

Contributions

from the Museum of Paleontology, University of Michigan

VOL. 35, NO. 1, PP. 1-33

SEPTEMBER 11, 2023

PHYLOGENY AND EVOLUTION OF NORTH AMERICAN NOTHARCTINAE (MAMMALIA, PRIMATES) IN THE EARLY EOCENE OF WYOMING

BY

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Abstract — The Bighorn Basin and adjacent Clarks Fork Basin of northwestern Wyoming both have an exceptionally dense and continuous fossil record documenting notharctine primate evolution through early Eocene time. The Bridger Basin of southwestern Wyoming has a similarly rich fossil record extending notharctine evolution into the early middle Eocene. Both areas have been productive for more than a century. Thousands of new specimens have been collected in the past fifty years, which reinforce a pattern of gradual change from one species to another. New specimens have also added to known diversity. In basins where the fossil record is dense and continuous, it is possible to characterize population variation and trace this through time. The Bighorn Basin has a single lineage of *Cantius* in the early Wasatchian land-mammal age. The genus made its first appearance in the Paleocene-Eocene Thermal Maximum (PETM). One and sometimes two notharctine lineages are present in the middle Wasatchian (*Cantius* and *Copelemur*), and a minimum of three notharctine lineages of different sizes are present in the late Wasatchian (*Cantius*, *Copelemur*, and, briefly, *Pelycodus*). The Bridger Basin has two and sometimes three notharctine lineages of different sizes (*Smilodectes*, *Notharctus*) in the Bridgerian land-mammal age. The range of body sizes expanded through time with the addition of new lineages of larger species. Overall, the rise and fall of notharctine diversity paralleled warming and cooling during the Early Eocene Climatic Optimum (EECO).

INTRODUCTION

Notharctinae are relatively large-bodied primates that weighed some 1–8 kg in life and ranged through the early and middle Eocene of North America (Rose, 2006; Fleagle, 2013). They had monkey-like spatulate incisors and projecting canines, and molar teeth indicating a plant-based frugivorous to folivorous diet. Notharctines retained a primitive dental formula of 2.1.4.3 / 2.1.4.3, and a lemur-like, ring-shaped, ectotympanic bone in the middle ear. The five genera reviewed here are known from the Western Interior of North America: *Cantius*,

Copelemur, *Pelycodus*, *Notharctus*, and *Smilodectes*. A sixth notharctine, *Hesperolemur*, is known from the middle Eocene of southern California.

The subfamily Notharctinae was named by Trouessart (1879), based on the genus and species *Notharctus tenebrosus* Leidy, 1870 (see below). In the same publication, Trouessart named the family Adapidae (on page 225) and the family Notharctidae (on page 230). Adapidae has priority as a family-group name, and Adapinae and Notharctinae are generally included in Adapidae. Alternatively, Adapidae and Notharctidae are included as families in a superfamily Adapoidea.

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Notharctinae are important in representing one of the two groups of true primates (Adapoidea and Tarsioidea) that made their first appearance in the fossil record during the Paleocene-Eocene Thermal Maximum (PETM), the intense global greenhouse-warming event that marks the beginning of the Eocene epoch of geological time. Notharctinae are also important because many of the constituent species are represented by large samples that enable quantitative study of population variation and evolutionary change through geological time.

William D. Matthew (1915) studied the Eocene primates collected by the American Museum of Natural History's early 20th-century expeditions to northwestern Wyoming. In his report, Matthew named *Pelycodus ralstoni* as a new species from Sand Coulee or 'basal Wasatch' strata of the Clarks Fork Basin, a northward extension of the Bighorn Basin. He named *Pelycodus trigonodus* as a new species from what he called lower Graybull or lower middle Wasatchian strata of the central Bighorn Basin. Matthew also recorded *Pelycodus jarrovii* (Cope, 1874) and *Pelycodus frugivorus* Cope, 1875, from upper Graybull and Lysite or upper middle and upper Wasatchian strata of the Bighorn Basin. A century ago Matthew wrote — anticipating subsequent studies:

The species of [Notharctinae] from successive horizons of lower and middle Eocene, from the Sand Coulee to the upper Bridger illustrate very clearly the progressive change in the upper molars from tritubercular to fully quadritubercular type, the development of the mesostyle, the complication of the fourth premolar, and increase in size... It is not the gradual replacement of one species by another distinct and more progressive species, but so far as one may judge from the characters of the teeth the *gradual conversion of one species into its successor by the progressive elimination of the more primitive and increase in numbers of the more advanced individuals*. The detailed geologic record of these phyla appears therefore to afford direct proof of continuity in their evolution. (Matthew, 1915: 434-435; italics added)

Sixty years later, I attempted to update our understanding of notharctine evolution through the Wasatchian Land-Mammal Age in lower Eocene strata of the Bighorn and Wind River basins of northwestern Wyoming (Gingerich, 1976: fig. 7). The study was based principally on specimens in the collection of the Peabody Museum of Natural History at Yale University, with additions from the American Museum of Natural History and the Department of Geology at Princeton University. The temporal framework for the study was a Willwood Formation stratigraphic section that Leonard Radinsky and Grant Meyer measured in the central Bighorn Basin (Gingerich, 1976: fig. 2). Latest Wasatchian notharctines from the adjacent Wind River Basin were added, based on the Lostcabinian (Wa-7) study of Daniel Guthrie (1971). This initial interpretation of notharctine evolution was compromised chronologically by a Bighorn Basin stratigraphy that was less well known and less stable than it is today. For example, the Clarkforkian Land-Mammal Age was

erroneously included in the Eocene epoch of geological time, and samples of the early notharctine *Pelycodus ralstoni* were incorrectly considered to be Clarkforkian in age.

A more thorough systematic analysis of the Yale collection from the central Bighorn Basin followed in 1977, co-authored with Elwyn Simons, and again tied to the Radinsky-Meyer stratigraphic section in the central Bighorn Basin (Gingerich and Simons, 1977). The 1977 study included new specimens from the Clarks Fork Basin collected in 1975 and 1976 by University of Michigan field parties. In the 1977 study, the early notharctine *Pelycodus ralstoni* was acknowledged to come from Sandcouleean strata of early Wasatchian age and not from Clarkforkian strata. The new species *Pelycodus mckennai* was named as an intermediate form connecting stratigraphically-lower *P. ralstoni* to stratigraphically-higher *P. trigonodus*. The new species *Pelycodus abditus* was named as an intermediate connecting stratigraphically-lower *P. trigonodus* and stratigraphically-higher *P. jarrovii*. In addition, two short-lived lineages of the new genus *Copelemur* were recognized: one lineage with questionably-identified *Copelemur praetutus* (Gazin, 1962) appeared in middle Wasatchian strata of the Bighorn Basin, and the other lineage with the new species *Copelemur feretutus* and *Co. consortutus* ranged through upper Wasatchian strata of the Bighorn Basin.

In a follow-up study, I analyzed Bridgerian Land-Mammal Age specimens of *Smilodectes* and *Notharctus* described by Gregory (1920), Robinson (1957), and others (Gingerich, 1979). Then, in a second follow-up study with Richard Haskin, we clarified morphological differences distinguishing the genera *Pelycodus* Cope (1875) and *Cantius* Simons (1962), and moved most Bighorn Basin species identified as *Pelycodus* to *Cantius* (Gingerich and Haskin, 1981). Kenneth Rose and Thomas Bown recognized and described two Bighorn Basin specimens that actually are *Pelycodus* (Rose and Bown, 1984). William Clyde and I analyzed rates of evolution in *Cantius* from the Clarks Fork Basin (Clyde and Gingerich, 1994). Later, Gregg Gunnell (2002) described two new species, *Cantius simonsi* and *Smilodectes sororis*, from the Bighorn Basin and Green River Basin, respectively.

Two Johns Hopkins University doctoral dissertations contributed greatly to our understanding of Bighorn Basin notharctines. Both were based on large new U. S. Geological Survey and U. S. National Museum collections from the central part of the basin. In the first dissertation, Maureen O'Leary (1996) traced a single lineage of *Pelycodus* [now *Cantius*] through Willwood Formation strata of early and middle Wasatchian age, quantifying size and shape characteristics of the premolars and molars. The initial *Pelycodus* [now *Cantius*] lineage became three distinct lineages of *Copelemur* and *Cantius* in the late Wasatchian. O'Leary recently published a summary of her dissertation results (O'Leary, 2021), with a link to a large table including natural-log values for the crown area ($L \times W$) of M_1 — for 1,046 specimens from the central Bighorn Basin. In the second dissertation, Amy Chew (2005) made a comprehensive study of mammalian faunas in the central Bighorn Basin, which involved measuring 1,101 specimens identified as *Cantius* or *Copelemur* that preserve M_1 . Chew generously provided

her unpublished notharctine identifications and measurements for use here. When merged, the O'Leary and Chew data sets provide $\ln(L \times W)$ of M_1 values for a total of 1,598 specimens. Of these, 569 specimens were measured independently by each author (measurements that were averaged here for each specimen).

The purpose of this review is to bring our understanding of the phylogeny and evolution of notharctine primates in Wyoming up to date. Many unpublished tooth size measurements for samples of known geological age are included as documentation.

INSTITUTIONAL ABBREVIATIONS

ACM	—	Pratt Museum of Geology, Amherst College, Amherst, Massachusetts, U.S.A.
AMNH	—	American Museum of Natural History, New York, New York, U.S.A.
CM	—	Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, U.S.A.
FMNH	—	Field Museum of Natural History, Chicago, Illinois, U.S.A.
NMMNH	—	New Mexico Museum of Natural History, Albuquerque, New Mexico, U.S.A.
SDSNH	—	San Diego Society of Natural History, San Diego, California, U.S.A.
TMM	—	Texas Memorial Museum, University of Texas, Austin, Texas, U.S.A.
UALP	—	University of Arizona Laboratory of Paleontology, Tucson, Arizona, U.S.A.
UCM	—	University of Colorado Museum, Boulder, Colorado, U.S.A.
UM	—	University of Michigan Museum of Paleontology, Ann Arbor, Michigan, U.S.A.
USGS	—	U. S. Geological Survey, Denver, Colorado, U.S.A.
USNM	—	U. S. National Museum of Natural History, Washington, D.C., U.S.A.
UW	—	University of Wyoming Geological Museum, Laramie, Wyoming, U.S.A.
YPM	—	Peabody Museum of Natural History, Yale University, New Haven, Connecticut, U.S.A.

LOCALITY ABBREVIATIONS

SC	—	University of Michigan Sand Coulee localities in the Clarks Fork and northern Bighorn basins, Wyoming, U.S.A.
MP	—	University of Michigan McCullough Peaks localities in the northern Bighorn Basin, Wyoming, U.S.A.
USGS	—	United States Geological Survey localities in the central Bighorn Basin, Wyoming, U.S.A.

YM or YPM — Yale-Michigan or Yale Peabody Museum localities in the central Bighorn Basin, Wyoming, U.S.A.

STRATIGRAPHIC SECTIONS IN THE CENTRAL BIGHORN BASIN

Four stratigraphic sections showing fossil localities have been measured in the central Bighorn Basin. The first section was measured by Leonard Radinsky and Grant Meyer of Yale University, and the second was measured by John Niesham and Carl Vondra of Iowa State University. The two were integrated and published in Gingerich (1976). The third section, by David Schankler and Scott Wing of Yale University, hereafter the Schankler section, was published in Schankler (1980). The fourth section, by Thomas Bown of the U. S. Geological Survey and Mary Kraus of the University of Colorado, hereafter the Bown section, was first described by Bown and Kraus (1993) and then fully published in Bown et al. (1994: tables 2 and 3).

The ranges of agreement and disagreement between the Schankler and Bown stratigraphic sections are shown graphically in Figure 1, which illustrates the meter levels for Yale and Yale-Michigan localities recorded by each author. Chew (2005) developed a similar graph, and the meter levels for localities plotted in Figure 1 are taken from Chew's appendix 3 (omitting levels for Yale locality Y-126, which is actually two localities at substantially different stratigraphic levels). If there were perfect agreement between the Schankler and Bown sections, then all of the localities plotted in Figure 1 would fall on the dashed diagonal line with a slope of 1.00 and an intercept of 0.00.

Figure 1 shows almost perfect consistency between the Schankler and Bown stratigraphic sections for points representing localities at meter levels ranging from 50 to 400 meters (localities in biochrons Wa-2, Wa-3, Wa-4, and early Wa-5). The solid line superimposed over these points, with a linear-model slope of 1.00 and intercept of -4.99, corroborates the consistency.

Figure 1 also shows almost perfect consistency for points representing localities with meter levels ranging from 530 to 730 meters in the Schankler section (localities in biochrons Wa-6 and Wa-7) — as indicated again by the solid line with a linear-model slope of 1.01 fit to and superimposed over the points. However, here the intercept is more negative (-87.41), and Bown levels for localities in this range are, on average, about 76 meters lower stratigraphically than Schankler levels for the same localities. This difference was acquired in the Wa-5 interval from 400 to 530 meters in the Schankler section, which corresponds to the interval from 400 to 448 meters in the Bown section. An accumulation of 130 meters in the former section corresponds to an accumulation of only 48 meters in the latter section. In Figure 1, localities that represent the interval of stratigraphic-level inconsistency are overprinted with an '×.'

According to Schankler (1980: p. 106), the first appearance of *Bunophorus* marking the beginning of biochron Wa-5 is at the 380 meter level in the Schankler section and the first appearance

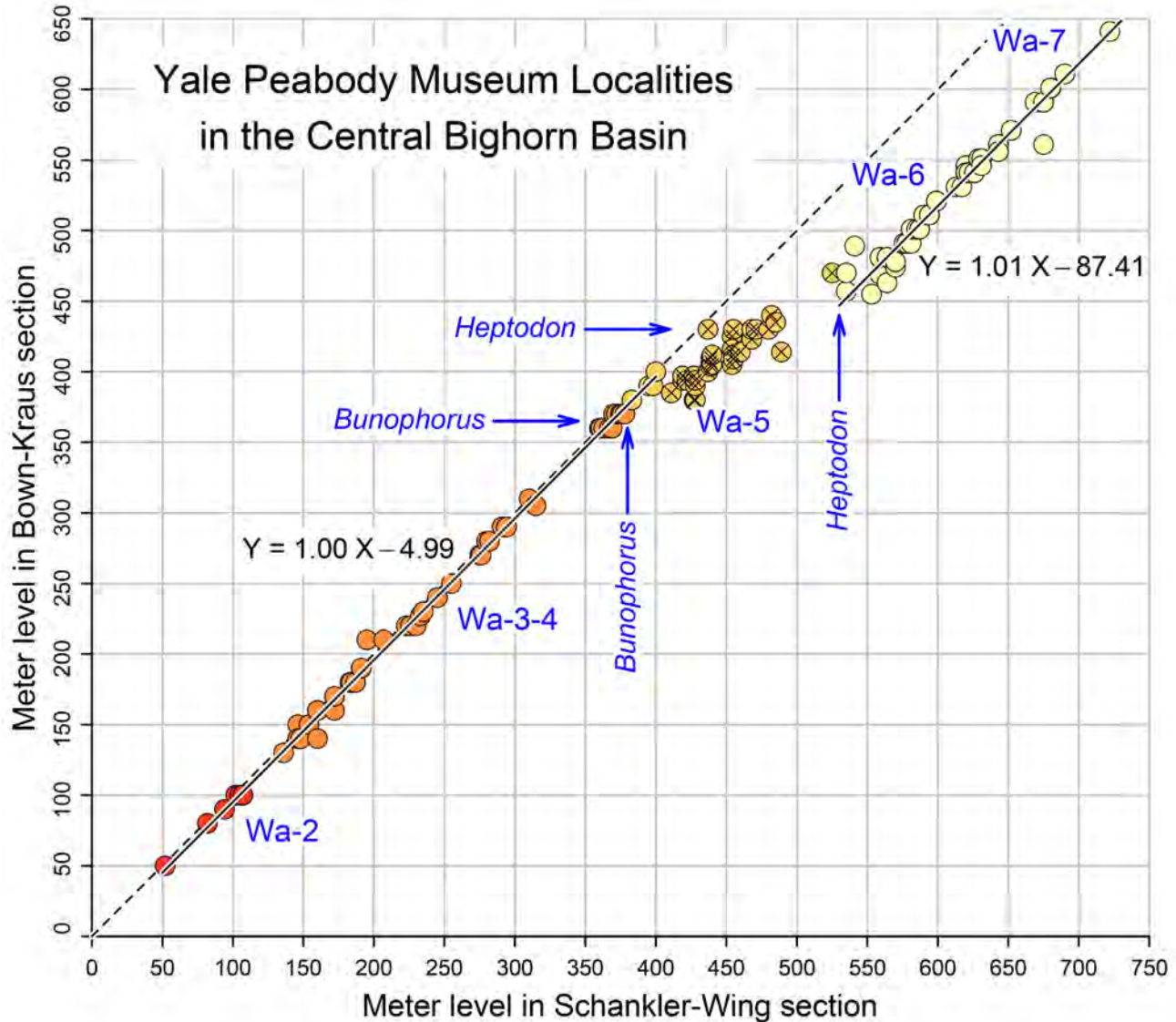


FIGURE 1 — Meter levels for Yale fossil localities in the Bighorn Basin published by Bown et al. (1994) compared to those of Schankler (1980). Numerical values for both are from Chew (2005: appendix 3). Note close agreement below 400 meters in both sections, and close agreement in the upper part of both sections. Agreement in the upper part is offset by about 76 meters, a difference acquired in biochron Wa-5. *Bunophorus*, marking the beginning of Wa-5, appears slightly lower in the Bown-Kraus section than in the Schankler-Wing section. *Heptodon*, marking the beginning of biochron Wa-6, appears much lower in the Bown-Kraus section than in the Schankler-Wing section. Localities are color-coded by biochron; those in the region of discrepancy between the Schankler and Bown sections are overprinted with an x.

of *Heptodon* marking the beginning of biochron Wa-6 is at the 530 meter level. This difference in levels suggests that biochron Wa-5 as a whole is 150 meters thick in the central Bighorn Basin.

In contrast, according to Bown et al. (1994: p. 56), the first appearance of *Bunophorus* marking the beginning of biochron Wa-5 is at the 365 meter level in the Bown section and the first appearance of *Heptodon* marking the beginning of biochron Wa-6 is at the 430 meter level. This difference in levels suggests

that biochron Wa-5 as a whole is only 65 meters thick in the central Bighorn Basin. However, Chew (2005, 2009) records the first appearance of *Bunophorus* at the 385 or 392 meter level in the Bown section, and the first appearance of *Heptodon* at the 430 m level in the Bown section. Thus the Wa-5 interval in the central Bighorn Basin is possibly only 38–45 m thick.

In the northern Bighorn Basin, for comparison, the Wa-5 interval is about 205 meters thick in the McCullough-

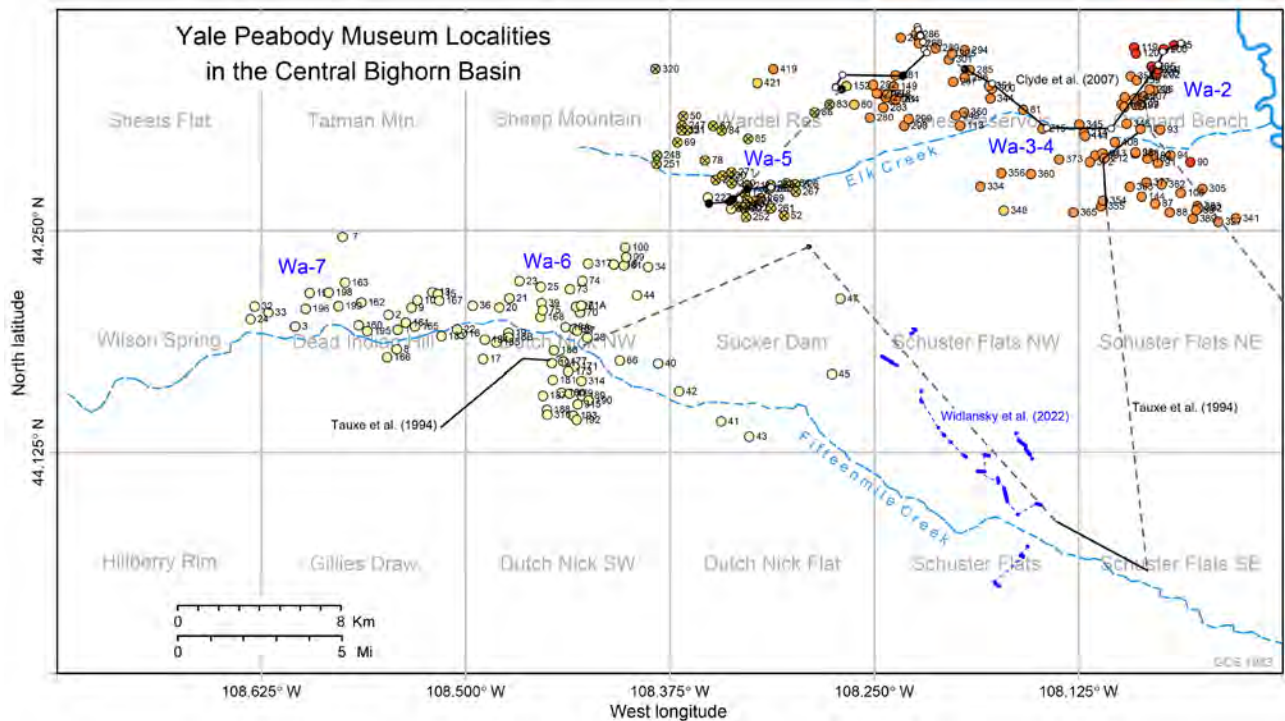


FIGURE 2 — Geographic map of the central Bighorn Basin showing the distribution of Yale-Michigan fossil localities in relation to Elk Creek, Fifteenmile Creek, and the underlying 7.5-minute topographic quadrangle maps in gray (Sheets Flat, etc.). Localities are color-coded by biochron, as in Figure 1, and localities in the region of discrepancy are again overprinted with an ×. Solid and dashed black lines north and south of Elk Creek trace the paleomagnetic traverse of Clyde et al. (2007), with sites of reversed polarity in white and normal polarity in black. Solid and dashed black lines north and south of Fifteenmile Creek trace the paleomagnetic traverse of Tauxe et al. (1994; site coordinates were not published, and the trace here is from Clyde et al., 2007). Reversal from magnetochron 24R to 24N lies within biochron Wa-5. Blue lines north and south of Fifteenmile Creek are isotope sections of Widlansky et al. (2022) recording early Eocene

Peaks-Northwest composite section of Clyde (1997: p. 44), and the Wa-5 interval is about 257 meters thick in the McCullough-Peaks-Southeast composite section of Clyde (1997: p. 44). Both of these McCullough Peaks Wa-5 intervals are substantially thicker than the central Bighorn Basin Wa-5 intervals reported by Schankler (1980), Bown et al. (1994), and Chew (2005, 2009).

Areas of agreement and disagreement in stratigraphic thickness are shown geographically on the map of Figure 2, where Yale and Yale-Michigan localities are color-coded to match the graph in Figure 1. For simplicity, many localities (USGS, USNM, and UW) that make up the Bown et al. (1994) composite section are not shown. Localities in the Wa-5 interval of stratigraphic-level inconsistency are again overprinted with an ‘×’ in Figure 2. These are in the upper reaches of Elk Creek, in or near the southwestern portion of the Wardel Reservoir 7.5’ quadrangle map. There is no easy way to resolve the discrepancy in reported thicknesses of the Wa-5 stratigraphic intervals published by Schankler (1980) and by Bown et al. (1994). However, there are field tools available now — including high-resolution satellite imagery of outcrops, a satellite-based global positioning system

(GPS), and computer-based three-dimensional modeling of outcrops, bedding planes, and stratigraphic sections — that were not available to Schankler and Wing or to Bown and Kraus when their sections were measured. In the future, detailed mapping, tracing, and projection of fossil localities and associated marker beds can and should be used to resolve the stratigraphic levels of localities.

Pending resolution, most authors studying early Eocene Notharctinae in the central Bighorn Basin have chosen to use the biostratigraphy of Bown et al. (1994). This lead is followed here — with the understanding that the Wa-5 biochron in the central Bighorn Basin may prove to be substantially thicker than currently recognized.

Tauxe et al. (1994) and Clyde et al. (2007) described the paleomagnetic stratigraphy of the central Bighorn Basin in two independent studies. However, the geospatial data and magnetic characteristics of the Tauxe et al. (1994) samples were never archived, which makes comparison difficult. The Clyde et al. (2007) polarities on the map in Figure 2 came from sections in the vicinity of Elk Creek. These data are available at <https://earthref.org/MagIC/18023>. The reversal from magnetochron

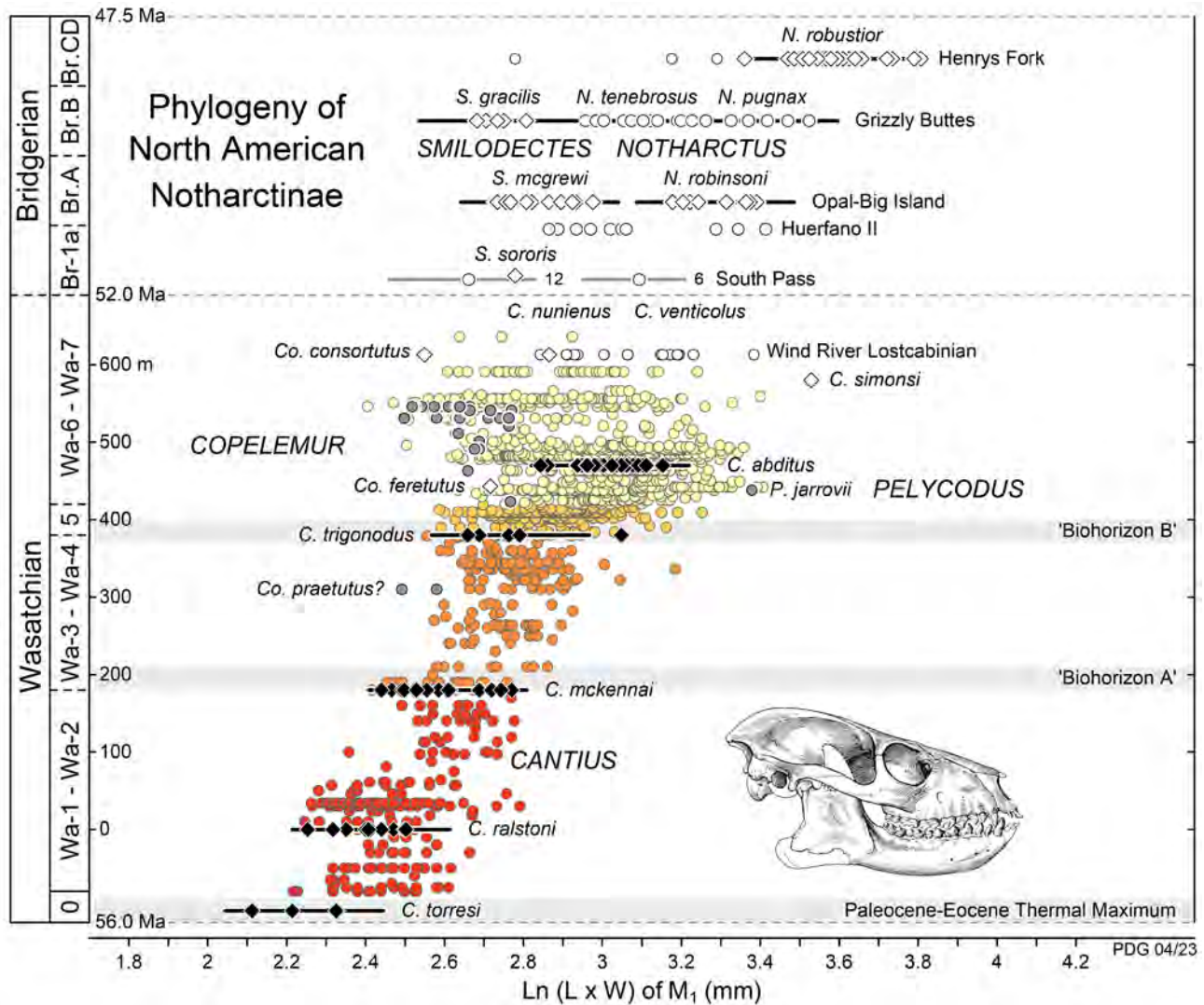


FIGURE 3 — Phylogeny of Notharctinae from the Western Interior of North America based on early and earliest middle Eocene specimens from localities in northwestern and southwestern Wyoming. Abscissa is the natural logarithm of tooth-crown area for lower first molars. Ordinate is stratigraphic superposition through some 8.5 million years of geological time. Meter levels are shown for central Bighorn Basin samples. The Wasatchian land-mammal age ranges from about 56.0 to 52.0 Ma, and the Bridgerian land-mammal age from about 52.0 to 47.5 Ma (Speijer et al., 2020). In the Wasatchian, colored circles represent individual Clarks Fork Basin and Bighorn Basin specimens studied by Clyde and Gingerich (1994), Chew (2005), and O’Leary (2021). These are colored by biochron as in Figures 1 and 2. Solid black diamonds are type samples for species in the Clarks Fork and Bighorn basins. In the latest Wasatchian and Bridgerian, open diamonds represent samples containing the holotype, and open circles are samples from other localities (Gregory, 1920; Gingerich, 1979; Gunnell, 2002). Horizontal black lines are 95% confidence intervals for ranges of tooth size variation (mean ± 2 standard deviations). Horizontal gray lines are ranges for South Pass samples of Gunnell (2002), where 12 and 6 are sample sizes. Note the continuity of intermediate forms representing most lineages of successive species, with occasional immigrants appearing from elsewhere (e.g., gray circles of *Copelemur* and *Pelycodus*). Abbreviations: *C.*, *Cantius*; *Co.*, *Copelemur*; *N.*, *Notharctus*; *P.*, *Pelycodus*; and *S.*, *Smilodectes*. Biohorizons A and B are from Schankler (1980) and Chew (2015). Inset illustration of a *Notharctus* skull is from Gregory (1916).

24R to 24N lies within biochron Wa-5 here (Clyde et al., 2007), as it does in McCullough Peaks sections farther north (Clyde et al., 1994; Abels et al., 2012, 2016).

Carbon isotope stratigraphy in the central Bighorn Basin was studied by Widlansky et al. (2022). Their isotope sections north and south of Fifteenmile Creek are plotted on the

map in Figure 2. The sections include the early Eocene negative $\delta^{13}\text{C}$ excursions and corresponding hyperthermals that are generally referred to as ETM2, H2, and I1. Again, all lie within biochron Wa-5 (Abels et al., 2012, 2016; Widlansky et al., 2022).

PHYLOGENY OF NOTHARCTINAE IN WYOMING

The geologically oldest notharctine primates in North America come from the Wa-0 biochron in the Paleocene-Eocene Thermal Maximum (PETM) that marks the beginning of the Eocene epoch of geological time. The Wa-0 biochron marks the first appearance of mammalian Artiodactyla, Perissodactyla, and true Primates in the fossil record of North America (Gingerich, 1989). The current phylogeny of notharctines in Wyoming is shown in Figure 3. This is a phylogeny in the traditional sense, a pattern of change through evolutionary time (e.g., Simpson, 1944: fig. 4).

The backbone of the phylogeny in Figure 3 is the dense and continuous sequence of central Bighorn Basin specimens studied by O’Leary (1996, 2021) and Chew (2005), where each specimen is plotted as an open circle. These are color-coded by stratigraphic interval, matching the colors in Figures 1 and 2. The O’Leary and Chew specimens range from 18 to 636 meters on the meter scale shown for the central Bighorn Basin. However, the lower part of the central Bighorn Basin stratigraphic section is condensed and poorly fossiliferous. The 18-meter level there lies near the base of biochron Wa-2, and the Wa-0 and Wa-1 biochrons are condensed or missing in the central Bighorn Basin stratigraphic section.

The central Bighorn Basin record shown in Figure 3 is augmented by addition of specimens studied by Gingerich (1989) and Clyde and Gingerich (1994) from the adjacent Clarks Fork Basin. Ninety-three specimens ranging from 1520 to 1630 meters in the Clarks Fork Basin section are plotted in Figure 3, with 1620 subtracted from their meter levels. Thus Wa-0 specimens in the PETM at the 1520 meter level in the Clarks Fork Basin plot at the -100 meter level in Figure 3. Wa-1 specimens at the 1630 meter level in the Clarks Fork Basin plot at the 10 meter level in Figure 3. The full set of Clyde and Gingerich meter levels and M_1 measurements is included in Appendix I.

In the following text, type specimens (holotypes or neotypes) and type samples (specimens from the type locality) for each species are described, genus by genus. Within each genus, species are listed in order of their stratigraphic appearance. Measurements of M_1 length and width for type samples of each species shown in Figure 3 are listed in Appendix II.

Genus *Cantius* Simons, 1962

Species of *Cantius* have an unfused mandibular symphysis and differ from species of other notharctines in having a less developed hypoconid and mesostyle on upper molars, anteroposteriorly less compressed lower premolars, retaining a distinct paraconid cusp on the trigonid of lower molars, and generally lacking a notch or valley between the entoconid and

hypoconid on the talonid of lower molars. Species of *Cantius* are chiefly distinguished on the basis of size and stratigraphic position, but later species also have more strongly developed hypocone cusps and mesostyles on upper molars.

The type species of the genus *Cantius* is the European early Eocene *Cantius eppsi*. This was first described from Abbey Wood in southern England and named *Protoadapis eppsi* by Forster Cooper (1932). Thirty years later, Simons (1962) moved *P. eppsi* to the new genus *Cantius*, which he regarded as an omomyid. Russell et al. (1967) recognized *Cantius* to be a notharctid or notharctine very similar to North American *Pelycodus*. In a subsequent study, Gingerich and Haskin (1981) restricted *Pelycodus* to the species *P. jarrovi* and moved the remaining species of *Pelycodus* to *Cantius*. The contemporary late Wasatchian species *Cantius nunienus* and *C. venticolus* are sometimes classified in *Cantius* and sometimes classified in *Notharctus*. Here they are retained in *Cantius* because they rarely have the fused mandibular symphysis typically found in mature individuals of *Notharctus* (Gingerich, 1979; Beecher, 1983; Rosenberger et al., 1985; Ravosa, 1996). With these inclusions, eight species of *Cantius* are known from Wyoming.

Cantius torresi Gingerich, 1986, is the oldest notharctine primate known from North America (Gingerich, 1986, 1989, 1995). It comes from the Wa-0 biochron of Wasatchian early Eocene age, a biochron lying within the PETM. The holotype is UM 83470 from locality SC-67 at the southwest end of Polecat Bench in the northern Bighorn Basin. Samples of *C. torresi* are not large, but ten specimens are known from the type locality (Gingerich, 1995). Two specimens are known from locality SC-69 nearby (Gingerich, 1995), and several specimens are known from Sand Creek Divide in the southeastern Bighorn Basin (Rose et al., 2012).

Cantius ralstoni, originally *Pelycodus ralstoni* Matthew, 1915, is present in biochrons Wa-1 and Wa-2. It is larger than *C. torresi* but connected by many intermediate specimens. The holotype, AMNH 16089, was found “three miles SE of the mouth of Pat O’Hara Creek” in the Clarks Fork Basin of northwestern Wyoming. This is UM locality SC-40 of Wa-1 age. *C. ralstoni* is known from hundreds of specimens in addition to the type sample.

Cantius mckennai, originally *Pelycodus mckennai* Gingerich and Simons, 1977, is present in biochrons Wa-3 and Wa-4. It is larger than *C. ralstoni* but connected to it by many specimens intermediate in size and form. The holotype, UM 67113, was found at UM locality SC-133, Wa-3 in age, in the Clarks Fork Basin of northwestern Wyoming. *C. mckennai* is known from hundreds of specimens in addition to the type sample.

Cantius trigonodus, originally *Pelycodus trigonodus* Matthew, 1915, is present in biochron Wa-5. It is larger than *C. mckennai* but connected to it by many specimens intermediate in size and form. The type specimen, AMNH 15017, was found five miles south of Otto in the central Bighorn Basin. *C. trigonodus* is known from hundreds of specimens in addition to the type sample.

Cantius abditus, originally *Pelycodus abditus* Gingerich and Simons, 1977, is present in biochron Wa-6. It is larger than *C.*

trigonodus but connected to it by many specimens intermediate in size and form. The holotype, UM 66000, was found at locality YM-45 in the central Bighorn Basin. *C. abditus* is known from hundreds of specimens in addition to the type sample.

Cantius nunienus, originally *Pelycodus nunienum* Cope, 1881, is present in Wasatchian biochron Wa-7 and Bridgerian biochron Br-1a of Clyde et al. (2001). It is smaller than *C. abditus* but connected to it by many specimens intermediate in size and form. The holotype, AMNH 4734, is a right dentary with P₃–M₃ from the Wind River Basin of central Wyoming. Guthrie (1971) regarded *Notharctus limosus* Gazin, 1952, as a synonym. Guthrie (1971) published statistics for a sample of 32 first lower molars of what he called *Notharctus nunienus* from Wa-7 localities in the Wind River Basin. Judging from the range of tooth sizes, the Guthrie (1971) sample almost certainly includes specimens of *Copelemur consortutus*. Gunnell (2002) extended the range of *C. nunienus* to Bridgerian biochron Br-1a at South Pass in the greater Green River Basin, but here too small specimens suggest inclusion of *Co. consortutus*.

Cantius venticolus Osborn, 1902, is present in Wasatchian biochron Wa-7 and Bridgerian biochron Br-1a of Clyde et al. (2001). It is larger than *C. abditus* but connected to it by many specimens intermediate in size and shape. The holotype, AMNH 4715b, is a maxilla and associated dentary collected in 1880 by Jacob Wortman in the Wind River Basin of Wyoming. Cope (1884) identified this as *Pelycodus tutus* and illustrated it in figures 1–2 of his plate XXVa. Later Osborn (1902) recognized the species as new and placed it in *Notharctus*. Guthrie (1971: table 10) published statistics for a sample of 35 first lower molars of what he called *Notharctus venticolus* from Wa-7 localities in the Wind River Basin, but measurements of individual specimens will be required to evaluate his identifications. Gunnell (2002) extended the range of what he called *N. venticolus* to Bridgerian biochron Br-1a at South Pass in the greater Green River Basin, but here again measurements of individual specimens will be required to evaluate his identifications. The sample of *C. venticolus* listed in Appendix II here probably includes some specimens of *C. nunienus*, and these two late Wasatchian species may have overlapped to some degree in size.

Cantius simonsi Gunnell, 2002, is present in biochron Wa-7. It is the largest species of *Cantius* and possibly also a descendant of the earlier-appearing *C. abditus*. The holotype of *C. simonsi*, UM 91592, is a right dentary with P₄–M₂ that was found at locality MP-78 in the northern Bighorn Basin. The holotype is seemingly unique and no additional specimens have been referred to the species.

Genus *Copelemur* Gingerich and Simons, 1977

Species of *Copelemur* differ from those of other notharctines in having the hypocone and mesostyle poorly developed on upper molars. *Copelemur* differs from *Cantius* in generally having a distinct entoconid notch or valley between the entoconid and hypoconulid on the talonid of lower molars (Gingerich and Simons, 1977). Species of *Copelemur* differ from those of *Smilodectes* in having less compressed lower premolars and more distinct paraconids on lower molars.

Species of *Copelemur* differ from those of *Notharctus* in having an unfused mandibular symphysis.

The type species of *Copelemur* is the North American early Eocene *Copelemur tutus*, originally *Tomitherium tutum* Cope, 1877, from New Mexico. Three species of *Copelemur* have been reported from the Bighorn Basin in Wyoming. Each is generally smaller than the contemporary species of *Cantius*.

Copelemur praetutus, originally *Pelycodus? praetutus* Gazin, 1962, is based on a holotype dentary, USNM 22262, from a middle Wasatchian-age locality near Bitter Creek Station in southwestern Wyoming. This was illustrated by Gazin (1962, pl. 4, fig. 4). The species is also present, questionably, at the 310 meter level, biochron Wa-4, in the central Bighorn Basin. Two specimens are known from the Bighorn Basin, both from locality YM-365. These are close to *Co. praetutus* in size, but neither has the deep entoconid notch seen in the holotype.

Copelemur feretutus Gingerich and Simons, 1977, is based on a small collection of specimens from the Lysite member, Wa-6, of the Wind River Formation in the Wind River Basin, Wyoming. These were included in *Pelycodus frugivorus* by Kelley and Wood (1954) and Guthrie (1967). The holotype, ACM 4326, is an isolated right M₁. Two specimens of *Co. feretutus* preserving M₁ are present in Yale collections from the central Bighorn Basin (YPM 18669 and 28199). More *Co. feretutus* are present among the *Copelemur* specimens identified by O'Leary (1996) and Chew (2005) in newer USGS and USNM collections.

Copelemur consortutus Gingerich and Simons, 1977, is based on a small collection of specimens from the Lost Cabin member, Wa-7, of the Wind River Formation in the Wind River Basin, Wyoming. This probably includes some specimens identified as *Pelycodus nunienus* by Guthrie (1971). The holotype, YPM-PU 18282, is a left dentary with M₁₋₃ from Alkali Creek five miles northwest of Arminto, Wyoming. Eighteen specimens of *Co. consortutus* that preserve M₁ are present in Yale collections from the central Bighorn Basin. More *Co. consortutus* are almost certainly present among the *Copelemur* specimens identified by O'Leary (1996) and Chew (2005) in newer USGS and USNM collections.

Genus *Pelycodus* Cope, 1875

Species of *Pelycodus* are distinctive in having relatively flat upper molars with a straight centrocrista connecting the paracone and metacone (Gingerich and Haskin, 1981). The styler shelf on upper molars is narrow and lacks styler cusps. Lower molars are relatively broad and flat. The paraconid is reduced on the trigonid, and the hypoconid and entoconid are small and broadly separated on the talonid.

The type species of *Pelycodus* is the North American early Eocene *Pelycodus jarrovii*, originally *Prototomus jarrovii* Cope, 1874, from New Mexico. In 1874, Cope had only a fragmentary dentary available, with the posterior crown of M₂ and crown of M₃, which he interpreted to represent a carnivore (Cope, 1874). A year later, with better specimens, Cope referred *Pelycodus jarrovii* to 'Quadrumana' or Primates (Cope, 1875). The original type, now lost, was illustrated in Cope (1877, pl. xxxix, fig.

17). By this time, Cope referred the species to *Tomitherium*, a synonym of *Notharctus*.

Gingerich and Haskin (1981) described new specimens of Cope's *Pelycodus jarrovii* from the San Juan Basin of New Mexico, designated AMNH 16282 from Arroyo Almagre as a neotype for the species, and transferred all other species identified as *Pelycodus* to the genus *Cantius*.

Rose and Bown (1984) described the first specimen correctly identified as *Pelycodus jarrovii* from the Bighorn Basin. The Rose and Bown (1984) specimen, USGS 6549, came from USGS locality D-1459 at about the 438 m level in the central Bighorn Basin (Bown et al., 1994). The measurement plotted here is from O'Leary (2021: supplemental table S1). According to Rose and Bown (1984), a second specimen from the same stratigraphic interval, YPM 40286 from Yale locality 448, may also represent *P. jarrovii*.

Genus *Notharctus* Leidy, 1870

Notharctus differs from earlier *Cantius*, *Copelemur*, and *Pelycodus* in having stronger mesostyles and hypocones on upper molars and generally having at least partial fusion of the mandibular symphysis (Osborn, 1902; Gregory, 1920). It differs from contemporary *Smilodectes* in being larger, having relatively larger teeth compared to skull size, having a larger and relatively narrower skull, and generally having at least partial fusion of the mandibular symphysis (Gazin, 1958; Gingerich, 1979). *Notharctus* also differs from *Smilodectes* in having a protoconid-directed flexure of the cristid obliqua on M₃ and in having distinct paraconid cusps on M₁ and M₂.

The type species of *Notharctus* is the North American early Eocene species *Notharctus tenebrosus* Leidy, 1870. Four species of *Notharctus* are known from Wyoming: *N. robinsoni*, *N. tenebrosus*, *N. pugnax*, and *N. robustior*.

Notharctus robinsoni Gingerich, 1979, is present in Bridger Formation unit A of Matthew (1909) or Bridgerian biochron Br-1b of Clyde et al. (2001). It is probably a descendant of *Cantius venticolus*. The holotype, UW 3007, includes left and right dentaries with C₁ and P₄-M₃ from locality 19-67 of McGrew and Sullivan (1970). This locality is in Bridger Formation unit A near the town of Opal in southwestern Wyoming. Gunnell (1998) described a large collection of Br-1b specimens of *N. robinsoni*.

Bown (1982) reported several teeth identified as *Notharctus* sp. from early Bridgerian-age faunas of the Aycross Formation in the southwestern part of the Bighorn Basin, Wyoming. These are certainly teeth of *Notharctus* and their size suggests that they represent *N. robinsoni*.

Notharctus tenebrosus Leidy, 1870, is present in Bridger Formation unit B of Matthew (1909) or Bridgerian biochron Br-2 of Clyde et al. (2001). It is a smaller-bodied descendant of *Notharctus robinsoni*. The holotype, USNM 3752, is a right dentary with C₁ and P₃-M₃ collected by Ferdinand Hayden in 1870 from the Blacks Fork of the Green River, possibly near Jackson Ridge (Murphey and Evanoff, 2011: fig. 4). This is in the Bridger Basin of southwestern Wyoming. Leidy (1873) described and illustrated the *N. tenebrosus* type, comparing it

to the extant South American primate *Cebus*. A large sample of *N. tenebrosus* of Br-2 age is available from Grizzly Buttes, 25 kilometers south of Jackson Ridge. The Grizzly Buttes sample includes holotypes of a number of junior synonyms of *N. tenebrosus*: *N. anceps*, *N. affinus*, *N. osborni*, and *N. tyrannus*.

Notharctus pugnax Granger and Gregory, 1917, is present in Bridger Formation unit B of Matthew (1909) or Bridgerian biochron Br-2 of Clyde et al. (2001). It is a larger descendant of *Notharctus robinsoni*. The holotype, AMNH 11461, is a left dentary with P₃-M₂ collected by Walter Granger near Millersville, Wyoming. This is several kilometers south of Jackson Ridge, near the junction of the Blacks Fork and Smiths Fork of the Green River in the Bridger Basin. A large sample of *N. pugnax* of Br-2 age is available from Grizzly Buttes farther to the south.

Notharctus robustior Leidy, 1872, is present in Bridger Formation units C and D of Matthew (1909) or Bridgerian biochron Br-3 of Clyde et al. (2001). It is a larger descendant of *Notharctus pugnax*. The holotype, USNM 3750, is a left dentary with M₂ collected by Ferdinand Hayden in 1870 from Henrys Fork of the Green River in the Bridger Basin of Wyoming. A large sample of *N. robustior* of Br-3 age is available from Henrys Fork. This includes the holotype of *N. crassus*, which is a junior synonym of *N. robustior* (Gazin, 1934).

Genus *Smilodectes* Wortman, 1903

Smilodectes differs from earlier *Cantius*, *Copelemur*, and *Pelycodus* in having stronger mesostyles and hypocones on upper molars and in having more anteroposteriorly compressed premolars (Gingerich, 1979). It has an entoconid notch like those of *Copelemur* and *Notharctus*. *Smilodectes* differs from contemporary *Notharctus* in being smaller, having relatively smaller teeth compared to skull size, having a shorter and relatively broader skull with a broader and more inflated frontal region, lacking symphyseal fusion of the mandibular rami, and lacking a protoconid-directed flexure on the cristid obliqua of M₃ (Gingerich, 1979). P₂ tends to be single-rooted in *Smilodectes*, and lower molar paraconids are reduced to a crest or lost.

The type species of *Smilodectes* is the North American early Eocene species *Smilodectes gracilis*, originally *Hyopsodus gracilis* Marsh, 1871, from Grizzly Buttes in the Bridger Basin of Wyoming. Wortman (1903) placed Marsh's *H. gracilis* in the new genus *Smilodectes*. Three species of *Smilodectes* have been named from Wyoming:

Smilodectes sororis Gunnell, 2002, is present in Gardnerbuttean-age strata of the Wasatch Formation or Bridgerian biochron Br-1a of Clyde et al. (2001). Its evolutionary origin is unclear. The holotype of *S. sororis*, UM 104807, is a right dentary with M₁₋₂ from University of Michigan South Pass locality SP-24. This is part of a small collection of South Pass Br-1a specimens (Gunnell, 2002). *S. sororis* is similar in size to contemporary Br-1a specimens identified as *Cantius nunienus* (see below).

Smilodectes mcgrewi Gingerich, 1979, is present in Bridger Formation unit A of Matthew (1909) or Bridgerian biochron Br-1b of Clyde et al. (2001). It may be a larger

descendant of *Smilodectes sororis*. The holotype, UW 5021, is a left dentary with P₃–M₃ from Bridger Formation unit A at locality V-16 of Kistner (1973). This was found in badlands east of the Green River some 50 kilometers east of Opal, Wyoming, but the species is also found near Opal (McGrew and Sullivan, 1970). Gunnell (1998) described a large collection of Br-1b *S. mcgrewi* specimens.

Smilodectes gracilis, originally *Hyopsodus gracilis* Marsh, 1871, is present in Bridger Formation unit B of Matthew (1909) or Bridgerian biochron Br-2 of Clyde et al. (2001). The holotype, YPM 11800, is a left dentary with P₃–M₁ collected by O. C. Marsh on September 5, 1870, at Grizzly Buttes in the Bridger Basin of southwestern Wyoming.

Gunnell et al. (1992) described a dentary identified as *Smilodectes mcgrewi* with P₃₋₄ and M₃, UM 80644, from early Bridgerian locality NF-6 in Wapiti unit III of the Willwood Formation on the western flank of the Bighorn Basin. They also described an upper molar identified as *S. gracilis* from middle Bridgerian locality NF-4 in Wapiti unit V of the Aycross Formation at a higher stratigraphic level.

NORTH AMERICAN NOTHARCTINES FROM OTHER BASINS

Gazin (1952) named *Notharctus limosus* from La Barge in the Green River Basin of southwestern Wyoming based on USNM 19294, which includes left and right dentaries with the teeth P₃ through M₃ (M₁ = 4.5 × 3.3 mm in anteroposterior length and buccolingual width). *Notharctus limosus* is the size of late Wasatchian *Notharctus nunienus* and associated with the larger species *Notharctus venticolus*, which led Guthrie (1971) to synonymize *N. limosus* with *N. nunienus*.

Dorr (1952) incorrectly referred an early Wasatchian-age artiodactyl M₃ from UM locality Sub-Wy 2 in the Hoback Basin of western Wyoming to *Pelycodus ralstoni*. Later Gingerich and Simons (1977) identified *P. ralstoni* from this locality, based on a previously uncataloged dentary from Sub-Wy 2 that preserves P₄–M₁. This specimen is now cataloged as UM 67569.

McKenna (1960) described a collection of specimens from the early Wasatchian-age Four Mile fauna of northwestern Colorado that was intermediate between what he called *Pelycodus ralstoni* and *P. trigonodus*, which led him to synonymize the two species. Twenty-one first lower molars from the East Alheit locality yielded a mean Ln (L × W) of M₁ value of 2.64. Gingerich and Simons (1977) referred these to the new species *Pelycodus* [now *Cantius*] *mckennai*.

Gazin (1962) named *Pelycodus? praetutus* [now *Copelemur praetutus*] from a Wasatchian-age locality 1¼ miles (2 km) south of Bitter Creek Station in the Washakie Basin of southwestern Wyoming. The holotype of *P. praetutus* is a right dentary with P₃–M₂ (M₁ = 3.8 × 3.0 mm in anteroposterior length and buccolingual width).

Jepsen (1963) identified three Wasatchian-age notharctine teeth from Golden Valley in North Dakota as *Pelycodus* cf. *P. ralstoni*. Gingerich and Simons (1977) re-identified these as *Pelycodus* [now *Cantius*] *trigonodus*.

Robinson (1966) described notharctines from two intervals of the Huerfano Formation in southern Colorado. The lower fauna, Lostcabinian or late Wasatchian in age, has a notharctine Robinson called *Notharctus nunienus*: this may be correctly identified to species (here placed in *Cantius*). The upper fauna, Gardnerbuttean or early Bridgerian in age, has notharctines of two distinct sizes. These are identified as *Smilodectes mcgrewi* and *Notharctus robinsoni* (see Gingerich, 1979).

Delson (1971) described a maxilla and a collection of 40 isolated teeth from 26 Wasatchian-age localities in the Powder River Basin of Wyoming. The specimens were identified as *Pelycodus ralstoni*, but based on measurements given for M₁ they are more likely to represent *Cantius mckennai*.

Dorr and Steidtmann (1971) recorded two isolated Wasatchian-age upper molars from UM locality Sub-Wy 29 in the Hoback Basin of western Wyoming as *Pelycodus ralstoni*. These were later re-identified by Gingerich and Simons (1977) as *Pelycodus* [now *Cantius*] *mckennai*.

West (1982) described an isolated partial M₃ from the Uintan middle Eocene Whistler Squat local fauna of Texas that he identified as *Notharctus tenebrosus*. The specimen, TMM 41444-18, is relatively large and probably notharctine, but generic and specific identifications are questionable.

Beard (1988) designated AMNH 55511 from Wasatchian-age Gavilan Arroyo in the San Jose Formation, New Mexico, as a neotype for *Pelycodus angulatus* Cope, 1875. He placed the species in the genus *Cantius*. Cope's (1875) measurements for the original type M₁, now lost, are 3.4 × 2.7 mm in anteroposterior length and buccolingual width, making it the smallest of North American middle Wasatchian notharctines. Similarly, Beard (1988) designated CM 37448 from Carnegie Museum locality 945 in the San Jose Formation as a neotype for *Pelycodus frugivorus* Cope, 1875. This too he placed in *Cantius*. Cope's (1875) measurements for the original type M₂, now lost, are 4.5 × 4.0 mm in anteroposterior length and buccolingual width, showing that it was substantially larger than *C. angulatus*.

Beard (1988) designated UALP 10233 from University of Arizona Wasatchian-age locality 7745 in the San Jose Formation of New Mexico as a neotype for *Tomitherium tutum* Cope, 1877, the type species of *Copelemur*. Cope (1877) gave measurements for the original type M₁, now lost, as 5.0 × 4.5 mm in anteroposterior length and buccolingual width. Beard (1988) also named *Copelemur australotutus* from Fossil Butte in southwestern Wyoming as a new species, based on USNM 22261, a left dentary with P₃–M₁ (M₁ = 4.65 × 3.65 mm in anteroposterior length and buccolingual width). *Co. australotutus* is based on a single specimen preserving a single molar, which precludes evaluation of likely variation. The age of the type is also uncertain (Wa-6 or Wa-7). No comparison was made with known *Co. feretutus* and *Co. consortutus*, with which it may be synonymous. Large samples of *Co. feretutus* and *Co. consortutus* available now from the Bighorn Basin (O'Leary, 1996; Chew, 2005) and *Co. australotutus* available from South Pass (Gunnell, 2002) make careful quantitative comparison of *Co. australotutus* possible, but this has not yet been attempted.

Beard (1988) named *Smilodectes gingerichi* from Carnegie Museum locality 941 in the Wasatchian-age San Jose Formation

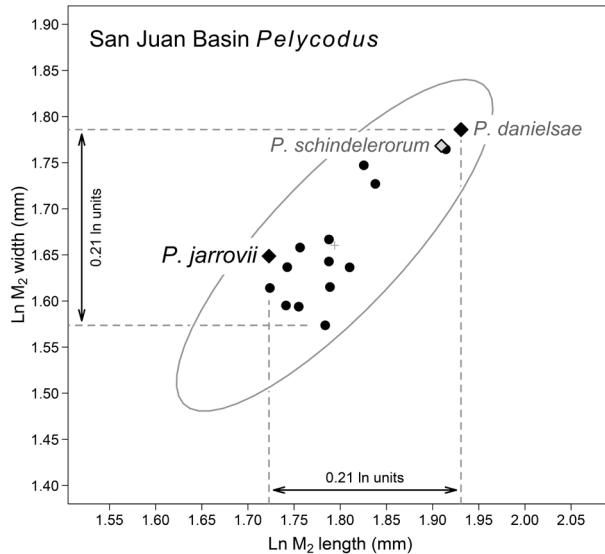


FIGURE 4 — M_2 molar crown size for 15 specimens of *Pelycodus jarrovii* Cope, 1874, from the San Jose Formation in the San Juan Basin of New Mexico (filled symbols). These are middle Wasatchian (Wa-5) in age. Measurements for the neotype of *Pelycodus jarrovii* (filled diamond) are from Gingerich and Haskin (1981). Measurements for the holotype of *Pelycodus danielsae* (filled diamond) are from Froehlich and Lucas (1991). The remaining San Jose Formation specimens were digitized from Froehlich and Lucas (1991: fig. 2). The ellipse surrounding the points is a 95% confidence ellipse computed for the entire set of San Juan Basin specimens. Ranges of 0.21 natural log units observed for M_2 length and M_2 width in the San Juan Basin specimens are ranges typical for linear measurements of molars within a mammalian species. It appears that *P. danielsae* is conspecific with *P. jarrovii*, a synonymy to be tested as more specimens are found. The gray diamond represents the holotype of Wa-7 late Wasatchian *P. schindelerorum* Kihm, 1992, from the Debeque Formation in the Piceance Basin of northwestern Colorado. Here too synonymy of *P. schindelerorum* with *P. jarrovii* and *P. danielsae* will be tested as more specimens are found.

of New Mexico. The type is CM 37451, a left maxilla with P^3-M^1 ($M^1 = 4.15 \times 4.90$ mm in anteroposterior length and buccolingual width). *S. gingerichi* is based on a single specimen preserving a single molar, which again precludes evaluation of likely variation. Gunnell (2002) considered *S. gingerichi* to be a junior synonym of *C. angulatus*. On the question of phylogenetic relationships, Beard (1988) regarded *Smilodectes* as a descendant of *Copelemur*, with *Notharctus* as an independently-derived descendant of *Cantius*, but analysis by Covert (1990) supported derivation of *Smilodectes* and *Notharctus* both from *Copelemur*. Gunnell (2002) found *Smilodectes* to be a sister taxon of *Copelemur*, with both derived from *Cantius* — so the broader relationships remain unclear.

Beard's (1988) idea that *Cantius frugivorus* and *C. trigonodus* might be synonymous is consistent with a Wasatchian Wa-5 age for the San Jose Formation fauna of New Mexico.

The San Jose Formation fauna lacks earlier Wa-1 through Wa-4 *Haplomyilus* and *Ectocion*, does contain Wa-5 *Bunophorus* and *Anacodon*, and lacks later Wa-6 *Heptodon* (Lucas et al., 1981; Robinson et al., 2004). However, if synonymous, *C. frugivorus* would be the only San Jose species found in Wa-5 strata of Wyoming. *Cantius angulatus*, *Copelemur tutus*, and *Pelycodus jarrovii* are not found in this interval in Wyoming, although *P. jarrovii* makes a brief appearance a little later in Wa-6.

Emry (1990) described a single upper molar of *Notharctus tenebrosus*, USNM 417415, a right M^2 , from the Sheep Pass Formation of Elderberry Canyon in eastern Nevada. The age, supported by many species in the fauna, is Bridger B or Bridgerian biochron Br-2 of Clyde et al. (2001). Later a second specimen, USNM 529039, was described from the same site. This has a virtually complete upper and lower dentition (Perry et al., 2017).

Froehlich and Lucas (1991) named the new species *Pelycodus danielsae* from New Mexico Museum of Natural History locality L-386 in the Wasatchian-age San Jose Formation of New Mexico. The holotype is NMMNH P-3052, a left dentary with M_{2-3} ($M_2 = 6.9 \times 5.9$ mm in anteroposterior length and buccolingual width). The holotype of *P. danielsae* is clearly larger than the holotype of *P. jarrovii* from the same formation (Fig. 4). However, all of the 15 San Jose Formation specimens of *P. danielsae*, taken together, have M_2 crown lengths and widths falling within a range of 0.21 natural-log units — very close to the range of 0.20 expected for a single species (Gingerich, 2014). The San Jose Formation *Pelycodus* specimens have molar crown areas spanning a range of 0.38 natural-log units — slightly less than the range of 0.40 expected for contemporaneous representatives of a single species (Gingerich, 2014). Thus *P. danielsae* is plausibly a junior synonym of contemporary *P. jarrovii*. Additional specimens will be required to demonstrate that they are different.

Kihm (1992) named two new notharctine species, one of *Cantius* and one of *Pelycodus*, from the Debeque Formation in the Piceance Basin of northwestern Colorado. Both are Lostcabinian late Wasatchian (Wa-7) in age. *Cantius antediluvius* was found at University of Colorado Museum locality 84122. The holotype is UCM 52023, a right maxilla preserving P^4-M^2 ($M^1 = 5.72 \times 6.22$ mm in anteroposterior length and buccolingual width). All of Kihm's measurements of *C. antediluvius* fall within the range published by Guthrie (1971) for contemporary *Notharctus venticolus* (here *C. venticolus*). Thus, *Cantius antediluvius* is almost certainly a junior synonym of *C. venticolus*. *C. antediluvius* may have a less developed mesostyle than some *C. venticolus*, as Kihm (1992) claimed in distinguishing the two species, but *C. antediluvius* does have a mesostyle.

Kihm (1992) also named *Pelycodus schindelerorum* based on four Field Museum of Natural History specimens. The holotype is FMNH P-26895, a right dentary preserving M_{2-3} ($M_2 = 6.75 \times 5.86$ mm in anteroposterior length and buccolingual width). Three other specimens preserve M_2 . The measurements and statistics given by Kihm (1992) for *P. schindelerorum* indicate that known specimens fall in the upper range of *Pelycodus jarrovii*. The holotype of Wa-7 *P. schindelerorum* is nearly identical in size to the holotype of Wa-5 *P. danielsae*

(Fig. 4). It is possible that *P. schindelerorum*, as a later species, is significantly larger than *P. jarrovii*, and it may differ in other ways. However, justification will require a larger sample. Wa-5 *P. danielsae* and Wa-7 *P. schindelerorum* are both regarded as junior synonyms of Wa-5 *P. jarrovii*.

Gunnell (1995) named the new genus and species *Hesperolemur actinus* from San Diego Society of Natural History locality 3413, Azuaga 11, site 5 in the Sespe Formation of southern California. The holotype is SDSNH 35233, a partial skull with left and right P⁴–M³ (M¹ = 5.2 × 6.2 mm in anteroposterior length and buccolingual width). *H. actinus* is part of the Poway fauna of early Uintan age (middle Eocene). It is the latest-surviving of named notharctines known from North America.

Finally, Robinson (2018) named two new genera and three new species of Notharctinae from Wasatchian-age strata in the Powder River Basin, east of the Bighorn Basin, in northern Wyoming. The holotype of *Cantius lohseorum* is a left M₃ (type: UCM 53537). The holotype of *Megaceralemur matthewi* is a set of associated teeth ranging from P₃ to M₃ (type: UCM 70000; M₁ = 4.07 × 3.25 mm in anteroposterior length and buccolingual width). Finally, the holotype of *Pinolophus meikei* is a right dentary with M₁₋₂ (type: UCM 62763; M₁ = 4.79 × 3.57 mm in anteroposterior length and buccolingual width). Most of the teeth involved were collected from anthills. All are recorded as coming from biochron Wa-2 in Sandcouleean strata, but Powder River exposures of Eocene strata are generally small and isolated, making localities difficult to relate to each other. The Powder River Basin species overlap in size with successive species of the Bighorn Basin lineage *C. ralstoni* – *C. mckennai* – *C. trigonodus* and may represent a parallel lineage of conspecifics in the Powder River Basin.

RELATED STUDIES OF NOTHARCTINAE

Various authors have described aspects of the skeletal and dental morphology of North American Notharctinae that are important, but do not have a direct bearing on the species-level phylogeny and evolution of notharctines reviewed here. The skeletal and dental studies include the classic *Notharctus* monograph by Gregory (1920). More recent studies of notharctine morphology, starting with the skeleton as a whole and proceeding to more narrowly focused studies on teeth, include:

- Rose and Walker (1985) on the postcranial skeleton;
- Hamrick and Alexander (1996), Boyer et al. (2013a), and Boyer et al. (2016) on the hand skeleton;
- Koenigswald et al. (2012), Maiolino et al. (2012), Boyer et al. (2013b, 2018) on pedal grooming claws;
- Rose et al. (1999) on cranial anatomy;
- Harrington et al. (2016) on brain morphology;
- Beecher (1983), Rosenberger et al. (1985), and Ravosa (1996) on symphyseal fusion and the anterior dentition;
- Krishtalka et al. (1990), Alexander (1994), and Gingerich (1995) on canine dimorphism;
- Gingerich and Smith (2010) on the sequence of premolar eruption;
- Anemone et al. (2012) on the homology of a ‘pseudohypocone.’

All of these studies contribute to our understanding of the skeletal and dental morphology of *Cantius* and *Notharctus* and their close relatives.

DISCUSSION

Cantius torresi appeared in the Wyoming fossil record at about 56 Ma, and *Notharctus robustior*, the last of Wyoming notharctines, disappeared at about 47.5 Ma (Fig. 3). During this 8.5 m.y. interval, the length of the M₁ crown changed from a geometric mean of 3.34 to a geometric mean of 6.56 mm, which is nearly a 2¹ = 2-fold increase. The area (L × W) of the M₁ crown changed from a mean of 9.44 mm² in *C. torresi* to a mean of 35.90 mm² in *N. robustior*, which is nearly a 2² = 4-fold increase. Finally, body weight, estimated from tooth size, changed from a mean of about 1.0 kg in *C. torresi* to a mean of about 7.4 kg in *N. robustior* (Gingerich et al., 1982), which is nearly a geometrically-expected 2³ = 8-fold increase.

Successive notharctine species have mean ln (L × W) of M₁ values differing from those of the previous species by about two standard deviation units (Fig. 3). The successive species are generally larger than their predecessors, but sometimes they are smaller. Where the record is dense and virtually continuous, as it is in the Bighorn and Clarks Fork basins, there are many intermediates, temporally and morphologically, documenting the change. In addition to evolution in situ, some less-well-known species — such as *Copelemur praetutus*, *Co. feretutus*, *Pelycodus jarrovii*, and possibly *Cantius simonsi* — appear suddenly, seemingly as immigrants from elsewhere. Later lineages of *Smilodectes* and *Notharctus* are plausibly derived from Wasatchian *Copelemur* and *Cantius*, but the relationships and transitions remain unclear.

Godinot (1992, 1998) made San Juan Basin *Cantius angulatus* Cope, 1875, the type species of a new subgenus, *Neocantius*, where he also placed the San Juan Basin species *C. frugivorus* and Wind River Basin species *C. nunienus* (but not Bighorn Basin *C. trigonodus*). This grouping appears somewhat arbitrary and it has not been accepted by subsequent authors. Nevertheless, *Neocantius* remains available as a genus-level name if *C. angulatus* proves to differ significantly from *Cantius eppi* and other species now included in *Cantius*.

Transitions from the late Wasatchian species *Copelemur consortutus*, *Cantius nunienus*, and *C. venticolus* to the early Bridgerian species *Smilodectes mcgrewi* and *Notharctus robinsoni* remain uncertain, and the South Pass collection of Gunnell (2002) deserves further study. Gunnell (2002) recognized three species at South Pass: *Cantius nunienus*,

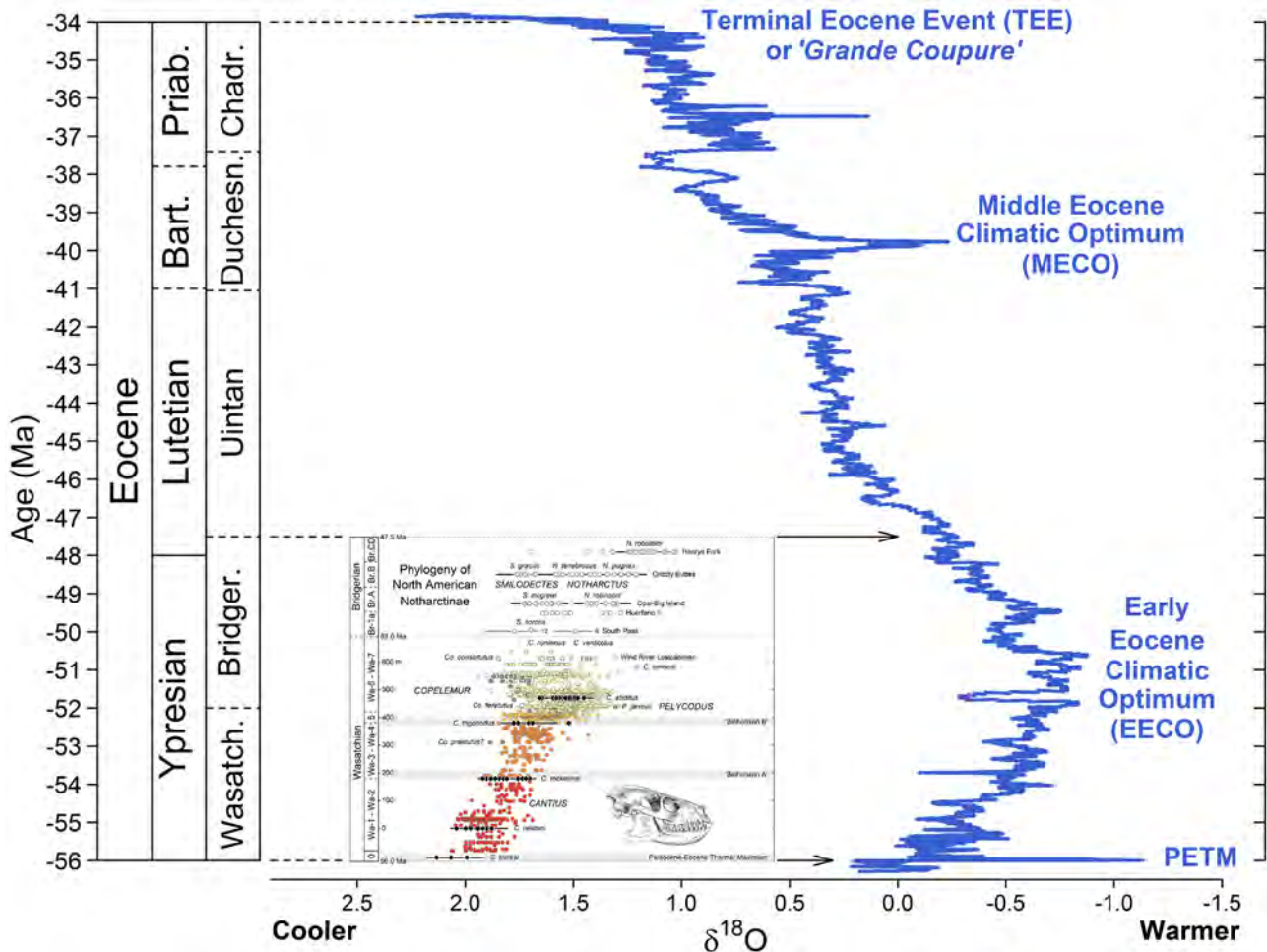


FIGURE 5 — Phylogeny of Notharctinae from the Western Interior of North America viewed in the context of Eocene climate change. The first notharctine species in Wyoming, *Cantius torresi*, appeared in the Paleocene–Eocene Thermal Maximum (PETM) marking the beginning of the Eocene, and the last notharctine species in Wyoming, *Notharctus robustior*, disappeared soon after the Early Eocene Climatic Optimum (EECO). The PETM–EECO interval in the early Eocene is the time when the $\delta^{18}\text{O}$ stable isotope curve was the most negative (note that the abscissa runs positive-to-negative) and temperature the warmest. Primates prefer warm climates, and cooling that followed the EECO meant that notharctine primates disappeared from Wyoming and other areas of similar northern latitude. Inset phylogeny shows the stratigraphic range of Notharctinae (Fig. 3). Oxygen isotope curve in blue is from Speijer et al. (2020).

Smilodectes sororis, and *Notharctus venticolus*. The smallest of these, which Gunnell (2002) called *C. nunienus*, spans a size range that does not include the holotype of Wind River *C. nunienus* — making it questionable that South Pass *C. nunienus* is correctly identified. Gunnell’s *S. sororis* matches South Pass *C. nunienus* closely in size, and no differences from *C. nunienus* were specified — making recognition of distinct taxa questionable. Finally, in light of these uncertainties, South Pass *N. venticolus* (or *C. venticolus*) deserves more careful comparison with Wind River *C. venticolus*.

Gazin (1958) considered the species *Notharctus gracilis* of Marsh (1871) and Robinson (1957) to be distinctive, based on cranial morphology, and he placed it in the genus *Smilodectes* of Wortman (1903). Virtually all subsequent authors have

followed Gazin in distinguishing *Smilodectes* from *Notharctus*. Robinson (1957) and Gazin (1958) recognized two species within *Notharctus*: *N. tenebrosus* from Bridger B or Br-2, and *N. robustior* from Bridger C–D or Br-3. Both authors synonymized Br-2 *Notharctus pugnax* with Br-2 *N. tenebrosus*. Later, Gingerich (1979) separated *N. pugnax* from contemporary *N. tenebrosus* because the two span a distribution of molar sizes that is clearly too large to represent a single species (Fig. 3).

The principal conclusion derived from the fossil record of Notharctinae in Wyoming is one of anagenesis yielding a pattern of gradual evolution. Here the focus is on tooth size as representative of overall body size, but it is also possible to see gradual change through time in the development of mesostyles and hypocones on upper molars and on the development of an

entoconid notch on lower molars (Matthew, 1915; Gingerich and Simons, 1977). O’Leary (1996, 2021) quantified change in tooth size and shape in Bighorn Basin notharctines using a variety of innovative measures applied to a wider range of upper and lower cheek teeth. She concluded that when the fossil record is densely sampled, change through time is continuous and consistent with gradual evolution (O’Leary, 2021). The pattern in Figure 3, where O’Leary’s measurements are combined with those of Chew (2005), reinforces this conclusion. Variation is ubiquitous whenever a stratigraphic level is well sampled, and in the Bighorn Basin the ranges of variation representing species overlap extensively from one level to the next.

Change can be quantified in terms of rate, which has been studied in the Clarks Fork Basin sample of the *Cantius* lineage (Clyde and Gingerich, 1994; Gingerich, 2019). The generation time for early *Cantius* is estimated to be a little under two years, which yields a rate distribution for M_1 length centered on $10^{-2.333} = 0.005$ standard deviations per generation on a time scale of one generation (Gingerich, 2019). On a log-rate-interval plot, the rate distribution scales with a slope of -0.534 , which is close to the -0.500 slope expected for a random walk. M_1 size increased slowly over time, but the underlying process was statistically little different from the expectation for random change. *Cantius* M_1 shape (length/width), on the other hand, scales with a slope of -1.079 , which is close to the slope of -1.000 expected for stasis (no change).

Here taxonomy is inextricably linked to stratigraphy and time. The emphasis in the preceding tabulation of notharctine species — and the emphasis in the graphic representation of Figure 3 — is on type samples of the contemporary or successive species. Each of the type samples in Figure 3 is illustrated by a solid line that spans a range of 0.4 units on the natural-log scale of the horizontal abscissa. This range is equivalent to a mean value ± 2 standard deviations of tooth size variability.

In an evolutionary context like this, where time is plotted on the ordinate and the record is virtually continuous through time, it makes little sense to attempt to divide species ‘vertically’ based solely on morphology. It makes more sense to divide species by drawing boundaries horizontally, so each spans an interval of time and is separated in time from its immediate ancestor and from any descendants. Both approaches to species delimitation, vertical and horizontal, are equally arbitrary, but making divisions parallel to time keeps contemporary samples — interbreeding or potentially interbreeding populations — of a lineage together. Each level in Figure 3 is then a sample of one or more notharctine species on a landscape, and the figure as a whole shows how the lineage segments changed and sometimes diversified through time.

Finally, it is instructive to place the diversification of Notharctinae in the context of Eocene climate change (Fig. 5). The warmest interval of global climate for the entire Cenozoic was during the Paleocene-Eocene Thermal Maximum or PETM. Temperatures remained warm through the Early Eocene Climatic Optimum or EECO (Speijer et al., 2020), and this is when notharctines diversified. The first genus and species, *Cantius torresi*, appeared during the PETM. A second genus and species, *Copelemur praetutus*, appeared in the middle

Wasatchian of southern Wyoming (Gazin, 1962), and possibly the Bighorn Basin (Fig. 3). The late Wasatchian had the greatest notharctine diversity, with three and possibly four contemporary lineages of *Copelemur*, *Cantius*, and *Pelycodus*. Notharctine diversity remained high through the early and middle Bridgerian (Bridger 1a, A, and B). However, a single species, *Notharctus robustior*, is known with certainty from the late Bridgerian (Bridger C and D). Notharctines are not known from Wyoming later in the Eocene. Primates prefer warm climates, and cooling following the EECO meant that notharctine primates disappeared from the Western Interior of North America.

ACKNOWLEDGMENTS

John Fleagle initiated this review by requesting that I update the notharctine phylogeny shown in previous editions of his *Primate Adaptation and Evolution* textbook to reflect a current understanding of notharctine evolution in Wyoming. I thank Amy Chew for providing unpublished measurements of notharctine specimens from her Bighorn Basin dissertation research, and Maureen O’Leary for including measurements in the supplement to her 2021 publication. William Clyde provided a copy of table 1 from Clyde et al. (2007). Adam Rountrey provided access to notharctine specimens at the University of Michigan, and I am grateful, as before, to curators and collection managers at the AMNH, USGS, USNM, UW, YPM, and other museums for providing access to notharctine fossils analyzed here.

The manuscript was reviewed by Amy Chew and Luke Weaver, and I thank each of them for comments that improved the presentation substantially.

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Contributions from the Museum of Paleontology, University of Michigan, is a medium for publication of reports based chiefly on museum collections and field research sponsored by the museum.

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APPENDIX I — Notharctine specimens from University of Michigan localities in or near the Clarks Fork Basin of northwestern Wyoming. Specimens of *Cantius torresi* and *Cantius ralstoni* from the 1520 through 1630 m levels are plotted in Figure 3 (see text for explanation). M₁ lengths and widths are in mm.

Locality	Specimen	M ₁ len.	M ₁ wid.	Ln L×W of M ₁	Locality	Specimen	M ₁ len.	M ₁ wid.	Ln L×W of M ₁
1520 meter level: <i>Cantius torresi</i>					1550 meter level: <i>Cantius ralstoni</i>				
SC067	UM 83470	3.19	2.87	2.214	SC182	UM 68761	3.80	3.10	2.466
SC067	UM 87341	3.47	2.96	2.329	SC182	UM 68778	3.40	3.00	2.322
SC067	UM 87852	3.49	2.93	2.325	1555 meter level: <i>Cantius ralstoni</i>				
SC067	UM 101958	3.24	2.55	2.112	SC026	UM 65188	3.60	2.90	2.346
1540 meter level: <i>Cantius ralstoni</i>					SC026	UM 65194	3.60	2.90	2.346
SC006	UM 64822	3.80	3.20	2.498	SC026	UM 65205	3.50	2.90	2.318
SC006	UM 64829	3.80	3.20	2.498	SC026	UM 65217	3.60	2.80	2.311
SC006	UM 64850	3.70	3.10	2.440	1560 meter level: <i>Cantius ralstoni</i>				
SC006	UM 66338	3.60	3.00	2.380	SC039	UM 76830	3.90	3.20	2.524
SC006	UM 66346	3.60	3.10	2.412	1570 meter level: <i>Cantius ralstoni</i>				
SC006	UM 68008	3.90	3.20	2.524	SC004	UM 64589	3.40	3.10	2.355
SC006	UM 72905	3.20	2.90	2.228	SC004	UM 64593	3.60	2.90	2.346
SC006	UM 79393	3.50	2.90	2.318	SC004	UM 64613	3.60	3.10	2.412
SC006	UM 79417	3.60	3.10	2.412	SC004	UM 64614	3.60	3.20	2.444
SC006	UM 80591	3.80	3.30	2.529	SC004	UM 64646	4.00	3.30	2.580
SC006	UM 83451	3.60	3.00	2.380	SC004	UM 64662	3.80	3.60	2.616
SC006	UM 85576	3.40	2.70	2.217	SC004	UM 65133	4.00	3.20	2.549
SC006	UM 87838	3.70	3.00	2.407	SC004	UM 65135	3.70	3.10	2.440
SC006	UM 87840	3.60	3.10	2.412	SC004	UM 65143	3.70	2.90	2.373
1545 meter level: <i>Cantius ralstoni</i>					SC004	UM 65324	3.70	2.90	2.373
SC040	UM 69378	3.50	2.90	2.318	SC004	UM 65769	3.70	3.40	2.532
SC040	UM 69381	3.70	3.20	2.472	SC004	UM 66485	3.70	3.20	2.472
SC040	UM 80387	3.50	3.00	2.351	SC004	UM 66491	3.80	3.10	2.466
SC040	UM 80391	3.90	3.10	2.492	SC004	UM 66863	3.80	3.10	2.466
SC040	UM 87545	4.00	3.40	2.610	SC004	UM 67363	3.70	3.00	2.407
SC040	UM 87546	3.70	3.10	2.440	SC004	UM 67377	3.80	3.10	2.466
SC040	UM 87551	3.50	3.00	2.351	SC004	UM 72848	3.80	3.30	2.529
SC040	UM 87565	3.50	2.90	2.318	SC004	UM 72890	3.80	3.20	2.498
SC040	UM 88330	3.80	3.30	2.529	SC004	UM 73889	3.50	3.20	2.416
SC124	UM 76447	3.50	3.00	2.351	SC004	UM 80790	3.60	3.10	2.412
SC124	UM 76459	3.70	3.20	2.472	SC004	UM 83080	3.70	3.20	2.472
SC125	UM 66894	3.60	3.00	2.380	SC004	UM 85565	3.60	3.10	2.412
SC125	UM 83763	3.90	3.40	2.585	SC004	UM 85569	3.50	2.90	2.318
SC142	UM 67261	4.00	3.30	2.580	SC004	UM 85572	3.70	3.20	2.472

Locality	Specimen	M ₁ len.	M ₁ wid.	Ln L×W of M ₁	Locality	Specimen	M ₁ len.	M ₁ wid.	Ln L×W of M ₁
1590 meter level: <i>Cantius ralstoni</i>					SC007	UM 80169	3.80	3.40	2.559
SC316	UM 80174	3.70	3.30	2.502	SC007	UM 83307	3.70	2.90	2.373
SC316	UM 80197	3.60	3.10	2.412	SC038	UM 65368	3.60	3.20	2.444
SC316	UM 80202	3.80	3.20	2.498	SC038	UM 75803	3.80	3.10	2.466
SC316	UM 80215	3.60	3.10	2.412	SC038	UM 75804	3.60	2.80	2.311
SC316	UM 80217	3.80	3.10	2.466	SC038	UM 76111	3.70	3.20	2.472
SC316	UM 80300	3.70	3.20	2.472	SC038	UM 76123	3.70	3.00	2.407
SC316	UM 80301	3.90	3.30	2.555	SC038	UM 76125	3.70	3.00	2.407
SC316	UM 80313	4.10	3.50	2.664	SC038	UM 76126	3.60	2.90	2.346
SC316	UM 80327	3.80	3.20	2.498	SC042	UM 65407	3.90	3.20	2.524
SC316	UM 80331	3.80	3.00	2.434	SC042	UM 65409	3.80	3.20	2.498
1600 meter level: <i>Cantius ralstoni</i>					SC151	UM 67435	3.80	3.20	2.498
C017	UM 64964	3.70	3.00	2.407	SC210	UM 74124	3.80	3.30	2.529
SC017	UM 64983	3.60	3.20	2.444	SC210	UM 75358	3.80	3.00	2.434
SC017	UM 73742	4.00	3.30	2.580	SC210	UM 75661	3.60	3.00	2.380
1610 meter level: <i>Cantius ralstoni</i>					SC210	UM 75662	3.70	3.30	2.502
SC094	UM 66357	3.90	3.30	2.555	SC210	UM 76638	3.80	3.30	2.529
SC094	UM 66366	3.70	3.30	2.502	SC210	UM 83089	4.00	3.20	2.549
SC094	UM 77016	3.90	3.30	2.555	SC210	UM 83090	3.60	3.10	2.412
SC304	UM 75751	3.70	3.20	2.472	SC210	UM 83099	3.80	3.40	2.559
1620 meter level: <i>Cantius ralstoni</i>					SC210	UM 87411	3.70	3.20	2.472
SC018	UM 64988	3.60	3.00	2.380	SC210	UM 87440	3.70	3.00	2.407
SC018	UM 76030	3.90	3.20	2.524	SC210	UM 87473	4.00	3.30	2.580
1630 meter level: <i>Cantius ralstoni</i>					SC305	UM 76066	3.50	2.80	2.282
SC015	UM 75299	3.80	3.30	2.529	SC305	UM 76068	3.90	3.30	2.555
SC015	UM 75324	3.50	2.70	2.246	SC305	UM 76074	3.60	3.20	2.444
SC016	UM 64916	3.70	3.00	2.407	SC305	UM 76081	3.60	3.20	2.444
SC016	UM 64919	3.60	3.40	2.505	SC305	UM 76083	3.50	2.70	2.246
SC016	UM 64925	3.50	3.00	2.351	SC305	UM 76098	3.90	3.40	2.585
SC016	UM 64926	3.80	3.10	2.466	SC305	UM 76105	3.70	3.00	2.407
SC016	UM 64927	3.60	3.00	2.380	SC305	UM 76106	3.80	3.10	2.466
SC016	UM 75355	3.50	2.80	2.282	1665 meter level: <i>Cantius ralstoni</i>				
SC037	UM 69429	3.50	3.00	2.351	SC001	UM 68160	3.80	3.00	2.434
SC037	UM 75762	3.50	2.80	2.282	SC001	UM 75968	3.50	2.80	2.282
SC037	UM 75942	3.60	3.00	2.380	SC001	UM 75973	4.10	3.60	2.692
1645 meter level: <i>Cantius ralstoni</i>					SC001	UM 81969	3.70	3.20	2.472
SC007	UM 64689	3.90	3.30	2.555	SC161	UM 68192	4.10	3.40	2.635
SC007	UM 67550	3.90	3.40	2.585	SC161	UM 68332	3.70	2.90	2.373
					SC161	UM 68395	3.80	3.20	2.498
					SC161	UM 68643	3.70	3.10	2.440
					SC161	UM 68657	4.20	3.20	2.598

Locality	Specimen	M ₁ len.	M ₁ wid.	Ln L×W of M ₁	Locality	Specimen	M ₁ len.	M ₁ wid.	Ln L×W of M ₁
SC161	UM 68661	3.80	3.20	2.498	SC046	UM 76594	4.00	3.20	2.549
SC161	UM 68670	3.90	3.10	2.492	SC046	UM 83368	3.60	3.20	2.444
SC161	UM 68711	3.70	3.10	2.440	SC046	UM 86371	3.80	3.20	2.498
SC161	UM 68829	4.00	3.10	2.518	SC046	UM 86386	4.00	3.10	2.518
SC161	UM 68842	3.90	3.10	2.492	SC046	UM 86400	4.00	3.00	2.485
SC161	UM 77472	3.90	3.20	2.524	SC046	UM 86409	3.70	3.20	2.472
SC161	UM 77491	3.80	3.30	2.529	SC046	UM 86445	4.10	3.20	2.574
SC161	UM 79044	4.00	3.10	2.518	SC046	UM 86474	3.80	3.20	2.498
SC161	UM 79065	3.70	3.10	2.440	SC054	UM 65571	3.90	3.10	2.492
SC161	UM 79093	3.80	3.00	2.434	SC054	UM 65615	4.10	3.40	2.635
SC161	UM 79096	4.10	3.50	2.664	SC054	UM 66929	4.10	3.70	2.719
SC161	UM 79112	3.90	3.20	2.524	SC054	UM 66941	3.90	3.10	2.492
SC161	UM 79121	3.90	3.10	2.492	SC054	UM 66948	4.20	3.60	2.716
SC161	UM 80522	3.70	3.10	2.440	SC054	UM 66967	4.00	3.30	2.580
SC161	UM 80541	3.70	3.20	2.472	SC054	UM 66995	4.00	3.20	2.549
SC161	UM 80690	3.80	3.10	2.466	SC054	UM 67006	4.20	3.40	2.659
SC161	UM 80698	3.80	3.30	2.529	SC054	UM 68553	4.00	3.30	2.580
SC161	UM 80702	3.80	3.10	2.466	SC054	UM 68583	4.00	3.00	2.485
SC161	UM 82269	4.00	3.20	2.549	SC054	UM 80062	3.80	3.30	2.529
SC161	UM 82282	4.10	3.50	2.664	SC054	UM 80096	3.70	2.90	2.373
SC161	UM 82467	4.00	3.60	2.667	SC054	UM 82229	3.90	3.40	2.585
SC161	UM 82472	3.60	3.20	2.444	SC054	UM 82234	4.00	3.50	2.639
SC161	UM 86033	3.60	3.10	2.412	SC054	UM 83420	3.70	3.20	2.472
SC161	UM 86072	3.70	3.00	2.407	SC311	UM 76618	3.90	3.30	2.555
SC161	UM 86084	4.00	3.40	2.610					
SC161	UM 86108	3.80	3.00	2.434	1720 meter level: <i>Cantius mckennai</i>				
SC211	UM 73843	3.80	3.00	2.434	SC002	UM 64747	3.90	3.50	2.614
SC211	UM 73845	3.70	3.00	2.407	SC002	UM 66563	4.00	3.10	2.518
SC211	UM 73847	4.00	3.30	2.580	SC002	UM 67493	3.80	3.30	2.529
SC211	UM 73849	4.10	3.20	2.574	SC002	UM 68296	4.00	3.50	2.639
					SC002	UM 68297	4.00	3.50	2.639
1690 meter level: <i>Cantius mckennai</i>					SC002	UM 68303	3.90	3.50	2.614
SC047	UM 66381	4.00	3.50	2.639	SC002	UM 68315	4.10	3.50	2.664
SC047	UM 74118	3.90	3.40	2.585	SC002	UM 68316	3.90	3.20	2.524
SC047	UM 74121	3.70	3.10	2.440	SC002	UM 71247	4.00	3.40	2.610
SC047	UM 86312	4.00	3.20	2.549	SC002	UM 71251	3.90	3.00	2.460
SC047	UM 86317	3.90	3.20	2.524	SC002	UM 76342	3.70	3.10	2.440
SC047	UM 86524	3.80	3.20	2.498	SC002	UM 76351	4.10	3.50	2.664
					SC002	UM 76364	3.80	3.40	2.559
1700 meter level: <i>Cantius mckennai</i>					SC002	UM 78929	4.00	3.40	2.610
SC046	UM 65448	4.00	3.20	2.549	SC002	UM 80029	4.00	3.60	2.667
SC046	UM 67412	4.00	3.20	2.549	SC002	UM 80477	3.80	3.10	2.466

Locality	Specimen	M ₁ len.	M ₁ wid.	Ln L×W of M ₁	Locality	Specimen	M ₁ len.	M ₁ wid.	Ln L×W of M ₁
SC002	UM 80482	3.90	3.30	2.555	SC133	UM 79721	3.90	3.10	2.492
SC002	UM 80484	3.80	3.20	2.498	SC133	UM 79729	4.00	3.40	2.610
SC002	UM 80835	3.90	3.20	2.524	SC133	UM 79736	4.20	3.70	2.743
SC002	UM 81934	3.90	3.20	2.524	SC133	UM 79748	3.90	3.10	2.492
SC002	UM 85852	3.80	3.20	2.498	SC133	UM 79760	4.20	3.60	2.716
SC002	UM 85880	3.90	3.30	2.555	SC133	UM 79764	3.90	3.30	2.555
SC002	UM 87370	4.20	3.40	2.659	SC133	UM 82702	3.80	3.20	2.498
SC002	UM 87381	3.70	3.30	2.502	SC133	UM 82742	3.70	3.10	2.440
SC012	UM 64772	3.80	3.20	2.498	SC133	UM 82752	4.20	3.80	2.770
SC160	UM 68126	4.10	3.30	2.605	SC133	UM 83582	3.80	3.30	2.529
SC160	UM 68143	3.90	3.30	2.555	SC133	UM 83588	4.20	3.50	2.688
SC160	UM 68495	4.00	3.20	2.549	SC133	UM 83607	4.10	3.70	2.719
SC160	UM 68498	3.70	3.40	2.532	SC133	UM 85821	4.20	3.70	2.743
SC160	UM 68502	3.90	3.30	2.555	SC207	UM 69464	4.10	3.50	2.664
SC160	UM 68505	4.00	3.30	2.580	SC207	UM 69467	4.00	3.70	2.695
SC160	UM 75107	3.80	3.20	2.498	SC207	UM 69501	4.10	3.70	2.719
SC160	UM 75108	4.00	3.50	2.639	SC207	UM 69502	4.30	3.40	2.682
SC160	UM 82793	3.90	3.10	2.492	SC207	UM 69506	4.00	3.30	2.580
SC160	UM 82794	3.90	3.10	2.492	SC207	UM 69528	4.30	3.60	2.740
1740 meter level: <i>Cantius mckennai</i>					SC207	UM 69561	4.20	3.50	2.688
SC131	UM 76727	3.90	3.20	2.524	SC207	UM 79997	4.40	3.30	2.676
SC300	UM 77546	4.00	3.30	2.580	SC207	UM 79999	4.10	3.60	2.692
SC300	UM 83323	4.20	3.60	2.716	SC207	UM 82803	4.00	3.50	2.639
1750 meter level: <i>Cantius mckennai</i>					SC207	UM 82811	3.90	3.50	2.614
SC005	UM 76415	4.10	3.60	2.692	SC207	UM 82814	3.80	3.10	2.466
SC005	UM 81927	3.80	3.10	2.466	SC207	UM 82828	4.30	3.60	2.740
SC088	UM 66245	4.00	3.40	2.610	SC207	UM 83495	3.80	3.30	2.529
SC088	UM 86170	3.80	3.60	2.616	SC207	UM 86331	4.00	3.20	2.549
SC088	UM 86194	4.50	3.90	2.865	SC212	UM 69748	3.90	3.50	2.614
SC133	UM 68090	4.20	3.50	2.688	SC310	UM 84766	4.00	3.50	2.639
SC133	UM 68101	4.00	3.40	2.610	SC310	UM 84771	3.80	3.60	2.616
SC133	UM 68111	3.90	3.50	2.614	SC310	UM 84772	4.00	3.50	2.639
SC133	UM 68117	3.90	3.20	2.524	SC310	UM 84773	3.90	3.30	2.555
SC133	UM 68471	3.80	3.20	2.498	SC310	UM 84774	3.80	3.30	2.529
SC133	UM 68476	4.10	3.30	2.605	SC310	UM 84776	3.80	3.30	2.529
SC133	UM 68483	4.00	3.40	2.610	SC310	UM 84783	3.80	3.10	2.466
SC133	UM 75067	4.20	3.80	2.770	SC310	UM 85621	4.20	3.50	2.688
SC133	UM 75084	3.90	3.40	2.585	SC310	UM 86552	4.10	3.70	2.719
SC133	UM 79698	3.80	3.10	2.466	1760 meter level: <i>Cantius mckennai</i>				
SC133	UM 79708	3.80	3.30	2.529	SC031	UM 65280	4.20	3.80	2.770
					SC031	UM 76502	3.90	3.10	2.492

Locality	Specimen	M ₁ len.	M ₁ wid.	Ln L×W of M ₁	Locality	Specimen	M ₁ len.	M ₁ wid.	Ln L×W of M ₁
SC087	UM 66221	3.90	3.10	2.492	SC213	UM 82164	3.70	3.30	2.502
SC087	UM 66237	4.00	3.40	2.610	SC213	UM 82184	4.10	3.30	2.605
SC087	UM 66279	4.10	3.60	2.692	SC213	UM 82187	4.10	3.70	2.719
SC087	UM 66281	4.10	3.50	2.664	SC213	UM 84675	4.20	3.50	2.688
SC087	UM 68529	4.20	3.70	2.743	SC213	UM 85500	4.20	3.40	2.659
SC087	UM 68536	4.10	3.40	2.635	SC221	UM 71158	4.30	3.50	2.711
SC087	UM 68541	4.10	3.20	2.574	SC221	UM 79787	4.00	3.40	2.610
SC087	UM 76511	4.10	3.60	2.692	SC221	UM 79804	4.00	3.50	2.639
SC087	UM 79825	3.80	3.10	2.466	SC312	UM 76662	4.00	3.50	2.639
SC087	UM 79830	4.00	3.30	2.580	SC312	UM 76666	3.80	3.60	2.616
SC087	UM 82155	4.00	3.40	2.610	SC312	UM 76667	3.90	3.50	2.614
SC087	UM 85535	4.00	3.40	2.610	SC312	UM 76668	4.00	3.50	2.639
SC087	UM 85536	4.00	3.70	2.695	SC312	UM 76669	4.30	3.60	2.740
SC095	UM 76645	3.80	3.20	2.498	SC312	UM 76671	4.40	3.90	2.843
SC095	UM 82538	3.90	3.50	2.614	SC312	UM 76677	3.90	3.40	2.585
SC213	UM 69828	4.10	3.30	2.605	SC312	UM 82548	4.00	3.50	2.639
SC213	UM 69837	4.10	3.40	2.635	SC312	UM 82558	4.50	3.70	2.812
SC213	UM 71055	4.50	3.60	2.785	SC312	UM 82561	4.20	3.50	2.688
SC213	UM 71075	4.10	3.70	2.719	SC312	UM 82563	4.10	3.60	2.692
SC213	UM 71076	4.00	3.30	2.580	SC341	UM 84893	4.30	3.70	2.767
SC213	UM 71077	3.90	3.40	2.585					
SC213	UM 71098	4.00	3.60	2.667	1810 meter level: <i>Cantius mckennai</i>				
SC213	UM 71101	4.10	3.70	2.719	SC321	UM 83527	4.20	3.50	2.688
SC213	UM 71104	4.20	3.60	2.716	1815 meter level: <i>Cantius mckennai</i>				
SC213	UM 71109	4.00	3.40	2.610	SC224	UM 71292	4.20	3.40	2.659
SC213	UM 71125	3.90	3.20	2.524	SC224	UM 82978	4.30	3.80	2.794
SC213	UM 71137	4.00	3.40	2.610	SC290	UM 73824	3.90	3.40	2.585
SC213	UM 71149	4.10	3.60	2.692	1840 meter level: <i>Cantius mckennai</i>				
SC213	UM 71392	3.90	3.40	2.585	SC033	UM 78974	4.30	3.70	2.767
SC213	UM 71401	3.90	3.20	2.524	SC225	UM 83541	4.30	3.40	2.682
SC213	UM 71667	4.30	3.70	2.767	SC225	UM 83544	4.30	3.60	2.740
SC213	UM 79495	4.00	3.40	2.610	SC236	UM 71541	4.20	3.40	2.659
SC213	UM 79533	4.00	3.40	2.610	SC236	UM 71543	4.40	3.70	2.790
SC213	UM 79564	4.10	3.40	2.635	SC236	UM 71593	4.00	3.30	2.580
SC213	UM 79604	4.20	2.70	2.428	1850 meter level: <i>Cantius mckennai</i>				
SC213	UM 79618	4.10	3.50	2.664	SC034	UM 71534	4.30	3.60	2.740
SC213	UM 79636	4.20	3.60	2.716	SC034	UM 73815	4.20	3.60	2.716
SC213	UM 79656	4.00	3.30	2.580	SC034	UM 73916	4.40	3.60	2.763
SC213	UM 81835	4.00	3.40	2.610	SC034	UM 76768	4.30	3.80	2.794
SC213	UM 81839	4.00	3.30	2.580	SC128	UM 67034	4.20	3.50	2.688
SC213	UM 81844	4.20	3.30	2.629					
SC213	UM 82153	4.00	3.40	2.610					

Locality	Specimen	M ₁ len.	M ₁ wid.	Ln L×W of M ₁	Locality	Specimen	M ₁ len.	M ₁ wid.	Ln L×W of M ₁
SC128	UM 67155	4.10	3.60	2.692	1970 meter level: <i>Cantius trigonodus</i>				
SC128	UM 67162	4.20	3.50	2.688	SC064	UM 65763	4.20	3.60	2.716
SC128	UM 79161	4.30	3.70	2.767	SC064	UM 66651	4.10	3.40	2.635
SC192	UM 69101	4.10	3.60	2.692	SC064	UM 66660	4.00	3.60	2.667
SC192	UM 69109	4.30	3.40	2.682	SC064	UM 66667	4.00	3.40	2.610
SC192	UM 69151	4.10	3.70	2.719	SC064	UM 72825	4.20	3.50	2.688
SC192	UM 69154	4.50	3.90	2.865	SC064	UM 72921	4.40	3.70	2.790
SC192	UM 69185	4.10	3.40	2.635	SC064	UM 72923	4.40	3.70	2.790
SC192	UM 69202	4.20	3.60	2.716	SC064	UM 72942	4.40	3.80	2.817
SC192	UM 69663	4.30	3.60	2.740	SC064	UM 72952	4.20	3.50	2.688
SC192	UM 79205	4.20	3.70	2.743	SC064	UM 74060	4.30	3.40	2.682
SC192	UM 79240	4.30	3.50	2.711	SC064	UM 79428	4.30	3.60	2.740
SC192	UM 79281	4.20	3.50	2.688	1995 meter level: <i>Cantius trigonodus</i>				
SC192	UM 79302	4.20	3.50	2.688	C324	UM 79446	4.30	3.50	2.711
SC192	UM 79314	4.10	3.50	2.664	SC324	UM 79447	4.40	3.50	2.734
SC192	UM 79329	4.50	3.80	2.839	SC324	UM 79452	4.60	3.80	2.861
SC192	UM 82855	4.40	3.80	2.817	2005 meter level: <i>Cantius trigonodus</i>				
SC192	UM 82905	4.10	3.30	2.605	SC111	UM 72960	4.30	3.70	2.767
SC192	UM 82934	4.00	3.40	2.610	SC111	UM 79902	4.40	3.50	2.734
SC192	UM 85743	4.10	3.40	2.635	SC111	UM 87621	4.10	3.50	2.664
SC237	UM 71602	4.20	3.90	2.796	2020 meter level: <i>Cantius trigonodus</i>				
SC237	UM 76802	4.30	3.80	2.794	SC112	UM 72972	4.00	3.30	2.580
SC237	UM 76812	4.30	3.70	2.767	SC112	UM 72979	4.50	3.90	2.865
SC237	UM 79016	4.10	3.50	2.664	2050 meter level: <i>Cantius trigonodus</i>				
SC237	UM 83069	4.00	3.50	2.639	SC113	UM 73633	4.30	3.60	2.740
1860 meter level: <i>Cantius mckennai</i>					SC113	UM 79941	4.40	3.30	2.676
SC314	UM 76820	4.00	3.10	2.518	SC148	UM 67343	4.30	3.80	2.794
1870 meter level: <i>Cantius mckennai</i>					SC148	UM 69716	4.40	3.40	2.705
SC035	UM 73938	4.50	3.90	2.865	SC255	UM 73086	4.40	3.60	2.763
SC035	UM 73940	4.10	3.40	2.635	SC255	UM 73117	4.50	3.90	2.865
1895 meter level: <i>Cantius mckennai</i>					SC255	UM 73167	4.40	3.70	2.790
SC036	UM 83025	4.30	3.80	2.794	SC255	UM 73183	4.20	3.60	2.716
SC036	UM 83032	4.10	3.70	2.719	SC255	UM 73209	4.50	3.60	2.785
SC036	UM 83036	4.10	3.40	2.635	SC255	UM 73238	4.40	3.60	2.763
SC232	UM 71718	4.40	3.60	2.763	SC255	UM 73279	4.30	3.60	2.740
1915 meter level: <i>Cantius mckennai</i>					SC255	UM 73281	4.00	3.30	2.580
SC114	UM 73026	3.90	3.30	2.555	SC255	UM 73282	4.40	3.50	2.734
1935 meter level: <i>Cantius mckennai</i>					SC255	UM 73304	4.40	3.50	2.734
SC003	UM 64549	4.30	3.50	2.711	SC255	UM 73310	4.50	3.60	2.785
					SC255	UM 75682	4.30	3.50	2.711

Locality	Specimen	M ₁ len.	M ₁ wid.	Ln L×W of M ₁	Locality	Specimen	M ₁ len.	M ₁ wid.	Ln L×W of M ₁
SC255	UM 75683	4.30	3.60	2.740	SC265	UM 73486	4.50	3.80	2.839
SC255	UM 75705	4.50	3.90	2.865	SC265	UM 80725	4.20	3.40	2.659
SC255	UM 80114	4.50	3.90	2.865	SC265	UM 80728	4.10	3.50	2.664
SC255	UM 80139	4.40	3.50	2.734	SC265	UM 83672	4.30	3.40	2.682
2065 meter level: <i>Cantius trigonodus</i>					SC265	UM 83688	4.30	3.40	2.682
SC145	UM 67296	4.40	3.60	2.763	SC265	UM 83690	4.30	3.50	2.711
SC146	UM 69713	4.40	3.60	2.763	SC265	UM 83715	4.40	3.70	2.790
SC147	UM 67312	4.20	3.40	2.659	SC265	UM 87704	4.00	3.50	2.639
SC147	UM 67314	4.40	3.60	2.763	2110 meter level: <i>Cantius trigonodus</i>				
SC297	UM 75024	4.60	3.80	2.861	SC303	UM 75717	4.50	3.60	2.785
2095 meter level: <i>Cantius trigonodus</i>					SC303	UM 80738	4.20	3.40	2.659
SC253	UM 74635	4.60	3.80	2.861	2240 meter level: <i>Cantius trigonodus</i>				
SC265	UM 73461	4.10	3.40	2.635	SC295	UM 87730	4.60	4.20	2.961

APPENDIX II — Type and related samples of notharctine species plotted in Figure 3. These are listed by genus for *Cantius*, *Copelemur*, *Pelycodus*, *Notharctus*, and *Smilodectes*. M₁ lengths and widths are in mm. Stratigraphic levels are in meters. Wyoming locality abbreviations: BB, Bridger Basin; BI, Big Island; MP, McCullough Peaks in the northern Bighorn Basin; SC, Sand Coulee in the northern Bighorn Basin; YM, Yale-Michigan in the central Bighorn Basin. The San Juan Basin is in New Mexico. Measurement sources (Meas.): AEC, Amy E. Chew; DAG, Daniel A. Guthrie; GFG, Gregg F. Gunnell; MAO, Maureen A. O'Leary; PDG, Philip D. Gingerich.

Specimen	Description	Locality	Bio-chron	M ₁ len.	M ₁ wid.	Ln L×W of M ₁	Level as plotted	Meas.	Remarks
Genus <i>Cantius</i> Simons 1962									
<i>Cantius torresi</i> Gingerich, 1986									
UM 83470	L dent P ₃ -M ₁	SC067	Wa-0	3.19	2.87	2.214	-105	PDG	Holotype
UM 87341	L and R dentaries	SC067	Wa-0	3.47	2.96	2.329	-105	PDG	
UM 87852	L and R dentaries	SC067	Wa-0	3.49	2.93	2.325	-105	PDG	
UM 101958	L and R dentaries	SC067	Wa-0	3.24	2.55	2.112	-105	PDG	
<i>Cantius ralstoni</i> (Matthew, 1915)									
AMNH 16088	Specimen w. M ₁	SC040	Wa-1	3.70	3.10	2.440	0	PDG	Holotype
AMNH 16089	R maxilla	SC040	Wa-1	—	—	—	0	PDG	
AMNH 16091	Specimen w. M ₁	SC040	Wa-1	3.50	3.00	2.351	0	PDG	
AMNH 16091	Specimen w. M ₁	SC040	Wa-1	3.60	3.10	2.412	0	PDG	
AMNH 16093	R dent. P ₃ -M ₂	SC040	Wa-1	3.70	3.20	2.471	0	PDG	
AMNH 16096	L dent. M ₁₋₃	SC040	Wa-1	3.70	3.20	2.471	0	PDG	
AMNH 16097	Specimen w. M ₁	SC040	Wa-1	3.80	3.20	2.498	0	PDG	
AMNH 94313	Specimen w. M ₁	SC040	Wa-1	3.70	3.10	2.440	0	PDG	
AMNH 94316	Specimen w. M ₁	SC040	Wa-1	3.50	2.90	2.317	0	PDG	
AMNH 94405	Specimen w. M ₁	SC040	Wa-1	3.80	2.90	2.400	0	PDG	
AMNH 94408	Specimen w. M ₁	SC040	Wa-1	3.70	3.00	2.407	0	PDG	
AMNH 94421	Specimen w. M ₁	SC040	Wa-1	3.40	2.80	2.253	0	PDG	
AMNH 94434	Specimen w. M ₁	SC040	Wa-1	3.70	3.30	2.502	0	PDG	
<i>Cantius mckennai</i> (Gingerich and Simons, 1977)									
UM 67087	L dent. w. M ₁	SC133	Wa-3	4.10	3.60	2.692	200	PDG	Holotype
UM 67089	Dent. w. M ₁	SC133	Wa-3	3.90	3.20	2.524	200	PDG	
UM 67102	R dent. w. M ₁	SC133	Wa-3	4.20	3.70	2.743	200	PDG	
UM 67113	Left max. M ₁₋₃	SC133	Wa-3	—	—	—	200	PDG	
UM 67123	R dent. w. M ₁	SC133	Wa-3	3.90	3.40	2.585	200	PDG	
UM 68090	R dent., L iso. lower	SC133	Wa-3	4.20	3.50	2.688	200	PDG	
UM 68101	L dent. w. M ₁	SC133	Wa-3	4.00	3.40	2.610	200	PDG	
UM 68111	L dent. w. M ₁	SC133	Wa-3	3.90	3.50	2.614	200	PDG	
UM 68117	R dent. w. M ₁	SC133	Wa-3	3.90	3.20	2.524	200	PDG	
UM 68471	L dent. w. M ₁	SC133	Wa-3	3.80	3.20	2.498	200	PDG	
UM 68476	L and R dent. w. M ₁	SC133	Wa-3	4.10	3.30	2.605	200	PDG	
UM 68483	R dent. w. M ₁	SC133	Wa-3	4.00	3.40	2.610	200	PDG	
UM 75067	R dent. w. M ₁ , L iso. upper	SC133	Wa-3	4.20	3.80	2.770	200	PDG	
UM 75084	L dent. w. M ₁	SC133	Wa-3	3.90	3.40	2.585	200	PDG	

Specimen	Description	Locality	Bio-chron	M ₁ len.	M ₁ wid.	Ln L×W of M ₁	Level as plotted	Meas.	Remarks
UM 79698	R dent. w. M ₁	SC133	Wa-3	3.80	3.10	2.466	200	PDG	
UM 79708	L dent. w. M ₁	SC133	Wa-3	3.80	3.30	2.529	200	PDG	
UM 79721	R dent. w. M ₁	SC133	Wa-3	3.90	3.10	2.492	200	PDG	
UM 79729	R dent. w. M ₁	SC133	Wa-3	4.00	3.40	2.610	200	PDG	
UM 79736	R dent. w. M ₁	SC133	Wa-3	4.20	3.70	2.743	200	PDG	
UM 79748	R dent. w. M ₁	SC133	Wa-3	3.90	3.10	2.492	200	PDG	
UM 79760	L dent. w. M ₁	SC133	Wa-3	4.20	3.60	2.716	200	PDG	
UM 79764	L dent. w. M ₁	SC133	Wa-3	3.90	3.30	2.555	200	PDG	
UM 82702	L dent. w. M ₁	SC133	Wa-3	3.80	3.20	2.498	200	PDG	
UM 82742	R iso. M ₁	SC133	Wa-3	3.70	3.10	2.440	200	PDG	
UM 82752	L dent. w. M ₁	SC133	Wa-3	4.20	3.80	2.770	200	PDG	
UM 83582	R dent. w. M ₁	SC133	Wa-3	3.80	3.30	2.529	200	PDG	
UM 83588	L dent. w. M ₁	SC133	Wa-3	4.20	3.50	2.688	200	PDG	
UM 83607	L dent. w. M ₁	SC133	Wa-3	4.10	3.70	2.719	200	PDG	
UM 85821	R iso. M ₁	SC133	Wa-3	4.20	3.70	2.743	200	PDG	
<i>Cantius trigonodus</i> (Matthew, 1915)									
AMNH 15017	R max. P ₄ -M ₃ , L dent. P ₃ -M ₃	5 mi. S Otto	Wa-5	4.40	3.60	2.763	390	PDG	Holotype
AMNH 15029	Specimen w. M ₁	5 mi. S Otto	Wa-5	4.90	4.30	3.048	390	PDG	
AMNH 15050	Specimen w. M ₁	5 mi. S Otto	Wa-5	4.40	3.60	2.763	390	PDG	
AMNH 15054	Specimen w. M ₁	5 mi. S Otto	Wa-5	4.20	3.50	2.688	390	PDG	
AMNH 15054	Specimen w. M ₁	5 mi. S Otto	Wa-5	4.20	3.40	2.659	390	PDG	
AMNH 15054	Specimen w. M ₁	5 mi. S Otto	Wa-5	4.20	3.40	2.659	390	PDG	
AMNH 15057	Specimen w. M ₁	5 mi. S Otto	Wa-5	4.40	3.70	2.790	390	PDG	
<i>Cantius abditus</i> (Gingerich and Simons, 1977)									
UM 65956	Specimen w. M ₁	YM045	Wa-6	4.90	4.20	3.024	470	PDG	
UM 65960	Specimen w. M ₁	YM045	Wa-6	4.80	4.00	2.955	470	PDG	
UM 66000	L and R dents. P ₃ -M ₃	YM045	Wa-6	4.80	4.40	3.050	470	PDG	Holotype
USGS 402	L M ₁₋₃	YM045	Wa-6	5.21	4.00	3.037	470	AEC	
USGS 403	L P ₃ -M ₁	YM045	Wa-6	5.22	4.06	3.054	470	AEC	
USGS 462	L M ₁₋₂	YM045	Wa-6	5.21	4.00	3.037	470	AEC	
USGS 1101	R P ₂₋₃ , R M ₁₋₂	YM045	wa-6	4.83	4.14	2.996	470	AEC	
USGS 1251	R M ₁ , R M ₂	YM045	Wa-6	5.31	4.09	3.078	470	AEC	
USGS 1258	L P ₄ , R M ₁	YM045	Wa-6	5.26	4.43	3.149	470	AEC	
USGS 1324	R M ₁₋₃	YM045	Wa-6	4.74	3.97	2.935	470	AEC	
USGS 1325	L P ₃ -M ₂	YM045	Wa-6	4.89	3.90	2.948	470	AEC	
USGS 4496	R M ₁₋₃	YM045	Wa-6	5.02	4.36	3.086	470	AEC	
USGS 6012	R P ₃ -M ₂	YM045	Wa-6	5.05	4.17	3.047	470	AEC	
USGS 6014	L P ₄ -M ₂	YM045	Wa-6	4.85	3.89	2.937	470	AEC	
USGS 6016	L M ₁	YM045	Wa-6	4.88	3.98	2.966	470	AEC	
USGS 6020	L M ₁	YM045	Wa-6	5.14	3.85	2.985	470	AEC	
USGS 6022	L M ₁	YM045	Wa-6	5.03	4.01	3.004	470	AEC	
USGS 6024	L M ₁	YM045	Wa-6	5.00	4.03	3.003	470	AEC	

Specimen	Description	Locality	Bio-chron	M ₁ len.	M ₁ wid.	Ln L×W of M ₁	Level as plotted	Meas.	Remarks
USGS 6102	L M ₁₋₃	YM045	Wa-6	5.24	4.14	3.077	470	AEC	
USGS 13735	L M ₁₋₃	YM045	Wa-6	5.13	4.16	3.061	470	AEC	
USGS 25178	L M ₂ , R M ₁₋₃ , R P ₃₋₄	YM045	Wa-6	5.05	4.38	3.096	470	AEC	
USNM 540663	R dent. P ₄ -M ₂	YM045	Wa-6	5.13	4.34	3.103	470	AEC	
USNM 540664	R dent. P ₂ -M ₂	YM045	Wa-6	4.46	3.92	2.861	470	AEC	
YPM 18639	Specimen w. M ₁	YM045	Wa-6	5.00	4.50	3.114	470	PDG	
YPM 18641	Specimen w. M ₁	YM045	Wa-6	5.00	4.40	3.091	470	PDG	
YPM 18642	Specimen w. M ₁	YM045	Wa-6	4.60	4.10	2.937	470	PDG	
YPM 18643	Specimen w. M ₁	YM045	Wa-6	4.70	4.10	2.959	470	PDG	
YPM 18644	Specimen w. M ₁	YM045	Wa-6	5.10	4.40	3.111	470	PDG	
YPM 18649	Specimen w. M ₁	YM045	Wa-6	4.90	4.20	3.024	470	PDG	
YPM 18679	Specimen w. M ₁	YM045	Wa-6	4.60	4.30	2.985	470	PDG	
YPM 23218	Specimen w. M ₁	YM045	Wa-6	5.20	4.50	3.153	470	PDG	
YPM 23284	Specimen w. M ₁	YM045	Wa-6	4.40	3.90	2.843	470	PDG	
YPM 23285	Specimen w. M ₁	YM045	Wa-6	4.90	4.30	3.048	470	PDG	
YPM 23323	Specimen w. M ₁	YM045	Wa-6	4.90	4.20	3.024	470	PDG	
YPM 27148	Specimen w. M ₁	YM045	Wa-6	4.80	4.10	2.980	470	PDG	
YPM 31010	Specimen w. M ₁	YM045	Wa-6	4.60	4.20	2.961	470	PDG	
<i>Cantius nunienus</i> (Cope, 1881)									
AMNH 4734	R dent. P ₃ -M ₃	Wind River B.	Wa-7	4.50	3.90	2.865	613	PDG	Holotype
AMNH 4736	Specimen w. M ₁	Wind River B.	Wa-7	4.40	3.90	2.843	613	PDG	
AMNH 4737c	Dent. M ₁₋₂	Wind River B.	Wa-7	4.60	4.10	2.937	613	PDG	
AMNH 12736	L and R dent. P ₂ -M ₃	Wind River B.	Wa-7	4.60	4.00	2.912	613	PDG	
Various	Mean values (n = 32)	Wind River B.	Wa-7	4.29	3.43	2.689	613	DAG	
Various	Mean values (n = 12)	South Pass	Br-1a	4.27	3.35	2.661	710	GFG	
<i>Cantius venticolus</i> Osborn, 1902									
AMNH 4715b	Specimen w. M ₁	Wind River B.	Wa-7	—	—	—	613	—	Holotype (not seen)
AMNH 4726	Dent. w. P ₃ -M ₁ , M ₃	Wind River B.	Wa-7	5.30	4.40	3.149	613	PDG	
AMNH 4728	Specimen w. M ₁	Wind River B.	Wa-7	5.10	4.20	3.064	613	PDG	
AMNH 14638	Dent. w. M ₁₋₃	Wind River B.	Wa-7	4.80	3.90	2.930	613	PDG	
AMNH 14639	Specimen w. M ₁	Wind River B.	Wa-7	4.70	3.90	2.909	613	PDG	
AMNH 14640	Specimen w. M ₁	Wind River B.	Wa-7	5.30	4.50	3.172	613	PDG	
AMNH 14641	Specimen w. M ₁	Wind River B.	Wa-7	5.10	4.20	3.064	613	PDG	
AMNH 14642	Specimen w. M ₁	Wind River B.	Wa-7	4.80	4.20	3.004	613	PDG	
AMNH 14646	Specimen w. M ₁	Wind River B.	Wa-7	5.20	4.50	3.153	613	PDG	
AMNH 14647	Specimen w. M ₁	Wind River B.	Wa-7	5.30	4.60	3.194	613	PDG	
AMNH 14650	Specimen w. M ₁	Wind River B.	Wa-7	5.30	4.60	3.194	613	PDG	
AMNH 14653	Specimen w. M ₁	Wind River B.	Wa-7	5.10	4.20	3.064	613	PDG	
AMNH 14655	Partial skull and jaws	Wind River B.	Wa-7	5.90	5.00	3.384	613	PDG	
AMNH 14657	Specimen w. M ₁	Wind River B.	Wa-7	5.40	4.50	3.190	613	PDG	
AMNH 93605	Dent. w. M ₁₋₂	Wind River B.	Wa-7	5.50	4.60	3.231	613	PDG	
Various	Mean values (n = 35)	Wind River B.	Wa-7	5.40	4.37	3.161	613	DAG	

Specimen	Description	Locality	Bio-chron	M ₁ len.	M ₁ wid.	Ln L×W of M ₁	Level as plotted	Meas.	Remarks
Various	Mean values (n = 6)	South Pass	Wa-7	5.30	4.16	3.093	710	GFG	
<i>Cantius simonsi</i> Gunnell, 2002									
UM 91592	R dent. P ₄ -M ₂	MP078	Wa-7	6.20	5.50	3.529	580	GFG	Holotype
Genus <i>Copelemur</i> Gingerich and Simons, 1977									
<i>Copelemur praetutus</i> (Gazin, 1962)									
USNM 22262	R dent. P ₃ -M ₂	Washakie B.	Wa-4	3.80	3.00	2.434	—	PDG	Holotype
YPM 31003	Specimen w. M ₁	YM365	Wa-4	3.90	3.10	2.492	310	PDG	
YPM 31072	Specimen w. M ₁	YM365	Wa-4	4.00	3.30	2.580	310	PDG	
<i>Copelemur feretutus</i> Gingerich and Simons, 1977									
ACM 4326	R M ₁	Wind River B.	Wa-6	4.20	3.60	2.716	443	PDG	Holotype
YPM-PU 18166	Specimen w. M ₁	Wind River B.	Wa-6	4.10	3.50	2.664	—	PDG	
YPM 18669	Specimen w. M ₁	YM044	Wa-6	4.20	3.40	2.659	463	PDG	
YPM 28199	Specimen w. M ₁	YM320	Wa-6	4.30	3.70	2.767	423	PDG	
<i>Copelemur consortutus</i> Gingerich and Simons, 1977									
YPM-PU 18282	L dent. M ₁₋₃	Wind River B.	Wa-7	4.00	3.20	2.549	613	PDG	Holotype
YPM-PU 20591	Specimen w. M ₁	Wind River B.	Wa-7	3.80	3.40	2.559	—	PDG	
YPM-PU 20593	Specimen w. M ₁	Wind River B.	Wa-7	4.00	3.40	2.610	—	PDG	
YPM-PU 20593	Specimen w. M ₁	Wind River B.	Wa-7	3.90	3.20	2.524	—	PDG	
YPM-PU 20595	Specimen w. M ₁	Wind River B.	Wa-7	4.10	3.30	2.605	—	PDG	
YPM 30419	Specimen w. M ₁	YM019	Wa-7	4.40	3.60	2.763	521	PDG	
YPM 17467	Specimen w. M ₁	YM016	Wa-7	4.00	3.50	2.639	541	PDG	
YPM 17703	Specimen w. M ₁	YM016	Wa-7	4.00	3.50	2.639	541	PDG	
YPM 23220	Specimen w. M ₁	YM077	Wa-7	4.20	3.50	2.688	501	PDG	
YPM 27466	Specimen w. M ₁	YM175	Wa-7	4.10	3.20	2.574	531	PDG	
YPM 27822	Specimen w. M ₁	YM177	Wa-7	4.10	3.40	2.635	511	PDG	
YPM 27829	Specimen w. M ₁	YM175	Wa-7	4.10	3.40	2.635	531	PDG	
YPM 27830	Specimen w. M ₁	YM175	Wa-7	3.80	3.20	2.498	531	PDG	
YPM 27831	Specimen w. M ₁	YM175	Wa-7	4.20	3.60	2.716	531	PDG	
YPM 27952	Specimen w. M ₁	YM185	Wa-7	4.20	3.30	2.629	531	PDG	
YPM 28125	Specimen w. M ₁	YM176	Wa-7	4.10	3.40	2.635	531	PDG	
YPM 28127	Specimen w. M ₁	YM176	Wa-7	4.00	3.50	2.639	531	PDG	
YPM 28128	Specimen w. M ₁	YM193	Wa-7	4.10	3.50	2.664	546	PDG	
YPM 28138	Specimen w. M ₁	YM193	Wa-7	3.90	3.30	2.555	546	PDG	
YPM 28152	Specimen w. M ₁	YM181	Wa-7	4.00	3.30	2.580	541	PDG	
YPM 28167	Specimen w. M ₁	YM181	Wa-7	4.20	3.80	2.770	541	PDG	
YPM 28168	Specimen w. M ₁	YM178	Wa-7	4.30	3.50	2.711	531	PDG	
YPM 28173	Specimen w. M ₁	YM185	Wa-7	4.30	3.70	2.767	531	PDG	
YPM 28178	Specimen w. M ₁	YM174	Wa-7	4.00	3.30	2.580	531	PDG	
YPM 28186	Specimen w. M ₁	YM185	Wa-7	4.30	3.60	2.740	531	PDG	
YPM 28191	Specimen w. M ₁	YM018A	Wa-7	4.20	3.50	2.688	491	PDG	
YPM 28192	Specimen w. M ₁	YM018A	Wa-7	4.40	3.30	2.676	491	PDG	

Specimen	Description	Locality	Bio-chron	M ₁ len.	M ₁ wid.	Ln L×W of M ₁	Level as plotted	Meas.	Remarks
YPM 28194	Specimen w. M ₁	YM190	Wa-7	4.20	3.60	2.716	541	PDG	
YPM 28196	Specimen w. M ₁	YM193	Wa-7	4.20	3.40	2.659	546	PDG	
YPM 28200	Specimen w. M ₁	YM176	Wa-7	4.40	3.60	2.763	531	PDG	
YPM 28217	Specimen w. M ₁	YM192	Wa-7	4.10	3.50	2.664	546	PDG	
YPM 28225	Specimen w. M ₁	YM193	Wa-7	4.10	3.20	2.574	546	PDG	
YPM 28231	Specimen w. M ₁	YM190	Wa-7	4.20	3.40	2.659	541	PDG	
YPM 28235	Specimen w. M ₁	YM192	Wa-7	4.00	3.40	2.610	546	PDG	
YPM 28239	Specimen w. M ₁	YM192	Wa-7	4.10	3.10	2.542	546	PDG	
YPM 28258	Specimen w. M ₁	YM192	Wa-7	4.10	3.50	2.664	546	PDG	
YPM 28274	Specimen w. M ₁	YM192	Wa-7	4.10	3.40	2.635	546	PDG	
YPM 28278	Specimen w. M ₁	YM192	Wa-7	3.90	3.20	2.524	546	PDG	
YPM 28517	Specimen w. M ₁	YM192	Wa-7	4.00	3.10	2.518	546	PDG	
YPM 29008	Specimen w. M ₁	YM181	Wa-7	4.10	3.50	2.664	541	PDG	
YPM 29758	Specimen w. M ₁	YM193	Wa-7	4.00	3.50	2.639	546	PDG	

Genus *Pelycodus* Cope, 1875

Pelycodus jarrovii Cope, 1874

AMNH 16298	L dent. M ₁₋₂	San Juan B.	Wa-6	5.6	4.7	3.270	—	PDG	Neotype
USGS 6549	L and R max., L dent. M ₁₋₃	USGS D-1459	Wa-6	—	—	3.379	438	MAO	

Genus *Notharctus* Leidy, 1870

Notharctus robinsoni Gingerich, 1979

AMNH 17478	R dent. P ₄ -M ₂	Huerf-ano II	Br-1b	5.70	4.70	3.288	775	PDG	
AMNH 55275	R dent. P ₃ -M ₂	Huerf-ano II	Br-1b	6.20	4.90	3.414	775	PDG	
UCM 29943	L dent. P ₃ -M ₁	Huerf-ano II	Br-1b	5.90	4.80	3.344	775	PDG	
UM 94862	R dent. P ₄ -M ₁	BB011	Br-1b	6.29	4.72	3.391	810	PDG	
UM 95607	L M ₁ , R dent. P ₃ , M ₁	BB037	Br-1b	5.60	4.48	3.222	810	PDG	
UM 99654	L M ₁	BB101	Br-1b	5.67	4.85	3.314	810	PDG	
UM 99923	L dent. P ₃ -M ₁ , R dent. M ₁ , M ₃	BB018	Br-1b	5.91	4.94	3.374	810	PDG	
UM 100435	R M ₁	BI007	Br-1b	5.42	4.43	3.178	810	PDG	
UM 100687	R M ₁	BI030	Br-1b	5.82	4.40	3.243	810	PDG	
UW 3007	L dent. P ₄ -M ₃	Opal 19-67	Br-1b	5.90	4.90	3.364	810	PDG	Holotype
UW 3020	Specimen R M ₁	Opal 34-67	Br-1b	5.60	4.40	3.204	810	PDG	

Notharctus tenebrosus Leidy, 1870

USNM 3752	R dent. C ₁ and P ₃ -M ₃	Blacks Fork	Br-2	5.70	4.20	3.176	915	PDG	Holotype
AMNH 11466	Specimen w. M ₁	Grizzly Buttes	Br-2	5.20	3.80	2.984	915	PDG	<i>N. osborni</i>
AMNH 11467	Specimen w. M ₁	Grizzly Buttes	Br-2	5.30	4.00	3.054	915	PDG	
AMNH 11469	Specimen w. M ₁	Grizzly Buttes	Br-2	5.30	4.30	3.126	915	PDG	
AMNH 11473	Specimen w. M ₁	Grizzly Buttes	Br-2	5.30	4.20	3.103	915	PDG	
AMNH 11481	Specimen w. M ₁	Grizzly Buttes	Br-2	5.20	3.70	2.957	915	PDG	
AMNH 12002	Specimen w. M ₁	Grizzly Buttes	Br-2	5.50	4.10	3.116	915	PDG	

Specimen	Description	Locality	Bio-chron	M ₁ len.	M ₁ wid.	Ln L×W of M ₁	Level as plotted	Meas.	Remarks
AMNH 13029	Specimen w. M ₁	Grizzly Buttes	Br-2	5.40	4.10	3.097	915	PDG	
AMNH 18985	Specimen w. M ₁	Grizzly Buttes	Br-2	5.30	4.00	3.054	915	PDG	
AMNH 18989	Specimen w. M ₁	Grizzly Buttes	Br-2	5.30	4.10	3.079	915	PDG	
AMNH 18990G	Specimen w. M ₁	Grizzly Buttes	Br-2	5.20	3.80	2.984	915	PDG	
AMNH 18990H	Specimen w. M ₁	Grizzly Buttes	Br-2	5.40	4.50	3.190	915	PDG	
USNM 21968	Specimen w. M ₁	Grizzly Buttes	Br-2	5.70	4.40	3.222	915	PDG	
USNM 21983	Specimen w. M ₁	Grizzly Buttes	Br-2	5.70	4.30	3.199	915	PDG	
USNM 21984	Specimen w. M ₁	Grizzly Buttes	Br-2	5.60	4.50	3.227	915	PDG	
YPM 11786A	Specimen w. M ₁	Grizzly Buttes	Br-2	5.40	4.00	3.073	915	PDG	<i>N. anceps</i>
YPM 11786B	Specimen w. M ₁	Grizzly Buttes	Br-2	5.40	4.20	3.121	915	PDG	
YPM 11795	Specimen w. M ₁	Grizzly Buttes	Br-2	5.30	3.80	3.003	915	PDG	<i>N. affinis</i>
YPM 11856	Specimen w. M ₁	Grizzly Buttes	Br-2	5.30	4.20	3.103	915	PDG	<i>N. tyrannus</i>
YPM 16223	Specimen w. M ₁	Grizzly Buttes	Br-2	5.50	4.20	3.140	915	PDG	
<i>Notharctus pugnax</i> Granger and Gregory, 1917									
AMNH 11461	L dent. P ₃ -M ₃	Millersville	Br-2	6.10	4.70	3.356	—	PDG	Holotype
AMNH 11480	R dent. C ₁ and P ₂ -M ₃	Grizzly Buttes	Br-2	6.40	5.30	3.524	915	PDG	
AMNH 12575	Specimen w. M ₁	Grizzly Buttes	Br-2	5.70	5.10	3.370	915	PDG	
AMNH 13022	Specimen w. M ₁	Grizzly Buttes	Br-2	5.80	4.80	3.326	915	PDG	
AMNH 14568	Specimen w. M ₁	Grizzly Buttes	Br-2	5.80	4.50	3.262	915	PDG	
YPM 12932A	Specimen w. M ₁	Grizzly Buttes	Br-2	6.10	5.00	3.418	915	PDG	
YPM 16224	Specimen w. M ₁	Grizzly Buttes	Br-2	6.30	5.10	3.470	915	PDG	
<i>Notharctus robustior</i> Leidy, 1872									
AMNH 11475	Specimen w. M ₁	Henrys Fork	Br-3	6.50	5.50	3.577	995	PDG	
AMNH 11982	Specimen w. M ₁	Henrys Fork	Br-3	6.50	5.50	3.577	995	PDG	
AMNH 11983	Specimen w. M ₁	Henrys Fork	Br-3	7.50	6.00	3.807	995	PDG	
AMNH 11992	Specimen w. M ₁	Henrys Fork	Br-3	6.50	5.20	3.520	995	PDG	
AMNH 11995	Specimen w. M ₁	Henrys Fork	Br-3	6.70	5.60	3.625	995	PDG	
USNM 3750	L dent. w. M ₂	Henrys Fork	Br-3	—	—	—	—	—	Holotype
USNM 3754	Specimen w. M ₁	Henrys Fork	Br-3	6.00	4.80	3.360	995	PDG	
USNM 13237	Specimen w. M ₁	Henrys Fork	Br-3	6.40	5.10	3.486	995	PDG	
USNM 13236	Specimen w. M ₁	Henrys Fork	Br-3	6.70	5.70	3.643	995	PDG	
USNM 30-258	Specimen w. M ₁	Henrys Fork	Br-3	7.00	5.50	3.651	995	PDG	
USNM 46-60	Specimen w. M ₁	Henrys Fork	Br-3	6.50	5.40	3.558	995	PDG	
USNM 13238	Specimen w. M ₁	Henrys Fork	Br-3	7.50	5.90	3.790	995	PDG	
YPM 11782	L max. M ₁₋₃ ; L dent P ₃ -M ₃	Henrys Fork	Br-3	6.80	5.70	3.657	995	PDG	<i>N. crassus</i>
YPM 12908	Specimen w. M ₁	Henrys Fork	Br-3	6.30	5.40	3.527	995	PDG	
YPM 12912	Specimen w. M ₁	Henrys Fork	Br-3	6.30	5.40	3.527	995	PDG	
YPM 12913	Specimen w. M ₁	Henrys Fork	Br-3	6.60	5.60	3.610	995	PDG	
YPM 12913	Specimen w. M ₁	Henrys Fork	Br-3	6.70	5.70	3.643	995	PDG	
YPM 12914	Specimen w. M ₁	Henrys Fork	Br-3	6.30	5.20	3.489	995	PDG	
YPM 12914	Specimen w. M ₁	Henrys Fork	Br-3	6.40	5.40	3.543	995	PDG	
YPM 12914	Specimen w. M ₁	Henrys Fork	Br-3	6.30	5.10	3.470	995	PDG	
YPM 12914	Specimen w. M ₁	Henrys Fork	Br-3	6.30	5.50	3.545	995	PDG	

Specimen	Description	Locality	Bio-chron	M ₁ len.	M ₁ wid.	Ln L×W of M ₁	Level as plotted	Meas.	Remarks
YPM 12915	Specimen w. M ₁	Henrys Fork	Br-3	6.00	5.90	3.567	995	PDG	
YPM 12928	Specimen w. M ₁	Henrys Fork	Br-3	6.50	5.60	3.595	995	PDG	
YPM 12928	Specimen w. M ₁	Henrys Fork	Br-3	7.10	5.90	3.735	995	PDG	
YPM 12930	Specimen w. M ₁	Henrys Fork	Br-3	7.00	5.90	3.721	995	PDG	
YPM 12934	Specimen w. M ₁	Henrys Fork	Br-3	6.50	5.10	3.501	995	PDG	
YPM 12934	Specimen w. M ₁	Henrys Fork	Br-3	6.40	5.60	3.579	995	PDG	
YPM 16227	Specimen w. M ₁	Henrys Fork	Br-3	6.40	5.10	3.486	995	PDG	
YPM 16228	Specimen w. M ₁	Henrys Fork	Br-3	6.30	5.50	3.545	995	PDG	
YPM 16230	Specimen w. M ₁	Henrys Fork	Br-3	6.30	5.30	3.508	995	PDG	
YPM 16231	Specimen w. M ₁	Henrys Fork	Br-3	6.40	5.30	3.524	995	PDG	
YPM 16232	Specimen w. M ₁	Henrys Fork	Br-3	6.80	5.60	3.640	995	PDG	

Genus *Smilodectes* Wortman, 1903

Smilodectes sororis Gunnell, 2002

UM 104807	R dent. M ₁₋₂	South Pass SP-24	Br-1a	4.60	3.50	2.779	715	GFG	Holotype
Various	Mean values (n = 7)	South Pass	Br-1a	4.47	3.52	2.756	715	GFG	

Smilodectes mcgrewi Gingerich, 1979

AMNH 17481	L dent. P ₄ -M ₂	Huerfano II	Br-1b	4.70	4.00	2.934	775	PDG	
AMNH 17494	L dent. C ₁ , P ₄ -M ₂ ; R dent. M ₁₋₂	Huerfano II	Br-1b	5.00	4.10	3.020	775	PDG	
AMNH 55157	Cranium, dentary w. teeth	Huerfano II	Br-1b	4.90	4.30	3.048	775	PDG	
AMNH 55158	R dent. P ₃ -M ₁ , M ₃	Huerfano II	Br-1b	5.20	4.10	3.060	775	PDG	
AMNH 55159	L C ₁ , M ₁ , M ₂	Huerfano II	Br-1b	5.00	3.90	2.970	775	PDG	
AMNH 55227	L dent. M ₂₋₃ ; R dent. M ₁₋₃	Huerfano II	Br-1b	4.60	3.90	2.887	775	PDG	
UCM 21478	R dent. M ₁₋₂	Huerfano II	Br-1b	4.50	3.90	2.865	775	PDG	
UM 94882	L dent. M ₁	BB016	Br-1b	4.55	3.69	2.821	810	PDG	
UM 99676	R dent. P ₄ -M ₁	BB105	Br-1b	4.70	3.73	2.864	810	PDG	
UM 100671	R dent. M ₁	BI030	Br-1b	4.43	3.46	2.730	810	PDG	
UM 100716	L dent. M ₁	BI031	Br-1b	5.08	3.56	2.895	810	PDG	
UM 100764	R dent. P ₃ -M ₁	BI034	Br-1b	4.89	3.84	2.933	810	PDG	
UM 100776	L dent. P ₄ -M ₁ , M ₃	BI034	Br-1b	4.50	3.42	2.734	810	PDG	
UM 100876	L dent. P ₄ -M ₁	BI016	Br-1b	4.65	3.54	2.801	810	PDG	
UM 101045	L dent. P ₃ -M ₁	BB007	Br-1b	4.47	3.52	2.756	810	PDG	
UM 101541	L M ₁	BB018	Br-1b	4.67	3.98	2.922	810	PDG	
UW 2977	Dent. w. M ₁₋₂	Opal 3-67	Br-1b	4.60	3.60	2.807	810	PDG	
UW 2978	R dent. w. P ₃ -M ₂	Opal 3-67	Br-1b	4.30	3.70	2.767	810	PDG	
UW 5021	L dent. w. P ₃ -M ₃	Blue Rim V-16	Br-1b	4.90	3.80	2.924	810	PDG	Holotype
UW 5031	Specimen w. M ₁	Blue Rim V-16	Br-1b	4.90	4.00	2.976	810	PDG	

Specimen	Description	Locality	Bio- chron	M ₁ len.	M ₁ wid.	Ln L×W of M ₁	Level as plotted	Meas.	Remarks
<i>Smilodectes gracilis</i> Wortman, 1903									
YPM 11800	L dent. P ₃ -M ₁	Grizzly Buttes	Br-2	4.40	3.40	2.705	915	PDG	Holotype
AMNH 12011	Specimen w. M ₁	Grizzly Buttes	Br-2	4.30	3.40	2.682	915	PDG	<i>N. matthewi</i>
AMNH 12589	Specimen w. M ₁	Grizzly Buttes	Br-2	4.60	3.40	2.750	915	PDG	
USNM 21956	Specimen w. M ₁	Grizzly Buttes	Br-2	4.40	3.50	2.734	915	PDG	
USNM 22038	Specimen w. M ₁	Grizzly Buttes	Br-2	4.60	3.60	2.807	915	PDG	