A Description and Phylogenetic Analysis of Three New Earliest Paleocene (Puercan) Periptychid ‘Condylarths’ from the Great Divide Basin, Wy

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A DESCRIPTION AND PHYLOGENETIC ANALYSIS OF THREE NEW EARLIEST PALEOCENE (PUERCAN) PERIPTYCHID ‘CONDYLARTHS’ FROM THE GREAT DIVIDE BASIN, WY

by

MADELAINE ATTEBERRY

B.S., University of Miami, 2016

A thesis submitted to the

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Department of Geological Sciences

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This thesis entitled:
A description and phylogenetic analysis of three new earliest Paleocene (Puercan) periptychid ‘condylarths’ from the Great Divide Basin, WY
Written by Madelaine Atteberry
has been approved for the Department of Geological Sciences.

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The final copy of this thesis has been examined by the signatories, and we find that both the content and the form meet acceptable presentation standards of scholarly work in the above-mentioned discipline.
A description and phylogenetic analysis of three new earliest Paleocene (Puercan) periptychid ‘condylarths’ from the Great Divide Basin, WY

Thesis directed by Professor & Curator of Fossil Vertebrates Dr. Jaelyn J. Eberle

An earliest Paleocene (Puercan) locality discovered by James and Jeannine Honey in the lower China Butte Member of the Fort Union Formation in Wyoming’s Great Divide Basin (GDB) contains a diverse mammalian faunal assemblage, including a number of ‘condylarth’ taxa. Previous studies have suggested that this faunal assemblage may be correlative with the early Puercan (Pu1) Littleton fauna in the Denver Basin, due to multiple shared taxa. From the University of Colorado Museum of Natural History (UCM) locality 2011035, I describe three new periptychid ‘condylarths’, in addition to the first occurrences of Maiorana noctiluca, Ampliconus antoni, and Conacodon harbourae from the GDB. The first new genus and species, Beornus honeyi, is based on a left dentary containing p3–m3. B. honeyi is 10–12% larger than Conacodon delphae (the largest documented species of Conacodon) and is similar in morphology to Auraria urbana, but differs in its relatively smaller molar paraconid, absence of a lingual cingulid, and more posteriorly-projecting m3 hypoconulid. A new species of Conacodon, C. hettingeri, is based on left and right dentaries containing Lp3–m3 and Rp4–m3, respectively. C. hettingeri is close in molar morphology to species of Conacodon, differing in its larger size and relatively less posteriorly-projecting m3 hypoconulid. Finally, the third new genus and species of periptychid from the GDB, Miniconus jeanninae, is based on two right dentaries containing p4–m3 and p3–m3, as well as a left dentary containing p4–m2. This new taxon is close in morphology to Oxyacodon archibaldi, sharing a distinct paraconulid, but differs
primarily in the more anterior placement of the entoconid. Based on its morphological similarity to *M. jeanninae* and its differences from other species of *Oxyacodon, O. archibaldi* is placed here within the new genus *Miniconus*. To examine the relationships of the three new GDB taxa to each other and to other Puercan periptychidss from the Western Interior of North America, a phylogenetic analysis was performed using 26 Puercan ‘condylarth’ taxa and 58 dental characters. Characters were aggregated from previous phylogenetic analyses of ‘condylarth’ taxa and scored based on comparative study with specimens from several museum collections as well as descriptions from the literature. The resulting strict consensus tree of 216 steps indicates that the three new periptychid species from the GDB are nested within Periptychidae. *B. honeyi* is closely related to *A. urbana* from the Denver Basin, whereas *C. hettingeri* belongs within the genus *Conacodon*, and *M. jeanninae* forms a clade with *Miniconus archibaldi*. The new genus *Miniconus* appears to be monophyletic, whereas the genus *Conacodon* is paraphyletic in my analysis. Additionally, the primitive, early Puercan ‘condylarth’ taxa *Mimatuta spp.* and *Maiorana noctiluca* fall within Periptychidae, supporting the traditional placement of these taxa within that family. *C. harbourae, A. antoni*, and *M. noctiluca*, which I report from the GDB, have been previously described elsewhere. The presence of *C. harbourae* in both the GDB and the Denver Basin suggests that the Littleton fauna is correlative with UCM locality 2011035. Also, the presence of *C. harbourae, A. antoni*, and *M. noctiluca* in Wyoming’s Hanna Basin confirms the hypothesis that the Great Divide and Hanna Basins were contiguous at the start of the Paleocene. Finally, the occurrence of the three new periptychid taxa in the GDB suggests that mammalian diversity is higher than previously thought for the early Puercan.
ACKNOWLEDGMENTS

Without the tremendous collecting and mapping efforts by the late James Honey and Malcolm McKenna, this window into a new early Puercan fauna would not exist. I want to thank Jeannine Honey for her valuable insight and logistical assistance with fossil collection and Bob Hettinger for his decades of careful and precise mapping of the stratigraphy of the Fort Union Formation. The fossil locality is on land administered by Wyoming Game and Fish and is located within the Red Rim-Daley Wildlife Habitat Management Area. This organization made collection of the fossil specimens included in this study possible through permits to James Honey and Jaelyn Eberle. More recent fieldwork associated with my thesis research was funded by a grant awarded to Dr. Jaelyn Eberle by the David B. Jones Foundation. The Department of Geological Sciences at the University of Colorado Boulder awarded me with a travel grant to attend the Geological Society of America (GSA) Rocky Mountain and Cordilleran Joint Section Meeting (2018) and the GSA Annual Meeting (2018), alongside a grant provided by the University of Colorado United Government of Graduate Students (UGGS). The University of Colorado Graduate School also awarded me a domestic travel scholarship to attend the 2018 GSA Annual Meeting in Indianapolis, IN.

I thank Toni Culver and Jacob Van Veldhuizen for providing access to the UCM specimens for the duration of my research, and Virginia Scott in the University of Colorado Museum’s Entomology Section for providing access to their superior imaging system. This research was also greatly assisted by Thomas Williamson (NMMNH) who provided access to the collection at the New Mexico Museum of Natural History. I thank Nicole Neu-Yagle for training me on using the imaging system in my very first week as a graduate student, and I thank the rest of my cohort of graduate students for their invaluable support and acceptance over the past years.
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I.

INTRODUCTION

Mammalian extinction levels spanning the Cretaceous-Paleogene (K-Pg) boundary are estimated to be as high as 75–93% (Wilson, 2014; Longrich et al., 2016). Nevertheless, a number of mammalian species survived into the Cenozoic, diversifying and taking advantage of resources made available by the K-Pg extinction. Recent studies have determined local faunal turnover to have occurred earlier than previously hypothesized, with mammalian recovery underway within the first ~320 ky after the K-Pg extinction (Smith et al., 2018). Additionally, the local recovery faunas in NE Montana reported by Smith et al. (2018, p. 12) “broadly resemble” other earliest Paleocene (Puercan; specifically, Pu1) faunas throughout the Western Interior of North America. Puercan mammalian faunas are documented at fossil localities in New Mexico, Wyoming, Montana, Colorado, Utah, Texas, North Dakota, and Canada (Lofgren et al., 2004, fig. 3.2). In particular, the Hanna Basin in south-central Wyoming has produced early–late Puercan faunas (Eberle & Lillegraven, 1998a, 1998b), and the Littleton fauna in the Denver Formation of Colorado preserves a diverse early Puercan fauna that includes a number of taxa that have yet to be documented anywhere else (Middleton & Dewar, 2004). Below, I describe six early Puercan periptychid ‘condylarth’ taxa, including three new periptychids, from the University of Colorado Museum of Natural History (UCM) locality 2011035 in the lower China Butte Member of the Fort Union Formation in the Great Divide Basin (GDB) of south-central Wyoming. These are only the second report of Puercan ‘condylarths’ from the GDB. The first, a new arctocyonid ‘condylarth,’ was described by McComas & Eberle (2015).

Some authors hypothesize that local mammal diversity was amplified by immigrant taxa following the K-Pg extinction event (Clemens, 2010; Wilson, 2013). Species whose ancestors or
sister taxa that do not precede them in the surrounding geographic area are classified as immigrant taxa, whereas species that are present or represented by a sister taxon in a fauna of the preceding NALMA are residents (Clemens, 2002). Immigrant taxa in the earliest Paleocene were dominated by ‘condylarths’, and immigrant taxa outnumbered resident taxa by nine to five at the generic level (Clemens, 2010). ‘Condylarths’ are paraphyletic and phylogenetically poorly understood archaic ungulates (Archibald, 1998). Morphologically primitive, generalized taxa have been assigned to ‘Condylarthra’ for decades (e.g., Van Valen, 1978; Archibald, 1982, 1998; Luo, 1991; Eberle & Lillegraven, 1998b; Middleton & Dewar, 2004), and ‘condylarths’ are widely represented in early Paleocene faunas. There is cause for the disuse of the term ‘Condylarthra’, given its paraphyly and status as a “waste-basket taxon” (Archibald, 1998). However, until a more appropriate taxonomic designation exists, I use the name ‘Condylarthra’ to refer to the taxa described below, and I follow others in placing quotation marks around it to indicate that it is non-monophyletic.

Taxa belonging to Periptychidae, a traditional ‘condylarth’ family, were among the first mammalian taxa to appear following the K-Pg extinction (Shelley et al., 2018). Periptychidae includes approximately 40 species (Shelley, 2018) and the family ranges from the early Puercan (Pu1) through middle Tiffanian (Ti4) of the Paleocene. Periptychids are known primarily from dental material, and their bulbous cheek teeth, which in some taxa possess crenulated enamel, are distinctive among early Paleocene mammals (Rose, 2006). The body size among Periptychidae ranges from approximately the size of a rat to the size of a sheep. Wilson (2013) estimated the body mass of Mimatuta minuial to be about 0.33 kg, Dewar (2003) found Conacodon harbourae to be about 1.3 kg, and Shelley et al. (2018) estimated Ectoconus to be about 100 kg. To the exclusion of Archibald (1982, 1993), McComas & Eberle (2015), and the currently unpublished
PhD dissertation by Shelley (2018), few phylogenetic studies in the past have included very many periptychid taxa in their analyses. When they have, they have focused on the basal ‘condylarths’ *Mimatuta* spp. and *Maiorana noctiluca* which were traditionally placed in the periptychids, although more recent analyses have suggested that they may instead belong in Arctocyonidae (Luo, 1991; Williamson & Carr, 2007; Tabuce *et al*., 2011; De Bast & Smith, 2013; McComas & Eberle, 2015; Shelley, 2018). Here, I have conducted a phylogenetic analysis that includes 26 ‘condylarth’ taxa to determine the phylogenetic relationships of the three new taxa from the GDB described below.
II.

GEOLOGIC SETTING AND HISTORY OF COLLECTING

The Great Divide Basin (GDB) is located in south-central Wyoming, in the eastern part of the Greater Green River Basin (GGRB; Figure 1; Hettinger et al., 2008). The GDB is bounded on the southwest by the Rock Springs Uplift (Kirschbaum et al., 1994), and on the south by the Wamsutter Arch (Love, 1961) which separates it from the Washakie Basin. The Granite Mountains Uplift bounds the Great Divide Basin to the north (Hettinger et al., 2008), and to the east is the Rawlins Uplift, which separates the GDB from the Hanna Basin (Lillegraven et al., 2004). The Rawlins Uplift is a Laramide, anticlinal fold that was elevated due to basement-involved faulting in the latest Paleocene and early Eocene (Barlow, 1953; Lillegraven et al., 2004). During the early Paleocene, the GDB and the Hanna Basin were contiguous as components of the GGRB, but by the end of the Paleocene they were separated by the Rawlins Uplift (Lillegraven et al., 2004). It is hypothesized that the Rawlins Uplift and other uplifts in the GGRB are Laramide in origin due to their similarity to other Wyoming foreland Laramide uplifts whose specific structural style fundamentally involves the basement craton (Barlow, 1953; Brown, 1988; Lillegraven et al., 2004; Otteman & Snoke, 2005). Lillegraven (2015) noted that his original field work in the Hanna Basin raised questions involving the specific timing of those structural events beyond simply “Laramide” (Lillegraven et al., 2004). Otteman & Snoke (2005) noted that concentrated study of the stratigraphy and paleontology around the Rawlins Uplift would help to constrain the timing of its structural development. Flat Top anticline in the northeastern Hanna Basin, at least, is constrained to be very late Paleocene or early Eocene in age because nearly the entire thickness of the Hanna Basin existed prior to that uplift, which preserves lower Paleocene strata that was thrust onto the anticline as it was uplifted (Lillegraven
et al., 2004). Additionally, Lillegraven (2015) commented that the Hanna and Ferris formations of the Hanna Basin must have extended westward before the GGRB was subdivided, and their correlatives in the GDB are now referred to as the Lance, Fort Union, and Wasatch formations. These formations can be correlated on the basis of mammalian biostratigraphy.

The Paleocene Fort Union Formation in the GDB documents the complicated early Cenozoic basin evolution following the recession of the Western Interior Seaway, and its beds preserve fluvial and coal deposits of southeast-flowing rivers and peat swamps, respectively (Lynds & Carroll, 2015). The stratigraphy of the Fort Union Formation has been characterized by a number of studies (Hettinger et al., 1991; Hettinger & Kirschbaum, 1991; Honey & Hettinger, 2004; Hettinger et al., 2008). Hettinger et al. (2008) provide the most detailed report of the formation and its members, placing particular emphasis on coal-bearing strata. Honey and Hettinger (2004) subdivided the Fort Union Formation into three members spanning the Great Divide, Washakie, and Sand Wash Basins: the oldest China Butte Member (lower Paleocene), the Blue Gap Member (lower Paleocene), and the Overland Member (upper middle and upper Paleocene).

The Overland Member, comprised of successive light-gray sandstone, siltstone, and mudstone, unconformably overlies the Blue Gap and China Butte Members (Honey & Hettinger, 2004), and its basal strata have produced a diverse early Tiffanian mammalian fauna recently described by Halverson and Eberle (2018). The poorly exposed Blue Gap Member is comprised of claystone and mudstone interbedded with thin layers of fine-grained sandstone, siltstone, ironstone, and carbonaceous shale. While it has not yet produced any fossil vertebrates, the age of the Blue Gap Member is constrained by the late Paleocene palynomorphs and vertebrate fossils collected from the overlying basal Overland Member, and by the early Paleocene fossil
mammals collected from the underlying China Butte Member (Honey & Hettinger, 2004). The Blue Gap Member does not crop out in the area of study (Hettinger et al., 2008). The fossils that I describe below are from the China Butte Member, which consists of interbedded conglomerate, sandstone, mudstone, siltstone, carbonaceous shale, and coal (Hettinger et al., 2008). These authors assigned an early Paleocene age (zone P2 of Nichols & Ott, 1978) to the China Butte Member, based on the palynomorphs *Momipites wyomingensis* and *Momipites waltmanensis* in particular, as well as vertebrate fossils from Swain Quarry in the Washakie Basin (Rigby, 1980) and other localities in both the Washakie and Great Divide Basins (Hettinger et al., 1991; Honey & Hettinger, 2004).

The China Butte Member ranges from approximately 150 to 570 m in thickness; it is thinnest in the Washakie Basin but increases in thickness northward, where it measures 570 m in northern parts of the Great Divide Basin (Hettinger et al., 2008). The base of the China Butte Member is characterized by a chert pebble conglomerate, above which are fining-upward sequences of sandstone, siltstone, claystone, carbonaceous shale, and coal units. The strata are interpreted as an alluvial sequence of channel, overbank, floodplain, swamp, and pond deposits that typically have southerly to southeasterly paleocurrents (Kirschbaum et al., 1994; Hettinger et al., 2008). The China Butte Member is well exposed and mappable, forming valleys and ridges at the surface with outcrops of red clinker coal zones (Honey & Hettinger, 2004).

UCM locality 2011035, the fossil locality that produced the mammalian fossils that I describe below, is in the lower part of the China Butte Member, approximately 46 m stratigraphically above the unconformable contact with the Upper Cretaceous, dinosaur-bearing Red Rim Member of the Lance Formation (Figure 2; McComas & Eberle, 2015). At UCM locality 2011035, the China Butte Member reaches its near maximum thickness of 565 m (Figure
2; McComas & Eberle, 2015). The locality occurs at the top of the basal sandstone unit of the China Butte Member (Figure 2) which was characterized by Honey & Hettinger (2004) as a multistoried sandstone unit that fines upwards from a conglomerate to a medium- to coarse-grained sandstone. Based on my personal observation, this unit is visible at UCM locality 2011035, and it fans outward from the quarry. The rock is “light to yellowish gray” as reported by Hettinger et al. (2008), and some mineral-filled stress fractures can be seen on the surface of the basal sandstone unit (Figure 3). A number of fossils were collected from UCM locality 2011035 that have yet to be prepared from the surrounding sedimentary matrix and are housed in the UCM Fossil Vertebrate Collection at CU Boulder. Analysis of this material confirms observations from James Honey’s field notes: the fossils were collected from a medium- to coarse-grained conglomeritic layer consisting of clay clasts in a quartz sandstone matrix with weak iron-oxide cementation. The light gray pebbles found in the matrix are angular, ranging from 1.5–25 mm in diameter, and consist of fine-grained mudstone and claystone with some potential iron-oxide staining.

UCM locality 2011035 is in Carbon County, approximately 13 miles southwest of Rawlins on Wyoming Game and Fish land. The locality was discovered by James and Jeannine Honey in 2001 and has also been listed under the following field names in James Honey’s field notes: UW-V-2001-092, 01RR02, Washakie’s Lowest, Dubbya Quarry, and Gooneyballs. The site was quarried by the Honeys and the late Malcolm McKenna for about a decade, producing more than 420 mammalian fossils including jaws and isolated teeth. James Honey believed that the productive layer at UCM locality 2011035 had been exhausted, and the quarry was filled in shortly after his quarrying was completed in 2011. When a UCM field crew visited the site in 2017 and 2018 (Figure 4), it appeared that the fossil horizon had indeed been exhausted,
although some fossils found weathering out of the tailings pile left by the Honeys were collected by the UCM team.

The GDB preserves an abundance of coal-bearing units, especially in the China Butte Member of the Fort Union Formation, which were comprehensively mapped and reported by Hettinger et al. (2008). These coal zones have extensive north-south continuity and have facilitated the designation of the three members within the Fort Union Formation as well as the correlation of fossil mammal localities throughout the basin (Hettinger et al., 1991; Honey & Hettinger, 2004). UCM locality 2011035 is the stratigraphically lowest Cenozoic mammal locality found in the Great Divide Basin to date (McComas & Eberle, 2015). Based on the fauna collected from UCM locality 2011035 and using North American Land Mammal Ages (NALMA) as the biochronologic framework, the locality appears to be early Puercan (Pu1) in age. An early Puercan age for UCM locality 2011035 is based upon the presence of Protungulatum donnae, which defines the onset of the Puercan NALMA, the early Puercan index taxon Oxyprimus, and characteristic Pu1 taxa Mesodma ambigua (Eberle et al., 2013).

Similar to UCM locality 2011035, Pu1 taxa P. donnae and Oxyprimus galadrielae are present in the Littleton fauna in Colorado’s Denver Basin, which others have hypothesized is late Pu1 in age (Eberle & Lillegraven 1998a, 1998b; Middleton & Dewar, 2004). An early Puercan age for UCM locality 2011035 and the Littleton fauna is also supported by the absence of the periptychid Ectoconus, which defines the onset of middle Puercan (Pu2) time (Lofgren et al., 2004). Templeman (2018) described the multituberculates from UCM locality 2011035, several of which also occur in the Littleton fauna, including Kimbetohia mziae. The presence of Kimbetohia further supports a Puercan age for UCM locality 2011035 because the last occurrence of this genus is in the late Puercan (Pu3) (Lofgren et al., 2004). Thus far, only one
eutherian – a new genus and species of arctocyonid coined Sigynorum magnadivisus – has been formally described from UCM locality 2011035 (McComas & Eberle, 2015).
FIGURE 1. Geographical and geologic context of the study area. A. Map of the Greater Green River Basin showing the study area, indicated by a star. B. Geologic map showing the location of UCM locality 2011035 (A and B modified from Hettinger et al., 2008; McComas, 2014; McComas & Eberle, 2015).
FIGURE 2. Stratigraphic section modified from Hettinger et al. (2008) showing the position of UCM locality 2011035 within the China Butte Member of the Fort Union Formation (from McComas and Eberle, 2015, fig. 1).
FIGURE 3. Image showing the basal sandstone unit near UCM locality 2011035 taken June 2017. The mineral-filled stress fractures are visible on the surface of the unit that is slightly down section from the study area. This image was taken looking northeast; UCM locality 2011035 is to the left, just off of the image.
FIGURE 4. Image showing UCM locality 2011035 in June, 2017. Atteberry sits in the filled-in quarry that is UCM locality 2011035.
III. MATERIALS AND METHODS

The fossil material included in this study was quarried and surface-collected by the late James Honey, his wife Jeannine Honey, and the late Malcolm McKenna from UCM locality 2011035 between 2001 and 2011, at which point the productive layer was deemed exhausted. UCM locality 2011035 is in the southeastern region of the Great Divide Basin, at approximately 41° 38’ N, 107° 33’ W. The locality is in Carbon County on land administered by Wyoming Game and Fish. More complete locality information is available to qualified researchers at the University of Colorado Museum of Natural History (UCM). All specimens are catalogued and housed in the UCM Fossil Vertebrate Collection at CU Boulder.

To identify the periptychid species from UCM locality 2011035, the fossils were compared with specimens and casts from the UCM Fossil Vertebrate Collection as well as specimens and casts from other collections including the: American Museum of Natural History, New Mexico Museum of Natural History, Princeton University Museum of Natural History, St. Paul Science Museum, University of California Museum of Paleontology, University of New Mexico, University of Minnesota Vertebrate Paleontology, United States Geological Survey, and University of Wyoming Geological Museum. If casts of holotypes could be found, they were used for comparison, along with descriptions, images, and tooth measurements from the literature. Teeth were measured using an Ehrenreich Photo-Optical Industries, Inc., Shopscope™ on loan from Jason Lillegraven (University of Wyoming) as well as Mitutoyo Absolute Digimatic™ calipers for larger specimens. Cusp terminology follows Taylor (1984) and Szalay (1969) (Figure 5). Dental measurement standards follow Archibald (1982) (Figure 6).
Below, I refer to a small cusp positioned lingual to slightly anterolingual of the paraconid on the lower molars as a paraconulid (Figure 5). This term has been used by a number of authors (Goldman, 1918; Lundelius, 1960; Baskin, 1989; Honey, 1990; Giannini & Barquez, 2003) for various taxa in the Carnivora, Chiroptera, Artiodactyla, Primates, and Rodentia. Here I apply it to periptychid lower molars. A number of taxa described below have a paraconulid, which previous authors have referred to as a “tiny cusp anterolingual to the paraconid” or “small cuspules on lingual cingulid below paraconid… that increase in prominence from m1 to m3” (Eberle & Lillegraven, 1998b; Middleton & Dewar, 2004).

The specimens were photographed using a Canon 5D Mark II and Canon MP-E 65mm f/2.8DG Macro Lens in the Entomology Imaging Station at the UCM. Images were imported into Adobe Lightroom and then into Helicon Focus to be combined into a single, focus-stacked image (Wolfson et al., 2015; Seyler et al., 2017). Images were subsequently processed, and a scale bar was added in Adobe Photoshop CC 2018.

Phylogenetic analysis was conducted using PAUP* v.4.0 beta 10 Win (Swofford, 2002). Detailed methods are presented below in the Phylogenetic Analysis section.

**Institutional abbreviations**

Dental terminology and measurements

Lower-case letters, designate teeth from lower jaws; Upper-case letters, designate teeth from upper jaws; L, Left tooth; R, Right tooth; P/p, Upper/lower premolar; M/m, Upper/lower molar; A-P length, Anteroposterior length; Wtri, Width of trigonid; Wtal, Width of talonid.
FIGURE 5. Nomenclature for mammalian molars (Modified from Taylor, 1984). A. Upper molar; B. Lower molar. Labial perspective is top.
FIGURE 6. Diagram of molar measurements. **A.** Upper molar; **B.** Lower molar (from Archibald, 1982).
IV.

SYSTEMATIC PALEONTOLOGY

Infraclass **EUTHERIA** Gill, 1872

Grandorder **UNGULATA** Linnaeus, 1766

Family **PERIPTYCHIDAE** Cope, 1882b

*Maiorana* Van Valen, 1978

*Maiorana noctiluca* Van Valen 1978

(Figures 7, 8, 9, 10, 11, 12; Table 1)

**Holotype & type locality.** PU 16667, skull fragment with left C, P3–M3 from UCM locality 82030, Polecat Bench Formation, Bighorn Basin, Park County, Wyoming (early Puercan).

**Referred specimens.** UCM 103131, incomplete left dentary with emerging p3–p4 visible in alveoli, and m1–m3; UCM 103093, incomplete left dentary containing p4–m3; UCM 103130, incomplete left dentary with p3–m3; UCM 103158, incomplete left dentary containing m1–m3; UCM 103147, incomplete right dentary with p3–m3; UCM 103167, incomplete right dentary with m2–m3; all from UCM locality 2011035.

**Occurrence.** Polecat Bench Formation, Bighorn Basin, Wyoming (Van Valen, 1978); UCM locality 2011035, China Butte Member of the Fort Union Formation, Great Divide Basin, Wyoming (both early Puercan).

**Description & discussion.** UCM specimens 103130, 103131, 103158, 103147, 103093, and 103167, all dentary fragments from UCM locality 2011035, are identified as *M. noctiluca* based upon morphologic similarity to casts and specimens of *M. noctiluca* from the Fort Union
Formation in the Bighorn Basin (PU specimens 16710, 16711, 16667, and 14171). The UCM specimens also fit the revised diagnosis of *Maiorana* given by Eberle & Lillegraven (1998b). As in *Maiorana noctiluca* specimens from the Bighorn Basin, the p3 and p4 on UCM 103130, UCM 103147, and UCM 103093 are narrow and uninflated, and they possess a small paraconid low and anterolingual to the protoconid, a narrow anterior cingulid, and a trenchant talonid bearing a single cusp. Where the p3 is present (on UCM 103130 and 103147), it is smaller than the p4. Where both the p4 and m1 are preserved (on UCM 103093, UCM 103147, and UCM 103130), the p4 is smaller than m1.

As on molars of *Maiorana noctiluca*, the molars on the UCM specimens have an anterior cingulid that decreases in size posteriorly, a wide labial cingulid, and a narrow postcingulid. The apices of the trigonid cusps on the UCM specimens are relatively uninflated and narrow, and a tiny paraconulid is present lingual to the paraconid, as on molars of *M. noctiluca* from the Bighorn Basin. The paraconulid is variable in size among the molars on the UCM specimens as well as specimens of *M. noctiluca* from the Bighorn Basin. The paraconulid on the m2 of UCM 103093, in particular, is larger than paraconulids on the other GDB as well as Bighorn Basin specimens of *M. noctiluca*, and it is also larger than paraconulids on molars of the new genus from the GDB described below. The m2 paraconulid on UCM 103093 is the same size and nearly the same height as its paraconid, and its large size gives the m2 trigonid a more widely-basined appearance than the trigonid basin on other specimens of *M. noctiluca* (Figure 8). The paraconid on the UCM specimens is lingual to the midline on m1–m2, but more medially-positioned on m3, as on molars of *M. noctiluca* from the Bighorn Basin. Additionally, the paraconid is relatively smaller than the other trigonid cusps, and it does not project anteriorly.
The talonid notch on molars of the UCM specimens is closed, as on molars of *Maiorana noctiluca* from the Bighorn Basin. However, the entocristid morphology on m2 of specimens of *M. noctiluca* from the Bighorn Basin is unique. The entocristid extends from the base of the entoconid to meet the base of the metaconid, and directly lingual to the entocristid is a cingulid that starts higher on the entoconid than the entocristid and extends anteriorly towards the lingual edge of the trigonid. Of the UCM specimens here referred to *M. noctiluca*, only UCM 103131 shares this m2 entocristid morphology with the Bighorn Basin specimens. The m2 on UCM 103130, UCM 103158, and UCM 103147 possess the wide lingual cingulid as seen on m2s of *M. noctiluca* from the Bighorn Basin, but the entocristid is shorter and does not meet the base of the entoconid. The m2s on UCM 103093 and UCM 103167 possess an entocristid that closes the talonid notch and a narrower lingual cingulid, compared to m2s of *M. noctiluca* from the Bighorn Basin. On all of the molars of the UCM specimens, the hypoconulid is closest to the entoconid, which, in turn, is positioned opposite the hypoconid. The UCM specimens differ the most from *M. noctiluca* from the Bighorn Basin in the morphology of the m3. Specifically, the m3s on the UCM specimens have a relatively narrower trigonid and talonid, and a more posteriorly-projecting hypoconulid, than on m3s of *M. noctiluca* from the Bighorn Basin. The m3 on UCM 103093 also differs from m3s on specimens of *M. noctiluca* from the Bighorn Basin in its relatively more lingually-placed paraconid.

Of the UCM specimens, UCM 103167 differs the most from specimens of *Maiorana noctiluca* from the Bighorn Basin. Specifically, UCM 103167 differs in the anterior shift of the entoconid on m2–m3, and the lingual shift of the hypoconid on m3 which makes the m3 talonid basin shallower and narrower. However, the revised diagnosis of *Maiorana* and the supplemental description of the m2–m3 of *M. noctiluca* by Eberle & Lillegraven (1998b, p. 72) describe the
position of the entoconid of *M. noctiluca* from the Bighorn Basin as “either opposite the hypoconid, or slightly anterior to it”. The molar morphology of UCM 103167 is therefore aligned with Eberle & Lillegraven’s (1998b) revised diagnosis of *Maiorana* and the description of *M. noctiluca* lower molars of these authors as well as Van Valen (1978). Therefore, I place UCM 103167 within *M. noctiluca*, chalking up its morphologic differences from the other GDB and Bighorn Basin specimens to intraspecific variation.

Measurements of the UCM specimens of *Maiorana noctiluca* are given in Table 1.
FIGURE 7. *Maiorana noctiluca*, UCM 103131, incomplete left dentary with emerging p3–p4 visible in alveoli and m1–m3; A, lingual view; B, occlusal view; C, labial view.
FIGURE 8. *Maiorana noctiluca*, UCM 103093, incomplete left dentary with p4–m3; A, lingual view; B, occlusal view; C, labial view.
**FIGURE 9.** *Maiorana noctiluca*, UCM 103130, incomplete left dentary with p3–m3; A, lingual view; B, occlusal view; C, labial view.
FIGURE 10. *Maiorana noctiluca*, UCM 103158, incomplete right dentary with m1–m3; A, lingual view; B, occlusal view; C, labial view.
FIGURE 11. Maiorana noctiluca, UCM 103147, incomplete right dentary with p3–m3; A, labial view; B, occlusal view; C, lingual view.
FIGURE 12. *Maiorana noctiluca*, UCM 103167, incomplete right dentary with m2–m3; A, labial view; B, occlusal view; C, lingual view.
**TABLE 1.** Measurements (in mm) of *Maiorana noctiluca* from UCM locality 2011035, China

Butte Member of the Fort Union Formation, Great Divide Basin, WY.

<table>
<thead>
<tr>
<th>Specimen</th>
<th>Position</th>
<th>A-P length</th>
<th>Width</th>
<th>Wtri</th>
<th>Wtal</th>
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<td>2.108</td>
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</tbody>
</table>

*Estimated due to breakage and/or wear.
Ampliconus Eberle & Lillegraven, 1998b

Ampliconus antoni Eberle & Lillegraven, 1998b

(Figures 13, 14; Table 2)

Holotype & type locality. UW 26200, incomplete left dentary containing p2–m3 from UW locality V-91005, upper Ferris Formation, western Hanna Basin, Carbon County, Wyoming (earliest middle Puercan).

Referred specimens. UCM 103150, incomplete right dentary containing p3–m3; UCM 103151, incomplete left dentary with p3–m2; both from UCM locality 2011035.

Occurrence. Upper Ferris Formation, western Hanna Basin, Wyoming (Eberle & Lillegraven, 1998b) (earliest middle Puercan); UCM locality 2011035, China Butte Member of the Fort Union Formation, Great Divide Basin, Wyoming (early Puercan).

Description & discussion. UCM 103150 and UCM 103151, incomplete right and left dentaries respectively, are identified as A. antoni based upon similarity in size and morphology to the holotype of A. antoni, UW 26200, a left dentary fragment with p2–m3 from the Hanna Basin, and to the diagnosis of A. antoni given by Eberle & Lillegraven (1998b).

The cusp apices on the premolars and molars of UCM 103150 and UCM 103151 are not so heavily worn as on the holotype of Ampliconus antoni, preserving more detail than has previously been recorded. Like those on the holotype of A. antoni, the premolars are wide and simple without a paraconid or metaconid, although the wear pattern on the p4 of UCM 103150 suggests that a ridge-like metaconid may have been located high on the protoconid. The talonid on p3 and p4 is anteroposteriorly shortened relative to the length of the trigonid, and the p4 talonid bears a single, medially-placed cusp. Wear on the p3 talonid of both UCM 103150 and UCM 103151 makes it difficult to ascertain whether it bore a cusp. The p4 is larger than the p3,
and it is the widest tooth in the lower dentition, as on the holotype of *A. antoni*, and it is also the tallest tooth on UCM 103150 in particular. The lower molars on the UCM specimens have anterior cingulids that decrease in width posteriorly, but they lack labial and lingual cingulids. However, the lower molars possess a tiny ectostylid, as on molars of *A. antoni*. The trigonid cusps of UCM 103150 and UCM 103151 are inflated, and the paraconid is large, medially-placed, and not appressed to the protoconid and metaconid. The trigonid of m2 is wider than the talonid, as seen on the m2 of the holotype of *A. antoni*. Also like the molars on the holotype of *A. antoni*, the talonid notch is closed on the m1 and m2 of UCM 103150 and UCM 103151, but open on the m3 preserved on UCM 103150. Additionally, the hypoconulid is positioned slightly closer to the entoconid than to the hypoconid, and the entoconid is opposite the hypoconid.

Whereas UCM 103151 is virtually identical in morphology to the holotype of *Ampliconus antoni*, UCM 103150 shows some minor differences. Specifically, the m2 and m3 on UCM 103150 are noticeably wider than the m2 and m3 on the holotype. However, UCM 103150 has previously been repaired, and the teeth were not properly aligned when they were glued back together. Had the teeth been properly repaired, the widths of m2–m3 on UCM 103150 would be closer to the widths of the m2–m3 on *A. antoni*. Unfortunately, UCM 103150 is fragile enough that to re-break and re-glue it would probably do more damage to the specimen. However, there are other minor differences between UCM 103150 and the holotype of *A. antoni*, including in the morphology of the m3, whose hypoconulid is less posteriorly-extended than the m3 hypoconulid on the holotype. Additionally, a tiny cuspule is present in the talonid notch of m3 on UCM 103150 which is not present on the holotype of *A. antoni*. This tiny cuspule may also have been present in the talonid notch of m2 on UCM 103150, but it has been obscured due to breakage.
Finally, the paraconid on molars of UCM 103150 is slightly more lingually-positioned than the paraconid on UCM 103151 and on the holotype of *A. antoni*.

The identification of the UCM specimens as *Ampliconus antoni* extends the geographic range of *A. antoni* into the Fort Union Formation of the Great Divide Basin in Wyoming. The holotype of *A. antoni* (UW 26200) was identified from the Ferris Formation of the Hanna Basin in Wyoming, which is hypothesized to represent the earliest middle Puercan (early Pu2) (Eberle & Lillegraven, 1998b). The presence of *A. antoni* in the Great Divide Basin fauna from UCM locality 2011035 also extends the temporal range of *A. antoni* into the late early Puercan (late Pu1) (Lofgren *et al.*, 2004; McComas & Eberle, 2015; Templeman, 2018).

Measurements of the UCM specimens of *Ampliconus antoni* are given in Table 2.
FIGURE 13. *Ampliconus antoni*, UCM 103150, incomplete right dentary with p3–m3; A, lingual view; B, occlusal view; C, labial view.
FIGURE 14. *Ampliconus antoni*, UCM 103151, incomplete left dentary with p3–m2; **A**, lingual view; **B**, occlusal view; **C**, labial view.
TABLE 2. Measurements (in mm) of *Ampliconus antoni* from UCM locality 2011035, China Butte Member of the Fort Union Formation, Great Divide Basin, WY.

<table>
<thead>
<tr>
<th>Specimen</th>
<th>Position</th>
<th>A-P length</th>
<th>Width</th>
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*Estimated due to breakage and/or wear.
Miniconus gen. nov.

Type species. Miniconus archibaldi (Middleton & Dewar, 2004.)

Included species. Type species; Miniconus jeanninae sp. nov. (this thesis).

Occurrence. Denver Formation, Denver Basin, Colorado (Middleton & Dewar, 2004); and UCM locality 2011035, China Butte Member of the Fort Union Formation, Great Divide Basin, Wyoming (both early Puercan).

Etymology. L. minim, least or smallest, and G. conus, cone; refers to the small accessory cusp (paraconulid) that is lingual to the molar paraconid.

Diagnosis. Medium-sized periptychid similar in size to Ampliconus browni; molars 9–10% larger than Oxyacodon apiculatus; p3–p4 are wide and have talonids with at least one cusp; lower molars low, bunodont, subquadrate, and bearing a distinct anterior cingulid and lingual cingulid with a small paraconulid that increases in size posteriorly. Upper molars have smaller, less lingually-extended hypocone compared to species of Oxyacodon (except Oxyacodon josephi), but hypocone is larger and more lingual than that of A. browni (Middleton & Dewar, 2004). Lower molars differ from A. browni and species of Oxyacodon in having a small cuspule (i.e. paraconulid in this thesis) on the lingual cingulid (Middleton & Dewar, 2004). Differs from species of Oxyacodon in having lower molars with a relatively larger, more medially-placed paraconid and a less posteriorly-projecting molar hypoconulid. Differs from A. browni in having a closed talonid notch. Differs from Ampliconus antoni in its smaller size, relatively larger molar paraconid, and wider anterior and lingual cingulids. Differs from Mimatuta and Maiorana in having a relatively larger, more medially-placed molar paraconid, and differs from Maiorana in its larger size, smaller p4 metaconid, and taller paracristid on m2–m3. Differs from Mithrandir in having a larger, more lingually-placed paraconid and lacking a continuous labial cingulid.
Differs from *Alticonus gazini* in its smaller size, wider anterior cingulid, subquadrate m2, and relatively smaller molar paraconid.

**Discussion.** Although *Alticonus gazini*, *Maiorana noctiluca*, and *Ampliconus antoni* variably possess a tiny paraconulid on the m1–m3, the size and morphologic differences between those taxa and species of *Miniconus* that are listed in the diagnosis above designate them as separate from this new genus. Of the other taxa that variably possess a paraconulid, *Miniconus* is most similar to *Maiorana* in its size and its alignment to the generic diagnosis of *Maiorana* of Van Valen (1978, p. 61) which reads: “Upper molars only weakly transverse, protocone apex tall and central, hypocone small, its base not projecting lingually; molar paraconid and entoconid large; canines small; mandibular condyle high.” The specimens here placed within *Miniconus* require assignment to a new genus despite their similarity to the generic diagnosis of *Maiorana* because the characters diagnosed by Van Valen (1978) are vague at best and apply to a number of other small early Puercan periptychids. On the other hand, *Miniconus* does align with portions of the revised diagnosis of *Maiorana* given by Eberle & Lillegraven (1998b, p. 72), in that the p4 of *Miniconus* is “relatively wider than that in species of *Mimatuta*, with smaller, lower paraconid, and wider talonid heel,” and it is subequal to slightly smaller than the m1. Additionally, the m2 of *Miniconus* is subquadrate, the molar entoconid is positioned either opposite or slightly anterior relative to the hypoconid, and the entoconid and hypoconulid are “distinct cusps with wear”. However, *Miniconus* differs from the revised diagnosis of *Maiorana* given by Eberle & Lillegraven (1998b, p. 72) in possessing a small or absent p4 metaconid, inflated molar trigonid, appressed entoconid and hypoconulid, and an anteriorly-projecting entocristid as opposed to an anterolabially-projecting entocristid.
In Middleton & Dewar’s (2004) diagnosis and description of *Oxyacodon archibaldi* (below referred to *Miniconus archibaldi*), the authors mention that this species differs from other species of *Oxyacodon*, except *Oxyacodon josephi*, in having a smaller and less lingual hypocone on its upper molars. Middleton & Dewar’s (2004) mention of the exception of *O. josephi* initially led me to believe that *O. josephi* might not belong in *Oxyacodon* either. The brief diagnosis of *O. josephi* given by Van Valen (1978) is based on the holotype (PU 21087), a right maxillary fragment containing partial M1–M3 from the Mantua Lentil in the Bighorn Basin. However, Van Valen (1978) lists a left dentary containing m1–m3 (PU 13338, also from the Mantua Lentil) identified as *Oxyacodon* sp. by Jepsen (1930) as also belonging to *O. josephi*. Based on size comparison alone, it is feasible that PU 13338 and PU 21087 could belong in the same species, although without more material it is difficult to say whether these specimens represent the upper and lower dentitions of *O. josephi*. If PU 13338 represents the lower dentition of *O. josephi* (which was diagnosed by its upper dentition), then based on my diagnosis of *Miniconus*, it is unlikely that *O. josephi* should be placed within this new genus. Further, the smaller and less lingually-extended hypocone shared by upper molars of *O. josephi* and species of *Miniconus* is a distinct character that should preclude their placement within the genus *Oxyacodon* altogether according to Archibald (1982). Before a definitive placement of *O. josephi* may be determined, more material from both upper and lower dentitions must be identified.
**Miniconus archibaldi**

(Figures 15, 16, 17, 18, 19, 20, 21, 22; Tables 3, 4).

*Oxyacodon archibaldi* Middleton & Dewar, 2004

**Holotype & type locality.** UCM 34958, incomplete right maxilla with partial P3 and P4–M3 in nodule from UCM locality 77267, Denver Formation, Denver Basin, Arapahoe County, Colorado (early Puercan).

**Hypodigm.** UCM 34607, right P4; UCM 34953, left P4; UCM 34610, right P3; UCM 34613 incomplete left dentary with crushed p3–4; UCM 34942, incomplete right dentary containing partial p3–m1 and complete m2–3; UCM 35087, incomplete right dentary containing m2–3; UCM 40700, incomplete right dentary with roots of c1–p3, and crushed p4, and m1–3; all from UCM locality 77267 (from Middleton & Dewar, 2004).

**Occurrence.** Only known at type locality, UCM locality 77267, Denver Formation, Denver Basin, Arapahoe County, Colorado (Middleton & Dewar, 2004).

**Revised diagnosis.** Periptychid larger than species of *Oxyacodon*, and similar in size to *Ampliconus browni*; 9–10% larger than *Oxyacodon apiculatus*; lower premolars with talonid possessing one or two cusps; p3 lacking a paraconid and metaconid; p4 with small paraconid and small, variably present metaconid; molars with paraconid lingual to the midline and not appressed to the other trigonid cusps, and small paraconulid; m1–m2 have closed talonid notch and large entoconid positioned opposite the hypoconid; m3 with small entoconid and open talonid notch. Upper molars with smaller, less lingually-extended hypocones compared to species of *Oxyacodon* (except *Oxyacodon josephi*), but hypocone larger and more lingual than on *Ampliconus browni* (Middleton & Dewar, 2004). Differs from *A. browni* and species of *Oxyacodon* in having lower molars with a small cuspule (i.e. paraconulid in this thesis) on
lingual cingulid (Middleton & Dewar, 2004). Differs from *Alticonus gazini* in its smaller size, and having lower molars with a wider anterior cingulid, relatively smaller protoconid, and m2–m3 with wider talonid than the trigonid. Differs from *Ampliconus antoni* in its smaller size, relatively larger paraconid, wider anterior and lingual cingulids, and small m3 entoconid. Differs from *Maiorana noctiluca* in its larger size, more inflated premolars, smaller p4 metaconid, relatively larger molar paraconid, taller paracristid on m2–m3, and small m3 entoconid. Differs from species of *Conacodon* in having a relatively larger molar paraconid, narrower lingual cingulid, and possessing a paraconulid. Differs from new species of *Miniconus* from the Great Divide Basin (described below) in its slightly smaller size, more medially-placed paraconid, wider anterior cingulid, entoconid positioned opposite the hypoconid on m1–m2, small m3 entoconid, and open talonid notch on m3.

**Description & discussion.** When Middleton & Dewar (2004) diagnosed *Oxyacodon archibaldi* based on upper and lower dentitions from the Denver Formation housed in the UCM Fossil Vertebrate Collection, these authors noted that it had multiple characters not shared by other species of *Oxyacodon* (except *Oxyacodon josephi*). Specifically, the molars are larger and the hypocone is smaller and less lingually-extended than on other documented species of *Oxyacodon* (except *O. josephi*). Here, I consider those characters to warrant its placement in the new genus, *Miniconus*. The upper dentition of *Miniconus archibaldi* is 9–10% larger than, the largest species of *Oxyacodon*, *O. apiculatus*, whereas the size of the lower dentitions of *M. archibaldi* overlap with the observed range for *O. apiculatus*. However, lower molars morphologically differ from those of species of *Oxyacodon* in having a relatively larger paraconid and a paraconulid. Whereas a paraconulid is variably present on specimens of *Maiorana noctiluca, Maiorana ferrisensis, Ampliconus antoni*, and *Alticonus gazini*, it is
consistently present on molars of *M. archibaldi* and the new species of *Miniconus* from the Great Divide Basin described below. Middleton (1983) and subsequently Middleton & Dewar (2004) placed the Denver Formation specimens within *Oxyacodon* based on characters primitive to the anisonchines, including relatively small, unspecialized premolars, a separate postcingulum and metacingulum, absence of a protostyle, and a well-developed stylar shelf (Middleton & Dewar, 2004). These characters are shared by many early Paleocene ‘condylarths’. Furthermore, Archibald (1982) indicated that the less lingually-extended hypocone compared to other species of *Oxyacodon* is enough to preclude the placement of certain taxa within the genus *Oxyacodon*. Specifically, Archibald (1982) did not agree with Van Valen’s (1978) placement of *O. josephi* within *Oxyacodon*. The phylogenetic analysis conducted for this thesis (below) finds *M. archibaldi* to be closer to the new species of *Miniconus* from the Great Divide Basin described below than to species of *Oxyacodon*. For these reasons, *M. archibaldi* is here placed within the new genus *Miniconus*.

Measurements of *Miniconus archibaldi* are given in Tables 3 and 4.
FIGURE 16. *Miniconus archibaldi*, UCM 34607, isolated right P4; A, labial view; B, occlusal view; C, lingual view.

2 mm

FIGURE 17. *Miniconus archibaldi*, UCM 34953, isolated left P4; A, labial view; B, occlusal view; C, lingual view.

2 mm
FIGURE 18. *Miniconus archibaldi*, UCM 34610, isolated right P3; A, labial view; B, occlusal view; C, lingual view.
FIGURE 19. *Miniconus archibaldi*, UCM 34613, incomplete left dentary with crushed p3–4; A, lingual view; B, occlusal view; C, labial view.
FIGURE 20. *Miniconus archibaldi*, UCM 34942, incomplete right dentary containing partial p3–m1 and complete m2–3; **A**, lingual view; **B**, occlusal view; **C**, labial view.
FIGURE 21. *Miniconus archibaldi*, UCM 35087, incomplete right dentary containing m2–3; A, lingual view; B, occlusal view; C, labial view.
FIGURE 22. *Miniconus archibaldi*, UCM 40700, incomplete right dentary with roots of c1–p3, and crushed p4, and m1–3; A, lingual view; B, occlusal view; C, labial view.
TABLE 3. Measurements (in mm) of upper dentition of *Miniconus archibaldi* from UCM locality 77267, Denver Formation, Denver Basin, Arapahoe County, CO.

<table>
<thead>
<tr>
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<th>Width</th>
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</tr>
<tr>
<td>34958</td>
<td>M1</td>
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<td>5.553</td>
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<tr>
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<td>M2</td>
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<td>7.140</td>
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<tr>
<td>34958</td>
<td>M3</td>
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*Estimated due to breakage and/or wear.
**TABLE 4.** Measurements (in mm) of lower dentition of *Miniconus archibaldi* from UCM locality 77267, Denver Formation, Denver Basin, Arapahoe County, CO.

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<th>Width</th>
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<td>p4</td>
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<td>2.5*</td>
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*Estimated due to breakage and/or wear.*
**Miniconus jeanninae** sp. nov.

(Figures 23, 24, 25; Table 5).

**Holotype & type locality.** UCM 103181, incomplete right dentary with partial p3 alveolus and p4–m3 from UCM locality 2011035, China Butte Member of the Fort Union Formation, Great Divide Basin, Carbon County, Wyoming (early Puercan).

**Hypodigm.** UCM 103084, incomplete right dentary containing partial p1 alveolus, p2 alveoli, and p3–m3; and UCM 103171, incomplete left dentary containing a single root of p2, both p3 roots, and complete p4–m2; all from UCM locality 2011035.

**Etymology.** Named for Jeannine Honey in recognition of her valuable insight on this project and others, and for her many years of prospecting and fossil collection alongside James Honey and Malcolm McKenna in the Great Divide Basin.

**Occurrence.** Only known at type locality, UCM locality 2011035, China Butte Member of the Fort Union Formation, Great Divide Basin, Carbon County, Wyoming (early Puercan).

**Diagnosis.** Medium-sized periptychid, similar in size to *Ampliconus browni*; p3–p4 lack a paraconid; p4 with small, appressed metaconid; molar paraconid projects anteriorly and is positioned slightly lingual to the midline on m1 and m3 but at the midline on m2; lower molars with a paraconulid, entocristid closes talonid notch, and entoconid is shifted anteriorly on m1 and m2. Differs from *Miniconus archibaldi* in its slightly larger size, more lingually-placed paraconid, narrower anterior cingulid, anteriorly-shifted entoconid on m1–m2, and m3 with a larger entoconid and closed talonid notch. Differs from species of *Oxyacodon* in its larger size, more inflated premolars, relatively larger, more medially-placed paraconid, and relatively larger entoconid. Differs from species of *Conacodon* in having a narrower labial cingulid, less inflated molars, and possessing a paraconulid. Differs from *Alticonus gazini* in its smaller size,
subquadrate m2, relatively smaller protoconid, and anteriorly-shifted entoconid on m1–m2.

Differs from *A. browni* in having a closed talonid notch, relatively smaller and less anteriorly-projecting paraconid, subquadrate m1, and anteriorly-shifted entoconid on m1–m2. Differs from *Ampliconus antoni* in its smaller size, relatively larger molar paraconid, wider lingual and anterior cingulids on the molars, and anteriorly-shifted entoconid on m1–m2. Differs from *Maiorana noctiluca* in its larger size, smaller metaconid on p4, narrower labial cingulid on molars, relatively larger molar paraconid, more posteriorly-extended hypoconulid, and anteriorly-shifted entoconid on m1–m2.

**Description.**

**Dentary.** The best-preserved dentary is that of the holotype, UCM 103181. The dentary is incomplete anterior to the p4 but retains much of the posterior details of the dentary despite a break across the angular process. The mandibular condyle is located well above the occlusal plane of the molars, and the jaw is moderately deep through the ascending ramus. The posterior mental foramen is preserved on two specimens (UCM 103084 and UCM 103171) below the p2 position.

**P1–2.** The crowns of the first two premolars are not preserved on any of the UCM specimens. A partial p1 alveolus is preserved on UCM 103084, followed by the two root sockets for p2.

**P3–4.** The p3 is known from only one specimen (UCM 103084), whereas the p4 is preserved on three specimens (UCM 103181, UCM 103171, and UCM 103084). The premolars from UCM specimens 103084 and 103181 are in poor condition, obscuring much of the detail and enamel. However, what can be discerned is that the p3 and p4 increase in size and complexity posteriorly. The p3 on UCM 103084 is narrower and less inflated than the p4, although they are subequal in
length. The p3 has a large protoconid and a small talonid bearing a single cusp. There is no trace of a paraconid or metaconid on the p3, although wear obscures this region of the tooth.

Whereas the p4 on UCM 103181 and UCM 103084 is shorter and narrower than m1, however the p4 on UCM 103171 is wider than, but subequal in length to, its m1. The p4 has a large protoconid with heavy apical wear, and the wear pattern suggests that there was a small, ridge-like metaconid located high on the protoconid. A weak ridge descends the posterolingual face of the protoconid from the metaconid to meet the talonid of the p4. There is an anterior cingulid on p4 that does not extend across the entire width of the tooth. A break across the enamel base of the tooth had previously been repaired, and by result the tooth is offset, making it difficult to determine whether there was a lingual cingulid. The talonid of the p4 is wider than the p3 talonid and bears a single, lingually-placed cusp. There is a posterior cingulid present on p4.

M1–3. The molars are bunodont and inflated, with m1 being wider than p4 on UCM 103181 and UCM 103084. The molar paraconid is slightly smaller than the protoconid and metaconid, and projects anteriorly, whereas the protoconid and metaconid are more closely appressed to one another and connected by a protocrisid. The paraconid is positioned slightly lingual to the midline on m1 and m3, but it is medially-placed on m2. A curved paracristid connects the paraconid with the protoconid. A lingual cingulid is present below the paraconid and possesses a paraconulid which increases in size from m1–m3. On m1–m3 there is a well-developed anterior cingulid that is mostly concentrated on the labial side of the tooth. A short, somewhat rugose lingual cingulid is present below the talonid notch. The molars have narrow, discontinuous labial cingulids that are present only in the hypoflexid region. On m1, the talonid is subequal in width to the trigonid, but on m2, the talonid is wider than the trigonid. The molar talonids are shorter
than the trigonids, and the hypoconulid is closer to the entoconid than to the hypoconid. The entoconid is shifted anteriorly towards the metaconid, especially on m2, with an entocristid that extends anteriorly from it, closing the talonid notch. The hypoconulid on m3 is a distinct cusp with a slight posterior extension. A short postcingulid is present between the hypoconid and hypoconulid on the m3 of the holotype (UCM 103181).

Measurements of Miniconus jeanninae are given in Table 5.

Discussion. Miniconus jeanninae sp. nov. is slightly larger than Miniconus archibaldi and similar in size to Ampliconus browni. Like Mimatuta minuial, the mandibular condyle is located well above the occlusal plane of the molars, a character typically shared by herbivores, suggesting that M. jeanninae may have had an herbivorous diet (Crompton, 1969). The molar morphology of M. jeanninae is most similar to M. archibaldi in that it has: inflated and appressed trigonid cusps, a lingual molar paraconid on m1 and m3, a medial paraconid on m2, a paraconulid, a distinct m3 hypoconulid with slight posterior extension, an anterior cingulid, a short discontinuous labial cingulid present only in the hypoflexid region, and a narrow lingual cingulid. However, M. jeanninae differs from M. archibaldi in lacking a paraconid on its p4, possessing an anteriorly-shifted entoconid relative to the hypoconid on its molars, and having a relatively larger entoconid and closed talonid notch on its m3. M. jeanninae shares the anterior shift of its molar entoconid with Conacodon harbourae, Conacodon delphae, certain specimens of Maiorana noctiluca, and Maiorana ferrisensis.

On Miniconus jeanninae, the molar paraconid is positioned lingual to the midline on m1 and m3, but at the midline on m2, similar to Conacodon harbourae and Miniconus archibaldi. Whereas the molar paraconid of M. archibaldi is lingual to the midline on m1 and m3, it is relatively more medially-positioned than on M. jeanninae. The molar paraconid on M. jeanninae
is smaller than the other trigonid cusps and slightly anteriorly-projecting; however it is not so far-projecting as on molars of *Ampliconus antoni*. Additionally, whereas the molar paraconid on *M. jeanninae* is relatively smaller than the protoconid and metaconid, it is not as small as the paraconid on on molars of *Conacodon delphae*. A paraconulid is variably present on specimens of *Maiorana noctiluca, Maiorana ferrisensis, A. antoni, and Alticonus gazini*. However, all known lower molars of *M. jeanninae* and *M. archibaldi* bear this cuspule. Although the talonid cusps of *M. jeanninae* are appressed to one another, they are not so inflated that their bases merge as on other periptychids such as *Hemithlaeus kowalevskianus* and *C. delphae*. The m3 hypoconulid on *M. jeanninae* is a distinct cusp with slight posterior extension as on *Mithrandir gillianus* and *M. archibaldi*, but it is not so posteriorly-projecting as in *Oxyacodon priscilla.  

Whereas *M. jeanninae* and *M. archibaldi* are aligned by several morphologic characters (described above), *M. jeanninae* is distinguished from *M. archibaldi* by the traits it shares with other early Puercan periptychids. Namely, the anteriorly-shifted molar entoconid on *M. jeanninae* also occurs on molars of *Conacodon harbourae, C. delphae*, certain specimens of *Maiorana noctiluca*, and *M. ferrisensis*. Additionally, the m3 entoconid on *M. jeanninae* is relatively larger than on *M. archibaldi*. *M. archibaldi* shares its small m3 entoconid with species of *Oxyacodon*. Furthermore, the m3 talonid notch is open on *M. archibaldi*, whereas it is closed on *M. jeanninae.*  

The placement of *Miniconus jeanninae* within the new genus *Miniconus* extends the geographic range of the genus into the Fort Union Formation of the Great Divide Basin of Wyoming. *Miniconus archibaldi*, the other species of *Miniconus*, is only known from the Denver Formation’s Littleton fauna in Colorado (Middleton & Dewar, 2004), which is hypothesized to represent the late early Puercan (late Pu1). Previous studies (Lofgren *et al.*, 2004; McComas &
Eberle, 2015; Templeman, 2018) have suggested that the Great Divide Basin fauna from UCM locality 2011035 may also represent late early Puercan time, due to taxa shared with the Littleton fauna, *Mesodma ambigua* and *Kimbetohia mziae*, and absence of Pu2 index taxon *Ectoconus*, The presence of *Miniconus* in both the GDB and Denver Basin helps corroborate this correlation.
FIGURE 23. *Miniconus jeanninae* sp. nov., UCM 103181, holotype, incomplete right dentary with p4–m3; A, labial view; B, occlusal view; C, lingual view. Inset image shows occlusal view in detail.
FIGURE 24. *Miniconus jeanninae* sp. nov., UCM 103084, incomplete right dentary with p3–m3; **A**, lingual view; **B**, occlusal view; **C**, labial view.
FIGURE 25. *Miniconus jeanninae* sp. nov., UCM 103171, incomplete left dentary with p4–m2; A, lingual view; B, occlusal view; C, labial view.
TABLE 5. Dental measurements (in mm) of *Miniconus jeanninae* sp. nov. from UCM locality 2011035, China Butte member of the Fort Union Formation, Great Divide Basin, Carbon County, WY.

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<th>Specimen</th>
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* Estimated due to breakage and/or wear.
Beornus gen. nov.

**Type and only known species.** Beornus honeyi sp. nov.

**Etymology.** Beorn, a character from J.R.R. Tolkien’s “The Hobbit”, is known for his massive size; in reference to the significant premolar and molar inflation of this taxon when compared to Conacodon delphae, the largest documented species of Conacodon.

**Occurrence.** Only known at type locality, UCM locality 2011035, China Butte Member of the Fort Union Formation, Great Divide Basin, Carbon County, Wyoming (early Puercan).

**Diagnosis.** As for the type species.

*Beornus honeyi* sp. nov.

(Figure 26; Table 6).

**Holotype & type locality.** UCM 103183, an incomplete left dentary containing p3–m3 from UCM locality 2011035, China Butte Member of the Fort Union Formation, Great Divide Basin, Carbon County, Wyoming (early Puercan).

**Etymology.** Named for the late James G. Honey in recognition of his decades of field research in the Great Divide Basin. His fieldwork produced a diverse assemblage of fossil mammals, including the research materials for this thesis.

**Occurrence.** Only known at type locality, UCM locality 2011035, China Butte Member of the Fort Union Formation, Great Divide Basin, Carbon County, Wyoming (early Puercan).

**Diagnosis.** Large periptychid, at least 14% larger than Conacodon delphae; larger than other documented species of Conacodon, Auraria, Alticonus, and Ampliconus; premolars are inflated with large protoconid and small, ridge-like metaconid; p3 lacks a paraconid; p4 has a paraconid and is wider than p3 and m1; molars are inflated with rugose enamel and appressed trigonid cusps, lacking lingual cingulid and possessing a narrow anterior cingulid, labial cingulid.
present only in hypoflexid region, and short postcingulid on m3; molar paraconid small, anteriorly-projecting, and positioned lingual to the midline on m1 and m3 and at the midline on m2; tiny cuspule occurs in open talonid notch; another cuspule is located between the hypoconid and hypoconulid on m1–m2. Differs from species of *Conacodon* in possessing a narrower anterior cingulid, a tiny cuspule between the hypoconulid and hypoconid on m1–m2, open talonid notch, and less posteriorly-projecting hypoconulid. Differs from *C. delphae* in having anteroposteriorly shorter premolars, a relatively larger and anteriorly-projecting molar paraconid on m1–m3, and narrower posterior cingulid on m3. Differs from *Conacodon matthewi* in its more inflated premolars and relatively larger molar paraconid. Differs from *Conacodon entoconus* in lacking lingual cingulid and having a relatively larger molar paraconid. Differs from *Auraria urbana* in its relatively smaller molar paraconid, absence of lingual cingulid, and more posteriorly-projecting m3 hypoconulid. Differs from *Ampliconus antoni* in its more inflated premolars, relatively smaller molar paraconid, narrower anterior cingulid, and less posteriorly-projecting hypoconulid on m3. Differs from *Alticonus gazini* in lacking a lingual cingulid, possessing a relatively smaller and more medially-placed molar paraconid, and a bearing relatively larger entoconid on m3.

**Description.**

**Dentary.** The dentary of the holotype (UCM 103183) is poorly preserved and shows little morphologic detail. No part of the ventral surface of the jaw is present. The roots of the premolars and molars are partially exposed on the labial side of the jaw.

**P2.** Neither the crown nor the roots of the p2 are preserved, although there are root sockets signifying that p2 was double-rooted.
**P3–p4.** On UCM 103183, the lower premolars increase in size and complexity posteriorly. Both p3 and p4 are laterally inflated, with a large protoconid, simple talonid, and a posterior cingulid. The premolars are taller than the molars, with a moderate backward pitch. The p3 bears weak crenulation on its anterior surface but has no trace of a paraconid or an anterior cingulid. The p3 apex is heavily worn on UCM 103183, and the wear pattern suggests that there probably was a small, ridge-like metaconid located high on the protoconid. The p3 talonid is weakly crenulated and shortened anteroposteriorly relative to the trigonid. The talonid has a high point appressed to the p4 at the midline of the tooth; however, there is no distinct cusp on the talonid of p3.

The p4 is noticeably more inflated than both p3 and m1, and it is subequal in length to m1. There is a narrow, anterior cingulid low on the tooth with a small cusp in the position of a paraconid. The apical wear pattern on p4 of UCM 103183 indicates the presence of a ridge-like metaconid appressed to, and located high on, the protoconid. A weak ridge descends the posterolingual face of the protoconid from the metaconid to meet the talonid of the p4. The p4 talonid is longer relative to the trigonid compared to the talonid of p3, it is rugose, and bears a single cusp on the midline. Lingual to the central cusp is a small swelling that may have been a second talonid cusp; however, the glue used to repair the teeth on UCM 103183 obscures this region.

**M1–m3.** The molars of UCM 103183 are long and laterally inflated with heavy apical wear, especially on m1 and m2. The molars are bunodont, and the trigonids are only slightly taller than the talonids. The trigonid cusps are appressed to one another, with the bases of the protoconid and metaconid merging on m2 and m3. The paraconid is smaller than the other trigonid cusps, low on the tooth, and shifted anteriorly, especially on m3. The paraconid is lingual to the midline on m1 and m3, but it is close to the midline on m2. A weak, curved paracristid connects the
protoconid to the paraconid, and is crenulated on m3. The molars bear weak anterior cingulids that become increasingly narrower from m1 to m3. The anterior cingulid of m1 has a small swelling where the cingulid meets the talonid of p4. The molars have narrow, discontinuous labial cingulids with some rugosity that are present only in the hypoflexid region. There is no lingual cingulid on the molars on UCM 103183. However, a crenulated postcingulid is present on m3.

On UCM 103183, the talonid is narrower than the trigonid on m1 and m3, but subequal in width to the trigonid on m2. The talonid notch is open, with no entocristid. There are tiny cuspules in the talonid notch throughout the molar series that lie in front of the entoconid but are not connected to the entoconid by any cristids. The talonid cusps are significantly inflated, their bases merging, resulting in a shallow talonid basin. The hypoconid is the largest talonid cusp and lies directly opposite the entoconid on all three molars. A tiny cuspule lies between the hypoconulid and entoconid on m2 and less distinctly on m1. The hypoconulid is closer to the entoconid than to the hypoconid on m1 and m3, but it is more equidistant between the two cusps on m2. The hypoconulid on m2 also does not project posteriorly, so the three talonid cusps lie almost in a straight line. The hypoconulid on m3 is distinct with a slight posterior extension.

Measurements of *Beornus honeyi* are given in Table 6.

**Discussion.** *Beornus honeyi* is larger than both *Conacodon delphae* and *Conacodon entoconus*. Whereas the premolars of *C. delphae* are longer than those on UCM 103183, the opposite occurs with the molars. On *B. honeyi*, m1 is 7% longer, m2 is 18% longer, and m3 is 17% longer than m1, m2, and m3, respectively, of *C. delphae* (UCM 45587, UCM 38042, UCM 43740, UCM 47587, USGS-D10; Appendix D). UCM 103183 is similar to *Ampliconus antoni* and *C. entoconus* in lacking a paraconid on its premolars but differs from species of *Conacodon*
in having a small, ridge-like metaconid on its p3 and p4. The wear pattern indicating a small, ridge-like metaconid appressed to the p3 and p4 protoconid on *B. honeyi* is a character shared by *Ampliconus browni*, although the premolars of *A. browni* are narrower and less inflated than the premolars on *B. honeyi*. Based on comparison with *C. delphae*, it is possible that the p4 of *B. honeyi* has two cusps on the talonid; however, the glue used to repair and consolidate UCM 103181 has obscured the region where a second cusp would be expected to occur.

The morphology of the molars of *Beornus honeyi* is most similar to *Auraria urbana* and *Ampliconus antoni*. The molar trigonid cusps are inflated and appressed to one another, as on most of the conacodontines, with the paraconid small and anteriorly-projecting relative to the protoconid and metaconid, as in *Conacodon matthewi* and *A. urbana*. Whereas *B. honeyi* differs from species of *Conacodon* and *Oxyacodon* in lacking lingual cingulids on its molars, *B. honeyi* shares this character with species of *Ampliconus*. The labial cingulid on molars of *B. honeyi* is narrower than on molars of *Conacodon entoconus*. The talonid notch is open, as on *A. urbana*, but differs from *A. urbana* in that there is a tiny cuspule anterior to the entoconid. Similar to other conacodontines, the talonid cusps of *B. honeyi* are inflated, and the hypoconid is the largest cusp positioned opposite the entoconid. On m2, the hypoconulid does not project posteriorly, so the three talonid cusps lie almost in a straight line, similar to the m2 on specimens of *Conacodon cophater*; however, this characteristic differs from the m2 on specimens of *C. entoconus* and *Hemithlaeus kowalevskianus*. Similar to *Ampliconus browni*, *B. honeyi* has a tiny cuspule that lies between the hypoconulid and entoconid on m1, although this cuspule is variably present on specimens of *A. browni*. The m3 hypoconulid on *B. honeyi* is a distinct cusp with only slight posterior extension, similar to m3s of *Alticonus gazini*, but it is not nearly so posteriorly-
extended as on m3s of *H. kowalevskianus*. A crenulated postcingulid lies below the postcristid on m3, similar to *Conacodon delphae*, although it is shorter and narrower on *B. honeyi*.

That *Beornus honeyi* belongs in its own genus is based on its differences from other large periptychids. Whereas *B. honeyi* shares large size, inflated cusps, and simple premolars with *Conacodon delphae*, *C. entoconus*, *Auraria urbana*, and *Ampliconus antoni*, *B. honeyi* is noticeably larger than all of these species, and possesses characters that distinguish it, such as an open talonid notch, absence of lingual cingulids, and a small paraconid. The presence of tiny cuspules in the talonid notch and between the hypoconulid and entoconid on m1 and m2 appears to be unique among periptychids, although *Ampliconus browni* also possesses a tiny cuspule between its hypoconulid and entoconid on m1.
FIGURE 26. *Beornus honeyi* gen. et sp. nov., UCM 103183, holotype, incomplete left dentary with p3–m3; A, lingual view; B, occlusal view; C, labial view.
**TABLE 6.** Dental measurements (in mm) of *Beornus honeyi* sp. nov. from UCM locality 2011035, China Butte Member of the Fort Union Formation, Great Divide Basin, Carbon County, WY.

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Conacodon Matthew, 1897

Conacodon hettingeri sp. nov.

(Figures 27, 28; Table 7).

Holotype & type locality. UCM 103374, an incomplete left dentary containing p3–m3; and incomplete right dentary containing partial c1 alveolus, root sockets for p1–p3, and complete p4–m3 from UCM locality 2011035, China Butte Member of the Fort Union Formation, Great Divide Basin, Carbon County, Wyoming (early Puercan).

Etymology. Named for Robert D. Hettinger in recognition of his decades of field research in the Great Divide Basin, carefully mapping the stratigraphy of the region with James G. Honey.

Occurrence. Only known at type locality, UCM locality 2011035, China Butte Member of the Fort Union Formation, Great Divide Basin, Carbon County, Wyoming (early Puercan).

Diagnosis. Large periptychid approximately 5% larger than Conacodon entoconus; premolars are inflated with small, ridge-like paraconid; p4 wider than m1 with appressed metaconid; molar paraconid is medial and small compared to metaconid and protoconid; anterior cingulid increases in size posteriorly; wide, continuous lingual cingulid on m2–m3, but discontinuous and present only in talonid notch region on m1; labial cingulid narrow and only present in hypoflexid region. Differs from other species of Conacodon in having a less posteriorly-extended hypoconulid. Larger than C. entoconus, Conacodon harbourae, and Conacodon cophater; smaller than Conacodon matthewi and Conacodon delphae. Differs from C. entoconus in its relatively larger paraconid, wider, more continuous lingual cingulid on m2–m3, and anteroposteriorly shorter talonid compared to length of trigonid. Differs from C. matthewi in its relatively larger trigonid cusps and wider talonids. Differs from C. harbourae in
having a narrower lingual cingulid. Differs from *C. cophater* in its relatively larger and more medially-placed paraconid, narrower and less continuous labial cingulid, and more posteriorly-extended m2 hypoconulid. Differs from *C. delphae* in its relatively larger molar paraconid and wider lingual cingulid. Differs from species of *Oxyacodon* in its larger size, less anteriorly-projecting molar paraconid, wider lingual cingulid, and less posteriorly-extended hypoconulid. Differs from species of *Ampliconus* in having a wider lingual cingulid, relatively smaller and more appressed molar paraconid, and less posteriorly-extended hypoconulid.

**Description.**

**Dentary.** The left dentary of UCM 103374 is broken anterior to the p3 and preserves a single mental foramen below the p3, positioned medially between the anterior and posterior root sockets. The right dentary of UCM 103374 possesses the masseteric fossa as well as two mental foramina: one below the p3, positioned medially between the anterior and posterior root sockets, and the other positioned below the anterior root socket of the p2.

**Canine.** Neither the crown nor root of the canine remains, although the right dentary of UCM 103374 preserves a portion of the alveolus.

**P1–p2.** The crowns and roots of p1 and p2 are not preserved. However, the right dentary of UCM 103374 preserves the alveoli indicating that p1 only possessed a single root, whereas p2 had two roots.

**P3–p4.** The premolars of UCM 103374 are inflated and heavily worn, erasing most of the apical details. The wear pattern on p3 indicates that a small, ridge-like paraconid was located high on the anterior face of the protoconid, but there is no trace of a metaconid. A weak anterior cingulid is present on the lingual side of p3. The p3 talonid is shortened relative to the trigonid. The p3 has a narrow posterior cingulid.
The p4 of UCM 103374 is shorter, although wider, than the p3. The p4 is noticeably wider and more inflated than the m1, although the m1 is longer than p4. The apical wear on p4 suggests that a ridge-like paraconid and metaconid were located on the protoconid, appressed to it. The weak ridge descends the anterior face of the protoconid from the paraconid to meet a short anterolingual cingulid. The p4 talonid is similar to p3 in size and complexity. The p4 talonid has rugose enamel, and there are no discernible cusps, although a narrow posterior cingulid is present.

M1–m3. The molar trigonids are heavily worn, especially on m1. The molar trigonid cusps are appressed with bases merging. The molar paraconid is close to the midline on m2–m3, but appears to be more lingually-positioned from what can be determined on m1. The protoconid and metaconid are larger than the paraconid, with the protoconid being the largest cusp. The molars possess anterior cingulids that increase in width posteriorly. There are discontinuous, crenulated labial cingulids present in the hypoflexid region of all of the molars. The m2–m3 on UCM 103374 have wide, well-developed lingual cingulids that extend from the base of the paraconid to the base of the entoconid. The m1, however, bears a cingulid just below the talonid notch.

The talonid basin on the molars is relatively shallow and shortened relative to the length of the trigonid. The talonid cusps are internally inflated into the basin, their bases merging. On all three molars, the hypoconid is the largest talonid cusp and is positioned opposite the entoconid. On m2, the hypoconulid does not project posteriorly, so the talonid cusps lie almost in a straight line. On m1 and m3, the hypoconulid is closer to the entoconid than to the hypoconid. However, on m2, the talonid cusps are nearly equidistant. The hypoconulid on m3 is a distinct cusp, but it is not extended posteriorly. A postcingulid occurs on m3.

Measurements of Conacodon hettingeri are given in Table 7.
**Discussion.** *Conacodon hettingeri* is slightly larger than *Conacodon entoconus* by 5% and slightly smaller than *Conacodon matthewi* by 6%. The premolars are wide and inflated, similar to other species of *Conacodon*, and the premolar talonids of *C. hettingeri* are simple and do not possess cusps, similar to *Alticonus gazini*. The morphology of the molars of *C. hettingeri* is most similar to *C. entoconus*, but *C. hettingeri* has more inflated trigonid cusps, a relatively larger molar paraconid, a wider lingual cingulid, and a relatively shorter talonid compared to its trigonid, when compared to lower molars of *C. entoconus*. As on other species of *Conacodon*, *C. hettingeri* possesses a medially-placed molar paraconid that is smaller than the other trigonid cusps, wide lingual cingulids on m2 and m3, a labial cingulid in the hypoflexid region, and the talonid basins are shortened anteroposteriorly relative to the trigonid. The hypoconulid, whereas it is a distinct cusp, is not nearly so posteriorly-projecting as on molars of *Hemithlaeus kowalevskianus* and species of *Oxyacodon* and *Amplusicus*.

*Conacodon hettingeri* is placed in the genus *Conacodon* due to both its similarity to other species of *Conacodon* and its alignment with the revised diagnosis of the lower dentition of *Conacodon* given by Matthew (1937, p. 145) which reads: “Lower molars with distinct paraconid. Cusps robust. Lower premolars with small talonids bearing single cusps on p2–p4 otherwise much like premolars of *Hemithlaeus*. The lower molars also have much the proportions and cusp construction of those of *Hemithlaeus*, but protoconid somewhat higher than metaconid.” *C. hettingeri* is distinguished from other species of *Conacodon* by its size – it is larger than *Conacodon entoconus*, *Conacodon harbourae*, and *Conacodon cophater* and smaller than *Conacodon matthewi* and *Conacodon delphae* – and its less posteriorly-extended m3 hypoconulid.
While no other species of *Conacodon* have yet been identified from UCM locality 2011035 besides *Conacodon hettingeri* and *Conacodon harbourae* (described below), a number of species of *Conacodon* were described from the Ferris Formation in the Hanna Basin by Eberle & Lillegraven (1998b). Those taxa included *C. harbourae*, *Conacodon cophater*, and *Conacodon delphae*. The Hanna Basin was contiguous with the Great Divide Basin in the early Paleocene, so it is not too surprising to find *Conacodon* at UCM locality 2011035.
FIGURE 27. *Conacodon hettingeri* sp. nov. UCM 103374, holotype, incomplete right dentary with p4–m3; A, lingual view; B, occlusal view; C, labial view.
FIGURE 28. Conacodon hettingeri sp. nov. UCM 103374, holotype, incomplete left dentary with p3–m3; A, lingual view; B, occlusal view; C, labial view.
**TABLE 7.** Dental measurements (in mm) of *Conacodon hettingeri* sp. nov. from UCM locality 2011035, China Butte Member of the Fort Union Formation, Great Divide Basin, Carbon County, WY.

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<td>6.413</td>
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* Estimated due to breakage and/or wear.
*Conacodon harbourae* Eberle & Lillegraven, 1998b

(Figures 29, 30, 31; Table 8).

*Conacodon harbourae* Eberle & Lillegraven, 1998b.


**Holotype & type locality.** UCM 40150, an incomplete left dentary with p2–m3 from UCM locality 78169, Denver Formation, Denver Basin, Arapahoe County, Colorado (early Puercan).

**Referred specimens.** UCM 108749, incomplete right dentary containing m2–m3; UCM 103155, incomplete right dentary with partial m1 and m2–m3; UCM 103085, incomplete right dentary with dp4 and emerging p3 visible in alveoli, and m1–m3; all from UCM locality 2011035.

**Occurrence.** Denver Formation, Denver Basin, Colorado (Middleton, 1983) (early Puercan); Upper Ferris Formation, western Hanna Basin, Wyoming (Eberle & Lillegraven, 1998b) (earliest middle Puercan); UCM locality 2011035, China Butte Member of the Fort Union Formation, Great Divide Basin, Wyoming (early Puercan).

**Description & discussion.** UCM specimens 108749, 103085, and 103155, all incomplete dentaries from UCM locality 2011035, are identified as *C. harbourae* because they are virtually identical to the holotype (UCM 40150), and they fit the revised diagnosis of *C. harbourae* given by Eberle & Lillegraven (1998b). As is characteristic of the species, the lower molars on the UCM specimens are inflated and close in morphology to other conacodontines, such as *Conacodon entoconus*. The trigonid cusps on UCM 108749, UCM 103085, and UCM 103155 are appressed to one another, and the talonid is shortened relative to the length of the trigonid, with an anteriorly-shifted entoconid and entocristid that closes the talonid notch. On UCM
108749, UCM 103085, and UCM 103155, the molar paraconid is small and medially-placed on m2, and larger and more lingual on m1 and m3, and connected to the protoconid by a well-developed paracristid. There is a tiny ectostylid on m1 and m2. The molar trigonid possesses wide anterior and lingual cingulids, as on *C. harbourae* from the Hanna Basin (Eberle & Lillegraven, 1998b). The cingulids are best developed on UCM 108749. On the talonid of m1 and m2, the hypoconulid is nearer to the entoconid than to the hypoconid, as on molars of *C. harbourae*. The m3 hypoconulid is not as large as other conacodontines such as *C. entoconus* and does not project posteriorly. There is a short postcingulid on the m3 of UCM 108749, UCM 103085, and UCM 103155.

UCM 103085 differs the most from the holotype of *Conacodon harbourae* in that it possesses a dp4 and an emerging p3 of which only the protoconid is visible within the alveolus (Figure 23). The dp4 is molariform, with distinct trigonid and talonid cusps, although it is 5% smaller than the m1, with a small, medially-placed paraconid and equidistant talonid cusps. The dp4 has a short anterior cingulid, and a tiny cuspule below the talonid notch.

Measurements of *Conacodon harbourae* are given in Table 8.
FIGURE 29. *Conacodon harbourae*, UCM 108749, incomplete right dentary containing m2–m3; A, labial view; B, occlusal view; C, lingual view.
FIGURE 30. *Conacodon harbourae*, UCM 103155, incomplete right dentary with partial m1 and complete m2–m3; A, labial view; B, occlusal view; C, lingual view.
FIGURE 31. *Conacodon harbourae*, UCM 103085, incomplete right dentary with dp4 and emerging p3 visible in alveolus, and m1–m3; **A**, lingual view; **B**, occlusal view; **C**, labial view.
TABLE 8. Dental measurements (in mm) of *Conacodon harbourae* from UCM locality 2011035, China Butte Member of the Fort Union Formation, Great Divide Basin, Carbon County, WY.

<table>
<thead>
<tr>
<th>Specimen</th>
<th>Position</th>
<th>A-P length</th>
<th>Wtri</th>
<th>Wtotal</th>
</tr>
</thead>
<tbody>
<tr>
<td>103085</td>
<td>dp4</td>
<td>4.123</td>
<td>2.618</td>
<td>2.658</td>
</tr>
<tr>
<td>103155</td>
<td>m1</td>
<td>4.2*</td>
<td>3.4*</td>
<td>3.288</td>
</tr>
<tr>
<td>103085</td>
<td>m1</td>
<td>4.468</td>
<td>3.503</td>
<td>3.229</td>
</tr>
<tr>
<td>108749</td>
<td>m2</td>
<td>4.555</td>
<td>4.193</td>
<td>3.919</td>
</tr>
<tr>
<td>103155</td>
<td>m2</td>
<td>4.226</td>
<td>3.926</td>
<td>3.578</td>
</tr>
<tr>
<td>103085</td>
<td>m2</td>
<td>4.466</td>
<td>3.873</td>
<td>3.441</td>
</tr>
<tr>
<td>108749</td>
<td>m3</td>
<td>5.100</td>
<td>3.637</td>
<td>2.962</td>
</tr>
<tr>
<td>103155</td>
<td>m3</td>
<td>4.790</td>
<td>3.466</td>
<td>3.162</td>
</tr>
<tr>
<td>103085</td>
<td>m3</td>
<td>5.065</td>
<td>3.412</td>
<td>2.802</td>
</tr>
</tbody>
</table>

* Estimated due to breakage and/or wear.
V.

PHYLOGENETIC ANALYSIS

In order to examine the relationships among *Miniconus jeanninae*, *Beornus honeyi*, *Conacodon hettingeri*, and other Puercan ‘condylarths’, a phylogenetic analysis was performed. There have been a number of previous phylogenetic analyses that focused on early Paleocene ‘condylarths’ (Archibald, 1982; Luo, 1991; Zack *et al*., 2005; Williamson & Carr, 2007; De Bast & Smith, 2013; McComas & Eberle, 2015), as well as studies that examined the phylogeny of placental mammals that included several ‘condylarthran’ taxa (e.g., Wible *et al*., 2007, 2009; O’Leary *et al*., 2013). The goal of my cladistic analysis is primarily to resolve the phylogenetic position of the new periptychids described above from the early Puercan of the Great Divide Basin, and not to resolve the phylogeny of all Periptychidae (which range in age from the early Puercan (Pu1) to the middle Tiffanian (Ti4)). An unpublished PhD dissertation by Shelley (2018), with a published meeting abstract (Shelley, 2018), focuses on the phylogeny of the Periptychidae.

Methodology

The analysis included 26 species of Arctocyonidae and Periptychidae known from early-middle Puercan localities in the Western Interior of North America. The arctocyonids used in the analysis are *Protungulatum donnae*, which served as the outgroup taxon, as well as *Oxyprimus galadrielae, Oxyprimus erikseni, Sigynorum magnadivusis*, and *Carcinodon olearyi*. The 21 periptychid species included *Mimatuta minuial, Maiorana noctiluca, Oxyacodon priscilla, Oxyacodon apiculatus, Oxyacodon josephi, Miniconus archibaldi, Miniconus jeanninae, Ampliconus browni, Ampliconus antoni, Alticonus gazini, Mithrandir gillianus, Auraria urbana,*

Protungulatum donnae was chosen as the outgroup for this analysis following Archibald (1982), Thewissen & Domning (1992), and Muizon & Cifelli (2000). It is a well-known species in the Puercan whose first appearance defines the onset of the NALMA, and it is considered the oldest species of placental mammal (O’Leary et al., 2013). Furthermore, study materials were abundant and available for comparison and scoring of dental characters.

The 26 taxa were scored for 58 dental characters, primarily sourced and adapted from a number of previous analyses (Archibald, 1982; Archibald et al., 1983b; Williamson & Carr, 2007; Wible et al., 2009; De Bast & Smith, 2013; McComas & Eberle, 2015; see Appendix A). Due to the absence of cranial and post-cranial material for the majority of the taxa included here, only dental characters were included in the cladistic analysis. Characters were scored by direct comparison to specimens and casts in the UCM collection where available, as well as specimens and casts from AMNH, NMMNH, PU, SMSP, UCMP, UMVP, UNM, USGS, and UW (Appendix B includes a comprehensive list of referred specimens). Additionally, characters were scored by utilizing the primary literature (e.g., Matthew, 1937; Van Valen, 1978; Archibald, 1982; Archibald et al., 1983a, 1983b; Eberle & Lillegraven, 1998b; Middleton & Dewar, 2004) and/or scores from previous phylogenetic analyses (Archibald, 1982; Archibald et al., 1983b; Wible et al., 2009; De Bast & Smith, 2013; McComas & Eberle, 2015) where comparative material was unavailable.

The characters in this analysis were treated as unweighted and unordered and were polarized by outgroup comparison. No a priori assumptions were made about the primitive or derived status of various dental characters, in part because previous workers on early Puercan
‘condylarths’ have not agreed on the primitive/derived status of many of the characters scored for this analysis (e.g., Archibald, 1982; Luo, 1991).

The data matrix was analyzed using PAUP* v.4.0 beta 10 Win (Swofford, 2002). A Heuristic search with random step-wise addition of taxa was performed at 1000 replications using tree-bisection-reconnection (TBR) branch-swapping. Bremer Index values were calculated to measure branch support within the resulting strict consensus tree. A study conducted on the efficiency of different methods of confidence estimation (bootstrap, jackknife, decay indices) found that bootstrapping does not necessarily result in higher branch support than the other methods, although it can be more computationally efficient than Bremer Indices for large data sets (Müller, 2005). Given the small size of my data set, I follow others (Tabuce, 2011; Williamson et al., 2012; Williamson et al., 2014; De Bast & Smith, 2013; McComas & Eberle, 2015) in using Bremer Index values to indicate branch support.

**Results**

The analysis resulted in two equally most parsimonious trees of 215 steps (CI=0.35, RI=0.55), and the strict consensus of those trees has 216 steps (CI=0.35, RI=0.55). The consensus tree is partly unresolved only within the arctocyonids, with the two equally most parsimonious trees in disagreement on the position of *Sigynorum magnadivisus* and *Oxyprimus erikseni* (see Appendix E). Individual Bremer support values for many clades are low (1s and 2s), with most tree branches collapsing in the strict consensus of all trees one or two steps longer than the most parsimonious trees. The low Bremer support values, as well as the low consistency and retention indices of the strict consensus tree, indicate a high degree of homoplasy within the tree. Homoplasy in my analysis may be due to the absence of complete dental material and
therefore the inability to score many of the characters for several taxa as well as the low ratio of taxa to characters – an issue encountered by other phylogenetic analyses that include only dental characteristics (e.g., Williamson & Carr, 2007; Tabuce et al., 2011; Williamson et al., 2014; McComas & Eberle, 2014; Eberle et al., 2019). The strict consensus tree is presented in Figure 32.

The results of the cladistic analysis support that the new GDB species *Beornus honeyi*, *Conacodon hettingeri*, and *Miniconus jeanninae* are nested within the Periptychidae, which was predicted because their teeth are morphologically more similar to the teeth of other Puercan periptychids than they are to arctocyonids. Additionally, the results show a well-supported periptychid clade [Bremer Index: 4].

Within the clade identified as Periptychidae (indicated on Figure 32), the strict consensus tree shows a group comprised of taxa traditionally considered to be periptychids – *Oxyacodon priscilla*, *Oxyacodon apiculatus*, *Oxyacodon josephi*, *Miniconus archibaldi*, *Ampliconus browni*, *Ampliconus antoni*, *Alticonus gazini*, *Mithrandir gillianus*, *Auraria urbana*, *Hemithlaeus kowalevskianus*, and the six previously documented species of *Conacodon* – as well as the new GDB species *Beornus honeyi*, *Conacodon hettingeri*, and *Miniconus jeanninae*. The new genus *Miniconus* appears to be a sister taxon to the clade that contains *C. matthewi*, *C. kohlbergeri*, *C. harbourae*, *C. delphae*, *C. entoconus*, *C. cophater*, *C. hettingeri*, *H. kowalevskianus*, *Alticonus gazini*, and *Ampliconus antoni*. The phylogenetic position of *Miniconus* is supported by the following characters: a p4 with a small, single-cusped talonid (character 11), a consistently-present paraconulid on the molars (character 25), and a distinct m3 hypoconulid with only slight posterior extension (character 28). The genus *Conacodon* is polyphyletic according to the analysis, with *C. matthewi*, *C. kohlbergeri*, and *C. harbourae* falling outside of the clade that
contains C. delphae, C. entoconus, C. cophater, C. hettingeri, as well as H. kowalevskianus, *Alticonus gazini*, and *Ampliconus antoni*.

*B. honeyi* appears to be most closely allied to *Auraria urbana* from the early Puercan Littleton fauna in the Denver Basin, and together these taxa form a sister group to a clade containing *C. harbourae* and *C. kohlbergeri*. The position of the clade formed by *A. urbana* and *B. honeyi* is supported by a single character: an open talonid notch (character 13). *A. browni* appears to be basal relative to most of the other periptychids, except for *O. josephi*, *M. gillianus*, *O. apiculatus*, and *O. priscilla*. However, as noted above, Bremer branch support is low, and therefore I consider the phylogenetic results to be preliminary that require more complete dental material.

Within Periptychidae, three subfamilies have been traditionally recognized: Periptychinae, Anisonchinae, and Conacodontinae as well as a handful of genera *incertae sedis* (Archibald, 1983b; McKenna & Bell, 1997; Archibald, 1998). The subfamilies Anisonchinae and Conacodontinae are not “mutually exclusive” (McKenna et al., 2008) and Eberle & Lillegraven (1998b) decided against using Conacodontinae altogether, instead assigning several new taxa to Anisonchinae. However, other authors (Archibald, 1983b; Middleton & Dewar, 2004) have classified new periptychid species within the Conacodontinae, despite the fact that the diagnosis for the subfamily overlaps with the diagnoses for both Anisonchinae and Periptychinae. According to Archibald (1998), periptychids belonging to any of the three subfamilies can be small in size, periptychids belonging to Conacodontinae and Anisonchinae may either possess or lack a P3 protocone, and the paraconid on p3 and p4 of periptychids belonging to Anisonchinae may range from large and distinct to completely absent. This overlapping of characters makes it difficult to assign new taxa to a subfamily and might instead force researchers to shoehorn taxa
into a subfamily that doesn’t entirely fit. Placing periptychids into subfamilies therefore only
creates confusion within an order that is already considered to be polyphyletic (‘Condylarthra’).
My phylogenetic analysis included periptychid taxa that traditionally were placed within these
three subfamilies. However, the strict consensus tree (Figure 32) shows that the taxa do not align
with their traditional placement within the Periptychinae, Anisonchinae, and Conacodontinae.
Nevertheless, for the sake of comparison with other studies that refer to the three traditional
subfamilies (e.g., Archibald, 1983b; Shelley, 2018), I tentatively refer to the node in the strict
consensus tree (Figure 32) that contains *Oxyacodon priscilla, Oxyacodon apiculatus, Miniconus
archibaldi, Miniconus jeanninae, A. gazini, Ampliconus antoni, Conacodon delphae, C.
entoconus, C. cophater, C. hettingeri, H. kowalevskianus, C. matthewi, C. harbourae, C.
kohlbergeri, A. urbana, Beornus honeyi, and Ampliconus browni* tentatively as the
Conacodontinae. Therefore, I place *A. gazini, A. antoni, A. browni, and H. kowalevskianus* into
that group. *Mithrandir gillianus*, traditionally considered to be an anisonchine, does in fact fall
outside of the node containing the Conacodontinae in the strict consensus tree (Figure 32), along
with *Oxyacodon josephi*.

The taxa I include in Conacodontinae variably align with the original diagnosis by
Archibald et al. (1983b). Those authors include the genera *Conacodon* and *Oxyacodon* into
Conacodontinae, and state that Conacodontinae are “periptychids with hypocone on M1–3 large
and lingually expanded, and protocone on P3 absent” (Archibald et al., 1983b, p. 3). The original
diagnosis was later expanded upon to also include that the molar precingulum tends to contact
the hypocone across the protocone (Archibald, 1998). Although the majority of the taxa I include
in Conacodontinae possess these characters, the original diagnosis is general and allows for some
intraspecific variation, such as the P3 protocone on *Oxyacodon apiculatus* being reduced to a
lingual swelling rather than absent altogether, and the hypocone on *Ampliconus browni* being
lingually expanded but not large in comparison to the protocone. *Alticonus gazini, A. browni,
Hemithlaeus kowalevskianus,* and *Miniconus archibaldi* do not possess a molar precingulum that
contacts the hypocone. Furthermore, Archibald (1983b, 1998) only diagnosed upper molar
characteristics for Conacodontinae, and the upper dentition is currently unknown for *A. antoni,
Conacodon harbourae, C. delphae, C. matthewi, C. hettingeri, Auraria urbana, Miniconus
jeanninae,* and *Beornus honeyi.* I therefore refrain from assigning the three new taxa from the
GDB described above, *Beornus honeyi, Conacodon hettingeri,* and *Miniconus jeanninae,* to any
of the existing periptychid subfamilies, in order to avoid adding to the confusion among
Periptychinae, Conacodontinae, and Anisonchinae.

The other major phylogenetic division shown in the strict consensus tree (Figure 32) is
comprised of four arctocyonid taxa. The arctocyonids *Oxyprimus galadrielae* and *Carcinodon
olearyi* form a clade, that, in turn, forms an unresolved polytomy with *Oxyprimus erikseni* and
*Sigynorum magnadivisus.* McComas & Eberle (2015) also found *S. magnadivisus* and *O.
erikseni* to form a clade with mild Bremer support [2], where my analysis found that the
positions of *S. magnadivisus* and *O. erikseni* change between the two equally most parsimonious
trees (see Appendix E) with *S. magnadivisus* and *O. erikseni* lying outside of a clade formed by
*O. galadrielae* and *C. olearyi.* Whereas my analysis found the four arctocyonids to form a clade,
similar to McComas & Eberle (2015), the difference in the relative positions of *S. magnadivisus*
and *O. erikseni* may be due to differences in the characters scored for this analysis. McComas &
Eberle (2015) scored 73 characters for 23 taxa in their analysis and sourced the majority of their
characters from previous phylogenetic analyses (e.g., Archibald, 1982; Archibald et al., 1983b;
Wible et al., 2009; De Bast & Smith, 2013) to capture the dental morphology of their new
arctocyonid species relative to other members of Arctocyonidae. Although I sourced a number of
characters for this analysis from the same primary literature, including McComas & Eberle
(2015), the characters used in my cladistic analysis were chosen to represent the morphology of
my three new periptychid species relative to Periptychidae.

*Oxyacodon apiculatus* was included in the study to help refine the relationship of the
species of *Oxyacodon* to one another. The analysis suggests that *O. apiculatus* and *O. priscilla*
do not form a clade, nor is either species contained in the clade that includes *Miniconus archibaldi* and *Miniconus jeanninae*. When considered alongside the morphologic differences
between *M. archibaldi* and the other species of *Oxyacodon*, the results of the phylogenetic
analysis support the removal of *M. archibaldi* from the genus *Oxyacodon* and its placement in
the new genus *Miniconus*.

It is important to note the clade formed by *Oxyacodon josephi* and *Mithrandir gillianus*
[Bremer Index: 2]. Despite the vague diagnosis and dubious nature of the two known specimens
of *O. josephi* detailed above in the discussion of Miniconus, *O. josephi* was included in this
analysis. If PU 13338, a left dentary containing m1–m3 identified as *Oxyacodon sp.* by Jepsen
(1930), is in fact the lower dentition of *O. josephi* as Van Valen (1978) claimed it to be, then the
position of *O. josephi* in this analysis may be accurate. *O. josephi* may not belong within the
genus *Oxyacodon*, and instead might be an anisonchine, given that it forms a clade with
*Mithrandir gillianus*. This solution would align with conclusions made by Archibald (1982,
1998) that *O. josephi* does not possess any synapomorphies that would ally it with *Oxyacodon*.
However, without more associated upper and lower dentitions of *O. josephi*, the clade formed by
*O. josephi* and *M. gillianus* should be treated as questionable. Two characters support this clade:
a medial m2 paraconid (character 22) and an M2 preparacrista that extends mesially to meet the parastylecone on the precingulum (character 51).

Finally, the placement of *Mimatuta minuial* and *Maiorana noctiluca* within this phylogenetic analysis is notable. The arctocyonids *Oxyprimus galadrielae, Oxyprimus erikseni, Sigynorum magnadivisus,* and *Carcinodon olearyi* were included in part to resolve the position of *M. noctiluca* and *Mimatuta minuial* in relation to other early Puercan periptychids. This analysis places *Mimatuta* and *Maiorana* within the Periptychidae, although outside the Conacodontinae. This is in contrast to some studies (Luo, 1991; Williamson & Carr, 2007; Tabuce *et al.*, 2011; De Bast & Smith, 2013; McComas & Eberle, 2015; Shelley, 2018) that place these two taxa within the Arctocyonidae.

**Comparison with other phylogenetic analyses**

The phylogenetic analysis conducted as part this thesis focused primarily on early Puercan periptychids, with some members of the Arctocyonidae included. Archibald (1982, 1993) and subsequently McComas & Eberle (2015) included a number of the periptychids discussed here in their phylogenetic analyses, although their results do not mirror the results of this analysis. Additionally, an unpublished (and currently embargoed) dissertation by Shelley (2018) focuses on the phylogenetic relationships of Periptychidae, and it contains a much larger character matrix that includes both cranial and post-cranial material. Due to the scarcity of published phylogenetic analyses that include Periptychidae, it is difficult to comment on the relative placement of periptychids within my cladogram compared to that of previous analyses. Studies that have included various families within the polyphyletic order ‘Condylarthra’ show periptychids and arctocyonids appearing throughout their phylogenies (Archibald, 1993;
Williamson & Carr, 2007; Wible et al., 2007, 2009; Tabuce et al., 2011; De Bast & Smith, 2013; McComas & Eberle, 2015).

Shelley (2018) reported that her phylogenetic analysis placed *Auraria urbana* as the most basal member of the Conacodontinae. My results do not seem to support this finding, although as noted earlier, the Bremer Indices are low for the clade containing the conacodontines. Shelley (2018) also reported *Alticonus gazini* as the most basal periptychid, a similar result to McComas & Eberle (2015). My results do not support *A. gazini* as the most basal periptychid, but rather this species forms a clade with *Ampliconus antoni* that is nested within the Conacodontinae (Figure 32). However, the discrepancy between my results and that of Shelley (2018) may also be due to the absence of post-cranial and cranial characters in my phylogenetic analysis. A recent study by Sansom et al. (2017) found that using characters solely from dental morphology or solely from osteological morphology in a phylogenetic analysis results in a less phylogenetically informative tree. Ideally, characters should be sourced from across morphological partitions; i.e., evenly sampling from dental, cranial, and post-cranial material (O’Leary & Gatesy, 2008; Spaulding & Flynn, 2012; Sansom et al., 2017). However, the great majority of the early–middle Puercan taxa used in my analysis are known only from their dentitions, so I was not able to incorporate cranial and postcranial characters into the analysis.

This phylogenetic analysis focused primarily on early Puercan periptychid ‘condylarthrs’ to specifically determine the position of the new GDB taxa *Beornus honeyi, Conacodon hettingeri*, and *Miniconus jeanninae*. Of the other ‘condylarthan’ taxa I have included in this analysis, it is primarily the more primitive arctocyonids *Protungulatum donnae* and *Oxyprimus spp.* and the periptychids *Mimatuta minuial* and *Maiorana noctiluca* that appear in previous studies. A monophyletic clade formed by *P. donnae* and *Oxyprimus spp.* is supported by a
number of analyses (Williamson & Carr, 2007; Wible et al., 2007, 2009; Tabuce et al., 2011; De Bast & Smith, 2013) which also is positioned as the immediate outgroup to Placentalia in broader studies (Wible et al., 2007, 2009; De Bast & Smith, 2013). This clade is relatively basal in comparison to a number of other Paleocene ‘condylarths’ (De Bast & Smith; 2013) and appears closely allied with the Paleocene plesiadapiform *Purgatorius* in some analyses (Wible et al., 2007, 2009; De Bast & Smith, 2013) as well as the small early Paleocene arctocyonid *Prolatidens waudruae* (De Bast & Smith, 2013). Wible et al. (2007, 2009) determined the clade formed by *Oxyprimus spp.* and *P. donnae* to be separate from other late Paleocene – early Eocene ‘condylarths’, and to represent the immediate outgroup to Placentalia (Wible et al., 2007). This conclusion contradicts O’Leary et al. (2013, p. 665) who recognized *P. donnae* “as the oldest undisputed species within crown Placentalia.”

*Mimatuta minuial* and *Maiorana noctiluca* also appear as a monophyletic clade nested within the arctocyonids in multiple previous analyses (Williamson & Carr, 2007; Tabuce et al., 2011; De Bast & Smith, 2013), closely related to the clade formed by *Protungulatum donnae* and *Oxyprimus spp.* and basal to other Paleocene ‘condylarths’ (De Bast & Smith, 2013). Whereas I also find *M. minuial* and *M. noctiluca* to be basal, this analysis here suggests that they represent basal periptychids, not arctocyonids. Disagreement on the phylogenetic position of *Maiorana* and *Mimatuta* is rampant among previous workers, with some researchers placing them among the Periptychidae (Van Valen, 1978; Archibald, 1982; Honey, 1990; Lofgren, 1995; Eberle & Lillegraven, 1998b) and others placing them within the Arctocyonidae (Luo, 1991; Williamson & Carr, 2007; Tabuce et al., 2011; De Bast & Smith, 2013; McComas & Eberle, 2015; Shelley, 2018).
Sansom et al. (2017) noted that mammalian dental characters are less compatible with molecular phylogenies than osteological data. Other authors have also pointed out that mammalian dental characters are not independent of one another, which may obscure certain phylogenies when those characters are used as significant markers in evolutionary taxonomy (Kangas et al., 2004). The available fossil material for this thesis is entirely dental and does not allow for scoring characters other than the dental morphology. This limitation has also been encountered by other phylogenetic studies assessing early Paleocene fossil mammals (e.g., Williamson & Carr, 2007; Williamson et al., 2012; McComas & Eberle, 2015). This at least partly explains the disagreement among previous workers on certain phylogenetic positions and taxonomic assignments of ‘condylarths’, and it may explain the low Bremer support for my strict consensus tree (Figure 32). As mentioned above, these results are preliminary. More complete material, and in particular the addition of upper dentitions (for some taxa) as well as cranial and postcranial materials, should help increase individual branch support and provide more conclusive results. Nevertheless, the results of the phylogenetic analysis demonstrate that the new GDB taxa – Beornus honeyi, Conacodon hettingeri, and Miniconus jeanninae – are nested within the Periptychidae, satisfying the primary goal of this cladistic analysis.
FIGURE 32. Strict consensus tree (216 steps, CI=0.35, RI=0.55) derived from the 2 most parsimonious trees with Bremer Index values located above the branches and new taxa highlighted in red.
VI.

CONCLUSIONS AND FUTURE RESEARCH

The six periptychid ‘condylarths’, including the two new genera and three new species described above from the lower China Butte Member of the Fort Union Formation in the Great Divide Basin contribute to the growing reservoir of knowledge of mammalian diversity in the earliest Paleocene. Three of the taxa described above from the GDB are known from elsewhere. Eberle & Lillegraven (1998b) described Maiorana noctiluca, Ampliconus antoni, and Conacodon harbourae from three localities of earliest middle Puercan age in the Ferris Formation in Wyoming’s Hanna Basin; Middleton & Dewar (2004) described C. harbourae from the Denver Basin, Colorado (early Puercan); and Van Valen (1978) diagnosed M. noctiluca from the Mantua lentil in Wyoming (early Puercan). My report of M. noctiluca, A. antoni, and C. harbourae from the China Butte Member extends the geographic ranges of all three taxa to the GDB, and it extends the temporal range of A. antoni from the middle Puercan (Hanna Basin) to the early Puercan (GDB). Above, I also describe three new periptychids from the GDB – Beornus honeyi, Conacodon hettingerii, and Miniconus jeanninae.

The phylogenetic analysis has a number of implications for early Puercan Periptychidae. My hypothesis that Beornus honeyi, Conacodon hettingerii, and Miniconus jeanninae from the GDB are nested within the Periptychidae is supported, with Beornus honeyi allied with the early Puercan periptychid Auraria urbana from the Denver Basin. Additionally, the new genus Miniconus, which comprises M. archibaldi and M. jeanninae, appears to be monophyletic, whereas the genus Conacodon appears to be paraphyletic. Conacodon hettingerii is included within the clade containing the traditional species of Conacodon, to the exclusion of C. matthewi, C. kohlbergeri, and C. harbourae. No previous phylogenetic analyses have found
Conacodon to be paraphyletic. However, Shelley (2018) noted that the genus Oxyacodon formed a paraphyletic stem to Conacodon in her analysis, which my results do not support. Finally, my phylogenetic analysis finds the early Puercan taxa Mimatuta spp. and Maiorana noctiluca to fall within the Periptychidae, supporting the traditional placement of these taxa as basal members of that family, although several studies contrast this placement (Luo, 1991; Williamson & Carr, 2007; Tabuce et al., 2011; De Bast & Smith, 2013; McComas & Eberle, 2015; Shelley, 2018). This may also be due to differences in included taxa and characters between my phylogenetic analysis and others.

Some recent work (Clemens, 2010; Wilson, 2013) has estimated ‘condylarthran’ diversity in the Western Interior of North America to be low in the early Puercan in spite of ‘condylarth’ taxa comprising a large portion of the total faunal diversity following the K-Pg boundary. In contrast to these findings, UCM locality 2011035 and the correlative Littleton fauna in Colorado’s Denver Basin both preserve high taxonomic diversity in the early Puercan. The Littleton fauna, hypothesized to be late Pu1 in age (Eberle & Lillegraven, 1998a, 1998b; Eberle, 2003; Middleton & Dewar, 2004), has high taxonomic diversity with nine genera and 12 species of ‘condylarths’ (Eberle, 2003; Middleton & Dewar, 2004). The presence of the three new periptychid taxa in the GDB in addition to the new genus and species of arctocyonid ‘condylarth’ described by McComas & Eberle (2015) further increases the known mammalian diversity during early Puercan time (Pu1), thus supporting the conclusion that local faunal diversity was higher than previously documented (Eberle & Lillegraven, 1998b; McComas & Eberle, 2015; Templeman, 2018). Similar to what has been hypothesized for the Littleton fauna, it is possible that the GDB samples a slightly later Puercan temporal window than the traditional, low diversity Pu1 faunas in NE Montana (e.g., Clemens, 2010; Wilson, 2013; Sprain et al., 2015;
Smith et al., 2018), which could explain the higher taxonomic diversity in the GDB and in the Denver Basin. Alternatively, the more southerly locations of the Great Divide and Denver Basins in comparison to other Pu1 fossil localities may be reflecting geographic differences in taxonomic diversity.

Previous studies of UCM locality 2011035 have suggested a late early Puercan (Pu1) age for the fauna, given faunal similarities to the Littleton fauna in the Denver Basin (Eberle et al., 2013; McComas & Eberle, 2015). The Littleton fauna is hypothesized to be late early Puercan in age because, though it falls within the biostratigraphic constraints of the early Puercan (Pu1) (Lofgren et al., 2004), it is also similar to the earliest middle Puercan (Pu2) of the Hanna Basin in its high taxonomic diversity and faunal composition (Eberle, 2003). My study of the periptychids supports correlation of UCM locality 2011035 with the Littleton fauna, as it shares another species - Conacodon harbourae. An early Puercan age for the fauna preserved at UCM locality 2011035 is also supported by the presence of Maiorana noctiluca, an early Puercan ‘condylarth’ (Van Valen, 1978; Eberle & Lillegraven, 1998b). Therefore, all faunal evidence thus far supports an early Puercan (Pu1) age assignment for UCM locality 2011035, which has produced a diverse fauna that likely includes other new taxa in addition to the recently-described arctocyonid Sigynorum magnadivisus (McComas & Eberle, 2015), a new eucosmodontid multituberculate (Templeman, 2018), and the three new periptychids described above.

In the earliest Paleocene, the Hanna and Great Divide Basins were components of the Greater Green River Basin which originally represented part of a foreland basin or “ponded depocenter” (Lillegraven et al., 2004; Lynds & Carroll, 2015). Late in the Laramide Orogeny, however, the Greater Green River Basin was subdivided by basement-involved thrust faulting and the Hanna and Great Divide Basins were subsequently split by the Rawlins Uplift.
(Lillegraven, et al., 2004). *Maiorana noctiluca*, *Ampliconus antoni*, and *Conacodon harbourae*, described above from UCM locality 2011035, have also been identified from localities in the Ferris Formation in the Hanna Basin that are considered earliest middle Puercan (Pu2) in age by Eberle & Lillegraven (1998b). The documentation of these taxa from UCM locality 2011035 in the GDB further supports the hypothesis by Lillegraven et al. (2004) that the Hanna and Great Divide Basins were contiguous during the early Paleocene. A number of studies report that the GDB and the Hanna Basin were not separated by the Rawlins Uplift until the late Paleocene/early Eocene (Kirschbaum et al., 1994; Lillegraven, 2004; Lynds & Carroll, 2015).

The high taxonomic diversity at UCM locality 2011035 in the GDB is incentive enough to continue studying this particular fauna. From this locality, a small percentage of the specimens collected by James Honey and Malcolm McKenna has been formally described thus far (McComas & Eberle, 2015; Templeman, 2018; this thesis). It is likely that there are additional new taxa to be described from the more than 420 mammalian fossils housed in the UCM collection. In order to more completely sample the early Puercan mammalian fauna from the GDB, additional prospecting is needed in the lower China Butte Member of the Fort Union Formation, as UCM locality 2011035 has been exhausted. Extensive efforts to describe the stratigraphy of the GDB have already been completed by Robert Hettinger and others (Hettinger et al., 1991; Hettinger & Kirschbaum, 1991; Honey & Hettinger, 2004; Hettinger et al., 2008). The work by those authors has been essential in determining the stratigraphic positions of Puercan – Tiffanian fossil localities in the GDB and will continue to play a central role as we discover new localities.
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Wolfson, K.B., Blanchard, M., Lobber, B., Scott, V., and Bowers, D. 2015. Imagine All the Imaging: One Entomology Collection’s Quest for the Prefect Insect Image. Poster Session at: AAAS; February 2015; San Jose, CA.

APPENDIX A. List of dental characters and definitions of character states. Reference provided after each character when applicable, with modifications to characters and/or character states indicated by an asterisk.

Lower Premolars

1. *p1 roots*: two (0); one (1); first lower premolar is absent (2) (De Bast & Smith 2013: character 40).
2. *p2 talonid*: bears distinct 'heel' (0); lacks distinct heel (1) (Williamson & Carr 2007: character 38).
3. *p3 paraconid*: distinct (0); small, or present as a ridge (1); absent (2) (Archibald et al. 1983b: table 3, character 13).
4. *p3 metaconid*: present as a ridge or cusp (0); very small or absent (1) (Archibald 1982: table 56, character 1).
5. *p4 length compared to m1*: shorter (0); subequal (within 0.25 mm) (1); longer (2) (Williamson & Carr 2007: character 46*; Archibald 1982: table 56, character 12*).
6. *p4 width compared to m1*: p4 narrower than m1 (0); subequal or slight inflation (1); p4 wider than m1 (2) (Archibald 1982: table 56, character 12*; Archibald et al. 1983b: table 3, character 5*).
7. *p4 paraconid*: small to distinct but low and lingual (0); absent or present as crest/bulge (1); moderately large, slightly lingual (2) (Archibald 1982: table 56, character 6*).
8. *p4 metaconid*: present as cusp (0), present as ridge (1), absent (2) (Archibald et al. 1983b: table 3, character 14*).
9. *p4 shape (length vs width)*: length exceeds width (0); length approximately equal to width (1) (Archibald et al. 1983b: table 3, character 5*).
10. *p4* talonid cusps: trenchant with small posterior cusp (0); one or more cuspids and/or with talonid basin (1); wide and well-developed with 2 or more cusps (2) (Archibald 1982: table 56, character 7*).

11. *p3*-4 protoconid: tall and not inflated to slightly inflated (0); relatively shorter and more inflated (1); moderately tall and well-inflated (2) (Archibald 1982: table 56, character 9).

**Lower Molars**

12. *m1*-2 talonid notch [scored by m2]: open (0); closed (1) (Archibald 1982: table 56, character 4*).

13. trigonid cusps: narrow and not inflated to slightly inflated (0); widened and more inflated (1) (Williamson & Carr 2007: character 53*).

14. trigonid cusps: not appressed (0); appressed (1), metaconid and protoconid appressed but paraconid is projected anteriorly (2) (Archibald *et al.* 1983b: table 3, character 3*; Williamson & Carr 2007: character 49*).

15. *m1* talonid vs. trigonid: talonid narrower than trigonid (0); subequal (1); talonid wider than trigonid (2) (Archibald 1982: table 56, character 13*).

16. *m2* talonid vs. trigonid: talonid narrower than trigonid (0); subequal (1); talonid wider than trigonid (2) (Archibald 1982: table 56, character 13*).

17. molar lingual cingulid: absent (0); discontinuous, narrow (1); prominent cingulid starting below paraconid reaching the base of the entoconid (2) (Archibald *et al.* 1983b: table 3, character 2).

18. molar labial cingulid around trigonid: discontinuous or absent (0); narrow and continuous (1); wide and continuous (2) (Archibald 1982: table 56, character 5*).
19. discontinuous labial cingulid in hypoflexid region [on one or more molars, potentially with rugosity]: present (0); absent (1), present as ectostylid (2) (De Bast & Smith 2013: character 77*).

20. m1 paraconid position: lingual to midline (0); slightly less lingual, closer to midline (1); on midline (2) (Archibald et al. 1983b: table 3, character 4).

21. m2 paraconid position: lingual to midline (0); slightly less lingual, closer to midline (1); on midline (2) (Archibald et al. 1983b: table 3, character 4).

22. m3 paraconid position: lingual to midline (0); slightly less lingual, closer to midline (1); on midline (2) (Archibald et al. 1983b: table 3, character 4).

23. paraconid size relative to other trigonid cusps: not reduced (large) (0); slightly reduced (1); small ridge or cusp (2) (Archibald 1982: table 56, character 14*; Archibald et al. 1983b: table 3, character 11).

24. presence of paraconulid [variably or consistently across specimens on one or more molars]: absent (0), variably present (1), consistently present (2) (this thesis).

25. placement of talonid cusps [scored by m1]: hypoconulid is nearest to entoconid (0), all three cusps are equidistant (1) (Archibald et al., 1983b: table 56, character 4*).

26. entoconid placement [scored by m1]: posteriorly shifted relative to hypoconid (0), opposite from hypoconid (1), anteriorly shifted relative to hypoconid (2) (this thesis).

27. m3 hypoconulid: well-developed, distinct posterior extension (0); distinct cusp, not extended posteriorly (1); distinct cusp, slight posterior extension (2) (Archibald 1982: table 56, character 3*).

**Upper Premolars**

28. P1 roots: two (0); one (1) (De Bast & Smith 2013: character 2).
29. *P3 roots*: two (0); three (1); one (2) (Wible *et al.* 2009: character 39).

30. *P3 shape*: length approximately equal to width (0); length exceeds width (1) (Williamson & Carr 2007: character 6).

31. *P3 protocone*: present as distinct cusp or reduced to lingual swelling (0); absent and lingual heel low (1) (Williamson & Carr 2007: character 7*).

32. *P3 metacone*: absent (0); present as a distinct cusp (1) (De Bast & Smith 2013: character 5*).

33. *P4 paracone and protocone*: uninflated (0); inflated (1) (Archibald 1982: table 55, character 7*).

34. *P4 paracone to protocone height*: paracone much taller (0); paracone slightly taller (1) (Archibald 1982: table 55, character 10).

35. *P4 metacone*: present (0); absent (1) (Williamson & Carr 2007: character 8).

36. *P4 parastyle and metastyle*: labial to paracone (0); shifted lingually and aligned with paracone (1) (Archibald 1982: table 55, character 8).

37. *preparacrista on P4*: absent (0); present (1) (De Bast & Smith 2013: character 11).

38. *labial cingulum on P4*: absent (0); present (1) (De Bast & Smith 2013: character 12).

39. *P4 precingulum*: absent (0); present (1) (Wible *et al.* 2009: character 43).

40. *P4 postcingulum*: absent (0); present, not reaching the labial margin of the tooth (1); present, reaching the labial margin of the tooth (2) (De Bast & Smith 2013: character 14).

41. *P4 paraconule*: absent (0); present (1) (De Bast & Smith 2013: character 15).

42. *P4 size relative to M1*: P4 smaller (0); P4 subequal (1); P4 larger (2) (Archibald 1982: table 55, character 5*).
Upper molars

43. *molar occlusal shape*: subquadrate (0); triangular (1) (Archibald 1982: table 55, character 12*).

44. *M1-2 relative size*: M2 larger than M1 (0); M1 is subequal or larger than M2 (1) (Williamson & Carr 2007: character 33).

45. *M3 size relative to M1*: M3 subequal to M1 (0); M3 moderately to greatly smaller than M1 (1) (Williamson & Carr: character 34).

46. *molar protocone position*: base is not expanded lingually (0); lingual expansion of base and apex is labially shifted (1) (Archibald et al. 1983b: table 3, character 1).

47. *molar paracone and metacone*: close so that bases merge (0); separated but connected by centrocrista (1) (Williamson & Carr 2007: character 20).

48. *M1-2 size of paracone relative to metacone*: subequal (0); paracone somewhat larger (1); paracone twice as large (2) (Williamson & Carr 2007: character 22).

49. *M1-2 hypocone size & position*: small or absent, posterolingual to protocone (0); distinct, posterolingual to protocone (1); distinct, more lingual than posterior to protocone (2) (Archibald 1982: table 55, character 9*).

50. *M2 preparacrista*: extends labially to labial stylocone (0); extends mesially to parastylolcone on the precingulum (1) (Williamson & Carr 2007: character 15).

51. *M2 parastylar cusps*: multiple (0); single cusp mesial to paracone (1) (Williamson & Carr 2007: character 14).

52. *molar mesostyle*: absent (0); present on some or all molars (1) (Williamson & Carr 2007: character 26*).
53. *molar stylar shelf*: wide shelf and continuous (0); narrow ridge and sometimes discontinuous (1); narrow ridge but continuous (2) (Archibald *et al.* 1983b: table 3, character 10*).

54. *M3 parastylar lobe*: projects mesiolabially to near the labial edge of M2 (0); broadly rounded and not projecting (1) (Williamson & Carr 2007: character 36).

55. *molar precingulum*: does not encircle protocone and does not contact hypocone (0); encircles protocone and contacts hypocone on some or all upper molars (1) (Archibald *et al.* 1983b: table 3, character 9).

56. *molar postcingulum and metacingulum*: distinct and not connected (0); form a continuous shelf (1); absent (2) (Archibald 1982: table 55, character 4).


58. *M1-2 metaconules*: present (0); absent (1) (Williamson & Carr 2007: character 29).
APPENDIX B. Data matrix including 58 dental characters scored for 26 taxa. Missing data are scored as ‘?’.

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<tr>
<th>Species</th>
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APPENDIX C. List of referred specimens

Protungulatum donnae
SPSM 62-2028 (cast), UMVP 5216 (cast), UMVP 5217 (cast)

Oxyprimus galadrielae
PU 16703 (cast), PU 16712 (cast), PU 16863 (cast), PU 16866 (cast), UCM 34567d, UCM 34622

Oxyprimus erikseni
UMVP 1561 (cast), UCMP 132315 (cast), UCMP 132250 (cast), UCMP 116506 (cast), UCMP 116514, UCMP 132496, UCMP 134623, UCMP 134698, UCMP 134783, UCMP 133796

Sigynorum magnadivisus
UCM 103133 (holotype), UCM 103086, UCM 103088, UCM 103089, UCM 103092, UCM 103128, UCM 103137, UCM 103139, UCM 103142, UCM 103154, UCM 103159, UCM 103175, UCM 108714, UCM 108715

Carcinodon olearyi
AMNH 801 (cast), AMNH 3216 (cast), AMNH 16350 (cast), NMMNH 2745 (cast), NMMNH 12415 (cast), NMMNH 12417 (cast)

Mimatuta minuial
PU 14453 (cast), PU 16702 (cast), PU 14211 (cast), PU 14172 (cast)

Mimatuta morgoth
UCMP 116522 (cast), UCMP 116523 (cast), UMVP 1664 (cast)

Maiorana noctiluca
PU 16710 (cast), PU 16667 (cast), PU 14171 (cast), PU 16711 (cast), UCM 103093, UCM 103131, UCM 103167
Maiorana ferrisensis
UW 26148 (cast)

Oxyacodon priscilla
AMNH 3547a (cast), AMNH 16386 (cast)

Oxyacodon archibaldi
UCM 34958 (holotype), UCM 34607, UCM 34610, UCM 34613, UCM 34942, UCM 34953,
UCM 34958, UCM 35087, UCM 40700

Oxyacodon apiculatus
AMNH 16489 (cast), AMNH 16369 (cast)

Alticonus gazini
UCM 34895 (holotype), UCM 34166

Ampliconus browni
UCM 34163 (holotype), UCM 34635, UCM 34637, UCM 34619

Ampliconus antoni
UW 26200 (cast), UCM 103150, UCM 103151

Conacodon harbourae
UCM 40150 (holotype), UCM 108749, UCM 103155, UCM 103085

Conacodon delphae
UCM 45587 (holotype), UCM 38042, UCM 43740, UCM 47587, USGS-D10 (cast)

Conacodon cophater
AMNH 16435 (cast), AMNH 16481 (cast), AMNH 3488 (cast)

Conacodon entoconus
AMNH 16424 (cast), AMNH 3467 (cast)
Conacodon kohlbergeri
NMMNH P-79975 (holotype)

Conacodon matthewi
UCM 33880 (holotype), UCM 33881, UCM 34324

Auraria urbana
UCM 34935 (holotype)

Hemithlaeus kowalevskianus
AMNH 16441 (cast), AMNH 3556 (cast), NMMNH P-47186, NMMNH P-15045, NMMNH P-15086, NMMNH P-15122

Mithrandir gilli
UNM B-029 (cast), AMNH 16461 (cast), AMNH 15452 (cast)

Beornus honeyi
UCM 103183 (holotype)

Conacodon hettingeri
UCM 103374 (holotype)

Miniconus jeanninae
UCM 103181 (holotype), UCM 103084, UCM 103171
APPENDIX D. Measurements (in mm.) of *Conacodon delphae*.

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* Estimated due to breakage and/or wear.
APPENDIX E. Two equally most parsimonious trees with new taxa highlighted in red.