oconostotae, its occurrence at Roche Percée would represent the first record of this taxon from Saskatchewan and the youngest yet known.

Genus THRYPTACODON Matthew, 1915

Thryptacodon MATTHEW, 1915, p. 7.

Type species.—Thryptacodon antiquus Matthew, 1915.

Included species.—Thryptacodon pseudarctus Simpson, 1928; T. orthogonius (Russell, 1929); T. australis Simpson, 1935b; T. barae Gingerich, 1989.

THRYPTACODON AUSTRALIS Simpson, 1935b

Figure 17.6-17.18; Table 24

Thryptacodon australis SIMPSON, 1935b, p. 20.

Holotype.—AMNH 17384, incomplete left dentary containing c, p1, p3-4, m1-3, and associated right dentary having c, p1-4, m1-3, possibly associated LM2, and postcranial remains (Simpson, 1935b, p. 20). Mason Pocket locality, Animas Formation of Colorado, late Paleocene (late middle Tiffanian, Ti4, Plesiadapis churchilli/P. simonsi Lineage Zone of Lofgren et al., 2004).

Material examined.—UALVP 9639, incomplete right maxilla with M1 and alveoli for P3-4, M2; UALVP 9640, 9641, M2; UALVP 51453, m1; UALVP 9645, 9647, m2; UALVP 51454, m3.

Age and occurrence.—Late Paleocene (late early Tiffanian, Ti2, Plesiadapis anceps/P. rex Lineage Zone to latest Clarkforkian, Cf3, Phenacodus/Ectocion Acme-Zone of Lofgren et al., 2004) of the Western Interior of North America.

Description.—Upper dentition, M1: The M1 of T. australis is subrectangular in occlusal outline. The principal cusps are inflated, especially near their bases, and subequal in height; collectively, these cusps and their associated crests enclose a deep trigon basin. The parastylar and metastylar lobes are reduced and only a faint ectoflexus indents the labial margin between these lobes. The paracone is slightly smaller and more labial than the metacone; the preparacrista, postmetacrista, and centrocrista are short and poorly developed. Both conules are robust and swollen, although the metaconule is slightly larger and more lingual than the paraconule. The base of the protocone is more massive than that of the paracone or metacone; the apex of the protocone is almost directly lingual to that of the paracone. The prominent but low basal cingulum is continuous around the entire crown and supports a small parastyle at the base of the preparacrista, a small accessory cusp lingual to the protocone, and a robust hypocone at the posterolingual corner of the crown.

M2: The M2 closely resembles M1 but differs as follows: slightly larger size, the metaconule is more swollen, the conular crests are slightly more pronounced, and the hypocone is more inflated, while the protocone is slightly more compressed anteroposteriorly.

Lower dentition, m1: The heavily worn m1 closely resembles that of T. australis from early middle Tiffanian (Ti3) localities in central Alberta (Scott, 2008). The trigonid is narrower than the talonid. The paraconid is anteroposteriorly compressed and projects anteriorly; the metaconid is positioned somewhat posterior to the level of the protoconid. The base of the hypoconid is slightly more massive than that of the entoconid, while the hypoconulid appears to be smaller than both of these. The ectocingulid is prominent and continuous across the hypoflexid.

m2: The m2 is subrectangular in occlusal outline, but there are slight constrictions between the trigonid and the wider talonid. The trigonid is taller than the talonid and dominated by a swollen protoconid and metaconid; a short protocristid extends between these cusps. The paracristid is anteriorly arcuate and partially supports a small, bulbous paraconid that is positioned internally from the lingual margin of the crown and leans slightly anteriorly. The low hypoconid is greatly enlarged and occupies nearly half the width of the talonid; the hypoconulid and the slightly larger entoconid are closely appressed to each other. The talonid basin is shallow and enclosed on all margins. The ectocingulid is strong and complete across the labial margin of the crown.

m3: The m3 is the longest tooth in the molar row and teardrop-shaped in occlusal outline, narrowing posteriorly towards the finger-like hypoconulid. The trigonid is more anteroposteriorly compressed than on m1 and m2 and only slightly taller than the talonid. The protoconid and metaconid are inflated, with smoothly rounded apices that are connected by a thick protocristid. The paracristid is anteriorly convex and the paraconid forms a small, anterolingual swelling on this crest. The basin of the talonid is shallow and enclosed on all margins. The hypoconid is massive, and the cristid obliqua and hypocristid are robust. The hypoconulid and the entoconid are closely appressed and connected by a short postcristid. A small entoconulid is developed on the entocristid. The precingulid is weak but continuous around the labial base of the protoconid and across the hypoflexid; however, the cingulid does not extend around the base of the hypoconid and does not join with the postcingulid.

Discussion.—Thryptacodon australis is both temporally long ranging (early Tiffanian to late Clarkforkian) and geographically widespread (Colorado to Alberta), and has been previously described by Simpson (1935b), Holtzman (1978), Rose (1981), and Scott (2008). The specimens from Roche Percée are virtually identical to homologous teeth of T. australis from middle Tiffanian (Ti3-4) localities in Alberta (Webb, 1996; Scott, 2008) and North Dakota (Holtzman, 1978), differing only in their slightly larger size and more massive hypocone on

M2. The citation of T. australis at the Roche Percée localities by Fox (1990) was the first record of this taxon in western Canada.

Family ARCTOCYONIDAE Giebel, 1855

Genus ARCTOCYON Blainville, 1841

Arctocyon BLAINVILLE, 1841, p. 73.
Paleocyon BLAINVILLE, 1841, p. 73.
Heteroborus COPE, 1880, p. 79.
Hyodectes COPE, 1880, p. 79.
Mioclaenus COPE, 1881b: COPE, 1883c, p. 547.
Claenodon SCOTT, 1892, p. 298.
Arctotherium LEMOINE, 1896, p. 342.
Neoclaenodon GIDLEY, 1919, p. 547 (in part).
Arctocyonides LEMOINE, 1891: VAN VALEN, 1978, p. 55 (in part).
Mentoclaenodon WEIGELT, 1960: VAN VALEN, 1978, p. 55 (in part).

Type species.—Arctocyon primaevus Blainville, 1841

Included species.—Arctocyon ferox (Cope, 1883c); A. corrugatus (Cope, 1883c); A. matthesi Russell, 1964; A. acrogenius (Gazin, 1956); A. mumak (Van Valen, 1978).

ARCTOCYON MUMAK (Van Valen, 1978)

Figure 18.1-18.5; Table 25

Arctocyonides mumak VAN VALEN, 1978, p. 55.

Holotype.—YPM-PU 17406, incomplete left maxilla containing P4 and M1-3 (Van Valen, 1978, p. 55). Type locality unknown, reportedly from “southeast side of Polecat Bench, east border of S10, T56, R99W (near SC-243)” (Secord, 2008, p. 139), Fort Union Formation of Wyoming, early late Paleocene (late middle Tiffanian, Ti4, Plesiadapis churchilli/P. simonsi Lineage Zone of Lofgren et al., 2004).

Material examined.—UALVP 9691, M1; UALVP 9689, incomplete left dentary with p3-4, m1-3 and alveoli for i1-3, c, p1-2; UALVP 51458, m3.

Age and occurrence.—Early late Paleocene (late middle Tiffanian, Ti4, Plesiadapis churchilli/P. simonsi Lineage Zone to early late Tiffanian, Ti5, P. simonsi/P. gingerichi Lineage Zone of Lofgren et al., 2004) of the Western Interior of the United States.

Description.—Upper dentition, M1: The margins of the crown are considerably inflated and only a shallow ectoflexus indents the labial side of the crown between the swollen stylar lobes. The paracone and metacone are robust and subconical. The centrocrista is serrated and forms an acute, V-shaped notch between the paracone and metacone; a conspicuous extension of the premetacrista continues from the deepest part of the centrocrista labially to the ectocingulum. Both conules are inflated; the conular cristae are faint and a small, bulbous cusp is developed posterolabially on the postmetaconule crista, near its confluence with the metacingulum. The base of the protocone is more massive than those of the other principal cusps but the heights of these three cusps are nearly equal; the long labial face of the protocone is nearly flat, and bordered anteriorly and posteriorly by the low preprotocrista and postprotocrista, respectively. The large hypocone is positioned posterolingual to the protocone and directly lingual to the metaconule. The pre- and postcingulum are joined lingually. The enamel is heavily wrinkled on the crown.

Dentary and lower dentition, Dentary: UALVP 9689 is a well-preserved left dentary, broken and missing from the base of i1 anteriorly and posteriorly from m3. The medial and lateral margins of the horizontal ramus are greatly inflated beneath the two posteriormost premolars and the molars, but narrow considerably anteriorly from the level of the p3. The horizontal ramus is deep (depth of dentary beneath m1, at least, = 32.5 mm); the ventral margin of the ramus is nearly parallel to the alveolar margin, except anteriorly from beneath the canine, where the ventral margin rises steeply at the level of the symphysis. The roughened symphyseal surface is deeply convoluted, but there is no evidence that the mandibular rami were co-ossified in life; a thick crest that terminates beneath p2 posteriorly borders the superior and distal margins of the symphyseal surface. Beginning ventral to p2 and continuing anteriorly, the ventral margin is flared laterally and forms an anterolateral flange that would have likely protected the large upper canine when the jaws were occluded. Two mental foramina, one beneath p1 and the other beneath p3, are present on the lateral surface of the horizontal ramus.

Lower incisors: The three small, crowded lower incisors are represented only by their alveoli in UALVP 9689 and are exposed along the anterior break of in the dentary. Similar to the pattern in the oxyclaenid Thryptacodon australis (see Scott, 2008), two of these alveoli, corresponding to i1 and i2, are developed medially, adjacent to the symphyseal surface. The i1 alveolus lies immediately anterior and ventral to the canine alveolus; the root that it contains is subcircular in cross section. With reference to the broken surface, the alveolus for i2 is ventral to the i1 alveolus and only a thin partition of bone separates the two alveoli; the i2 aperture is subequal in size to that of i1 and also subcircular in outline. The i3 alveolus is smaller than the other incisor alveoli, and the aperture is smaller and slightly compressed mediolaterally; it is developed lateral to the i2 alveolus.

Lower canine: The aperture of the lower canine alveolus is slightly damaged but would have been anteroposteriorly elongate and strongly compressed labiolingually in life. The alveolus, itself, is directed slightly anteroventrally, rather than vertically, and extends posteriorly to at least beneath p2.

p1: The alveolus is immediately posterior to the canine alveolus and directed anteroventrally. The aperture is ovate and the p1 would likely have been labiolingually compressed.

p2: Most of p2 has been broken away and only the roots, preserved within their alveoli, are present in UALVP 9689. The aperture of the anterior alveolus is circular in cross section; the root occupies only a small portion of the alveolus.

The posterior alveolus appears to have been circular but the aperture and root are partially covered by bone. Based on this condition, I interpret here that (1) the crown of the two-rooted p2 was likely lost during the life of the animal, (2) the alveoli were remodeled (in the case of UALVP 9689, the posterior alveolus was in the process of being remodeled before the anterior alveolus), and (3) a large diastema between p1 and p3 was present in the later life of the animal.

Notably, Gazin (1956) observed that there was a single depression between p1 and p3 in the holotype of A. acrogenius (USNM 20634), and suggested that p2 was likely single-rooted and that the crown was probably lost in life. Secord (2008) later distinguished specimens he referred to Arctocyon cf. A. mumak from A. acrogenius by having a double-rooted, rather than a single-rooted, p2; however, based on the evidence provided by UALVP 9689, the taxonomic significance of the number of roots observed for p2 is less useful than proposed by Secord (2008).

p3: The crown of p3 is rectangular in occlusal outline, with only a slight labiolingual expansion posteriorly, and is dominated by a massive protoconid and short talonid heel, bearing two cusps. The protoconid is centrally positioned on the crown and leans slightly posteriorly. The low paracristid is robust and serrated [similar to the paracristid in homologous specimens of A. ferox from the Birchwood and Blindman River localities (see Scott, 2008)]; the crest turns lingually near the base of the cusp before joining the precingulid. A second serrated crest descends posteriorly from the apex of the protoconid to the swollen medial talonid cusp. A smaller cusp is developed lingual to the medial talonid cusp on the posterolingual corner of the cingulid. The precingulid is moderately developed and forms a narrow ledge at the anterior base of the protoconid; the cingulid continues a short distance onto the labial and lingual margins of the crown before fading. The postcingulid is more prominent than the precingulid and, similar to the precingulid, forms a narrow shelf posterolabially and posterolingually. The enamel is weakly wrinkled.

p4: The p4 is considerably taller and wider than p3. As on p3, an enlarged protoconid and a broad, but short talonid dominate the crown. The robust, serrated paracristid is directed anteriorly and slightly more lingually from the apex of the protoconid than that on the p3; a paraconid is not developed, but a faint swelling occurs at the contact between the paracristid and precingulid, suggesting its incipient development. A metaconid is not present. The talonid on p4 is better developed than on p3, and the medial talonid cusp is more robust. The posterolingual and posterolabial corners of the crown are damaged, and the development of any cusps in these areas cannot be determined. The pre- and postcingulid are prominent but discontinuous labially. The enamel is more heavily wrinkled than on p3.

m1: The m1 crown is pyriform in occlusal outline, with the talonid slightly wider than the trigonid, and the principal cusps are bunodont. The protoconid and metaconid are inflated and subequal in size; the small paraconid is high and closely appressed to the metaconid. The long, anteriorly arcuate paracristid extends from the apex of the protoconid to the anterior surface of the paraconid. As in other arctocyonines, broad crests descend from the apices of the protoconid and metaconid into the shallow trigonid basin, and join mid-sagittally to form a elongate, notched transverse crest; a heavily worn protocristid is developed posterior to this crest. Protostylid and metastylid crests extend down the postvallid surface of the trigonid to the hypoflexid and entocristid, respectively. The talonid basin is shallow and V-shaped. The hypoconid is massive and dominates the talonid; the entoconid is slightly lower than and approximately half the size of the hypoconid. A reduced hypoconulid is wedged between the other, larger talonid cusps. The ectocingulid is continuous labially and developed high on the crown. The enamel is weakly wrinkled.

m2: m2 is more rectangular than pyriform, with the trigonid and talonid subequal in width. The protoconid and metaconid are massive like those on m1 but slightly lower; the anterolingual corner of the crown is broken and missing, obscuring details of the paraconid. The paracristid does not extend as far anteriorly as that on m1 and instead runs almost directly anterolingually from the apex of the protoconid. The transverse crests that descend from the protoconid and metaconid into the trigonid basin are more robust than those seen on m1. The talonid of the m2 is very similar to that in m1 differing, however, in having more inflated cusps and crests, and a small talonid notch separating the metastylid and the entocristid. The ectocingulid is equal in height to that on m1.

m3: The m3 is narrower and only slightly longer than m2. The crown is subrectangular in occlusal outline, and the trigonid is wider than the talonid. The trigonid cusps are heavily worn and the paraconid appears to have been indistinct from the robust paracristid. The base of the metaconid is larger than that of the protoconid and positioned further posteriorly. The talonid cusps are massive but reduced relatively to those in m1 and m2, with the exception that the hypoconulid is expanded and more lobate. A small, inflated mesoconid and entoconulid are developed between the postvallid surface and the hypoconid and entoconid, respectively. The high ectocingulid is complete across the labial margin of the crown.

Discussion.—Since the original diagnosis of the species was presented, the taxonomy of Arctocyon mumak has been somewhat unclear and an attempt to rectify some of this confusion is undertaken here. The holotype of Arctocyon mumak was first described by Van Valen (1978) as “Arctocyonides” mumak; Van Valen (1978) considered Claenodon a synonym of Arctocyonides, rather than Arctocyon as Russell (1964) had proposed. Russell (1980), however, retained Claenodon as a synonym of Arctocyon but did not comment on the taxonomy of “Arctocyonides” mumak, likely assuming that this species was a member of Arctocyon. Subsequent authors either purposely ignored these revisions and recognized “Claenodon” mumak (e.g., Winterfeld, 1982) or, more commonly, recognized Arctocyon mumak as a valid taxon (e.g., Secord, 1998; Archibald, 1998). More recently, Kondrashov and Lucas (2004) considered Arctocyon mumak a subjective junior synonym of Arctocyon (=Mentoclaenodon) acrogenius (Gazin, 1956); yet, Secord (2008), without citing Kondrashov and Lucas (2004), assigned specimens from the Bighorn Basin, Wyoming, to Arctocyon mumak and Arctocyon cf. A. mumak.

Much of this taxonomic confusion can be largely attributed to the considerable variability in size and morphology observed within species of

Arctocyon and other closely related forms, and also to the small sample sizes known for many of these species. The latest emendments proposed by Kondrashov and Lucas (2004) appear in part an attempt to simplify the taxonomy of *Arctocyon*, with only three valid species [*A*. *corrugatus*, *A*. *ferox*, and *A*. *acrogenius*] recognized within the genus and principally distinguished from each other on the basis of size (i.e., all “large” specimens referable to the genus are assigned to *A*. *acrogenius*, while all “intermediate-sized” specimens pertain to *A*. *ferox*, etc.). However, the new specimens from Roche Percée, combined with specimens of *A*. *mumak* from the Bighorn Basin (Secord, 2008) do not support this abridged classification; rather, these specimens suggest that *A*. *mumak* is distinct from all other members of the genus *Arctocyon* and is a valid species.

As noted by Van Valen (1978) in the original diagnosis of the species, *A*. *mumak* is larger than other species of *Arctocyon*, including *A*. *acrogenius*, (e.g., mean length, m1 = 14.5 mm combined samples of *A*. *mumak* from the Williston and Bighorn Basins, versus mean length, m1 = 12.2 mm, *A*. *acrogenius* from the Bison Basin). *A*. *mumak* differs further from *A*. *ferox* in having upper molars that are more squarish, with the margins of the crown considerably more inflated, lower cusps and conules, more closely approximated paracone and metacone, and a less prominent cingulum (also see Secord, 2008). Kondrashov and Lucas (2004) assigned the first upper dentition, a maxillary fragment containing P4, M1-2 (YPM-PU 13215), to *A*. *acrogenius* based on its large size and resemblance to *A*. *ferox*; although the specimen was not figured, it compares closely in size to *A*. *mumak* and could potentially belong to this species.

The occurrence of *A*. *mumak* at Roche Percée documents the first record of this taxon in western Canada and extends the known geographical range of this taxon northwards from Wyoming.

ARCTOCYON CORRUGATUS (Cope, 1883c)

Figure 18.6-18.12

Claenodon *corrugatus* COPE, 1883c, p. 556.

Neoclaenodon montanensis GIDLEY, 1919, p. 547.
?Neoclaenodon latidens GIDLEY, 1919, p. 554.
?Claenodon vecordensis SIMPSON, 1935a, p. 232.

Holotype.—AMNH 3258, incomplete right maxilla with P4 and M1-3 (Cope, 1883c, p. 556). Type locality unknown, but described by Matthew (1937, p. 36) as “middle Paleocene, Torrejon Formation, San Juan Basin, New Mexico”, possibly the late early Paleocene (middle Torrejonian, To2, Protoselene opisthacus/Mixodectes pungens Interval Zone, or latest Torrejonian, To3, Mixodectes pungens/Plesiadapis praecursor Interval Zone of Lofgren et al., 2004).

Material examined.—UALVP 51459, M1 (L=7.4; W=8.1); UALVP 51460, M2 (L=9.3; W=12.8); UALVP 10877, m3 (L=9.8; TrW=6.9; TaW=5.9).

Age and occurrence.—Early to late Paleocene (late Torrejonian, To3, Mixodectes pungens/Plesiadapis praecursor Interval Zone to late middle Tiffanian, Ti4, P. churchilli /P. simonsi Lineage Zone of Lofgren et al., 2004) of the Western Interior of North America.

Description.—Upper dentition, M1: The M1 is subquadrate in occlusal outline, with the crown slightly wider than long. A shallow ectoflexus indents the labial margin midway along the crown, between the weak, smoothly rounded parastylar and metastylar lobes. The ectocingulum is faint and discontinuous labial to the paracone. The subconical paracone and metacone are swollen, especially near their bases, and subequal in size and height; the preparacrista, centrocrista, and postmetacrista are only weakly developed. The metaconule is much larger than the paraconule and extends further lingually; the internal conular cristae are short, while the preparaconule crista and postmetaconule crista are confluent with the para- and metacingulum, respectively. The apex of the protocone is transversely opposite to the apex of the paracone; broad preprotocrista and postprotocrista extend between the protocone and the conules. The low, bulbous hypocone is positioned lingual to the metaconule and immediately posterior to the protocone. The anterior and posterior cingula are joined lingually.

M2: The crown is worn but is more rectangular in occlusal outline than M1, being longer but also wider. The subequal paracone and metacone are low and massive; a short, crenulated crest runs directly labially from the notch between the paracone and metacone to the ectocingulum. The base of the metaconule is larger and more lingually positioned than the paraconule. The protocone is nearly worn flat, but the base of the cusp is wider than that of the other principal cusps; the trigon basin is shallow and broad. The hypocone is also heavily worn, but the base is inflated and is positioned posterior and slightly lingual to the protocone. The pre- and postcingulum are not continuous lingually, and are terminated labially by the para- and metacingulum, respectively; these latter cingula are confluent with the ectocingulum. The enamel is wrinkled.

Lower dentition, m3: The crown of m3 is roughly rectangular in occlusal outline, narrowing posteriorly towards the enlarged, lobate hypoconulid. The trigonid is slightly taller than the talonid, and dominated by a swollen, low protoconid and metaconid; the metaconid is larger and taller than the protoconid. The paraconid is low and closely appressed to the metaconid. As in A. mumak, the trigonid basin is V-shaped and extends mid-sagittally between the protoconid and metaconid; this basin interrupts the robust paracristid, transverse crests, and protocristid. The talonid is shallowly basined and its cusps are inflated. The hypoconid is the largest cusp, followed by the subequal entoconid and hypoconulid; a small cusp is wedged between the hypoconid and hypoconulid. Thick protostylid and metastylid crests extend down the postvallid. The continuous ectocingulid bears small serrations, and the enamel of the crown is wrinkled.

Discussion.—In their recent review of Arctocyon, Kondrashov and Lucas (2004) considered “Neoclaenodon montanensis” a junior synonym of A. corrugatus and, without a larger collection of small arctocyonines at hand, this opinion is followed here. The referred specimens are virtually identical to specimens assigned to A. corrugatus by Kondrashov and Lucas (2004), with the exception that M1 is considerably smaller [e.g., mean length, M1 = 7.4, A. corrugatus from Roche Percée, Saskatchewan, versus mean length, M1 = 8.9, combined samples of A. corrugatus from localities in the Western Interior of the United States (Kondrashov and Lucas, 2004)] and less transverse relative to its length. Potentially, this single specimen could belong to a smaller, yet unknown species of Arctocyon; however, a larger sample is needed to resolve this question. The occurrence of A. corrugatus at Roche Percée represents the youngest record of this stratigraphically long-ranging taxon.

Order CONDYLARTHRA Cope, 1881d
Family HYOPSODONTIDAE Trouessart, 1879
Genus DORRALETES Gingerich, 1983

Haplaletes DORR, 1952, p. 86 (in part).
Dorraletes GINGERICH, 1983, p. 244.

Type species.—Haplaletes diminutivus (Dorr, 1952), by monotypy.

DORRALETES DIMINUTIVUS (Dorr, 1952)
Figure 19.1-19.3; Table 26

Haplaletes diminutivus DORR, 1952, p. 86, original description.
Dorraletes diminutivus GINGERICH, 1983, p. 245, new combination.

Holotype.—UM 27231, incomplete left maxilla containing P4 and M1-2 (Dorr, 1952, p. 86; Gingerich, 1983, p. 245). Dell Creek Quarry, Hoback Formation of Wyoming, late Paleocene (late Tiffanian, Ti5, Plesiadapis simonsi/P. gingerichi Lineage Zone of Lofgren et al., 2004).

Material examined.—UALVP 9664, 51524-51527 (total: 5), m2.

Age and occurrence.—Early late Paleocene (early middle Tiffanian, Ti3, Plesiadapis rex /P. churchilli Lineage Zone to early late Tiffanian, Ti5, P. simonsi /P. gingerichi Lineage Zone of Lofgren et al., 2004) of the Western Interior of North America.

Description.—m2: The crown is subrectangular in occlusal outline, and markedly exodaenodont, with enamel overhanging both roots labially. The trigonid is slightly taller than the talonid, and dominated by the swollen, closely appressed protoconid and metaconid; the cusp apices are acute and connected by a low, V-shaped protocristid. A faint paracristid descends directly anteriorly from the apex of the protoconid before turning abruptly lingually to end anterior to the apex of the metaconid; no paraconid is developed. The talonid is longer than the trigonid and deeply basined. The hypoconid is larger and directly opposite to the entoconid; the hypoconulid is smaller and slightly lower than the hypoconid and entoconid, and rests on the prominent, shelf-like postcingulid. The cristid obliqua contacts the postvallid surface slightly labial to the deepest part of the protocristid and can support a small mesoconid (e.g., UALVP 51527); distinct notches are developed in the hypocristid and postcristid. The prominent precingulid originates high on the anterior surface of the metaconid, just ventral to the paracristid, but descends steeply as it runs transversely towards the base of the trigonid beneath the protoconid. The cingulid continues onto the labial margin of the crown and can terminate just posterior to the hypoflexid, or continue around the base of the hypoconid and join the postcingulid (three of five specimens).

Discussion.—Hyopsodontids are small-bodied, herbivorous mammals that are conventionally placed within the Condylarthra (e.g., Van Valen, 1978; Rose, 1981; McKenna and Bell, 1997; Archibald, 1998), although several recent studies (Zack et al., 2005a, 2005b) have revealed an intriguing relationship between several members of the group and afrotherian macroscelideans (elephant shrews). The late Paleocene hyopsodontid “Haplaletes” diminutivus was originally described by Dorr (1952), based on a single specimen (UM 27231) from the Dell Creek Quarry in Wyoming. Dorr (1952) compared UM 27231 with specimens of H. disceptatrix, known only from the late early Paleocene (middle Torrejonian, To2), and considered the two forms virtually identical in anatomy and differing only in size. With the discovery of a larger sample of the species, however, including an important collection from the Judson locality in North Dakota

(Holtzman, 1978), Gingerich (1983) recognized the distinctiveness of this taxon and placed it within a new monotypic genus, Dorraletes.

The specimens referred here closely resemble comparable teeth in Dorraletes diminutivus, but differ in several ways. Most notably, the specimens from Roche Percée are larger (e.g., mean length, m2= 2.38 mm, D. diminutivus from Roche Percée, Saskatchewan, versus mean length, m2 = 2.07 mm, D. diminutivus from Type Chappo locality, Wyoming), and have more pronounced labial exodaenodonty, a weaker paracristid, and a better developed, more nearly complete ectocingulid. The development of this latter feature was initially noted as completely absent in the diagnosis provided by Gingerich (1983); however, Zack et al. (2005b), in their phylogenetic analysis of the hyopsodontids, scored the ectocingulid as “strong and complete at least around the trigonid” (Zack et al., 2005b, Appendix 2, p. 828 and Appendix 3, p. 830) on D. diminutivus. Unfortunately, a cast of the lower molars of D. diminutivus is not available for comparison and only illustrations, in which a distinct ectocingulid does not appear present, are given by Gingerich (1983). Hence, this feature, combined with the difference in size and the other features cited above, could prove to be taxonomically significant but more detailed comparisons are needed.

Despite the relatively small sample size, the discovery of a hyopsodontid condylarth in late middle Tiffanian of western Canada is especially noteworthy because of the dramatic decrease in abundance this group appears to have experienced beginning after the earliest parts of the Tiffanian in the region (Youzwhyshyn, 1988; Zack et al., 2005b; Scott, 2008). In fact, previous to the identification of D. diminutivus at the Roche Percée localities, hyopsodontids were only documented at two post-earliest Tiffanian localities in western Canada and by only a single, fragmentary specimen at each site (see MacDonald, 1996; Webb, 1996). Previously, Gingerich (1983), reporting on a similar decline of hyopsodontids from middle to late Tiffanian localities in Wyoming, suggested that competitive exclusion by plesiadapiform primates and other small, eutherian mammals was the most plausible explanation for this trend. Scott (2008) agreed with this hypothesis but further suggested that the decline in hyopsodontids could represent a small part of a broader, more encompassing faunal and floral reorganization that culminated at the Paleocene-Eocene Thermal Maximum (Rose, 1981; Wing, 2004; Gingerich, 2006). Although a more complete understanding of this faunal change must await further collections and studies, the recognition of *D*. *diminutivus* at the Roche Percée localities represents an important contribution to understanding the decline of the Hyopsodontidae in western Canada and, more broadly, North America.

Family PHENACODONTIDAE Cope, 1881d

Genus PHENACODUS Cope, 1873b

Phenacodus COPE, 1873b, p. 3; COPE, 1885, p. 428; Granger, 1915, p. 332; West, 1973b, p. 135; West, 1976, p. 19; Rose, 1981, p. 70; Thewissen, 1990, p. 45.
Opisthotomus COPE, 1875, p. 15.
Eohyus MARSH, 1894, p. 259 (in part).
Almogaver CRUSAFONT and VILLALTA, 1955, p. 9.

Type species.—*Phenacodus primaevus* Cope, 1873b.

Included species.—*Phenacodus vortmani* (Cope, 1880); *P*. *trilobatus* Cope, 1881a; *P*. *intermedius* Granger, 1915; *P*. *teilhardi* Simpson, 1929b; *P*. *grangeri* Simpson, 1935b; *P*. *matthewi* Simpson, 1935b; *P*. *condali* (Crusafont and Villalta, 1955); *P*. *bisonensis* Gazin, 1956; *P*. *magnus* Thewissen, 1990; *P*. *lemoinei* Thewissen, 1990.

PHENACODUS MAGNUS Thewissen, 1990

Figure 19.4-19.26, Table 27-28

Phenacodus primaevus WEST, 1976, p. 33; HOLTZMAN, 1978, p. 58; WINTERFELD, 1982, p. 100.

Holotype.—YPM-PU 20165, right c, p4, m1-2, left p1-2 fragments, right P4, M1-2, two incisors, and numerous bone fragments (Thewissen, 1990, p. 55).

From Sec 14, T57N, R100W, Fort Union Formation of Wyoming, late Paleocene [late middle Tiffanian, Ti4, Plesiadapis churchilli/P. simonsi Lineage Zone of Lofgren et al., 2004 (see Secord, 2008)]. Thewissen (1990) mistakenly reported YPM-PU 21065 as the holotype but, as noted by Secord (2008), this catalogue number pertains to a specimen of Ptilodus from the Cedar Point Quarry of Wyoming.

Material examined.—UALVP 9651, DP3; UALVP 9692, 51463, P4; UALVP 9691, M2; UALVP 9694, M3; UALVP 9650, 51467, p3; UALVP 51468, p4; UALVP 9697, m1; UALVP 9696, 9701-9702, 51470 (total: 4), m2; UALVP 9695, m3.

Age and occurrence.—Early late Paleocene (late middle Tiffanian, Ti4, Plesiadapis churchilli/P. simonsi Lineage Zone to early late Tiffanian, Ti5, P. simonsi/P. gingerichi Lineage Zone of Lofgren et al. 2004) of the Western Interior of North America.

Description.—Upper dentition, DP3: The crown of DP3 is subtriangular in outline and the principal cusps are massive and closely approximated to each other. The parastylar lobe is considerably elongated and projects anterolabially, while both the stylar shelf and metastylar lobe are reduced. The paracone and slightly smaller metacone arise from a common base and remain joined for much of their total height; the centrocrista is strong and forms a narrow, V-shaped notch between these cusps. The preparacrista has been heavily worn along the anterolingual face of the paracone, but is sharp and well developed between the base of the cusp and the low parastyle; the strong postmetacrista bears a small, bulbous metastylar cusp that separates the ectocingulum and metacingulum. The protocone is inflated but lower than the other principal cusps; the paraconule is small and no metaconule is present. The precingulum is well developed but discontinuous lingually with the postcingulum.

P4: The P4 is triangular in occlusal outline. The principal cusps are swollen, especially near their bases, and their apices are blunted. The paracone is larger and slightly taller than the metacone and the strong centrocrista forms an acute notch between these cusps. Both the preparacrista and postmetacrista are robust; the preparacrista extends almost directly anteriorly from the paracone to join the parastyle, while the postmetacrista joins the ectocingulum+postcingulum posteriorly. The paraconule is bulbous and wedged between the paracone and protocone, whereas the metaconule can be much smaller and low (UALVP 9692) or completely undeveloped (UALVP 51563). The protocone is the largest and tallest cusp; the preprotocrista is stronger than the postprotocrista. The pre- and postcingulum are not continuous lingually and only a small, incipient hypocone is developed on the postcingulum. The enamel on much of the crown is heavily wrinkled, especially on the internal walls of the trigon basin.

M2: The M2 is subrectangular in occlusal outline and the principal cusps are bunodont. The smoothly rounded parastylar lobe is considerably expanded labially and slightly anteriorly. The paracone is only slightly larger than the metacone and extends further labially; the centrocrista is deflected labially to the base of a bulbous mesostyle. Both the paraconule and metaconule are inflated; however, the paraconule is slightly larger and more labial than the metaconule. The base of the protocone is more massive than that of either the paracone or metacone. The hypocone is inflated and supported on the expanded postcingulum. The prominent basal cingulum is continuous around most of the crown and generally low, except as it wraps along the anterolabial and posterolingual corners of the crown. The enamel is wrinkled.

M3: The M3 is more ovate than the M2; the parastylar lobe is expanded anterolabially but the metastyle is more reduced. The cingulum is like that in M2 but discontinuous labial to the paracone. The centrocrista is more robust than on M2,; however, the mesostyle is smaller; a small swelling lingual to the mesostyle is developed on the ectocingulum. The metaconule is half the size of the paraconule and closely appressed to the metacone. The postcingulum is irregularly cuspate and, although distinct, the hypocone is much smaller than on M2. The enamel is heavily wrinkled, and small, irregular cuspules are developed within and along the crests of the trigon basin.

Lower dentition, p3: The p3 of _P_. _magnus_ consists of a massive protoconid and a short talonid. The crown is subrectangular in occlusal outline, with a slight labiolingual expansion posteriorly. A robust crest extends down the anterior surface of the protoconid, but no paraconid is developed. The talonid supports a single, small cusp. The anterior and posterior cingulids are low and discontinuous labially.

p4: The single, isolated p4 (UALVP 51568) is heavily worn and its referral to P. magnus is based primarily on its relatively large size and narrow trigonid. The trigonid is roughly triangular in occlusal outline, with swollen labial and lingual margins; a large interdental facet flattens the anterior margin. From the dimensions of their bases, the protoconid and metaconid would have been inflated and likely equal in size. The talonid is subquadrate in outline, and consists of a large hypoconid and considerably smaller entoconid. The cristid obliqua extends from the hypoconid towards the apex of the metaconid.

m1: UALVP 9697 is a fragmentary m1 missing much of the lingual half and base of the crown. If the crown were complete, the m1 would likely have been pyriform in occlusal outline, with the talonid only slightly wider than the trigonid. The trigonid cusps have been worn nearly flat; the base of the metaconid is massive and there is little evidence that the paraconid was distinct from the paracristid. The base of the hypoconid is enlarged and occupies nearly half the width of the talonid; the base of the entoconid is slightly larger than that of the hypoconulid and the two cusps are closely approximated. The shallow talonid basin is circular and small; there is a small notch between the robust metastylid and entocristid.

m2: In occlusal outline, the m2 crown is subrectangular and small constrictions are developed between the trigonid and talonid. The trigonid is dominated by the low, massive protoconid and metaconid; the paraconid is high and closely appressed to the metaconid, but poorly differentiated from the robust paracristid. A short, broad protocristid encloses the small trigonid basin posteriorly. The hypoconid is massive, and the cristid obliqua is robust and extends slightly on the postvallid towards the apex of the metaconid; the hypoconulid is half the size of the entoconid and more posteriorly positioned than in m1. The talonid basin is even smaller than on m1. No cingulid is developed.

m3: The m3 is nearly the same length as m2, but narrower. The trigonid is higher and slightly wider than the talonid. As on m2, the protoconid and metaconid are massive and dominate the trigonid; however, the metaconid is positioned slightly posterolingual to the protoconid, rather than directly opposite. The swollen paraconid is more distinct than on m1 and m2, and positioned further from the lingual margin; the paracristid extends from the apex of protoconid to the anterior surface of the metaconid. The talonid cusps are swollen and nearly equal in size; the talonid basin is elongate, and open between the entoconid and robust metastylid. A faint anterior cingulid is developed but it does not extend labially.

Discussion.—Phenacodus magnus was first described by Thewissen (1990) in his comprehensive review of the Phenacodontidae and based on specimens from middle-late Tiffanian (Ti4-Ti5) localities in the Western Interior of the United States. Thewissen (1990) distinguished P. magnus from other Paleocene phenacodontids primarily by its large size, but also in having more inflated cusps and a narrower trigonid basin on p4. Secord (2008), however, noted the considerable size overlap between P. magnus and the contemporaneous P. grangeri, and, although recognizing both as valid taxa, suggested that further study might reveal that the two species are members of a single evolutionary lineage; I follow the opinions of Secord (2008) here.

The referred specimens are larger than those of P. grangeri and compare most closely in size with those of P. magnus (e.g., mean length, m2 = 15.1 mm, P. magnus from Roche Percée, Saskatchewan, versus mean length, m2= 15.3 mm, combined samples of P. magnus from localities in the Western Interior of the United States). Additionally, the trigonid of the referred p4 (UALVP 51568) is relatively narrow and compares closely with that in P. magnus (e.g., mean trigonid width, p4 = 9.5 mm, UALVP 51568, versus mean trigonid width, p4 = 9.4 mm, combined samples of P. magnus from localities in the Western Interior of the United States). The specimens differ, however, from homologous teeth of P. magnus in having a more anterolabially projecting parastylar lobe in the upper molars and a wider trigonid relative to the talonid on m2.

Genus ECTOCION Cope, 1882c

Oligotomus COPE, 1873b: COPE, 1882d, p. 182 (in part).
Ectocion COPE, 1882c, p. 522.
Gidleyina SIMPSON, 1935a, p. 240.
Prosthecion PATTERSON and WEST, 1973, p. 2.

Type species.—Oligotomus osbornianus Cope, 1882d.

Included species.—Ectocion parvus Granger, 1915; E. superstes Granger, 1915; E. collinus Russell, 1929; E. major (Patterson and West, 1973); E. mediotuber Thewissen, 1990; E. cedrus Thewissen, 1990; E. ignotum Novacek, Ferrusquia-Villafranca, Flynn, Wyss, and Norell, 1991; E. borealis new species.

ECTOCION BOREALIS new species

Figure 20.1-20.23; Table 29-30

Ectocion osbornianus 1882c, p. 182: FOX, 1990, p. 66.
Ectocion cedrus THEWISSEN, 1990: WEBB, 1996, p. 110.
Ectocion cf. E. cedrus SCOTT, 2008, p. 1064.

Diagnosis.—A species most closely resembling Ectocion cedrus in dental features but differing as follows: slightly smaller, P4 subtriangular in occlusal outline, rather than rectangular, with weak posterior cingulum and paracone and metacone closely appressed, upper molars narrower, relative to their lengths, and metastylar area more reduced, p3 with undeveloped metaconid, p4 paraconid more lingual and metaconid more posterior, and lower molar trigonids narrower and less anteroposteriorly compressed. Also differing from E. collinus as follows: smaller size, upper molar mesostyle stronger and centrocrista more labially deflected, molar paracristids terminating low on anterior surface of metaconid (i.e., not ascending the anterior surface of metaconid), and lower molar trigonids more anteroposteriorly compressed.

Description.—A detailed description of the dentition of Ectocion borealis is provided by Scott (2008), under his presentation of specimens of Ectocion cf. E. cedrus from central Alberta (see discussion below). Specimens of E. borealis recovered from the Roche Percée local fauna are virtually identical to those from Alberta (Scott, 2008). P3 is subtriangular in occlusal outline, the parastylar lobe is expanded anterolabially and supports a small parastyle, the paracone and metacone are closely appressed to each other, and the pre- and postcingulum are strong. P4 is broadly similar to P3 but the parastylar lobe is less projecting, the protocone is better developed, and the postcingulum is much weaker. The upper molars are subrectangular in outline, the swollen principal cusps and slightly lower hypocone are strongly quadritubercular in their arrangement, the parastyle is better developed than on the premolars, the centrocrista extends labially from the apices of the paracone and metacone to an acute mesostyle, and both conules are considerably inflated.

The dentary of E. borealis, previously undescribed, is similar to that of other species of Ectocion (Thewissen, 1990): the horizontal ramus is deep relative to the height of the tooth crowns, the articular surface of the symphysis is elongate anteroposteriorly and roughly rectangular in medial outline, and mental foramen are present beneath the p1 and the p4. None of the crowns for the lower incisors, canine, nor the single rooted p1 is known; however, based on the number and position of the alveoli, these teeth were similar to those in other species of the genus. The p2 consists of an inflated protoconid and a short talonid, bearing a single minute cuspule; the crown of p3 is much like that of p2, but a small paraconid is developed at the anterolingual base of the protoconid, and the talonid basin supports a distinct hypoconid and small entoconid. Both the trigonid and talonid of p4 are better developed than on p3, the paraconid is discrete and is positioned anterior and slightly lingual to the protoconid, the metaconid is developed, and the hypoconid is large and positioned opposite to the smaller entoconid, while the hypoconulid is commonly undeveloped. The lower molars are subrectangular in occlusal outline, the small paraconid is low and closely appressed to the metaconid (but with only minor wear can become completely indistinct from the long, anteriorly arcuate paracristid), the metaconid is taller and larger than the protoconid, and the hypoconid dominates the talonid, while the subequal hypoconulid and entoconid are smaller and more closely approximated.

Etymology.—From borealis, Latin, northern, in reference to the northern distribution of the species.

Holotype.—UALVP 9579, incomplete right dentary with p2-4 and m1-3 (Figs. 20.15-20.17). Roche Percée local fauna, Ravenscrag Formation of Saskatchewan, early late Paleocene [late Tiffanian, Ti4 (see Krause, 1978; Fox, 1990) Plesiadapis churchilli/P. simonsi Lineage Zone of Lofgren et al., 2004].

Other material examined.—In addition to material from the early middle Tiffanian (Ti3) of central Alberta referred elsewhere (see Scott, 2008), UALVP 51474, DP3; UALVP 51473, P3; UALVP 10851, 51475, DP4; UALVP 9684, 9687, 51476, P4; UALVP 9597, 9610, 9685, 10905, 51477-51480 (total: 8), M1; UALVP 9598, 51481-51488 (total: 9), M2; UALVP 9578, 9599, 9600, 9688, 51489-51494 (total: 10), M3; UALVP 9580, incomplete right dentary with p4, m1-3, and alveoli for i3, c, p1-2; UALVP 9581, incomplete right dentary with m1-2, and alveoli for c, p1-3, m3; UALVP 9582, incomplete right dentary containing p2-4, and alveoli for c, p1; UALVP 51495-51496, p3; UALVP 9595, 51497-51499 (total: 4), dp4; UALVP 9583, 9596, 9682, 51500-51507 (total: 11), p4; UALVP 9588, 9589, 9591, 9592, 9601, 9607, 51508-51511 (total: 10), m1; UALVP 9584, 9587, 9590, 9605, 9606, 9678, 9679, 51512-51516 (total: 12), m2; UALVP 9586, 9593, 9608, 9609, 9677, 9683, 51517-51522 (total: 12), m3.

Occurrence.—Early late Paleocene (early middle Tiffanian, Ti3, Plesiadapis rex/P. churchilli Lineage Zone to late middle Tiffanian, Ti4, P. churchilli/P. simonsi Lineage Zone of Lofgren et al. 2004) of the northern part of the Western Interior of North America.

Discussion.—During his studies on the early middle Tiffanian (Ti3) mammals from the DW-2 and Birchwood localities of central Alberta, Scott (2008) described a small sample of teeth that he referred to Ectocion cf. E. cedrus.

Specimens of Ectocion cf. E. cedrus from these two localities can be differentiated from those of E. cedrus primarily by features of the highly diagnostic posterior premolars (Thewissen, 1990), including: P4 with a weaker postcingulum, and more closely approximated paracone and metacone, and p3 with a undeveloped metaconid. Scott (2008) suggested that his referred specimens likely represent a new species of Ectocion, but deferred the naming of this species until a larger sample could be obtained.

The referred specimens from Roche Percée are virtually identical to homologous teeth of Ectocion cf. E. cedrus from DW-2 and Birchwood, and, as recognized here, represent the same taxon. With this large addition, more detailed comparisons between specimens of this previously undescribed species and those of E. cedrus were conducted, and many of the differences cited by Scott (2008) were independently corroborated. Additionally, these comparisons revealed that specimens from DW-2, Birchwood, and Roche Percée have upper molars that are narrower, relative to their lengths, and have more reduced metastylar lobes than those of E. cedrus. Taken together, these differences indicated that specimens from Alberta and Saskatchewan represent a species distinct from E. cedrus and are referred here to a new species of Ectocion, E. borealis.

CONCLUSIONS

Age of the Roche Percée local fauna

The age and correlation of Cenozoic mammal assemblages in North America is based principally on the system of North American Land Mammal ages (NALMAs) and their subdivisions, initially proposed as "provincial ages" by the Wood Committee (Wood et al., 1941). Despite recent advances in magnetostratigraphy and radioisotopic dating (e.g., Secord et al., 2006), the vast majority of these NALMAs remain as informal geochronologic ages (see NACSN, 2005), largely because they are not defined on fossil sequences in measured stratigraphic sections (Secord et al., 2006). Most NALMAs, rather, are biochronological units and "recognize distinct intervals of time based on the evolution of fossil mammals" (Woodburne, 2004b, p. 15); for example, the Tiffanian NALMA is described as the interval between the first appearance of the plesiadapiform primate Plesiadapis and the first appearance of rodents (Lofgren et al., 2004). Although lacking a more direct tie to the rock record, mammal-based biochronology continues to provide some of the finest resolution possible for non-marine sections of the Cenozoic in North America, and the zonation scheme provided by Woodburne (2004a) is followed here.

Within the Paleocene, four NALMAs are currently recognized, from oldest to youngest: Puercan, Torrejonian, Tiffanian, and Clarkforkian (Lofgren et al. 2004). The mammal assemblage recovered from the Roche Percée localities can be easily correlated with the Tiffanian, based on the presence of the plesiadapiform primate Carpodaptes (see Krause, 1978; Fox, 2002), Litolestes, Raphictis, Arctocyon (=Mentoclaenodon, see Kondrashov and Lucas, 2004), and hyopsodontid Dorraletes, taxa that are restricted elsewhere in North American to the Tiffanian (Lofgren et al., 2004). This correlation is further supported by the taxa present in the fauna that make their first appearances during the Tiffanian, including the ptilodontid multituberculate Prochetodon (see Krause, 1987), Palaeosinopa, Titanoides, Didymictis, Thryptacodon, and Ectocion.

Building on the work of earlier authors (e.g., Gingerich, 1976; Archibald et al., 1987), Lofgren et al. (2004) further subdivided the Tiffanian into six lineage zones, with each zone being defined on the successive first and last appearances of species of Plesiadapis that collectively are thought to represent a single evolving lineage. Based in part on the presence of P. churchilli, Krause (1978) suggested that the age of the Roche Percée local fauna is late middle Tiffanian, within the P. churchilli/P. simonsi Lineage Zone (Ti4) of Lofgren et al. (2004). In support of Krause's (1978) assignment, 25 of the 39 taxa identified by Lofgren et al. (2004) as being characteristic of the late middle Tiffanian [e.g., Litocherus, Mimetodon (see Krause, 1977), Unuchinia, and Carpodaptes] are now known to be present in the Roche Percée local fauna, while an additional three supraspecific taxa previously known only before and after the late middle Tiffanian were recovered within the fauna.

Secord et al. (2006) recently redefined several Tiffanian NALMA subdivisions within the Bighorn Basin of Wyoming, based on new material, a newly restrictive stratigraphic range for Plesiadapis churchilli, and the first radioisotopic calibration point for the late Paleocene. Relevant to the current discussion, Secord et al. (2006) split the P. churchilli/P. simonsi Lineage Zone (Ti4) of Lofgren et al. (2004) into two zones, the P. churchilli Lineage Zone (Ti4a) and the temporally younger Phenacolemur Interval Zone (Ti4b). While these revised subdivisions are still unproven outside of the Bighorn Basin, the occurrence of P. churchilli and Carpodaptes stonleyi (see Fox, 2002) suggest that the age of the Roche Percée local fauna is early in the middle late Tiffanian, part of the P. churchilli Lineage Zone (Ti4a) of Secord et al. (2006). The presence of Ptilodus kummae (see Krause, 1977), Prochetodon foxi (see Krause, 1987), Litolestes, Bessoecetor pilodontus, Palaeosinopa, Arctocyon mumak, Phenacodus magnus, and Cyriacotherium (see Rose and Krause, 1982), taxa that make their first appearances within the Bighorn Basin during this time interval (Secord et al., 2006; Secord, 2008), as well as the absence of the plesiadapiform primate Phenacolemur, strengthens this age assignment.

Faunal comparisons

With several notable exceptions (e.g., Rose, 1981; Gunnell, 1994; Scott, 2008; Secord, 2008), middle Tiffanian mammal assemblages in North America remain relatively poorly sampled and studied, especially in comparison to slightly older and younger faunas. Of reliably comparable middle Tiffanian faunas, the Roche Percée local fauna is most similar to the early middle Tiffanian (Ti3) assemblage of mammals from the Blindman River localities in central Alberta (Scott, 2008), both in general composition and in possessing several uniquely shared taxa (Figure 31). Based on the latest, exhaustive faunal list of the Blindman River local fauna (Scott, 2008), 25 genera and 11 species are identified as occurring at both localities, and among these, two species (Bessoecetor krausei and Raphictis machaera) are shared uniquely. The Birchwood locality fauna (Webb, 1996) is smaller and less taxonomically diverse than the Blindman River fauna but similar in composition, and also closely resembles the local fauna from the Roche Percée localities (see faunal lists provided by Scott, 2008).

Two other middle Tiffanian faunas show a close similarity with the Roche Percée local fauna. The early middle Tiffanian (Ti3) Chappo Type locality fauna of Wyoming shares 23 genera and 7 species with the Roche Percée assemblage, while the middle Tiffanian (Ti3 and Ti4, respectively) faunas from the Brisbane and Judson localities of North Dakota share 21 genera and 7 species. Both these faunas are slightly more similar to the Roche Percée local fauna than the early middle Tiffanian (Ti3) Cedar Point Quarry fauna of northern Wyoming (Figure 31).

The fauna of the late middle Tiffanian (Ti4) Divide Quarry in the Bighorn Basin of northern Wyoming also bears a strong resemblance to that from the Roche Percée localities, with the two faunas sharing 21 genera in common and 10 species, the second highest number of shared species among the local faunas used in this comparison. One taxon is uniquely shared (Carpodaptes stonleyi) between these faunas and, as noted earlier, is an index taxon for the P. churchilli Lineage Zone of Secord et al. (2006). In addition, the number of known shared genera and species between these two faunas increases if several of the tentative taxonomic assignments reported in the latest faunal list for the Divide Quarry (e.g., ?Mimetodon silberlingi, ?Raphictis, and cf. Prodiacodon sp.) are confirmed (Secord, 2008). Other late middle Tiffanian faunas from the northern parts of the United States, the Long Draw Quarry and the Croc Tooth Quarry, although considerably smaller in sample size, closely resemble the Roche Percée local fauna (Secord, 2008).

In comparison to late middle Tiffanian (Ti4) faunas from western Canada, the Roche Percée assemblage is remarkably similar in general composition to that of the smaller Swan Hills local fauna from central Alberta (Stonley, 1988), especially in light of the relatively small number of specimens collected from the Swan Hills localities. Based on the most recent faunal list provided by Fox (1990), 19 genera and 9 species are shared between the two faunas (Figure 31). The Police Point fauna (Krishtalka, 1973) from the Cypress Hills area of southeastern Alberta is smaller than the Swan Hills local fauna and is less similar to that of the Roche Percée assemblage (see Fox, 1990). The comparable fauna overlapping the least with the Roche Percée is the early late Tiffanian (Ti5) Princeton Quarry fauna from northern Wyoming, with 18 genera and only 2 species occurring at both localities.

Given the late middle Tiffanian (Ti4) age of the Roche Percée localities and the strong resemblance it bears to the early middle Tiffanian (Ti3) Blindman River local fauna, it could be suggested that the Roche Percée local fauna may be very early within the late middle Tiffanian and slightly older than other, more typical late middle Tiffanian faunas (e.g., Divide Quarry fauna, Swan Hills local fauna). It must be noted, however, that many of the shared taxa between the Roche Percée local fauna and the early middle Tiffanian Blindman River local fauna are stratigraphically long ranging (e.g., the ptilodontid multituberculate Mesodma pygmaea, Diacocherus, and Arctocyon) and all of the uniquely shared taxa between these faunas are newly described mammals whose stratigraphic and geographic ranges have yet to be fully understood. Furthermore, aside from the Blindman River local fauna, the Roche Percée local fauna is more similar to the

Divide Quarry fauna than it is to any of the other early middle Tiffanian assemblages in this comparison and, as noted earlier, the similarity between the Divide Quarry and Roche Percée localities would be increased with the confirmation of several tentative identifications. I therefore consider the Roche Percée local fauna to be nearly contemporaneous to the early middle Tiffanian (Ti4) Divide Quarry fauna and the Swan Hills local fauna.

Implications for further research

With over 2000 catalogued specimens and nearly 50 described species (see Appendix 1), the Roche Percée local fauna is the largest and most taxonomically diverse late middle Tiffanian (Ti4) mammal assemblage yet known. The identifications and descriptions provided for these mammals permit, for the first time, detailed and thorough comparisons to near contemporaneous localities in the Western Interior of North America; these types of comparisons are fundamental in our understanding of the evolutionary history of mammals, and provide the opportunity to test and refine the NALMAs beyond the American mammalian succession, on which they are largely based. Comprehensive descriptions of mammals from the Roche Percée localities and taxonomically similar faunas additionally help to address broader questions on paleoecology, diversity, and the phylogeny and evolution of Paleogene mammals following the K/Pg transition.

REFERENCES

ALROY, J. 1998. Cope’s rule and the dynamics of body mass evolution in North American fossil mammals. Science, 280:731-734.

ARCHIBALD, J. D. 1982. A study of Mammalia and geology across the Cretaceous-Tertiary boundary in Garfield County, Montana. The University of California Publications in Geological Sciences, 122:1-286.

ARCHIBALD, J. D. 1983. Structure of the K-T mammal radiation in North America: speculation on turnover rates and trophic structure. Acta Palaeontologica Polonica, 28:7-17.

ARCHIBALD, J. D. 1998. Archaic ungulates “Condylarthra”, p. 292-331. In C. M. Janis, K. M. Scott, and L. L. Jacobs (eds.), Evolution of Tertiary Mammals of North America. Volume 1: Terrestrial Carnivores, Ungulates, and Ungulatelike Mammals. Cambridge University Press, Cambridge, United Kingdom.

ARCHIBALD, J. D., W. A. CLEMENS, P. D. GINGERICH, D. W. KRAUSE, E. H. LINDSAY, and K. D. ROSE. 1987. First North American land mammal ages of the Cenozoic era, p. 24-76. In M. O. Woodburne (ed.), Cenozoic Mammals of North America: Geochronology and Biostratigraphy. University of California Press, Berkeley.

ASHER, R. J., M. J. NOVACEK, and J. H. GEISLER. 2003. Relationships of endemic African mammals and their fossil relatives based on morphological and molecular evidence. Journal of Mammalian Evolution, 10:131-194.

ASHER, R.J., M. C. MCKENNA, R. J. EMRY, A. R. TABRUM, and D. G. KRON. 2002. Morphology and relationships of Apternodus and other extinct, zalambdodont, placental mammals. Bulletin of the American Museum of Natural History, 273:1-117.

BLAINVILLE, de, H. M. D. 1841. Ostéographie, et description iconographique des Mammifères récents et fossils (Carnivores), Volume. I et II. Paris.

BLOCH, J.I. 2001. Mammalian paleontology of freshwater limestones from the Paleocene-Eocene of the Clarks Fork Basin, Wyoming. Unpublished Ph. D. dissertation, The University of Michigan, Ann Arbor, 358 p.

BLOCH, J. I. and D. M. BOYER. 2001. Taphonomy of small mammals in freshwater limestones from the Paleocene of the Clarks Fork Basin, p. 185-198. In P.D. Gingerich (ed.), Paleocene-Eocene Stratigraphy and Biotic Change in the Bighorn and Clarks Fork Basins, Wyoming. The University of Michigan Papers on Paleontology, 33.

BLOCH, J. I., R. SECORD, and P. D. GINGERICH. 2004a. Systematics and phylogeny of late Paleocene and early Eocene Palaeoryctinae (Mammalia, Insectivora) from the Clarks Fork and Bighorn basins, Wyoming. Contributions from the Museum of Paleontology, The University of Michigan, 31:119-154.

BLOCH, J. I., D. M. BOYER, M. T. SILCOX, and P. HOUDE. 2004b. New skeletons of Paleocene-Eocene Labidolemur kayi (Mammalia, Apatemyidae): ecomorphology and relationship of apatemyids to primates and other mammals. Journal of Vertebrate Paleontology, 24, Supplement to Number 3: 40A.

BOWDICH, T. E. 1821. An analysis of the natural classifications of Mammalia for the use of students and travellers. J. Smith, Paris, 115 p.

BOWN, T. M. and D. SCHANKLER. 1982. A review of the Proteutheria and Insectivora of the Willwood Formation (Lower Eocene), Bighorn Basin, Wyoming. U. S. Geological Survey, Bulletin 1523:1-79.

BOWN, T. M. and E. L. SIMONS. 1987. New Oligocene Ptolemaiidae (Mammalia: ?Pantolesta) from the Jebel Qatrani Formation, Fayum depression, Egypt. Journal of Vertebrate Paleontology, 7:311-324.

BUTLER, P. M. 1956. The skull of Ictops and the classification of the Insectivora. Proceedings of the Zoological Society of London, 126:453-481.

BUTLER, P. M. 1988. Phylogeny of the insectivores, p. 253-265. In M. J. Benton (ed.), The Phylogeny and Classification of the Tetrapods. Volume 2:

Mammals. Systematics Association Special Volume 35B, Clarendon Press, Oxford.

CLEMENS, W. A. 1964. Records of the fossil mammal Sinclairella, Family Apatemyidae, from the Chadronian and Orellan. University of Kansas Publications, Museum of Natural History, 14:483-491.

CLEMENS, W. A. 1966. Fossil mammals of the type Lance Formation, Wyoming. Part II. Marsupialia. The University of California Publications in Geological Sciences, 62:1-122.

CLEMENS, W. A. 2002. Evolution of the mammalian fauna across the Cretaceous-Tertiary boundary in northeastern Montana and other areas in the Western Interior, p. 217-245. In. J. H. Hartman, K. R. Johnson, and D. J. Nichols (eds.), The Hell Creek Formation and the Cretaceous-Tertiary Boundary in the Northern Great Plain: An Integrated Continental Record of the End of the Cretaceous. Geological Society of America Special Paper, 361.

CLEMENS, W. A. 2006. Early Paleocene (Puercan) peradectid marsupials from northeastern Montana, North American Western Interior. Palaeontographica Abteilung A, 277:19-31.

COPE, E. D. 1872. Second account of new Vertebrata from the Bridger Eocene. Proceedings of the American Philosophical Society, 12 (separata Paleontological Bulletin no. 2):466-468. [dated August 3]

COPE, E. D. 1873a. On the short-footed Ungulata of the Eocene of Wyoming. Proceedings of the American Philosophical Society, 13:38-74.

COPE, E. D. 1873b. On the extinct Vertebrata of the Eocene of Wyoming observed by the expedition of 1872 with notes on the geology. United States Geological Survey of Montana, Idaho, Wyoming, and Utah. Sixth Annual Report of the United States Geological Survey of the Territories by F. V. Hayden:546-649.

COPE, E. D. 1874. Report of the vertebrate fossils discovered in New Mexico, with descriptions of new species. Annual Report, Chief of Engineers, 1874, Appendix FF, Washington (Government Printing Office) 1874:3-18.

COPE, E. D. 1875. Systematic catalogue of Vertebrata of the Eocene of New Mexico collected in 1874. Geographical Surveys west of the 100th Meridian, G. M. Wheeler, Corps of Engineers, United States Army, Washington:1-37.

COPE, E. D. 1880. On the genera of the Creodonta. Proceedings of the American Philosophical Society, 19:76-82.

COPE, E. D. 1881a. On the Vertebrata of the Wind River Eocene beds of Wyoming. Bulletin of the U. S. Geographical and Geological Survey of the Territories, 6:183-202.

COPE, E. D. 1881b. Mammalia of the lower Eocene beds. American Naturalist, 15:337-338.

COPE, E. D. 1881c. Notes on Creodonta. American Naturalist, 15:1018-1020.

COPE, E. D. 1881d. On some Mammalia of the lowest Eocene beds of New Mexico. Proceedings of the American Philosophical Society, 19:484-495.

COPE, E. D. 1882a. Synopsis of the Vertebrata of the Puerco Eocene epoch. Proceedings of the American Philosophical Society, 20:461-471.

COPE, E. D. 1882b. Notes on Eocene Mammalia. American Naturalist, 16:522.

COPE, E. D. 1882c. Contributions to the history of the Vertebrata of the lower Eocene of Wyoming and New Mexico, made during 1881. Proceedings of the Academy of Natural Sciences Philadelphia, 20:139-197.

COPE, E. D. 1883a. The ancestor of Coryphodon. American Naturalist, 17:406-407.

COPE, E. D. 1883b. On the mutual relationships of the bunotherian Mammalia. Proceedings of the Academy of Natural Sciences Philadelphia, 35:77-83.

COPE, E. D. 1883c. First addition to the fauna of the Puerco Eocene. Proceedings of the American Philosophical Society, 20:545-563.

COPE, E. D. 1884a. Second addition to the knowledge of the fauna of the Puerco Epoch. Proceedings of the American Philosophical Society, 21: 309-324.

COPE, E. D. 1884b. The Creodonta. American Naturalist, 18:255-267.

COPE, E. D. 1885. The Vertebrata of the Tertiary Formations of the West. United States Geological Survey of the Territories, 3:1-1009.

COPE, E. D. 1888. Synopsis of the vertebrate fauna of the Puerco Series. Transactions of the American Philosophical Society, 15, new series:298-361.

CROCHET, J.-Y. 1977a. Les Didelphidae (Marsupicarnivora, Marsupialia) holartiques tertiares. Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences, Série D, 284:357-360.

CROCHET, J.-Y. 1977b. Les didelphidés paléocènes holartiques: historique et tendances évolutives. Géobios, Mémoire Special, 1:124-134.

CROCHET, J.-Y. 1979. Diversité systématique des Didelphidae (Marsupialia) Européens Tertiares. Géobios, 12:365-378.

CRUSAFONT, M. and J. F. VILLALTA. 1955. Almogaver, un nuevo primate del Eocene Pirenaico. Il cursillo Estudios Geologicos, Madrid, 22:1-11.

DORR, J. A. 1952. Early Cenozoic stratigraphy and vertebrate paleontology of the Hoback Basin, Wyoming. Bulletin of the Geological Society of America, 63:59-94.

DORR, J. A. 1958. Early Cenozoic vertebrate paleontology, sedimentation, and orogeny in central western Wyoming. Bulletin of the Geological Society of America, 69:1217-1244.

DORR, J. A. 1977. Partial skull of Paleosinopa [Palaeosinopa] simpsoni (Mammalia, Insectivora), latest Paleocene Hoback Formation, central western Wyoming, with some general remarks on the family Pantolestidae. Contributions from the Museum of Paleontology, The University of Michigan, 24:281-307.

EBERLE, J. J. and M. C. MCKENNA. 2002. Early Eocene Leptictida, Pantolesta, Creodonta, Carnivora, and Mesonychidae (Mammalia) from the Eureka Sound Group, Ellesmere Island, Nunavut. Canadian Journal of Earth Sciences, 39:899-910.

FISCHER DE WALDHEIM, G. 1817. Adversaria zoologica. Part 2. De systemata mammalium. Mémoire de lat Societé Imperiale Naturalistes, Mosquae, 5:368-391.

FLYNN, J. J. and H. GALIANO. 1982. Phylogeny of early Tertiary Carnivora, with a description of a new species of Protictis from the middle Eocene of northwestern Wyoming. American Museum Novitates, Number 2725:1-64.

FOOTE, M., J. P. HUNTER, C. M. JANIS, and J. J. SEPKOSKI. 1999. Evolutionary and preservational constraints on origins of biologic groups: divergence times of eutherian mammals. Science, 283:1310-1314.

FOX, R. C. 1984. First North American record the Paleocene primate Saxonella. Journal of Paleontology, 58:892-894.

FOX, R. C. 1987. Palaeontology and the early evolution of marsupials, p. 161-169. In M. Archer (ed.), Possums and Opossums: Studies in Evolution, Volume 1. Surrey Beatty and Sons and the Royal Zoological Society of New South Wales, Sydney.

FOX, R. C. 1990. The succession of Paleocene mammals in western Canada, pp. 51-70. In T. M. Bown and K. D. Rose (eds.), Dawn of the Age of Mammals in the Northern Part of the Rocky Mountain Interior. Geological Society of America Special Paper, 243.

FOX, R. C. 1991. Saxonella (Plesiadapiformes; ?Primates) in North America: S. naylori, sp. nov., from the late Paleocene of Alberta, Canada. Journal of Vertebrate Paleontology, 11:334-349.

FOX, R. C. 2002. The dentition and relationships of Carpodaptes cygneus (Russell) (Carpolestidae, Plesiadapiformes, Mammalia), from the late Paleocene of Alberta, Canada. Journal of Paleontology, 76:864-881.

FOX, R. C. and G. P. YOUZWYSHYN. 1994. New primitive carnivorans (Mammalia) from the Paleocene of western Canada, and their bearing on relationships of the order. Journal of Vertebrate Paleontology, 14:382-404.

FRASER, F. J., F. D. MCLEARN, L. S. RUSSELL, P. S. WARREN, and R. T. D. WICKENDEN. 1935. Geology of southern Saskatchewan. Geological Survey of Canada Memoir 176, 137 p.

GAZIN, C. L. 1952. The Lower Eocene Knight Formation of western Wyoming and its mammalian faunas. Smithsonian Miscellaneous Collections, 117:1-82.

GAZIN, C. L. 1956. Paleocene mammalian faunas of the Bison Basin in south-central Wyoming. Smithsonian Miscellaneous Collections, 131:1-57.

GHEERBRANT, E. 1991. Todralestes variabilis, n.g., n.sp., new proteutherian (Eutheria, Todralestidae fam. nov.) from the Paleocene of Morocco. Comptes Rendus de l’Académie des Sciences Paris, 312:1249-1255.

GIDLEY, J. W. 1917. Notice of a new Paleocene mammal, a possible relative of the titanotheres. Proceedings of the United States National Museum, 52:431-435.

GIDLEY, J. W. 1919. New species of claenodonts from the Fort Union (basal Eocene) of Montana. Bulletin of the American Museum of Natural History, 41:541-556.

GIEBEL, C. G. 1855. Die Säugetiere in zoologischer, anatomischer und palaeontologischer Beziehung umfassend dargestellt. Abel, Leipzig, 1108 p.

GILL, T. 1872. Arrangement of the families of mammals with analytical tables. Smithsonian Miscellaneous Collections, 11:1-98.

GINGERICH, P. D. 1976. Cranial anatomy and evolution of Early Tertiary Plesiadapidae (Mammalia, Primates). The University of Michigan Papers on Paleontology, 15:1-141.

GINGERICH, P. D. 1980. A new species of Palaeosinopa (Insectivora: Pantolestidae) from the late Paleocene of western North America. Journal of Mammalogy, 61:449-454.

GINGERICH, P. D. 1982a. Aaptoryctes (Palaeoryctidae) and Thelysia (Palaeoryctidae?): New insectivorous mammals from the late Paleocene and early Eocene of western North America. Contributions from the Museum of Paleontology, The University of Michigan, 26:37-47.

GINGERICH, P. D. 1982b. Studies of Paleocene and early Eocene Apatemyidae (Mammalia, Insectivora). II. Labidolemur and Apatemys from the early

Wasatchian of the Clarks Fork Basin, Wyoming. Contributions from the Museum of Paleontology, The University of Michigan, 26:57-69.

GINGERICH, P. D. 1983. New Adapisoricidae, Pentacodontidae, and Hyopsodontidae (Mammalia, Insectivora and Condylarthra) from the late Paleocene of Wyoming and Colorado. Contributions from the Museum of Paleontology, The University of Michigan, 26:227-255.

GINGERICH, P. D. 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. Journal of Paleontology, 60:1135-1137.

GINGERICH, P. D. 1987. Early Eocene bats (Mammalia, Chiroptera) and other vertebrates in freshwater limestones of the Willwood Formation, Clark's Fork Basin, Wyoming. Contributions from the Museum of Paleontology, The University of Michigan, 27:275-320.

GINGERICH, P. D. 1989. New earliest Wasatchian mammalian fauna from the Eocene of northwestern Wyoming: composition and diversity in a rarely sampled high-floodplain assemblage. The University of Michigan Papers on Paleontology, 28:1-97.

GINGERICH, P. D. 1996. New species of Titanoides (Mammalia, Pantodonta) from the middle Clarkforkian (late Paleocene) of northwestern Wyoming. Contributions from the Museum of Paleontology, The University of Michigan, 29:403-412.

GINGERICH, P. D. 2001. Biostratigraphy of the continental Paleocene-Eocene boundary interval on Polecat Bench in the northern Bighorn Basin, p. 37-71. In P.D. Gingerich (ed.), Paleocene-Eocene Stratigraphy and Biotic Change in the Bighorn and Clarks Fork Basins, Wyoming. The University of Michigan Museum Papers on Paleontology, 33.

GINGERICH, P. D. 2006. Environment and evolution through the Paleocene-Eocene thermal maximum. Trends in Ecology and Evolution, 21:246-253.

GINGERICH, P. D. and D. A. WINKLER. 1979. Patterns of variation and correlation in the dentition of the red fox, Vulpes vulpes. Journal of Mammalogy, 60:691-704.

GINGERICH, P. D. and K. D. ROSE. 1982. Studies of Paleocene and early Eocene Apatemyidae (Mammalia, Insectivora). I. Dentition of Clarkforkian Labidolemur kayi. Contributions from the Museum of Paleontology, The University of Michigan, 26:49-55.

GINGERICH, P. D. and D. A. WINKLER. 1985. Systematics of Paleocene Viverravidae (Mammalia, Carnivora) in the Bighorn Basin and Clark's Fork Basin, Wyoming. Contributions from the Museum of Paleontology, The University of Michigan, 27:87-128.

GRANGER, W. 1915. Part III: Order Condylarthra. In W. D. Matthew and W. Granger (auths.), A revision of the lower Eocene Wasatch and Wind River faunas. Bulletin of the American Museum of Natural History, 39:329-361.

GREGORY, W. K. 1910. The orders of mammals. Bulletin of the American Museum of Natural History, 27:1-254.

GUNNELL, G. F. 1988. New species of Unuchinia (Mammalia: Insectivora) from the middle Paleocene of North America. Journal of Paleontology, 62:139-141.

GUNNELL, G. F. 1994. Paleocene mammals and faunal analysis of the Chappo Type Locality (Tiffanian), Green River Basin, Wyoming. Journal of Vertebrate Paleontology, 14:81-104.

GUNNELL, G. F, T. M. BOWN, J. I. BLOCH, and D. M. BOYER. 2008. "Proteutheria", p. 63-81. In C. M. Janis, G. F. Gunnell, and M. D. Uhen (eds.), Evolution of Tertiary Mammals of North America. Volume 2: Small Mammals, Xenathrans, and Marine Mammals. Cambridge University Press, Cambridge, United Kingdom.

HAECKEL, E. 1866. Generelle Morphologie der Organismen. Volume 2: Systematische Einteinlung in die allgemeine Entwickelungsgeschichte. Georg Reimer, Berlin.

HARTMAN, J. H. and A. J. KIHM. 1991. Stratigraphic distribution of Titanoides (Mammalia: Pantodonta) in the Fort Union Group (Paleocene) of North Dakota, p. 207-215. In J. E. Christopher and F. M. Haidl (eds.), Sixth International Williston Basin Symposium. Saskatchewan Geological Society, Special Publication 11.

HOLTZMAN, R. C. 1978. Late Paleocene mammals of the Tongue River Formation, western North Dakota. Report of Investigation, North Dakota Geological Survey, 65:1-88.

HOOKER, J. J. 2001. Tarsals of the extinct insectivoran family Nyctitheriidae (Mammalia): evidence for archontan relationships. Zoological Journal of the Linnean Society, 135:501-529.

ILLIGER, C. 1811. Prodromus systematis mammalium et avium additis terminis zoographicus ultriusque classis. C. Salfeld, Berlin, 301 p.

JENKINS, F. A. and D. W. KRAUSE. 1983. Adaptations for climbing in North American Multituberculates (Mammalia). Science, 220:712-715.

JEPSEN, G. L. 1930. Stratigraphy and paleontology of the Paleocene of northeastern Park County, Wyoming. Proceedings of the American Philosophical Society, 69:463-528.

JEPSEN, G. L. 1934. A revision of the American Apatemyidae and the description of a new genus, Sinclairella, from the White River Oligocene of South Dakota. Proceedings of the American Philosophical Society, 74:287-305.

JEPSEN, G. L. 1940. Paleocene faunas of the Polecat Bench Formation, Wyoming. Proceedings of the American Philosophical Society, 83: 217-340.

JOHANSON, Z. 1996. New marsupial from the Fort Union Formation, Swain Quarry, Wyoming. Journal of Paleontology, 70:1023-1031.

JOHNSON, G. D., P. A. MURRY, and J. E. STORER. 1994. Recovery of vertebrate microfossils. Proceedings of the South Dakota Academy of Science, 73:211-230.

KELLNER and M. C. MCKENNA. 1996. A leptictid mammal from the Hsanda Gol Formation (Oligocene), central Mongolia, with comments on some Palaeoryctidae. American Museum Novitates, Number 3168, 13 p.

KENT, D. M. and J. E. CHRISTOPHER. 1994. Geological history of the Williston Basin and Sweetgrass Arch, p. 421-429. In G. D. Mossop and I. Shetson (comp.), Geological Atlas of the Western Canada Sedimentary Basin. Canadian Society of Petroleum Geologists and Alberta Research Council.

KIHM, A. J. and J. H. HARTMAN. 2004. A reevaluation of the biochronology of the Brisbane and Judson local faunas (late Paleocene) of North Dakota. Bulletin of Carnegie Museum of Natural History, 36:97-107.

KOENIGSWALD, W. V. 1980. Das Skelett eines Pantolestiden (Proteutheria, Mammalia) aus dem mittleren Eozän von Messel bei Darmstadt. Paläontologische Zeitschrift, 54:267-287.

KOENIGSWALD, W. v. 1987a. Apatemyiden-Skelette aus dem Mitteleozän von Messel und ihre paläobiologische Aussage. Carolinea, 45:31-35.

KOENIGSWALD, W. V. 1987b. Ein zweites Skelett von Buxolestes (Pantolestidae, Proteutheria, Mammalia) aus dem Mitteleozän von Messel bei Darmstadt. Carolinea, 45:36-42.

KOENIGSWALD, W. v. 1990. Die Paläobiologie der Apatemyiden (Insectivora s. l.) und die Ausdeutung der Skelettfunde von Heterohyus nanus aus dem Mitteleozän von Messel bei Darmstadt. Palaeontographica Abteilung A, 210:41-77.

KOENIGSWALD, W. v. and H.-P. SCHIERNING. 1987. The ecological niche of an extinct group of mammals, the early Tertiary apatemyids. Nature, 326:595-597.

KOENIGSWALD, W. v., K. D. ROSE, L. GRANDE, and R. D. MARTIN. 2005a. Die Lebensweise eozäner Säugetiere (Pantolestidae und Apatemyidae) aus Messel (Europa) im Vergleich zu neuen Skelettfunden aus dem Fossil Butte Member von Wyoming. Geologisches Jahrbuch Hessen, 132:43-52.

KOENIGSWALD, W. v., K. D. ROSE, L. GRANDE, and R. D. MARTIN. 2005b. First apatemyid skeleton from the lower Eocene Fossil Butte Member

Wyoming, compared to the European apatemyid from Messel, Germany. Palaeontographica Abteilung A, 272:149-169.

KONDRASHOV, P. E. and S. G. LUCAS. 2004. Arctocyon (Mammalia, Arctocyonidae) from the Paleocene of North America, p. 11-20. In S. G. Lucas, K. E. Zeigler, and P. E. Kondrashov (eds.), Paleogene Mammals. Bulletin of the New Mexico Museum of Natural History and Science, 26.

KÖPPEN, W. and GEIGER, R. 1936. Handluch der Klimatologie. Volume 1. Das geographische System der Klimate. Verlag von Gebrüder Borntraeger, Berlin, 144 p.

KORTH, W. W. 2008. Marsupialia, p. 39-47. In C. M. Janis, G. F. Gunnell, and M. D. Uhen (eds.), Evolution of Tertiary Mammals of North America. Volume 2: Small Mammals, Xenathrans, and Marine Mammals. Cambridge University Press, Cambridge, United Kingdom.

KRAUSE, D. W. 1977. Paleocene multituberculates (Mammalia) of the Roche Percée local fauna, Ravenscrag Formation, Saskatchewan, Canada. Palaeontographica Abteilung A, 159:1-36.

KRAUSE, D. W. 1978. Paleocene primates from western Canada. Canadian Journal of Earth Sciences, 15: 1250-1271.

KRAUSE, D. W. 1987. Systematic revision of the genus Prochetodon (Ptilodontidae, Multituberculata) from the late Paleocene and early Eocene of the western North America. Contributions from the Museum of Paleontology, The University of Michigan, 27:221-236.

KRAUSE, D. W. and P. D. GINGERICH. 1983. Mammalian fauna from Douglass Quarry, earliest Tiffanian (late Paleocene) of eastern Crazy Mountain Basin, Montana. Contributions from the Museum of Paleontology, University of Michigan, 26:157-196.

KRAUSE, D. W. and F. A. JENKINS. 1983. The postcranial skeleton of North American multituberculates. Bulletin of the Museum of Comparative Zoology, 150:199-246.

KRISHTALKA, L. 1973. Late Paleocene mammals from the Cypress Hills, Alberta. Special Publication of the Museum, Texas Tech University, 2:1-77.

KRISHTALKA, L. 1976a. Early Tertiary Adapisoricidae and Erinaceidae (Mammalia, Insectivora) of North America. Bulletin of Carnegie Museum of Natural History, 1:1-40.

KRISHTALKA, L. 1976b. North American Nyctitheriidae (Mammalia, Insectivora). Annals of Carnegie Museum, 46:7-28.

KRISHTALKA, L. and T. SETOGUCHI. 1977. Paleontology and geology of the Badwater Creek Area, Central Wyoming. Part 13. Annals of Carnegie Museum, 46:71-99.

KRISHTALKA, L. and R. K. STUCKY. 1983. Paleocene and Eocene marsupials of North America. Annals of Carnegie Museum, 52:229-263.

KUMAR, S. and S. B. HEDGES. 1998. A molecular timescale for vertebrate evolution. Nature, 329:917-920.

LEMOINE, V. 1883. Etude sur le <u>Neoplagiaulax</u> de la faune éocène inférieure des environs de Reims. Bulletin de la Société Géologique de France, 3e série, 11:249-271.

LEMOINE, V. 1891. Études d'ensemble sur les dents des mammifères fossiles des environs Reims. Bulletin de la Société Geologique de France, 3e série, 19:263-290.

LEMOINE, V. 1896. Études sur les couches de l'Éocène inférieur remois qui continental la faune Cernaysienne, et sur deux types nouveux de cette faune. Bulletin de la Société Geologique de France, 3 série, 24:333-344.

LERBEKMO, J. F. 1985. Magnetostratigraphic and biostratigraphic correlations of Maastrichtian to early Paleocene strata between south-central Alberta and southwestern Saskatchewan. Bulletin of Canadian Petroleum Geologists, 33:213-226.

LILLEGRAVEN, J. A. 1969. Latest Cretaceous mammals of upper part of the Edmonton Formation of Alberta, Canada, and review of marsupial-placental dichotomy in mammalian evolution. The University of Kansas Paleontological Contributions, 50 (Vertebrata 12):1-122.

LILLEGRAVEN, J. A. and J. J. EBERLE. 1999. Vertebrate faunal changes through Lancian and Puercan time in southern Wyoming. Journal of Paleontology, 73:691-710.

LINNAEUS, C. 1758. Systema naturae per regna tria naturae, secundum classes, ordines, genera, species cum characteribus, differentiis, synonymis, locis. Tomus I: Regnum animale. Editio decima, reformata. Laurentii Salvii, Stockholm [Facsimile reprinted in 1956 by the British Museum of Natural History].

LINNAEUS, C. 1766. Systema naturae per regna tria naturae, secundum classes, ordines, genera, species cum characteribus, differentiis, synonymis, locis. Tomus I: Regnum animale. Editio decima, reformata. Laurentii Salvii, Stockholm [12th edition].

LOFGREN, D. L. 1995. The Bug Creek problem and the Cretaceous-Tertiary transition at McGuire Creek, Montana. The University of California Publications in Geological Sciences, 140:1-185.

LOFGREN, D. L., M. C. MCKENNA, and S. L. WALSH. 1999. New records of Torrejonian-Tiffanian mammals from the Paleocene-Eocene Goler Formation, California. Journal of Vertebrate Paleontology, 19, Supplement to Number 3:60A.

LOFGREN, D. L., J. A. LILLEGRAVEN, W. A. CLEMENS, P. D. GINGERICH, and T. E. WILLIAMSON. 2004. Paleocene biochronology: The Puercan through Clarkforkian Land Mammal Ages, p. 43-105. In M. O. Woodburne (ed.), Late Cretaceous and Cenozoic Mammals of North America: Biostratigraphy and Geochronology. Columbia University Press, New York.

LUCAS, S. G. 1993. Pantodonts, tillodonts, unitatheres, and pyrotheres are not ungulates, p. 182-194. In F. S. Szalay, M. J. Novacek, and M. C. McKenna (eds.), Mammal Phylogeny: Placentals. Springer-Verlag, New York.

LUCAS, S. G. 1998. Pantodonta, p. 274-283. In C. M. Janis, K. M. Scott, and L. L. Jacobs (eds.), Evolution of Tertiary Mammals of North America. Volume 1: Small Mammals, Xenathrans, and Marine Mammals. Cambridge University Press, Cambridge, United Kingdom.

MACDONALD, T. E. 1996. Late Paleocene (Tiffanian) mammal-bearing localities in superposition, from near Drumheller, Alberta. Unpublished M. Sc. thesis, University of Alberta, 276 p.

MACINTYRE, G. T. 1966. The Miacidae (Mammalia, Carnivora). Part I. The systematics of Ictidopappus and Protictis. Bulletin of the American Museum of Natural History, 131:115-210.

MARSH, O. C. 1872. Preliminary description of new Tertiary Mammals. Parts I-IV. American Journal of Science, 4:122-128, 202-224.

MARSH, O. C. 1889. Discovery of Cretaceous Mammalia. Part II. American Journal of Science, 38:177-180.

MARSH, O. C. 1894. Description of Tertiary artiodactyls. American Journal of Science, 48:259-274.

MARSHALL, L. G. and C. DE MUIZON. 1988. The dawn of the Age of Mammals in South America. National Geographic Research, 4:23-55.

MATTHEW, W. D. 1897. A revision of the Puerco Fauna. Bulletin of the American Museum of Natural History, 9:259-323.

MATTHEW, W. D. 1899. A provisional classification of the freshwater Tertiary of the West. Bulletin of the American Museum of Natural History, 12:19-75.

MATTHEW, W. D. 1901. Additional observations on the Creodonta. Bulletin of the American Museum of Natural History, 14:1-38 p.

MATTHEW, W. D. 1909. The Carnivora and Insectivora of the Bridger Basin, middle Eocene. Memoirs of the American Museum of Natural History, 9:291-567.

MATTHEW, W. D. 1914. Evidence of the Paleocene vertebrate fauna on the Cretaceous-Tertiary problem. Bulletin of the American Geological Society, 25:381-402.

MATTHEW, W. D. 1915. Part I: Order Ferae (Carnivora), Suborder Creodonta. In W. D. Matthew and W. Granger (auths.), A revision of the lower Eocene Wasatch and Wind River faunas. Bulletin of the American Museum of Natural History, 34:4-103.

MATTHEW, W. D. 1918. Part V: Insectivora (continued), Glires, Edentata. In W. D. Matthew and W. Granger (auths.), A revision of the lower Eocene Wasatch and Wind River faunas. Bulletin of the American Museum of Natural History, 34:565-657.

MATTHEW, W. D. 1921a. Fossil vertebrates and the Cretaceous-Tertiary problem. American Journal of Science, 22:107-140

MATTHEW, W. D. 1921b. Stehlinius, a new Eocene insectivore. American Museum Novitates, Number 14, 5 p.

MATTHEW, W. D. 1929. Preoccupied names. Journal of Mammalogy, 10:171.

MATTHEW, W. D. 1937. Paleocene faunas of the San Juan Basin, New Mexico. Transactions of the American Philosophical Society, New Series, 30:1-510.

MATTHEW, W. D. and W. GRANGER. 1921. New genera of Paleocene mammals. American Museum Novitates, Number 13, 7 p.

MCIVER, E. E. and J. F. BASINGER. 1993. Flora of the Ravenscrag Formation (Paleocene) southwestern Saskatchewan, Canada. Palaeontographica Canadiana, 10, 167 p.

MCKENNA, M. C. 1960. Fossil Mammalia from the early Wasatchian Four Mile fauna, Eocene of northwest Colorado. The University of California Publications in Geological Sciences, 37:1-130.

MCKENNA, M. C. 1963. Primitive Paleocene and Eocene Apatemyidae (Mammalia, Insectivora) and the primate-insectivore boundary. American Museum Novitates, Number 2160, 39 p.

MCKENNA, M. C. 1975. Towards a phylogenetic classification of the Mammalia, p. 21-46. In W. P. Luckett and F. S. Szalay (eds.), Phylogeny of the Primates: A Multidisciplinary Approach. Plenum Press, New York.

MCKENNA, M. C. and S. K. BELL. 1997. Classification of Mammals Above the Species Level. Columbia University Press, New York, 631 p.

MEEHAN, T. J. and R. W. WILSON. 2002. New viverravids from the Torrejonian (middle Paleocene) of Kutz Canyon, New Mexico and the oldest skull of the Order Carnivora. Journal of Paleontology, 76:1091-1101.

MISSIAEN, P. and T. SMITH. 2005. A new Paleocene nyctitheriid insectivore from Inner Mongolia (China) and the origin of Asian nyctitheriids. Acta Palaeontologica Polonica, 50:513-522.

MOSSOP, G. D. and I. SHETSON. 1994. Geological atlas of the Western Canadian Sedimentary Basin. Canadian Society of Petroleum Geologists and Alberta Research Council, 510 p.

NASCN. 2005. North American Stratigraphic Code, North American Commission on Stratigraphic Nomenclature. American Association of Petroleum Geologists Bulletin, 89:1547-1591.

NAYLOR, B. G. 1987. The earliest known Necturus (Amphibia, Urodela), from the Paleocene Ravenscrag Formation of Saskatchewan. Journal of Herpetology, 12:565-569.

NAYLOR, B. G. and D. W. KRAUSE. 1981. Piceoerpeton, a giant early Tertiary salamander from western North America. Journal of Paleontology, 55:507-523.

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

NOVACEK, M. J., T. M. BOWN, and D. SCHANKLER. 1985. On the classification of the early Tertiary Erinaceomorpha (Insectivora, Mammalia). American Museum Novitates, Number 2822, 22 p.

NOVACEK, M. J., I. FERRUSQUIA-VILLAFRANCA, J. J. FLYNN, A. R. WYSS, and M. A. NORELL. 1991. Wasatchian (early Eocene) mammals and other vertebrates from Baja California, Mexico: the Lomas Las Tetas de Cabra fauna. Bulletin of the American Museum of Natural History, 208:1-88.

OWEN, R. 1837. Teeth, p. 864-935. In R. B. Todd (ed.), The Encyclopedia of Anatomy and Physiology. Volume 4. Part 2. Sherwood, Gilbert, and Piper, London.

PARKER, T. J. and W. A. HASWELL. 1897. A Text-book of Zoology. Volume 2. Macmillan Press, London, 310 p.

PATTERSON, B. 1934. A contribution to the osteology of Titanoides and the relationships of the Amblypoda. Proceedings of the American Philosophical Society, 73:71-101.

PATTERSON, B. 1939. New Pantodonta and Dinocerata from the upper Paleocene of western Colorado. Geological Series of Field Museum of Natural History, 6:351-384.

PATTERSON, B. and R. M. WEST. 1973. A new late Paleocene phenacodont (Mammalia, Condylarthra) from western Colorado. Breviora, 403:1-7.

PENGILLY, D. 1984. Development versus functional explanations for patterns of variability and correlation in the dentitions of foxes. Journal of Mammalogy, 65:34-43.

PFRETZSCHNER, H. U. 1993. Muscle reconstruction and aquatic locomotion in the Middle Eocene Buxolestes piscator from Messel near Darmstadt. Kaupia, 3:75-87.

POLLY, P. D. 1997. Ancestry and species definition in paleontology: a stratocladistic analysis of Viverravidae (Carnivora, Mammalia) from Wyoming. Contributions from the Museum of Paleontology, The University of Michigan, 30:1-53.

POSTNIKOFF, A. C. L. 2009. Flora of the Ravenscrag Formation of the Big Muddy Valley, Willow Bunch Lake Map Area (72H) Saskatchewan. Unpublished M. Sc. thesis, University of Saskatchewan, 230 p.

RANKIN, B. D. and R. C. FOX. 2008. Early late Paleocene carnivorans from the Roche Percée local fauna, southeastern Saskatchewan, Canada. Journal of Vertebrate Paleontology, 28, Supplement to Number 3:129A.

RIGBY, J. K. JR. 1980. Swain Quarry of the Fort Union Formation, middle Paleocene (Torrejonian), Carbon County, Wyoming: Geologic setting and mammalian fauna. Evolutionary Monographs, 3, 179 p.

ROBINSON, P. 1966. Fossil Mammalia of the Huerfano Formation, Eocene, of Colorado. Bulletin of the Peabody Museum of Natural History, 21:1-95.

ROBINSON, P., G. F. GUNNELL, S. L. WALSH, W. C. CLYDE, J. E. STORER, R. K. STUCKY, D. J. FROEHLICH, I. FERRUSQUIA-VILLAFRANCA, and M. C. MCKENNA. 2004. Wasatchian through Duchesnean biochronology, p. 106-155. In M. O. Woodburne (ed.), Late Cretaceous and Cenozoic Mammals of North America: Biostratigraphy and Geochronology. Columbia University Press, New York.

ROSE, K. D. 1981. The Clarkforkian Land Mammal Age and mammalian faunal composition across the Paleocene-Eocene boundary. The University of Michigan Papers on Paleontology, 26:1-197.

ROSE, K. D. 1999. Postcranial skeleton of Eocene Leptictidae (Mammalia), and its implications for behavior and relationships. Journal of Vertebrate Paleontology, 19:355-372.

ROSE, K. D. 2006. The Beginning of the Age of Mammals. The John Hopkins University Press, Baltimore, 640 p.

ROSE, K. D. and D. W. KRAUSE. 1982. Cyriacotheriidae, a new family of early Tertiary pantodonts from western North America. Proceedings of the American Philosophical Society, 126:26-50.

ROSE, K. D. and W. VON KOENIGSWALD. 2005. An exceptionally complete skeleton of Palaeosinopa (Mammalia, Cimolesta, Pantolestidae) from the Green River Formation, and other postcranial elements of the Pantolestidae from the Eocene of Wyoming. Palaeontographica Abteilung A, 273:55-96.

ROWE, T. 1988. Definitions, diagnosis, and origin of Mammalia. Journal of Vertebrate Paleontology, 8:241-264.

RUSSELL, D. E. 1964. Les Mammifères Paléocènes d'Europe. Mémoirs du Museum National d'Histoire Naturelle (France), Nouvelle Séries, Séries C, 13:1-321.

RUSSELL, D. E. 1980. Sur les condylarthres Cernaysiens Tricuspiodon et Landenodon (Paléocène supérieur de France). Palaeovertebrata, Mémoire Jubilaire en Hommage à René Lavocat:127-166.

RUSSELL, D. E. and D. DASHZEVEG. 1986. Early Eocene insectivores (Mammalia) from the People's Republic of Mongolia. Palaeontology, 29:269-291.

RUSSELL, L. S. 1929. Paleocene vertebrates from Alberta. American Journal of Science, 17:162-178.

RUSSELL, L. S. 1949. Preliminary report, the geology of the southern part of the Cypress Hills, southwestern Saskatchewan. Report of the Saskatchewan Geological Survey, Petroleum Geology Series, 1:1-47.

RUSSELL, L. S. 1950. Correlation of the Cretaceous-Tertiary transition in Saskatchewan and Alberta. Bulletin of the Geological Society of America, 61:27-42.

RUSSELL, L. S. 1974. Fauna and correlation of the Ravenscrag Formation (Paleocene) of southwestern Saskatchewan. Contributions in Life Sciences from the Royal Ontario Museum, 102:1-52.

RUTHERFORD, R. L. 1927. Geology along the Bow River between Cochrane and Kananaskis, Alberta. Scientific and Industrial Research Council of Alberta Report, 17:1-46.

SCHLOSSER, M. 1887. Die Affen, Lemuren, Chiropteren, Insektivoren, Marsupialier, Creodontier und Carnivoren des Europäischen Tertiärs und deren Bezeihungen zu ihren lebenden und fossilen auβereuropäischen Verwandten. Part 1. Beitrage zur Palaontologie und Geologie, Osterreich-Ungarns und des Orients, 6:1-224.

SCOTT, C. S. 2003. Late Torrejonian (middle Paleocene) mammals from south central Alberta, Canada. Journal of Paleontology, 77:745-768.

SCOTT, C. S. 2006. A new erinaceid (Mammalia, Insectivora) from the late Paleocene from western Canada. Canadian Journal of Earth Sciences, 43:1695-1709.

SCOTT, C. S. 2008. Late Paleocene mammals from near Red Deer, Alberta, and a phylogenetic analysis of the earliest lipotyphla (Mammalia, Insectivora). Unpublished Ph. D. dissertation, University of Alberta, 1377 p.

SCOTT, C.S. and D. M. BOYER. 2006. First skeletal material of <u>Litocherus notissimus</u> (Simpson) (Mammalia, Erinaceomorpha) from the late Paleocene of south central Alberta. Journal of Vertebrate Paleontology, 26, Supplement to Number 3:123A.

SCOTT, C. S., R. C. FOX, and G. P. YOUZWYSHYN. 2002. New earliest Tiffanian (late Paleocene) mammals from Cochrane 2, southwestern Alberta, Canada. Acta Palaeontologica Polonica, 47:691-704.

SCOTT, W. B. 1892. A revision of the North American Creodonta, with notes on some of the genera which have been referred to that group. Proceedings of the Academy of Natural Sciences Philadelphia, 44:291-323.

SCOTT, W. B. and G. L. JEPSEN. 1936. The mammalian fauna of the White River Oligocene. Part I, Insectivora and Carnivora. Transactions of the American Philosophical Society, New Series, 28:1-153.

SECORD, R. 1998. Paleocene mammalian biostratigraphy of the Carbon Basin, southeastern Wyoming, and age constraints on local phases of tectonism. Rocky Mountain Geology, 33:119-154.

SECORD, R. 2008. The Tiffanian Land-Mammal Age (middle-late Paleocene) in the northern Bighorn Basin, Wyoming. The University of Michigan Papers on Paleontology, 35:1-192.

SECORD, R. P. D. GINGERICH, M. E. SMITH, W. C. CLYDE, P. WILF, and B. S. SINGER. 2006. Geochronology and mammalian biostratigraphy of middle and upper Paleocene continental strata, Bighorn Basin, Wyoming. American Journal of Science, 306:211-245.

SETOGUCHI, T. 1978. Paleontology and geology of the Badwater Creek area, central Wyoming. Part 16. The Cedar Ridge local fauna (late Oligocene). Bulletin of Carnegie Museum of Natural History, 9:1-61.

SIGÉ, B. 1971. Les Didelphoidea de Laguna Umayo (Formation Vilquechico, Crétacé Supérieur, Pérou), et la peuplement marsupial d'Amérique du Sud. Comptes Rendus Hebdomadiares des Séances de l'Académie des Sciences, Série D, 273:2479-2481.

SIGÉ, B. 1976. Insectivores primitif de l' Éocène supérieur et Oligocène inférieur d'Europe occidentale. Nyctitheriidés. Mémoire du Musée Nationale d'Histoire Naturelle, Série C, 34:1-140.

SIGÉ, B, T. SEMPRE, R. F. BUTLER, L. G. MARSHALL, AND J.-Y. CROCHET. 2004. Age and stratigraphic reassessment of the fossil-bearing Laguna Umayo red mudstone unit, SE Peru, from regional stratigraphy, fossil record, and paleomagnetism. Géobios, 37:771-794.

SILCOX, M. T., J. I. BLOCH, D. M. BOYER, and P. HOUDE. 2007. Cranial anatomy of Labidolemur kayi and the relationships of the Apatemyidae. Journal of Vertebrate Paleontology, 27, Supplement to Number 3: 147A.

SIMONS, E. L. 1960. The Paleocene Pantodonta. Transactions of the American Philosophical Society, New Series, 50:1-99.

SIMPSON. G. G. 1927. Mammalian fauna and correlation of the Paskapoo Formation of Alberta. American Museum Novitates, Number 268:1-10.

SIMPSON, G. G. 1928. A new mammalian fauna from the Fort Union of southern Montana. American Museum Novitates, Number 297, 15 p.

SIMPSON, G. G. 1929a. A collection of Paleocene mammals from Bear Creek, Montana. Annals of Carnegie Museum, 19:115-122.

SIMPSON, G. G. 1929b. Paleocene and lower Eocene mammals of Europe. American Museum Novitates, Number 354, 17 p.

SIMPSON, G. G. 1935a. New Paleocene mammals from the Fort Union of Montana. Proceedings of the United States National Museum, 83:221-244.

SIMPSON, G. G. 1935b. The Tiffany fauna, upper Paleocene. III. Primates, Carnivora, Condylarthra, and Amblypoda. American Museum Novitates, Number 817, 28 p.

SIMPSON, G. G. 1936. A new fauna from the Fort Union of Montana. American Museum Novitates, Number 873, 27 p.

SIMPSON, G. G. 1937a. The Beginning of the Age of Mammals. Biological Reviews, 12:1-46.

SIMPSON, G. G. 1937b. Unuchinia, a new name for Apator Simpson, not Semenow. Journal of Paleontology, 11:78.

SIMPSON, G. G. 1937c. Additions to the upper Paleocene fauna of the Crazy Mountain Field. American Museum Novitates, Number 940, 15 p.

SIMPSON, G. G. 1937d. The Fort Union of the Crazy Mountain Field, Montana and its mammalian faunas. Bulletin of the United States Museum, 169:1-287.

SIMPSON, G. G. 1937e. Notes on the Clark Fork, upper Paleocene, fauna. American Museum Novitates, Number 954, 24 p.

SIMPSON, G. G. 1940. Studies on the earliest primates. Bulletin of the American Museum of Natural History, 77:185-212.

SIMPSON, G. G. 1945. The principles of classification and a classification of mammals. Bulletin of the American Museum of Natural History, 85:14-350.

SKWARA, T. 1988. Mammals of the Topham local fauna: early Miocene (Hemingfordian), Cypress Hills Formation, Saskatchewan. Natural History Contributions, Saskatchewan Museum of Natural History, Number 9, 169 p.

SLOAN, R. E. 1987. Paleocene and latest Cretaceous mammals, rates of sedimentation and evolution, p. 165-200. In J. E. Fassett and J. K. Rigby, Jr. (eds.), The Cretaceous-Tertiary Boundary in the San Juan and Raton Basins, New Mexico and Colorado. Geological Society of America Special Paper, 209.

SLOAN, R. E. and L. VAN VALEN. 1965. Cretaceous mammals from Montana. Science, 148:220-227.

SMITH, R. 1997. Palaeosinopa russelli (Mammalia, Pantolesta), une espèce nouvelle du Membre de Dormaal, proche de la limite Paléocène-Eocène. Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Sciences de le Terre, 67:153-159.

SMITH, T. 1996. Leptacodon dormaalensis (Mammalia, Lipotyphla), un nyctithère primitif de lat transition Paléocène-Éocène de Belgique. Belgian Journal of Zoology, 126:153-167.

SPRINGER, M. S. 1997. Molecular clocks and the timing of the placental and marsupial radiations in relation to the Cretaceous-Tertiary boundary. Journal of Mammalian Evolution, 4:285-302.

SPRINGER, M. S., W. J. MURPHY, E. EIZIRIK, and S. J. O'BRIEN. 2003. Placental mammal diversification and the Cretaceous-Tertiary boundary. Proceedings of the National Academy of Science of the United States of America, 100:1056-1996.

STOCK, C. 1936. Sespé Eocene didelphids. Proceedings of the National Academy of Science, 22:122-124.

STONLEY, G. J. 1988. Late Paleocene mammals from the Swan Hills Local Fauna (Paskapoo Formation), Alberta. Unpublished M. Sc. thesis, University of Alberta, Edmonton, 265 p.

STORER, J. E. 1975. Middle Miocene mammals from the Cypress Hills, Canada. Canadian Journal of Earth Sciences, 12:520-522.

STORER, J. E. 1993. Additions to the mammalian paleofauna of Saskatchewan. Modern Geology, 18:475-487.

STORER, J. E. 1996. Eocene-Oligocene faunas of the Cypress Hills Formation, Saskatchewan, p. 240-261. In D. R. Prothero and R. J. Emry (eds.), The Terrestrial Eocene-Oligocene Transition in North America. Cambridge University Press, Cambridge, United Kingdom.

SZALAY, F. S. 1968. Origins of the Apatemyidae (Mammalia, Insectivora). American Museum Novitates, Number 2352, 11 p.

SZALAY, F. S. 1969. Mixdoectidae, Microsyopsidae, and the insectivore-primate transition. Bulletin of the American Museum of Natural History, 140:193-330.

THEWISSEN, J. G. M. 1990. Evolution of Paleocene and Eocene Phenacodontidae (Mammalia, Condylarthra). The University of Michigan Papers on Paleontology, 29:1-107.

TROUESSART, E. L. 1879. Catalogue des Mammifères vivants et fossiles. Revue et Magazine de Zoologie pure et appliqué, Séries 3, 7:219-285.

TURNBULL, W. D. 1970. Mammalian masticatory apparatus. Fieldiana: Geology, 18:147-356.

VAN VALEN, L. 1966. Deltatheridia, a new order of mammals. Bulletin of the American Museum of Natural History, 132:1-126.

VAN VALEN, L. 1967. New Paleocene insectivores and insectivore classification. Bulletin of the American Museum of Natural History, 132:1-126.

VAN VALEN, L. 1978. The beginning of the Age of Mammals. Evolutionary Theory, 4:45-80.

VAN VALEN, L. and R. E. SLOAN. 1965. The earliest primates. Science, 150:743-745.

WEBB, M. W. 1996. Late Paleocene mammals from near Drayton Valley, Alberta. Unpublished M. Sc. thesis, University of Alberta, Edmonton, 258 p.

WEIGELT, J. 1960. Die Arctocyoniden von Walbeck. Freiberger Forschungshefte, 77:1-241.

WEST, R. M. 1973a. Antemolar dentitions of the Paleocene apatemyid insectivorans Jepsenella and Labidolemur. Journal of Mammalogy, 54:33-40.

WEST, R. M. 1973b. Geology and mammalian paleontology of the New Fork-Big Sandy Area, Sublette County, Wyoming. Fieldiana, Geology, 29:1-193.

WEST, R. M. 1974. New North American middle Eocene nyctithere (Mammalia, Insectivora). Journal of Paleontology, 48:983-987.

WEST, R. M. 1976. The North American Phenacodontidae (Mammalia, Condylarthra). Contributions in Biology and Geology, Milwaukee Public Museum, 6:1-78.

WHITTAKER, S, B. J. ROSTRON, D. KHAN, Z. HAJNAL, H. QING, L. PENNER, H. MAATHUIS, and S. GOUSSEV. 2004. Geological characterization, p. 15-69. In M. Wilson and M. Monea (eds.), IEA GHG Weyburn CO_2 Monitoring and Storage Project Summary Report 2000-2004. Seventh International Conference on Greenhouse Gas Control Technologies. Petroleum Technology Research Centre.

WIBLE, J. R., G. W. ROUGIER, M. J. NOVACEK, M. C. MCKENNA, and D. DASHZEVEG. 1995. A mammalian petrosal from the Early Cretaceous of Mongolia: implications for the evolution of the ear region and mammaliamorph interrelationships. American Museum Novitates, Number 3140, 19 p.

WILSON, M. V. H. 1980. Oldest known Esox (Pisces: Esocidae), part of a new Paleocene teleost fauna from western Canada. Canadian Journal of Earth Sciences, 17:307-312.

WING, S. L., G. J. HARRINGTON, F.A. SMITH, J. I. BLOCH, D. M. BOYER, and K. H. FREEMAN. 2004. Transient floral change and the rapid global warming at the Paleocene-Eocene Boundary. Science, 310:993-996.

WINTERFELD, G. F. 1982. Mammalian paleontology of the Fort Union Formation (Paleocene), eastern Rock Springs Uplift, Sweetwater County, Wyoming. University of Wyoming Contributions to Geology, 21:73-112.

WOOD, H. E. II, R. W. CHANEY, J. CLARK, E. H. COLBERT, G. L. JEPSEN, J. B. REESIDE, JR., and C. STOCK. 1941. Nomenclature and correlation of the North American continental Tertiary. Bulletin of the Geological Society of American, 52:1-48.

WOODBURNE, M. O. 2004a. Late Cretaceous and Cenozoic Mammals of North America: Biostratigraphy and Geochronology. Columbia University Press, New York, 391 p.

WOODBURNE, M. O. 2004b. Principles and Procedures, p. 1-20. In M. O. Woodburne (ed.), Late Cretaceous and Cenozoic Mammals of North America: Biostratigraphy and Geochronology. Columbia University Press, New York.

WORTMAN, J. L. 1901. Studies of Eocene Mammalia in the Marsh Collection, Peabody Museum. Part I. Carnivora. American Journal of Science, 11:1-145.

WORTMAN, J. L. and W. D. MATTHEW. 1899. The ancestry of certain members of the Canidae, the Viverridae, and Procyonidae. Bulletin of the American Museum of Natural History, 12:109-139.

YOUZWYSHYN, G. P. 1988. Paleocene mammals from near Cochrane, Alberta. Unpublished M. Sc. thesis, University of Alberta, Edmonton, 484 p.

ZACK, S. P., T. A. PENKROT, J. I. BLOCH, and K. D. ROSE. 2005a. Affinities of 'hyopsodontids' to elephant shrews and a Holarctic origin of Afrotheria. Nature, 434:497-501.

ZACK, S. P., T. A. PENKROT, D. W. KRAUSE, and M. C. MAAS. 2005b. A new apheliscine "condylarth" mammal from the late Paleocene of Montana and Alberta and the phylogeny of "hyopsodontids". Acta Palaeontologica Polonica, 50:809-830.

Table 1.—Measurements and descriptive statistics of the dentition of Prodiacodon cf. P. concordiarcensis from the late middle Tiffanian (Ti4) Roche Percée local fauna, Ravenscrag Formation, Saskatchewan.

Element	P	N	OR	M	SD	CV
M2	L	3	1.9-2.0	1.97	0.06	2.94
	W	2	2.7-2.8	2.75	0.07	2.57

Table 2.—Measurements and descriptive statistics of the upper dentition of Diacocherus cf. D. meizon from the late middle Tiffanian (Ti4) Roche Percée local fauna, Ravenscrag Formation, Saskatchewan.

Element	P	N	OR	M	SD	CV
P3	L	1	1.8	—	—	—
	W	1	1.4	—	—	—
P4	L	8	1.6-1.8	1.74	0.09	5.27
	W	10	1.8-2.0	1.94	0.08	4.35
M1	L	13	1.7-1.8	1.78	0.04	2.47
	W	11	2.3-2.4	2.36	0.05	2.13
M2	L	11	1.7-1.9	1.78	0.06	3.38
	W	11	2.5-2.6	2.55	0.05	2.05
M3	L	5	1.3-1.4	1.32	0.04	3.39
	W	5	1.9-2.0	1.96	0.05	2.79

Table 3.—Measurements and descriptive statistics of the lower dentition of Diacocherus cf. D. meizon from the late middle Tiffanian (Ti4) Roche Percée local fauna, Ravenscrag Formation, Saskatchewan.

Element	P	N	OR	M	SD	CV
p4	L	7	1.7-2.0	1.83	0.10	5.20
	W	7	0.9-1.0	0.94	0.05	5.67
m1	L	16	1.6-1.9	1.77	0.07	3.98
	TrW	18	1.1-1.3	1.21	0.08	6.26
	TaW	17	1.2-1.4	1.26	0.07	5.66
m2	L	24	1.7-1.8	1.76	0.05	2.81
	TrW	24	1.3-1.5	1.38	0.08	5.77
	TaW	24	1.2-1.5	1.34	0.08	5.75
m3	L	20	1.6-1.8	1.68	0.10	5.66
	TrW	21	1.0-1.3	1.13	0.08	6.94
	TaW	19	0.9-1.1	0.99	0.05	5.27

Table 4.—Measurements and descriptive statistics of the lower dentition of "Xynolestes denommei" from the late middle Tiffanian (Ti4) Roche Percée local fauna, Ravenscrag Formation, Saskatchewan.

Element	P	N	OR	M	SD	CV
p2	L	1	1.0	—	—	—
	W	1	0.5	—	—	—
p4	L	4	1.2-1.3	1.25	0.06	4.62
	W	4	0.8	0.80	0	0
m1	L	3	1.2-1.4	1.33	0.12	8.66
	TrW	3	0.8-1.0	0.90	0.10	11.11
	TaW	3	0.8-1.0	0.90	0.10	11.11
m2	L	4	1.1-1.2	1.18	0.05	4.26
	TrW	4	0.8-1.0	0.88	0.10	10.94
	TaW	4	0.8-0.9	0.85	0.06	6.79
m3	L	3	1.1-1.2	1.13	0.06	5.09
	TrW	3	0.7-0.8	0.77	0.06	7.53
	TaW	3	0.6-0.7	0.67	0.06	8.66

Table 5.—Measurements and descriptive statistics of the upper dentition of Litocherus lacunatus from the late middle Tiffanian (Ti4) Roche Percée local fauna, Ravenscrag Formation, Saskatchewan.

Element	P	N	OR	M	SD	CV
P4	L	11	2.5-3.1	2.88	0.18	6.17
	W	10	3.3-3.6	3.39	0.11	3.25
M1	L	15	2.3-2.7	2.45	0.14	5.54
	W	14	3.2-3.5	3.29	0.11	3.47
M2	L	14	2.2-2.7	2.38	0.16	6.63
	W	14	3.4-3.8	3.56	0.11	3.06
M3	L	9	1.5-1.7	1.63	0.07	4.33
	W	7	2.5-2.7	2.57	0.08	2.94

Table 6.—Measurements and descriptive statistics of the lower dentition of Litocherus lacunatus from the late middle Tiffanian (Ti4) Roche Percée local fauna, Ravenscrag Formation, Saskatchewan.

Element	P	N	OR	M	SD	CV
p3	L	2	2.2-2.3	2.25	0.07	3.14
	W	2	1.3-1.5	1.4	0.14	10.10
p4	L	13	3.0-3.3	3.15	0.09	2.78
	W	13	1.8-2.1	1.97	0.12	6.00
m1	L	19	2.6-2.8	2.70	0.07	2.47
	TrW	19	1.8-2.1	1.97	0.09	4.50
	TaW	21	2.0-2.4	2.12	0.12	5.43
m2	L	33	2.2-2.7	2.42	0.09	3.83
	TrW	32	1.9-2.4	2.12	0.14	6.52
	TaW	35	1.8-2.3	2.04	0.13	6.42
m3	L	19	2.0-2.4	2.20	0.13	5.87
	TrW	19	1.4-1.8	1.59	0.11	7.23
	TaW	19	1.3-1.7	1.48	0.13	8.77

Table 7.—Measurements and descriptive statistics of the lower dentition of Litocherus cf. L. zygeus from the late middle Tiffanian (Ti4) Roche Percée local fauna, Ravenscrag Formation, Saskatchewan.

Element	P	N	OR	M	SD	CV
p4	L	4	2.8-2.9	2.85	0.06	2.03
	W	4	1.7-1.8	1.78	0.05	2.82
m1	L	4	2.5-2.6	2.55	0.06	2.26
	TrW	3	1.8-2.0	1.93	0.12	5.97
	TaW	4	2.0-2.3	1.98	0.05	2.53
m2	L	5	2.2-2.3	2.24	0.05	2.45
	TrW	5	1.8-2.0	1.90	0.10	5.26
	TaW	5	1.7-2.0	1.84	0.11	6.20
m3	L	5	1.9-2.1	2.00	0.07	3.54
	TrW	4	1.4-1.5	1.45	0.06	3.98
	TaW	4	1.4	1.40	—	—

Table 8.—Measurements and descriptive statistics of the dentition of Adapisorex sp. from the late middle Tiffanian (Ti4) Roche Percée local fauna, Ravenscrag Formation, Saskatchewan.

Element	P	N	OR	M	SD	CV
M1	L	1	2.5	—	—	—
	W	1	3.0	—	—	—
m1	L	2	2.6-2.7	2.65	0.07	2.67
	TrW	1	1.7	—	—	—
	TaW	2	1.9	1.90	0	0

Table 9.—Measurements and descriptive statistics of the lower dentition of Pararyctes pattersoni from the late middle Tiffanian (Ti4) Roche Percée local fauna, Ravenscrag Formation, Saskatchewan.

Element	P	N	OR	M	SD	CV
M2	L	1	1.4-1.5	1.43	0.06	4.03
	W	1	2.3-2.5	2.40	0.14	5.89
m1	L	3	1.4-1.5	1.47	0.06	3.94
	TrW	3	1.0-1.2	1.13	0.12	10.19
	TaW	3	1.0	1.00	—	—
m3	L	1	1.6	—	—	—
	TrW	1	1.1	—	—	—
	TaW	1	0.8	—	—	—

Table 10.—Measurements and descriptive statistics of the lower dentition of cf. Paleotomus sp. 1 from the late middle Tiffanian (Ti4) Roche Percée local fauna, Ravenscrag Formation, Saskatchewan.

Element	P	N	OR	M	SD	CV
p2	L	1	3.7	—	—	—
	W	1	1.7	—	—	—
p4	L	3	5.6-5.7	5.67	0.06	1.02
	W	3	2.4-2.6	2.5	0.10	4.00
m1	L	1	4.7	—	—	—
	TrW	1	3.3	—	—	—
	TaW	1	2.5	—	—	—
m2	L	1	5.5	—	—	—
	TrW	1	3.7	—	—	—
	TaW	1	2.7	—	—	—
m3	L	1	5.8	—	—	—
	TrW	2	3.9-4.2	4.05	0.21	5.24
	TaW	2	2.4-2.6	2.5	0.14	5.66

Table 11.—Measurements and descriptive statistics of the upper dentition of Unuchinia cf. U. dysmathes from the late middle Tiffanian (Ti4) Roche Percée local fauna, Ravenscrag Formation, Saskatchewan.

Element	P	N	OR	M	SD	CV
I1	D	5	3.1-3.5	3.24	0.17	5.16
	W	8	1.7-2.0	1.84	0.12	6.46
I2	D	6	3.4-3.8	3.62	0.15	4.07
	W	6	1.7-2.0	1.92	0.12	6.10
P4	L	1	2.4	—	—	—
	W	1	2.5	—	—	—
M1	L	1	2.9	—	—	—
	W	1	3.4	—	—	—
M2	L	1	2.7	—	—	—
	W	1	4.7	—	—	—

Table 12.—Measurements and descriptive statistics of the lower dentition of Unuchinia cf. U. dysmathes from the late middle Tiffanian (Ti4) Roche Percée local fauna, Ravenscrag Formation, Saskatchewan.

Element	P	N	OR	M	SD	CV
i2	D	1	3.0	—	—	—
	W	1	1.9	—	—	—
p2	L	2	3.4	3.40	0	0
	W	2	1.4	1.40	0	0
m1	L	4	2.5-2.7	2.60	0.08	3.14
	TrW	4	1.7-1.8	1.75	0.06	3.30
	TaW	4	1.6-1.7	1.68	0.05	2.99
m2	L	4	2.7-3.0	2.83	0.15	5.31
	TrW	5	1.8-2.0	1.92	0.08	4.36
	TaW	4	1.8-2.0	1.85	0.10	5.41
m3	L	2	3.2-3.3	3.25	0.07	2.18
	TrW	2	1.9-2.0	1.95	0.07	3.63
	TaW	2	1.5	1.50	—	—

Table 13.—Measurements and descriptive statistics of the upper and lower dentition of Bessoecetor pilodontus from the late middle Tiffanian (Ti4) Roche Percée local fauna, Ravenscrag Formation, Saskatchewan.

Element	P	N	OR	M	SD	CV
P4	L	2	2.7	2.70	0	0
	W	2	3.0	3.00	0	0
M1	L	6	2.6-2.7	2.67	0.05	1.94
	W	6	3.4-3.8	3.52	0.16	4.56
M2	L	4	2.5-2.9	2.75	0.19	6.96
	W	4	4.1-4.4	4.25	0.17	4.08
p4	L	1	2.8	—	—	—
	W	1	1.4	—	—	—
m1	L	6	2.5-2.7	2.60	0.06	2.43
	TrW	7	1.6-1.9	1.77	0.13	7.08
	TaW	6	1.7-2.0	1.92	0.13	6.93
m2	L	5	2.7-2.8	2.74	0.05	2.00
	TrW	5	2.0-2.2	2.06	0.09	4.34
	TaW	5	1.9-2.2	2.00	0.12	6.12

Table 14.—Measurements and descriptive statistics of the lower dentition of Bessoecetor krausei n. sp. from the late middle Tiffanian (Ti4) Roche Percée local fauna, Ravenscrag Formation, Saskatchewan.

Element	P	N	OR	M	SD	CV
p2	L	1	1.5	—	—	—
	W	1	0.6	—	—	—
m1	L	1	1.9	—	—	—
	TrW	1	1.1	—	—	—
	TaW	1	1.2	—	—	—
m2	L	1	2.0	—	—	—
	TrW	1	1.3	—	—	—
	TaW	1	1.3	—	—	—
m3	L	2	2.0	2.00	0	0
	TrW	2	1.2-1.3	1.25	0.07	5.66
	TaW	1	1.0	—	—	—

Table 15.—Measurements and descriptive statistics of the upper dentition of Palaeosinopa sp. from the late middle Tiffanian (Ti4) Roche Percée local fauna, Ravenscrag Formation, Saskatchewan.

Element	P	N	OR	M	SD	CV
P4	L	10	3.4-3.8	3.58	0.13	3.68
	W	11	3.9-4.5	4.19	0.18	4.20
M1	L	8	4.0-4.2	4.04	0.07	1.84
	W	8	5.0-5.8	5.33	0.26	4.89
M2	L	10	3.9-4.4	4.15	0.17	4.13
	W	9	6.1-6.8	6.38	0.21	3.31
M3	L	8	2.5-3.1	2.84	0.22	7.98
	W	9	5.2-6.5	5.81	0.35	6.05

Table 16.—Measurements and descriptive statistics of the lower dentition of Palaeosinopa sp. from the late middle Tiffanian (Ti4) Roche Percée local fauna, Ravenscrag Formation, Saskatchewan.

Element	P	N	OR	M	SD	CV
p2	L	7	2.3-2.7	2.56	0.16	6.33
	W	7	1.3-1.5	1.39	0.08	6.49
p3	L	3	3.0-3.1	3.07	0.06	1.88
	W	3	1.6-1.8	1.70	0.10	5.88
p4	L	14	3.3-3.6	3.48	0.11	3.22
	W	14	2.0-2.2	2.09	0.07	3.49
m1	L	12	3.6-3.9	3.81	0.10	2.62
	TrW	12	2.4-2.9	2.74	0.16	5.71
	TaW	12	2.5-3.1	2.83	0.19	6.79
m2	L	28	3.9-4.3	4.10	0.12	2.93
	TrW	29	3.0-3.6	3.31	0.15	4.42
	TaW	27	2.9-3.5	3.15	0.18	5.86
m3	L	26	4.1-4.7	4.49	0.18	3.98
	TrW	27	2.9-3.5	3.10	0.13	4.29
	TaW	27	2.3-2.7	2.50	0.12	4.63

Table 17.—Measurements and descriptive statistics of the dentition of Didymictis cf. D. dellensis from the late middle Tiffanian (Ti4) Roche Percée local fauna, Ravenscrag Formation, Saskatchewan.

Element	P	N	OR	M	SD	CV
p2	L	1	4.3	—	—	—
	W	1	1.7	—	—	—
p4	L	1	7.5	—	—	—
	W	1	3.2	—	—	—
m1	L	1	7.4	—	—	—
	TrW	1	4.9	—	—	—
	TaW	1	3.8	—	—	—
m2	L	3	4.8-5.2	5.00	0.21	4.14
	TrW	3	2.9-3.1	3.00	0.10	3.33
	TaW	3	2.5-2.7	2.60	0.10	3.85

Table 18.—Measurements and descriptive statistics of the dentition of Protictis cf. P. paralus from the late middle Tiffanian (Ti4) Roche Percée local fauna, Ravenscrag Formation, Saskatchewan.

Element	P	N	OR	M	SD	CV
P4	L	3	4.1-4.4	4.25	0.15	3.61
	W	3	1.7-1.8	1.75	0.06	3.27

Table 19.—Measurements and descriptive statistics of the dentition of Raphictis "iota" from the late middle Tiffanian (Ti4) Roche Percée local fauna, Ravenscrag Formation, Saskatchewan.

Element	P	N	OR	M	SD	CV
P4	L	1	3.4	—	—	—
	W	1	2.2	—	—	—
p4	L	1	3.1	—	—	—
	W	1	1.2	—	—	—
m1	L	2	3.1-3.3	3.20	0.14	4.42
	TrW	2	1.9-2.1	2.00	0.14	7.07
	TaW	2	1.5-1.6	1.55	0.07	4.56

Table 20.—Measurements and descriptive statistics of the upper dentition of Raphictis machaera n. sp. from the late middle Tiffanian (Ti4) Roche Percée local fauna, Ravenscrag Formation, Saskatchewan.

Element	P	N	OR	M	SD	CV
P4	L	1	5.7	5.70	—	—
	W	1	3.6	3.60	—	—
M1	L	4	3.4-3.8	3.60	0.18	5.07
	W	3	4.8-5.4	5.15	0.31	5.95
M2	L	2	1.9-2.0	1.95	0.07	3.63
	W	2	3.6-3.7	3.65	0.07	1.94

Table 21.—Measurements and descriptive statistics of the lower dentition of Raphictis machaera n. sp. from the late middle Tiffanian (Ti4) Roche Percée local fauna, Ravenscrag Formation, Saskatchewan.

Element	P	N	OR	M	SD	CV
p3	L	1	4.2	4.20	—	—
	W	1	1.8	1.80	—	—
p4	L	2	4.6	4.60	0	0
	W	2	1.7-1.8	1.75	0.07	4.04
m1	L	2	4.6-4.9	4.75	0.21	4.47
	TrW	9	2.8-3.1	2.90	0.11	3.86
	TaW	2	2.1-2.2	2.15	0.07	3.29
m2	L	2	3.2-3.3	3.25	0.07	2.18
	TrW	3	1.9-2.1	2.00	0.10	5.00
	TaW	2	1.5-1.6	1.55	0.07	4.56
	TrH	3	1.8-2.0	2.60	0	0

Table 22.—Measurements and descriptive statistics of the dentition of Raphictis nanoptexis n. sp. from the late middle Tiffanian (Ti4) Roche Percée local fauna, Ravenscrag Formation, Saskatchewan.

Element	P	N	OR	M	SD	CV
P4	L	1	2.8	—	—	—
	W	1	1.9	—	—	—
M1	L	1	2.0	—	—	—
	W	1	3.1	—	—	—
p4	L	1	2.2	—	—	—
	W	1	0.8	—	—	—
m1	L	1	2.4	—	—	—
	TrW	2	1.2-1.4	1.30	0.14	10.88
	TaW	1	1.1	—	—	—

Table 23.—Measurements and descriptive statistics of the dentition of Chriacus cf. C. baldwini from the late middle Tiffanian (Ti4) Roche Percée local fauna, Ravenscrag Formation, Saskatchewan.

Element	P	N	OR	M	SD	CV
M1	L	2	5.7-5.8	5.75	0.07	1.23
	W	2	6.7	6.70	—	—

Table 24.—Measurements and descriptive statistics of the dentition of Thryptacodon australis from the late middle Tiffanian (Ti4) Roche Percée local fauna, Ravenscrag Formation, Saskatchewan.

Element	P	N	OR	M	SD	CV
M1	L	1	6.3	—	—	—
	W	1	7.8	—	—	—
M2	L	1	6.6	—	—	—
	W	1	8.2	—	—	—
m1	L	1	6.3	—	—	—
	TrW	1	3.7	—	—	—
	TaW	1	4.5	—	—	—
m2	L	1	6.9	—	—	—
	TrW	2	4.8-5.2	5.00	0.28	5.66
	TaW	1	6.0	—	—	—
m3	L	1	6.9	—	—	—
	TrW	1	4.8	—	—	—
	TaW	1	4.1	—	—	—

Table 25.—Measurements and descriptive statistics of the dentition of Arctocyon mumak from the late middle Tiffanian (Ti4) Roche Percée local fauna, Ravenscrag Formation, Saskatchewan.

Element	P	N	OR	M	SD	CV
M1	L	1	13.5	—	—	—
	W	1	17.0	—	—	—
p3	L	1	11.4	—	—	—
	W	1	6.5	—	—	—
p4	L	1	15.4	—	—	—
	W	1	7.9	—	—	—
m1	L	1	14.1	—	—	—
	TrW	1	9.6	—	—	—
	TaW	1	11.6	—	—	—
m2	L	1	15.3	—	—	—
	TrW	1	12.4	—	—	—
	TaW	1	12.6	—	—	—
m3	L	2	15.2-16.0	15.60	0.57	3.63
	TrW	1	9.8	—	—	—
	TaW	2	8.7-9.7	9.20	0.71	7.69

Table 26.—Measurements and descriptive statistics of the dentition of Dorraletes diminutivus from the late middle Tiffanian (Ti4) Roche Percée local fauna, Ravenscrag Formation, Saskatchewan.

Element	P	N	OR	M	SD	CV
m2	L	5	2.3-2.5	2.38	0.08	3.52
	TrW	4	1.8-2.0	1.93	0.10	4.97
	TaW	5	1.8-2.2	1.98	0.15	7.49

Table 27.—Measurements and descriptive statistics of the upper dentition of Phenacodus magnus from the late middle Tiffanian (Ti4) Roche Percée local fauna, Ravenscrag Formation, Saskatchewan.

Element	P	N	OR	M	SD	CV
DP3	L	1	10.4	—	—	—
	W	1	10.5	—	—	—
P4	L	2	11.3-11.8	11.55	0.35	3.06
	W	2	12.6-13.9	13.25	0.92	6.94
M2	L	1	13.1	—	—	—
	W	1	16.9	—	—	—
M3	L	1	11.6	—	—	—
	W	1	13.3	—	—	—

Table 28.—Measurements and descriptive statistics of the lower dentition of *Phenacodus magnus* from the late middle Tiffanian (Ti4) Roche Percée local fauna, Ravenscrag Formation, Saskatchewan.

Element	P	N	OR	M	SD	CV
p3	L	2	11.1-11.3	11.2	0.14	1.26
	W	2	7.3-7.9	7.6	0.42	5.58
p4	L	1	13.0	—	—	—
	W	1	9.5	—	—	—
m2	L	1	15.1	—	—	—
	TrW	2	12.8-12.9	12.85	0.35	2.75
	TaW	2	12.3-14.1	13.20	1.27	9.64
m3	L	1	14.6	—	—	—
	TrW	—	—	—	—	—
	TaW	1	8.6	—	—	—

Table 29.—Measurements and descriptive statistics of the upper dentition of Ectocion borealis n. sp. from the late middle Tiffanian (Ti4) Roche Percée local fauna, Ravenscrag Formation, Saskatchewan.

Element	P	N	OR	M	SD	CV
DP3	L	1	4.5	—	—	—
	W	1	5.1	—	—	—
P3	L	1	4.9	—	—	—
	W	1	5.1	—	—	—
DP4	L	2	5.5-6.0	5.75	0.35	6.15
	W	2	5.7-6.5	6.1	0.57	9.27
P4	L	2	5.1-5.4	5.25	0.21	4.04
	W	2	6.3-6.4	6.35	0.07	1.11
M1	L	4	5.3-6.0	5.63	0.30	5.31
	W	5	7.3-7.6	7.44	0.15	2.04
M2	L	7	5.8-6.3	6.00	0.20	3.26
	W	6	7.7-9.0	8.22	0.47	5.73
M3	L	8	4.5-5.3	5.00	0.28	5.66
	W	8	6.1-7.1	6.69	0.41	6.06

Table 30.—Measurements and descriptive statistics of the lower dentition of Ectocion borealis n. sp. from the late middle Tiffanian (Ti4) Roche Percée local fauna, Ravenscrag Formation, Saskatchewan.

Element	P	N	OR	M	SD	CV
p2	L	2	2.7-3.1	2.90	0.28	9.75
	W	2	1.8-2.3	2.05	0.35	17.2
p3	L	3	4.3-5.0	4.60	0.36	7.83
	W	3	2.8-3.3	3.03	0.25	8.30
dp4	L	4	5.7-6.3	6.10	0.28	4.64
	TrW	4	2.9-3.3	3.10	0.18	5.89
	TaW	3	3.5-3.8	3.53	0.25	7.12
p4	L	9	5.2-5.9	5.50	0.25	4.55
	W	10	3.5-4.1	3.80	0.19	5.11
m1	L	11	5.3-5.8	5.51	0.16	2.98
	TrW	12	3.8-4.3	4.08	0.17	4.07
	TaW	11	3.9-4.7	4.18	0.23	5.54
m2	L	15	5.5-6.2	5.86	0.22	3.86
	TrW	15	4.1-5.1	4.57	0.24	5.34
	TaW	13	4.1-4.8	4.42	0.20	4.54
m3	L	11	5.7-6.7	6.13	0.30	4.83
	TrW	13	3.6-4.1	3.85	0.17	4.45
	TaW	13	3.3-4.0	3.56	0.22	6.23

Table 31.—Taxonomic comparison of mammals from the late middle Tiffanian (Ti4) Roche Percée local fauna, Ravenscrag Formation, Saskatchewan, with those of select middle to late Tiffanian localities in the Western Interior of North America. “G” and “s” refer to similar occurrences in the comparable fauna at the generic and species level, respectively, while “Gs” indicates a match at both the generic and species levels; “—“ indicates no match. Locality abbreviations, with respective sources of faunal data are: CPQ = Cedar Point Quarry (Secord, 2008); CHT = Chappo Type locality (Gunnell, 1994); BMR = Blindman River local fauna (Scott, 2008); BJ = Brisbane and Judson localities (Holtzman, 1978; Kihm and Hartman, 2004); DVQ = Divide Quarry (Secord, 2008); SH = Swan Hills local fauna (Stonley, 1988; Fox, 1990); PRQ = Princeton Quarry (Secord, 2008). Sources of faunal data for the Roche Percée local fauna include Krause (1977, 1978, 1987), Rose and Krause (1982), Fox (1990, 2002), and Scott (2006). Table adapted from Webb (1996) and Scott (2008).

Roche Percée taxa	Localities						
	CPQ	CHT	BMR	BJ	SH	DVQ	PRQ
Ptilodus kummae	G	Gs	G	G	Gs	Gs	—
Prochetodon foxi	—	—	G	Gs	Gs	Gs	G
Mesodma pygmaea	—	G	Gs	Gs	Gs	—	—
Mimetodon silberlingi		—	Gs	—	—	—	G
Ectypodus cf. E. powelli	—	G	G	G	—	—	G
Neoplagiaulax hunteri	Gs	G	G	Gs	Gs	G	G
Neoplagiaulax cf. N. hazeni							
Microcosmodon conus	—	—	G	—	Gs	—	Gs
Perad. cf. P. protinnominatus	G	G	G	G	—	—	G
Diacocherus cf. D. meizon	G	G	G	—	G	G	G
“Xynolestes denommei”	—	—	Gs	—	—	—	—
Litocherus lacunatus	G	Gs	G	G	Gs	—	—
Litocherus cf. L. zygeus						—	—
Adapisorex sp.	—	—	—	—	—	—	—
Oncocherus krishtalkai	—	—	—	—	Gs	—	—
Litolestes cf. L. ignotus	—	—	G	—	—	G	G
Nyctitherium sp.	—	—	—	—	G	—	—
Prod. cf. P. concordiarcensis	—	G	—	—	G	—	G
Pararyctes pattersoni	—	—	Gs	Gs	—	—	—
Palaeoryctes sp.	G	G	—	G	G	G	G
Paleotomus cf. P. junior	G	G	G	G	—	G	—
cf. Paleotomus sp. 1	—	—	—	—	—	—	—
cf. Paleotomus sp. 2	—	—	—	—	—	—	—
Unuchinia cf. U. dysmathes	—	G	G	G	—	G	G
Labidolemur soricoides	Gs	Gs	—	—	G	Gs	—
Bessoecetor pilodontus	G	G	G	G	G	Gs	—
Bessoecetor krausei		s					—
Palaeosinopa sp.	—	—	—	—	—	G	—
Titanoides cf. T. primaevus	G		—	G	G	G	—
Cyriacotherium cf. C. argyreum	—	—	—	—	—	G	—

	Localities						
Roche Percée taxa	CPQ	CHT	BMR	BJ	SH	DVQ	PRQ
Didymictis dellensis	—	—	Gs	—	G	G	G
Didymictis cf. *D*. *dellensis*	—	—		—			s
Protictis cf. *P*. *paralus*	G	G	—	G	—	—	—
Raphictis “*iota*”	G	G	Gs	—	—	—	—
Raphictis nanoptexis				—	—	—	—
Raphictis machaera			s	—	—	—	—
Plesiadapis churchilli	G	G	—	G	Gs	Gs	G
Micromomys vossae	—	—	G	—	—	—	G
Ignacius frugivorous	Gs	Gs	Gs	Gs	Gs	Gs	—
Carpodaptes stonleyi	G	G	G	G	G	Gs	—
Chriacus cf. *C*. *baldwini*	G	G	G	—	—	—	—
Chriacus cf. *C*. *oconostotae*				—	—	—	—
Thryptacodon australis	Gs	Gs	Gs	Gs	—	Gs	G
Arctocyon mumak	G	—	G	G	—	Gs	G
Arctocyon corrugatus		—	s		—		
Dorraletes diminutivus	—	Gs	—	Gs	—	—	—
Phenacodus magnus	G	G	—	G	—	Gs	G
Ectocion borealis	G	G	Gs	G	G	G	G
TOTALS	19G	23G	25G	21G	19G	21G	18G
	4s	7s	11s	7s	9s	10s	2s

Figure 1.—Outline map of Saskatchewan and Alberta. White symbol indicates the location of the hamlet of Roche Percée and the nearby late middle Tiffanian (Ti4) Roche Percée local fauna, Ravenscrag Formation, Saskatchewan. Figured adapted and modified from Scott (2006).

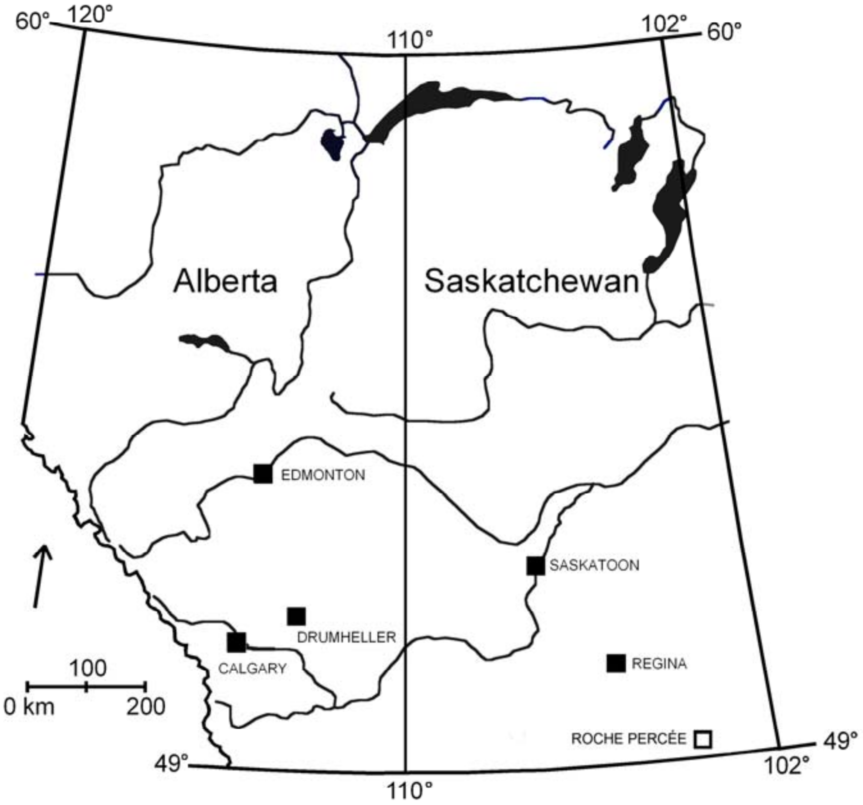
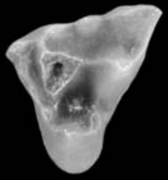
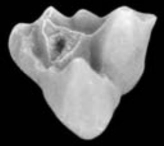

60°
120°
110°
102°
60°
Alberta
Saskatchewan
EDMONTON
SASKATOON
DRUMHELLER
CALGARY
REGINA
ROCHE PERCÉE
100
0 km
200
49°
110°
102°
49°

Figure 2.—1-5. Peradectes cf. P. protinnominatus from the late middle Tiffanian (Ti4) Roche Percée local fauna, Ravenscrag Formation, Saskatchewan. 1-2, UALVP 51528, left M1 in 1, occlusal, and 2, lingual views; 3-5, UALVP 9435, right mx in 5, labial, 6, lingual, and 7, occlusal views. Scale bar = 1 mm.



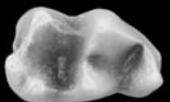
1



2

3

4

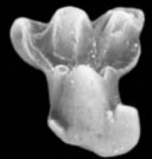


5

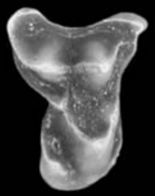
Figure 3.—1-4. Prodiacodon cf. P. concordiarcensis from the late middle Tiffanian (Ti4) Roche Percée local fauna, Ravenscrag Formation, Saskatchewan. 1-2, UALVP 9408, left M2 in 1, occlusal, and 2, lingual views; 3-4, UALVP 9407, right M2 in 3, occlusal, and 4, lingual views.

Scale bar = 1 mm.

1



2



3

4

Figure 4.—1-22. Diacocherus cf. D. meizon from the late middle Tiffanian (Ti4) Roche Percée local fauna, Ravenscrag Formation, Saskatchewan. 1-2, UALVP 9442, left P4 in 1, occlusal, and 2, lingual views; 3-4, UALVP 9443, right P4 in 3, occlusal, and 4, lingual views; 5-6, UALVP 9420, right M1 in 5, occlusal, and 6, lingual views; 7-8, UALVP 9413, left M1 in 7, occlusal, and 8, lingual views; 9-10, UALVP 51766, right M2 in 9, occlusal, and 10, lingual views; 11-12, UALVP 9427, right M2 in 11, occlusal, and 12, lingual views; 13-14, UALVP 9326, right M3 in 13, occlusal, and 14, lingual views; 15-16, UALVP 9265, right M3 in 15, occlusal, and 16, lingual views; 17-19, UALVP 9182, incomplete right dentary with p4, m1-3 and alveoli for p3 in 17, occlusal, 18, labial, and 19, lingual views; 20-22, UALVP 51767, incomplete right dentary with m2-3 and talonid of m1 in 20, occlusal, 21, labial, and 22, lingual views.

23-31. “Xynolestes denommei” from the late middle Tiffanian (Ti4) Roche Percée local fauna, Ravenscrag Formation, Saskatchewan. 23-25, UALVP 10872, incomplete right dentary with p2, p4, m1-3, and alveoli for c, p1, p3 in 23, occlusal, 24, labial, and 25, lingual views; 26-28, UALVP 51784, incomplete right dentary with m1-3 in 26, occlusal, 27, labial, and 28, lingual views; 29-31, UALVP 51782, incomplete right dentary with p4, and alveoli for p3, m1 in 29, occlusal, 30, labial, and 31, lingual views.

Scale bar = 2 mm.

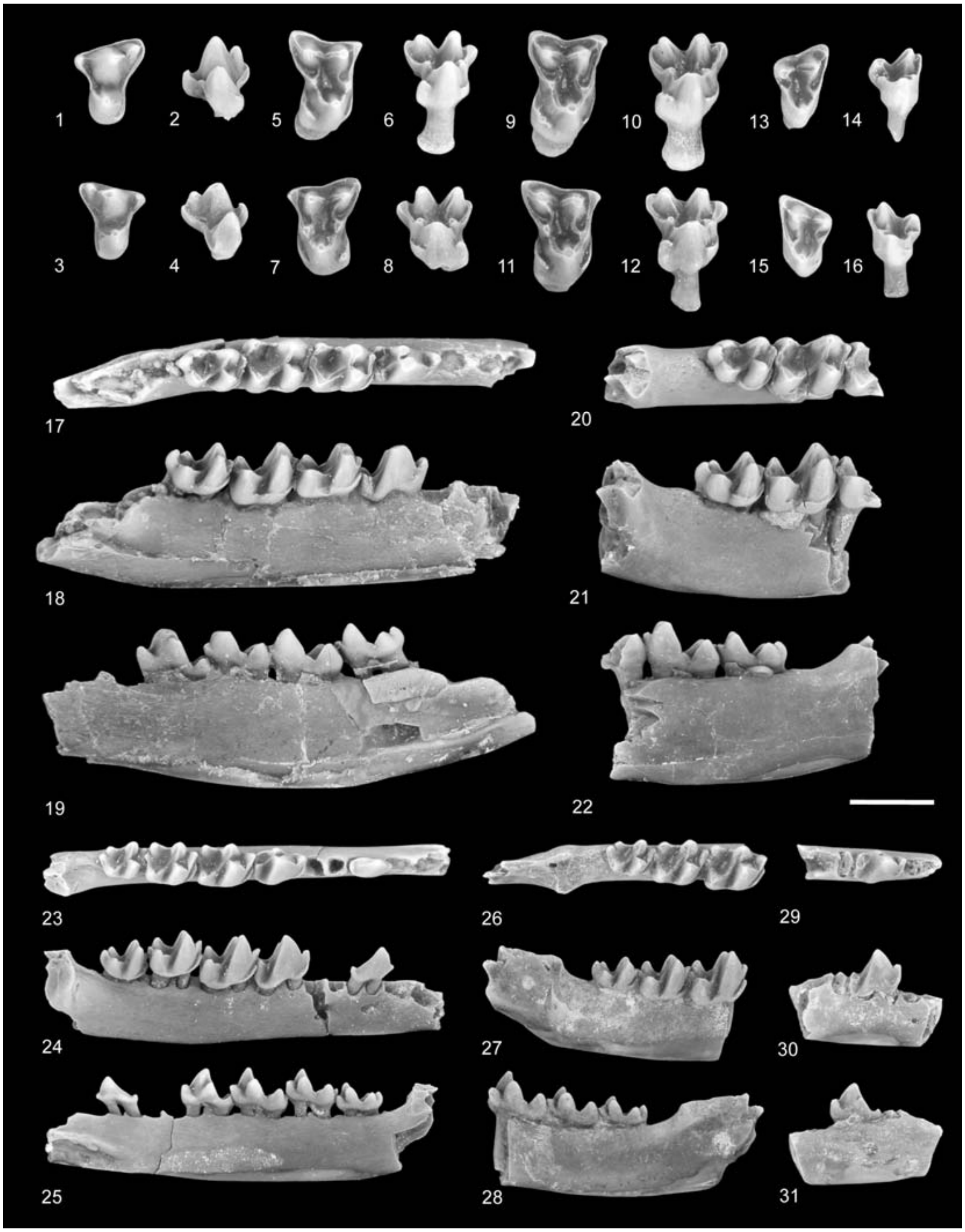

1
2
5
6
9
10
13
14
3
4
7
8
11
12
15
16
17
20
18
21
19
22
23
26
29
24
27
30
25
28
31

Figure 5.—1-25. Litocherus lacunatus from the late middle Tiffanian (Ti4) Roche Percée local fauna, Ravenscrag Formation, Saskatchewan. 1-2, UALVP 9448, right P4 in 1, occlusal, and 2, lingual views; 3-4, UALVP 51795, left P4 in 3, occlusal, and 4, lingual views; 5-6, UALVP 9238, right M1 in 5, occlusal, and 6, lingual views; 7-8, UALVP 51523, left M1 in 7, occlusal, and 8, lingual views; 9-10, UALVP 9234, right M2 in 9, occlusal, and 10, lingual views; 11-12, UALVP 9711, right M2 in 11, occlusal, and 12, lingual views; 13-14, UALVP 9268, right M3 in 13, occlusal, and 14, lingual views; 15-16, UALVP 9270, right M3 in 15, occlusal, and 16, lingual views; 17-19, UALVP 51818, incomplete left dentary with p3-4, m1-3 in 17, occlusal, 18, labial, and 19, lingual views; 20-22, UALVP 9623, incomplete left dentary with m1-3 and posterior alveolus of p4 in 20, occlusal, 21, labial, and 22, lingual views; 23-25, UALVP 51835, left p4 in 23, occlusal, 24, labial, and 25, lingual views.

26-31. Litocherus cf. L. zygeus from the late middle Tiffanian (Ti4) Roche Percée local fauna, Ravenscrag Formation, Saskatchewan. 26-28, UALVP 8924, incomplete right dentary with p4, and alveoli for p3 and m1 in 26, occlusal, 27, labial, and 28, lingual views; 29-31, UALVP 9637, incomplete left dentary with m1-3 and posterior alveolus of p4 in 29, occlusal, 30, labial, and 31, lingual views.

Scale bar = 2 mm.

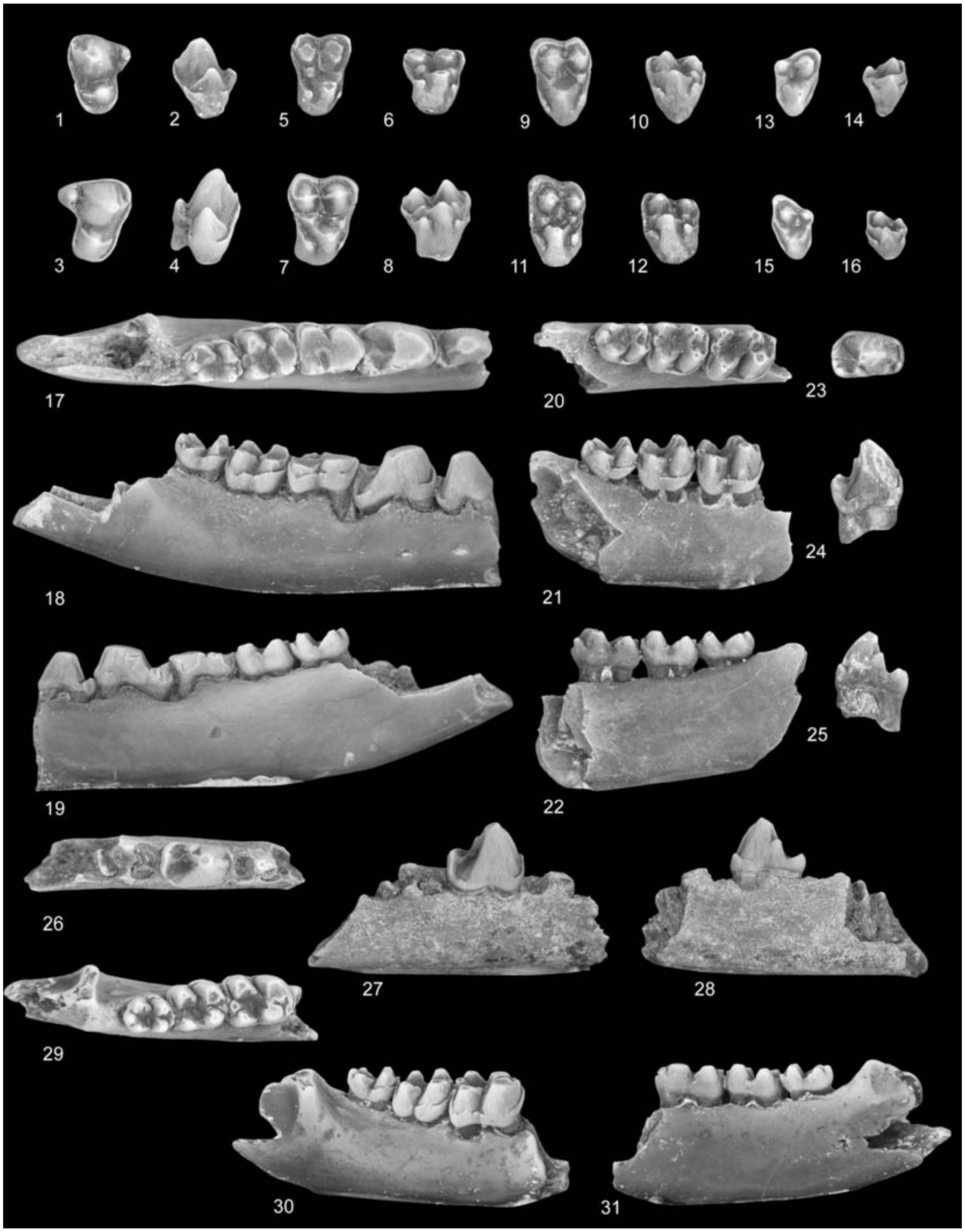

1
2
5
6
9
10
13
14
3
4
7
8
11
12
15
16
17
20
23
18
21
24
19
22
25
26
27
28
29
30
31

Figure 6.—1-5. Adapisorex sp. from the late middle Tiffanian (Ti4) Roche Percée local fauna, Ravenscrag Formation, Saskatchewan. 1-2, UALVP 51850, right M1 in 1, occlusal, and 2, lingual views; 3-5, UALVP 51851, right m1 in 3, occlusal, 4, labial, and 5, lingual views.

6-7. Litolestes cf. L. ignotus from the late middle Tiffanian (Ti4) Roche Percée local fauna, Ravenscrag Formation, Saskatchewan. 6-7, UALVP 10885, left M1 in 6, occlusal, and 7, lingual views.

8-9. Nyctitherium sp. from the late middle Tiffanian (Ti4) Roche Percée local fauna, Ravenscrag Formation, Saskatchewan. 8-9, UALVP 51853, left M2 in 8, occlusal, and 9, lingual views.

Scale bar = 2 mm.

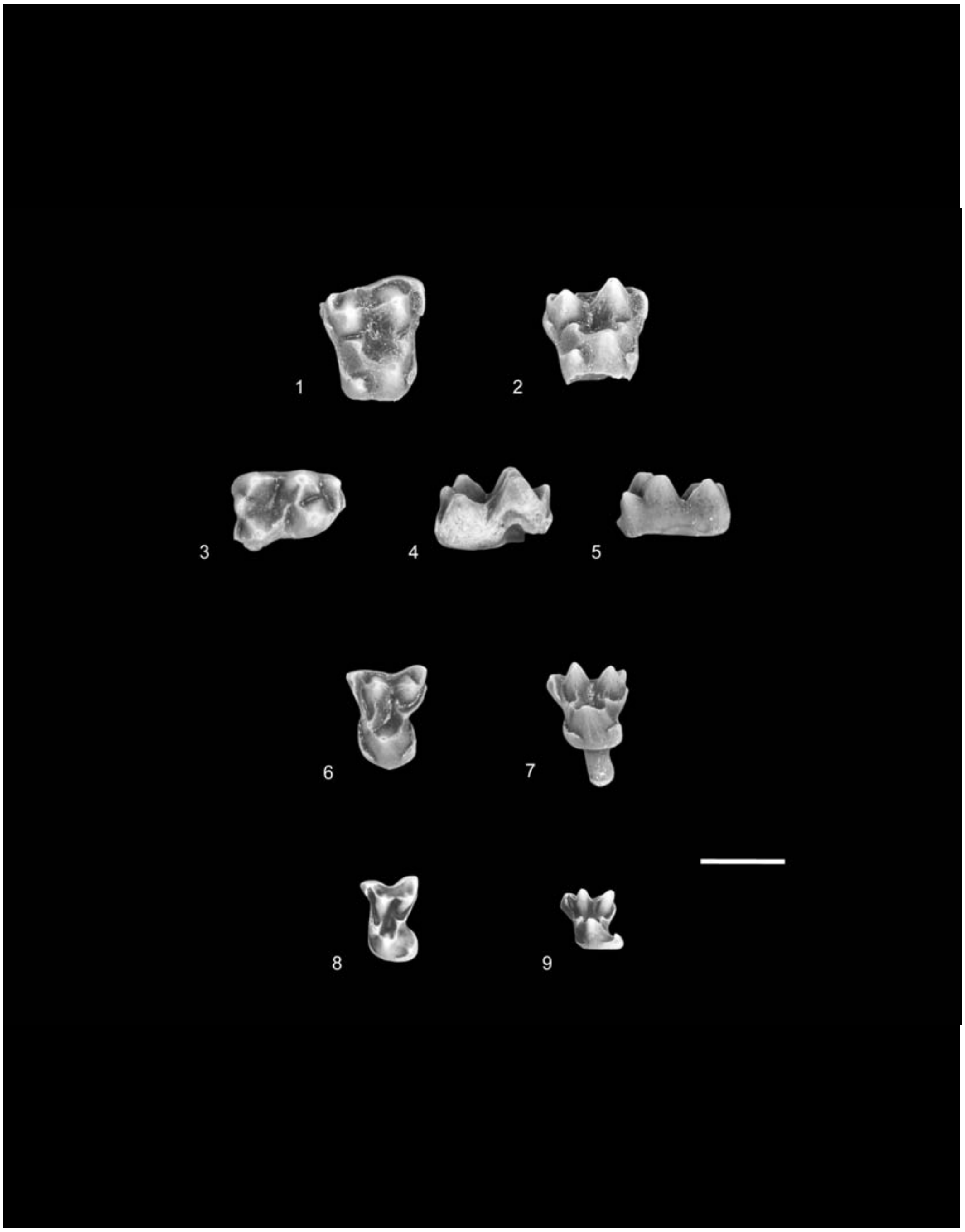

1
2
3
4
5
6
7
8
9

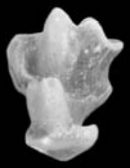
Figure 7.—1-10. Pararyctes pattersoni from the late middle Tiffanian (Ti4) Roche Percée local fauna, Ravenscrag Formation, Saskatchewan. 1-2, UALVP 51757, right M2 in 1, occlusal, and 2, lingual views; 3-4, UALVP 51756, left M2 in 3, occlusal, and 4, lingual views; 5-7, UALVP 9307, right m1 in 5, occlusal, 6, labial, and 7, lingual views; 8-10, UALVP 9305, left m3 in 8, occlusal, 9, labial, and 10, lingual views.

Scale bar = 1 mm.

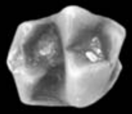
1

2

3



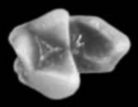
4



5

6

7



8

9

10

Figure 8.—1-3. Paleotomus cf. P. junior from the late middle Tiffanian (Ti4) Roche Percée local fauna, Ravenscrag Formation, Saskatchewan. 1-3, UALVP 8875, left m1 in 1, occlusal, 2, labial, and 3, lingual views.

4-19. cf. Paleotomus sp. 1 from the late middle Tiffanian (Ti4) Roche Percée local fauna, Ravenscrag Formation, Saskatchewan. 4-5, UALVP 51592, right M3 in 4, occlusal, and 5, lingual views; 6-8, UALVP 51593, left p2 in 6, occlusal, 7, labial, and 8, lingual views; 9-11, UALVP 8776, right p4 in 9, occlusal, 10, labial, and 11, lingual views; 12-14, UALVP 8871, left m1 in 12, occlusal, 13, labial, and 14, lingual views; 15-17, UALVP 8780, left m2 in 15, occlusal, 16, labial, and 17, lingual views; 18-20, UALVP 8778, left m3 in 18, occlusal, 19, labial, and 20, lingual views.

21-23. cf. Paleotomus sp. 2 from the late middle Tiffanian (Ti4) Roche Percée local fauna, Ravenscrag Formation, Saskatchewan. 21-23, UALVP 51595, right p2 in 21, occlusal, 22, labial, and 23, lingual views.

Scale bar = 2mm.

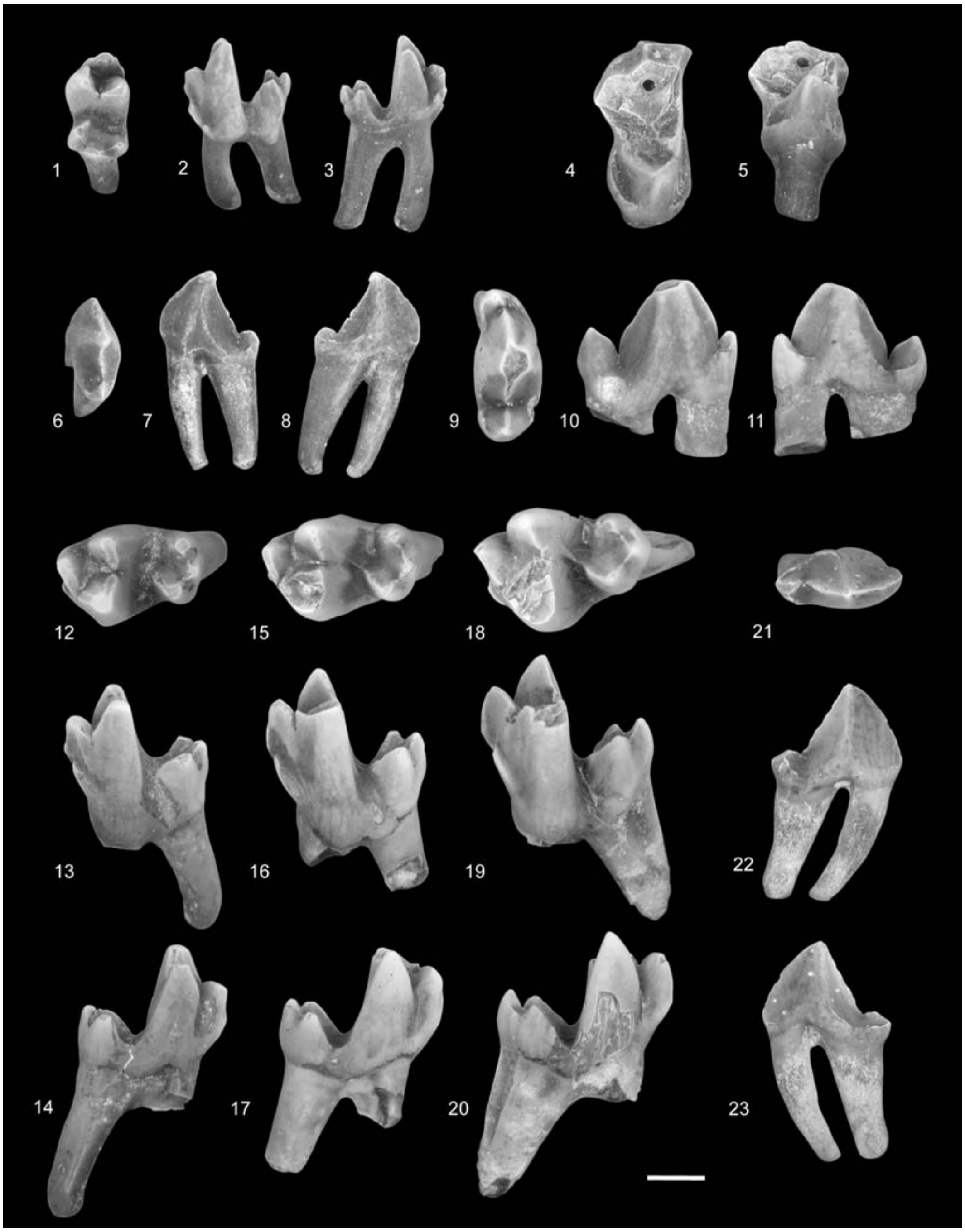

1
2
3
4
5
6
7
8
9
10
11
12
15
18
21
13
16
19
22
14
17
20
23

Figure 9.—1-36. Unuchinia cf. U. dysmathes from the late middle Tiffanian (Ti4) Roche Percée local fauna, Ravenscrag Formation, Saskatchewan. 1-3, UALVP 51530, right I1 in 1, lateral, 2, medial, and 3, occlusal views; 4-6, UALVP 51531, right I1 in 4, lateral, 5, medial, and 6, occlusal views; 7-9, UALVP 51537, left I2 in 7, lateral, 8, medial, and 9, anterior views; 10-11, UALVP 51542, left P4 in 10, occlusal, and 11, lingual views; 12-13, UALVP 51543, right M1 in 12, occlusal, and 13, lingual views; 14-15, UALVP 51544, left M2 in 14, occlusal, and 15, lingual views; 16-18, UALVP 51545, right i2 in 16, lateral, 17, medial, and 18, occlusal views; 19-21, UALVP 51546, right p2 in 19, lateral, 20, medial, and 21, occlusal views; 22-24, UALVP 51548, left m1 in 22, labial, 23, lingual, and 24, occlusal views; 25-27, UALVP 51551, left m1 in 25, labial, 26, lingual, and 27, occlusal views; 28-30, UALVP 51553, right m2 in 28, labial, 29, lingual, and 30, occlusal views; 31-33, UALVP 51549, left m2 in 31, labial, 32, lingual, and 33, occlusal views; 34-36, UALVP 51754, left m3 in 34, labial, 35, lingual, and 36, occlusal views.

37-39. Labidolemur soricoides from the late middle Tiffanian (Ti4) Roche Percée local fauna, Ravenscrag Formation, Saskatchewan. 37-39, UALVP 51755, left m1 in 37, labial, 38, lingual, and 39, occlusal views

Scale bar = 2mm.

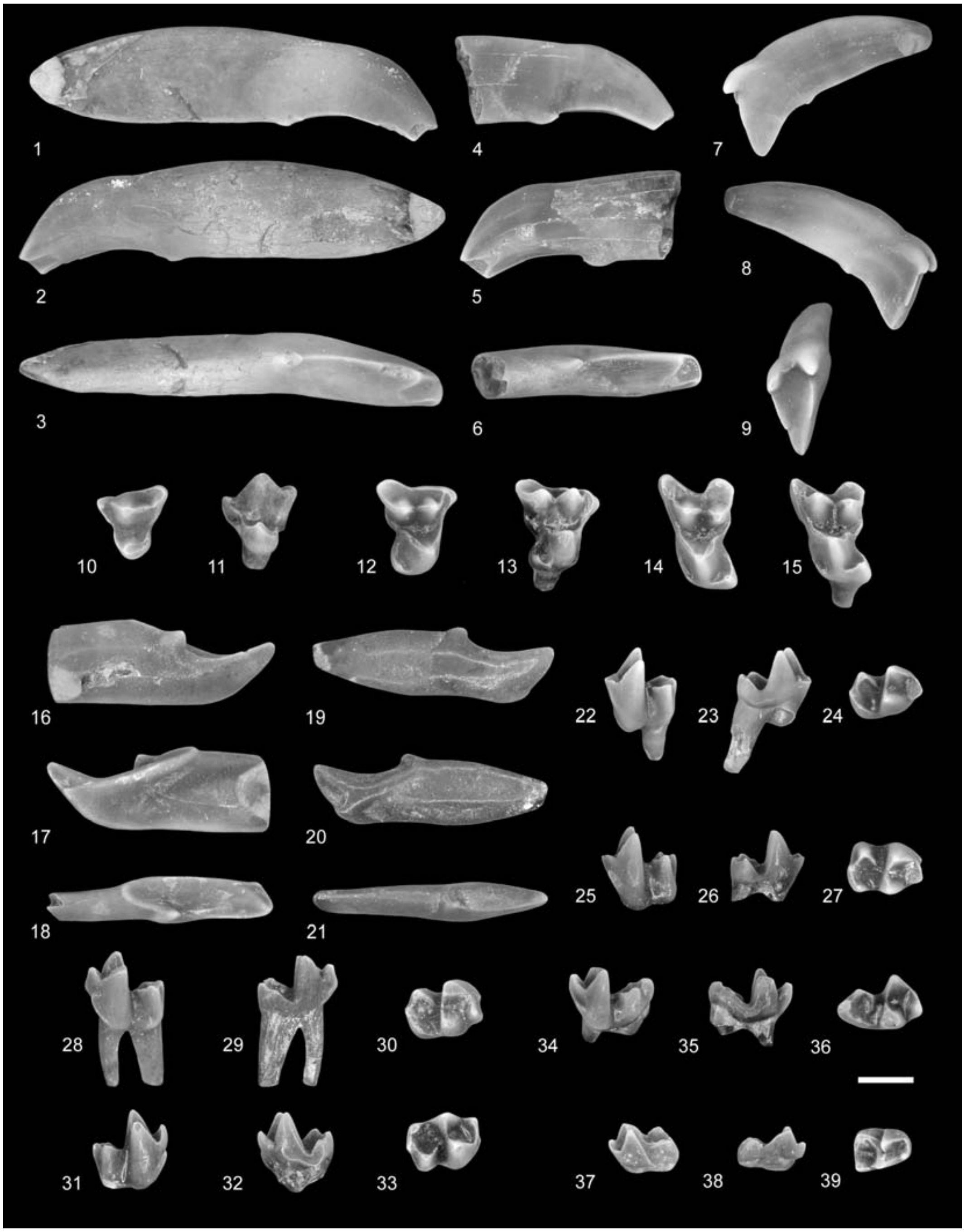

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39

Figure 10.—1-10. Titanoides cf. T. primaevus from the late middle Tiffanian (Ti4) Roche Percée local fauna, Ravenscrag Formation, Saskatchewan. 1-2, UALVP 8765, incomplete right maxilla with M2-3 in 1, occlusal, and 2, lingual views; 3-4, UALVP 8768, right M3 in 3, occlusal, and 4, lingual views; 5-7, UALVP 51529, left mx in 5, labial, 6, lingual, and 7, occlusal views; 8-10, UALVP 8770, right mx in 8, labial, 9, lingual, and 10, occlusal views.

Scale bar = 10 mm.

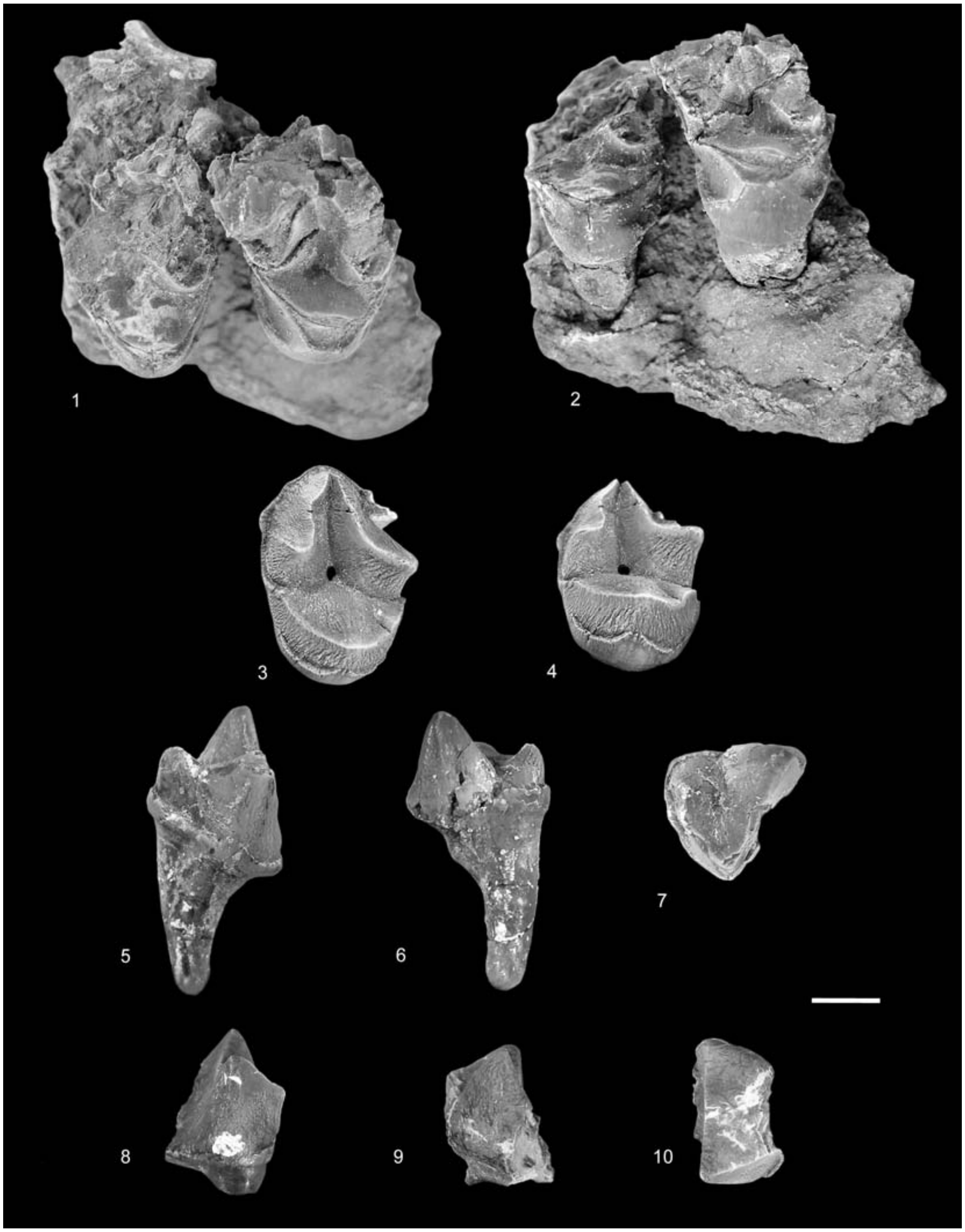

1
2
3
4
5
6
7
8
9
10

Figure 11.—1-22. Bessoecetor pilodontus from the late middle Tiffanian (Ti4) Roche Percée local fauna, Ravenscrag Formation, Saskatchewan. 1-2, UALVP 51455, right P4 in 1, occlusal, and 2, lingual views; 3-4, UALVP 51037, left M1 in 3, occlusal, and 4, lingual views; 5-6, UALVP 51031, right M1 in 5, occlusal, and 6, lingual views; 7-8, UALVP 51038, left M2 in 7, occlusal, and 8, lingual views; 9-10, UALVP 51041, right M2 in 9, occlusal, and 10, lingual views; 11-13, UALVP 51043, incomplete right dentary containing p4, m1 and alveoli for p2-3, m2 in 11, labial, 12, lingual, and 13, occlusal views; 14-16, UALVP 9632, left m1 in 14, labial, 15, lingual, and 16, occlusal views; 17-19, UALVP 51044, incomplete right dentary containing m2 and alveoli for p2-4, m1, m3 in 17, labial, 18, lingual, and 19, occlusal views; 20-22, UALVP 51050, incomplete right dentary with m2 and alveoli for m1, m3 in 20, labial, 21, lingual, and 22, occlusal views.

Scale bar = 2 mm.

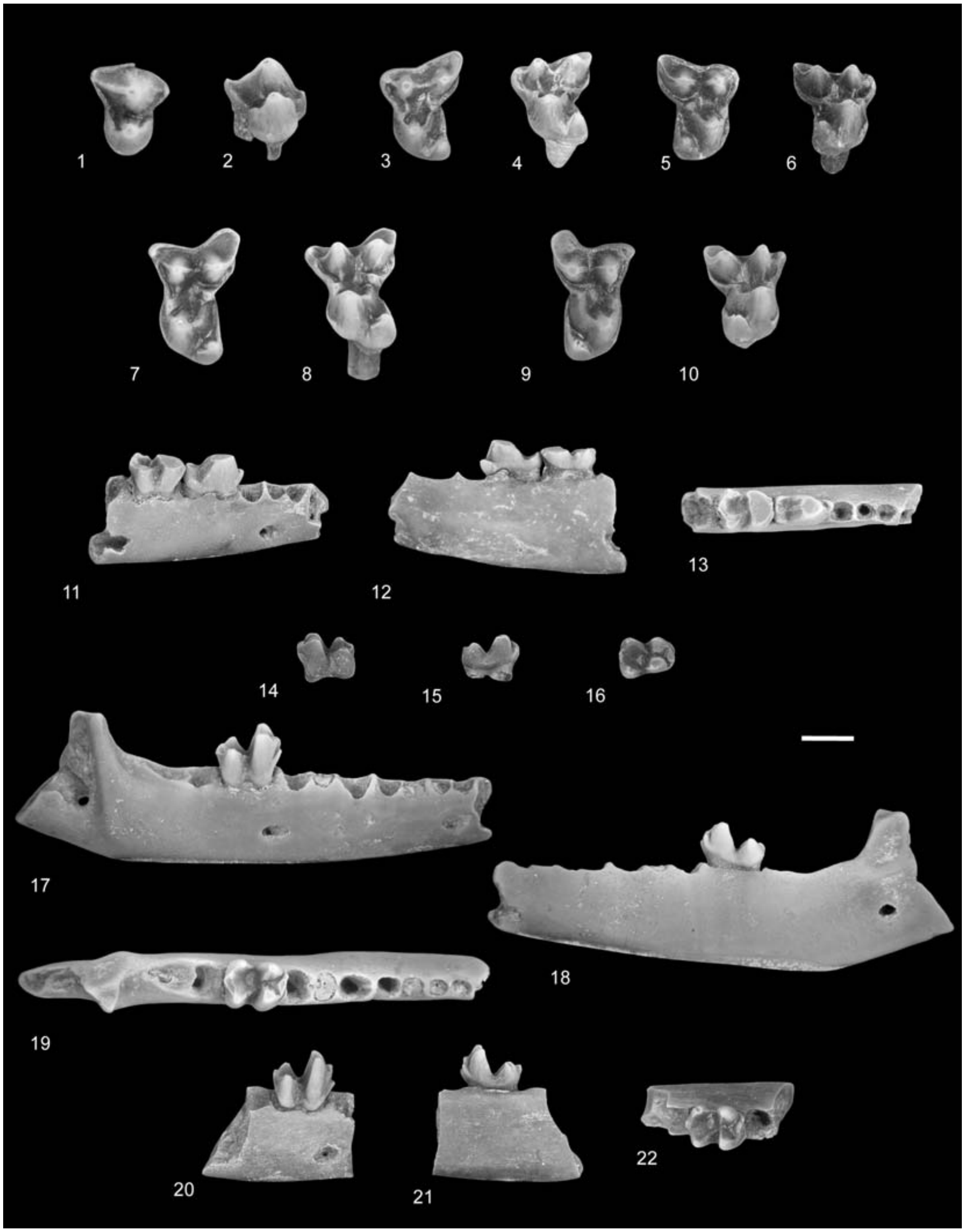

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22

Figure 12.—1-6. Bessoecetor krausei n. sp. from the late middle Tiffanian (Ti4) Roche Percée local fauna, Ravenscrag Formation, Saskatchewan. 1-3, UALVP 9300 (holotype), incomplete right dentary containing i1, p2, m1-3, and alveoli for ?i2-3, p3-4 in 1, labial, 2, lingual, and 3, occlusal views; inset shows UALVP 9300 in oblique labial view with alveoli for i1, ?i2-i3, and c labeled; 4-6, UALVP 10908, left m3 in 4, labial, 5, lingual, and 6, occlusal views.

Scale bar = 2 mm.

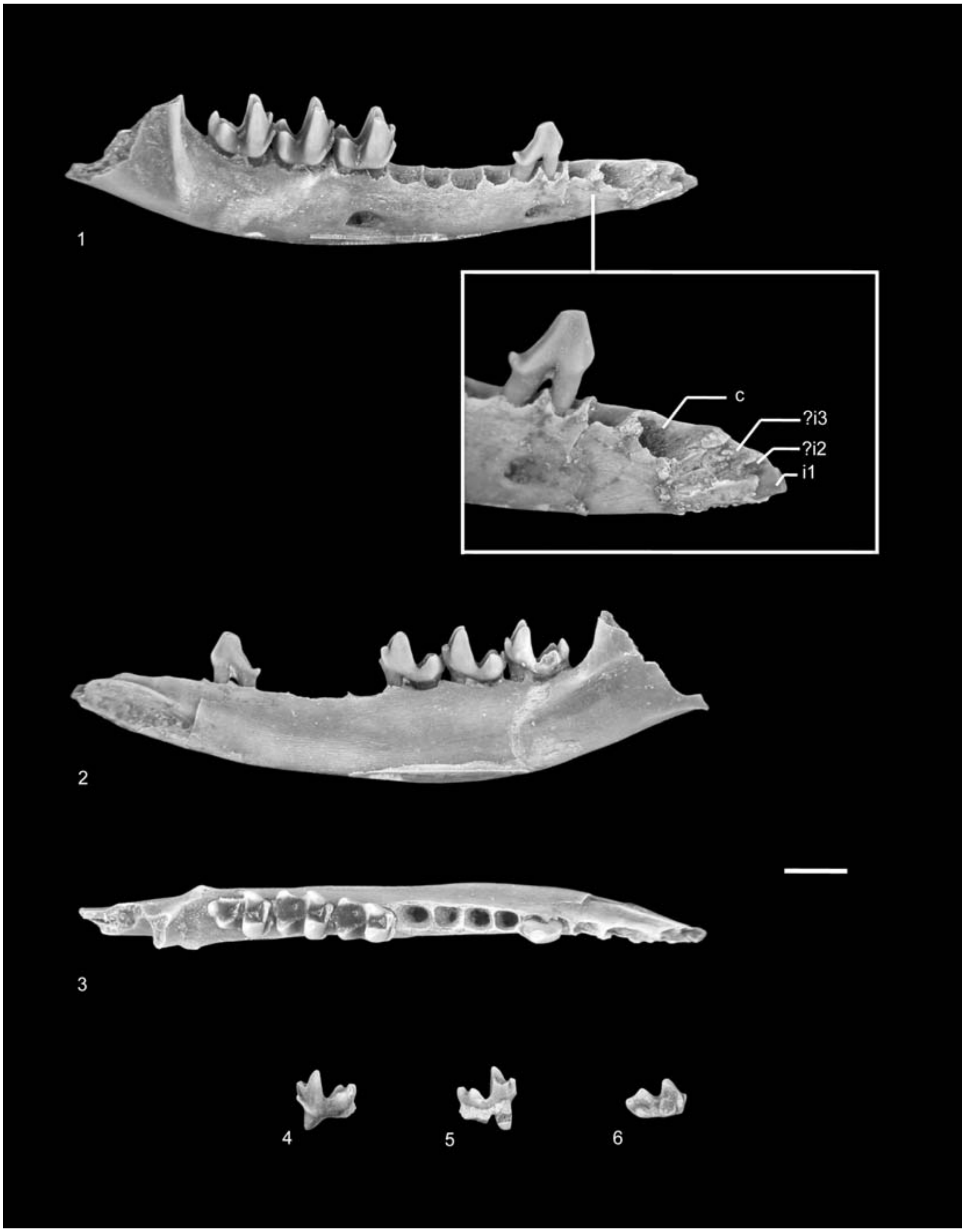

1
c
?i3
?i2
i1
2
3
4
5
6

Figure 13.—1-22. Palaeosinopa sp. from the late middle Tiffanian (Ti4) Roche Percée local fauna, Ravenscrag Formation, Saskatchewan. 1-2, UALVP 9725, left P4 in 1, occlusal, and 2, lingual views; 3-4, UALVP 51053, left P4 in 3, occlusal, and 4, lingual views; 5-6, UALVP 51577, left M1 in 5, occlusal, and 6, lingual views; 7-8, UALVP 51578, right M1 in 7, occlusal, and 8, lingual views; 9-10, UALVP 51077, right M2 in 9, occlusal, and 10, lingual views; 11-12, UALVP 51078, right M2 in 11, occlusal, and 12, lingual views; 13-14, UALVP 9072, right M3 in 13, occlusal, and 14, lingual views; 15-16, UALVP 51080, left M3 in 15, occlusal, and 16, lingual views; 17-19, UALVP 51088, incomplete right dentary containing p2, p4, m1-3 in 17, occlusal, 18, labial, and 19, lingual views; 20-22, UALVP 34129, incomplete left dentary containing p2-4, m1-3 in 20, occlusal, 21, labial, and 22, lingual views.

Scale bar = 4 mm.

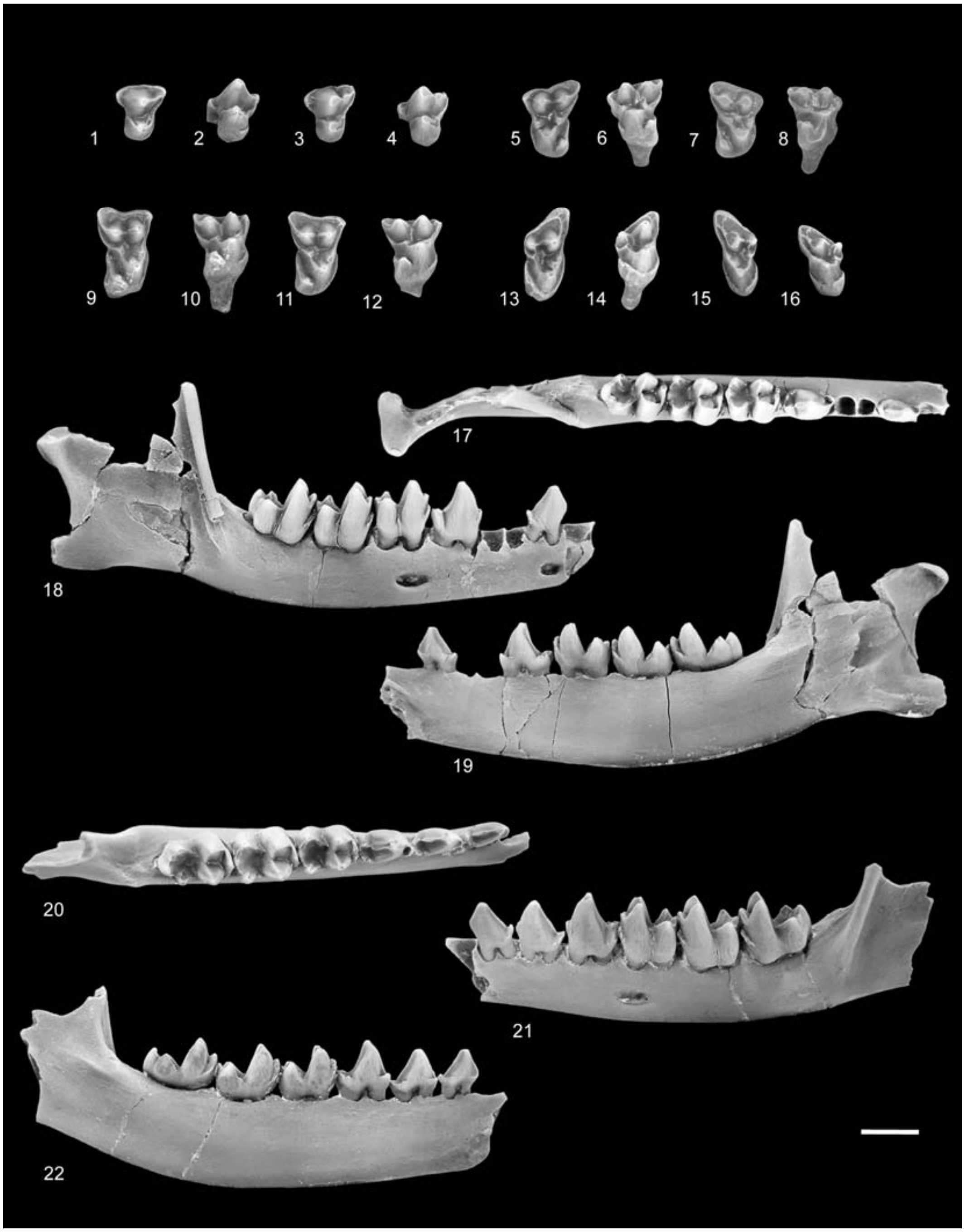

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22

Figure 14.—Bivariate scatter plot of natural logarithm of m1 length and width (after Gingerich and Winkler, 1985, p. 91, fig. 2) of Didymictis dellensis, Didymictis cf. D. dellensis, Raphictis machaera, R. gausion, R. “iota”, and R. nanoptexis. White symbols represent viverravid specimens from Paleocene localities in northern Wyoming (Gingerich and Winkler, 1985), whereas solid symbols represent viverravid specimens from the Roche Percée localities in southeastern Saskatchewan. Circles are 0.2 units in diameter and represent the typical range of variation in a single, non-sexually dimorphic carnivoran species (see discussion of D. dellensis); I assume that the data points represent average values and center the circles on the mean of each species. As interpreted here, D. dellensis is likely not a sexually dimorphic species and Didymictis cf. D. dellensis is distinct from D. dellensis.

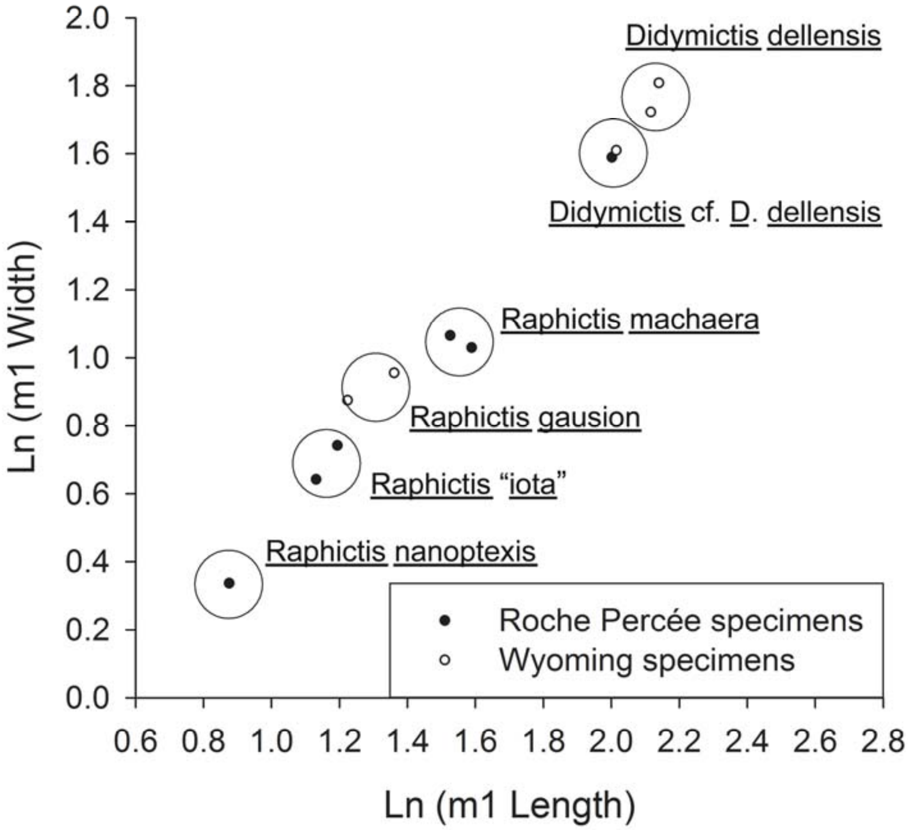

Didymictis dellensis
Didymictis cf. D. dellensis
Raphictis machaera
Raphictis gausion
Raphictis "iota"
Raphictis nanoptexis
● Roche Percée specimens
○ Wyoming specimens
Ln (m1 Width)
Ln (m1 Length)
2.0
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
0.6
0.8
1.0
1.2
1.4
1.6
1.8
2.0
2.2
2.4
2.6
2.8

Figure 15.—1-6. Didymictis dellensis from the late middle Tiffanian (Ti4) Roche Percée local fauna, Ravenscrag Formation, Saskatchewan. 1-3, UALVP 51555, left P4 in 1, occlusal, 2, labial, and 3, lingual views.; 4-6, UALVP 8781, left trigonid of m1 in 4, occlusal, 5, labial, and 6, lingual views.

7-12. Didymictis cf. D. dellensis from the late middle Tiffanian (Ti4) Roche Percée local fauna, Ravenscrag Formation, Saskatchewan. 7-9, UALVP 8774, incomplete left dentary containing p2, p4, m1, and alveoli for p1, p3, m2 in 7, occlusal, 8, labial, and 9, lingual views; 10-12, UALVP 10918, right m2 in 10, occlusal, 11, labial, and 12, lingual views.

13-18. Protictis cf. P. paralus from the late middle Tiffanian (Ti4) Roche Percée local fauna, Ravenscrag Formation, Saskatchewan. 13-15, UALVP 8867, left p4 in 13, occlusal, 14, labial, and 15, lingual views; 16-18, UALVP 51557, right p4 in 16, occlusal, 17, labial, and 18, lingual views.

Scale bar = 5 mm.

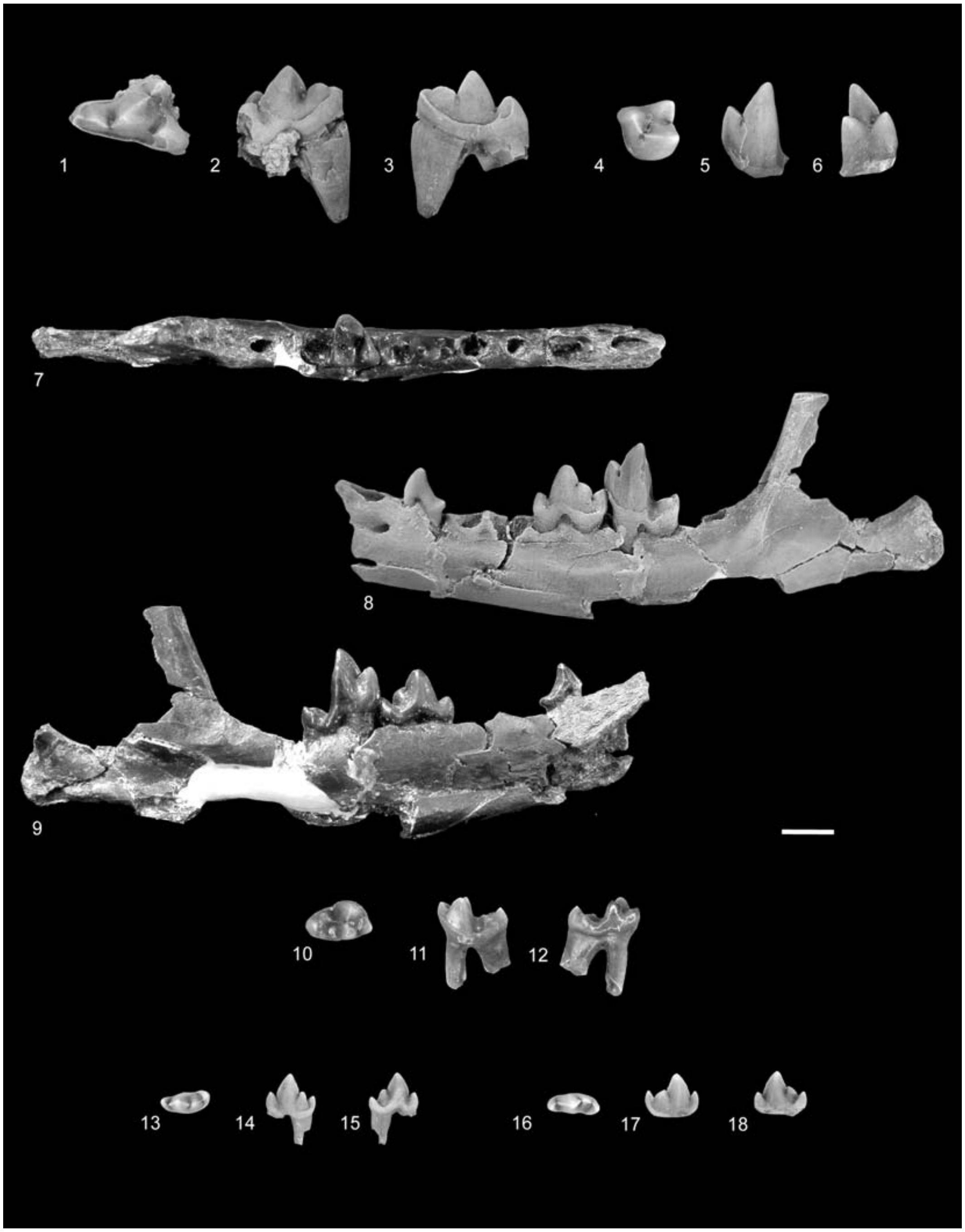

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18

Figure 16.—1-9. Raphictis “iota” from the late middle Tiffanian (Ti4) Roche Percée local fauna, Ravenscrag Formation, Saskatchewan. 1-3, UALVP 51558, left P4 in 1, occlusal, 2, labial, and 3, lingual views.; 4-6, UALVP 9063, left m1 in 4, occlusal, 5, labial, and 6, lingual views; 7-9, UALVP 9062, incomplete right dentary with p4 and m1 and alveoli for p3 in 7, occlusal, 8, labial, and 9, lingual views.

10-25. Raphictis machaera n. sp. from the late middle Tiffanian (Ti4) Roche Percée local fauna, Ravenscrag Formation, Saskatchewan. 10-12, UALVP 51563, left P4 in 10, occlusal, 11, labial, and 12, lingual views; 13-14, UALVP 51565, right M1 in 13, occlusal, and 14, lingual views; 15-16, UALVP 9066, right M2 in 15, occlusal, and 16, lingual views; 17-19, UALVP 8775 (holotype), incomplete left dentary with p4, m1, roots for the c, p3, and alveoli for p2, m2 in 17, occlusal, 18, labial, and 19, lingual views; 20-22, UALVP 9060, left p3 in 20, occlusal, 21, labial, and 22, lingual views; 23-25, UALVP 51573, right m2 in 23, occlusal, 24, labial, and 25, lingual views.

26-36. Raphictis nanoptexis n. sp. from the late middle Tiffanian (Ti4) Roche Percée local fauna, Ravenscrag Formation, Saskatchewan. 26-28, UALVP 51560, right P4 in 26, occlusal, 27, labial, and 28, lingual views; 29-30, UALVP 51561, right M1 in 29, occlusal, and 30, lingual views; 31-33, UALVP 9070, left p4 in 31, occlusal, 32, labial, and 33, lingual views; 34-36, UALVP 8876 (holotype), left m1 in 34, occlusal, 35, labial, and 36, lingual views.

Scale bar = 2 mm.

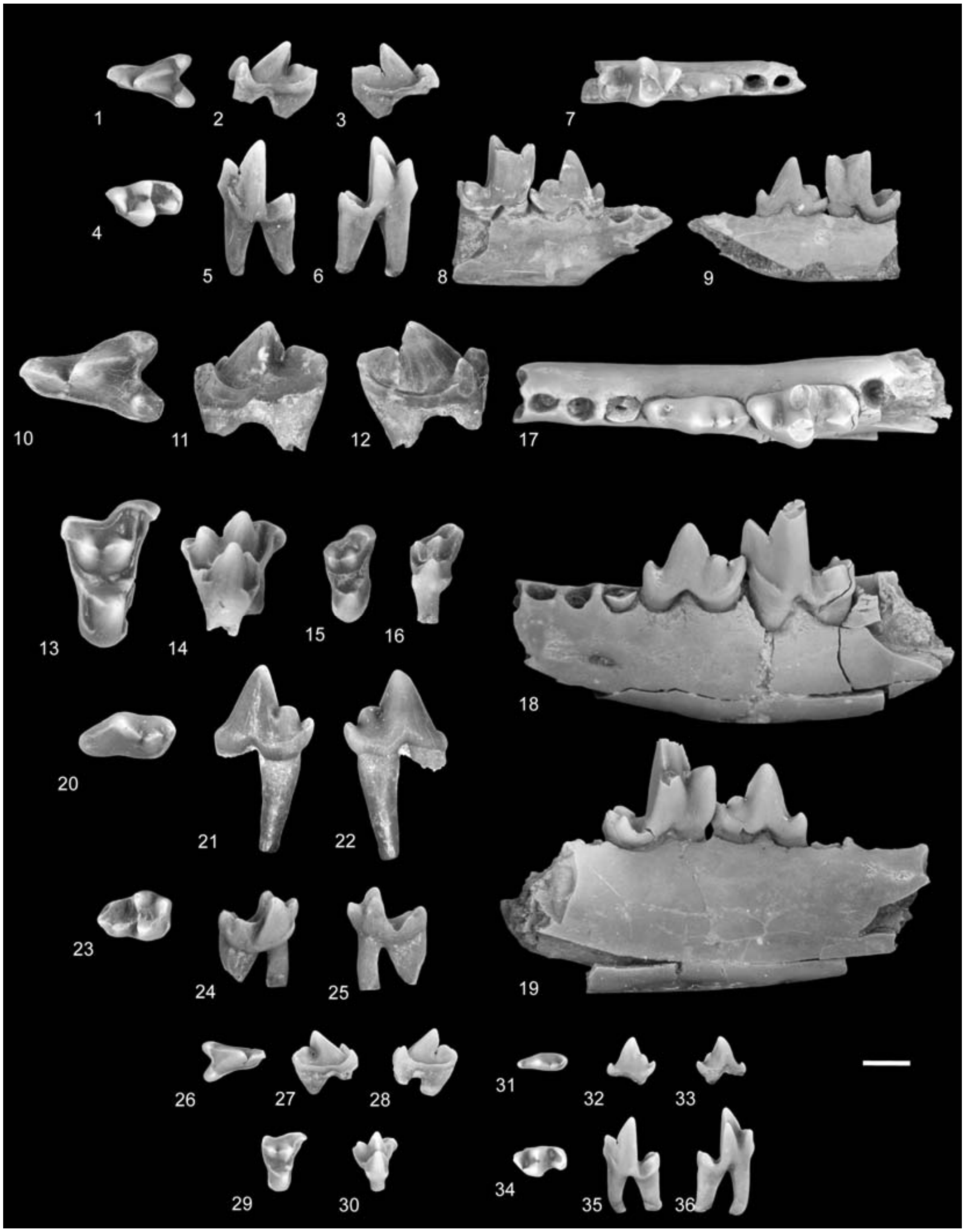

1
2
3
7
4
5
6
8
9
10
11
12
17
13
14
15
16
18
20
21
22
23
24
25
19
26
27
28
31
32
33
29
30
34
35
36

Figure 17.—*1*-*2*. *Chriacus* cf. *C*. *baldwini* from the late middle Tiffanian (Ti4) Roche Percée local fauna, Ravenscrag Formation, Saskatchewan. *1*-*2*, UALVP 9643, left M1 in *1*, occlusal, and *2*, lingual views.

3-*5*. *Chriacus* cf. *C*. *oconostotae* from the late middle Tiffanian (Ti4) Roche Percée local fauna, Ravenscrag Formation, Saskatchewan. *3*-*5*, UALVP 51452, left m2 talonid in *3*, occlusal, *4*, labial, and *5*, lingual views.

6-*18*. *Thryptacodon* *australis* from the late middle Tiffanian (Ti4) Roche Percée local fauna, Ravenscrag Formation, Saskatchewan. *6*-*7*, UALVP 9639, incomplete right maxilla with M1 and alveoli for P3-4, M2 in *6*, occlusal, and *7*, lingual views; *8*-*9*, UALVP 9640, right M2 in *8*, occlusal, and *9*, lingual views; *10*-*12*, UALVP 51453, left m1 in *10*, occlusal, *11*, labial, and *12*, lingual views; *13*-*15*, UALVP 9645, left m2 in *13*, occlusal, *14*, labial, and *15*, lingual views; *16*-*18*, UALVP 51454, left m3 in *16*, occlusal, *17*, labial, and *18*, lingual views.

Scale bar = 5 mm.

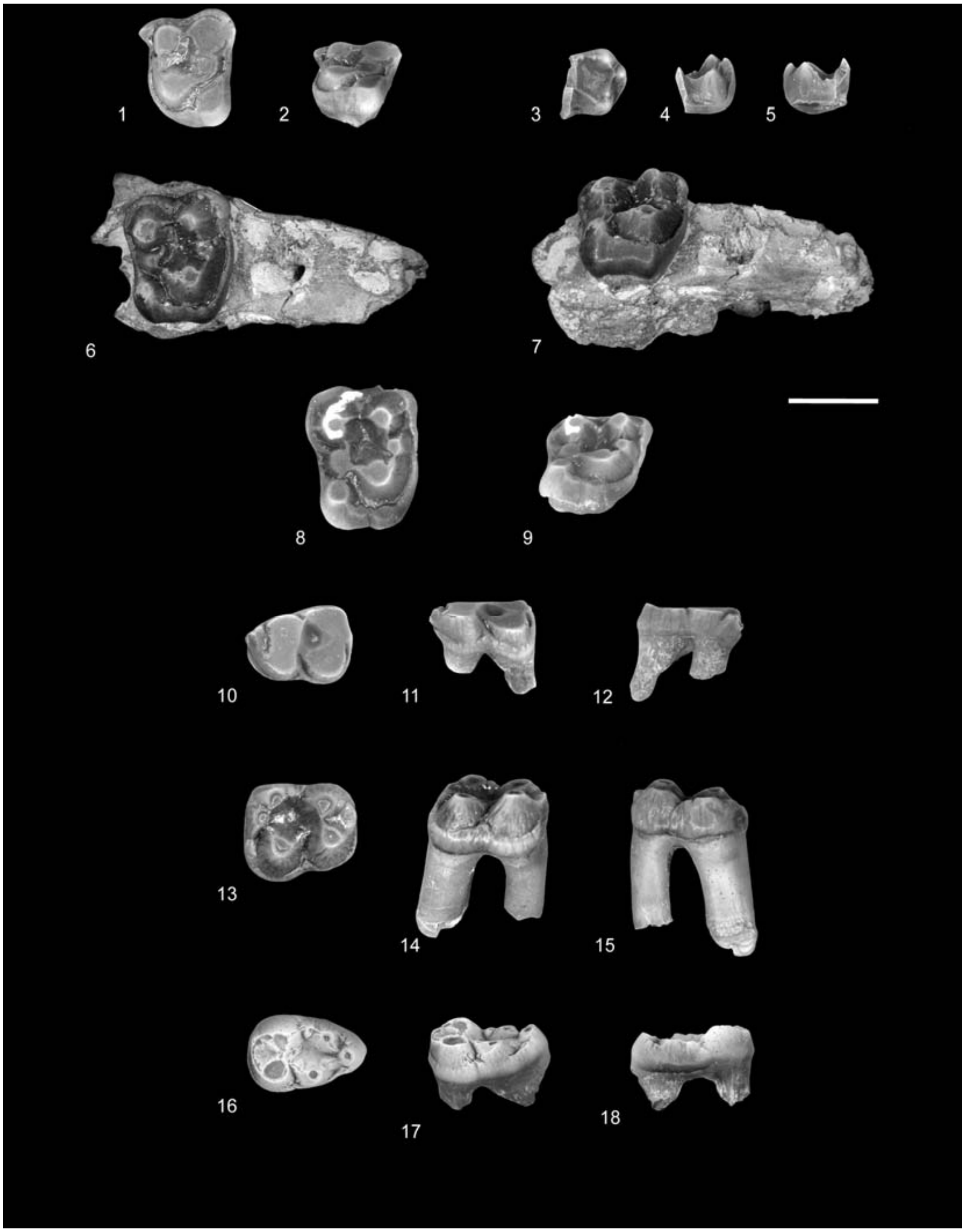

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18

Figure 18.—*1*-*5*. *Arctocyon mumak* from the late middle Tiffanian (Ti4) Roche Percée local fauna, Ravenscrag Formation, Saskatchewan. *1*-*2*, UALVP 9691, left M1 in *1*, occlusal, and *2*, lingual views; *3*-*5*, UALVP 9689, incomplete left dentary with p3-4, m1-3 and alveoli for i1-3, c, p1-2 in *3*, occlusal, *4*, labial, and *5*, lingual views.

6-*12*. *Arctocyon corrugatus* from the late middle Tiffanian (Ti4) Roche Percée local fauna, Ravenscrag Formation, Saskatchewan. *6*-*7*, UALVP 51459, left M1 in *6*, occlusal, and *7*, lingual views; *8*-*9*, UALVP 51460, right M2 in *8*, occlusal, and *9*, lingual views; *10*-*12*, UALVP 10877, right m3 in *10*, occlusal, *11*, labial, and *12*, lingual views.

Scale bar = 10 mm.


1
2
3
4
UA9689
5
6
7
8
9
10
11
12

Figure 19.—1-3. Dorraletes diminutivus from the late middle Tiffanian (Ti4) Roche Percée local fauna, Ravenscrag Formation, Saskatchewan. 1-3, UALVP 51527, right m2 in 1, occlusal, 2, labial, and 3, lingual views.

Scale bar in top left corner = 2 mm (applies only for figs. 3.1-3.3).

4-26. Phenacodus magnus from the late middle Tiffanian (Ti4) Roche Percée local fauna, Ravenscrag Formation, Saskatchewan. 4-5, UALVP 9651, right DP3 in 4, occlusal, and 5, lingual views; 6-7, UALVP 51463, left P4 in 6, occlusal, and 7, lingual views; 8-9, UALVP 9691, left M2 in 8, occlusal, and 9, lingual views; 10-11, UALVP 9694, right M3 in 10, occlusal, and 11, lingual views; 12-14, UALVP 9650, right p3 in 12, occlusal, 13, labial, and 14, lingual views; 15-17, UALVP 51468, left p4 in 15, occlusal, 16, labial, and 17, lingual views; 18-20, UALVP 9697, right m1 in 18, occlusal, 19, labial, and 20, lingual views; 21-23, UALVP 9696, left m2 in 21, occlusal, 22, labial, and 23, lingual views; 24-26, UALVP 9695, left m3 in 24, occlusal, 25, labial, and 26, lingual views.

Scale bar in bottom right corner = 10 mm (applies only for figs. 3.4-3.26).

.

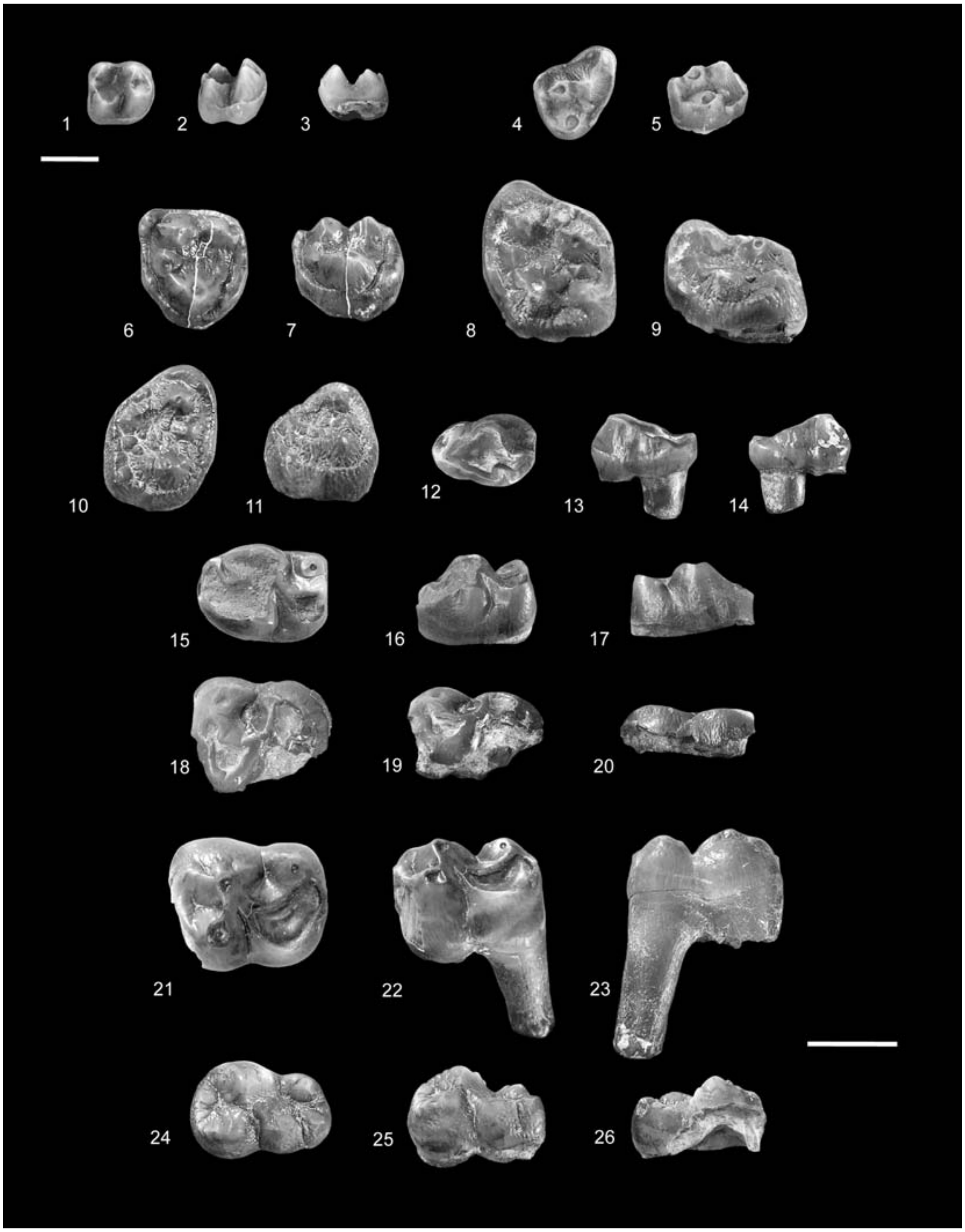
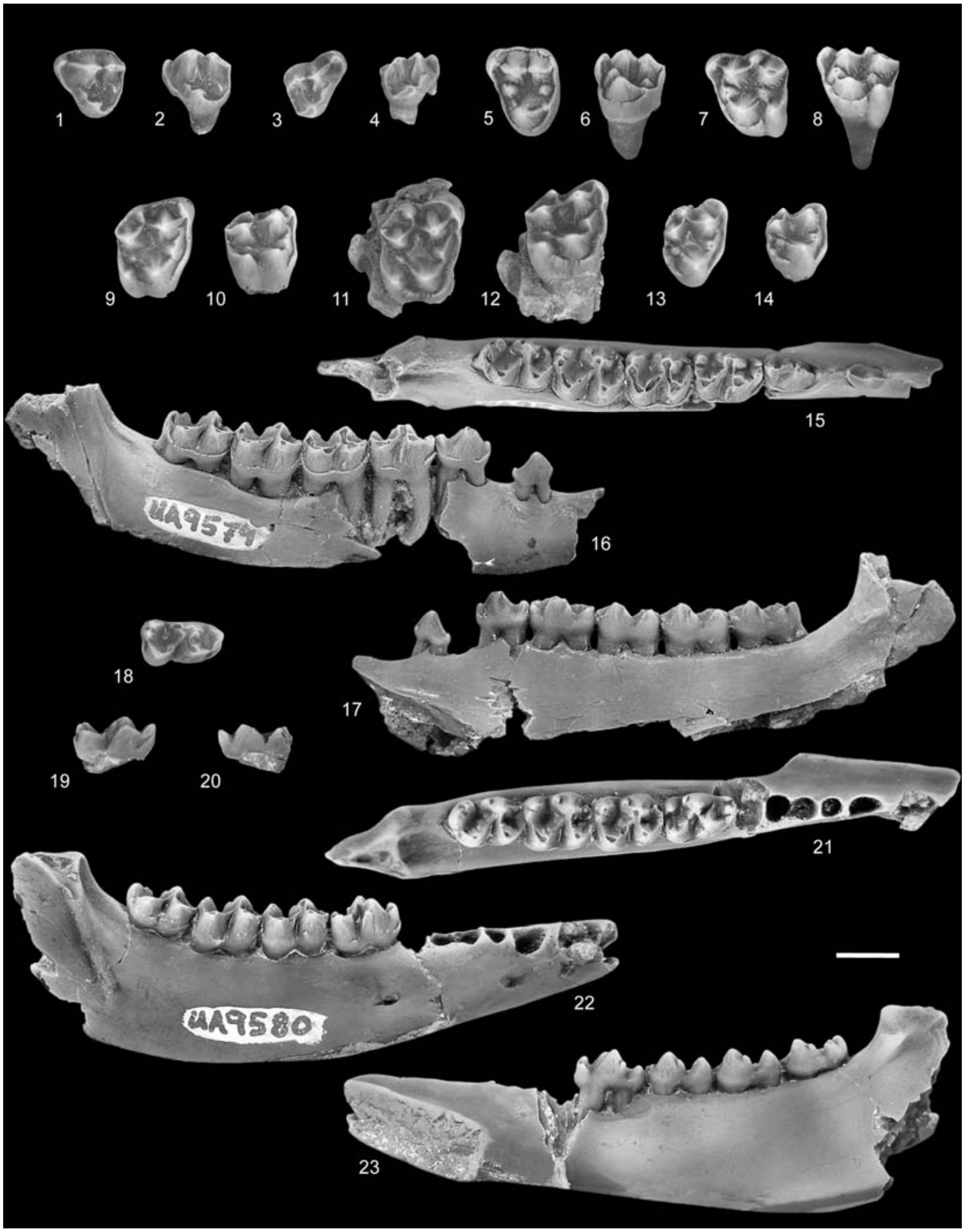

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26

Figure 20.—*1*-*23*. *Ectocion* *borealis* n. sp. from the late middle Tiffanian (Ti4) Roche Percée local fauna, Ravenscrag Formation, Saskatchewan. *1*-*2*, UALVP 51473, left P3 in *1*, occlusal, and *2*, lingual views; *3*-*4*, UALVP 51474, right DP3 in *3*, occlusal, and *4*, lingual views; *5*-*6*, UALVP 9684, left P4 in *5*, occlusal, and *6*, lingual views; *7*-*8*, UALVP 51475, left DP4 in *7*, occlusal, and *8*, lingual views; *9*-*10*, UALVP 51477, right M1 in *9*, occlusal, and *10*, lingual views; *11*-*12*, UALVP 51481, right M2 in *11*, occlusal, and *12*, lingual views; *13*-*14*, UALVP 51489, right M3 in *13*, occlusal, and *14*, lingual views; *15*-*17*, UALVP 9579 (holotype), incomplete right dentary with p2-4, m1-3 in *15*, occlusal, *16*, labial, and *17*, lingual views; *18*-*20*, UALVP 51497, right dp4 in *18*, occlusal, *19*, labial, and *20*, lingual views; *21*-*23*, UALVP 9580, incomplete right dentary with p4, m1-3, and alveoli for i3, c, p1-2 in *21*, occlusal, *22*, labial, and *23*, lingual views.

Scale bar = 5 mm.


1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
UA9579
16
18
17
19
20
21
22
UA9580
23

Appendix 1.—Taxonomic listing of mammals from the late middle Tiffanian (Ti4) Roche Percée local fauna, Ravenscrag Formation, Saskatchewan.

- Class Mammalia
  - Subclass Theriiformes
    - Infraclass Allotheria
      - Order Multituberculata
        - Suborder Cimolodonta
          - Family Ptilodontidae
            - Subfamily Neoplagiaulacinae
              - *Mesodma pygmaea* Sloan
              - *Mimetodon silberlingi* (Simpson)
              - *Ectypodus* cf. *E. powelli*
              - *Neoplagiaulax hunteri* (Simpson)
              - *Neoplagiaulax* cf. *N. hazeni*

            - Subfamily Ptilodontinae
              - *Ptilodus kummae* Krause
              - *Prochetodon foxi* Krause

          - Family Microcosmodontidae
            - *Microcosmodon conus* Jepsen

    - Infraclass Holotheria
      - Supercohort Theria
        - Cohort Marsupialia
          - Order Didelphimorphia
            - Family Peradectidae
              - *Peradectes* cf. *P. protinnominatus*

Cohort PLACENTALIA

Superorder LEPTICTIDA

Family LEPTICTIDAE

PRODIACODON CF. *P*. *CONCORDIARCENSIS*

Grandorder LIPOTYPHLA

Order ERINACEOMORPHA

Family uncertain

DIACOCHERUS CF. *D*. *MEIZON*

“*XYNOLESTES* *DENOMMEI*” Scott

LITOCHERUS *LACUNATUS* (Gazin)

LITOCHERUS CF. *L*. *ZYGEUS*

Family ADAPISORICIDAE

ADAPISOREX SP.

Family ERINACEIDAE

ONCOCHERUS *KRISHTALKAI* Scott

LITOLESTES CF. *L*. *IGNOTUS*

Order SORICOMORPHA

Family NYCTITHERIIDAE

NYCTITHERIUM SP.

Grandorder FERAE

Order CIMOLESTA

Family uncertain

PARARYCTES *PATTERSONI* Van Valen

Family PALAEORYCTIDAE

PALAEORYCTES SP.

Suborder DIDELPHODONTA

Family CIMOLESTIDAE

PALEOTOMUS CF. P. JUNIOR

CF. PALEOTOMUS SP. 1

CF. PALEOTOMUS SP. 2

Suborder APATOTHERIA

Family APATEMYIDAE

UNUCHINIA CF. U. DYSMATHES

LABIDOLEMUR SORICOIDES Matthew and Granger

Suborder PANTODONTA

Superfamily PANTOLAMBDOIDEA

Family TITANOIDEIDAE

TITANOIDES CF. T. PRIMAEVUS

Family CYRIACOTHERIIDAE

CYRIACOTHERIUM CF. C. ARGYREUM

Suborder PANTOLESTA

Family PANTOLESTIDAE

BESSOECETOR PILODONTUS Secord

BESSOECETOR KRAUSEI

PALAEOSINOPA SP.

Order CARNIVORA

Family VIVERRAVIDAE

DIDYMICTIS DELLENSIS Dorr

DIDYMICTIS CF. D. DELLENSIS

Protictis cf. *P. paralus*
Raphictis "*iota*" Scott
Raphictis nanoptexis
Raphictis machaera

Grandorder Archonta
Order Primates
Suborder Plesiadapiformes
Family Micromomyidae
Micromomys vossae Krause

Family Plesiadapidae
Plesiadapis churchilli Gingerich

Family Carpolestidae
Carpodaptes stonleyi Fox

Superfamily Paromomyoidea
Family Paromomyidae
Ignacius frugivorous Matthew and Granger

Grandorder Ungulata
Order Procreodi
Family Oxyclaenidae
Chriacus cf. *C. baldwini*
Chriacus cf. *C. oconostotae*
Thryptacodon australis Simpson

Family Arctocyonidae
Subfamily Arctocyoninae

ARCTOCYON MUMAK (Van Valen)
ARCTOCYON CORRUGATUS (Cope)

Order CONDYLARTHRA
  Family HYOPSODONTIDAE
    DORRALETES DIMINUTIVUS (Dorr)

  Family PHENACODONTIDAE
    PHENACODUS MAGNUS Thewissen
    ECTOCION BOREALIS