VERTEBRATE PALEONTOLOGY OF MONTANA

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(1) INTRODUCTION

Montana is renowned for its rich paleontological treasures, particularly those of vertebrate animals such as fishes, dinosaurs, and mammals. For example, the most speciose fish fauna in the world comes from Fergus County. The first dinosaur remains noted from the western hemisphere came from an area near the mouth of the Judith River in what would become Fergus County. The first *Tyrannosaurus rex* skeleton, and many more since, have come from Garfield and McCone Counties. The first dinosaur recognized to show the relationship between dinosaurs and birds came from Carbon County, and the first dinosaur eggs, embryos, and nests revealing dinosaur social behaviors were found in Teton County. The first dinosaur confirmed to have denned in burrows was found in Beaverhead County.

Although Montana is not often thought of for mammal fossils, a great diversity of late Mesozoic and Cenozoic mammals also occurs within the State. Especially noteworthy are the mid to Late Cretaceous primitive mammals found within the great dinosaur-producing formations of eastern Montana, the early and late Paleocene mammals of the Fort Union Formation in central and eastern Montana, and the late Eocene/early Oligocene deposits in southwestern Montana. Additionally, middle Eocene and middle Miocene strata contain important mammal fossils, in some cases representing unique occurrences.

This chapter highlights Montana's most significant vertebrate fossils, and the environments in which the animals lived and died. We have chosen to list representative Holotypes, and taxa that have been formally described in the literature, rather than listing all of the species reported in "faunal lists," since these lists often contain very fragmentary remains, and only best guesses of their identities. The taxa listed here are what we consider to be the most representative, from which important and interesting hypotheses have been derived concerning the evolution, behavior, and paleoecology of vertebrate fossil taxa from Montana.

All Paleozoic vertebrates from Montana come from marine sediments, whereas the Mesozoic assemblages are derived from transgressive–regressive alternating marine and freshwater deposits, and the Cenozoic faunas are derived strictly from freshwater terrestrial environments.

(2) PALEOZOIC VERTEBRATES

Two vertebrate assemblages are known from the Paleozoic, one of Early Devonian age, and the other of Late Mississippian age.

a. Early Devonian (Emsian: 407–397 Ma) Beartooth Butte Formation

The oldest vertebrate remains found in Montana come from the Beartooth Butte Formation exposed in the Big Belt and Big Snowy Mountains of central Montana. These Devonian sediments, representing an estuarine environment at the edge of the continent (Dorf, 1934; Sandberg, 1961), yield bony plates (fig. 1) of armored fishes called arthrodires and antiarchs (see Fiorillo, 2000), which are both groups within the Placodermi, the "dominant vertebrates of the Devonian Period" (Young, 2010). The Beartooth Butte Formation, yielding the best examples of these fishes, is named for Beartooth Butte, located along the Beartooth Highway in Wyoming, adjacent to the Montana border. Twenty-one species have been described from the Wyoming site (Bryant, 1935; Elliot and Ilyes, 1996; Fiorillo, 2000). Although some placoderms in other regions of North America grew to gigantic proportions, the specimens from Montana and Wyoming represent individuals of about 20 to 30 cm in length.

Fiorillo (2000) presented data from a stable oxygen and carbon isotope study of the various sites in Wyoming and Montana, and was able to hypothesize that the Montana sites had a higher freshwater component as opposed to the Wyoming sites, which had

Figure 1. Dermal armor plate from the placoderm, *Cyrtaspidichthys sculptus* from the Beartooth Butte Formation, Wyoming/Montana border. Photo by James St. John.

higher salinity. This study helps to confirm that these Devonian fishes lived in both freshwater and marine environments (Young, 2010), and that a shallow embayment existed in Wyoming at the time (see fig. 2).

b. Late Devonian, Early Mississippian (361 Ma) Sappington Formation

No vertebrates have been formally described from this unit, although fish remains have been reported (Gutschick and others, 1962).

c. Late Mississippian (Serpukhovian: 330.9–323.2 Ma) Bear Gulch Limestone

Fish fossils were first discovered in the Bear Gulch Limestone of Fergus County in 1968 by Chuck Allen, a man from Beckett, Montana who was quarrying building stone. The first fish he found was a coelacanth, which he reported to the University of Montana, Museum of Paleontology. Bill Melton, the curator, and his field assistant, J. Horner, went to the site the following year and opened a quarry to evaluate the rock's potential. In less than a week they had discovered a plethora of fishes and soft-bodied animals, all new to science. Paleozoic fish expert Richard Lund from New York was brought in, and so began what would eventually produce hundreds of new species, and the world's most diverse Paleozoic fish fauna.

The Bear Gulch Limestone is a facies of the Heath Formation, and therefore part of the Late Mississippian, Big Snowy Group (Horner, 1985). The Bear Gulch Limestone was deposited in an embayment of the "Montana Trough" (see Williams, 1983), a narrow seaway that connected the Panthalassic Ocean to the Williston Basin (fig. 3), which at the time was located about 10º North latitude (Grogan and Lund, 2002).

The Bear Gulch Limestone sediments consist of fine-grained micritic muds deposited rhythmically that now form a plattenkalk lagerstätte (Williams, 1983), preserving exquisite soft-bodied organisms and fishes (see Lund and Grogan, 2013). Evaluation of the sediments together with paleoclimatology models suggests that the climate fluctuated from semi-arid to tropical, and that deposition within the seaway alternated between slow during arid conditions to rapid during tropical seasons (Grogan and Lund, 2002). This alternating deposition is reflected in specimen preservation: slow depositional periods produced disarticulated skeletal remains scattered about on the sediment floor, whereas rapid deposition preserved whole bodies and soft tissues.

The Bear Gulch fish fauna is extraordinary and is represented by more than 3,000 catalogued specimens (fig. 4), representing more than 130 different species, the majority of which are chondrichthyans (see table 1), which include sharks and their kin (Horner and Lund, 1985; Lund and others, 2012). Among the bony fish, the paleoniscoids are the most speciose of the ray-fin fishes (Actinopterygii), and the coelacanths are

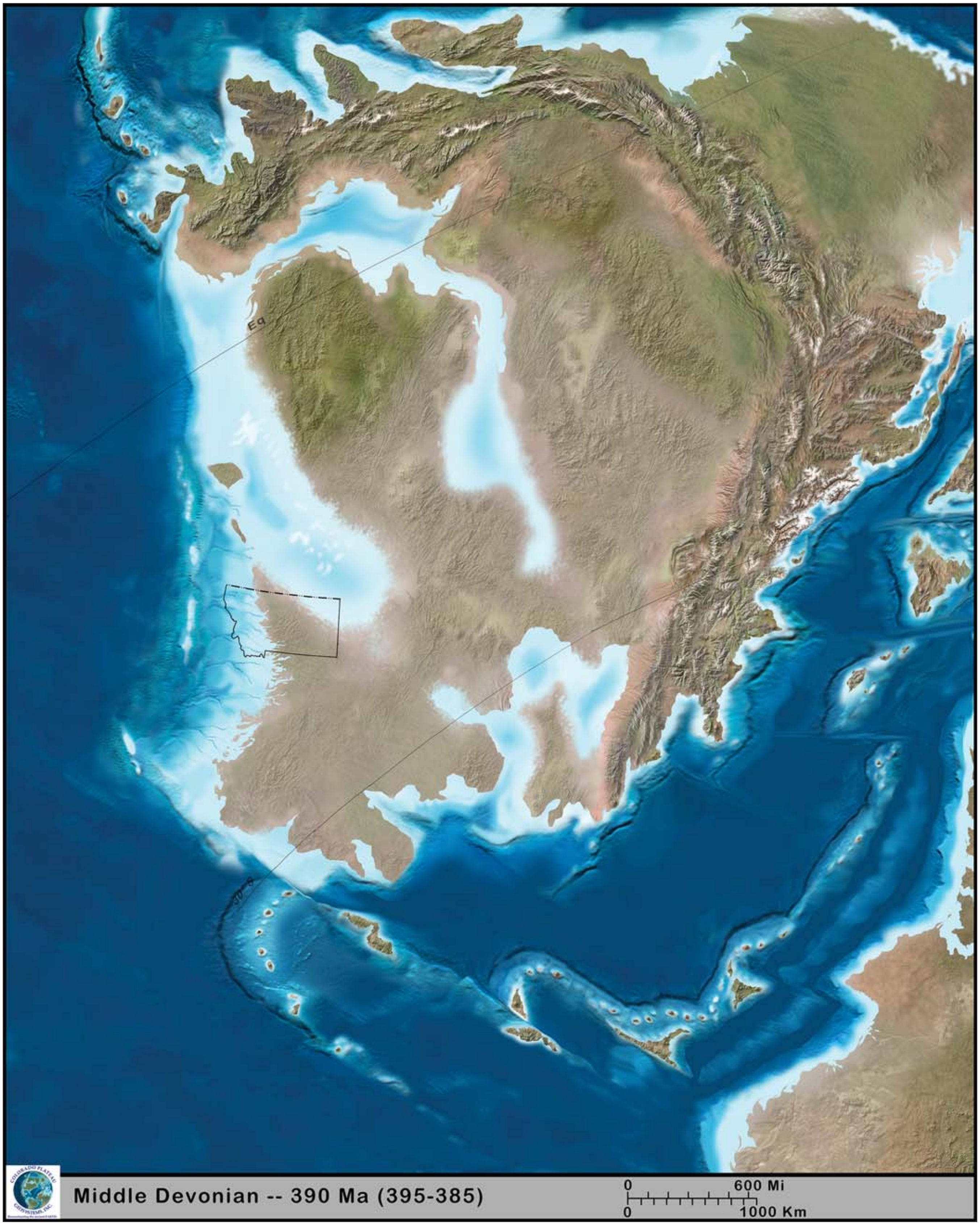

Figure 2. Paleogeographic map showing North America as it may have looked during the Early Devonian. Note the Beartooth embayment in western Montana. From Blakey, https://deeptimemaps.com, with permission (Blakey, 2016).

Figure 3. Paleogeographic map showing North America as it may have looked during the Late Mississippian. Note the Montana trough and Williston Basin Embayment. From Blakey, https://deeptimemaps.com, with permission (Blakey, 2016).

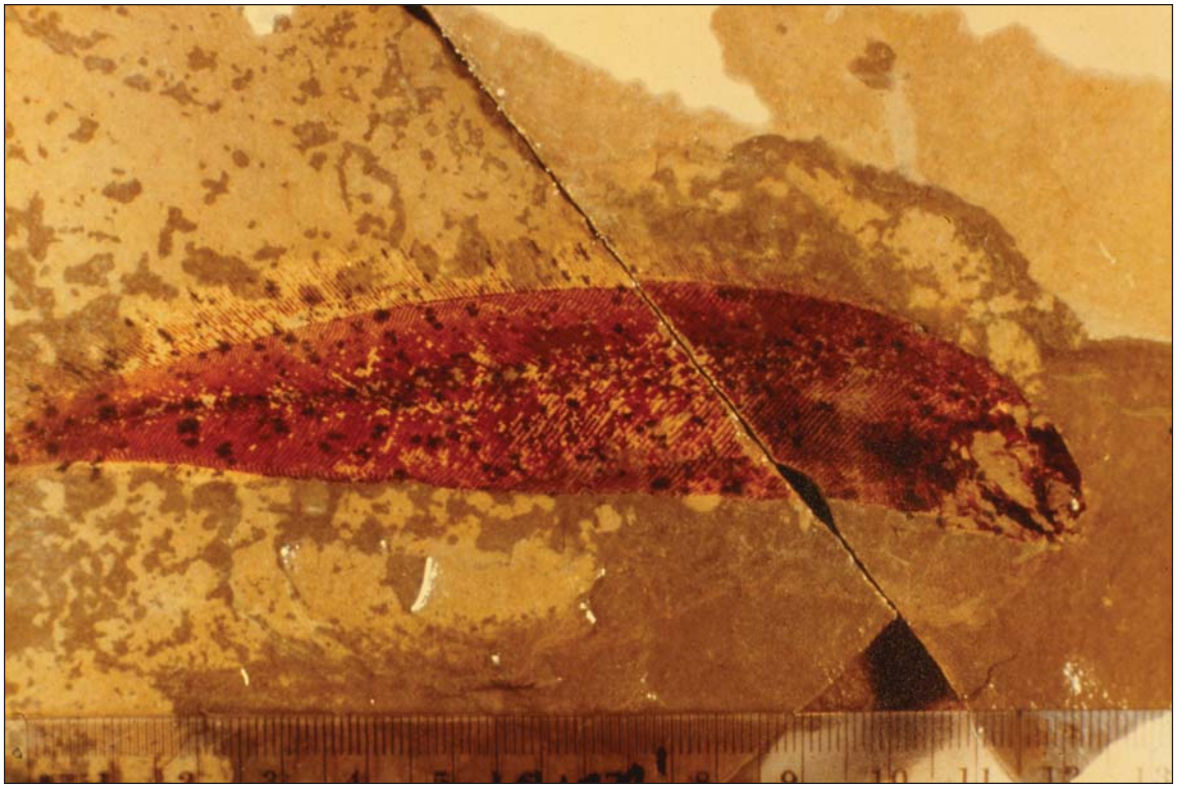

Figure 4. *Paratarrasius hibbardi*, a tarrasiiformes Actinopterygian fish from the Bear Gulch Limestone. J Horner photo, University of Montana specimen.

among the most speciose of the lobe-fin fishes (Sarcopterygii).

The fishes come in a wide variety of body shapes, some deep-bodied and laterally compressed, indicative of living high in the water column (e.g., Lund, 1990, 2000), and others dorso-ventrally flattened, indicative of being bottom dwellers (Lund and Zangerl, 1974).

The earliest known lamprey (Janvier and Lund, 1983) is found here, as is a spiny-finned fish called an acanthodian (Zidek, 1980). Some shark species clearly reveal their sexual dimorphic morphologies, the male *Falcatus falcatus*, for example, sporting a large dorsal spine (Lund, 1985). There is also a large stethacanthid shark named *Stethacanthus altonensis* that probably reached 5 ft in length, and had a large, dorsal, comb-like structure (Lund, 1974). There are specimens that show color patterns, last meals, and reproductive strategies (Grogan and Lund, 1995).

The Bear Gulch Bay teemed with a diverse variety of taxa (fig. 5), many of which are not preserved in any other location on earth (e.g., Lund and Lund, 1984; Lund and Grogan, 2004; Mickle and others, 2009). The Bear Gulch Limestone is arguably the most important Paleozoic fossil-bearing unit in the world.

Pennsylvanian and Permian rocks in Montana have not produced any described vertebrate remains.

(3) MESOZOIC VERTEBRATES

The marine Dinwoody Formation and the terrestrial Chugwater Formation, both deposited during the Triassic Period in Montana, have yet to yield vertebrate specimens, although fossils do occur in these formations in Wyoming.

a. Middle Jurassic (Callovian: 166–163 Ma) Sundance Formation, Hulett Member

A sliver of the Sundance Formation, deposited in the Sundance Sea, is exposed in south-central Montana (Carbon County). The Sundance Formation, primarily exposed in Wyoming, is equivalent to the Swift and Rierdon Formations of the marine Ellis Group in Montana (Parcell and Williams, 2005). To date, fishes reported from the Montana part of the Sundance Formation are referable only to *Hulettia americana*, although these beds have yet to be extensively sampled, and other taxa are found in Wyoming (see Schaeffer and Patterson, 1984).

Along the northern edge of the Sundance Sea, in tidal flat deposits located on the Montana–Wyoming border, enigmatic footprints have been reported (Harris and Lacovara, 2010).

No vertebrate remains have been described from the marine Jurassic Ellis Group.

Table 1. Vertebrate Paleontological Holotypes from Montana (not comprehensive).

(1) Paleozoic Vertebrates

a. Early Devonian (Emsian: 407–397 Ma) Beartooth Butte Formation

No Montana Holotypes: Antiarch and arthrodire indeterminate taxa (see Fiorillo, 2000).

b. Late Mississippian (Serpukhovian: 330.9–323.2 Ma; IUGS, 2020) Bear Gulch Limestone (Fergus County) (List from Lund and Grogen, 2013)

Chordata Incertae Sedis

Typhloesus wellsi Melton et Scott, 1973

i. Agnatha (jawless fish)

Hardistiella montanensis Janvier et Lund, 1983

ii. Acanthodii (spiny fish)

Acanthodes lundi Zidek, 1980

iii. Chondrichthyes (sharks)

Bealbonn rogaire Lund et Grogan, 2004
Gregorius rexi Lund et Grogan, 2004
Srianta dawsoni Lund et Grogan, 2004
Srianta srianta Lund et Grogan, 2004
Debeerius ellefseni Grogan et Lund, 2000
Heteropetalus elegantulus Lund, 1977b
Belantsea montana Lund, 1989
Harpacanthus fimbriatus Lund et Grogan, 2004
Delphyodontos dacriformes Lund, 1980
Harpagofututor volsellorhinus Lund, 1982
Echinochimaera meltoni Lund, 1977a
Echinochimaera snyderi Lund, 1988
Traquairius agkistrocephalus Lund et Grogan, 1997a
Traquairius spinosus Lund et Grogan, 1997b
Traquairius nudus Lund et Grogan 1997b
Polyrhizodus digitatus Lund, 1983
Netsepoye hawesi Lund, 1989
Siksika ottae Lund, 1989
Obruchevodus griffithi Grogan et al., 2014
Fissodopsis robustus Lund et al., 2014
Petalorhynchus beargulchensis Lund 1989
Janassa clarki Lund, 1989
Rainerichthys zangerli Grogan et Lund, 2009
Papilionichthys stahlae Grogan et Lund, 2009
Damocles serratus Lund, 1986
Falcatus falcatus Lund, 1985
Orestiacanthus fergusi Lund, 1984
Stethacanthus productus Lund, 1984
Squatinactis montanus Lund et Zangerl, 1974
Thrinacoselache gracia Grogen et Lund, 2008

iv. Osteichthyes (bony fish)

Paratarrasius hibbardi Lund et Melton, 1982
Discoserra pectinodon Lund, 2000
Guildayichthys carnegiei Lund, 2000
Aesopichthys erinaceus Poplin et Lund, 2000
Cyranorhis bergeraci Lund et Poplin, 1997
Kalops monophrys Poplin et Lund, 2002
Kaplops diophrys Poplin et Lund, 2002
Proceramala montanensis Poplin et Lund, 2000
Wendyichthys dicksoni Lund et Poplin, 1997
Wendyichthys lautreci Lund et Poplin, 1997
Allenypterus montanus Lund et Lund, 1984
Caridosuctor populosum Lund et Lund, 1984
Hadronector donbairdi Lund et Lund, 1984
Polyosteorhynchus beargulchensis Lund et Lund, 1984
Lochmocercus aciculodontus Lund et Lund, 1984
Lineagruan judithi Mickle et al., 2009
Lineagruan snowyi Mickle et al., 2009
Beagiacus pulcherrimus Mickle et al., 2009
Paphosiscus circulocaudus Grogan et Lund, 2015
Paphosiscus scalmocristus Grogan et Lund, 2015

Table 1—*Continued.*

(2) Mesozoic Vertebrates

- a. Middle Jurassic (Callovian: 166–163 Ma) Sundance Formation, Hulett Member
  - No Montana Holotypes: *Hulettia americana* (Eastman, 1899) see Schaeffer and Patterson, 1984
- b. Late Jurassic (Tithonian–Kimmerigian: 156–146 Ma) Morrison Formation
  - *Suuwassea emilieae* Harris et Dodson, 2004
- *c.* Early Cretaceous (Aptian-Albian: 120–110 Ma) Kootenai Formation
  - *Toxolophosaurus cloudi* Olson, 1960
- d. Early Cretaceous (Aptian-Albian: 120–110 Ma) Cloverly Formation
  - *Ceratodus frazieri* Ostrom, 1970
  - *Paramacellodus keebleri* Nydam et Cifelli, 2002
  - *Ptilotodon wilsoni* Nydam et Cifelli, 2002
  - *Deinonychus antirrhopus* Ostrom, 1969
  - *Tenontosaurus tilletti* Ostrom, 1970
  - *Zephyrosaurus schaffi* Sues, 1980
  - *Sauropelta edwardsorum* Ostrom, 1970
  - *Tatankacephalus cooneyorum** Parsons et Parsons, 2009
  - *Microvenator celer* Ostrom, 1970
  - *Aquilops americanus* Farke et al., 2014
  - *Rugocaudia cooneyi** Woodruff, 2012
  - *Gobiconodon ostromi* Jenkins Jr. et Schaff, 1988
  - *Argaliatherium robustum* Cifelli et Davis, 2015
  - *Carinalestes murensis* Cifelli et Davis, 2015
  - *Montanalestes keeblerorum* Cifelli, 1999
  - *Oklatheridium wiblei* Cifelli et Davis, 2015
- e. Middle Cretaceous (Albian–Cenomanian: 103–98 Ma) Thermopolis Shale
  - *Edgarosaurus muddi* Druckenmiller, 2002
- f. Late Cretaceous (Cenomanian: 95 Ma) Blackleaf Formation.
  - *Oryctodromeus cubicularis* Varricchio et al., 2007
- g. Late Cretaceous (Campanian: 80–74 Ma) Two Medicine Formation
  - i. Lower lithofacies
    - *Cerasinops hodgkissi* Chinnery et Horner, 2007
    - *Acristavus gagslarsoni* Gates et al., 2011
    - *Gryposaurus latidens* Horner, 1992
  - ii. Middle lithofacies
    - *Magnuviator ovimonsensis* DeMar et al., 2017
    - *Maiasaura peeblesorum* Horner et Makela, 1979
    - *Orodromeus makelai* Horner et Weishampel, 1988
    - *Bambiraptor feinbergi* Burnham et al., 2000
  - iii. Upper lithofacies
    - *Daspletosaurus horneri* Carr et al., 2017
    - *Palaeoscincus rugosidens** Gilmore, 1930
    - *Brachyceratops montanensis* Gilmore, 1914
    - *Achelousaurus horneri* Sampson, 1994
    - *Einiosaurus procurvicornis* Sampson, 1995
    - *Rubeosaurus ovatus* McDonald et Horner, 2010
    - *Oohkotokia horneri** Penkalski, 2013
    - *Prenoceratops pieganensis* Chinnery, 2004
    - *Hypacrosaurus stebingeri* Horner et Currie, 1994
    - *Prosaurolophus blackfeetensis** Horner, 1992
    - *Glishades ericksoni** Prieto-Marquez, 2010
    - *Avisaurus gloriae* Varricchio et Chiappe, 1995
    - *Piksi barbaruina* Varricchio, 2002 (See: Agnolin & Varricchio, 2012)
    - *Montanazhdarcho minor* Padian et al., 1995
- h. Late Cretaceous (Campanian: 78 Ma) Claggett Shale
  - *Hesperornis montana* Shufeldt, 1915
- i. Late Cretaceous (Campanian: 79–74.9 Ma) Judith River Formation
  - *Lepidotus occidentalis* Leidy, 1856
  - *Lepidotus haydeni** Leidy, 1856
  - *Myledaphus bipartitus* Cope, 1876
  - *Chiloscyllium missouriensis* Case, 1979
  - *Psammorhynchus longipinnis* Grande, 2006
  - *Scapherpeton tectum* Cope, 1876

Table 1—*Continued.*

*Scapherpeton laticolle** Cope, 1876
*Scapherpeton excisum** Cope, 1876
*Scapherpeton favosum** Cope, 1876
*Hemitrypus jordanianus** Cope, 1876
Nezpercius dodsoni Blob et al., 2001
Deinosuchus hatcheri Holland, 1909
Compsemys variolosus Cope, 1876
Compsemy imbricarius Cope, 1876
Polythorax missuriensis Cope, 1876
Champsosaurus profundus Cope, 1876
Champsosaurus annectens Cope, 1876
Champsosaurus brevicollis Cope, 1876
Champsosaurus vaccinsulensis Cope, 1876
Troodon formosus Leidy, 1856
Paronychodon lacustris Cope, 1876
*Deinodon horridus** Leidy, 1856
*Zapsalis abradens** Cope, 1876
*Aublysodon mirandus** Leidy, 1856
*Palaeoscincus costatus** Leidy, 1856
*Trachodon mirabilis** Leidy, 1856
*Pteropelyx grallipes** Cope, 1889
*Diclonius calamaris** Cope, 1876
*Diclonius pentagonius** Cope, 1876
*Diclonius perengulatus** Cope, 1876
*Dysganus peiganus** Cope, 1876
*Dysganus bicarinatus** Cope, 1876
*Dysganus haydenianus** Cope, 1876
*Dysganus encaustus** Cope, 1876
*Ceratops montanus** Marsh, 1888
Avaceratops lammersi Dodson, 1986
Mercuriceratops gemini Ryan et al., 2014
Judiceratops tigris Longrich, 2013
Medusaceratops lokii Ryan et al., 2010
Spiclypeus shipporum Mallon et al., 2016
Probrachylophosaurus bergei Freedman Fowler et Horner, 2015
*Brachylophosaurus goodwini** Horner, 1988
Zuul crurivastator Arbour et Evans, 2017
Cimexomys judithae Sahni, 1972
Cimexomys magnus Sahni, 1972
Cimolomys clarki Sahni, 1972
Pediomys clemensi Sahni, 1972
Alphadon halleyi Sahni, 1972
Gypsonictops lewisi Sahni, 1972

j. Late Cretaceous (Campanian–Maastrichtian: 70.5 Ma) Bearpaw Formation
Plioplatecarpus peckensis Cuthbertson et Holmes, 2015

k. Late Cretaceous (Maastrichtian: 72–66 Ma) St. Mary River Formation
Montanaceratops cerorhynchos Brown et Schlaikjer, 1942
Paracimexomys propriscus Hunter et al., 2010
Nidimys occultus Hunter et al., 2010
Leptalestes toevsi Hunter et al., 2010

l. Late Cretaceous (Maastrichtian: 66.8–66 Ma) Hell Creek Formation
Paleopsephurus wilsoni MacAlpin, 1947
Protoscaphirhynchus squamosus Wilimovsky, 1956
Phyllodus paulkatoi Estes et Hiatt, 1978
Melvius thomasi Bryant, 1987
Paranecturus garbanii Demar, 2013
Obamadon gracilis Longrich, 2013
Stygiochelys estesi Gaffney et Hiatt, 1971
Emarginachelys cretacea Whetstone, 1978
Brachychampsa montana Gilmore, 1911
Tyrannosaurus rex Osborn, 1905
Trierarchuncus prairiensis Fowler et al., 2020
*Nanotyrannus lancensis** (Gilmore, 1946)
*Triceratops maximus** Brown, 1933
*Ugrosaurus olsoni** CoBabe et Fastovsky, 1987

Table 1—*Continued.*

Ankylosaurus magniventris Brown, 1908
*Bugenasaura garbanii** (Galton, 1995)
Pachycephalosaurus grangeri Brown et Schlaikjer,
1942 *Stygimoloch spinifer** Galton et Sues, 1983
*Stenotholus kohleri** Giffin et al., 1987
*Sphaerotholus buchholtzae** Williamson et Carr, 2002
Acheroraptor temertyorum Evans et al., 2013
Belonoolithus garbani Jackson et Varricchio, 2016
Avisaurus archibaldi Brett-Surman et Paul, 1985
Neoplagiaulax burgessi Archibald, 1982
Essonodon browni Simpson, 1927
*Meniscoessus borealis** Simpson, 1927
Ectoconodon montanensis Simpson, 1927
Glasbius twitchelli Archibald, 1982
Protungulatum coombsi Archibald et al., 2011

(3) Cenozoic Vertebrates
a. Paleocene (66–55 Ma)
i. Puercan (Early Paleocene: 66–63.3 Ma) Tullock (incl. Bug Creek anthills fauna) and Ludlow Members of the Fort Union Formation, and Simpson Quarry in the Bear Formation (Crazy Mtn. Basin)
Polyodon tuberculata Grande et Bemis, 1991
Lisserpeton bairdi Estes, 1965
Derrisemys sterea Hutchison, 2009
Plastomenoides tetanetron Hutchison, 2009
*Atoposemys entopteros** Hutchison, 2013
Cimexomys hausoi Archibald, 1982
Cimexomys minor Sloan et Van Valen, 1965
*Mesodma garfieldensis** Archibald, 1982
Neoplagiaulax nelsoni Sloan, 1987
Acheronodon garbani Archibald, 1982
Stygimys kuszmauli Sloan et Van Valen, 1965
Catopsalis joyneri Sloan et Van Valen, 1965
Catopsalis waddleae Buckley, 1995
Taeniolabis lamberti Simmons, 1987
Peradectes minor Clemens, 2006
Thylacodon montanensis Williamson et al., 2012
Prodiacodon crustulum Novacek, 1977
Procerberus formicarum Sloan et Van Valen, 1965
Procerberus plutonis Van Valen, 1978
Crustulus fontanus Clemens, 2017
Leptacodon proserpinae Van Valen, 1978
Purgatorius ceratops Van Valen et Sloan, 1965
Purgatorius janisae Van Valen, 1994
Purgatorius unio Van Valen et Sloan, 1965
Ursolestes perpetior Fox et al., 2015
Pandemonium dis Van Valen, 1994
Protungulatum donnae Sloan et Van Valen, 1965
Protungulatum gorgun Van Valen, 1978
Protungulatum mckeeveri Archibald, 1982
Protungulatum sloani Van Valen, 1978
Oxyprimus erikseni Van Valen, 1978
Chriacus calenancus Van Valen, 1978
*Thangorodrim thalion** Van Valen, 1978
Ragnarok engdahli Archibald, 1982
*Ragnarok harbichti** Van Valen, 1978
Haplaletes andakupensis Van Valen, 1978
Mimatuta morgoth Van Valen, 1978
Tinuviel eurydice Van Valen, 1978
Eoconodon nidhoggi Van Valen, 1978
Eoconodon hutchisoni Clemens, 2011

Table 1—*Continued.*

ii. Torrejonian (Middle Paleocene: 63.3–60.2 Ma) Lebo Member of the Fort Union Formation (Gidley and Silberling Quarries of the Crazy Mtn. Basin, Bear Formation, and Medicine Rocks of southeastern Montana)

Polyodon tuberculata Bryant, 1989
Ammobatrachus montanensis Gilmore, 1928
Plastomenoides lamberti Hutchison, 2009
Ptilodus gidleyi Simpson, 1935
Ectypodus russelli Simpson, 1935
Mesodma pygmaea Sloan, 1987
Ptilodus gracilis Gidley, 1909
Ptilodus sinclairi Simpson, 1935
Ectypodus grangeri Simpson, 1935
Ectypodus aphronorus Sloan, 1987
Ectypodus szalayi Sloan, 1981
Ectypodus silberlingi Simpson, 1935
Ptilodus montanus Douglass, 1908d
Ptilodus douglassi Simpson, 1935
Baiotomeus lamberti Krause, 1987
Eucosmodon sparsus Simpson, 1937
Parectypodus jepseni Simpson, 1935
Stilpnodon simplicidens Simpson, 1935
Leptonysson basiliscus Van Valen, 1967
Prodiacodon concordiarcensis Simpson, 1935
Prodiacodon furor Novacek, 1977
Myrmecoboides montanensis Gidley, 1915
*Emperodon acmeodontoides** Simpson, 1935
Gelastops parcus Simpson, 1935
Avunculus didelphodonti Van Valen, 1966
Jepsenella praepropera Simpson, 1940
Pantolambda intermedius Simpson, 1935
Pantomimus leari Van Valen, 1967
Coriphagus montanus Douglass, 1908d
Aphronorus fraudator Simpson, 1935
*Palaeosinopa diluculi** Simpson, 1935
Didymictis tenuis Simpson, 1935
Ictidopappus mustelinus Simpson, 1935
Didymictis microlestes Simpson, 1935
Leptacodon ladae Simpson, 1935
*Mckennatherium libitum** Van Valen, 1965
Leptacodon munusculum Simpson, 1935
Pronothodectes matthewi Gidley, 1923
Palaechthon alticuspis Gidley, 1923
Palaechthon minor Gidley, 1923
Megopterna minuta Douglass, 1908d
Picrodus silberlingi Douglass, 1908d
Paromomys depressidens Gidley, 1923
Paromomys farrandi Clemens et Wilson, 2009
Paromomys maturus Gidley, 1923
Elpidophorus minor Simpson, 1937
Eudaemonema cuspidata Simpson, 1935
Elphidotarsius florencae Gidley, 1923
*Tricentes latidens** Simpson, 1935
*Spanoxyodon latrunculus** Simpson, 1935
*Metachriacus provocator** Simpson, 1935
Metachriacus punitor Simpson, 1935
*Chriacus pusillus** Simpson, 1935
Chriacus pugnax Simpson, 1935
Prothryptacodon furens Simpson, 1935
Mimotricentes angustidens Simpson, 1937
Deuterogonodon montanus Simpson, 1935
Neoclaenodon latidens Gidley, 1919
Neoclaenodon montanensis Gidley, 1919
Neoclaenodon silberlingi Gidley, 1919
*Claenodon vecordensis** Simpson, 1935

Table 1—*Continued.*

Litomylus dissentaneus Simpson, 1935
Haplaletes disceptatrix Simpson, 1935
Litaletes disjunctus Simpson, 1935
*Ellipsodon aquilonius** Simpson, 1935
*Tetraclaenodon symbolicus** Simpson, 1935

iii. Tiffanian (Late Paleocene: 60.2–56.0 Ma) Tongue River Member of the Fort Union Formation, the Douglass and Scarritt Quarries in the Bear Formation (Crazy Mtn. Basin), and the Melville Formation
Ectypodus hunteri Simpson, 1936
Neoplagiaulax donaldorum Scott et Krause, 2006
Paleotomus senior Van Valen, 1967
Palaeosinopa senior Simpson, 1937
Apator asaphes Simpson, 1936
Deltatherium durini Van Valen, 1978
*Bessoecetor thomsoni** Simpson, 1936
*Palaeosinopa simpsoni** Van Valen, 1967
Litolestes notissimus Simpson, 1936
Plesiadapis anceps Simpson, 1936
Plesiadapis praecursor Gingerich, 1975
Tetonius rex Gidley, 1923
*Elpidophorus patratus** Simpson, 1936
Carpodaptes hazelae Simpson, 1936
Gingerichia geoteretes Zack et al., 2005
*Gidleyina montanensis** Simpson, 1935
*Gidleyina silberlingi** Simpson, 1935
*Tetraclaenodon superior** Simpson, 1935
Lithornis celetius Houde, 1988
Lithornis plebius Houde, 1988

iv. Clarkforkian (Latest Paleocene: 56.0–55.5 Ma) Eagle Mine in the upper Bear Formation
Protentomodon ursirivalis Simpson, 1928
Leipsanolestes siegfriedti Simpson, 1928
Planetetherium mirabile Simpson, 1928
Carpolestes nigridens Simpson, 1928
Thryptacodon pseudarctos Simpson, 1928
*Parapheliscus bjorni** Van Valen, 1967

b. Eocene (55.0–33.7 Ma)
i. Uintan (Middle Eocene: 46.3–39.7 Ma)
Microparamys solis Dawson et Constenius, 2018
Tarkadectes montanensis McKenna, 1990
Desmatotherium kayi Hough, 1955
ii. Duchesnean (Middle Eocene: 39.7–37.0 Ma)
Mytonolagus ashcrafti Fostowicz-Frelik et Tabrum, 2009
Spurimus hoffmani Korth et Tabrum, 2017
Metanoiamys norejkoi Korth et Tabrum, 2017
Macrotarsius montanus Clark, 1941
iii. Chadronian (Late Eocene: 37.0–33.7 Ma)
Helodermoides tuberculatus Douglass, 1903
*Glyptosaurus montanus** Douglass, 1908c
Didelphidectes pumilis Hough, 1961
*Peratherium donohoei** Hough, 1961
Peratherium titanelix Matthew, 1903
Ictops acutidens Douglass, 1902
*Ictops intermedius** Douglass, 1905
Ictops major Douglass, 1905
Ictops montanus Douglass, 1905
*Ictops tenuis** Douglass, 1905
Ictops thomsoni Matthew, 1903
Palaeolagus brachyodon Matthew, 1903
Palaeolagus temnodon Douglass, 1902
Ischyromys douglassi Black, 1968

Table 1—*Continued.*

Ischyromys veterior Matthew, 1903
Sciurus (Prosciurus) vetustus Matthew, 1903
Dakotallomys whitei Korth, 2012
Sciurus jeffersoni Douglass, 1902
Pipestoneomys bisulcatus Donohoe, 1956
*Eumys minor** Douglass, 1902
Aulolithomys bounites Black, 1965
Gymnoptychus minimus Matthew, 1903
Namatomys lloydi Black, 1965
Montanamus bjorki Ostrander, 1983
Yoderimys burkei Black, 1965
Pseudocylindrodon medius Burke, 1938
Pseudocylindrodon neglectus Burke, 1935
Ardynomys occidentalis Burke, 1936
Cylindrodon fontis Douglass, 1902
Dolocylindrodon rahnensis Korth et Tabrum, 2016
Dolocylindrodon vukae Korth et Tabrum, 2016
Xenotherium unicum Douglass, 1905
*Hyaenodon minutus** Douglass, 1902
*Bunaelurus infelix** Matthew, 1903
*Cynodictis paterculus** Matthew, 1903
Parictis (Subparictis) montanus Clark et Guensburg, 1972
Centetodon kuenzii Lillegraven et Tabrum, 1983
Micropternodus borealis Matthew, 1903
Kentrogomphios strophensis White, 1954
Cryptoryctes kayi Reed, 1954
Apternodus baladontus Asher et al., 2002
Apternodus mediaevus Matthew, 1903
Domnina thompsoni Simpson, 1941
Stibarus montanus Matthew, 1903
Agriochoerus maximus Douglass, 1902
Agriochoerus minimus Douglass, 1902
Bathygenys alpha Douglass, 1902
Limnenetes anceps Douglass, 1902
Limnenetes platyceps Douglass, 1902
Montanatylopus matthewi Prothero, 1986
Leptotragulus profectus Matthew, 1903
*Trigenicus socialis** Douglass, 1903
Pipestoneia douglassi Tabrum et Metais, 2007
Mesohippus latidens Douglass, 1903
*Mesohippus montanensis** Osborn, 1904
*Mesohippus portentus** Douglass, 1908b
Triplopides rieli Radinsky, 1967

c. Oligocene (33.7–23.8 Ma)

i. Orellan (Early Oligocene: 33.7–32.0 Ma)

Pseudallomys nexodens Korth, 1992
Brachygaulus leistneri Korth et Tabrum, 2011
Brachygaulus nicholsi Korth et Tabrum, 2011
Brachygaulus xerobothrus Korth et Tabrum, 2011
Eumys cricetodontoides White, 1954
*Eumys latidens** White, 1954
*Eumys spokanensis** White, 1954
Scottimus longiquus Korth, 1981
Paradjidaumo spokanensis White, 1954
*Heliscomys gregoryi** Wood, 1933
Hyaenodon montanus Douglass, 1902
*Oreodon robustum** Douglass, 1902
*Eucrotaphus helenae** Douglass, 1902
*Oreodon macrorhinus** Douglass, 1903
Schizotheroides parvus Hough, 1955
Anchitherium agreste Leidy, 1873
*Hyrachyus priscus** Douglass, 1903
Colodon cingulatus Douglass, 1902

Table 1—*Continued.*

ii. Arikareean (Early Oligocene to Early Miocene: 30.0–18.8 Ma)
- *Testudo copei* Koerner, 1940
- *Megalagus dawsoni* Black, 1961b
- *Niglarodon blacki* Rensberger, 1981
- *Niglarodon koerneri* Black, 1961b
- *Niglarodon loneyi* Rensberger, 1981
- *Niglarodon progressus* Rensberger, 1981
- *Eutypomys montanensis* Wood et Konizeski, 1965
- *Eumys eliensis* Black, 1961b
- *Gregorymys montanensis* Hibbard et Keenmon, 1950
- *Mesocyon drummondanus** Douglass, 1903
- *Cynodesmus thooides* Scott, 1893
- *Stenoechinus tantalus* Rich et Rasmussen, 1973
- *Proscalops intermedius* Barnosky, 1982
- *Kukusepasutanka schultzi* Macdonald, 1956
- *Arretotherium acridens* Douglass, 1902
- *Cyclopidius loganensis** Koerner, 1940
- *Promerycochoerus grandis* Douglass, 1907a
- *Promerycochoerus hatcheri** Douglass, 1907a
- *Promerycochoerus hollandi** Douglass, 1907a
- *Promerycochoerus minor** Douglass, 1903
- *Mesoreodon chelonyx* Scott, 1893
- *Mesoreodon danai** Koerner, 1940
- *Mesoreodon intermedius** Scott, 1893
- *Mesoreodon latidens** Douglass, 1907a
- *Mesoreodon longiceps* Douglass, 1907b
- *Eucrotaphus montanus** Douglass, 1907a
- *Mesoreodon wheeleri** Koerner, 1940
- *Eporeodon meagherensis** Koerner, 1940
- *Ticholeptus bannackensis* Douglass, 1907a
- *Ticholeptus brachymelis** Douglass, 1907b
- *Ticholeptus breviceps* Douglass, 1907a
- *Leptomeryx transmontanus* Douglass, 1903
- *Pronodens silberlingi* Koerner, 1940

d. Miocene (23.8–5.3 Ma)

i. Hemingfordian (Early Miocene: 18.8–16.0 Ma)
- *Sciurus angusticeps* Matthew et Mook, 1933
- *Steneofiber hesperus* Douglass, 1902
- *Paciculus montanus* Black, 1961b
- *Dikkomys woodi* Black, 1961b
- *Mookomys altifluminis* Wood, 1931
- *Brachyerix macrotis* Matthew et Mook, 1933

ii. Barstovian (Middle Miocene: 16.0–12.4 mya)
- *Ogmophis arenarum* Douglass, 1903
- *Ansomys hepburnensis* Hopkins, 2004
- *Trilaccogaulus bettae* Sutton et Korth, 1995
- *Mylagaulus pristinus* Douglass, 1903
- *Mylagaulus proximus** Douglass, 1903
- *Sciurus angusticeps* Matthew et Mook, 1933
- *Palaearctomys macrorhinus** Douglass, 1903
- *Palaearctomys montanus* Douglass, 1903
- *Sciurus arctomyoides* Douglass, 1903
- *Spermophilus (Otospermophilus) jerae* Sutton et Korth, 1995
- *Steneofiber montanus* Scott, 1893
- *Steneofiber complexus** Douglass, 1902
- *Steneofiber hesperus* Douglass, 1902
- *Euroxenomys inconnexus* Sutton et Korth, 1995
- *Paciculus montanus* Black, 1961b
- *Cotimus alicae* Black, 1961a
- *Copemys lindsayi* Sutton et Korth, 1995
- *Dikkomys woodi* Black, 1961b
- *Peridiomys halis* Sutton et Korth, 1995
- *Mookomys thrinax* Sutton et Korth, 1995

Table 1—*Continued.*

Perognathoides madisonensis Dorr, 1956
Perognathus ancenensis Sutton et Korth, 1995
*?Canis anceps** Scott, 1893
Aelurodon brachygnathus Douglass, 1903
Aelurodon montanensis Wang et al., 2004
Dinocyon ossifragus Douglass, 1903
*Mustela minor** Douglass, 1903
Martes kinseyi Gidley, 1927
*Hypsoparia bozemanensis** Dorr, 1954
Parvericius montanus Koerner, 1940
Brachyerix macrotis Matthew et Mook, 1933
Mesoscalops montanensis Barnosky, 1981
Talpa? platybrachys Douglass, 1903
Ancenycteris rasmusseni Sutton et Genoways, 1974
Hesperhys vagrans Douglass, 1903
*Cyclopidius incisivus** Scott, 1893
*Cyclopidius quadratus** Koerner, 1940
*Promerycochoerus grinnelli** Koerner, 1940
*Promerycochoerus thorpei** Koerner, 1940
Merycoides cursor Douglass, 1907a
Merycochoerus compressidens Douglass, 1901
Merychyus smithi Douglass, 1903
*Poatrephes paludicola** Douglass, 1903
Merycochoerus altiramus Douglass, 1901
Merycochoerus elrodi Douglass, 1901
Merycochoerus laticeps Douglass, 1900
Merycochoerus madisonius Douglass, 1901
*Procamelus lacustris** Douglass, 1899
Procamelus elrodi Douglass, 1908e
*Procamelus madisonius** Douglass, 1899
Protolabis montanus Douglass, 1899
Gomphotherium serus Douglass, 1899
*Cosoryx agilis** Douglass, 1899
Blastomeryx antilopinus Scott, 1893
Blastomeryx borealis Cope, 1877
*Cranioceras kinseyi** Frick, 1937
Palaeomeryx americanus Douglass, 1899
*Palaeomeryx madisonius** Douglass, 1899
Achitherium (sic) *minimus* Douglass, 1899
Anchitherium equinum Scott, 1893
Desmatippus crenidens Scott, 1893
Altippus taxus Douglass, 1908b
Merychippus missouriensis Douglass, 1908b
*Aphelops ceratorhinus** Douglass, 1903
*Aphelops montanus** Douglass, 1908a

*Species challenged or no longer considered valid.

Note. Please see Smith and others, volume 1, for Quaternary vertebrate fossils.

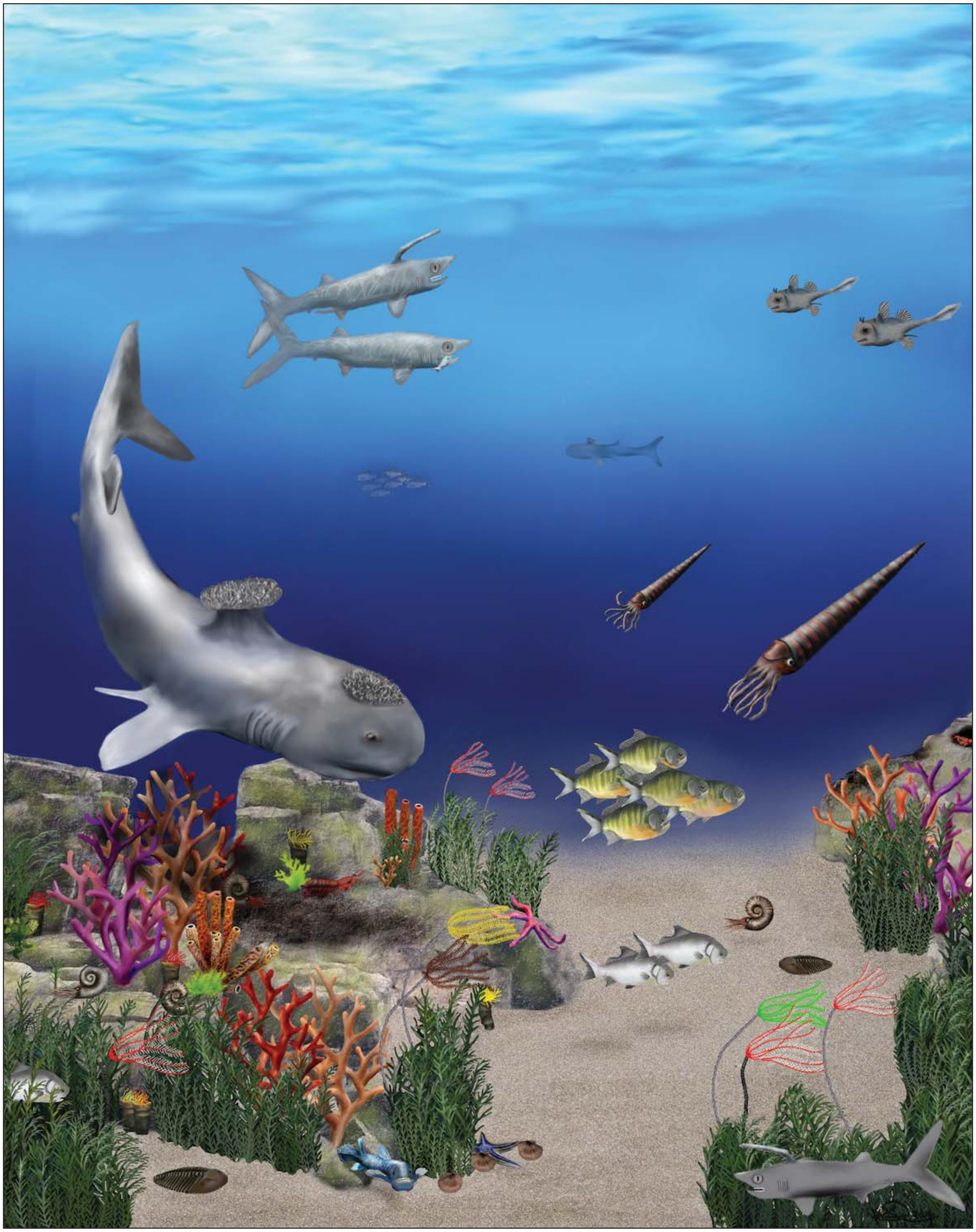

Figure 5. Depiction of the marine environment preserved in the Bear Gulch Limestone. The large shark is *Stethacanthus altonensis*, and a pair of *Falcatus falcatus* swim above it. Art by Kari Scannella, with permission.

Figure 6. Paleogeographic map showing North America as it may have looked during the Late Jurassic. Note the embayment reaches northern Montana and the Williston Basin. From Blakey, https://deeptimemaps.com, with permission (Blakey, 2016).

b. Late Jurassic (Tithonian–Kimmerigian: 156–146 Ma) Morrison Formation

The Morrison Formation of Montana is described as an anastomosed fluvial system deposited on a regressing distal coastal plain (Cooley and Schmitt, 1998). At this time the seaway was regressing to the north and west of southern Montana (fig. 6). Outcrops of the Morrison Formation are sparse in Montana, mostly exposed around the peripheries of mountain ranges, and most often covered by vegetation.

The Morrison Formation in Montana has produced a significant collection of dinosaur remains, but only one holotype, a sauropod named *Suuassea emilieae* Harris et Dodson, 2004. *Suuassea* has most recently been confirmed as a member of the sauropod family Dicraeosauridae (Tschopp and others, 2015). Besides *Suuassea*, other sauropods described from Montana include *Camarasaurus* (Woodruff and Foster, 2017), *Diplodocus* (Woodruff and others, 2018; fig. 7), and *Amphicoelias* (Wilson and Smith, 1996). The stegosaurid *Hesperosaurus mjosi* has also been recently described from Park County (Maidment and others, 2018). Unfortunately, the stratigraphic relationships of the various localities in Montana have not been established, nor have their relationships with other localities in the west (Turner and Peterson, 1999). The non-dinosaurian vertebrate fauna has also not yet been described.

Figure 7. Diplodocid (sauropod) bones from the Morrison Formation of Park County. Museum of the Rockies photo, with permission.

Most of the Morrison vertebrate fossils are found as associated skeletons, often with skulls, in the anastomosing channel deposits, but the Mother's Day Site, located in Carbon County, is a bonebed primarily composed of disarticulated elements in a muddy siltstone. Multiple individuals of diplodocid dinosaurs are represented (Myers and Storrs, 2007), possibly revealing aggregate, behavioral characteristics.

c. Early Cretaceous (Aptian–Albian: 120–110 Ma) Kootenai Formation

Disconformably overlying the Morrison Formation in Montana is the Kootenai Formation in the western parts of the State, and the Cloverly Formation in the central and south-central parts. The Kootenai was deposited in the Cordilleran foreland basin, and consists primarily of sediments deposited in fluvial and fluvio-lacustrine environments (DeCelles, 1986; fig. 8). One vertebrate, *Toxolophosaurus cloudi*, a sphenodontid lizard-like reptile, has been described from the Kootenai Formation in Silver Bow County (Olson, 1960).

d. Early Cretaceous (Aptian–Albian: 120–110 Ma) Cloverly Formation

The Cloverly Formation has been interpreted as a facies of the Kootenai Formation in south-central Montana, and consists primarily of braided stream deposits (Moberly, 1960). The Cloverly Formation, exposed best in Carbon and Wheatland Counties, produces an extensive vertebrate fauna that Oreska and colleagues (2013) describe as including a variety of fishes of both osteichthyes and chondrichthyes, amphibians, squamates, testudines, crocodilians, dinosaurs, and mammals (table 1). The dinosaurs, which dominate the fauna, were described initially by Ostrom (1969, 1970), and include the theropod *Deinonychus antirrhopus*, the coelurosaurian dinosaur that Ostrom (1969) highlighted in his study on the origin of birds (Ostrom, 1976). The Cloverly Formation of Montana has also produced an articulated specimen of the plant-eating dinosaur *Tenontosaurus tilletti* (fig. 9) thought to have been brought down by a group of *Deinonychus* (Maxwell and Ostrom, 1995), and offering the best evidence to date that dromaeosaurs might have been "pack hunters." The Cloverly of Montana is also the unit from which the best-known North American, Lower Cretaceous ceratopsian, *Aquilops*

Figure 8. Paleogeographic map showing North America as it may have looked during the Early Cretaceous. The western prong embayment extending into Montana was lake-like. From Blakey, https://deeptimemaps.com, with permission (Blakey, 2016).

Figure 9. The skull of *Tenontosaurus tilletti* from the Cloverly Formation of Carbon County. Museum of the Rockies photo, with permission.

americanus, is found (Farke and others, 2014), providing the earliest evidence of dinosaur migrations between Asia and North America. Dinosaurian egg remains and neonate bones are not uncommon in the Cloverly (Maxwell and Horner, 1994), and suggest the paleolandscape was conducive for nesting.

Rare, triconodont mammals are also described from the Montana beds (Jenkins and Schaff, 1988; Cifelli and others, 1998; Cifelli, 1999; table 1). *Gobiconodon ostromi* (Jenkins and Schaff, 1988) is represented by nearly complete skeletons, a rarity for this time period, and significantly, *Montanalestes keeblerorum* (Cifelli, 1999) is currently the earliest eutherian mammal known from North America.

e. Middle Cretaceous (Albian–Cenomanian: 103–98 Ma) Thermopolis Shale of the Colorado Group

Porter and others (1993) and Lash (2011) state that the Thermopolis Shale or Formation overlies the Kootenai Formation in south-central Montana, although this is also the area where the Cloverly Formation was recognized and described (see Moberly, 1960; Ostrom, 1970). Regardless, the Thermopolis Formation is represented primarily by marine black shale laid down along the western edge of the Western Interior Seaway (in Montana and Wyoming; fig. 10) that extended from the Gulf of Mexico to the Arctic Ocean. The Thermopolis Formation is overlain by the Mowry Shale (Lash, 2011). Lash describes a fossil zone at the bottom of the upper Thermopolis Member, a unit described by Porter and others (1993) as the Muddy Sandstone. Within the fossil zone Lash reported disarticulated remains of fishes (Osteichthyes and Chondrichthyes), testudines, plesiosaurs, and crocodilians, including an articulated marine crocodile (Lash, 2011). The sole described Holotype from the Montana part of the Thermopolis Formation is a polycotylid plesiosaur named *Edgarosaurus muddi* found in Carbon County (Druckenmiller, 2002).

f. Late Cretaceous (Cenomanian: 95 Ma) Blackleaf Formation

Overlying the Kootenai Formation in central and southwestern Montana is the Blackleaf Formation, which yields few vertebrate remains from its central locations, but a unique dinosaur from localities in the southwestern part of the State (Beaverhead County), very near the Idaho border. *Oryctodromeus cubicularis*, a “hypsilophodontid” dinosaur, was discovered to have nested in underground dens (Varricchio and others, 2007). This is the first dinosaur confirmed to have burrowed. A life restoration of *Orytodromeus* and its young in a burrow is on display in the Hall of Giants at the Museum of the Rockies in Bozeman. Other described taxa from this formation include a couple crocodilians, including *Bernissartia*, the cryptodiran

Figure 10. Paleogeographic map showing North America as it may have looked during the Middle Cretaceous, and the deposi-tion of the marine Colorado Group. From Blakey, https://deeptimemaps.com, with permission (Blakey, 2016).

turtle *Glyptops*, and two neopterygian fishes (Ullmann and others, 2012). These animals apparently lived within an intermontane basin.

g. Late Cretaceous (Campanian: 80–74 Ma) Two Medicine Formation

During the Late Cretaceous, the Western Interior Seaway underwent a series of three regressive–transgressive pulses that are recorded in foredeep, clastic wedge sediments exposed along the eastern front of the cordillera (fig. 11). The first regressive terrestrial sequence, following the recession of the marine Colorado transgressive pulse, deposited sediments of the lower Two Medicine Formation proximal to the cordillera, and the Eagle Sandstone more distally. A second transgressive pulse deposited marine shale of the Claggett Formation, which separates the underlying Eagle Sandstone from the overlying terrestrial Judith River Formation. Proximal to the Judith River Formation is the middle lithofacies of the Two Medicine Formation. Overlying the Judith River Formation and the eastern limit of the Two Medicine Formation is the Bearpaw Formation, which represents the third pulse of the seaway. The final regression of the Bearpaw sea from Montana was followed by the deposition of the terrestrial St. Mary River Formation proximal to the cordillera, and the Hell Creek Formation distally.

The Two Medicine Formation is exposed along the Rocky Mountain Front in Glacier, Pondera, Teton, and Lewis and Clark Counties. It is a 650-m-thick wedge of terrestrial sandstones and mudrocks deposited on the western side of the foredeep. The formation is divisible into three lithofacies with distinct faunal elements (see Lorenz and Gavin, 1984; Horner, 1989).

i. The lower lithofacies (top of the lower lithofacies, see fig. 8), dated from ~79 to 80 Ma (Rogers and others, 1993) and best exposed in Teton and Pondera Counties, yields a group of dinosaur taxa that reveal ancestral relationships with more derived taxa from younger sediments. Lower lithofacies dinosaur taxa include the protoceratopsian *Cerasinops* and the hadrosaurids *Avicristatus* and *Gryposaurus latidens* (table 1; Chinnery and Horner, 2007; Gates and others, 2011; Horner, 1992). There is also an undescribed species of *Daspletosaurus* from this horizon that provided information about the digestive tract of tyrannosaurid dinosaurs (Varricchio, 2001), and a provisionally described ceratopsian (Baker and others, 2011). No other taxa have been described.

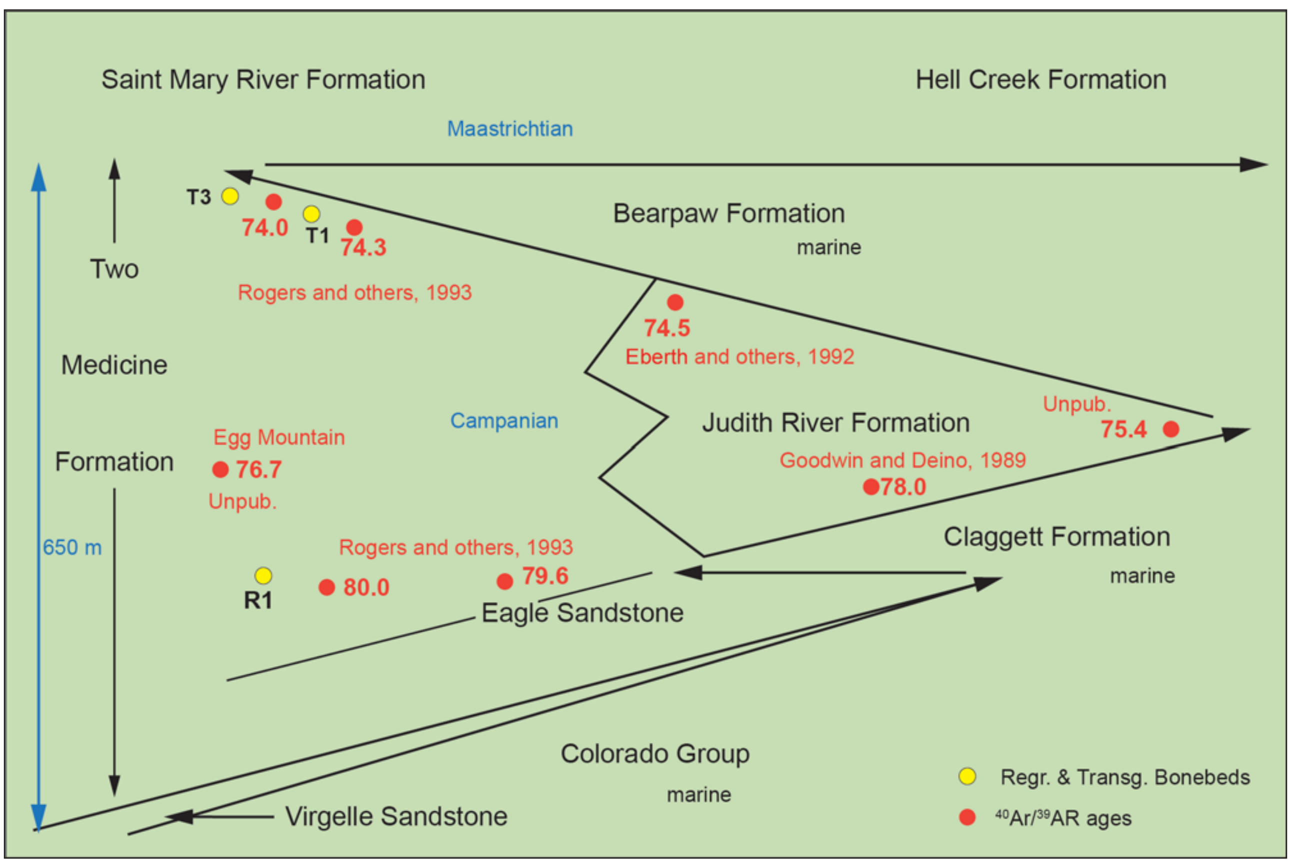

Figure 11. Diagram showing the facies relationships of the Late Cretaceous transgressive-regressive clastic wedge east of the cordillera.

ii. The middle lithofacies dated from ~78–79 Ma and exposed in Teton and Pondera Counties, yields three dinosaur taxa including the “hypsilophodontid” *Orodromeus* (Horner and Weishampel, 1988), the hadrosaurid *Maiasaura* (Horner and Makela, 1979; fig. 12), and the troodontid *Troodon* (see Varricchio and others, 2002). The site that produced the first skeletons of these taxa is the Willow Creek Anticline in Teton County. The 50-m-thick stratigraphic section exposed in the anticline consists of braided and anastomosing stream deposits, mudrocks containing caliche nodules, and lacustrine limestones (Lorenz and Gavin, 1984). The mudrock horizons yield associations of nests referable to *Maiasaura*, providing clues to dinosaur behavior, including parental care and feeding, colonial nesting, site fidelity, nest construction, and social aggregation, among others (Horner and Makela, 1979; Horner, 1982; Schmitt and others, 2014). The lacustrine sediments have produced an azdarchid pterodactyloid (Padian, 1984). *Maiasaura* is arguably the most comprehensively known dinosaur (see Woodward and others, 2015) because of the associations of its skeletons, ranging from embryos to full-grown adults, its eggs, nests, coprolites indicating food choice (Chin, 2007), and footprints. Another dinosaur, *Troodon formosus,* from a lacustrine horizon at the Willow Creek Anticline, is also represented by a plethora of specimens, including eggs, embryos, and skeletons (Varricchio and others, 1999, 2002). The first confirmed dinosaur embryos also came from the Willow Creek Anticline (Horner and Weishampel, 1988), and are attributed to *Troodon* (Varricchio and others, 2002). *Bambiraptor*, a small saurornitholestine theropod, is also found at this stratigraphic level (Burnham and others, 2000). In addition to the dinosaurs, the mammals *Alphadon* and *Cimexomys,* and a new iguanomorph lizard *Magnuviator ovimonsensis,* have also been described from the Willow Creek Anticline sediments (Montellano, 1988; Montellano and others, 2000; DeMar and others, 2017).

iii. The upper lithofacies (76.5 to 74.5 Ma) is best exposed in Glacier County and yields a very diverse vertebrate fauna, some species apparently indistinguishable from taxa found in the Dinosaur Park Formation of Alberta, and other species new and possibly transitional between Campanian and Maastrichtian taxa (e.g., Horner and others, 1992; Arbour and Currie, 2013; Carr and others, 2017). This upper horizon of the Two Medicine Formation was initially collected by Barnum Brown of the American Museum in New York, around the turn of the 20th century, and a bit later by Charles Gilmore of the Smithsonian Institution. Both early collectors made significant collections, but only Gilmore described new taxa (see Gilmore, 1914). Collection efforts by the Museum of the Rockies during the 1980s produced a wide variety of new taxa (table 1), including three new horned dinosaurs (Sampson, 1995; McDonald and Horner, 2010), and some “new” contested species (Horner, 1992; Prieto-Marquez, 2010; Penkalski, 2013). One new taxon, *Hypacrosaurus stebingeri,* is represented by eggs, embryos, and a suite of different growth stages, some

Figure 12.The skulls of an adult and juvenile *Maiasaura peeblesorum* (Montana’s State Fossil) from the middle lithofacies of the Two Medicine Formation. Museum of the Rockies photo, with permission.

of which are found in extensive bonebeds (Horner and Currie, 1994; Varricchio and Horner, 1993). *Hypacrosaurus stebingeri* is arguably the second most comprehensively represented dinosaur taxon.

In summary, the lower facies of the Two Medicine Formation yields isolated taxa that aid in more clearly understanding the phylogenetic relationships of later Campanian dinosaurs, whereas the middle facies yields nesting grounds and bonebed associations that provide clues to dinosaur behaviors. The upper facies yields both isolated taxa, revealing relationships of some later taxa, and additionally yielding nesting horizons and bonebeds.

h. Late Cretaceous (Campanian: 78 Ma) Claggett Shale

The Claggett Shale represents a trangressive pulse of the marine, Cretaceous intercontinental seaway. The Claggett yields isolated dinosaur remains (Fiorillo, 1990) and has produced a single described bird, *Hesperornis montana* (Shufeldt, 1915).

i. Late Cretaceous (Campanian: 79–74.9 Ma) Judith River Formation

The Judith River Formation is equivalent to the middle lithofacies of the Two Medicine Formation (see fig. 11), and represents the distal part of the regressive–transgressive clastic wedge (Rogers and others, 1993).

The Judith River Formation, exposed at the mouth of the Judith River in Fergus County, produced the first dinosaur fossils described from North America (Leidy, 1856). The specimens had been collected by F.V. Hayden during a geological expedition the preceding year. The collection consisted of isolated teeth, which formed the basis for creating several new dinosaur taxa that are mostly considered *nomen dubium*, although the taxon *Troodon formosus* is still in use.

Following Hayden's expedition, E.D. Cope, working for the Philadelphia Academy of Science, explored the Judith River Formation exposures along the Missouri River in 1876. The story of Cope's expedition is iterated in a book by Charles H. Sternberg (1909), one of Cope's field assistants. Sternberg noted that they had met in Helena in August and proceeded to Fort Benton and the Judith River even though the newspapers had that very month told of the massacre at the Little Bighorn. Cope and his field party were not deterred. Cope, Sternberg, and a fellow named Mr. Issac collected dinosaur remains for the remainder of August, the month of September, and into mid-October. Cope departed on the Josephine, the last steamboat of the year, with hundreds of pounds of fossils. The other two men made their journey home by stage and rail.

More than 10 years passed before John Bell Hatcher, collecting for Othniel Marsh and the Yale Peabody Museum in New Haven, Connecticut, came to Montana to explore the Judith River Formation for vertebrate remains. Hatcher found what Marsh would describe and name *Ceratops montanaus* (Marsh, 1888), based on a single orbital horn that is now considered a *nomen dubium.* The specimen was found in what would become Blaine County.

Asok Sahni, collecting for the American Museum in New York during the early 1970s, described a few new mammalian taxa as well as various vertebrate taxa represented by teeth and small bones recovered from microsite screenings (Sahni, 1972). A more recent summary of the mammalian fauna was published by Montellano (1992).

The first relatively complete dinosaur skeleton from the Judith River Formation was not described until 1986, with the naming of *Avaceratops lammersi* from Wheatland County (Dodson, 1986). Following another hiatus of more than 20 years, a number of new taxa were added from Hill and Fergus Counties. Most dinosaur specimens from the Judith River Formation occur as isolated individuals that have been described recently (e.g., Ryan and others, 2010, 2014; Longrich, 2013; Mallon and others, 2016; Freedman Fowler and Horner, 2015; Arbour and Evans, 2017). Dinosaur nests and embryos have also been described from Hill County (Horner, 1999).

Bonebeds, exquisitely preserved articulated skeletons of *Brachylophosaurus canadensis* (see Prieto-Marquez, 2005) with associated skin impressions and biomolecular preservation, have been described from the distal, eastern parts of the Judithian clastic wedge in Phillips County (see LaRock, 2001; Murphy and others, 2006; Schweitzer and others, 2009). This distal part of the Judith River Formation is called the Parkman Sandstone, which is the shore facies of the regressive Claggett Sea.

j. Late Cretaceous (Campanian–Maastrichtian: 70.5 Ma) Bearpaw Formation

The Bearpaw Formation, the last transgressive pulse of the Cretaceous Western Interior Seaway in Montana (fig. 13), yields a wide variety of vertebrates,

Figure 13. Paleogeographic map showing North America as it may have looked during the Late Cretaceous, and the deposi-tion of the marine Bearpaw Shale. From Blakey, https://deeptimemaps.com, with permission (Blakey, 2016).

but only one described mosasaur, *Plioplatecarpus peckensis* Cuthbertson et Holmes, 2015, and three dinosaurs of questionable identity, which include two hadrosaurids and a nodosaurid (Horner, 1979). It is likely that this unit will produce more skeletal remains with extraordinary preservation, such as skin and soft-tissue impressions, due to preservation of the specimens in concreted limestone nodules.

k. Late Cretaceous (Maastrichtian: 72–66 Ma) St. Mary River Formation

The St. Mary River Formation is exposed most extensively in southwestern Alberta, but a narrow wedge is exposed along the Rocky Mountain Front in Glacier and Lewis and Clark Counties. It is composed of braided stream deposits and mudrocks with caliche limestone lenses. The unit has yielded one described protoceratopsian dinosaur (*Montanoceratops cerorhynchos*), originally described as *Leptoceratops cerorhynchos* by Barnum Brown and Erich Schlaikjer in 1942, and later reassigned to *Montanoceratops cerorhynchos* by Charles Sternberg in 1951. The St. Mary River Formation has also yielded a few mammal taxa (see Hunter and others, 2010).

l. Late Cretaceous (Maastrichtian: 66.8–66 Ma) Hell Creek Formation

The Hell Creek Formation is arguably the most comprehensively collected and studied fossil-bearing unit in Montana. Ever since Barnum Brown collected the first *Tyrannosaurus rex* skeleton at the turn of the 20th century, paleontologists have been scouring the formation for fossil remains for museums and later testing hypotheses concerning the extinction of dinosaurs. The majority of specimens from this rock unit are curated in the American Museum of Natural History in New York; the Museum of Paleontology at the University of California, Berkeley; the Museum of the Rockies at Montana State University; The University of Washington Burke Museum; and the Burpee Museum in Rockford, Illinois (table 1). Interestingly, nearly all the vertebrate specimens were found as isolated individuals or in microsites. Bonebeds are rare in Montana, but more common in facies farther east in the Dakotas. Based on the most recent dinosaur census data from the formation, *Triceratops* is the most common (fig. 14), followed by *Edmontosaurus* and *Tyrannosaurus*, and then by other ornithischian taxa before additional saurischians (Horner and others, 2011).

Probably the most famous of all taxonomic interactions of any taxa in the fossil record is that between *Tyrannosaurus* and *Triceratops*, which have a long history of illustrations depicting head-to head aggressive conflicts. Here we avoid the argument of how *T. rex* might have acquired its meal, showing them simply together in their riverine environment (fig. 15).

Because the dinosaur taxa terminate at the K-Pg boundary, it is the mammalian taxa that provide the best perspectives of the transition between the Mesozoic and Cenozoic. Two hypotheses have prevailed for nearly 40 years: the catastrophic, asteroid hypotheses (Alvarez and others, 1980), and a more gradual extinction (see Archibald, 1982; Wilson and others, 2014). The problem is yet to be resolved.

Figure 14. The skull of a full-grown *Triceratops horridus* from the lower Hell Creek Formation. The skull is 3 m long. Museum of the Rockies photo, with permission.

Figure 15. Depiction of a feathered *Tyrannosaurus rex* and a vividly colored *Triceratops prorsus* on the edge of a river during deposition of the Hell Creek Formation. Art by Kari Scannella, with permission.

(4) CENOZOIC VERTEBRATES

Cenozoic sediments in Montana can be divided into two large-scale sediment regimes, the central and eastern Montana Paleocene–early Eocene regressive sediments, and the western Montana, late Eocene–Pliocene intermontane basin sediments.

a. Paleocene (66–55 Ma)

The early Paleocene sediments of the Fort Union Formation in eastern Montana were deposited contemporaneously with a change in base level apparently coinciding with the advancing Cannonball Sea to the east. This resulted in swamp or fen-like environments in the southeastern part of the State (see Brown, 1993). These swamp environments are now the massive coal deposits in Big Horn, Richland, and Rosebud Counties. In Garfield and McCone Counties, the coal lenses are much thinner and are replaced by braided stream and anastomosed river deposits. Important primitive mammal fossils from the early Paleocene sediments above the K-Pg boundary are the focus of many studies focused on faunal replacement and post extinction ecology. Farther to the west, middle and late Paleocene deposits in Sweetgrass County have yielded a bounty of mammalian specimens providing important insights concerning the early evolution of mammals. "Three of the best known Paleocene mammalian localities in North America—Silberling Quarry, Gidley Quarry, and Scarritt Quarry—lie on the eastern flank of the Crazy Mountains in south-central Montana" (Gingerich and others, 1983). These localities, together with those in eastern Montana and another locality near Bear Creek in Carbon County, have long been the focus of research exploring the evolution and relationships of our modern groups of mammalian taxa (e.g., Simpson references; Krause and Gingerich, 1983; O'Leary and others, 2013; see table 1). Paleognathus birds have also been reported from Crazy Mountain Basin Paleocene sediments in the Bangtail Hills near Bozeman (see Houde, 1988).

b. Eocene (55.0–33.7 Ma)

Only a few early Eocene fossils have been found in Montana, in the Wasatch Formation outcrops of southeastern Montana, from the early Wasatchian

North American Land Mammal Age (NALMA) at about 54 Ma, but none have been described. More records exist for middle Eocene fossils, albeit still relatively uncommon, from the southwestern part of the State in the Sage Creek basin southeast of Dillon, in Beaverhead County (Hough, 1955; Fostowicz-Frelik and Tabrum, 2009; Korth and Tabrum, 2017). Although this area contains probably the most temporally extensive suite of Cenozoic fossils known from any area of Montana (Tabrum, 2001), it is important principally because it provides the only Montana localities containing mid-Eocene fossils, primarily from the Bridgerian and Uintan North American Land Mammal Ages (NALMAs) at about 52 to 40 million years ago (mya), with a few records of Duchesnean and early Chadronian NALMA localities spanning 40 to 35 mya. The first of these mid-Eocene fossils was collected by Earl Douglass in 1897, which he reported on a few years later (Douglass, 1903). His report spurred collecting expeditions to the area through subsequent years, including A.E. Wood of Columbia University and Amherst College, J.L. Kay and Alan Tabrum of the Carnegie Museum, and Jean Hough of the U.S. Geological Survey.

The intermontane basins of southwestern Montana are especially well known for the late Eocene (middle to late Chadronian NALMA) and earliest Oligocene (Orellan NALMA) fossils found there, spanning a time frame from about 34 to 33 Ma. Localities such as Pipestone Springs, Little Pipestone, Thompson Creek, and Easter Lily in Jefferson County are frequently cited in publications (e.g., Douglass, 1901, 1905; Matthew, 1903; Black, 1965; Kuenzi and Fields, 1971; Nichols, 2001; Korth and Tabrum, 2016) discussing this time interval, and have produced an extensive variety of holotypes (table 1). Significant from the paleontological standpoint, these localities, as well as many others of similar age in Montana, have produced abundant small mammals such as rodents, lagomorphs, and artiodactyls, and small and medium sized perissodactyls. This is in contrast to many localities elsewhere that are dominated by large mammal remains.

c. Oligocene (33.7–23.8 Ma)

Very few fossil localities are known in Montana between the early Oligocene Orellan NALMA at about 33 Ma and the late Oligocene Arikareean NALMA at about 30 Ma, presenting difficulties for biostratigraphic correlations here and elsewhere in the United States. The late Oligocene (early to middle Arikareean NALMA) is, however, well represented in Montana primarily by three nearly contemporaneous areas: the Cabbage Patch deposits near Drummond, Granite County; the outcrops adjacent to Canyon Ferry Reservoir, Broadwater, and Lewis and Clark Counties; and regions near White Sulphur Springs, Meagher County. Additional Oligocene deposits are found in the high buttes in Carter County in southeastern Montana, but these are limited in exposure. The Cabbage Patch deposits consist of numerous small outcrops, often isolated from one another and challenging to correlate at the local level. These deposits have produced fossil leaves and other plant material, freshwater molluscs, fish, amphibian, turtle, bird, and mammal fossils (Calede and Rasmussen, 2015). Showing a long collecting history, the first record of these deposits was published in 1903 by Earl Douglass on three mammal specimens, and Jonathan Calede recently completed his Ph.D. dissertation on the paleontology of these deposits, in which he noted that as many as 30 new species remain to be described from the Cabbage Patch beds (Calede, 2016). The Canyon Ferry outcrops have also produced a variety of fossils of similar diversity, including insects, bird feathers, leaves, petrified wood, and mammals (CoBabe and others, 2012; White, 1954; Douglass, 1907a; Hanson, 2015), although these are found in disparate localities. One research quarry has produced a number of mostly intact Arikareean mammal skulls, including 13 examples of one species of a large oreodont *Megoreodon grandis* (a pig/sheep-like animal; fig. 16), a beaver, a sabertooth, several rodent taxa, and other significant finds. Another nearby locality contains numerous trackways of a large bird, probably a heron-like wader, and several specimens of two species of small marsupials, rare in other Montana deposits. Earl Douglass' primary Canyon Ferry Lake area locality has produced several additional examples of the same large oreodont, as well as other mammals of the same age. Hanson (2015) and Hanson and Scannella (2016) prepared brief reports on the Canyon Ferry faunas and geology. The fossiliferous outcrops near White Sulphur Springs have, at present, not been studied in a comprehensive manner, but many important specimens have been reported historically, beginning in 1893 by William Berryman Scott (Scott, 1893). For many years, the long time span that the White Sulphur Springs outcrops represent was not fully recognized, leading to some reports lumping together fossils spanning a time period of about 16 million years. The main

Figure 16. The skull of *Megoreodon grandis* (dorsal view) from the Canyon Ferry mammal Quarry, early Arikareean (Oligocene). Museum of the Rockies photo, with permission.

collecting level, historically termed the Deep River beds in the literature, has produced the majority of the published specimens, but this level is actually middle Miocene in age. The lower, more restricted level is often termed the Fort Logan beds. These lower beds appear to be nearly contemporaneous with the Cabbage Patch and Canyon Ferry localities (Scott, 1893; Koerner, 1940; Black 1961b).

d. Miocene (23.8–5.3 Ma)

A significant hiatus exists between these late Oligocene localities and the middle Miocene in Montana and elsewhere, which lasted in Montana from about 17.3 to 16.7 Ma (Barnosky and others, 2007), before deposition resumed on a broad basis during the latest Hemingfordian into the early Barstovian NALMA. Barstovian-aged sediments are scattered throughout southwestern Montana, often located in more rolling terrain. Very few natural exposures of these sediments occur, so some significant localities are found in highway road cuts, such as the Anceney locality (Dorr, 1956; Sutton and Korth, 1995) that produced the skull of the bear dog tentatively identified as *Protepicyon raki* (fig. 17; and Wang and others, 1999) and a bat *Ancenycteris rasmusseni* (Sutton and Genoways, 1974), and a roadcut on Interstate 90 that produced the Holotype and only known specimen of a robust canid *Aelurodon montanensis* (Wang and others, 2004). The few exceptions include extensive natural exposures of Barstovian-aged sediments in large outcrops of the Hepburn's Mesa Formation in the southern part of the Paradise Valley in Park County, where several researchers have studied the fossils and sediments (Burbank and Barnosky, 1990; Barnosky and LaBar, 1989), and the high bluffs to the east of the Madison River in Gallatin County, where Earl Douglass collected many fossils in his early years of collecting.

The Flint Creek beds are another area of Barstovian sediments in Granite County (Douglass, 1903; Black, 1961a; Barnosky and others, 2007), and as noted above, the Deep River beds near White Sulphur Springs have produced many important fossils from this time range. The Deep River beds produced some of the early major collections from the middle Miocene, and helped to shape the early understanding of this period (see Scott, 1893; Koerner, 1940; Black, 1961b; Barnosky, 1981, 1982; Rensberger, 1981). Today, the Miocene is best known from Nebraska and California, but the Montana formations, in some cases, contain taxa that are unknown from other locations, indicating a unique environment was probably present in this area during this time.

Since the late Barstovian, after about 13 Ma, deposition of fossiliferous sediments throughout Montana has been sporadic, influenced mainly by modern river course development and glaciation. Late Barstovian-, Clarendonian-, and Hemphillian-aged deposits (13 to 5 Ma) are known or suggested, but these are relatively isolated and contain sparse fossils, and are difficult to age precisely. Many of the recovered fossils have relatively long time ranges, adding to the challenge.

Figure 17. The skull of Protepicyon raki from the Anceney locality, Barstovian (Miocene). Museum of the Rockies photo, with permission.

e. Pliocene–Pleistocene (5.3–0.02 Ma)

Notable deposits near Deer Lodge (Powell County) and Logan (Gallatin County) have produced Pliocene or early Pleistocene animals, including *Gomphotherium*, an early elephantid typically found in deposits of Hemphillian age or younger. Typical Pleistocene faunas have been found in many river sediments, including commercial gravel operations, throughout Montana. Doeden's gravel operations near Miles City (Custer County) have produced a large fauna of early to mid-Pleistocene remains (Wilson, 2003), and isolated finds of fairly complete mammoths have been found in a few places. Some cave deposits have also produced Pleistocene remains. See Smith and others (2020) for more complete information about Quaternary vertebrate fossils.

An important consideration for the Montana Cenozoic deposits is their geographic and topographic relationships with other similarly aged deposits in North America. Fossiliferous late Eocene deposits occur in South Dakota, Nebraska, California, Wyoming, Utah, and the Gulf Coast. Oligocene deposits occur in South Dakota, Nebraska, Oregon, and New Mexico. Miocene fossils are best known from Nebraska, South Dakota, California, and Oregon. Although deposits of these similar ages occur in other areas in North America, often with more extensive vertical and lateral exposures, many of these areas represent paleoenvironments of low relief and corresponding extensive, monotonous landscapes of interior areas. The paleotopography of Oregon and California deposits are more similar to Montana's, but these areas are much closer to the Pacific Ocean, and were probably even closer in those earlier periods. The Montana fossil record, therefore, represents a sampling of a unique region of mountain ranges and valleys with probably a more varied seasonal climate, throughout the Cenozoic.

The scientific literature discussing vertebrate fossil specimens from Montana began with the early descriptions of fragmentary dinosaur remains and isolated teeth by Joseph Leidy and Edwin Drinker Cope, all collected along the Missouri River in what is now Fergus County. William Berryman Scott reported on some fossil mammals from Deep Creek, near Fort Logan in Meager County in 1893. But the true beginnings of paleontological publishing really began with Earl Douglass in 1902. Douglass moved to Montana to teach school in a one-room schoolhouse on the Madison River in 1894. During his free time, he wandered the hillsides near the school. On these walks, he began finding fossil mammals, and a lifelong ambition was born. He reported his finds and was encouraged to continue his searches. Although lacking a geologic or paleontologic background, he read numerous books and became self-educated on a par with his peers. He enrolled at the University of Montana, and in 1900 received what is reportedly the first ever Masters degree awarded by the University. During that period of time he discovered and collected the first dinosaur skeletons found in Montana. They were collected from the Bearpaw Shale in Wheatland and northern Stillwater Counties (see Horner, 1979). Marcus Farr, a paleontologist at Princeton University, hired Douglass to collect for him in 1900 and 1901, but in 1902, Douglass began to collect for the Carnegie Museum full-time in southwest Montana, as well as in North Dakota, Minnesota, Idaho, and eventually Utah. His most famous find occurred in northeastern Utah in 1908, where he discovered the Carnegie Quarry in the Jurassic Morrison Formation, which became what we now know as Dinosaur National Monument. He continued to explore in Montana for a few more years, before moving to Utah permanently. During his research on Montana paleontology, he published 12 papers describing mammal discoveries in the 10 years between 1899 and 1909. In those publications, as sole author, he erected 71 new taxa of mammals and three lizards from Montana, of which 46 mammals and 2 lizards are still valid species today.

Montana continues to offer great potential for significant new discoveries and research on fossil vertebrates and their paleoecological context. The Sappington Formation (Late Devonian–Early Mississippian) and formations of the Big Snowy Group, particularly facies of the Heath and Tyler Formations (Late Mississippian–early Pennsylvanian), offer exciting future prospects within the Paleozoic record. The Triassic Chugwater Formation in Carbon County, although not well exposed, has yet to produce any vertebrate fossils. The Late Jurassic Morrison Formation has produced a lot of fossil material that simply needs to be described. In the Cretaceous each of the marine units, and in particular the Thermopolis Formation in Carbon County, the Telegraph Creek Formation in Toole County, and the Bearpaw Shale in Phillips, Valley, and Wheatland Counties, deserves much more attention, as do the terrestrial units such as the Livingston Group in Park, Gallatin, and Madison Counties. The 1,500-m-thick Livingston Group, composed of several formations spanning the Late Cretaceous and early Paleocene, contains dinosaur remains, including skeletons, and yet the only described vertebrate specimen is a single fish (Schaeffer, 1949). Middle Eocene and middle Oligocene deposits in southwestern and southeastern Montana hold promise to produce significant finds, as previous studies have suggested. Montana is ideally suited to contribute important research on the effects of mountain valley paleoenvironments on mammal development and adaptation. There are so many more fossil vertebrate discoveries to be made in Montana.

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