A NEW PUERCAN ARCTOCYONID GENUS FROM THE GREAT DIVIDE BASIN, WYOMING

KATIE MCCOMAS Sc.B., Brown University, 2008

A thesis submitted to the Faculty of the Graduate School of the University of Colorado in partial fulfillment of the requirement for the degree of Master of Science Department of Museum and Field Studies 2014 This thesis entitled: A new Puercan arctocyonid genus from the Great Divide Basin, Wyoming written by Katie McComas has been approved for the Department of Museum and Field Studies.

Jaelyn J. Eberle

Christy M. McCain

William A. Clemens

Patricia A. Holroyd

Date

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. McComas, Katie (M.S., Museum and Field Studies) A new Puercan arctocyonid genus from the Great Divide Basin, Wyoming Thesis directed by Associate Professor & Curator of Fossil Vertebrates Jaelyn J. Eberle

A new genus and species of earliest Paleocene (Puercan) arctocyonid 'condylarth,' Sigynorum magnadivisus, is described from the Great Divide Basin of southern Wyoming. The fossils are from the China Butte Member of the Fort Union Formation, and the fauna as a whole suggests an early Puercan (Pu1) age. Based on a sample of 14 partial dentaries whose combined dentitions document the p2, p4, and m1–3, the new taxon appears most similar in size and molar morphology to the early Puercan arctocyonid Oxyprimus erikseni. There are, however, distinctive features possessed by the new arctocyonid, including a p4 with a tall single-cusped trigonid and anteroposteriorly-compressed molar trigonids that are lacking in *O. erikseni*. To examine the relationships among S. magnadivisus and other Puercan arctocyonids and periptychids from the Western Interior of North America, a phylogenetic analysis utilizing 18 taxa (including 16 'condylarths', the plesiadapiform *Purgatorius*, and outgroup taxon *Cimolestes*) and 52 dental characters was performed. Characters were aggregated from a number of previous phylogenetic analyses of 'condylarth' taxa, and scored based on direct comparative study of specimens and casts from several museum collections, as well as descriptions of dental morphology in the literature. The resulting strict consensus tree of 190 steps shows that S. magnadivisus is closely related to Oxyprimus spp. and Protungulatum donnae, while Purgatorius is the sister group to the monophyletic Puercan arctocyonids. The Periptychidae are paraphyletic, and the early Puercan periptychids Mimatuta morgoth, Mimatuta minuial, and Maiorana noctiluca appear in a tritomy as the sister clade to *Purgatorius* + Arctocyonidae, while the remaining

periptychid taxa (*Conacodon* spp., *Ampliconus browni*, *Oxyacodon priscilla*, and *Mithrandir gillianus*) form a monophyletic clade. This analysis is the first to focus on a large set of Puercan arctocyonid and periptychid taxa across geographically-widespread localities, and, with the addition of *S. magnadivisus* to the known early Puercan arctocyonids, suggests that diversity among early Puercan 'condylarths' may be higher than previously thought.

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INTRODUCTION

Recent studies have suggested that the radiation of placental mammals after the Cretaceous-Paleogene (K-Pg) extinction event fits the explosive model of diversification, and that ordinal-level diversification began in the earliest Paleocene within 400 thousand years of the K-Pg boundary (O'Leary et al., 2013). Others have suggested that immigration of new taxa played a large role in boosting local mammalian diversity after the K-Pg extinction (Clemens, 2002, 2010; Wilson, 2014). Earliest Paleocene faunas -particularly those of the Puercan, a North American Land Mammal Age (NALMA) or biozone which represents approximately the first million years of the Cenozoic (Lofgren et al., 2004) – contain valuable information that can be used to test such hypotheses. While there are documented Puercan faunal assemblages stretching from Saskatchewan to New Mexico (Lofgren et al., 2004), only one – the Hanna Basin in south-central Wyoming – preserves faunas representing the entirety of the Puercan (Eberle & Lillegraven, 1998b). Here I describe a new 'condylarth' from a recently discovered, diverse Puercan faunal assemblage in the Great Divide Basin (GDB) in south-central Wyoming, just west of the Hanna Basin and Rawlins Uplift (see Figure 1). Preliminary studies of the faunas suggest that the GDB may preserve nearly the entirety of Puercan time. The new 'condylarth' described below adds to the diversity of early Puercan faunas.

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FIGURE 1. Map showing the Greater Green River Basin (modified from Hettinger *et al.*, 2008). Study area is shaded and a detailed geologic map is shown in Figure 2.

As a result of decades of field work by the late James Honey and Malcolm McKenna, a thick stratigraphic sequence of fossil mammal localities (spanning the latest Cretaceous through early Eocene time) has been unearthed in the GDB. Included among these is a new Puercan fauna from the China Butte Member of the Fort Union Formation. A single locality (UCM locality 2011035) has produced 332 mammalian fossils and contains a large diversity of 'condylarths' (Eberle *et al.*, 2013), including the new genus and species described below.

'Condylarthra' is a paraphyletic, but important, assemblage of mammals thought to be precursors to a number of ungulate groups (Archibald, 1998). Members of 'Condylarthra' comprise the majority of the diversity of eutherian mammals in Puercan faunas, but their phylogenetic relationships are not well understood. Morphologically primitive taxa have been assigned to various families by different authors over time (e.g., Archibald, 1982, 1998; Luo, 1991). Some have argued for replacement of the term 'condylarth' with archaic ungulate - a phrase that implies no monophyly and refers simply to the age of the taxa (see Archibald, 1998 for a thorough discussion of the issue). However, I choose to retain the name 'Condylarthra' here informally for convenient reference to these taxa, and present the term in quotation marks, as is the standard for paraphyletic groups. The Arctocyonidae, a family traditionally included in the 'condylarths' but whose validity has recently been questioned (Williamson & Carr, 2007; Tabuce et al., 2011; De Bast & Smith, 2013), is used here to refer to the earliest and morphologically most primitive 'condylarth' taxa, including Protungulatum donnae, Oxyprimus spp., Oxyclaenus spp., and Baioconodon nordicum. While some authors have also included the primitive periptychids *Mimatuta* and/or *Maiorana* in

Arctocyonidae (Luo, 1991; Tabuce *et al.*, 2011), they are treated presumptively as periptychids based on their original allocation to the family by Van Valen (1978) and subsequent acceptance as such by most authors (Archibald, 1982, 1998; Lofgren, 1995; Eberle & Lillegraven, 1998b).

The description of the new genus and species of arctocyonid 'condylarth' from the Great Divide Basin is based upon 14 well-preserved partial dentaries. Comparisons are made with Puercan arctocyonid and periptychid taxa known from the Western Interior of North America. A phylogenetic analysis is performed to determine the relationship of the new taxon to other Puercan arctocyonids and periptychids, and the results are compared with phylogenies obtained in previous studies.

GEOLOGIC SETTING

The Great Divide Basin lies in the eastern subdivision of the Greater Green River Basin of Wyoming (see Figure 1). It is bounded to the southwest by the latest Cretaceous to earliest Paleocene-aged Rock Springs Uplift (Kirschbaum et al., 1994), and is separated from the more southerly Washakie Basin by the Wamsutter Arch (Love, 1961). During the Puercan, the Great Divide Basin was contiguous with the Hanna Basin to the east, and both comprised part of the Greater Green River Basin (Lillegraven et al., 2004). The geology and stratigraphy of the lower to upper Paleocene Fort Union Formation in the Great Divide Basin was provided by Hettinger et al. (2008) (see Figure 2). The formation was subdivided into three members (named in Honey & Hettinger, 2004): the oldest China Butte Member (lower Paleocene), the Blue Gap Member (lower Paleocene), and the Overland Member (upper middle and upper Paleocene). The lower Paleocene (early Puercan to Torrejonian) China Butte Member of the Fort Union Formation is composed of a generally fining-upward sequence of fineto medium-grained sandstone, siltstone, mudrock, carbonaceous shale, and coal units. The conglomerate that marks the base of the China Butte Member unconformably overlies the Red Rim Member of the Late Cretaceous-aged Lance Formation (Hettinger et al., 2008).

П.





The thickness of the China Butte Member increases from south to north in the Washakie and Great Divide Basins (Honey & Hettinger, 2004), reaching a nearmaximum thickness at UCM locality 2011035 where it measures approximately 565 m thick (Hettinger *et al.*, 2008). The abundance of mappable coal zones within the China Butte Member has facilitated the correlation of the many fossil mammal localities across the basin.

The quarry that yielded the study materials, UCM locality 2011035 (also listed in field notes and by other institutions under the following field names: UW-V-2001-092, 01RR02, Washakie's Lowest, Dubbya Quarry, and Gooneyballs), lies approximately 46 m above the contact between the Lance and Fort Union Formations (Hettinger *et al.*, 2008: sheet 3), and is at the top of the basal sandstone unit of the China Butte Member, which is characterized by "light-gray to white, medium- to coarse- grained, trough-crossbedded, multi-sorted sandstone as much as 220 ft [67 m] thick" (Hettinger *et al.*, 2008: sheet 1). UCM locality 2011035 is the stratigraphically lowest Cenozoic mammal-bearing locality yet found in the Great Divide Basin (see Figure 3). Based on a preliminary faunal list, the locality appears most similar to the late early Puercan (Pu1) Littleton Local Fauna in Colorado's Denver Basin (see Table 1). Due to the presence of characteristic Pu1 taxa (*Oxyprimus galadrielae, Protungulatum donnae*) and the absence of Pu2 index taxon *Ectoconus*, the fauna is assigned to Pu1 (Lofgren *et al.*, 2004; Eberle *et al.*, 2013).



FIGURE 3. Stratigraphic section showing the position of UCM locality 2011035 (modified from Hettinger *et al.*, 2008).

Denver Basin, Colorado	Hanna Basin, Wyoming	Great Divide Basin, Wyoming
Littleton fauna	Interval-zone Pu1 localities	UCM locality 2011035
Multituberculata	Multituberculata	Multituberculata
Mesodma cf. M. ambigua	Mesodma formosa	Mesodma cf. M. formosa
Xyronomys robinsoni	Mesodma ambigua	Mesodma ambigua
Kimbetohia mziae	Mesodma hensleighi	Eucosmodontidae gen. et sp. nov.
Catopsalis alexanderi	Mesodma cf. M. garfieldensis	
Cimexomys arapahoensis	Mesodma sp. indet.	
Cimexomys minor	?Mesodma sp.	
	Neoplagiaulacidae indet.	
Metatheria	Metatheria	Metatheria
Thylacodon pusillus	Peradectes cf. P. pusillus	Didelphidae indet.
Cimolesta	Cimolesta	Cimolesta
Procerberus andesiticus	Palaeoryctidae indet.	cf. Procerberus
Procerberus grandis	"Proteutheria" indet.	
"Proteutheria" indet.		
		Lipotyphla
		Geolabididae indet.
Ungulata	Ungulata	Ungulata
Oxyprimus cf. O. galadrielae	Protungulatum donnae	Sigynorum magnadivisus gen. et sp. nov.
Baioconodon cannoni	Protungulatum sloani	Protungulatum donnae
Baioconodon denverensis	Oxyprimus galadrielae	Oxyprimus galadrielae
Oxyclaenus subbituminus	Oxyprimus sp. indet.	Oxyclaenus subbituminus
Arctocyonidae indet.	Mimatuta sp. indet.	cf. Mimatuta
Ampliconus browni	Maiorana ferrisensis	Ampliconus sp.
Conacodon harbourae	Eoconodon sp.	cf. Conacodon
Conacodon matthewi		Conacodon sp.
Oxyacodon archibaldi		Conacodon cf. C. harbourae
Alticonus gazini		cf. Mithrandir
Auraria urbana		Oxyacodon sp.
		cf. Phenacoadaptes

TABLE 1. Comparative faunal lists for Pu1 localities in the Denver Basin (from: Middleton & Dewar, 2004), Hanna Basin (from: Eberle & Lillegraven, 1998a,b), and Great Divide Basin (preliminary identifications of specimens from UCM locality 2011035).

MATERIALS AND METHODS

UCM locality 2011035 was discovered in 2001 by James and Jeannine Honey, and was quarried by James Honey and Malcolm McKenna over the following decade. The locality resides in the southeast part of Wyoming's Great Divide Basin (at approximately 41° 38' N, 107° 33' W) in Carbon County on land administered by Wyoming Game & Fish. Detailed locality information is on file at the University of Colorado Museum of Natural History (UCM).

Material assigned to the new arctocyonid was compared with specimens and casts from the University of Colorado Museum of Natural History (UCM), American Museum of Natural History (AMNH), Denver Museum of Natural History (DMNH), Museum of Comparative Zoology (MCZ), University of Alberta (UA), University of California Museum of Paleontology (UCMP), University of Minnesota Museum of Paleontology (UMVP), University of New Mexico (UNM), and Yale Peabody Museum of Natural History (YPM). Casts of holotypes were utilized where available, as were descriptions and images in the literature. Teeth were measured using an Ehrenreich Photo Optical Shopscope on Ioan from J. Lillegraven (University of Wyoming). Dental measurement standards follow Archibald (1982) (see Figure 4). Other measurements, such as depth and width of dentaries, as well as the diameters of tooth alveoli, were measured with digital calipers. Cusp terminology follows Van Valen (1966).

Phylogenetic analysis was conducted using PAUP* v.4.0 beta 10 Win (Swofford

III.

2002). Detailed methods are presented below in the Phylogenetic Analysis methodology.

Specimens are catalogued and housed in the Fossil Vertebrate Collection at the UCM. Hypodigm specimens were molded and cast in the UCM molding and casting lab, where molds and master casts are retained.

Institutional abbreviations

AMNH, American Museum of Natural History; DMNH, Denver Museum of Natural
History; MCZ, Museum of Comparative Zoology, Cambridge, Massachusetts; UA,
University of Alberta; UCM, University of Colorado Museum of Natural History, Boulder,
Colorado; UCMP, University of California Museum of Paleontology, Berkeley, California;
UNM, University of New Mexico ; YPM, Yale Peabody Museum of Natural History, New
Haven, Connecticut.

Dental terminology and measurements

L, Left tooth; R, Right tooth; P/p, Upper/lower premolar; M/m, Upper/lower molar; A-P length, Anteroposterior length; Ltri, Length of trigonid; Ltal, length of talonid; Wtri, Width of trigonid; Wtal, Width of talonid.



FIGURE 4. Diagram of lower molar measurements (modified from Archibald, 1982).

SYSTEMATIC PALEONTOLOGY

IV.

Class **Mammalia** Linnaeus, 1758 Infraclass **Eutheria** Gill, 1872 Grandorder **Ungulata** Linnaeus, 1758 Family **Arctocyonidae** Murray, 1866 *Sigynorum* gen. nov.

Type species. Sigynorum magnadivisus gen. et sp. nov.

Diagnosis. As for the type species.

Derivation of name. From 'sigynos', Greek word for spear, in reference to the acute nature of the cusps and especially the tall spear-like cusp of the p4, and '-orum', neuter of the Latin suffix denoting possession of a condition.

Sigynorum magnadivisus gen. et sp. nov.

(Figures 5, 6, 7, 8; Tables 2, 4)

Diagnosis. Small arctocyonid similar in size to *Oxyprimus erikseni*; p4 with a tall central trigonid cusp lacking a para- and metaconid, and a crested talonid; molars with

uninflated bases and unreduced paraconids; anteroposteriorly compressed trigonid in m2–3. Differs from *Protungulatum donnae* and *Oxyprimus* spp. in absence of a p4 paraconid and metaconid, and in presence of a vestigial anterolabial cingulid on p4, a more labial molar paraconid, and an anteroposteriorly shorter trigonid than talonid in m2. Differs from *Mimatuta* spp. and *Maiorana noctiluca* in having uninflated premolars and molars, a p4 smaller than m1, a molar paraconid that is medially-placed or lingual to the groove between the metaconid and protoconid, with molar talonid cusps not 'closing', and discontinuous molar labial cingulids restricted to the precingulid, hypoflexid, and postcingulid. Differs from small species of *Conacodon* and *Oxyacodon* in lacking lingual cingulids, and in having an unreduced molar paraconid, and a p4 smaller than m1.

Derivation of name. From 'magnus', Latin for great, and 'divisus', Latin for cut or separated, in reference to the Great Divide Basin of Wyoming where the specimens on which the species is based were collected.

Holotype. UCM 103133, right mandible with p4–m3, alveoli p1–p3 (Figure 5).

Hypodigm. UCM 103086, right mandible with m2–3, m1 partial, alveoli p1–4; UCM 103088, right mandible with m2, alveoli c1–m1, m3; UCM 103089, right mandible with m1–3, alveoli c1–p4; UCM 103092, left mandible with p4–m1, m2 partial, alveoli c1–p3; UCM 103128, left mandible with m2–3, alveolus m1; UCM 103137, right mandible with p4–m3; UCM 103139, left mandible with m1–3, broken p4, alveoli c1–p3; UCM 103142, right mandible with p4–m2; UCM 103154, left mandible with p4–m3, alveoli p1–3; UCM



10 mm

FIGURE 5. *Sigynorum magnadivisus* gen. et sp. nov., UCM 103133, holotype, right mandible with p4–m3, alveoli p1–p3; top, lingual view; middle, occlusal view; bottom, labial view.

103159, right mandible with p2, p4–m2, alveoli c1–p1, p3, m3; UCM 103175, left mandible with worn p4–m2, alveoli c1–p3, m3 roots; UCM 108714, left mandible with m2–m3, m1 partial; and UCM 108715, left mandible with m3, m2 sheared.

Type locality. UCM locality 2011035, China Butte Member of the Fort Union Formation, Great Divide Basin, Carbon County, Wyoming, USA (earliest Paleocene, Puercan NALMA).

Distribution. Only known from type locality.

Description.

Mandible. Fourteen dentaries comprise the type series. The jaw is gracile with only slight labial torsion of the anterior portion of the dentary. UCM 103133 has a mandibular depth of 5.75 mm and width of 3 mm below the m2. Two mental foramina are present below the p1 and p3. The ascending ramus is most complete on UCM 103088, 103128, and 103137, and has a deep masseteric fossa bordered anteriorly by a strong ridge that rises at approximately 70° to the alveolar border. The inferior notch at the posterior margin of the mandible is preserved in UCM 103128 and 103137, while the superior notch is preserved in UCM 103088 (see Figure 6). In combination, these specimens delimit the positions of the coronoid, condyloid, and angular processes, but do not show the processes themselves. The mandibular condyle sits above the tooth row, but its size and shape are unknown.



FIGURE 6. Sigynorum magnadivisus gen. et sp. nov.; left column = labial; right column = lingual; top, UCM 103088, UCM 103088 and 103137 to show known posterior extent of the lower jaw, including superior and inferior notches. paratype, right mandible with m2; bottom, UCM 103137, paratype, right mandible with p4-m3; middle, overlay of

Canine. Although no canines are preserved, a large canine alveolus is preserved and appears shifted slightly labial relative to the tooth row. The alveolus measures approximately 1.8 mm in diameter.

Premolars. There are no diastemata evident anterior to or between the premolars.

p1: The p1 alveolus indicates a single-rooted tooth.

p2: The p2 is present on UCM 103159 (see Figure 7). It is double-rooted and dominated by a single posteriorly-keeled cusp. There are crests along the anterior and posterior faces of the cusp that bend lingually toward the base of the tooth. The posterior crest lies just labial of the midline and terminates at the very narrow lingually-trending shelf that constitutes the heel. The p2 apex on UCM 103159 is worn into a steep lingual facet.

p3: The p3 is not preserved in any of the study specimens, but the alveoli show that it has two roots that were probably similar in size and spacing to the roots of p2. Consequently, p3 was likely closer in size to p2 than p4.

p4: The largest of the premolar series, p4 is double-rooted and has a singlecusped trigonid without a paraconid or metaconid, and a simple crest-like talonid. The p4 is shorter in A-P length and narrower than the m1. It is widest at the posterior margin of the protoconid, and its A-P length is greater than its maximum width (see Table 2). The protoconid is slightly inflated, posteriorly-keeled, and taller than any molar cusps in its unworn condition. A weak labial precingulid is present on UCM 103133, 103159, and 103175, while the posterior surface of the central cusp is bordered by a distinct lingual ridge. In one specimen with a heavily-worn p4 (UCM 103175), the protoconid is reduced



10 mm

FIGURE 7. *Sigynorum magnadivisus* gen. et sp. nov., UCM 103159, paratype, right mandible with p2, p4–m2; top, lingual view; middle, occlusal view; bottom, labial view.

Specimen	Position	A-P length	Width	Ltri	Ltal	Ltri/Ltal	Wtri	Wtal	Wtri/Wtal
103159	p2	1.95	1.41						
103092	p4	2.52	1.86						
103133	p4	2.61	1.75						
103137	p4	2.70	1.76						
103142	p4	2.35	1.82						
103154	p4	2.65	1.81						
103159	p4	2.56	1.80						
103175	p4	2.62	1.78						
103089	m1	3.02		1.52	1.50	1.01	2.18	2.40	0.91
103092	m1	3.10		1.53	1.57	0.97	2.12	2.19	0.97
103133	m1	3.08		1.51	1.57	0.96	2.18	2.23	0.98
103137	m1	3.01		1.45	1.56	0.93	2.22	2.38	0.93
103139	m1	2.91			1.46			2.28	
103142	m1	2.83		1.47	1.36	1.08	2.17	2.33	0.93
103154	m1	2.92		1.51	1.41	1.07	2.19	2.35	0.93
103159	m1	3.01		1.48	1.53	0.97	2.13	2.23	0.96
103175	m1	3.10		1.57	1.53	1.03	2.35	2.43	0.97
103086	m2	3.26		1.58	1.68	0.94	2.64	2.60	1.02
103088	m2	3.56		1.74	1.82	0.96	2.59	2.41	1.07
103089	m2	3.14		1.54	1.60	0.96	2.54	2.57	0.99
103128	m2	3.30		1.56	1.74	0.90	2.51	2.45	1.02
103133	m2	3.31		1.57	1.74	0.90	2.60	2.56	1.02
103137	m2	3.33		1.55	1.78	0.87	2.73	2.70	1.01
103139	m2	3.21		1.43	1.78	0.80	2.64	2.60	1.02
103142	m2	3.28		1.57	1.71	0.92	2.61	2.57	1.02
103154	m2	3.17		1.54	1.63	0.94	2.60	2.58	1.01
103159	m2	3.30		1.51	1.79	0.84	2.70	2.47	1.09
103175	m2	3.57		1.75	1.82	0.96	2.86	2.61	1.10
108714	m2	3.25		1.50	1.75	0.86	2.76	2.59	1.07
103086	m3	3.69		1.54	2.15	0.72	2.15	1.72	1.25
103089	m3	3.92		1.63	2.29	0.71	2.29	1.94	1.18
103128	m3	3.54		1.45	2.09	0.69	2.22	1.96	1.13
103133	m3	4.10		1.64	2.46	0.67	2.30	2.03	1.13
103137	m3	4.31		1.68	2.63	0.64	2.39	2.03	1.18
103139	m3	4.00		1.57	2.43	0.65	2.31	2.02	1.14
103154	m3	4.14		1.64	2.50	0.66	2.28	2.00	1.14
108714	m3	3.90		1.53	2.37	0.65	2.41	2.08	1.16
108715	m3	4.31		1.58	2.73	0.58	2.50	2.14	1.17

TABLE 2. Measurements (in mm.) of *Sigynorum magnadivisus* gen. et sp. nov. All specimens are reposited at UCM.

to a broad lingually-angled surface that also includes a wear facet at the lingual base of the talonid (see Figure 8). The p4 talonid is crested and slopes steeply to the lingual base of the tooth. The majority of specimens with complete talonids have two centrally located cusps at the posterior margin of the tooth; one cusp sits just lingual and slightly posterior to the other. A single specimen, UCM 103154, has just one talonid cusp lingual to the midline.

Molars. The molars increase in A-P length from m1 to m3 (see Table 2). The ratio of Ltri/Ltal decreases from m1 to m3 as a result of the increased anteroposterior compression of the trigonid in m2 and m3, and the elongated talonid of m3. The molar metaconid and protoconid are approximately equal in height and size when unworn, and the paraconid is unreduced, closely appressed to the metaconid, and lies on or just lingual to the groove between the metaconid and paraconid. At all molar positions, the metaconid is the first trigonid cusp to show wear, but with more advanced wear, facets occur at the apices of the paraconid and protoconid, as well as along the paracristid and protocristid. The talonid basin is broad and cuplike, with cusp apices at its margins. The cristid obligua contacts the trigonid wall directly below the groove between the protoconid and metaconid. The entocristid is an anteroventrally-trending ridge that either terminates before reaching the metaconid or just contacts the metaconid at its base without climbing the metaconid wall, creating a talonid notch that only weakly encloses the talonid basin. All molars bear a small precingulid on the anterolabial surface of the protoconid with labial cingulids otherwise minimal or absent, while lingual cingulids are entirely absent.

Detailed descriptions specific to each molar position are below.



10 mm

FIGURE 8. *Sigynorum magnadivisus* gen. et sp. nov., UCM 103175, paratype, left mandible with worn p4–m2, showing advanced wear; top, labial view; middle, occlusal view; bottom, lingual view.

m1: The A-P lengths of the m1 trigonid and talonid are approximately equal, and the trigonid is slightly narrower than the talonid. The paraconid is less appressed to the metaconid in m1 than in m2–3, resulting in lesser anteroposterior compression of the trigonid. The shelf-like precingulid anterior to the protoconid is broader than on m2 and m3. An ectostylid is present in the hypoflexid and is associated with a short and narrow cingulid at the posterior margin of the protoconid. The hypoconid is the largest talonid cusp, while the hypoconulid is subequal in size and posterolabial to the entoconid. The postcingulid on m1 is small or altogether absent.

m2: The m2 is the widest molar. The trigonid length is always shorter than the talonid due to the close appression of the paraconid and metaconid, making the trigonid basin appear compressed. The trigonid is equal in width to, or slightly wider than, the talonid. The tooth is proportionally shorter in length and broader in width than the m1 or m3. The ectostylid is less developed than in m1, but the positions and sizes of the talonid cusps and postcingulid are as described for m1.

m3: The m3 trigonid displays a similar degree of anteroposterior compression as in m2. An ectostylid is not present, or only faintly so. The talonid is elongated due to the enlargement of the hypoconulid, which extends into a distal lobe and is approximately equal in size to the hypoconid; the entoconid is the smallest talonid cusp in m3. The width of the m3 trigonid is approximately equal to that of the m1 talonid on specimens where both teeth are present.

Sigynorum cf. S. magnadivisus

(Figure 9; Table 3)

Referred specimens. UCM 103140, right mandible with p4–m3, alveoli c1–p3; and UCM 103168, right mandible with partial m1–m3.

Description. Although similar in size and morphology to *Sigynorum magnadivisus*, UCM 103140 is only tentatively assigned to this species due to its outlier status in several characters (see Figure 9). Specifically, its p4 bears an incipient anterolingually-placed paraconid and is significantly larger in both A-P length and width than any of the p4s of *S. magnadivisus* (see Table 3). The m3 paraconid is less appressed to the metaconid and larger than in specimens assigned to the hypodigm. The apex of the paraconid on m2 and m3 also protrudes anteriorly, while the paraconid on specimens referred to *S. magnadivisus* is more vertical.

UCM 103168 is also assigned to *Sigynorum* cf. *S. magnadivisus* on the basis of the anteroposterior compression of the m2 trigonid. Measurements are not provided, because incompleteness and poor preservation of the specimen (i.e., lack of enamel) render them uninformative.

Specimen	Position	A-P length	Width	Ltri	Ltal	Ltri/Ltal	Wtri	Wtal	Wtri/Wtal
103140	p4	2.76	2.02						
103140	m1	3.07		1.54	1.53	1.01	2.27	2.41	0.94
103140	m2	3.51		1.74	1.77	0.98	2.80	2.71	1.03
103140	m3	4.36		1.94	2.42	0.80	2.47	2.15	1.15

TABLE 3. Measurements (in mm.) of UCM 103140, *Sigynorum* c.f. *S. magnadivisus*. Specimen is reposited at UCM.



10 mm

FIGURE 9. *Sigynorum* cf. *S. magnadivisus*, UCM 103140, referred, right mandible with p4–m3; top, lingual view; middle, occlusal view; bottom, labial view.

DISCUSSION

V.

Comparison with early Puercan arctocyonids and periptychids

Early Puercan 'condylarths' are morphologically conservative and difficult to distinguish from one another. The 'condylarths' most similar in size and morphology to *Sigynorum magnadivisus* include arctocyonid and periptychid taxa. *Protungulatum donnae* and *Oxyprimus* spp. are known widely from the Hanna Basin, northern Wyoming, Montana, and Canada; *Oxyprimus galadrielae* has also been recovered from the Denver Basin (Eberle & Lillegraven, 1998b). The small periptychid *Mimatuta* spp. is known from Wyoming and Montana, while *Maiorana noctiluca* was described from the northern Wyoming Mantua locality, but has not been documented elsewhere (Van Valen, 1978). These taxa will be the focus of the comparison between *S. magnadivisus* and early Puercan 'condylarths'.

The specimens here described require assignment to a new genus despite their alignment with the generic diagnosis for *Oxyprimus* provided by Van Valen (1978), which reads: "Trigonid walls nearly vertical; p4 rather narrow; molar talonids larger than in *Protungulatum*; upper molars rather rectangular. Includes the smallest known arctocyonids" (Van Valen, 1978: 53). The characters provided by Van Valen (1978) are simply insufficient to distinguish other small early Puercan arctocyonids from *Oxyprimus*.

Oxyprimus erikseni is the species most similar in size and morphology to

Sigynorum magnadivisus. Measurements of lower molars overlap between the two taxa, while those of *O. galadrielae* and *Protungulatum donnae* are moderately and significantly larger, respectively (see Table 4). The most striking difference between *O. erikseni* and *S. magnadivisus* is in p4 morphology. While *S. magnadivisus* has a p4 lacking a paraconid, metaconid, and anterolabial cingulid, the p4 of *O. erikseni* has a "large and divergent paraconid and metaconid" (Luo, 1991: 467) and an anterolabial cingulid. As a result, the average p4 of *O. erikseni* is nearly as long as the average m1 (97% of m1 length), whereas the p4 of *S. magnadivisus* is shorter (86% of m1 length; see Table 4). In its molar morphology, Archibald (1982, p. 190) noted that *O. erikseni* has a paraconid "more closely appressed to the metaconid" compared to *P. donnae*, but the relative length of its molar trigonid to talonid is still greater than in molars of *S. magnadivisus*.

Both *Oxyprimus galadrielae* and *Protungulatum donnae* have p4 and molar morphology that distinguish their dentitions from that of *Sigynorum magnadivisus*. While the trigonid accessory cusps on p4 are smaller than in *O. erikseni*, both a paraconid and metaconid are present and distinct in these species (Sloan & Van Valen, 1965; Middleton, 1983; Luo, 1991), unlike *S. magnadivisus*. The molar paraconid in *O. galadrielae* and *P. donnae* is not appressed to the metaconid and is lingual to the groove between the metaconid and protoconid (Archibald, 1982; Middleton, 1983; Luo, 1991; pers. observ.); consequently, the trigonid has a longer paracristid and larger trigonid basin than in *S. magnadivisus*.

Small early Puercan periptychids are distinguished from Sigynorum

Measurement	Sigynorum	Oxyprimus	Oxyprimus	Protungulatum
	magnadivisus	erikseni	galadrielae	donnae
/p4 A-P length	2.35–2.70 ∓=2.57 n=7	3.00–3.45 ∓=3.17 n=3	2.80–2.99 x=2.90 n=3	3.51 n=1
/p4 width	1.75–1.86 ⊽=1.80 n=7	1.62–1.80 ⊽=1.73 n=3	1.68–1.86 ≅ =1.77 n=3	2.27 n=1
/m1 A-P length	2.83–3.10	3.03–3.38	3.21–3.26	3.61−4.10
	≅=3.00	≅=3.27	≅ =3.23	x=3.84
	n=9	n=7	n=4	n=8
/m1 Wtri	2.13–2.35 〒2.21 n=8	1.97–2.24 〒2.10 n=7	2.09–2.21	2.60–3.15
/m1 Wtal	2.21–2.43	1.91–2.28	2.27–2.45	2.50–2.96
	≅ =2.32	≅=2.17	≅ =2.38	x=2.71
	n=9	n=7	n=4	n=8
/m2 A-P length	3.14–3.57	3.35–3.64	3.43–3.74	3.68–4.52
	⊼= 3.31	⊽=3.53	⊼= 3.60	⊽=4.19
	n=12	n=7	n=3	n=15
/m2 Wtri	2.51–2.86	2.40–2.82 x=2.59 n=7	2.64–2.73	2.89–3.87
/m2 Wtal	2.41–2.70	2.18–2.73	2.56–2.71	2.46–3.49
	x =2.56	⊼= 2.43	≅ =2.64	⊼ =3.13
	n=12	n=7	n=3	n=15
/m3 A-P length	3.54–4.31	3.83–4.52	3.76–4.31	4.42–5.56
	≅ =3.99	≅ =4.17	≅ =3.96	≅ =4.85
	n=9	n=7	n=3	n=7
/m3 Wtri	2.15–2.50 x=2.32 n=9	2.28–2.80 x=2.50 n=7	2.37–2.53 x=2.46 n=3	2.67–3.56
/m3 Wtal	1.72–2.14	1.76–2.08	1.96–2.10	2.11–2.85
	⊽=1.99	⊽=1.98	⊽=2.03	⊼= 2.39
	n=9	n=7	n=3	n=7

TABLE 4. Measurements (in mm.) of *Sigynorum magnadivisus*, *Oxyprimus erikseni*, *Oxyprimus galadrielae*, and *Protungulatum donnae*, including observed range, mean, and number of specimens measured. Measurements for *O. erikseni*, *O. galadrielae*, and *P. donnae* are from Lofgren (1995, tables 41, 42, 47).

magnadivisus by a number of features. In *Mimatuta morgoth* and *M. minuial*, as well as in *Maiorana noctiluca*, the p4 is inflated to nearly the size of m1 and is molarized with a paraconid and metaconid, the molar paraconid is small and labial, and molar bases are inflated (Archibald, 1982; Luo, 1991; Eberle & Lillegraven, 1998b; pers. observ.). In addition, *M. noctiluca* has a wide and continuous molar cingulid around the labial margin of the trigonid (Eberle & Lillegraven, 1998b; pers. observ.), unlike *S. magnadivisus* in which the cingulid is very narrow and discontinuous.

The larger Puercan anisonchine periptychids *Conacodon* spp., *Ampliconus browni*, *Oxyacodon priscilla*, and *Mithrandir gillianus* are readily distinguished from *S*. *magnadivisus*. The cheek teeth are inflated, molar paraconids are reduced and labially shifted, and p4 is as large as, or larger than, m1 (Middleton, 1983; Eberle & Lillegraven, 1998b; pers. observ.). A single-cusped p4 is present in *C. entoconus*, but the p4 is there modified into an oversized conical tooth, while the p4 in *Sigynorum magnadivisus* is gracile. Due to the differences in morphology of the p4s of these two species and the dissimilarity of the molars, the absence of accessory cusps on p4 likely evolved convergently in *C. entoconus* and *S. magnadivisus*.

PHYLOGENETIC ANALYSIS

In order to examine the relationship between Sigynorum magnadivisus and other Puercan 'condylarths', a phylogenetic analysis was performed. A number of phylogenetic analyses that focus on a variety of 'condylarth' taxa have been undertaken (e.g., Archibald, 1982; Luo, 1991; Zack et al., 2005; Williamson & Carr, 2007; De Bast & Smith, 2013), as well as studies that take a broader perspective on mammalian diversification and necessarily include 'condylarths' in their studies (e.g., O'Leary et al., 2013; Wible et al., 2007, 2009). Subsets of 'condylarth' taxa in Puercan faunas have been defined on their plesiomorphic dental characteristics (see Archibald, 1988 for a thorough discussion), and familial divisions then arose based on hypothesized ancestry to derived ungulate groups (Van Valen, 1978; Archibald, 1982, 1988). Early representatives of Arctocyonidae and Periptychidae, therefore, are likely to appear more similar to each other than to morphologically derived members of their respective families. The goals of this phylogenetic analysis are to discretize the dental variation among the Puercan 'condylarths', which are often difficult to differentiate from one another, and to determine the phylogenetic position of *S. magnadivisus*.

Methodology

The analysis included 16 Puercan members of Arctocyonidae and Periptychidae known from the Western Interior of North America. The taxa were selected based on

VI.

their similarity to *Sigynorum magnadivisus* and are representatives of early and middle Puercan faunas. Arctocyonid species included in the analysis are *Protungulatum donnae*, *Oxyprimus galadrielae*, *Oxyprimus erikseni*, *Oxyclaenus cuspidatus*, *Oxyclaenus simplex*, and *Baioconodon nordicum*. The periptychids used are *Mimatuta morgoth*, *Mimatuta minuial*, *Maiorana noctiluca*, *Oxyacodon priscilla*, *Ampliconus browni*, *Mithrandir gillianus*, and three species of *Conacodon*: *C. entoconus*, *C. cophater*, and *C. harbourae*.

The polyphyletic nature of the taxa included and uncertain phylogenetic and geographic origins of 'Condylarthra' make outgroup selection difficult. Possible outgroups suggested by recent phylogenetic analyses include the Paleocene plesiadapiform *Purgatorius* (Wible *et al.*, 2007, 2009), the zhelestids (Williamson & Carr, 2007), and Late Cretaceous insectivores *Cimolestes* and *Gypsonictops*, or a combination of multiple outgroup taxa (Luo, 1991; De Bast & Smith, 2013). *Cimolestes* was chosen as the outgroup because it is well known, comparative material was available for first-hand scoring of the majority of dental characters, and its dental morphology provides strong character state polarization for ingroup taxa. *Purgatorius* was also included to evaluate its close phylogenetic position to *Oxyprimus* and *Protungulatum* in recent analyses (Wible *et al.*, 2007, 2009; Rook & Hunter, 2014).

The taxa were scored for 52 dental characters, primarily sourced and adapted from a number of previous analyses (Archibald, 1982; Luo, 1991; Zack *et al.*, 2005; Williamson & Carr, 2007; De Bast & Smith, 2013; see Appendix A). Few of the taxa included are known from non-dental material, so no cranial or post-cranial characters were considered. Some dental characters from previous analyses were taxonomically uninformative among ingroup taxa, and were also excluded. Characters were scored by direct comparison where available, and by utilizing primary literature (Matthew, 1937; Sloan & Van Valen, 1965; Van Valen & Sloan, 1965; Clemens, 1974, 2004; Archibald, 1982; Luo, 1991; Lofgren, 1995; Eberle, 2003) and/or scores from previous analyses (Archibald, 1982; Luo, 1991; Zack *et al.*, 2005; Wible *et al.*, 2009; De Bast & Smith, 2013) where comparative material was unavailable (see Appendix B).

The characters were treated as unweighted and unordered, and were polarized based on outgroup comparison. No *a priori* assumptions were made about the primitive or derived status of dental characters, because of a lack of clear synapomorphies and the lack of agreement among previous workers [see Archibald (1982) and Luo (1991) for discussions].

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, and Bremer Index values were calculated to measure branch support within the resulting tree.

Results

The analysis resulted in eight equally most parsimonious trees of 181 steps (CI=0.40, RI=0.56) and a strict consensus of those trees measuring 190 steps (CI=0.38, RI=0.52). Variation among the output trees results from clade instability among periptychids *Maiorana noctiluca* and the two species of *Mimatuta*, the two species of *Oxyclaenus*, and between *Oxyprimus erikseni*, *Protungulatum donnae*, and *Sigynorum magnadivisus*. The strict consensus and 50% majority rule cladograms are presented in Figure 10.

Two major clades arose from the phylogenetic analysis of ingroup taxa. The first, whose topology is fully supported in the strict consensus tree, is a clade of periptychids: all three species of *Conacodon, Oxyacodon priscilla, Ampliconus browni*, and *Mithrandir gillianus*. While *C. entoconus* and *C. cophater* are sister taxa, *C. harbourae* appears as the sister taxon to *M. gillianus*. The other major phylogenetic division contains *Purgatorius* and both arctocyonid and periptychid taxa, including *Sigynorum magnadivisus*. The most basal branch is a polytomy that includes *Mimatuta morgoth, M. minuial*, and *Maiorana noctiluca*. Within the arctocyonid clade, the two species of *Oxyclaenus* are monophyletic in only 25% of trees, while *Oxyprimus erikseni*, *Protungulatum donnae*, and *S. magnadivisus* form a tritomy to the exclusion of *O. galadrielae* in 75% of tree topologies (see Figure 10).

Sigynorum magnadivisus is firmly nested within the arctocyonid 'condylarths'. The lack of clear resolution among *Oxyprimus erikseni*, *Protungulatum donnae*, and *S. magnadivisus* is likely due to missing data, and specifically the absent upper dentition for the new species. A few characters support the alignment of these three species to the exclusion of *O. galadrielae*: an unbasined p4 talonid (character 9), m1 trigonid subequal in width to talonid (character 13), and absence of lingual molar cingulids (character 30).

That *Mimatuta morgoth*, *M. minuial*, and *Maiorana noctiluca*, traditionally considered as basal members of Periptychidae (Van Valen, 1978; Archibald, 1982, 1998; Lofgren, 1995; Eberle & Lillegraven, 1998b), do not align with the other periptychid taxa is intriguing, though not entirely unexpected. Under further study,



FIGURE 10. Strict consensus and 50% majority rule trees (190 steps, CI=0.38, RI=0.52); **a.** Strict consensus tree derived from the eight most parsimonious trees with Bremer Index values located above the branches; **b.** 50% majority rule tree derived from the eight most parsimonious trees with percentage values at 50% or greater above the branches.

Mimatuta and *Maiorana* may be more strongly supported within Arctocyonidae, as they have been interpreted by Luo (1991) and Tabuce *et al.* (2011). It may also be that cranial and post-cranial characters, absent from the current analysis and unavailable for most of the included taxa, would unite *Mimatuta* and *Maiorana* with members of the family Periptychidae.

Comparison with previous phylogenetic studies

The current phylogenetic analysis provides a focused perspective on early Puercan 'condylarths'. A monophyletic clade including species of Oxyprimus and Protungulatum donnae appears in multiple previous phylogenetic studies, both broadly and narrowly based (Wible et al., 2007, 2009; Tabuce et al., 2011), and Sigynorum magnadivisus aligns with these taxa in this analysis. A number of taxonomically broader phylogenetic studies have questioned the validity of Arctocyonidae (Williamson & Carr, 2007; Tabuce et al., 2011; De Bast & Smith, 2013), while others have reallocated basal family members to other parts of the 'condylarth' tree, such as Hyopsodontidae, Cete, and unresolved placement(s) (Archibald, 1998). De Bast & Smith (2013) described Arctocyonidae as a polyphyletic wastebasket for a number of basal ungulate taxa, and their results support this conclusion; arctocyonids appear throughout their phylogeny. In the cladogram presented by Tabuce et al. (2011), arctocyonids are largely a paraphyletic stem grouping, with the exception of Oxyclaenus cuspidatus, which is an intermediate stem taxon of the triisodontids and mesonychians. In contrast, the trees resulting from my analysis support monophyly of the Puercan arctocyonids Oxyprimus spp., P. donnae, Oxyclaenus spp., Baioconodon nordicum, and S. magnadivisus.

Puercan 'condylarths' *Mimatuta* and *Maiorana* have been placed variably in

Arctocyonidae and Periptychidae. Luo (1991) included *M. morgoth* in his study of the morphologically-similar arctocyonid 'condylarth' taxa from the Bug Creek localities in Montana, alongside *Oxyprimus erikseni* and *Protungulatum donnae*. More recently, Tabuce *et al.* (2011) showed a monophyletic clade including *M. minuial* and *M. noctiluca* within a paraphyletic 'Arctocyonidae'. Although not formally discussed, their inclusion underscores the primitive morphology of these two genera. Additionally, Archibald (1998) suggested that *Mimatuta* may be paraphyletic at a generic level. The present phylogenetic analysis concurs with this conclusion, and finds little support for a monophyletic *Mimatuta* clade.

The plesiadapiform *Purgatorius* has previously appeared as the sister group to the monophyletic clade that includes *Protungulatum* and *Oxyprimus* (Wible *et al.*, 2007, 2009; Rook & Hunter, 2014). The strict consensus tree obtained here also supports *Purgatorius* as the sister taxon to Arctocyonidae, to the exclusion of the periptychids (including *Mimatuta* and *Maiorana*).

CONCLUSIONS AND FUTURE RESEARCH

VII.

The description of a new arctocyonid genus and species, Sigynorum magnadivisus, from the Great Divide Basin (GDB) in Wyoming increases the known diversity of Puercan 'condylarths', and especially among the morphologically most primitive members of Arctocyonidae, *Protungulatum* and *Oxyprimus*, to which the new taxon appears most closely allied. A number of previous phylogenetic analyses have attempted to untangle the poorly understood relationships among various 'condylarth' taxa and their hypothesized relatives in other orders of mammals (Wible et al., 2007, 2009; Tabuce et al., 2011; O'Leary et al., 2013), while others have included a broad selection of Paleocene taxa (Archibald, 1998; Zack et al., 2005; Williamson & Carr, 2007; De Bast & Smith, 2013). Both Archibald (1982) and Luo (1991) conducted analyses narrowly focused on the few Puercan 'condylarths' known from the Bug Creek fauna of Montana. The phylogenetic analysis presented in this study is unique for its comprehensive inclusion of arctocyonid and periptychid taxa from several Puercan faunas across the Western Interior of North America, along with its focus on the earliest and most basal members of these groups, and finds the following:

1. *Sigynorum magnadivisus* is closely related to early Puercan 'condylarths' *Protungulatum donnae* and *Oxyprimus* spp., a phylogenetic position supporting its inclusion in Arctocyonidae.

2. Their dental characters suggest that the Puercan Arctocyonidae included in this

analysis are monophyletic, and this clade is the sister group to the plesiadapiform *Purgatorius*.

3. Puercan Periptychidae are found to be paraphyletic, with *Mimatuta* and *Maiorana*, traditionally considered basal periptychids, excluded from the branch of the strict consensus tree containing the other Puercan periptychid taxa.

In addition to these phylogenetic implications, the discovery of Sigynorum magnadivisus in early Puercan strata of the GDB has implications for understanding post-K-Pg mammalian diversity. Much of the work on Puercan faunas has led to the conclusion that the diversity of 'condylarth' taxa in the Western Interior of North America, while it composed a significant portion of post-K-Pg boundary local faunal diversity, was initially quite low (Clemens, 2010; Wilson, 2014). The Pu1-aged Littleton local fauna of the Denver Formation in the Denver Basin, Colorado provides one striking example to the contrary, with nine genera and 12 species of 'condylarths' recognized (Middleton, 1983; Eberle, 2003). To explain the increased taxonomic diversity observed in the Denver Basin, Middleton (1983) proposed that the preserved fauna may sample a time interval intermediate between other typical Pu1 and Pu2 faunas (i.e., late Pu1), or that its more southerly geographic location may have provided a unique setting for earlier diversification (Eberle, 2003), especially among periptychids. Similar to the Denver Basin, the GDB preserves a diverse early Puercan fauna, UCM locality 2011035, with at least ten genera of 'condylarths' identified (a probably conservative estimate based on preliminary identifications; see Figure 3), including taxa also known from the Littleton local fauna. However, it likely also includes several new species, in addition to S. magnadivisus, which would add to the already higher than expected early

Puercan diversity of this fauna.

A number of directions for future research are called for in the GDB. First, as in Sigynorum magnadivisus, a number of taxa are represented by well-preserved dentaries in the UCM collection, but have only been preliminarily identified to genus and species; these taxa need to be described and definitively identified. In order to better assess their phylogenetic relationships, the research would benefit considerably from the discovery of upper dentitions (which are rare at this locality). In order to refine the biostratigraphic correlation between the Puercan fauna from the GDB and other Puercan faunas from the Western Interior, additional material must be collected from Puercan localities in the GDB. While UCM locality 2011035 contains more than 330 mammalian fossils, other Puercan localities in the GDB have considerably fewer specimens and require a concentrated collecting effort (e.g., dryscreening and screenwashing, as well as collection of anthill matrix). Fortunately, their stratigraphic relationships are well established (Hettinger et al., 2008), and so future research should concentrate on recovery of fossil mammals. In addition to the collection and study of fossil mammals, preliminary investigation of the applicability of dating techniques to Puercan strata of the GDB, and specifically magnetostratigraphic analysis and geochronology, will take place in the coming year. Refined temporal correlation of the GDB Puercan fauna with others from the Western Interior of North America will provide increased resolution that is necessary for the study of post-K-Pg extinction mammalian communities, and the radiation of mammals in the first few geologic 'minutes' of the Cenozoic.

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

Lower premolars

- 1) p3 metaconid: absent (0), present as a ridge or cusp (1) (Archibald, 1982: character x*)
- p3 paraconid: absent (0), small (1), distinct (2) (De Bast & Smith, 2013: character 43*)
- 3) p3 talonid cusps: two or more cuspids and/or basined (0), one central blade with no basin (1) (De Bast and Smith, 2013: character 44*)
- 4) p4 paraconid: large (0), small/vestigial (1), absent (2) (Luo, 1991; De Bast and Smith, 2013: character 49*)
- 5) p4 paraconid placement: lingual (0), close to midline (1) (Archibald, 1982: character x*)
- 6) p4 metaconid: large (0), small/vestigial (1), absent (2) (Luo, 1991; De Bast and Smith, 2013: character 50*)
- p4 protoconid inflation: uninflated/weak (0), moderate (1), strong inflation (2) (Zack *et al.*, 2005: character 4)
- 8) p4 protoconid distal face: smooth (0), distinct distally directed postprotoconid cristid (1) (De Bast and Smith, 2013: character 51)
- 9) p4 talonid: basined (0), one central blade with no basin (1) (De Bast and Smith, 2013: character 52*)
- 10) p4 anterolabial cingulid: absent/vestigial (0), distinct (1) (De Bast and Smith, 2013: character 54)
- 11) p4 width relative to m1: narrower (0), subequal (1), wider (2)
- 12) p4 length relative to m1: subequal to or smaller than m1 (0), markedly larger than m1 (1) (Zack *et al.*, 2005: character 1)

Lower molars

- 13) m1 trigonid to talonid width ratio: trigonid narrower (0), subequal (1), trigonid wider (2) (Luo, 1991; Zack *et al.*, 2005: character 11*)
- 14) m2 trigonid to talonid width ratio: trigonid narrower (0), subequal (1), trigonid wider (2) (Zack *et al.*, 2005: character 11*)
- m3 trigonid width relative to m2: subequal to or slightly wider (0), narrower (1) (Zack *et al.*, 2005: character 25*)
- 16) m2 trigonid length relative to talonid length: trigonid shorter (0), subequal (1), trigonid longer (2) (Archibald, 1982)
- 17) m3 length to m2 length: longer (0), subequal (1), shorter (2) (De Bast and Smith,

2013: character 73*)

- trigonid height relative to talonid: high (0), intermediate (1), low (2) (Zack *et al.*, 2005: character 9*)
- 19) m1-2 paraconid apex relative to groove between metaconid and protoconid: lingual (0), midline (1), labial (2) (De Bast and Smith, 2013: character 55*)
- 20) m3 paraconid apex relative to groove between metaconid and protoconid: lingual (0), midline (1), labial (2)
- 21) molar paraconid size: not reduced (0), intermediate (1), reduced (2) (Archibald, 1982)
- 22) m2 metaconid position: distolingual to protoconid (0), lingual to protoconid (1) (De Bast and Smith, 2013: character 58)
- 23) m2 hypoconid size relative to entoconid: subequal (0), hypoconid larger than entoconid (1) (De Bast and Smith, 2013: character 70)
- 24) m1-2 hypoconulid size relative to entoconid: subequal (0), entoconid larger than hypoconulid (1) (De Bast and Smith, 2013: character 71)
- 25) m1-2 hypoconulid placement: closer to entoconid (0), in median position (1) (Zack *et al.*, 2005: character 19)
- 26) m3 hypoconulid: long and protrudes as a separate distal lobe (0), short and does not protrude substantially (1) (De Bast and Smith, 2013: character 74*)
- 27) m1-2 entocristid: climbs the base of the metaconid wall, talonid basin enclosed lingually (0), extends around the base of the metaconid to the lingual cingulid (if present) (1), extends to the base of the metaconid wall but not climbing, creating a notch (2), entocristid absent or extremely faint, talonid basin widely open lingually (3) (De Bast and Smith, 2013: character 72*)
- 28) molar cristid obliqua contacts trigonid: labial to the notch between the protoconid and metaconid (0), at the notch (1)
- 29) molar labial cingulid around trigonid: discontinuous (0), narrow and continuous (1), wide and continuous (2) (Archibald, 1982)
- 30) lingual cingulid on one or more molars, especially the lingual face of the metaconid: absent (0), narrow/discontinuous (1), wide/continuous (2)

Upper premolars

- 31) P3 shape: length subequal to width (0), length greater than width (1) (De Bast and Smith, 2013: character 3)
- 32) P3 protocone: absent (0), present (1) (De Bast and Smith, 2013: character 4)
- 33) P4 paracone and protocone: uninflated (0), inflated (1) (Archibald, 1982)
- 34) P4 paracone to protocone height: paracone much taller (0), paracone slightly taller (1) (De Bast and Smith, 2013: character 10*)
- 35) P4 parastyle and metastyle: labial to paracone (0), shifted lingually and aligned with paracone (1) (Archibald, 1982)

36) P4 size relative to M1: P4 smaller (0), P4 subequal (1), P4 larger (2) (Archibald, 1982*)

Upper molars

- 37) molar occlusal shape: subquadrate (0), triangular (1) (Archibald, 1982)
- 38) M3 size relative to M1: M3 subequal to M1 (0), M3 moderately to greatly smaller than M1 (1) (De Bast and Smith, 2013: character 35)
- 39) trigon basin size: small (0), large (1) (Luo, 1991)
- 40) molar protocone apex position: lingual (0), labial shift (1) (De Bast and Smith, 2013: character 24*)
- 41) molar protocone labial inclination: vertical (0), moderate (1), strong (2) (Luo, 1991*)
- 42) M1-2 metacone position: approximately labial (0), lingual shift relative to protocone (1)
- 43) M1-2 hypocone position: posterolingual to protocone (0), more lingual than posterior (1) (Archibald, 1982)
- 44) M2 hypocone size: small swelling of the precingulum (0), circular cusp (1), enlarged projecting cusp (2) (De Bast and Smith, 2013: character 33*)
- 45) M2 preparacrista: extends labially to labial stylocone (0), extends mesially to parastylocone on the precingulum (1) (De Bast and Smith, 2013: character 18)
- 46) molar mesostyle: absent (0), present on some or all molars (1) (Archibald, 1982)
- 47) molar stylar shelf: narrow ridge (0), wide shelf (1) (Archibald, 1982)
- 48) M1-2 ectoflexus: deep (0), moderate (1), nearly straight (2)
- 49) molar postcingulum and metacingulum: distinct and not connected (0), form a continuous shelf (1), absent (2) (Archibald, 1982)
- 50) M2 conule morphology: crested (0), rounded (1) (Luo, 1991)
- 51) molar conule position: lingual (0), labial shift (1) (Archibald, 1982)
- 52) paraconule and metaconule size: small (0), intermediate (1), large (2), paraconule small with metaconule larger (3) (Luo, 1991*)

APPENDIX B. Character-taxon matrix used in the phylogenetic analysis. Missing data are scored as '?'; inapplicable characters are scored as '-.'

000000001 1111111112 222222223 333333334 444444445 55 1234567890 1234567890 1234567890 1234567890 1234567890 12

0011120110	0022121011	0110111100	1101111100	01 001120	10
0110021001	001?100111	0001102100	??01101?11	11 001100	02
???2-20010	0011100100	0110002100	???????????	???????????????????????????????????????	??
0110000011	0012110100	0111002100	01?0??1010	1001001101	02
1110010001	0001110100	0111001101	010000110	1001001100	02
1110010011	0012011100	0010001110	0100000110	2001001001	02
1210011001	0002110201	0010001100	0101011?01	2100001000	11
1210001001	1012110211	0010001111	0101011001	2100001100	10
1012 -12?00	2111121221	2010100002	0011121101	1112 -10210	13
0100112101	1111120211	20001?0022	0011121001	1112110210	13
0011112001	2011021221	1010110102	???????????	???????????????????????????????????????	??
0111111101	1012110211	1110000001	??11111001	?112011000	13
???1120111	0001102200	0111011111	1000110110	1100101101	02
???????????	??01120210	001?001?11	?????0010	1000101101	02
0111112001	1002121211	1010110001	0110111101	2102 -11200	11
1200112?01	2112020211	1011110111	0111111001	2102 -00210	11
0110011011	0011120211	0011111111	0100000110	1000011000	12
1211011001	0001111201	0000110121	0101010001	1100010101	11
	0011120110 0110021001 ???2-20010 0110000011 111001001 121001001 121001001 1012 -12?00 0100112101 0011112001 01111101 ??????????	001112011000221210110110021001001?100111???2-2001000111001000110000011001211010011100100100011101001100100110002110201121001100110121102111012 -12?002111121221010011210111112021101111200120110212210111111011012110211???11201110001102200??????????01120210011111200110021212111200112?0121120202110110011011001112021112110110010001111201	0011120110002212101101101111000110021001001?1001110001102100???2-200100011100100011000210001100000110012110100011100210011100100100011101000111001101111001001000211020100100011101210011001000211020100100011101210011001100211020100100011111012 -12?002111121221201010002010011210111112021120001?002200111120012011021221101011010111111011012110211111000001??????????01120210001?001?11011111200110021212111011100111200112?012112020211101111011011001101100111202110011111111210110010001111201000011012	0011120110002212101101101111001101111000110021001001?1001110001102100??01101?11???2-2001000111001000110002100????????0110000110012110100011100210001?0??10101110010010001110100011100110101000011011100100100011101001100011100100001101210011001000211020100100011000101011?01121001001101211021100100011000101011011012 -12?002111121221201010000200111210101011210111112021120001?002200111210101111200120110212211010110102????????01111110110121102111110000001?11111001??????????01120210001?001?11??????001001111120011002121211101011001011011101?????????211202021110111101101100001101210011011001112021100111111101000011012110110010011112011001111111010000110	001112011000221210110110111100110111110001 001120011002100100171001110001102100??01101?1111 001100???2-2001000111001000110002100?????????????????????????????????