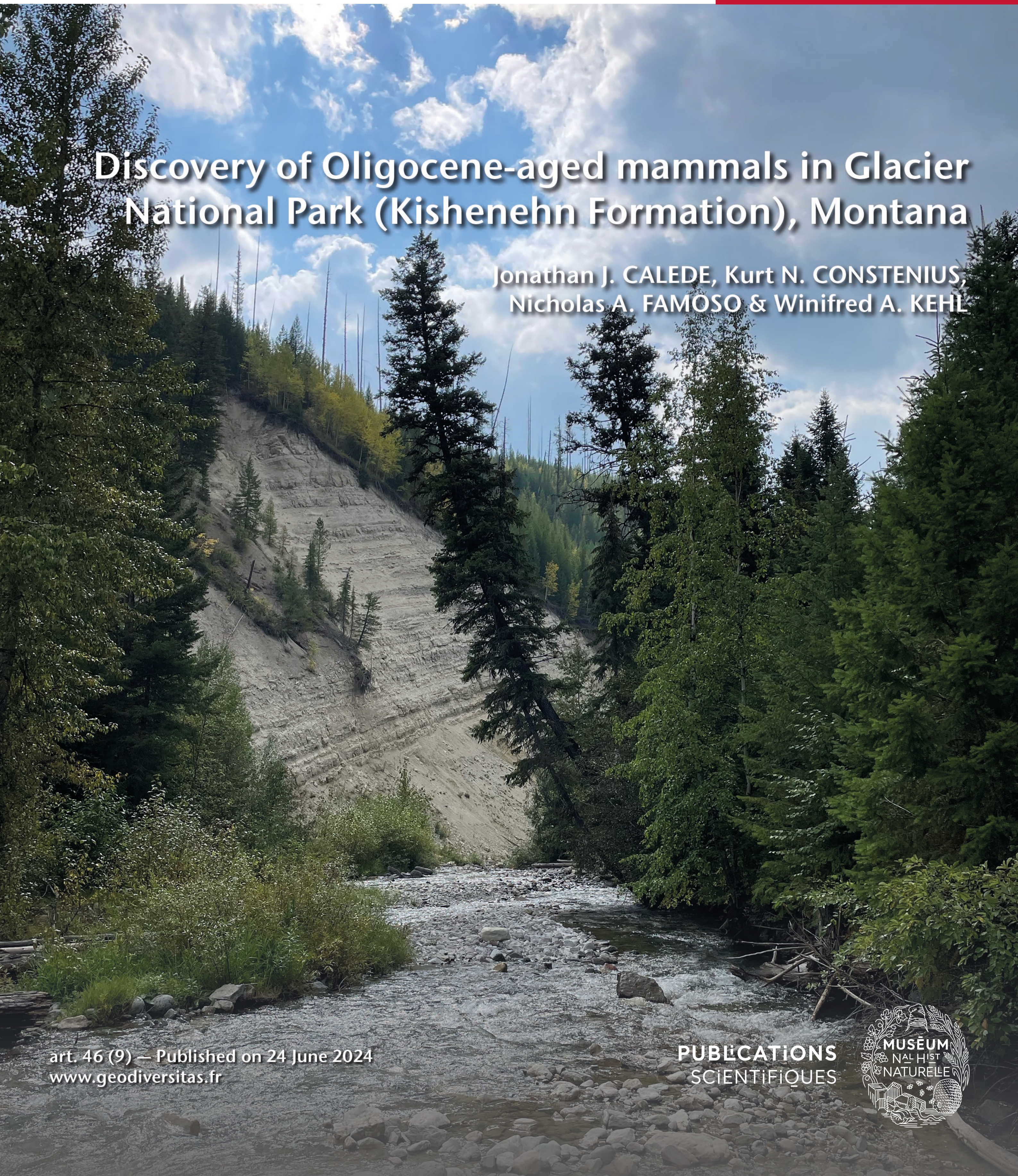
geodiversitas

2024 • 46 • 9

Discovery of Oligocene-aged mammals in Glacier National Park (Kishenehn Formation), Montana

Jonathan J. CALEDE, Kurt N. CONSTENIUS,
Nicholas A. FAMOSO & Winifred A. KEHL



art. 46 (9) — Published on 24 June 2024
www.geodiversitas.fr

PUBLICATIONS
SCIENTIFIQUES

MUSÉUM
NAL HIST
NATURELLE

DIRECTEUR DE LA PUBLICATION / *PUBLICATION DIRECTOR* : Gilles Bloch,
Président du Muséum national d'Histoire naturelle

RÉDACTEUR EN CHEF / *EDITOR-IN-CHIEF* : Didier Merle

ASSISTANT DE RÉDACTION / *ASSISTANT EDITOR* : Emmanuel Côtez (geodiv@mnhn.fr)

MISE EN PAGE / *PAGE LAYOUT* : Audrina Neveu

COMITÉ SCIENTIFIQUE / *SCIENTIFIC BOARD* :
Christine Argot (Muséum national d'Histoire naturelle, Paris)
Beatrix Azanza (Museo Nacional de Ciencias Naturales, Madrid)
Raymond L. Bernor (Howard University, Washington DC)
Henning Blom (Uppsala University)
Jean Broutin (Sorbonne Université, Paris, retraité)
Gaël Clément (Muséum national d'Histoire naturelle, Paris)
Ted Daeschler (Academy of Natural Sciences, Philadelphie)
Gregory D. Edgecombe (The Natural History Museum, Londres)
Ursula Göhlich (Natural History Museum Vienna)
Jin Meng (American Museum of Natural History, New York)
Brigitte Meyer-Berthaud (CIRAD, Montpellier)
Zhu Min (Chinese Academy of Sciences, Pékin)
Isabelle Rouget (Muséum national d'Histoire naturelle, Paris)
Sevket Sen (Muséum national d'Histoire naturelle, Paris, retraité)
Stanislav Štamberg (Museum of Eastern Bohemia, Hradec Králové)
Paul Taylor (The Natural History Museum, Londres, retraité)

COUVERTURE / *COVER* :
Affleurement d'un banc de coupe de la formation Oligocène de Kishenehn, Bowman Creek, Parc National des Glaciers, Montana. Crédits : Kurt Constenius./
Cut bank exposure of Oligocene Kishenehn Formation, Bowman Creek, Glacier National Park, Montana. Credits: Kurt Constenius.

Geodiversitas est indexé dans / Geodiversitas *is indexed in:*
- Science Citation Index Expanded (SciSearch®)
- ISI Alerting Services®
- Current Contents® / Physical, Chemical, and Earth Sciences®
- Scopus®

Geodiversitas est distribué en version électronique par / Geodiversitas *is distributed electronically by:*
- BioOne® (http://www.bioone.org)

Les articles ainsi que les nouveautés nomenclaturales publiés dans *Geodiversitas* sont référencés par /
Articles and nomenclatural novelties published in Geodiversitas *are referenced by:*
- ZooBank® (http://zoobank.org)

Geodiversitas est une revue en flux continu publiée par les Publications scientifiques du Muséum, Paris
Geodiversitas *is a fast track journal published by the Museum Science Press, Paris*

Les Publications scientifiques du Muséum publient aussi / *The Museum Science Press also publish:* ***Adansonia***, ***Zoosystema***, ***Anthropozoologica***, ***European Journal of Taxonomy***, ***Naturae***, ***Cryptogamie*** **sous-sections** ***Algologie***, ***Bryologie***, ***Mycologie, Comptes Rendus Palevol***

Diffusion – Publications scientifiques Muséum national d'Histoire naturelle
CP 41 – 57 rue Cuvier F-75231 Paris cedex 05 (France)
Tél. : 33 (0)1 40 79 48 05 / Fax : 33 (0)1 40 79 38 40
diff.pub@mnhn.fr / http://sciencepress.mnhn.fr

© Publications scientifiques du Muséum national d'Histoire naturelle, Paris, 2024
ISSN (imprimé / *print*) : 1280-9659/ ISSN (électronique / *electronic*) : 1638-9395

Discovery of Oligocene-aged mammals in Glacier National Park (Kishenehn Formation), Montana

Jonathan J. CALEDE
Department of Evolution, Ecology, and Organismal Biology, The Ohio State University at
Marion, 1459 Mount Vernon Avenue, Marion, OH 43302 (United States)
and Research Associate, Section of Vertebrate Paleontology, Carnegie Museum of Natural
History 4400 Forbes Avenue, Pittsburgh, PA 15213 (United States)
jonathan.calede@gmail.com (corresponding author)

Kurt N. CONSTENIUS
Research Associate, Section of Vertebrate Paleontology, Carnegie Museum of Natural History
4400 Forbes Avenue, Pittsburgh, PA 15213 (United States)
and Department of Geosciences, University of Arizona,
Tucson, AZ 85721 (United States)

Nicholas A. FAMOSO
John Day Fossil Beds National Monument, US National Park Service,
32651 Highway 19, Kimberly, OR 97848 (United States)
and Department of Earth Sciences, University of Oregon,
1272 University of Oregon, Eugene, OR 97403 (United States)

Winifred A. KEHL
3971 Hoover Road #52, Grove City, OH 43123 (United States)

Submitted on 15 July 2023 | Accepted on 20 December 2023 | Published on 24 June 2024

urn:lsid:zoobank.org:pub:FF29E123-8A23-4ACF-9D54-FA2191BAF6DA

Calede J. J., Constenius K. N., Famoso N. A. & Kehl W. A. — Discovery of Oligocene-aged mammals in Glacier National Park (Kishenehn Formation), Montana. *Geodiversitas* 46 (9): 367-386. https://doi.org/10.5252/geodiversitas2024v46a9. http://geodiversitas.com/46/9

ABSTRACT

The Kishnehn Formation crops out in Glacier National Park of northwest Montana where a rich fossil record of plant macrofossils, pollen and spores, insects, terrestrial and aquatic mollusks, and fish has been unearthed. Past research has also described an extensive mammal fauna from the Eocene (Uintan-Chadronian). Oligocene-aged fossil mammals have been reported before, but none has ever been published in the peer-reviewed literature. Here, we present the first Arikareean-aged fossil mammals from the Kishenehn Formation, the youngest fossil mammals ever discovered in the park. The fossils consist of a set of lower jaws of the leptomerycid *Pronodens transmontanus* (Douglas, 1903) and a partial lower jaw of the rodent *Paciculus montanus* Black, 1961, both endemics of the northern Rocky Mountains. These new fossils enable us to explore the morphological variation in *Pronodens* Koerner, 1940 and *Paciculus* Cope, 1879. Our analyses suggest the existence of a single widely distributed and sometimes locally abundant species of *Pronodens*, which may co-occur with a rare and very large second species. Our revised diagnoses for the genus and species show the need for additional work on this little-studied artiodactyl genus. Similar efforts on the systematics of cricetid rodents will benefit from building upon our analysis of tooth morphology in *Paciculus* to shed light on the rise of leidymines. The last fossil we describe, partial paired dentaries of *Miohippus* Marsh, 1874, is the northern-most occurrence of the genus in the Rocky Mountains and shows the potential for future work in the Kishenehn Formation to enable the study of faunal change across the Eocene-Oligocene boundary in the northern Rocky Mountains.

KEY WORDS
Arikareean,
Miohippus,
Paciculus,
Pronodens,
Rocky Mountains.

RÉSUMÉ

Découverte de mammifères de l'Oligocène dans le Parc National de Glacier (Formation de Kishenehn), Montana.

La formation Kishenehn est développée dans le Parc National de Glacier du nord-ouest du Montana, où un riche registre fossile de macroplantes, de spores, insectes, mollusques terrestres et aquatiques, et poissons ont été trouvés. Des recherches passées ont aussi décrit une faune de mammifères extensive datant de l'Éocène (Uintien-Chadronien). Des fossiles de mammifères de l'Oligocène ont déjà étés signalés, mais aucun n'a jamais été publié dans la littérature scientifique. Nous présentons ici les premiers fossiles de mammifères de l'Arikaréen provenant de la formation Kishenehn, les plus récents fossiles jamais découverts dans le parc. Ils consistent en un ensemble de mandibules du leptomérycide *Pronodens transmontanus* (Douglas, 1903) et une mandibule partielle de *Paciculus montanus* Black, 1961, tous deux endémiques du nord des montagnes Rocheuses. Ces nouveaux fossiles nous permettent d'explorer la variation morphologique au sein de *Pronodens* Koerner, 1940 et *Paciculus* Cope, 1879. Nos analyses suggèrent l'existence d'une seule espèce de *Pronodens*, largement distribuée et parfois abondante localement, qui pourrait coexister avec une seconde espèce, rare et plus grande. Nos diagnoses révisées pour le genre et l'espèce démontrent la nécessité d'un travail supplémentaire sur ce petit genre d'artiodactyle peu étudié. Des efforts similaires sur la systématique des rongeurs cricétidés pourront s'appuyer sur notre analyse de la morphologie dentaire chez *Paciculus* pour éclairer la diversification des leidymines. Le dernier fossile que nous décrivons, une paire d'os dentaires de *Miohippus* Marsh, 1874, atteste la présence la plus au nord de ce genre dans les montagnes Rocheuses et démontre le potentiel des travaux futurs dans la formation Kishenehn, pour permettre l'étude des changements fauniques autour de la limite Éocène-Oligocène dans les montagnes Rocheuses du nord.

MOTS CLÉS
Arikaréen,
Miohippus,
Paciculus,
Pronodens,
montagnes Rocheuses.

INTRODUCTION

The fossil record of the northern Rocky Mountains includes a rich Oligocene-aged mammalian fauna spanning the Orellan through Arikareean North American land mammal ages. Much of this fossil record is concentrated in southwestern Montana, especially the Orellan and Whitneyan-aged deposits. The richest Arikareean-aged assemblages are concentrated in the early part of the Arikareean (30-25 Ma) and located both in Montana and Idaho, across the Great Continental Divide (Fig. 1B; Tedford *et al.* 2004). West of the divide, the Peterson Creek Local Fauna, from the Lemhi Valley of east central Idaho, preserves a dozen rodent species as well as carnivores, lagomorphs, soricids, merycoidodontids, equids, and rhinocerotids (Nichols 1976, 1979; Fig. 1B). Farther north, in west central Montana and also on the western side of the divide, the Cabbage Patch beds, part of the Renova Formation, preserve the richest mammalian fauna of the region with over 90 species, mostly small mammals (Calede 2016a, 2020, 2022; Calede & Rasmussen 2020; Calede *et al.* 2022), which have been studied for well over a century (Douglass 1902, 1903). One fossil-bearing outcrop of the Cabbage Patch beds preserving two congeneric gopher species, oreodonts, and a carnivore is present on the eastern side of the continental divide (Rasmussen 1977; Calede & Rasmussen 2020). Also on the eastern side of the continental divide, the Fort Logan Formation preserves a little studied, but rich mammalian fauna that includes proscalopid moles and erinaceids (Koerner 1940; Barnosky 1982), several families of rodents (castorids [Calede 2014], aplodontiids [Rensberger 1979, 1981], and cricetids [Black 1961]), and lagomorphs (Black 1961) as well as carnivores and ungulates (Scott 1895; Koerner 1940). Hanson (2015) reported the existence of some Arikareean-aged fossils from outcrops of the Six Mile Creek Formation in the Canyon Ferry Reservoir area (east of the divide), but these remain unpublished. Whitneyan-aged fossils have been recovered from the Gravelly range and the White Hills Local Fauna as well as the Parrot Bench Local Fauna, all in southwest Montana, east of the divide (Kuenzi & Fields 1971; Tedford *et al.* 2004; Korth & Tabrum 2017; Lofgren *et al.* 2020). The Orellan-aged assemblages include the assemblages of the Cook Ranch and Matador Ranch local faunas of southwestern Montana (Korth 2019), the more northerly Easter Lily deposits (Kuenzi & Fields 1971; Garcia 1992; Prothero & Emry 2004), and the Canyon Ferry Reservoir east of Helena in west central Montana (White 1954; Korth 2012), all located in the southwestern part of the state of Montana on the eastern side of the Great Continental Divide (Fig. 1B). In this publication, we present new remains of Oligocene-aged fossil mammals from the northern Rockies. In contrast to previous findings,

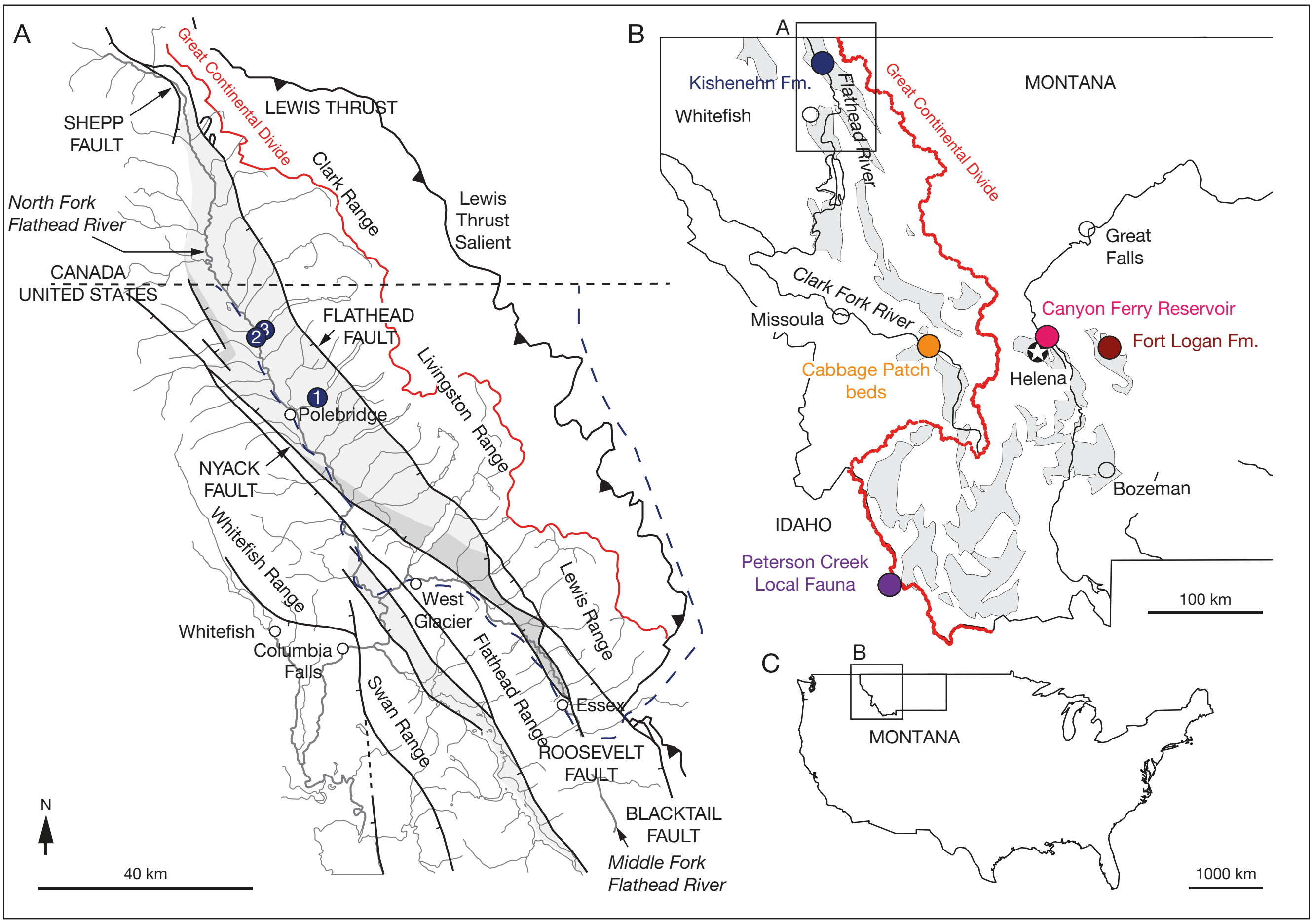


Fig. 1. — Geographic context of the Oligocene-aged fossils from Glacier National Park: **A**, detailed map of the Kishenehn basin showing the North Fork and Middle Fork areas, faults in the area (**continuous black lines**), continental divide (**red**), national park boundaries (**dashed blue line**), and water courses (**gray**). Localities of GLAC 26988 (**1**), GLAC 26987 (**2**), and CM 87801 (**3**) are also showed (modified from Dawson & Constenius 2018). Detailed geographic information is available to qualified researchers from repositories; **B**, map of western Montana showing the location of five coeval Arikareean-aged deposits bearing leptomerycid and/or equid fossils: the Kishenehn, Renova (Cabbage Patch beds), and Fort Logan formations as well as the Canyon Ferry Reservoir and the Peterson Creek Local Fauna (in Idaho). Select water bodies, cities, and the continental divide are also displayed. **Grey areas** represent basins with strata coeval with the Kishenehn Formation. **Black box** shows location of A; **C**, location of the state of Montana within the United States with **black box** showing location of B.

these fossils were found in northwest Montana just south of the 49th parallel, within Glacier National Park (National Park Service-administered lands), from outcrops of the Kishenehn Formation (Fig. 1A).

The Kishenehn Formation has already yielded a rich fossil record of plant macrofossils, pollen and spores, insects, terrestrial and aquatic mollusks, fish, and mammals from the middle Eocene and early Oligocene (summarized in Constenius *et al.* 1989; Pierce & Constenius 2001, 2014; Greenwalt & Labandeira 2013; Greenwalt *et al.* 2015; Liu *et al.* 2016; Dawson & Constenius 2018; Fan *et al.* 2021; Gardner & Wilson 2022), but the fossils presented herein are the youngest known mammal remains from the formation to be published. The first vertebrate fossils that were discovered in the formation are Duchesnean and/or Chadronian in age (late Eocene; Russell 1954, 1964; Dawson & Constenius 2018). An older, richer fauna of fossil mammals has been described from Uintan-aged horizons (Dawson & Constenius 2018). The youngest fossil mammals so far known from the Kishenehn Formation consists of Orellan-aged specimens, including a merycoidodontid (McMechan 1981; Constenius *et al.* 1989), which is currently lost, and some small mammals (see Pierce & Constenius 2001; Fan *et al.* 2021), all unpublished.

The fossils we describe herein consist of two sets of ungulate jaws, including a fossil horse, *Miohippus* Marsh, 1874, and a leptomerycid, *Pronodens* Koerner, 1940, as well as a partial jaw of a cricetid rodent, *Paciculus* Cope, 1879; the latter two can be identified to the species level. Fossils of *Pronodens* and *Paciculus* are already known from other Oligocene-aged deposits of the Rockies coeval with the Kishenehn Formation, offering the opportunity for an initial interpretation of the biostratigraphy and biogeography within the region during the early part of the Arikareean. Specifically, two different species of the leptomerycid genus *Pronodens* are already known from Montana. *Pronodens silberlingi* Koerner, 1940 has been described from the Fort Logan Formation (Koerner 1940) and *P. transmontanus* (Douglass, 1903) from the Cabbage Patch beds (Douglass 1903; Rasmussen 1977). *Pronodens silberlingi* is found in the Rosebud Formation of South Dakota in addition to the Fort Logan Formation (Taylor & Webb 1976), whereas *P. transmontanus* is restricted to the Cabbage Patch beds where it is considered an index taxon for the lower unit dated *c.* 30-28.1 Ma (Calede 2020). In addition to providing biostratigraphic and biogeographic insights, the new material we describe herein enables us to provide a revised diagnosis for the genus, the first differential diagnosis for the species *P. transmontanus*, and the first quantitative analysis of morphology for the genus. *Paciculus* is a widespread taxon found from the John Day Formation of Oregon to the Great Plains, including several localities in the Rocky Mountains (Nichols 1979; Lindsay *et al.* 2016). On the western side of the continental divide, *P. montanus* Black, 1961 has been found in the Peterson Creek Local Fauna (Nichols 1976). A similar form, *P.* cf. *P. montanus*, has also been recovered from the middle and upper units (*c.* 28.1-25.6 Ma) of the Cabbage Patch beds (Calede 2020). On the eastern side of the continental divide, *P. montanus* is also present in the Fort Logan Formation (Black 1961). The new fossil we present provides the opportunity to undertake a quantitative analysis of morphology in the genus *Paciculus*.

GEOLOGICAL CONTEXT

The Kishenehn Formation is deposited (in part) in the basin of the same name, a half graben divided into two regions corresponding to branches of the Flathead River: the North Fork and Middle Fork (Fig. 1B). The fossils described herein are from the North Fork region. This section of the basin is bordered to the northeast by the Flathead fault and to the southwest by the Nyack Fault (Constenius 1982, 1996). The formation itself consists of a thick accumulation of nonmarine alluvial fan, fluviolacustrine, and paludal deposits (Constenius *et al.* 1989; Fan *et al.* 2021). Many of the fluviolacustrine deposits are rich in mollusk remains, described by Pierce & Constenius (2001, 2014).

The Kishenehn Formation in the North Fork has been divided into three informal units, the basal, lower, and upper members (Price 1965; Jones 1969; McMechan & Price 1980; McMechan 1981; Constenius *et al.* 1989). The basal member is composed of 140 to 1 200 meters of fluvial sandstone and conglomerate. Correlative deposits of the Coal Creek Member in the Middle Fork region have been dated as middle Eocene with the fossil-bearing strata corresponding to the Uintan North American Land Mammal Age (NALMA). Strata of the Coal Creek Member have been dated radioisotopically with a tuff yielding a ^{40}Ar/^{39}Ar biotite age of 46.2 ± 0.4 Ma (Dawson & Constenius 2018). The 2 400-3 500-meter-thick lower member includes lacustrine, fluvial, paludal, and deltaic deposits of conglomerate, sandstone, mudstone, lignite, and coal that date back to the late Eocene and early Oligocene (Russell 1954, 1964; Hopkins & Sweet 1976; McMechan 1981; Pierce & Constenius 2001). The 1 500-2 000-meter-thick upper member is characterized by coarse clastic rocks and megabreccia in British Columbia that have been interpreted as alluvial fan deposits, whereas thick sequences of fluvial and lacustrine sandstone, mudstone and lessor conglomerate are more typical of the member in Montana. Limited age control suggests the age of the upper member spans the Oligocene and likely extends into the early Miocene (Orellan through Arikareean NALMAs; Price 1965; Jones 1969; McMechan 1981; Constenius *et al.* 1989; Pierce & Constenius 2001; Dawson & Constenius 2018; Fan *et al.* 2021). In the central part of the Kishenehn basin, the collective stratigraphic thickness of these three members is as much as 5 000 m and the vertical thickness of the basin fill based on gravity modeling is 3 350 m (Constenius 1988). The youngest dated horizon has previously been reported to be 28.2 ± 0.6 million years old (Fan *et al.* 2021). All fossils described herein are from the upper member.

Fossil-bearing strata of the Kishenehn Formation are exposed in cut banks of the Flathead River system, including in Kintla Creek and Bowman Creek, the outlets of two of the glacially dammed lakes that occupy the basin (Constenius *et al.* 1989; Dawson & Constenius 2018; Fan *et al.* 2021). The specimen of *Pronodens* we describe is from Bowman Creek where the youngest dated horizon crops out (Fig. 1A). In fact, the specimen was collected approximately 1-2 meters stratigraphically below where the horizon was sampled by Fan *et al.* (2021) in the cutbank. Other unidentifiable bone fragments as well as an extremely worn upper tooth of a small artiodactyl were recovered nearby this specimen. Little of the crown of that tooth is left and no morphology can be described, but the size of the tooth is consistent with it belonging to *Pronodens*. The cricetid specimen was recovered from Kintla Creek (Fig. 1A; KTL-3 in Pierce & Constenius 2001: fig. 2), which has been interpreted as early Arikareean in age by Mary Dawson (reported in Pierce & Constenius 2001: fig. 2). The equid specimen was collected as a float specimen in the North Fork of the Flathead River (Fig. 1A; NFF17 in Pierce & Constenius 2001: fig. 2; USNM locality 24FH01670), but its origin can be associated with a specific horizon in a nearby outcrop in the cutbank. Therefore, its stratigraphic origin is below two localities (KTL1 and KTL2) interpreted as Orellan on Kintla Creek by Mary Dawson (reported in Pierce & Constenius 2001: fig. 2). In addition, there is a locality to the north of the NFF17 locality on the North Fork (NFF12 in Pierce & Constenius 2001: fig. 2) that is along strike and characterized as "Duchesnean-Chadronian?" Consequently, we interpret the age of the equid specimen to be likely Chadronian-Orellan.

MATERIAL AND METHODS

The taxonomic framework of leptomerycids follows Métais & Vislobokova (2007), that of equids follows Prothero & Shubin (1989), MacFadden (2005), as well as Famoso (2017). The taxonomy of *Paciculus* was most recently reviewed by Lindsay *et al.* (2016). The dental nomenclature and measurements of equids are detailed in Eisenmann *et al.* (1988), those of leptomerycids are from Taylor & Webb (1976) as well as Heaton & Emry (1996). The dental nomenclature of *Paciculus* follows Lindsay *et al.* (2016). Some of the measurements were taken from the literature, others were measured using Mitutoyo Digimatic CD-6' CX calipers or from specimen photographs using ImageJ (Schneider *et al.* 2012). All ungulate specimen photographs were taken using a Canon EOS Rebel SL2 camera. Photos of *Paciculus* were taken by Amy Henrici (CM). Upper case letters (P, M) denote upper teeth and lower-case letters (c, p, m) denote lower teeth. The graphical representations of osteological and dental measurements were prepared in R 4.1.3 using R Studio (R Core Team 2023). The tests for significant differences among species of *Paciculus* were undertaken for species with three or more specimens and consisted of analyses of variance (ANOVAs) for each measurement (lengths and widths of m1 and m2) followed by Tukey's Honest Significant Difference (THSD) tests whenever the ANOVA was significant to explore pairwise differences. Linear regressions were run using the *lm* function and confidence intervals determined using the function *confint*. The mapping of the Arikareean-aged fossil-bearing deposits of Montana and continental divide was also undertaken in R using the packages maps 3.4.1 (Becker *et al.* 2022) and rnaturalearth 0.3.3 (Massicotte & South 2023). Data for the geographic location of the continental divide were taken from https://earthworks.stanford.edu/catalog/stanford-pw312bv3382. The comparative specimens studied include the collection of *Pronodens transmontanus* from the CM, KUVP, UMPC, and UWBM as well as MOR 951, a specimen of *Pronodens* sp. from the Six Mile Creek Formation, and published specimens from Koerner (1940), and Taylor & Webb (1976), the last peer-reviewed publication to study *Pronodens*. We also studied UMPC 4035, a specimen of *Miohippus*, Finally, we studied specimens in the collections of the John Day Fossil Beds National Monument, including JODA 15473, a cast of AMNH 7022.

Abbreviations

Repositories and institutional abbreviations

AMNH	American Museum of Natural History, New York City, New York;
CM	Carnegie Museum of Natural History, Pittsburgh, Pennsylvania;
GLAC	Glacier National Park, U.S. National Park Service, West Glacier, Montana;
JODA	John Day Fossils Beds National Monument, U.S. National Park Service, Kimberly, Oregon;
KUVP	University of Kansas Biodiversity Institute and Museum of Natural History, Lawrence, Kansas;
LACM	Natural History Museum of Los Angeles County, Los Angeles, California;
MOR	Museum of the Rockies, Bozeman, Montana;
SDNHM	San Diego Natural History Museum, San Diego, California;
SDSM	South Dakota School of Mines and Technology Museum of Geology, Rapid City, South Dakota;
UCMP	University of California Museum of Paleontology, Berkeley, California;
UMPC	University of Montana Paleontology Center, Missoula, Montana;
UNSM	University of Nebraska State Museum, Lincoln, Nebraska;
USNM	Smithsonian Institution, National Museum of Natural History, Washington D.C.;
UWBM	University of Washington Burke Museum of Natural History and Culture, Seattle, Washington;
YPM	Yale Peabody Museum, New Haven, Connecticut.

Other abbreviations

NALMA	North American Land Mammal Age;
THSD	Tukey's Honest Significant Difference.

SYSTEMATIC PALEONTOLOGY

Class MAMMALIA Linneaus, 1758
Order ARTIODACTYLA Owen, 1848
Family LEPTOMERYCIDAE Zittel, 1893

Genus *Pronodens* Koerner, 1940

Pronodens Koerner, 1940: 842, fig 3.

Type species. — *Pronodens siberlingi* Koerner, 1940 by original designation.

Emended diagnosis (revised from Taylor & Webb 1976; Métais & Vislobokova 2007; Tabrum & Métais 2007). — Larger size than *Pseudoparablastomeryx* Frick, 1937; dentition more selenodont than in *Hendryomeryx* Black, 1978*, Pipestoneia* Tabrum & Metais, 2007, and "*Leptomeryx mammifer* (Cope, 1885); p1 missing unlike in *Leptomeryx* Leidy, 1853 and *Pipestoneia*; shorter diastema between c and p2 than in *Leptomeryx* and *Pseudoparablastomeryx*; lower jaw symphysis extends posteriorly to a point below anterior root of p2 unlike in *Leptomeryx* and *Pseudoparablastomeryx*; dentary more robust and dorsoventrally deeper at the diastema than in *Pseudoparablastomeryx*; mental foramen smaller than in *Pseudoparablastomeryx* located more posteriorly, ventral or slightly anterior to p2 unlike in *Leptomeryx* and *Pseudoparablastomeryx*; premolars relatively smaller than in *Leptomeryx*; reduced paraconid size in premolars compared to *Leptomeryx*; paraconid of p4 not strongly inflected as in *Pipestoneia*.

Pronodens transmontanus Douglass, 1903
(Fig. 2; Appendix 1)

Leptomeryx transmontanus Douglass, 1903: 167, fig. 11.

Type material. — **Holotype. United States of America** • CM 726, partial skull with right and left P2-M3 lacking parts of skull anterior to P2 and posterior to the frontals.

Type locality. — CM 2377 (KU-MT-31, UMPC MV6203, UWBM C1709), United States of America, Montana, East of Drummond.

Material. — From GLAC-PALLOC-0001: GLAC 26988, partial left dentary bearing p2-m3 and partial right dentary bearing p3-m3.

Diagnosis. — Much smaller species than *Pronodens silberlingi*; dentary shallower than in *P. silberlingi*; p2 less mesiodistally elongated than in *P. silberlingi*; labial cusps of m3 (protoconid, hypoconid, and hypoconulid) more buccally expanded than in *P. silberlingi*; protocone of P3 smaller and more buccolingually elongated than in *P. silberlingi*.

Stratigraphic and geographic range. — Lower unit of the Cabbage Patch beds (Renova Formation, early Arikareean) and upper member of the Kishenehn Formation, western Montana, United States of America (early Arikareean).

TABLE 1. — Jaw measurements of GLAC 26988 and comparative leptomerycids. Abbreviations: **Dd**, depth of dentary; **GNP**, Glacier National Park specimen (Kishenehn Formation); **Ps**, *Pronodens silberlingi* Koerner, 1940; **Psp**, *Pronodens* sp.; **Pt**, *P. transmontanus* (Douglass, 1903). Sources: **1**, Rasmussen (1977); **2**, this paper; **3**, Koerner (1940); **4**, Taylor & Webb (1976). **L** (left) and **R** (right) denote the sides of the jaw measured for GLAC 26988.

Species	Specimen	Ddp2	Ddm1	Ddm2	Ddm3	Source
Pt	UMPC 1482	8.4	11.2	11.63	13.72	1-2
Pt	UMPC 3030	9.4	9.97	–	–	1-2
Pt	KUVP 20724	12.4	14.15	–	–	1-2
Pt	CM 8938	10.58	11.3	12.27	15.64	1-2
Ps	YPM 13952	13	–	17	–	3
Psp	MOR 951	–	14.04	13.89	15.90	2
GNP	GLAC 26988 - L	11.7	12.93	13.02	15.95	2
GNP	GLAC 26988 - R	12.2	–	–	–	2

TABLE 2. — Measurements of the premolars of GLAC 26988 and comparative leptomerycids. Abbreviations: **Ppf**, *Pseudoparablastomeryx francescita* (Frick, 1937); **Pps**, *P. Pseudoparablastomeryx scotti* (Frick, 1937). Sources: **1**, Rasmussen (1977); **2**, this paper; **3**, Koerner (1940); **4**, Taylor & Webb (1976). Abbreviations: **GNP**, Glacier National Park specimen (Kishenehn Formation); **Ppf**, *Pseudoparablastomeryx francescita* (Frick, 1937); **Pps**, *P. Pseudoparablastomeryx scotti* (Frick, 1937); **Ps**, *Pronodens silberlingi* Koerner, 1940; **Psp**, *Pronodens* sp.; **Pt**, *P. transmontanus* (Douglass, 1903).

Species	Specimen	p2L	p2W	p3L	p3W	p4L	p4W	Source
Pt	KUVP 18452	–	–	7.36	3.36	–	–	1
Pt	KUVP 18668	–	–	8.1	3.39	7.9	4.24	1
Pt	CM 8938	5.57	2.83	7.83	3.62	8.76	4.55	1-2
Pt	UWBM 97474	–	–	5.72	3.46	–	–	2
Pt	UWBM 97460	5.66	2.51	–	3.34	6.97	3.87	2
Ps	YPM 13952	6.4	2.9	8.5	3.9	8.4	4.6	3
Pps	Species means	4.43	2.13	5.69	3.06	6.14	3.12	4
Ppf	F:AM 53405	–	–	5.5	2.8	6.0	3.0	4
Ppf	F:AM 53407	–	–	6.0	3.1	6.5	3.5	4
GNP	GLAC 26988 - L	5.37	2.65	7.06	3.96	7.27	4.58	2
GNP	GLAC 26988 - R	–	–	6.91	3.69	7.35	4.66	2

DESCRIPTION

The *Pronodens* material from the Kishenehn Formation is composed of partial left and right dentaries. The left dentary preserves a little damaged or worn dentition including p2-m3, whereas the right dentary includes a sheared and worn dentition including p3-m3. The left jaw is only the second specimen including the entire cheektooth row ever discovered for the species after CM 8938, the most complete lower jaw known for the species. It is also one of the best-preserved dentition, albeit worn, available for description for *P. transmontanus* (Fig. 2).

The dentaries of GLAC 26988 are similar to those of *Pronodens transmontanus* in their robustness of the anterior portion of the jaw (Fig. 3A; Table 1). In the posterior portion of the molar row, the dentary of the Kishenehn Formation material is deeper than in the specimens from the Cabbage Patch beds, more closely resembling MOR 951. Overall, both the Kishenehn Formation specimen and Cabbage Patch material are dorsoventrally shallower than the dentary of *P. silberlingi* (Fig. 3A). Both the left and right jaws show evidence for the absence of p1 unlike in *Leptomeryx*, but like all known *Pronodens* material. The mental foramen can be observed on the left side (Fig. 1C); its position far anterior to the anterior edge of p2 is similar to that observed in three known specimens of *P. transmontanus*, UMPC 3030, UMPC 1782, and UWBM 97460. Two other specimens, an edentulous jaw assigned to *P. transmontanus* (KUVP 20724) as well as CM 8938, show a more posteriorly located foramen, immediately ventral to the anterior edge of p2, as in the type of *P. silberlingi*, a feature previously considered a characteristic of the genus (Taylor & Webb 1976). The postsymphysis is posterior to the mental foramen in the Kishenehn Formation material (Fig. 1C), unlike in CM 8938 and the holotype of *P. silberlingi*, YPM 13952. In both GLAC 26988 and YPM 13952, the postsymphysis terminates posteriorly halfway through p2; in CM 8938, it is fully anterior to p2, terminating posteriorly at the anterior edge of the tooth (Fig. 1C).

The dentition of GLAC 26988 is best preserved in the left jaw (Appendix 1). The m1 and m2 of the right jaw are damaged and p2 is missing (Fig. 1A); only the roots of the tooth are preserved. The size of the p2 of GLAC 26988 falls within the range of measurements observed in *Pronodens transmontanus* from the Cabbage Patch beds (the type area) for both length and width (Figs 3B; 4A; Table 2). The p2 of *P. silberlingi* is much more mesiodistally elongated. The shape of the p2 in the Kishenehn Formation specimen is very similar to that observed in the Cabbage Patch fossils (Fig. 1E). The protoconid and entoconid are more robust than in UWBM 97460, but this character varies across specimens in the sample from Cabbage Patch (see UMPC 3030, CM 8938, and UWBM 97460 in particular; Fig. 4A). The length of the p3 of *P. transmontanus* from Cabbage Patch overlaps the length of the p3 of the Kishenehn Formation material, but the buccolingual width of the latter is larger,

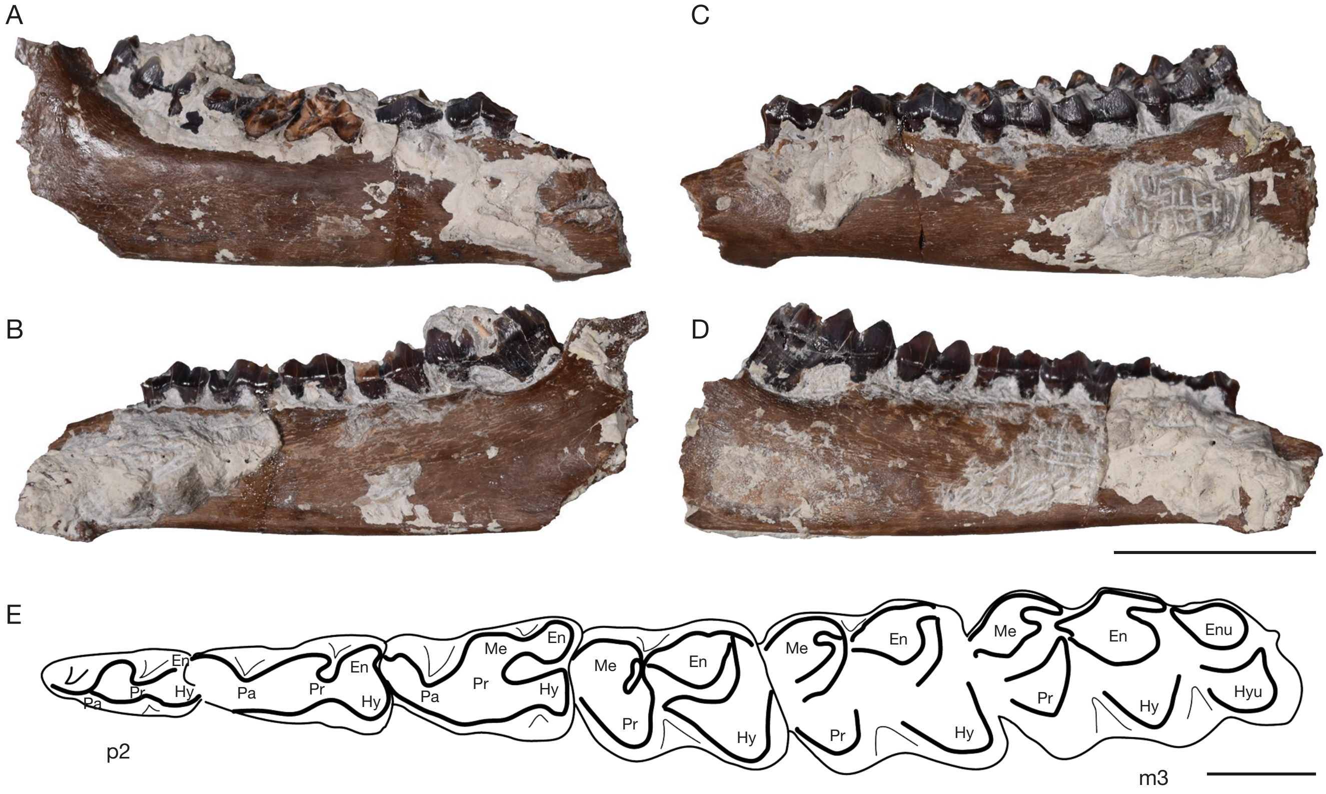


Fig. 2. — Morphology of GLAC 26988, *Pronodens transmontanus* (Douglass, 1903), from the Kishenehn Formation: **A**, lateral view of right dentary; **B**, medial view of right dentary; **C**, lateral view of left dentary; **D**, medial view of left dentary; **E**, line drawing of the occlusal view showing tooth morphology of the left dentary. A photo of the occlusal view of the teeth is showed in Appendix 1. Scale bars: A-D, 2 cm; E, 4 mm.

more similar in fact to *P. silberlingi* (Figs 3B; 4B; Table 2). In both the left and right jaws of GLAC 26988, the portion of the tooth anterior to the paraconid is heavily worn, much more so than the posterior portion of the tooth and cannot be described in detail (Fig. 1A, C, E). The paraconid itself is larger in GLAC 26988 than in KUVP 18452, KUVP 18668, and CM 8938. The same observation can be made of the protoconid, which is broader buccolingually in the Kishenehn Formation material than in the Cabbage Patch specimens. The ridge extending lingually from the protoconid is longer and narrower in the Cabbage Patch material than in the Kishenehn Formation specimen where it terminates more anteriorly (Fig. 1E). The anatomy of the posterior-most portion of the tooth, including the entoconid and hypoconid, varies greatly with wear across specimens within the Cabbage Patch sample; the Kishenehn Formation specimen is most similar to KUVP 18452 and CM 8938, although the ridge extending lingually from the entoconid is more lingually inflated in the Kishenehn Formation specimen than in the Cabbage Patch fossils. The length of p4 in the Kishenehn Formation specimen overlaps with the range of sizes observed in *P. transmontanus* from the Cabbage Patch beds (Fig. 3B; Table 2). GLAC 26988 is comparable in width to the largest measured specimen of *P. transmontanus* from Cabbage Patch as well as the type specimen of *P. silberlingi*, but it is proportionately broader (Fig. 4C). The anterior-most portion of the p4 of the Kishenehn Formation specimen is similar to that of UWBM 97460, the only well preserved p4 of *P. transmontanus* from Cabbage Patch, when accounting for wear. The more worn KUVP 18668 shows a similar paraconid morphology as the Kishenehn Formation specimen as well. The shape of the metaconid is complex, but once again, when accounting for wear, is essentially identical to that of UWBM 97460 and CM 8938 (Fig. 1E). The advanced wear stage of the Kishenehn Formation specimen leads to an uninterrupted connection between the metaconid and entoconid (Fig. 1E). The shape of the entoconid is simple, once more as a consequence of wear. It is larger, rounder, and more lingually inflated than in UWBM 97460 or CM 8938. There is, however, little difference in the morphology of the hypoconid between GLAC 26988 and UWBM 97460 when accounting for wear.

The m1 of GLAC 26988 is more heavily worn than in UWBM 97460, UMPC 1482, UMPC 3030, and CM 8938 (Fig. 1E). The Kishenehn Formation specimen overlaps in size with the Cabbage Patch fossils (Fig. 3C; Table 3) although it is broader for a given length than the specimens from the type area (Fig. 4D). All these specimens are much smaller than the type of *Pronodens silberlingi*. GLAC 26988 is heavily worn making the morphologies of the metaconid and entoconid difficult to compare between the Kishenehn Formation specimen and the Cabbage Patch fossils, but the overall shapes of these lingual cusps are consistent across all specimens. The protoconid and hypoconid are more

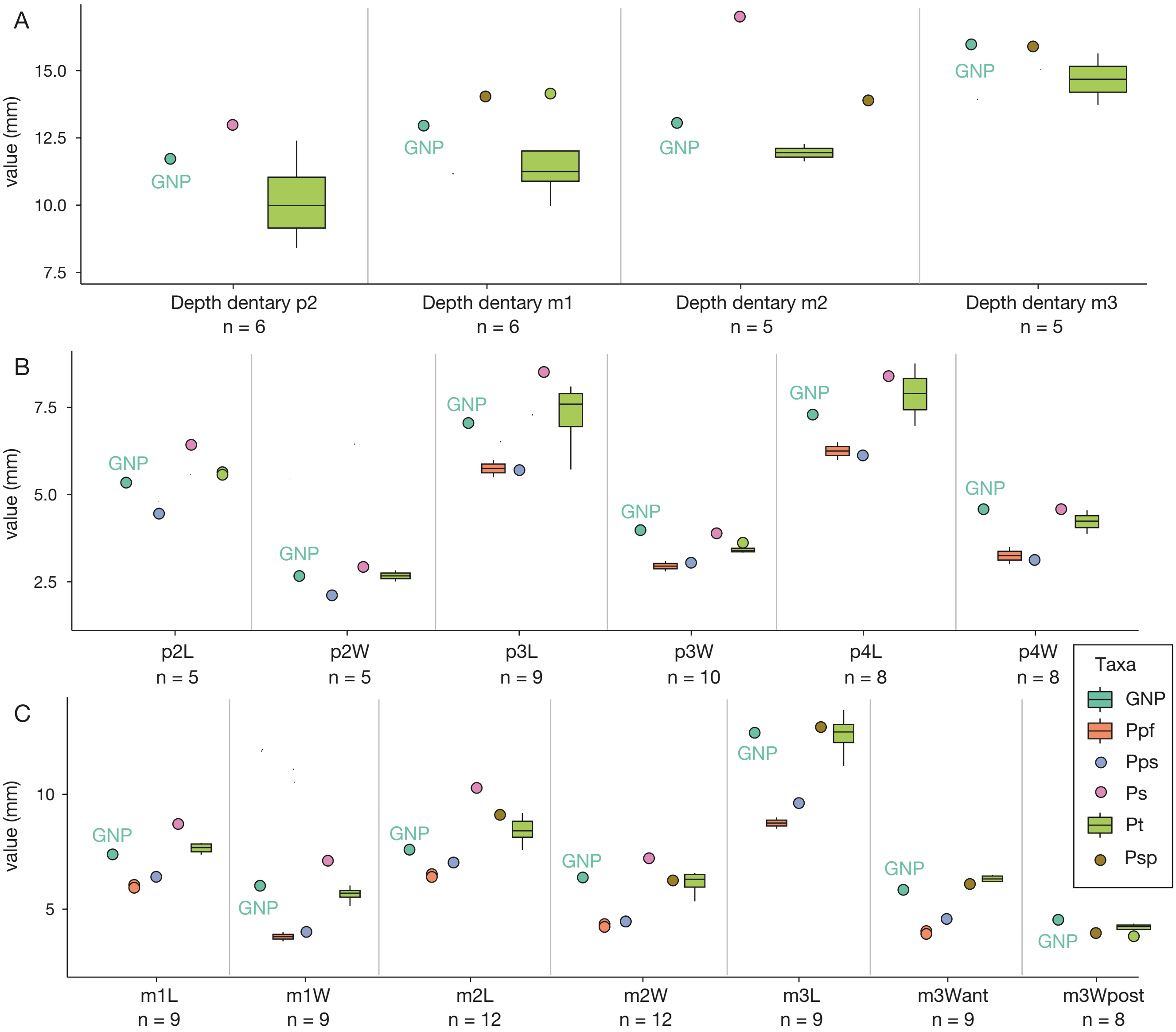


FIG. 3. — Size analysis of GLAC 26988 and other leptomerycids from the Arikareean and Hemingfordian: **A**, comparison of the depth of the dentary at different tooth positions; **B**, comparison of the size of the premolars; **C**, comparison of the size of the molars. **GNP** denotes the specimen from Glacier National Park (Kishenehn Formation); data from the left jaw. Note that the data for *Pseudoparablastomeryx* Frick, 1937 are in fact a species mean. Sample size is indicated for each comparison. See Tables 1-3 for data. Abbreviations: **ant**, anterior lophid; **post**, posterior lophid; **Ppf**, *Pseudoparablastomeryx francescita* (Frick, 1937); **Pps**, *P. Pseudoparablastomeryx scotti* (Frick, 1937); **Ps**, *Pronodens silberlingi* Koerner, 1940; **Psp**, *Pronodens* sp.; **Pt**, *P. transmontanus* (Douglass, 1903).

buccally extended in the Glacier National Park specimen (Fig. 1E), leading to the greater buccolingual width of the tooth in GLAC 26988 compared to the Cabbage Patch fossils. A similar pattern can be observed in the m2 with an overlap in size of the Kishenehn Formation specimen with the Cabbage Patch fossils (Fig. 3C; Table 3). The Kishenehn Formation specimen is once again slightly wider for a given length than the Cabbage Patch sample (Fig. 4E), but they are very similar, and even resemble a specimen of *Pronodens* from the Six Mile Creek Formation, MOR 951. The type of *P. silberlingi* is larger than any other specimen of the genus measured. The shape of the metaconid of GLAC 26988 is similar to the one in CM 8938; the shape of the entoconid is similar to that observed in UMPC 1482. The protoconid and hypoconid are buccally expanded in the Kishenehn Formation specimen compared to the Cabbage Patch sample. There are little to no differences in m3 size between the Glacier specimen and the sample of fossils from the Cabbage Patch beds (Fig. 3C; Table 3). Unlike in m1 and m2, the anterior lophid of the m3 of GLAC 26988 is buccolingually narrower than that observed in the sample of *P. transmontanus* from Cabbage Patch or MOR 951 (Fig. 4F). The buccal cusps (metaconid, entoconid, and entoconulid) of GLAC 26988 are most similar to those observed in CM 8938 and UMPC 1482 or MOR951; they are large and round with tapered mesial and distal ends. In the Kishenehn Formation specimen, the lingual surface of the entoconid is not as rounded as in CM 8938 and KUVP 18838. Instead, it resembles

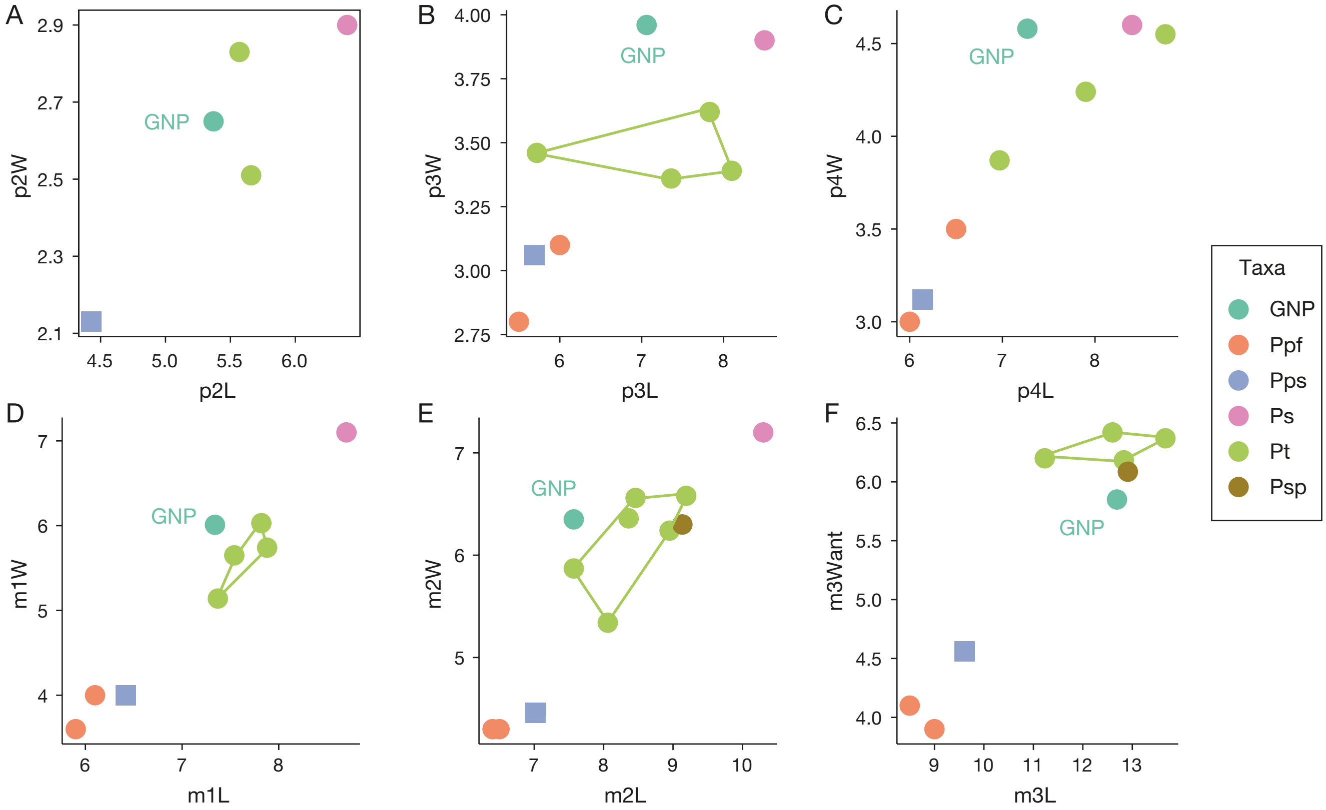


Fig. 4. — Shape analysis of GLAC 26988 and other leptomerycids from the Arikareean and Hemingfordian: **A**-**C**, comparison of the shape of the premolars; **D**-**F**, comparison of the shape of the molars. **GNP** denotes the specimen from the Glacier National Park (Kishenehn Formation); data from the left jaw. Note that the data for *Pseudoparablastomeryx* Frick, 1937 are in fact a species mean. Each point otherwise represents a specimen. Disparity is showed for *Pronodens transmontanus* (Douglass, 1903) from the Cabbage Patch beds when four or more specimens were measured. See Tables 1-3 for data. Abbreviations: **ant**, anterior lophid; **Ppf**, *Pseudoparablastomeryx francescita* (Frick, 1937); **Pps**, *P. Pseudoparablastomeryx scotti* (Frick, 1937); **Ps**, *Pronodens silberlingi* Koerner, 1940; **Psp**, *Pronodens* sp.; **Pt**, *P. transmontanus* (Douglass, 1903).

Table 3. — Measurements of the molars of GLAC 26988 and comparative leptomerycids. Abbreviations: **ant**: anterior lophid; **post**, posterior lophid. Sources: **1**, Rasmussen (1977); **2**, this paper; **3**, Koerner (1940); **4**, Taylor & Webb (1976). Abbreviations: **GNP**, Glacier National Park specimen (Kishenehn Formation); **Ppf**, *Pseudoparablastomeryx francescita* (Frick, 1937); **Pps**, *P. Pseudoparablastomeryx scotti* (Frick, 1937); **Ps**, *Pronodens silberlingi* Koerner, 1940; **Psp**, *Pronodens* sp.; **Pt**, *P. transmontanus* (Douglass, 1903).

Species	Specimen	m1L	m1W	m2L	m2W	m3L	m3Want	m3Wpost	Source
Pt	UMPC 1482	7.54	5.65	8.06	5.34	11.23	6.2	4.32	1-2
Pt	UMPC 3030	7.88	5.74	8.95	6.24	–	–	–	1-2
Pt	KUVP 18184	–	–	–	–	–	–	3.82	1
Pt	KUVP 18838	–	–	9.19	6.58	13.67	6.37	4.26	1
Pt	CM 8938	7.82	6.03	8.46	6.56	12.83	6.18	4.08	1-2
Pt	CM 20736	–	–	8.36	6.36	12.60	6.42	4.37	1-2
Pt	UWBM 97494	–	–	–	–	–	–	4.23	2
Pt	UWBM 97460	7.37	5.14	7.57	5.87	–	–	–	2
Ps	YPM 13952	8.7	7.1	10.3	7.2	–	–	–	3
Psp	MOR 951	–	–	9.13	6.30	12.91	6.09	3.96	2
Pps	Species means	6.42	4	7.02	4.46	9.61	4.56	–	4
Ppf	F:AM 31425	–	–	6.5	4.3	9.0	3.9	–	4
Ppf	F:AM 31397	5.9	3.6	–	–	–	–	–	4
Ppf	F:AM 53405	6.1	4.0	6.4	4.3	8.5	4.1	–	4
GNP	GLAC 26988 – L	7.34	6.01	7.57	6.35	12.69	5.85	4.49	2
GNP	GLAC 26988 – R	–	–	–	–	12.33	5.97	4.68	2

more closely the morphology observed in UWBM 97494 with a lingually displaced cusp point. The entoconulid is teardrop shaped with the narrow end at the mesial end of the lophid contacting the distal end of the entoconid as in KUVP 18838 and CM 8938; the shapes of the entoconid and entoconulid in UWBM 97494 differ from those found in the Kishenehn Formation fossil as well as other *P. transmontanus* specimens. The entoconulid of MOR 951 is more

TABLE 4. — Measurements of the lower jaw of GLAC 26987 (left [**L**] and right [**R**] dentaries) and UMPC 4035 (**P** referring to Peterson Creek; taken on the left side). Abbreviation: **Dd**, depth of the dentary at tooth position specified.

Side	Ddp2	Ddp4-m1
L	14.07	18.02
R	–	17.94
P	20.25	24.00

TABLE 5. — Measurements of the dentition of GLAC 26987 (left [**L**] and right [**R**] dentaries) and UMPC 4035 (**P** referring to Peterson Creek; taken on the left side).

Side	p2L	p2W	p3L	p3W	p4L	p4W	m1L	m1W	m2L	m2W	m3L	m3W
L	7.38	4.48	12.98	8.96	13.4	9.95	13.21	10.28	13.57	9.69	–	–
R	–	–	–	–	13.34	9.14	13.02	9.32	13.3	9.87	13.11	9.46
P	16.27	9.59	15.79	11.5	16.51	11.31	14.99	10.37	15.8	11.21	20.54	9.95

symmetrical than in *P. transmontanus* from Cabbage Patch or the Kishenehn Formation specimen. The protoconid is not as buccally expanded in the Kishenehn Formation specimen as they are in the Cabbage Patch sample at similar wear stages; this is also true of the other labial cusps, the hypoconid and the hypoconulid (Fig. 1E). However, these cusps are more buccally expanded than in *P. silberlingi* or MOR 951. Both the hypoconid and the hypoconulid are more mesiodistally expanded in GLAC 26988 than in the Cabbage Patch specimens, leading to more robust bulbous cusps.

REMARKS

The Kishenehn Formation specimen is very similar in size to the sample of *Pronodens transmontanus* from the type area, the Cabbage Patch beds (Tables 1-3). None of the measurements of the Kishenehn Formation specimen fall outside of the range of measurements observed in *P. transmontanus* ± 10%; only two measurements of the Kishenehn Formation specimen (Ddm2 and p3W) are more than 5% larger than the measurements observed in the Cabbage Patch sample; this despite the small size of our sample (two and five specimens respectively) that is unlikely to capture the range of size variation in *P. transmontanus*. In contrast, *P. silberlingi* is much larger, with the type specimen (YPM 13952) more than 5% larger than *P. transmontanus* from Cabbage Patch in 83% of measurements taken (10 out of 12). YPM 13952 is also more than 10% larger than the Kishenehn Formation specimen in nine measurements (out of 12) available for both specimens. On average, the teeth of YPM 13952 are 14.96% larger than those of the Kishenehn Formation specimen. Differences between the Kishenehn Formation specimen and MOR 951 are reduced; however, the two specimens differ by 11.9 and 20.7% for two dental measurements (m2L, m3Wpost). The morphology of the teeth in the Kishenehn Formation specimen more closely resembles *P. transmontanus* than *P. silberlingi* or *Pronodens* sp. However, the dentition of the type specimen of *P. silberlingi* is worn beyond the possibility of tooth crown morphological comparisons. We conservatively assign the material from Kishenehn Formation to *P. transmontanus.*

Order PERISSODACTYLA Owen, 1848
Family EQUIDAE Gray, 1821

Genus *Miohippus* Marsh, 1874

Miohippus Marsh, 1874: 397, fig 3.

TYPE SPECIES. — *Miohippus annectens* Marsh, 1874 by original designation.

Miohippus sp.
(Fig. 5)

MATERIAL EXAMINED. — From USNM locality 24FH01670: GLAC 26987, partial left dentary with p2-m2 and partial right dentary with p4-m3 from the same individual.

STRATIGRAPHIC AND GEOGRAPHIC RANGE. — Upper member of the Kishenehn Formation, western Montana, United States of America.

DESCRIPTION

GLAC 26987 is composed of two partial lower dentaries (left and right) and includes the left p2-m2 and the right p4-m3 (Fig. 5). The left dentary includes a small amount of the dentary mesial of the p2 (Fig. 5A). There is some of the dentary present distal of the m2 with no exposed roots, but the alveolus for the m3 is present with only the mesial portion remaining. A small portion of the mesial end of the right dentary is attached with matrix (Fig. 5B). This portion of the right dentary includes part of the diastema and the p2. The right p2 is broken at the root and what is present is mostly the empty alveolus. The remainder of the right dentary fragment is broken just mesial of the p4 and at the posterior root of the m3, exposing the distal root. All other teeth are in good condition with no missing cusps (Fig. 5C, F). The teeth are in a middle stage of wear.

REMARKS

Measurements of the dentition of GLAC 26987 are within the size range of *Miohippus annectens* (Marsh 1874) specimens found in the John Day Formation of Oregon affirming

Fig. 5. — Morphology of GLAC 26987, fossil *Miohippus* Marsh, 1874 from the Kishenehn Formation: **A**, lateral view of left dentary; **B**, medial view of left dentary; **C**, occlusal view of left dentary; **D**, lateral view of right dentary; **E**, medial view of right dentary; **F**, occlusal view of the right dentary. Scale bar: 2 cm.

this specimen is from the same genus (Tables 4; 5; Famoso 2017). There are no morphological characters in the lower jaw or dentition that can be used to distinguish between *Miohippus* and *Mesohippus* Marsh, 1875, let alone species of either genus (Famoso 2017). Stirton (1940) noted that *Miohippus* and *Mesohippus* are difficult to differentiate, and other recent workers have suggested *Mesohippus* is a junior synonym of *Miohippus* (Masciale 2010; Kocken 2022; Kocken & Pagnac 2022).

Order Rodentia Bowdich, 1821
Family Cricetidae Fischer von Waldheim, 1817

Genus *Paciculus* Cope, 1879

Paciculus Cope, 1879: 371.

Type species. — *Paciculus insolitus* Cope, 1879 by original designation.

Paciculus montanus Black, 1961
(Fig. 6; Appendix 2)

Paciculus montanus Black, 1961: 10, fig. 4.

Material examined. — From CM Locality 5084: CM 87801, partial right dentary with incisor and m1-m2.

Stratigraphic and geographic range. — Fort Logan Formation, upper member of the Kishenehn Formation, and middle as well as upper units of the Cabbage Patch beds (Renova Formation), western Montana, United States of America (early Arikareean). From Peterson Creek Local Fauna, eastern Idaho, United States of America (early Arikareean).

Description

CM 87801 is a large specimen of *Paciculus* (Fig. 6; Appendix 1). The m1 is as long as in *P. montanus*, *P. walshi* (Lindsay *et al.* 2016), *P. nebraskensis* (Alker 1969), and the sample of *Paciculus* from the Cabbage Patch beds identified as *P.* cf. *P. montanus* (Table 6; Fig. 7A). It is much longer than any other species of the genus. A similar pattern can be observed in the m2 (Table 6; Fig. 7B); the Kishenehn Formation specimen is longer than any other species of the genus with the exceptions of *P. nebraskensis* and *P. montanus.* The widths of the teeth also place CM 87801 among the very largest *Paciculus* specimens. The shape of m1 is nearly identical to *P. montanus* and the Cabbage Patch sample as well as one extreme of the shapes found in *P. insolitus* (Cope 1879; Fig. 8). The shape of the m2 overlaps the range observed in both *P. nebraskensis* and *P. montanus* (Fig. 8).

The m1 of the Kishenehn Formation specimen (Fig. 6) shares a number of features with *P. montanus* that also differentiate it from *P. walshi*, including: 1) the presence of a distinct anteroconid; 2) a protoconid arm that is short and

Table 6. — Measurements of CM 87801 and comparative specimens. Abbreviations: **Abb.**, abbreviation; **Ref.**, reference. Species means are summarized in Lindsay *et al.* (2016). References: **1**, this paper; **2**, Nichols (1976); **3**, Lindsay *et al.* (2016); **4**, Korth (2014); **5**, Martin (1973); **6**, Korth & Sullivan (2021); **7**, Alker (1969).

Specimen	Taxon	Abb.	Ref.	m1L	m1W	m2L	m2W
CM 87801	Glacier National Park specimen	GNP	1	2.07	1.44	1.93	1.58
UMPC 5104	*P. montanus* (Douglass, 1903)	Pm	2	2.2	1.53	2	1.55
UMPC 5105	*P. montanus*	Pm	2	2.1	1.45	1.8	1.64
UMPC 5106	*P. montanus*	Pm	2	2.1	1.43	1.8	1.6
LACM 122480	*P. montanus*	Pm	3	2.1	1.56	–	–
KUVP 18381	*P.* cf. *P. montanus*	PCP	1	2.45	1.67	–	–
KUVP 18382	*P.* cf. *P. montanus*	PCP	1	2.23	1.51	–	–
KUVP 18774	*P.* cf. *P. montanus*	PCP	1	2.31	1.37	–	–
KUVP 20607	*P.* cf. *P. montanus*	PCP	1	2.08	1.41	–	–
Species means	*P. cedrus* (Korth, 2014)	Pce	4	1.69	1.33	1.7	1.51
UNSM 11530	*P. mcgregori* (Macdonald, 1970)	Pmc	5	1.75	1.41	1.63	1.43
UNSM 11725	*P. mcgregori*	Pmc	5	1.63	1.22	1.57	1.48
UNSM 66159	*P. mcgregori*	Pmc	5	1.69	1.24	1.49	1.44
UNSM 11726	*P. mcgregori*	Pmc	5	1.75	1.23	1.53	1.61
UNSM 11535	*P. mcgregori*	Pmc	5	1.57	1.39	1.43	1.37
UNSM 11537	*P. mcgregori*	Pmc	5	1.51	1.20	1.33	1.41
UNSM 11552	*P. mcgregori*	Pmc	5	1.47	1.34	1.46	1.36
UNSM 66163	*P. mcgregori*	Pmc	5	1.57	1.39	1.44	1.48
SDNHM 73115	*P. walshi* Lindsay, Whistler, Kalthoff & von Koenigswald, 2016	Pwa	3	2.2	1.54	–	–
UCMP 75593	*P.* cf. *P. insolitus*	Pi	3	2.2	1.43	–	–
USNM 66157	*P. insolitus* Cope, 1879	Pi	7	1.65	1.40	1.65	1.50
USNM 66162	*P. insolitus*	Pi	7	1.75	1.40	1.60	1.50
USNM 66164	*P. insolitus*	Pi	7	1.85	1.45	1.75	1.60
USNM 14961	*P. insolitus*	Pi	7	1.65	1.25	1.65	1.40
USNM 66158	*P. insolitus*	Pi	7	–	–	1.75	1.50
USNM 66159	*P. insolitus*	Pi	7	1.75	1.30	1.60	1.50
LACM 15434	*P. gloveri* MacDonald, 1970	Pg	3	1.4	1.12	–	–
LACM 9358	*P. woodi* (Macdonald, 1963)	Pwo	3	1.5	1.34	–	–
CM 96345	*P. nebraskensis* Alker, 1969	Pn	6	–	–	1.85	1.39
CM 96351	*P. nebraskensis*	Pn	6	1.99	1.5	–	–
CM 96364	*P. nebraskensis*	Pn	6	–	–	1.91	1.64
CM 96366	*P. nebraskensis*	Pn	6	–	–	1.86	1.52
UNSM 24121	*P. nebraskensis*	Pn	1	2.38	1.58	–	–
UNSM 24122	*P. nebraskensis*	Pn	1	2.45	1.65	2.10	1.75
UNSM 24123	*P. nebraskensis*	Pn	1	2.06	1.56	1.95	1.71
UNSM 66166	*P. nebraskensis*	Pn	7	2.20	1.60	2.20	1.70
CM 96346	*P. dakotensis* Korth, 2010	Pd	6	–	–	1.73	1.63
CM 96358	*P. dakotensis*	Pd	6	1.81	1.39	–	–
CM 96365	*P. dakotensis*	Pd	6	1.89	1.32	–	–
CM 96386	*P. copiosus* (Korth, 2010)	Pco	6	–	–	1.65	1.36
CM 96387	*P. copiosus*	Pco	6	1.75	1.4	–	–
CM 96390	*P. copiosus*	Pco	6	1.75	1.31	–	–
CM 96391	*P. copiosus*	Pco	6	1.61	1.19	–	–
CM 96392	*P. copiosus*	Pco	6	1.71	1.32	–	–
CM 96393	*P. copiosus*	Pco	6	–	–	1.53	1.42

does not reach the anterior cingulum; 3) a short protolophid II, which, like half of the specimens of *P. montanus* observed by Lindsay *et al.* (2016), does not join the metaconid; and 4) a robust posterior arm of the protoconid that does not bifurcate, as in most specimens of *P. montanus* analyzed by Lindsay *et al.* (2016). Additionally, as in *P. montanus*, the m2 of the Kishenehn Formation specimen bears a long protolophid II. Unlike in *P. walshi* or *P. cedrus* Korth, 2014, but like in *P. montanus*, the anterior lingual cingulum of the m1 of CM 87801 extends from the anteroconid to the metaconid. The teeth of *P. nebraskensis* differ from those of CM 87801 by a shorter mesolophid of m1, a shorter protolophid II on m2, and the presence of an anterior cingulum of m2 (Korth 1992).

CM 87801 further differs from smaller species of *Paciculus* by several discrete morphological characters. The m1 of *P. gloveri* MacDonald, 1970 has a smaller protolophid I as well as a narrower, buccolingually straighter mesostylid than the Kishenehn Formation specimen. Additionally, *P. gloveri* bears a posterior spur on the metaconid of m2, has an isolated mesostylid, and has a very short protolophid II (Williams & Storer 1998), all characters not observed in the Kishenehn Formation fossil. *P. copiosus* (Korth 2010) bears an anteroconid on m2 unlike CM 87801. Unlike the Kishenehn Formation specimen, the m1 of *P. dakotensis* Korth, 2010 lacks a protolophid II and the protolophid II of the m2 does not reach the lingual edge of the tooth (Korth 2010). Additionally, the m2 of *P. dakotensis* (Korth 2010) bears an anterior cingulum extending lingually anterior to the metaconid, which is absent from the Kishenehn Formation fossil. *Paciculus mcgregori* (MacDonald, 1970) and the Kishenehn Formation fossil can be distinguished by the incomplete protolophid II of the former and very different anterior portions

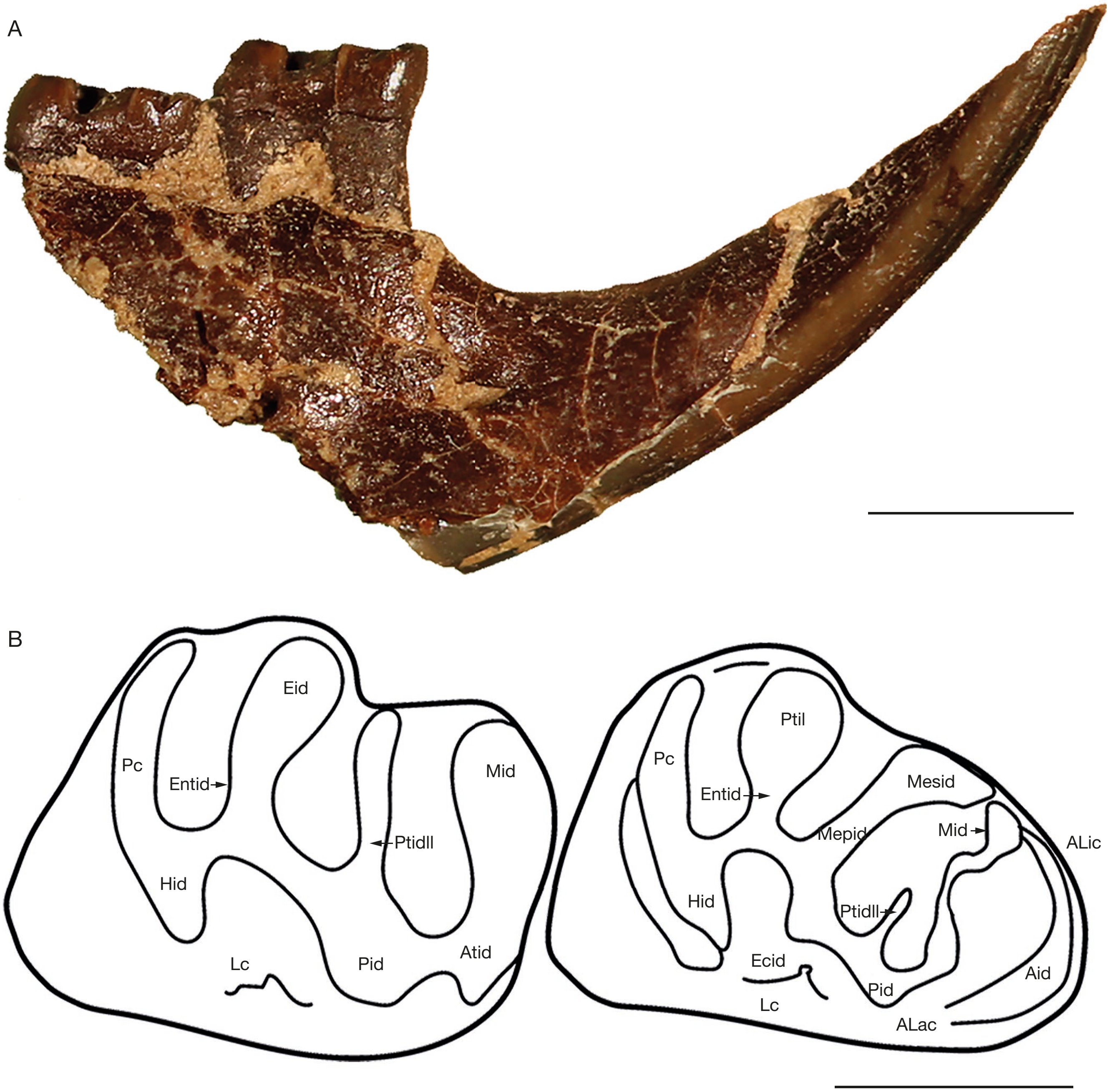


Fig. 6. — Morphology of CM 87801, *Paciculus* Cope, 1879 from the Kishenehn Formation: **A**, lateral view of right dentary; **B**, occlusal view of dentition, m1-2. Abbreviations: **Aid**, anteroconid; **ALac**, anterior labial cingulum; **ALic**, anterior lingual cingulum; **Atid**, anterolophid; **Ecid**, ectostylid; **Entid**, entolophid; **Eid**, entoconid; **Hid**, hypoconid; **Lc**, labial cingulum; **Mepid**, mesolophid; **Mesid**, mesostylid; **Mid**, metaconid; **Pc**, posterior cingulum; **Pid**, protoconid; **Ptil**, protolophid I; **PtidII**, protolophid II. A photo of the occlusal view of the teeth is showed in Appendix 2. Scale bars: A, 2 mm; B, 1 mm.

of m1 (Martin 1980). The m2 of *P. cedrus*, unlike the fossil from the Kishenehn Formation bears a short protolophid II disconnected from an isolated mesostylid as well as a distinct anterior cingulum (Korth 2014). The anterior portion of m1 of CM 87801 also differs from that observed in the type specimen (SDSM 56510). The Kishenehn Formation specimen, unlike *P. insolitus*, but like *P. walshi*, has a short ectolophid on m1 (Lindsay *et al.* 2016). *Paciculus insolitus* and CM 87801 can be further distinguished by differences in the shape of the mesostylid, the pattern of branching of the mesolophid and entolophid from the posterior mure, the size of the metaconid, and the morphology of the protoconid. The posterior cingula of the m1 and m2 of *P. woodi* are more mesiodistally oriented than in the Kishenehn Formation specimen, in which they are much more bucco-lingually oriented. In *P. woodi* (MacDonald 1963), the anterior mure is interrupted and therefore does not contact the protoconid in the m1; this is also the case in *P. cedrus* and *P. insolitus*, but not in CM 87801. The anterior cingulum of *P. woodi* lacks the long labial extension seen in CM 87801.

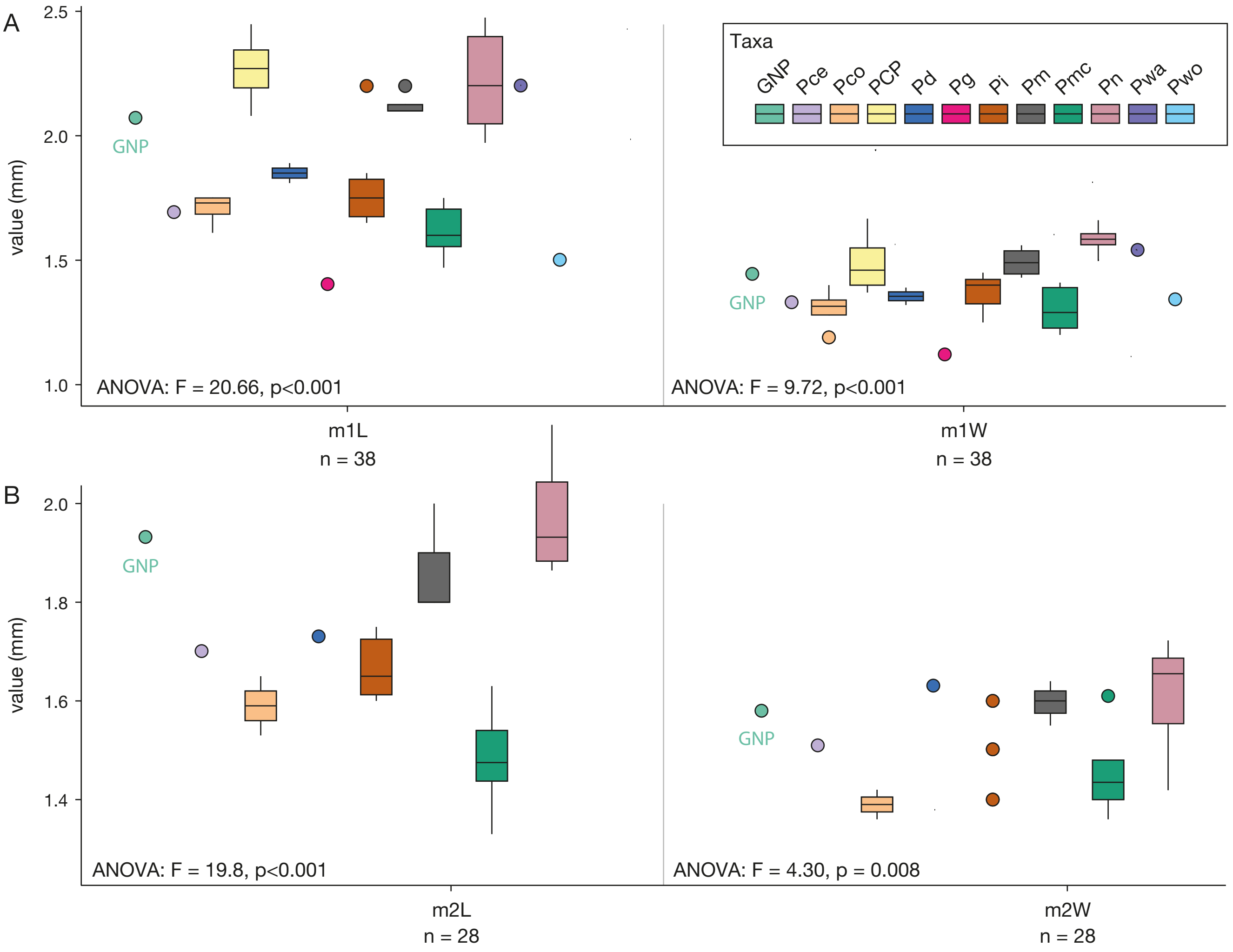


Fig. 7. — Size analysis of CM 87801 and other specimens of *Paciculus* Cope, 1879: **A**, comparison of the size of m1; **B**, comparison of the size of m2. GNP denotes the specimen from Glacier National Park (Kishenehn Formation). Note that the data for *P. cedrus* Korth, 2014 are in fact a species mean. Sample size is indicated for each comparison. See Table 6 for data. Abbreviations: **GNP**, Glacier National Park specimen; **Pce**, *P. cedrus*; **Pco**, *P. copiosus* Korth, 2010; **PCP**, *P.* cf. *P. montanus*; **Pd**, *P. dakotensis* Korth, 2010; **Pg**, *P. gloveri* MacDonald, 1970; **Pi**, *P. insolitus* Cope, 1879; **Pm**, *P. montanus* Black, 1961; **Pmc**, *P. mcgregori* MacDonald, 1970; **Pn**, *P. nebraskensis* Alker, 1969; **Pwa**, *P. walshi* Lindsay, Whistler, Kalthoff & von Koenigswald, 2016; **Pwo**, *P. woodi* MacDonald, 1963.

Remarks

The size and morphology of CM 87801 support it being assigned to *Paciculus montanus* (Table 6). The holotype of the species is an upper dentition (Black 1961), so it is not currently possible to directly compare the material from the Kishenehn Formation with the type area specimens, however, there is no identifiable difference between CM 87801 and the known lower dentition of *P. montanus.* The material from the Cabbage Patch beds (Calede 2020) cannot be assigned with confidence to the species based on the rarity of the material and its worn state. However, the size of the lower teeth as well as the morphology of the upper teeth recovered are consistent with *P. montanus* (Rasmussen 1977; this paper). Future discoveries of dental remains from the Cabbage Patch beds are expected to confirm the presence of the species in this area of Montana in addition to the type area, the Peterson Creek Local Fauna of Idaho and, now, the Kishenehn Formation.

DISCUSSION

The new fossils described herein represent the first occurrence of Oligocene-aged fossils, and the youngest fossil mammals, from the Kishenehn Formation. The *Miohippus* specimen is the northernmost occurrence of the genus in the Rocky Mountains. Unfortunately, the absence of upper teeth prevents a specific assignment to be made and therefore limits the significance of this well-preserved specimen. The fossils described also include the northernmost occurrence of the genus *Pronodens.* It is also the first occurrence of the species *P. transmontanus* outside of the Cabbage Patch beds. The Kishenehn Formation material differs little from the Cabbage Patch material. The differences between the two samples are concentrated in the relative proportion of the teeth and inflation of the cusps. A different species of the genus, *Pronodens silberlingi*, is present in the Fort Logan Formation (Koerner 1940) as well as the Rosebud Formation of South Dakota

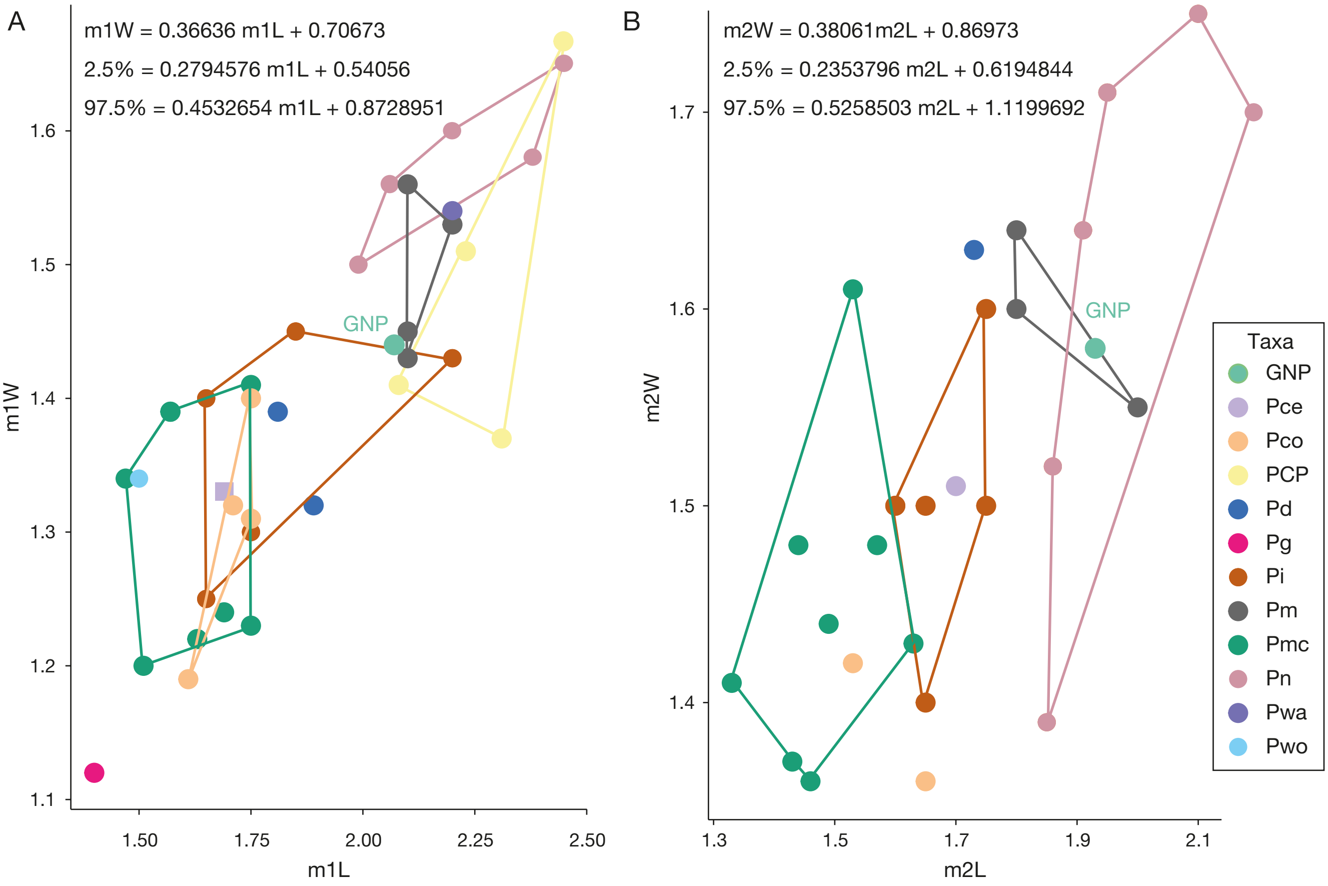


Fig. 8. — Shape analysis of CM 87801 and other specimens of *Paciculus* Cope, 1879: **A**, comparison of the shape of m1; **B**, comparison of the shape of m2. GNP denotes the specimen from the Glacier National Park (Kishenehn Formation). Note that the data for *P. cedrus* Korth, 2014 are in fact a species mean. Each point otherwise represents a specimen. Disparity is showed for species when three or more specimens were measured. See Table 6 for data. Abbreviations: **GNP**, Glacier National Park specimen; **Pce**, *P. cedrus* Korth, 2014; **Pco**, *P. copiosus* Korth, 2010; **PCP**, *P.* cf. *P. montanus*; **Pd**, *P. dakotensis* Korth, 2010; **Pg**, *P. gloveri* MacDonald, 1970; **Pi**, *P. insolitus* Cope, 1879; **Pm**, *P. montanus* Black, 1961; **Pmc**, *P. mcgregori* MacDonald, 1970; **Pn**, *P. nebraskensis* Alker, 1969; **Pwa**, *P. walshi* Lindsay, Whistler, Kalthoff & von Koenigswald, 2016; **Pwo**, *P. woodi* MacDonald, 1963.

(Taylor & Webb 1976). Interestingly, no leptomerycid is known from the Peterson Creek Local Fauna. This despite the fact that the fauna has been thoroughly sampled, from rhinocerotids to soricids (Nichols 1976, 1979), and regardless of the greater distance between Cabbage Patch and Glacier National Park than between Cabbage Patch and the Lemhi Valley of Idaho (Fig. 1). This difference between the assemblages from Montana and the fauna from nearby eastern Idaho has already been noted for other taxa and suggested to be a consequence of the isolation of intermontane basins at the time (Nichols 1976, 1979). This hypothesis remains to be rigorously tested. There is no significant difference in faunal composition between coeval deposits from different basins within the Cabbage Patch beds (Calede 2020), with the possible exception of a poor assemblage from the Blackfoot basin (Calede 2016b). A strong similarity between the mollusk assemblages of the Cabbage Patch beds and Kishenehn Formation has already been documented (Pierce & Constenius 2001). The *Pronodens* fossil from the Kishenehn Formation is coeval with the material recovered from the lower Cabbage Patch beds (Calede 2020). In fact, the species *Pronodens transmontanus* is restricted to this biostratigraphic unit in the Renova Formation and appears to be extinct (or at least extirpated) by 28.1 Ma (Calede 2020) in Cabbage Patch. The fossil from the Kishenehn Formation dated *c.* 28.2 Ma (Fan *et al.* 2021) does not expand the stratigraphic range of the taxon. Further work on vertebrates will help resolve the biogeography of the northern Rockies during the Arikareean. Such work will also require analyses of the fauna from the Fort Logan Formation.

Our quantitative analysis of the morphology of *Pronodens* suggests the need for additional studies of *P. silberlingi*. The type specimen of *P. silberlingi* is very large, much larger than MOR 951, which is more similar in size and shape to *P. transmontanus*. If the two specimens do represent two distinct taxa, *P. silberlingi* and a taxon possibly more appropriately identified as *P.* cf. *P. transmontanus*, a hypothesis for the biogeography of *Pronodens* emerges, one with a more geographically wide-ranging species (*P. transmontanus*) possibly present (albeit barely) across the Rockies with some morphological differences across populations; and a much larger, rarer species that has so far only been recovered on the eastern slope of the Rockies. The poor quality of the known lower dentitions of *P. silberlingi* precludes a comparison of the YPM

TABLE 7. — Post-hoc comparisons among species of *Paciculus* Cope, 1879 with three or more specimens measured. CM 87801 and the material from Cabbage Patch are included in the sample of *P. montanus* Black, 1961. Abbreviations: **Pco**, *P. copiosus* Korth, 2010; **Pd**, *P. dakotensis* Korth, 2010; **Pi**, *P. insolitus* Cope, 1879; **Pmc**, *P. mcgregori* Macdonald, 1970; **Pn**, *P. nebraskensis* Alker, 1969. **Bolded cells** indicate significant differences.

Taxon pair	m1L	m1W	m2L	m2W
Pd-Pco	0.790	0.972	0.836	0.258
Pi-Pco	0.858	0.777	0.916	0.607
Pi-Pd	0.997	1.000	0.990	0.760
Pmc-Pco	0.835	1.000	0.666	0.951
Pmc-Pd	0.214	0.948	0.170	0.399
Pmc-Pi	0.102	0.583	**0.015**	0.852
Pmc-Pm	**0.000**	**0.001**	**0.000**	0.112
Pm-Pco	**0.000**	**0.013**	**0.032**	0.114
Pm-Pd	0.079	0.393	0.793	0.999
Pm-Pi	**0.000**	0.147	**0.041**	0.598
Pn-Pco	**0.000**	**0.001**	**0.002**	**0.047**
Pn-Pd	0.073	0.048	0.327	1.000
Pn-Pi	**0.001**	**0.006**	**0.001**	0.279
Pn-Pm	0.999	0.441	0.786	0.999
Pn-Pmc	**0.000**	**0.000**	**0.000**	**0.022**

and MOR specimen beyond size and a definite conclusion as to the nature of the *Pronodens* material east of the Rocky Mountains. The sole upper dentition (P2-M2) referred to *P. silberlingi*, AMNH 13824 from the Rosebud Formation of South Dakota, as figured in Taylor & Webb (1976) is mostly indistinguishable in tooth shape and cusp morphology from the type specimen of *P. transmontanus* (CM 726); there is a larger and rounder protocone on P3 in the material from South Dakota. The two specimens are however much different in size with the P2-M2 length of AMNH 13824 documented at 38.5 mm (Taylor & Webb 1976) compared to 33.6 mm in CM 726, an almost 15% difference. A larger sample of *Pronodens* specimens will be necessary to revise the taxonomy of this little studied genus, especially in light of our finding that some morphological characters previously considered to be taxonomically informative may in fact vary within species, including the position of the postsymphysis relative to the mental foramen and relative to p2.

One reason why some aspects of the morphology of *Pronodens* may not be taxonomically informative is that they may be influenced by ecology. Thus, the Kishenehn Formation specimen displays several morphological characteristics that could be indicative of a more durophagous diet in Glacier National Park than Cabbage Patch. Indeed, GLAC 26988 displays very heavy wear concentrated on the anterior portion of the p3 and overall heavy wear of the teeth, a deeper posterior portion of the dentary, proportionately broader p3-m2, and inflated tooth cusps. The sole upper tooth recovered nearby the lower jaw and tentatively assigned to *Pronodens* (see Geological context above) is also very heavily worn.

Previous studies of the Oligocene-aged fossil assemblages of the Kishenehn Formation have shown that the mollusk fauna coeval with the mammals described herein is indicative of temperate environments following cooling contemporary with basin extension and slowed range uplift (Pierce & Constenius 2001; Fan *et al.* 2021). These environments may have resembled those of the Cabbage Patch beds. Indeed, the plant fossils as well as the mollusks of the Kishenehn Formation converge on a paleoenvironment of semi-permanently to permanently ponded/lacustrine to paludal vegetated lowlands associated with drier highlands (Constenius *et al.* 1989; Pierce & Constenius 2001). This mosaic of environments would certainly encompass the habitats inferred for the lower unit of the Cabbage Patch beds on the basis of sedimentary data, paleobotanical evidence, amphibian and fish bones, and invertebrate fossil remains (Calede 2016a, 2022); habitats in which *Pronodens* thrived (Calede 2020). It would also be consistent with the habitats previously inferred for the family Leptomerycidae. Indeed, leptomerycids as a whole have been interpreted to be browsers feeding on fruits and foliage, which inhabited open woodlands and/or scrubs (Métais & Vislobokova 2007; Janis & Theodor 2014). Habitat similarities across regions of the northern Rockies during the Arikareean may have been critical to biogeography; local differences in vegetation may have influenced the diet of the animals enough to impact the observable tooth morphology.

The new material of *Paciculus montanus* described herein is the northernmost occurrence of the genus in the Rocky Mountains. It is the fourth occurrence of the species, which was first described in the Fort Logan Formation (Black 1961) and has been recovered from the Lemhi Valley of Idaho (Nichols 1976) as well as the Cabbage Patch beds of Montana (Rasmussen 1977; Calede 2020; see Remarks section above). *Pronodens montanus* is the only species of the genus published to date for the northern Rocky Mountains. Unlike *Pronodens*, there are no major morphological differences that can be documented among specimens of *P. montanus* across deposits. Specifically, there are no differences between the fossils from the Peterson Creek Local Fauna and those from the Kishenehn Formation. The material from Cabbage Patch and the Fort Logan Formation cannot be compared (see Remarks above).

Our quantitative analysis of the dental morphology of the genus is the largest analysis ever undertaken, with all species represented in the analysis of m1 (38 specimens) and m2 (28 specimens). The ANOVAs show significant differences among species in the lengths and widths of m1 and m2 (Fig. 7). Post-hoc tests show that the pairwise differences between species are concentrated between the two largest species (*P. montanus* and *P. nebraskensis*) and the smaller species (Table 7). *Paciculus montanus* and *P. nebraskensis* are not significantly different in size from one another. In the absence of a large sample for *P. walshi*, our results support the conclusion from Lindsay *et al.* (2016) that the three largest species of *Paciculus* are indeed *P. montanus, P. walshi,* and *P. nebraskensis*; we cannot settle on a larger species among these. In both m1 and m2, width scales linearly with length with little deviation from the regression lines (all specimens fit within the 95% confidence interval; Fig. 8). Future analyses should explore quantitatively the morphological variation within *Leidymys*, the sister taxon to *Paciculus* (Lindsay *et al.* 2016), and include measurements for additional specimens previously unreported in the literature to inform differences in morphological disparity among species and between the two genera. This work should be combined with a phylogenetic study of Leidymini and more broadly Eucricetodontini to shed light on the origin of Cricetidae. Although fossils from the Great Plains (Martin 1980) and southern California (Whistler & Lander 2003) have been central to understanding the evolution of these clades as emphasized by Lindsay *et al.* (2016), this study shows that fossil leidymines from the Rocky Mountains will be helpful in analyzing the morphology of cricetids and central to understanding their biogeography.

Acknowledgements

This paper is dedicated to the memory of Dr Mary Dawson who shared her enthusiasm for the fossils of Montana with JC, was a longtime collaborator and friend of KC, and helped encourage NF to pursue mammal paleontology from a young age. We thank E. Côtez, G. Métais and an anonymous reviewer for their constructive feedback. Access to collections was provided by Christian Sidor and Paige Wilson (UWBM), Matt Lamanna and Amy Henrici (CM), Kallie Moore and George Stanley (UMPC), Desui Miao, David Burnham, and Chris Beard (KUVP), Darren Lewis (GLAC), and Dale Hanson (MOR). Amy Henrici photographed CM 87801. Kallie Moore shared photos of the *Miohippus* material from Peterson Creek. Christian Sidor and Kelsie Abrams provided access to prep facilities. Tara Carolin, Jean Tabbert, and Marlene Almos provided assistance with permitting, access, logistics, and specimen cataloging. Darren Lewis (Glacier National Park Archives) provided access to the fossil horse jaw and gathered descriptive notes regarding the discovery of the fossil. GLAC 26988 was collected under permit GLAC-2021-SCI-0011 from the National Park Service. Glacier National Park is located on the lands of the Blackfeet, Salish, Pend d'Oreille, and Kootenai tribes. Members of the Blackfeet Nation and Confederated Salish and Kootenai Tribes continue to tell their history and culture in the park as part of the longest running Indigenous speaker series in the National Park Service. Leona Constenius facilitated the logistics of field research. Don Rasmussen continues to share his wealth of knowledge about Rocky Mountain geology and paleontology. Funding for field work was provided in part by The Ohio State University at Marion to JC.

REFERENCES

Alker J. 1969. — *Paciculus* (Cricetinae, incertae sedis) teeth from the Miocene of Nebraska. *Journal of Paleontology* 43 (1): 171-174. https://www.jstor.org/stable/1302358

Barnosky A. D. 1982. — A new species of *Proscalops* (Mammalia, Insectivora) from the Arikareean Deep River Formation, Meagher County, Montana. *Journal of Paleontology* 56 (5): 1103-1111. https://www.jstor.org/stable/1304567

Becker R. A., Minka P. & Deckmyn A. 2022. — Maps: Draw Geographical Maps. R package version 3.4.1. Available at: https://CRAN.R-project.org/package=maps

Black C. C. 1961. — Rodents and lagomorphs from the Miocene Fort Logan and Deep River formations of Montana. *Postilla* 48: 1-20. https://www.biodiversitylibrary.org/page/10580084

Black C. C. 1978. — Paleontology and geology of the Badwater Creek Area, central Wyoming. Part 14. The Artiodactyls. *Annals of Carnegie Museum* 47: 223-259. https://doi.org/10.5962/p.215822

Bowdich T. E. 1821. — *An Analysis of the Natural Classifications of Mammalia: for the Use of Students and Travellers*. J. Smith, Paris, 115 p.

Calede J. J. 2014. — Skeletal morphology of *Palaeocastor peninsulatus* (Rodentia, Castoridae) from the Fort Logan Formation of Montana (early Arikareean): ontogenetic and paleoecological interpretations. *Journal of Mammalian Evolution* 21: 223-241. https://doi.org/10.1007/s10914-013-9231-8

Calede J. J. 2016a. — Comparative taphonomy of the mammalian remains from the Cabbage Patch beds of western Montana (Renova Formation , Arikareean): contrasting depositional environments and specimen preservation. *Palaios* 31 (11): 497-515. https://doi.org/10.2110/palo.2015.072

Calede J. J. 2016b. — *The Rise of Modern Mammalian Faunas: Tempo and Mode of Faunal Turnover in Western Montana During the Oligocene*. Unpublished PhD Dissertation, University of Washington, 427 p. https://digital.lib.washington.edu/researchworks/handle/1773/36498

Calede J. J. M. 2020. — Pattern and processes of the mammalian turnover of the Arikareean in the Northern Rocky Mountains. *Journal of Vertebrate Paleontology* 40 (1): 1-17. https://doi.org/10.1080/02724634.2020.1767117

Calede J. J. M. 2022. — The oldest semi-aquatic beaver in the world and a new hypothesis for the evolution of locomotion in Castoridae. *Royal Society Open Science* 9 (8): 220926. https://doi.org/10.1098/rsos.220926

Calede J. J. M. & Rasmussen D. L. 2020. — New gophers (Rodentia: Geomyidae) from the Cabbage Patch beds of Montana (Renova Formation) and the phylogenetic relationships within entoptychinae. *Annals of Carnegie Museum* 86 (2): 107-167. https://doi.org/10.2992/007.086.0202

Calede J. J. M., Tse Y. T. & Cairns K. D. 2022. — The first evidence of *Heosminthus* from North America and the phylogenetics of Sminthidae (Mammalia, Rodentia, Dipodoidea): biogeographical implications. *Journal of Systematic Palaeontology* 20: 1-21. https://doi.org/10.1080/14772019.2022.2111232

Constenius K. N. 1982. — Relationship between the Kishenehn basin, and the Flathead listric normal fault system and Lewis thrust salient, *in* Powers R. B. (ed.), *Geologic Studies of the Cordilleran Thrust Belt*. Rocky Mountain Association of Geologists, Denver: 817-830.

Constenius K. 1988. — Structural configuration of the Kishenehn Basin delineated by geophysical methods, northwestern Montana and southeastern British Columbia (USA, Canada). *Mountain Geologist* 25: 13-28.

Constenius K. N. 1996. — Late Paleogene extensional collapse of the Cordilleran foreland fold and thrust belt. *Geological Society of America Bulletin* 108 (1): 20-39. https://doi.org/10.1130/0016-7606(1996)108%3C0020:LPECOT%3E2.3.CO;2

Constenius K. N., Dawson M. R., Pierce H. G., Walter R. C. & Wilson M. V. H. 1989. — Reconnaissance paleontologic study of the Kishenehn Formation, northwestern Montana and southeastern British Columbia. *Montana Geological Society* 1: 189-203.

Cope E. D. 1879. — Second contribution to a knowledge of the Miocene fauna of Oregon. *Proceedings of the American Philosophical Society* 18: 370-376. https://biostor.org/reference/202783

Cope E. D. 1885. — The White River beds of Swift Current River, Northwest Territory. *American Naturalist* 19 (2): 163. https://doi.org/10.1086/273889

Dawson M. R. & Constenius K. N. 2018. — Mammalian fauna of the middle Eocene Kishenehn Formation, Middle Fork of the Flathead River, Montana. *Annals of Carnegie Museum* 85 (1): 25-60. https://doi.org/10.2992/007.085.0103

DOUGLASS E. 1902. — Fossil Mammalia of the White River beds of Montana. *Transactions of the American Philosophical Society* 20 (3): 237. https://doi.org/10.2307/1005478

DOUGLASS E. 1903. — New vertebrates from the Montana Tertiary. *Annals of the Carnegie Museum* 2: 145-199. https://doi.org/10.5962/p.78052

EISENMANN V., ALBERDI M. T., DE GIULI C. & STAESCHE U. 1988. — Studying fossil horses. *New York International Hipparion Conference* 1: 1-71.

FAMOSO N. A. 2017. — Statistical analysis of dental variation in the Oligocene equid *Miohippus* (Mammalia, Perissodactyla) of Oregon. *Journal of Paleontology* 91 (5): 1060-1068. https://doi.org/10.1017/jpa.2017.42

FAN M., CONSTENIUS K. N., PHILLIPS R. F. & DETTMAN D. L. 2021. — Late Paleogene paleotopographic evolution of the northern Cordilleran orogenic front: implications for demise of the orogen. *GSA Bulletin* 133 (11-12): 2549-2566. https://doi.org/10.1130/B35919.1

FISCHER VON WALDHEIM G. 1817. — Adversaria Zoologica: Memoires de la Société Impériale des Naturalistes de Moscou 5: 368-428.

FRICK C. 1937. — Horned ruminants of North America. *Bulletin of the American Museum of Natural History* 69: 669 p. http://hdl.handle.net/2246/362

GARCIA D. 1992. — *Fossil Mammalia from the Pipestone Creeks Region, Late Eocene and Oligocene (Chadronian and Orellan), Jefferson County, Montana*. Unpublished PhD Dissertation, University of Montana, Berkeley, 215 p.

GARDNER J. D. & WILSON M. V. H. 2022. — The most complete amiid fish from the Coal Creek member of the Eocene Kishenehn Formation in northwestern Montana. *Acta Palaeontologica Polonica* 67 (7): 493-508. https://doi.org/10.4202/app.00733.2020

GRAY J. E. 1821. — On the natural arrangement of vertebrose animals. *London medical repository* 15: 296-310.

GREENWALT D. & LABANDEIRA C. 2013. — The amazing fossil insects of the Eocene Kishenehn Formation in northwestern Montana. *Rocks and Minerals* 88 (5): 434-441. https://doi.org/10.1080/00357529.2013.809972

GREENWALT D. E., ROSE T. R., SILJESTROM S. M., GOREVA Y. S., CONSTENIUS K. N. & WINGERATH J. G. 2015. — Taphonomy of the fossil insects of the Middle Eocene Kishenehn Formation. *Acta Palaeontologica Polonica* 60 (4): 931-947. https://doi.org/10.4202/app.00071.2014

HANSON D. A. 2015. — An early Arikareean (middle Oligocene) mammal assemblage from west central Montana. Abstract for 75th Annual Meeting of the Society of Vertebrate Paleontology, 138 p.

HEATON T. H. & EMRY R. J. 1996. — Leptomerycidae, *in* PROTHERO D. R. & EMRY R. J. (eds), *The Terrestrial Eocene-Oligocene Transition in North America*. Cambridge University Press, Cambridge: 581-608.

HOPKINS W. S. & SWEET A. R. 1976. — A microflora from a short section of the Paleogene Kishenehn Formation, southeastern British Columbia. *Geological Survey of Canada, Paper* 76-1B: 307-309. https://doi.org/10.4095/104117

JANIS C. M. & THEODOR J. M. 2014. — Cranial and postcranial morphological data in ruminant phylogenetics. *Zitteliana Reihe B: Abhandlungen der Bayerischen Staatssammlung fur Palaontologie und Geologie* 32: 15-32. https://doi.org/10.5282/ubm/epub.22383

JONES P. B. 1969. — The Tertiary Kishenehn Formation, British Columbia. *Bulletin of Canadian Petroleum Geology* 17: 234-246. https://doi.org/10.35767/gscpgbull.17.2.234

KOCKEN C. M. 2022. — *Geographic and Temporal Variation in the Morphology of Diagnostic Tooth Characteristics in* Mesohippus *and* Miohippus. Unpublished Masters Thesis, South Dakota School of Mines and Technology, Rapid City, SD, 57 p.

KOCKEN C. & PAGNAC D. 2022. — Diagnostic tooth morphology of *Mesohippus* and *Miohippus*: a case for synonomization. *Geological Society of America Abstracts with Programs* 54 (5). https://doi.org/10.1130/abs/2022AM-378189

KOERNER H. E. 1940. — New vertebrates Part 1 of The geology and vertebrate paleontology of the Fort Logan and Deep River formations of Montana. *American Journal of Science* 238 (12): 837-862. https://doi.org/10.2475/ajs.238.12.837

KORTH W. W. 1992. — Fossil small mammals from the Harrison Formation (Late Arikareean : earliest Miocene), Cherry county, Nebraska. *Annals of Carnegie Museum* 61 (2): 69-131. https://doi.org/10.5962/p.215172

KORTH W. W. 2010. — Mammals from the Blue Ash Local Fauna (Late Oligocene), South Dakota. Rodentia Part 5: Family Cricetidae. *Paludicola* 7 (4): 117-136. https://paludicolavertpaleo.files.wordpress.com/2018/05/7-4-korth-2010.pdf

KORTH W. W. 2012. — Aplodontid rodents (Mammalia) from the Orellan (Early Oligocene) Canyon Ferry Fauna of Montana. *Paludicola* 9 (1): 1-6. https://paludicolavertpaleo.files.wordpress.com/2018/05/9-1-korth-2012a.pdf

KORTH W. W. 2014. — Rodents (Mammalia) from the Whitneyan (Middle Oligocene) Cedar Pass fauna of South Dakota. *Annals of Carnegie Museum* 82 (4): 373-398. https://doi.org/10.2992/007.082.0404

KORTH W. W. 2019. — Rodents (Mammalia) from the Early Oligocene (Orellan) Cook Ranch Local Fauna of southwestern Montana. *Annals of Carnegie Museum* 85 (3): 223. https://doi.org/10.2992/007.085.0303

KORTH W. W. & SULLIVAN J. S. 2021. — Mammals from the Blue Ash Local Fauna (Whitneyan, Oligocene), South Dakota. Carnivora, Artiodactyla, and additional Rodentia. *Paludicola* 13: 69-84.

KORTH W. W. & TABRUM A. R. 2017. — A unique rodent fauna from the Whitneyan (Middle Oligocene) of southwestern Montana. *Annals of Carnegie Museum* 84 (4): 319-340. https://doi.org/10.2992/007.084.0401

KUENZI W. D. & FIELDS R. W. 1971. — Tertiary stratigraphy, structure, and geologic history, Jefferson Basin, Montana. *Geological Society of America Bulletin* 82 (12): 3373-3394. https://doi.org/10.1130/0016-7606(1971)82[3373:TSSAGH]2.0.CO;2

LEIDY J. 1853. — Remarks on a collection of fossil Mammalia from Nebraska. *Proceedings of the Academy of Natural Sciences of Philadelphia* 6: 392-394.

LINDSAY E., WHISTLER D. P., KALTHOFF D. C. & VON KOENIGSWALD W. 2016. — *Paciculus walshi*, new species, (Rodentia, Cricetidae), the origin of the Cricetidae and an Oligocene intercontinental mammal dispersal event. *Historical Biology* 28 (1-2): 78-94. https://doi.org/10.1080/08912963.2015.1050389

LINNEAUS C. 1758. — *Systema naturae per regna tria naturae, secundum class, ordines, genera, species cum characteribus, differentiis, synonymis, locis*. Laurentii Salvi, Stockholm, 824 p.

LIU J., WILSON M. V. H. & MURRAY A. M. 2016. — A new catostomid fish (Ostariophysi, Cypriniformes) from the Eocene Kishenehn Formation and remarks on the North American species of †*Amyzon* Cope, 1872. *Journal of Paleontology* 90 (2): 288-304. https://doi.org/10.1017/jpa.2016.28

LOFGREN D., HANNEMAN D., BIBBENS J., GERKEN L., HU F., RUNKEL A., KONG I., TARAKJI A., HELGESON A., GERARD I., LI R., LI S. & JI Z. 2020. — Eocene and Oligocene mammals from the Gravelly Range of southwest Montana. *Paludicola* 12 (4): 263-297.

MACDONALD J. R. 1963. — The Miocene faunas from the Wounded Knee area of western South Dakota. *Bulletin of the American Museum of Natural History* 125:139-238. http://hdl.handle.net/2246/1259

MACDONALD J. R. 1970. — Review of the Miocene Wounded Knee faunas of southwestern South Dakota. *Bulletin of the Los Angeles County Museum of Natural History, Science* 8: 165-82.

MACFADDEN B. J. 2005. — Fossil horses – Evidence for evolution. *Science* 307 (5716): 1728-1730. https://doi.org/10.1126/science.1105458

Marsh O. C. 1874. — Notice of new equine mammals from the Tertiary formation. *Journal of Natural History* 13 (77): 397-400. https://doi.org/10.1080/00222937408680887

Marsh O. C. 1875. — Notice of new tertiary mammals, IV. *American Journal of Science* 9 (51): 239-250. https://doi.org/10.2475/ajs.s3-9.51.239

Martin L. D. 1973. — *The Mammalian Fauna of the Lower Miocene Gering Formation of Western Nebraska and the Early Evolution of the North American Cricetidae*. Unpublished PhD Dissertation, University of Kansas, Lawrence, KS, 264 p.

Martin L. D. 1980. — The early evolution of the Cricetidae in North America. *The University of Kansas Paleontological Contributions* 102: 1-41. http://hdl.handle.net/1808/3684

Masciale D. M. 2010. — *An Analysis of Anchitherine Equids Across the Eocene–Oligocene Boundary in the White River Group of the Western Great Plains*. Unpublished Masters Thesis, University of Nebraska, Lincoln, NE, 79 p. https://digitalcommons.unl.edu/geoscidiss/11/

Massicotte P. & South A. 2023. — rnaturalearth: World Map Data from Natural Earth. R package version 0.3.3. https://CRAN.R-project.org/package=rnaturalearth

McMechan R. D. 1981. — *Stratigraphy, Sedimentology, Structure and Tectonic Implications of the Oligocene Kishenehn Formation, Flathead Valley Graben, southeastern British Columbia*. Unpublished PhD Dissertation, Queen's University, Kingston, Ontario, 327 p.

McMechan R. D. & Price R. A. 1980. — Reappraisal of a reported unconformity in the Paleogene (Oligocene) Kishenehn Formation: implications for Cenozoic tectonics in the Flathead Valley graben, southeastern British Columbia. *Bulletin of Canadian Petroleum Geology* 28 (1): 37-45. https://doi.org/10.35767/gscpgbull.28.1.037

Métais G. & Vislobokova I. 2007. — Basal ruminants, *in* Prothero D. R. & Foss S. E. (eds), *The Evolution of Artiodactyls*. Johns Hopkins University Press, Baltimore: 189-212.

Nichols R. 1976. — Early Miocene mammals from the Lemhi valley of Idaho. *Tebiwa* 18: 9-47.

Nichols R. 1979. — Additional early Miocene mammals from the Lemhi Valley of Idaho. *Tebiwa* 17: 1-12.

Owen R. 1848. — Description of teeth and portions of jaws of two extinct anthracotherioid quadrupeds (*Hyopotamus vectianus* and *Hyop. bovinus*), discovered in the Eocene deposits on the N.W. coast of the Isle of Wight; with an attempt to develope Cuvier's idea of the class. *Quarterly Journal of the Geological Society, London* 4: 103-141. https://doi.org/10.1144/GSL.JGS.1848.004.01-02.21

Pierce H. G. & Constenius K. N. 2001. — Late Eocene-Oligocene nonmarine mollusks of the northern Kishenehn Basin, Montana and British Columbia. *Annals of the Carnegie Museum* 70 (1): 1-112. https://doi.org/10.5962/p.215142

Pierce H. G. & Constenius K. N. 2014. — Terrestrial and aquatic mollusks of the Eocene Kishenehn Formation, Middle Fork Flathead River, Montana. *Annals of Carnegie Museum* 82 (4): 305-329. https://doi.org/10.2992/007.082.0401

Price R. A. 1965. — Flathead map-area, British Columbia and Alberta. *Memoir of the Geological Survey of Canada* 336: 1-221.

Prothero D. R. & Shubin N. 1989. — The evolution of Oligocene Horses, *in* Prothero D. R. & Schoch R. M. (eds), *The Evolution of Perissodactyls*. Oxford University Press, New York: 142-175.

Prothero D. R. & Emry R. J. 2004. — 5. The Chadronian, Orellan, and Whitneyan North American Land Mammal Ages, *in* Woodburne M. O. (ed.), *Late Cretaceous and Cenozoic Mammals of North America.* Columbia University Press, New York: 156-168.

R Core Team 2023. — R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Rasmussen D. L. 1977. — *Geology and Mammalian Paleontology of the Oligocene-Miocene Cabbage Patch Formation, Central-Western Montana*. Unpublished PhD Dissertation, University of Kansas, Lawrence, KS, 775 p.

Rensberger J. M. 1979. — *Promylagaulus* progressive aplodontoid rodents of the Early Miocene. *Contributions in Science* 312: 1-18. https://doi.org/10.5962/p.208195

Rensberger J. M. 1981. — Evolution in a Late Oligocene-Early Miocene sucession of meniscomyine rodents in the Deep River Formation, Montana. *Journal Of vertebrate paleontology* 1 (2): 185-209. https://doi.org/10.1080/02724634.1981.10011891

Russell L. S. 1954. — Mammalian fauna of the Kishenehn Formation, southeastern British Colombia. *Bulletin, Annual Report of the National Museum for the Fiscal Year 1952-53* 132: 92-111.

Russell L. S. 1964. — Kishenehn Formation. *Bulletin of the Canadian Petroleum Geology* 12: 536-543.

Schneider C. A., Rasband W. S. & Eliceiri K. W. 2012. — NIH Image to ImageJ: 25 years of image analysis. *Nature Methods* 9: 671-675. https://doi.org/10.1038/nmeth.2089

Scott W. B. 1895. — The Mammalia of the Deep River Beds. *Transactions of the American Philosophical Society* 18 (2): 55-185. https://doi.org/10.2307/1005386

Stirton R. A. 1940. — Phylogeny of North American Equidae. *University of California Publications in Geological Sciences* 24: 165-197.

Tabrum A. R. & Métais G. 2007. — *Pipestoneia douglassi*, a new genus and species of selenodont artiodactyl from the Pipestone Springs area, Jefferson County, Montana. *Bulletin of Carnegie Museum of Natural History* 39: 83-96. https://doi.org/fpfzwb

Taylor B. E. & Webb S. D. 1976. — Miocene Leptomerycidae (Artiodactyla, Ruminantia) and their relationships. *American Museum Novitates* 2596: 1-22. http://hdl.handle.net/2246/5473

Tedford R. H., Albright L. B., Barnosky A. D., Ferrusquia-Villafranca I., Hunt R. M., Storer J. E., Swisher C. C., Voorhies M. R., Webb S. D. & Whistler D. P. 2004. — 6. Mammalian Biochronology of the Arikareean Through Hemphillian Interval (Late Oligocene Through Early Pliocene Epochs), *in* Woodburne M. O. (ed.), *Late Cretaceous and Cenozoic Mammals of North America*. Columbia University Press, New York: 169-231. https://doi.org/10.7312/wood13040-008

Whistler D. P. & Lander E. B. 2003. — Chapter 11. New Late Uintan to Early Hemingfordian Land Mammal assemblages from the undifferentiated Sespe and Vaqueros formations, Orange county, and from the Sespe and equivalent marine formations in Los Angeles, Santa Barbara, and Ventura counties, southern California. *Bulletin of the American Museum of Natural History*: 231-268. http://hdl.handle.net/2246/447

White T. E. 1954. — Preliminary analysis of the fossil vertebrates of the Canyon Ferry reservoir area. *Proceedings of the United States National Museum* 103: 395-438. https://doi.org/10.5479/si.00963801.103-3326.395

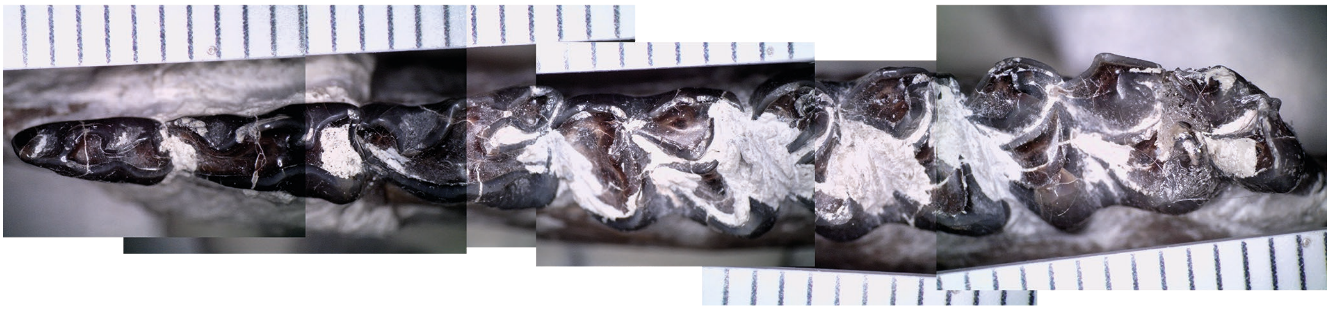
Williams M. R. & Storer J. E. 1998. — Cricetid rodents of the Kealey Springs Local Fauna (Early Ariakreean; Late Oligocene) of Saskatchewan. *Paludicola* 1: 143-149.

Zittel K. A. Von 1893. — *Handbuch der Palaeontologie. Abteilung I. Palaeozoologie. Band IV, Vertebrata (Mammalia)*. R. Oldenbourg, Munich, 799 p.

Submitted on 15 July 2023;
accepted on 20 December 2023;
published on 24 June 2024.

APPENDICES

Appendix 1. — Dental morphology in occlusal view of GLAC 26988, *Pronodens transmontanus* (Douglass, 1903), from the Kishenehn Formation.



Appendix 2. — Dental morphology in occlusal view of CM 87801, *Paciculus* Cope, 1879 from the Kishenehn Formation.