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The diversity of cimolestan mammals within the White River Group of South Dakota and Nebraska

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The synonymization of the cimolestan taxa *Cymaprimadon* and *Chadronia* from the Late Eocene Chadron Formation is consistently upheld, despite a lack of supporting evidence. Here we show that the synonymization is unjustified, owing to distinct differences between these taxa in the mandibular tooth count (1-1-3-3 vs. ?-1-4-3), the identity of the enlarged anterior mandibular tooth (incisor versus canine), and the morphology of the crown of m3 (e.g., paraconid on m3 in *Cymaprimadon*). We also refer a specimen recently collected from the Early Oligocene Brule Formation within the Badlands National Park (BADL 16917) to *Chadronia* sp., thus making it the youngest occurrence of a pantolestan from North America. Examination of an additional specimen (FMNH UC 349) revealed the presence of a further cimolestan taxon in the White River Group of South Dakota, although the poor quality of the locality and stratigraphic data associated with this specimen precludes erecting a formal name. In total, this study doubles the number of cimolestans from the Late Chadronian and Orellan (Ch4 to Or1) of North America from two to four, and extends the biostratigraphic range of Pantolesta into the North American Oligocene.

Key words: Mammalia, Pantolestidae, *Chadronia,* Cimolesta, *Cymaprimadon*, Pantolesta, Chadron Formation, Eocene, White River Group, South Dakota, Nebraska.

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Introduction

Chadronia margaretae Cook, 1954 is the only pantolestan, and, together with *Sinclairella* Jepsen, 1934, one of just two cimolestans currently recognized from the White River Group of North America. *C. margaretae* is known from two specimens from the Chadron Formation (latest Eocene) that are the youngest definitive representatives of both Pantolestidae and Pantolesta from North America: AMNH HC 750 (holotype) from Nebraska and FMNH PM 9567 from South Dakota (Gunnell et al. 2008). The latter specimen is the holotype of *Cymaprimadon kenni* Clark, 1968. An additional specimen from the White River Group of South Dakota (FMNH UC 349) was described by Clark (1968) as representing an "unnamed genus and species" (Clark 1968: 246) closely related to, but morphologically distinct from, *Cymaprimadon kenni*. However, he refrained from naming this new taxon owing to the poor quality of the associated stratigraphic data (i.e., "Oligocene of South Dakota, White River Badlands"; Clark 1968: 241).

Cymaprimadon was originally referred to its own clade within Insectivora (Cymaprimadontidae Clark, 1968), but was subsequently designated a subjective junior synonym of *Chadronia* sp. (McKenna and Bell 1997). Though subsequent authors have upheld this referral (e.g., Gunnell et al. 2008), no justification was provided to support this synonymization. In this study, we compare the morphologies of the holotypes of *Chadronia* and *Cymaprimadon*, and evaluate the prior synonymization of these taxa. We also redescribe FMNH UC 349, as well as a new specimen collected from the Scenic Member of the Brule Formation within the Badlands Nation-

al Park (BADL 16917), and assess their taxonomic affinities with respect to *Chadronia* and *Cymaprimadon*. Finally, we discuss the implications of this study for North American cimolestan diversity during the Eocene and Oligocene.

Institutional abbreviations.—AMNH HC, American Museum of Natural History, Hunter College Collection, New York, USA; BADL, Badlands National Park, Interior, USA; FMNH PM, Field Museum of Natural History, Paleomammals Collection, Chicago, USA; FMNH UC, Field Museum of Natural History, University of Chicago Collection, Chicago, USA; ROM, Royal Ontario Museum, Toronto, Canada.

Other abbreviations.—f, fresh surfaces; w, weathered surfaces; m, lower molar; p, lower premolar.

Material and methods

Observations regarding the morphology of *Chadronia margaretae* are based on the descriptions of Cook (1954) and Gunnell et al. (2008), as well as direct examination of casts of the lower jaws of the holotype (AMNH HC 750). The descriptions of BADL 16917 and FMNH UC 349 are based on personal observations. Observations regarding the morphology of *Cymaprimadon kenni* are based on the original description of Clark (1968) because the holotype specimen was unavailable for direct study. Comparisons between these three specimens and *Pantolestes* sp. Cope, 1872, based on specimens from the Adobe Town Member of the Washakie Formation (Eocene) within the collections of the Field Museum of Natural History, were also conducted to further evaluate the referral of BADL 16917 to Pantolesta. Finally, we also compared all of the studied specimens with the apatemyid *Sinclairella*, the only other cimolestan from the White River Group. Measurements of BADL 16917 were taken using digital calipers; all other measurements were obtained from the published literature (Table 1). Discussions related to the North American Land Mammal Ages (NALMAs) follow the definitions of Woodburne (2004). The use of the name Cimolesta follows Rose (2006).

Geological setting

The White River Group of North America is best exposed in south-central South Dakota; however, exposures are also known from Nebraska, North Dakota, Wyoming, and Colorado. This lithostratigraphic unit consists of the Chamberlain Pass, Chadron, and Brule formations, with the Chadron and Brule formations being more widely exposed (Terry 1998). The units were deposited in wide range of terrestrial environments, predominantly fluvial and lacustrine settings. Biostratigraphic assessment indicates a Late Eocene age for the Chamberlin Pass and Chadron formations, and an Early Oligocene age for the Brule Formation (Prothero and Emry 2004).

The holotype of *Chadronia margaretae* was collected from a locality within the Chadron Formation referred to as the "Chadronia Pocket" (Wood 1969). This site is located approximately 7.8 miles north of Crawford, Nebraska (NW. ¼, NE. ¼, NW. ¼, Sec. 36, T. 33N, R. 52W; Wood 1969). Only a single specimen of *C. margaretae* is known from this locality, although a variety of other taxa are present. Additional specimens referred to cf. *Chadronia* have been reported from Ellesmere Island (McKenna 1980), but so far have not been figured or discussed in detail, precluding their inclusion in this study. Furthermore, a single, unpublished specimen labeled *Chadronia* within the collections of the Royal Ontario Museum (ROM 46028) consists of a fragmentary left dentary from the Twin Buttes Member of the Bridger Formation, preserving only the alveoli for m1–3. Given the incomplete nature of this specimen, assessing this referral is difficult and is left for a future study.

The holotype of *Cymaprimadon kenni* was recovered from the top of the Crazy Johnson Member of the Chadron Formation, from a locality located on the northeastern face of the "Finney Breaks" in Pennington County, South Dakota (NW. ¼, NE. ¼, Sec. 25, T. 3S, R. 10E; Clark 1968). The sediment at this locality has been described as: "a slightly-cemented bentonitic mudstone with abundant, very fine sand grains" (Clark 1968).

The quality of the locality data preserved with specimen FMNH UC 349 is exceedingly poor. Collected in 1894, and the only associated field data state that the specimen came from the "Oligocene of South Dakota, White River Badlands" (Clark 1968). It was embedded in a matrix of fine sand that was slightly coarser and better cemented than that preserved with the holotype of *C. kenni*, leading Clark (1968) to estimate that it may have come from the "Lower Nodular Zone" of the Scenic Member of the Brule Formation, though it could not be ruled out that it came from the Chadron Formation. Thus, the exact stratigraphic position cannot be confidently resolved further than the White River Group.

BADL 16917, an anterior portion of a mandible, was collected from the "Owl's Roost" locality (BADL-LOC-0236), positioned within the Scenic Member of the Brule Formation in the North Unit of the Badlands National Park (contact Badlands National Park for further details). The stratigraphy of the locality was assessed with respect to two distinct, continuous units recognized within this area: the contact between the Brule Formation and the underlying Chadron Formation, and the Hay Butte Marker Bed (HBM) within the Scenic Member of the Brule Formation (Evanoff et al. 2010). Six distinct lithologic units are recognized at this locality (Fig. 1C). A full stratigraphic profile is exposed on the northeast face of the outcrop on which BADL16917 was collected (Fig. 1A, C), although only the upper portion of unit 3 and units 4–6 are exposed on the southwest face of the outcrop where the specimen was recovered (Fig. 1B). The sediments at this locality range from claystone to sandstone. All beds examined have a 335º strike and are dipping 1.5º to the south-

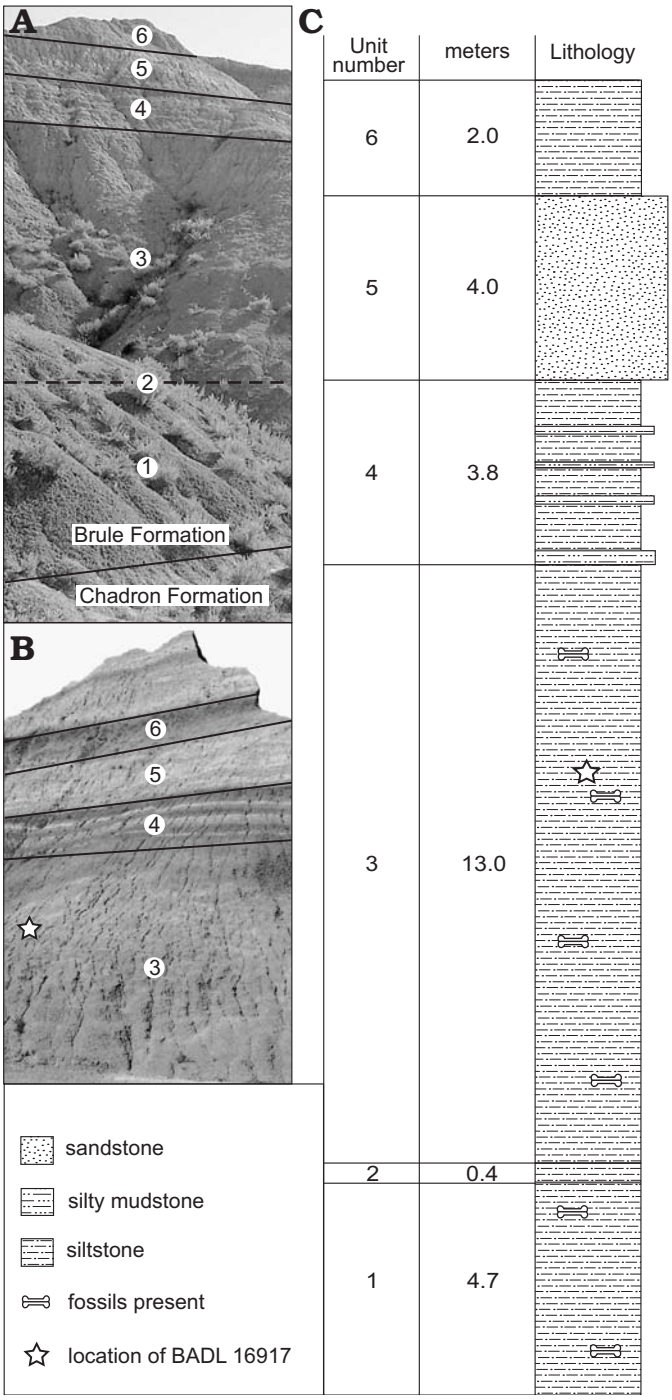

Fig. 1. Photographs of the back of the hillside (**A**) and the front face of the hillside (**B**) on which locality BADL-LOC-0236 (Badlands National Park, South Dakota, USA; Rupelian, Oligocene) is located, with Units 1–6 labeled (Unit 2 dashed, because its presence is not laterally continuous throughout the locality). **C**. Stratigraphic column based on A.

west. In the following descriptions, the colors of weathered and fresh surfaces are indicated by the abbreviations (w) and (f), respectively.

Unit 1 is a 4.65 meter, fossiliferous, reddish-rusty brown (w) to dark brown (f), somewhat platy claystone to siltstone that displays the characteristic "popcorn weathering" of swelling clay. The base of the unit has a diffuse to distinct contact with the Chadron Formation, and the top of the unit has a diffuse contact with unit 2, or unit 3 in areas where unit 2 is not present. Unit 2 averages 0.40 meter thick where present, but is not continuous throughout the locality, with deposition apparently reflecting paleotopography. When present, the unit consists of an unfossiliferous, greenish-gray (w) to a mottled green, red, and brown (f) platy claystone to siltstone that displays popcorn weathering. The top of the unit has a diffuse contact with unit 3. Unit 3 is a 13.0 meter reddish-brown (w) to light brown (f) blocky siltstone with fossils abundant throughout. BADL 16917 was exposed on the surface of this unit, approximately 3.5 meters below the base of unit 4. Based on the position of the specimen, the abundance of fossils in this unit (both on the surface and in situ), and the lack of fossils in the overlying units (see below), BADL 16917 likely originally derives from this layer. The top of the unit has a distinct contact with unit 4. Unit 4 is a 3.8 meter thick, unfossiliferous unit composed of four alternating sequences. Each sequence consists of grayish-white (w and f), blocky sandstone to muddy sandstone overlain by a reddish brown (w) to dark brown (f) platy to blocky silty mudstone. The top of each sequence has a distinct contact with the overlying sequence and the upper contact with unit 5 is also distinct. Unit 5 is a 4.0 meter, unfossiliferous, grayish-white (w and f), blocky sandstone with a nodular weathering pattern. The top of the unit has a clear contact with the distinctive basal carbonate of the HBM. Unit 6 is the HBM (see Evanoff et al. 2010 for a lithologic description) and is 2.0 meters thick at this locality.

Re-evaluating the synonymization of *Chadronia* and *Cymaprimadon*

Detailed comparisons between the published description and illustrations of the holotype of *Cymaprimadon kenni* (FMNH PM 9567) and personal examination of casts of the holotype of *Chadronia margaretae* (AMNH HC 750) revealed substantial differences between these specimens. Most significantly, the tooth count in the lower jaw of *Chadronia* is ?-1-4-3 with the lower canine being greatly enlarged and strongly recurved, whereas in *Cymaprimadon* the tooth count is 1-1-3-3 with a procumbent lower incisor (Clark [1968] gives ?3-1-3-3, but then later states that two of the incisors were likely absent). The overall length of the cheek tooth series in *Chadronia* exceeds that in *Cymaprimadon*, although the reverse is true with regards to the molar series (Table 1). In *Cymaprimadon*, the m3 entoconid is greatly reduced, whereas in *Chadronia* it is well developed. Also, the paraconid is present, though reduced, in *Cymaprimadon*, as opposed to being completely absent in *Chadronia*. Finally, the mandibular symphysis is smaller and narrower in *Cymaprimadon* than in *Chadronia*. Based on these differences, we conclude that the synonymization of *Chadronia* and *Cymaprimadon* is unjustified, and reinstate *Cymaprimadon kenni* as a distinct

taxon (see below; for a diagnosis of *Chadronia margaretae*; see Gunnell et al. 2008). In addition, we refer one new specimen to *Chadronia* sp. and Cimolesta incertae sedis, respectively.

Systematic paleontology

Class Mammalia Linnaeus, 1758

Order Cimolesta McKenna, 1975

Genus *Cymaprimadon* Clark, 1968

Type species: *Cymaprimadon kenni* Clarke, 1968, Chadronian (Late Eocene), "Finney Breaks," Pennington County, South Dakota.

Cymaprimadon kenni Clark, 1968

Holotype: FMNH PM 9567, right mandible preserving the crown of m3 and the greater portion of an enlarged incisor.

Type locality: Northeast face of the "Finney Breaks" (NW ¼ of NE ¼, Section 25, Township 3 South, Range 10 East) in Pennington County, South Dakota (Clark 1968).

Type horizon: Uppermost Crazy Johnson Member, Chadron Formation, White River Group; Late Eocene.

Material.—Holotype only.

Diagnosis.—Presence of an enlarged incisor in the mandible (enlarged canine in *Chadronia*); entoconid on m3 reduced to a small projection on the low ridge that forms the posterolingual corner of the talonid basin (only slightly smaller than the hypoconid in *Chadronia*); paraconid on m3 present (absent in *Chadronia*); presence of three cingulids on anterior margin of m3 (only the anterior cingulid present on the m3 in FMNH UC 349); presence of accessory cuspule on the posterobuccal margin of the hypoconid (absent in FMNH UC 349); tooth row straight in dorsal view (premolars aligned with mandibular body, but molars angle posterolingually in FMNH UC 349); alveolus for enlarged lower incisor extends to below the anterior alveolus for p4 (extends ventral to at least m3 in the apatemyid *Sinclairella*); presence of three lower premolars (two lower premolars in *Sinclairella*; four lower premolars in *Chadronia*).

Geographic and stratigraphic range.—White River Badlands, South Dakota, USA; upper-most Crazy Johnson Member, Chadron Formation, White River Group (Late Eocene).

Table 1. Measurements (in mm) of the cimolestan specimens analyzed in this study. Measurements for BADL 16917 were obtained via personal examination using digital calipers. Measurements for *Chadronia margaretae* were taken from Cook (1954), and measurements for *Cymaprimodon kenni* and FMNH UC 349 are from Clark (1937). Dashes indicate values that were either not reported or were not preserved in the examined specimens.

Dimension	*Chadronia margaretae* (AMNH HC 750)	*Chadronia* sp. (BADL 16917)	FMNH UC 349	*Cymaprimodon kenni* (FMNH PM 9567)
Length of skull	151.0	–	–	–
Depth of skull	38.0	–	–	–
Mandible depth below anterior m1 root	–	–	15.6	12.6
Mandible thickness below anterior m1 root	–	–	10.5	8.5
Temporal fossa to mental foramen	–	–	23.1	20.0
Lower incisor to molar length	71.0	–	–	–
c1–m3 alveolar length	–	–	–	41.4
Lower premolar-molar length	40.0	–	–	–
m1–3 alveolar length	16.0	–	24.3	20.6
Left c1 width	–	7.75	–	–
Left c1 depth	–	11.52	–	–
Right c1 width	–	8.09	–	–
Right c1 depth	–	11.55	–	–
Left p1 length	–	9.86	–	–
Left p1 width	–	4.44	–	–
Right p1 length	–	9.59	–	–
Right p1 width	–	4.40	–	–
Left p2 width	–	4.74	–	–
Right p2 width	–	4.76	–	–
p4 alveolus length	–	–	10.1	9.5
m1 alveolus length	–	–	7.5	7.5
m2 alveolus length	–	–	6.9	6.8
m3 length	–	–	7.8	5.6
m3 width	–	–	5.8	4.4
m3 protoconid height	–	–	6.4	4.9
m3 metaconid height	–	–	5.6	4.0
m3 hypoconid height	–	–	4.7	3.3

Class Mammalia Linnaeus, 1758
Order Cimolesta McKenna, 1975
Family incertae sedis
Gen. et sp. indet.

Fig. 2.

Material.—FMNH UC 349, partial left dentary preserving the crown of m3 from White River Badlands, South Dakota, USA; White River Group (Late Eocene–Early Oligocene).

Description.—This specimen was briefly described and poorly figured by Clark (1968). In dorsal view, the anterior portion of the tooth row is aligned with the mandibular body until the molar series, which is angled posterolingually as in *Chadronia* (Cook 1954: fig. 5). Ventral to the alveolus for p3, the posteriormost extent of the alveolus for an enlarged anterior tooth is exposed. The p3 was identified as single-rooted by Clark (1968), but breakage of the anterior margin of the alveolus makes it impossible to confirm this determination. Based on the morphology of the alveoli, p4 is double-rooted and the largest of the cheek teeth. The alveoli for the molar series decrease in size posteriorly. A deep coronoid fossa is present on the lateral surface of the mandible and bounded anteriorly by a prominent ridge (Fig. 2C, D). The mandibular body is robust, with a buccolingually wide and dorsoventrally deep posterior end. The buccal surface of the mandibular body is anteroposteriorly concave and bears two distinct mental foramina. The anterior mental foramen is circular and positioned ventral to the p3 alveolus. The posterior mental foramen is larger, ovate, and located ventral to the posterior margin of p4. The ramus is moderately steep and offset at a 50 degree angle from the body of the mandible.

The crown of m3 is rectangular in occlusal view (Fig. 2A, B). The trigonid is anteroposteriorly compressed. The paraconid is small, low, positioned along the midline of the tooth and is connected to the protoconid by a thin crest. The protoconid is triangular and is the tallest cusp of the crown. The metaconid is only slightly smaller in height and size. The anterolingual position of the paraconid gives the trigonid basin a closed appearance. There is a well-developed anterior cingulid, which extends from the base of the metaconid to the base of the protoconid. The anterior cingulid is highest in elevation below the paraconid, with the widest portion of the cingulid being located on the anterobuccal corner of the tooth. The buccolingual width of the trigonid is greater than that of the talonid. The hypoconid, the largest talonid cusp, is positioned on the posterobuccal corner of the tooth, and is conical with a small hypostylid on the anterior margin. A small accessory cuspule is present between the hypostylid and the trigonid wall. The presence of the three cusps gives the cristid obliqua, which attaches to the posterior face of the protoconid, an irregular appearance. The entoconid is incorporated into an elongate ridge on the posterolingual corner of the tooth, with its apex forming the highest point of the ridge. This ridge has an irregular occlusal surface and continues around the posterolingual corner of the tooth, ending near the anteroposterior midline. A distinct hypoconulid is absent and may have been incorporated into the posterolingual ridge. The talonid basin is shallow and open lingually.

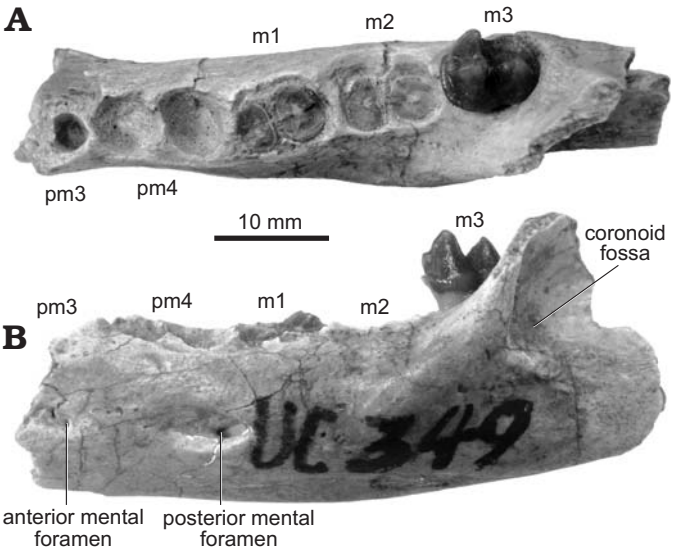

Fig. 2. Right mandible of the cimolestan mammal gen. et sp. indet. (FMNH UC 349) from the White River Badlands of South Dakota, Late Eocene–Early Oligocene, in dorsal (**A**) and buccal (**B**) views.

Remarks.—The dental formula for the lower jaw of FMNH UC 349 was reported as 1-0-2-3 by Clark (1968). However, because the anterior portion of the jaw is missing, the reported dental formula represents that author's interpretation, as opposed to a full tooth count. Reexamination of the specimen reveals the presence of the crown of m3 and alveoli for m2, m1, p4, and part of p3. The p4 through m3 were double rooted, with the number of alveoli for p3 uncertain owing to preservational issues. Based on the presence of the alveolus for an enlarged anterior tooth below p3 and comparisons with *C. kenni*, Clark (1968) interpreted that there was no room for any additional teeth. However, BADL 16917 (see below) and AMNH HC 750 have an alveolus for the enlarged anterior tooth that extends posteroventrally beneath the alveoli for p1 through to at least p3. Additionally, in apatemyids the alveolus for the enlarged incisor extends to beneath the alveolus for m3. Therefore, the assumption that p1 and p2 were absent cannot be confirmed. Similarly, the identification of the enlarged anterior tooth as an incisor is uncertain, and was based solely on the referral of this specimen to Cymaprimadontidae by Clark (1968).

The preserved morphology of FMNH UC 349 differs from apatemyids in that the posteriormost extent of the alveolus for the enlarged anterior tooth is located ventral to the posterior portion of p3 (extends to at least m3 in apatemyids). FMNH UC 349 also differs from *Chadronia* in the presence of the paraconid on m3 (absent in *Chadronia*) and in the reduction of the entoconid on m3 to a ridge on the posterolingual corner of the tooth (entoconid only slightly smaller than the hypoconid in *Chadronia*). While FMNH UC 349 does share some features with *Cymaprimadon* in the morphology of the m3 (e.g., retention of paraconid and reduction

of the entoconid), it also shows sufficient differences (e.g., presence of a hypostylid and an accessory cuspule along the cristid obliqua; number of cingulids on m3) to identify it as a distinct taxon. Nevertheless, the incomplete nature of FMNH UC 349, leading to an uncertain tooth count and the question of the identity (i.e., canine or incisor) of the enlarged anterior tooth, makes it difficult to decipher its taxonomic affinities. Therefore, given its general similarity to *Cymaprimadon*, we refer this new taxon to Cimolesta gen. et sp. indet. until more complete specimens are discovered.

Suborder Pantolesta McKenna, 1975

Family Pantolestidae Cope, 1884

Genus *Chadronia* Cook, 1954

Type species: *Chadronia margaretae* Cook, 1954, Chadronian (Late Eocene), Chadronia Pocket, Nebraska.

Chadronia sp.

Fig. 3.

Material.—BADL 16917, anterior portion of mandible with broken lower canines and the alveoli for p1–2 from "Owl's Roost" locality (BADL-LOC-0236), North Unit of Badlands National Park, South Dakota, USA; Scenic Member of the Brule Formation (Early Oligocene).

Description.—In anterior view, the mandible is distinctively concave dorsally and convex ventrally (Fig. 3D). The mandibular symphysis is very robust, extending from the anterior margin of the mandible to beyond the preserved posterior border of the specimen (Fig. 3B). The canines are separated by a 4.48 mm wide anterior extension of the mandible, which appears to have been highly vascularized (Fig. 3B). On the ventral surface there are two ovate foramina, one on each side of the mandibular symphysis (Fig. 3C, D). Muscle scars are present along the midline of the ventral surface (Fig. 3C, D). The latter is highly vascularized, with the density of vascularization increasing anterodorsally. Prominent, circular mental foramina are present (approximately 2.0 mm in diameter) on the lateral surfaces, just ventral to the anterior alveolus of p1 (Fig. 3A), which resembles that of *Pantolestes* sp. (FMNH PM 55996).

Incisors are lacking in the mandible of BADL 16917, as indicated by the absence of alveoli anterior to the canines. The enlarged lower canines are oriented anterodorsally, but broken just anterior to the level of the alveoli (Fig. 3A, C). The preserved portions of the canines are ovate in cross-section, with enamel remaining on the buccal, ventral, and partially on the dorsal margins of the teeth (Fig. 3B, D). The curvature of the canine cannot be confidently assessed, although it seems to have been recurved dorsally (Fig. 3B). Judging from the alveoli, p1 is double rooted with the roots angled posteroventrally into the mandible. The alveoli for p2 are slightly larger than those for p1, and its roots are angled more strongly posteriorly. Additionally, the p2 alveoli are obliquely oriented anterobuccally-posterolingually (Fig. 3B). See Table 1 for measurements of the preserved alveoli.

Remarks.—Based on comparison with casts of the holotype of *Chadronia margaretae* Cook, 1954 (AMNH HC 750), we tentatively refer this specimen to *Chadronia* sp. The only potential difference may be the presence of at least one lower incisor in AMNH HC 750 (Cook 1954). However, this observation was based on Cook's interpretation of associated fragments that were inferred to belong to the mandible, which is incomplete anterior to the enlarged lower canine in the holotype. In BADL 16917, the anteriormost portion of the mandible is complete and does not show any signs of an incisor (Fig. 3B, C, D). This difference may represent species-level variation between the Late Chadronian (Ch4; Gunnell and Bloch 2008) holotype and the Orellan (Or1) referred specimen, although this is currently difficult to determine given the small number of available specimens. Alternatively, the referral of the isolated incisor by Cook (1954) to the holotype mandible may be incorrect. Based on this difference and given the incomplete nature of BADL 16917, we refrain from referring this specimen to the species level at this time.

Discussion

Chadronia was placed within Pantolestinae by McKenna and Bell (1997); however, in their review of pantolestan relationships, Gunnell et al. (2008) removed *Chadronia* from the Pantolestinae and instead suggested that it occupied a basal position within Pantolestidae outside of both Pantolestinae and Pentacodontinae (Gunnell et al. 2008: fig. 5.2). We follow the latter classification because it was supported by a list of defining morphological characters, although it is important to note that these characters were not confirmed via a phylogenetic analysis.

Cymaprimadon kenni was originally placed within its own clade Cymaprimadontidae (= Cymaprimatontitae; Clark 1968: 242), with an uncertain position within Insectivora (Clark 1968). The synonymization of *Cymaprimadon* with *Chadronia* resulted in the clade Cymaprimadontidae being synonymized with either Pantolestidae (McKenna and Bell 1997: 217) or Pantolestinae (McKenna and Bell 1997: 218). The separation of *Chadronia* and *Cymaprimadon* proposed here thus requires the higher-level relationships of the latter taxon to be addressed.

The presence of enlarged incisors in *Cymaprimadon* precludes its referral to Pantolesta, which all possess enlarged canines. Within Cimolesta, apatemyids possess an enlarged incisor, but the morphology of the lower mandible of apatemyids differs substantially from that of *Cymaprimadon*. Specifically, p3 is double-rooted in *Cymaprimadon* versus the single-rooted and reduced or absent p3 in apatemyids. Equally, *Cymaprimadon* lacks the dorsoventral narrowing of the anterior portion of the mandible that results in the crown of p2 being offset ventrally relative to the p3–m3 tooth row in apatemyids. Additionally, the mandibular tooth count of *Cymaprimadon* is 1-1-3-3, while in apatemyids it is 2-0-3-3, 1-0-3-3, or 1-0-2-3, depending on the taxon (Rose 2006).

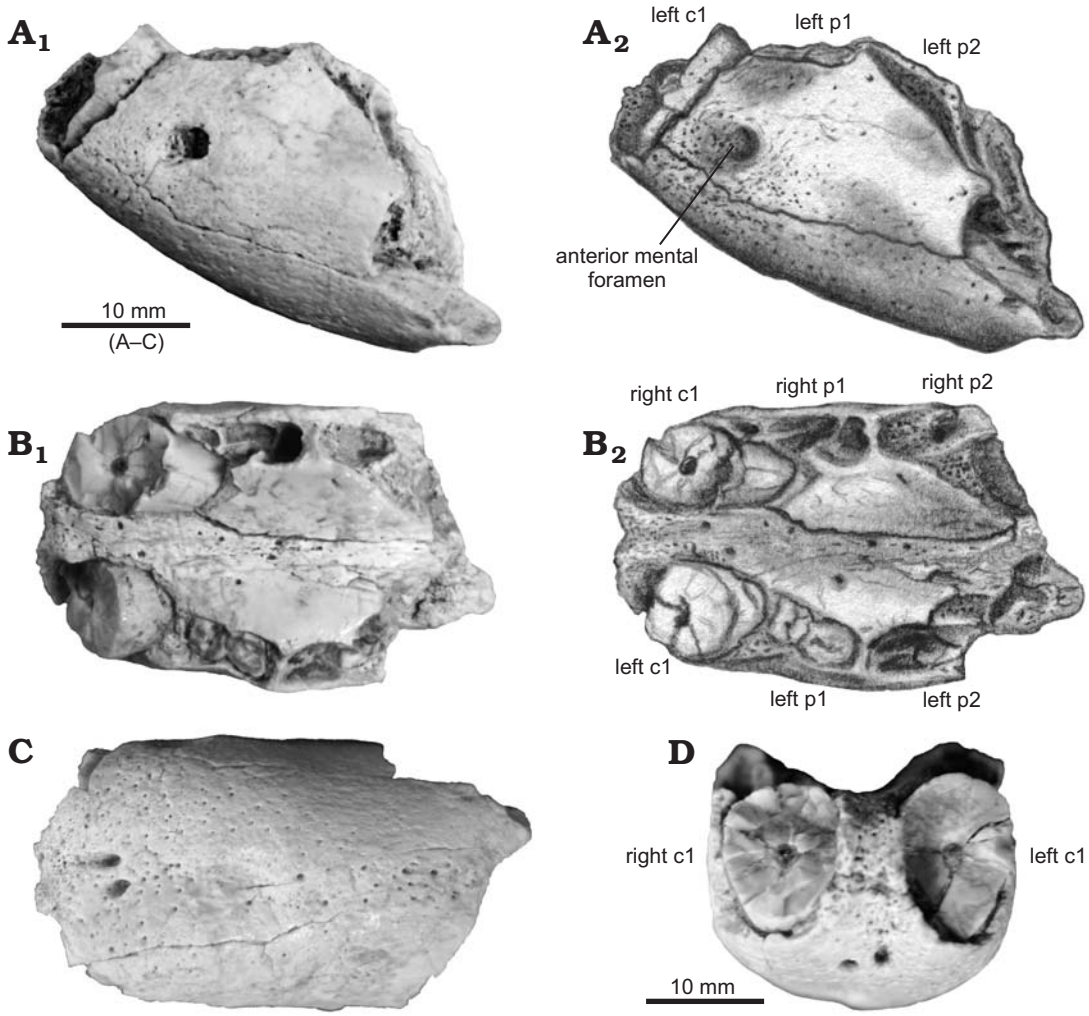

Fig. 3. Anterior portion of a mammalian mandible (BADL 16917) here tentatively referred to *Chadronia* sp., from the lower Scenic Member of the Brule Formation, South Dakota, in left buccal (**A**), dorsal (**B**), ventral (**C**), and anterior (**D**) views. Photographs (A_1, B_1, C, D) and explanatory drawings (A_2, B_2)

These differences argue against the referral of *Cymaprimadon* to Apatemyidae. The dental formula and morphology of *Cymaprimadon* conflicts with that of cimolestids, didymoconids, palaeoryctids, pantodonts, taeniodonts, tillodontians, and wyolestids, the remaining taxa referred to Cimolesta by Rose (2006). As a result, referral of *Cymaprimadon* is currently limited to Cimolesta incertae sedis, pending the publication of further information regarding the morphology of this taxon and/or a robust phylogenetic analysis of the relationships of basal eutherians.

Conclusions

Prior to this study, only two cimolestan taxa were recognized within the Late Eocene Chadron Formation (the pantolestid *Chadronia* and the apatemyid *Sinclairella*), and only a single taxon (*Sinclairella*) was recognized from the Early Oligocene Scenic Member of the Brule Formation (Gunnell and Bloch 2008). This study raises the diversity of cimolestan taxa within the Chadron Formation to at least three, based on the separation of *Cymaprimadon* from *Chadronia*. In addition, the tentative referral of BADL 16917 to *Chadronia* sp. extends the temporal range of pantolestids into the Early Oligocene (Or-1 biochron), corresponding to similar occurrences in Europe and Asia (Dashzeveg and Russell 1992; Rose 2006). McKenna and Bell (1997) also noted the presence of an unnamed pantolestid from the Early Oligocene of South Dakota, but did not cite a specific specimen. Though uncertainty surrounding the stratigraphic position of FMNH UC 349 prevents any definite observations regarding changes in cimolestan diversity across the Eocene/Oligocene boundary, the identification of FMNH UC 349 as a distinct taxon further raises the diversity of cimolestans within the White River Group. Overall, known cimolestan diversity during the combined Late Chadronian and Early Orellan biochrons (Ch4 to Or1) is here raised from two to four taxa, though cimolestans still show a general decrease in diversity from either three or four taxa during the late Late Eocene (Ch4), to a single taxon in the later Early Oligocene (Or4, *Sinclairella*), to the complete absence of cimolestans by the late Late Oligocene (Ar2) (Gunnell and Block 2008).

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