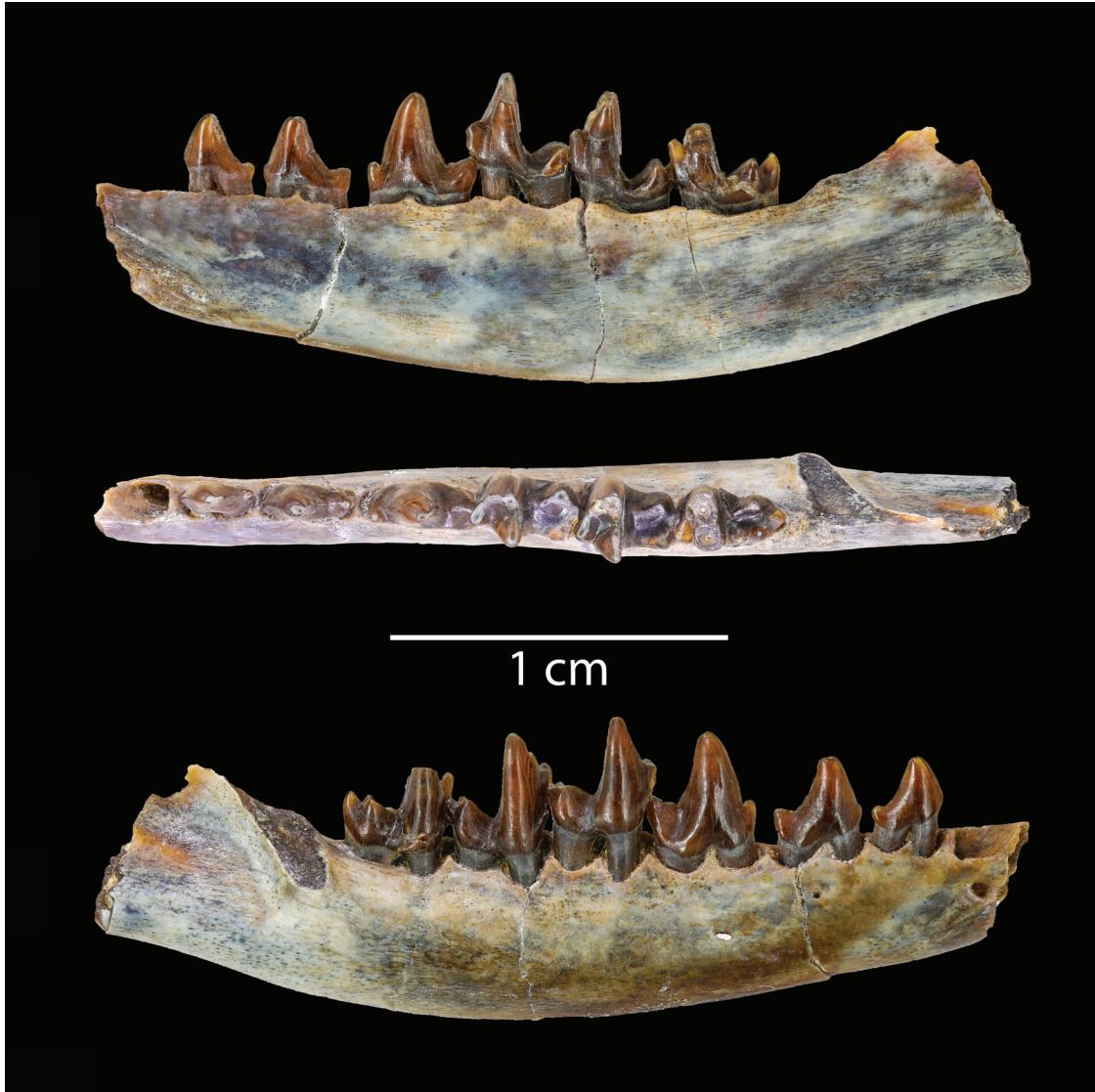


# *PaleoBios*

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**WILLIAM A. CLEMENS (2019).** *Puercolestes* and *Betonnia* (Cimolestidae, Mammalia) from the early Paleocene (Puercan 3 Interval Zone) of northeastern Montana, U.S.A.

**Cover:** *Cimolestes incisus* dentary preserving the lower cheek teeth p2 through m3. Images of UCMP 46874 by Dave Strauss.

**Citation:** Clemens, W.A. 2019. *Puercolestes* and *Betonnia* (Cimolestidae, Mammalia) from the early Paleocene (Puercan 3 Interval Zone) of northeastern Montana, U.S.A. *PaleoBios*, 36. ucmp\_paleobios\_42705.

# *Puercolestes* and *Betonnia* (Cimolestidae, Mammalia) from the early Paleocene (Puercan 3 Interval Zone) of northeastern Montana, U.S.A.

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In northeastern Montana, fossil localities in the Garbani Channel Complex and other early Paleocene (Puercan 3 Interval Zone) localities are preserved in the Tullock Member of the Fort Union Formation. They document an early phase in the recovery of the terrestrial fauna of the North American Western Interior after the mass extinction marking the Cretaceous-Paleogene (K-Pg) boundary. The cimolestids *Puercolestes simpsoni* and *Betonnia tsosia* were typified on fragmentary jaws and isolated teeth found in Puercan 2 and 3 Interval Zones (Pu2, Pu3) in the Nacimiento Formation, San Juan Basin, New Mexico. The available samples of these genera from both New Mexico and Montana are small and dominantly consist of isolated teeth. Characters of upper cheek teeth, P4 and M1–M3, justify provisional recognition of *Puercolestes* sp. cf. *Pu. simpsoni* and the somewhat smaller *Betonnia* sp. cf. *Be. tsosia* in Pu3 local faunas in the Tullock Member. In contrast, discovery of characters distinguishing the isolated lower cheek teeth, p4s and m1–m3s, of these species must await recovery of dentulous dentaries documenting the patterns of morphological variation of their lower dentitions. Fossils from the Tullock Member add support to the current interpretation that cimolestids were taxonomically diverse and geographically widespread but relatively rare members of the faunas of the North American Western Interior during approximately the first million years of the Paleocene.

**Keywords:** *Puercolestes*, *Betonnia*, Cimolestidae, Puercan, Tullock Member, Fort Union Formation, Montana

## INTRODUCTION

From Alberta southward to New Mexico, cimolestids have been recorded at many Puercan localities. Usually these records are based on a few isolated cheek teeth and a smaller number of dentulous fragments of maxillaries or dentaries. In a recent study, [Williamson et al. \(2011\)](#) described the cimolestids found in Puercan 2 (Pu2) and Puercan 3 (Pu3) Interval Zone faunal assemblages preserved in the Nacimiento Formation, San Juan Basin, New Mexico. They recognized three taxa, *Puercolestes simpsoni* [Reynolds, 1936](#), *Betonnia tsosia* [Williamson, Weil and Standhardt, 2011](#), and *Chacopterygus minimus* [Williamson et al., 2011](#), as well as a group of small, isolated molars simply dubbed “Cimolestidae, gen. et sp. undet.”

In northeastern Montana, fossil localities in the Garbani Channel Complex (GCC) and other early Paleocene Pu3 localities have been discovered in the Tullock Member of the Fort Union Formation (Fig. 1). They have yielded

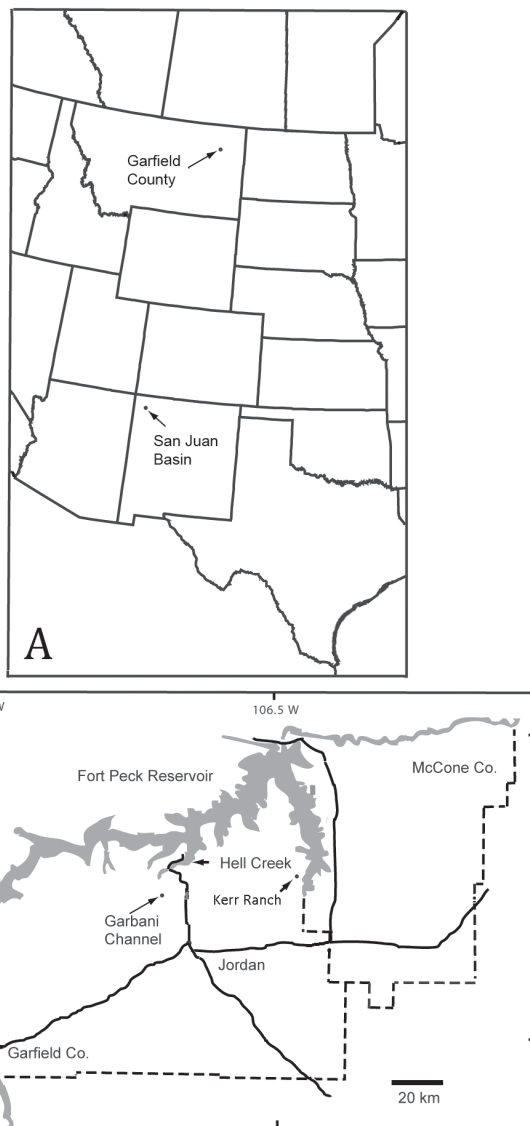
a remarkably large number of mammalian fossils, more than 7,800 cataloged mammalian specimens from just the localities mentioned in this paper. These document an early phase in recovery of the terrestrial fauna of the North American Western Interior after the mass extinction marking the Cretaceous-Paleogene (K-Pg) boundary. [Wilson \(2014\)](#) compiled a faunal list of what were then interpreted as undifferentiated Pu 2/Pu 3 Interval Zone faunal assemblages found in the GCC. Subsequent chronostratigraphic and biostratigraphic analyses ([Sprain et al. 2018](#)) constrain the ages of these faunal assemblages within an interval between approximately 375 and 850 ka after the K-Pg boundary and support the reference of those containing *Taeniolabis* [Cope, 1882](#) to the Pu3 Interval Zone.

Originally, the genus and species *Pu. simpsoni* [Reynolds, 1936](#) were typified on fossils from the Pu2 Interval Zone ([Williamson et al. 2011](#)) in the Nacimiento

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**Figure 1.** A. Map showing Garfield County, Montana, and the San Juan Basin, New Mexico. B. Map showing locations of the Garbani Channel and Kerr Ranch fossil localities in Garfield County, northeastern Montana.

Formation, San Juan Basin, New Mexico. On the basis of this material, Clemens (1973) argued that at the generic level, *Puercolestes* Reynolds, 1936 could not be distinguished from *Cimolestes* Marsh, 1889 and recognized *Cimolestes simpsoni*. Wilson (2014, table 1) recorded the presence of *Ci. cf. Ci. simpsoni* in the faunal assemblages of the GCC. With some additional material from the San Juan Basin, Williamson et al. (2011) provisionally concluded that *Puercolestes* was distinguishable. Accepting their working hypothesis, *Pu. simpsoni* is recognized here.

The goals of this study are to describe the available

samples and justify recognition of *Puercolestes* sp. cf. *Pu. simpsoni* and *Betonnia* sp. cf. *Be. tsosia* in Pu3 faunal assemblages in northeastern Montana. The upper distal premolars and molars of these two taxa are clearly distinguishable. Although larger in number than that of their upper counterparts, the sample of lower distal premolars and molars of appropriate size and morphology to be referable to these two taxa consists almost entirely of isolated teeth. Identification of criteria that might allow assignment of individual lower teeth to one or the other of the two taxa must await discovery of fossils documenting patterns of morphological variation within their lower dentitions.

## MATERIALS AND METHODS

### Geological setting and available fossil record

With the exception of UCMP 218933, all the mammalian fossils from northeastern Montana described here are from 15 localities (UCMP V72125, V72127, V72128, V72129, V72130, V72134, V72137, V73080, V73082, V74122, V74126, V75193, V75194, V75230, and V99438) in the GCC (Fig. 1). This is a complex of channel fillings in the Tullock Member of the Fort Union Formation exposed in Garfield County, Montana (Archibald 1982). On the basis of the occurrence of the multituberculate *Taeniolabis Cope* (1882), the local faunas found in this complex are broadly correlated with Pu3 Interval Zone local faunas in New Mexico and other areas in the North American Western Interior. Cutting and filling of the GCC occurred at times during the interval between  $65.677 \pm 0.041$  and  $65.202 \pm 0.057$  Ma (Sprain et al. 2018). This interval is approximately 375 to 850 ka after the K-Pg boundary ( $66.052 \pm 0.043$  Ma; Sprain et al. 2018).

The vast majority of the fossils from the GCC considered here are isolated teeth or fragments of teeth. They were recovered by hand quarrying and then washing the quarried sediments through 25 mesh screens. The only fossil from the GCC cited in this study that documents the association of cheek teeth is a fragment of dentary containing p4 and m1 (UCMP 281342). The only other fossil cited here that documents the association of cheek teeth was collected at a locality (UCMP V75196) on the Kerr Ranch, approximately 48 km east of outcrops of the GCC (Fig. 1). At this locality Richard Farrand discovered an associated P4, M1, and M2 identified below as cheek teeth of *Puercolestes* sp. cf. *Pu. simpsoni* (UCMP 218933). Archibald (1982, p. 33–34) briefly mentioned this and nearby localities at approximately the same stratigraphic

level in his detailed analysis of fossil occurrences in the Flat Creek area. He reported, "...the localities are at the base of a 20+ ft. (6.1 m) well-sorted sandstone channel deposit. The base of the channel is about 210 ft. (64.0 m) above the base of the lower Z coal." Archibald (1982) suggested the vertebrate fossils from these localities were of Puercan age. The stratigraphic height of the localities above the locally lowest coal of the Z coal complex, which probably approximates the K-Pg boundary, as well as the occurrence of both *Puercolestes* sp. cf. *Pu. simpsoni* and *Eoconodon hutchisoni* Clemens, 2011 support Archibald's interpretation. That the Kerr Ranch locality is broadly correlative with the GCC Pu3 localities is an appropriate working hypothesis.

Detailed descriptions of the GCC and Kerr Ranch localities are on file at the University of California Museum of Paleontology. In the following section on Systematic Paleontology UCMP locality numbers are those with a "V" prefix and are followed by specimen numbers, which lack this prefix.

### Dental terminology and measurements

**M/m**, molar. **P/p**, premolar. Elements of the upper dentition are identified with upper case letters, e.g., M1, while elements of the lower dentition are identified with lower case letters, e.g., m1. Descriptive dental terminology follows Williamson et al. (2011, fig. 3). All dental measurements were made with an Ehrenreich Photo-Optical Shopscope™ and are reported in millimeters.

### Institutional Abbreviations

**AMNH**, American Museum of Natural History. **KU**, University of Kansas Biodiversity Institute and Natural History Museum, **NMMNH**, New Mexico Museum of Natural History and Science. **UCMP**, University of California Museum of Paleontology.

#### SYSTEMATIC PALEONTOLOGY

EUTHERIA HUXLEY, 1880

CIMOESTA MCKENNA, 1975

CIMOESTIDAE MARSH, 1889

PUERCOLESTES REYNOLDS, 1936

*PUERCOLESTES SIMPSONI* REYNOLDS, 1936

*PUERCOLESTES* SP. CF. *PU. SIMPSONI*

FIGS. 2, 3

**Referred Specimens**—Kerr Butte 1 locality: UCMP V75196. **P4**, **M1–2**: UCMP 218933. Garbani Channel Complex localities: **P4**: UCMP V73080, UCMP 186460. **M1**: UCMP V72127, UCMP 258056; UCMP V73080,

UCMP nos. 187987, 187989, 258016; UCMP V99438, UCMP 218934. **M2**: UCMP V72128, UCMP 218935; UCMP V73080, UCMP nos. 258022, 258023; UCMP V73082, UCMP 258044. **M3**: UCMP V72129, UCMP 258052; UCMP V73080, UCMP nos. 258021, 258025.

**Basis for association**—The following descriptions of P4, M1, and M2 are founded on the associated, but worn, teeth preserved in UCMP 218933. Where possible, morphological details are added from isolated teeth found in GCC localities. Isolated M3s from GCC localities resembling those of other cimolestids and of appropriate size (Table 1) are tentatively referred.

### Description

**P4**—The parastylar lobe is mesially salient, situated directly mesial to the paracone, and supports a small parastyle (Fig. 2). The metacone is small, closely approximated to the paracone, and linked to the metastylar lobe by a short postmetacrista. An ectocingulum is not present. The protocone is not as high or as large as the paracone. The area delimited by the pre- and postprotocrista is not basined. Distinct conules, as well as pre- and postcingula are not present. Like the molars, the

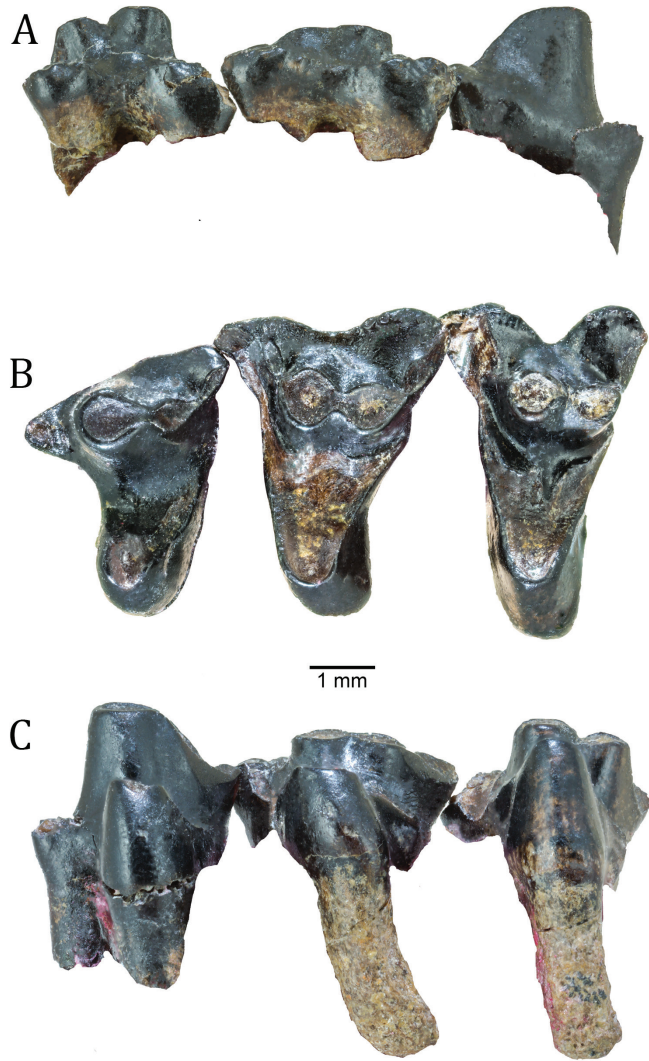
**Table 1.** Molar dimensions of *Puercolestes* sp. cf. *Pu. simpsoni*. All dimensions in millimeters. \*= estimated value.

#### Kerr Butte locality, V75196, specimen UCMP 218933

	Length	Mesial Width	Distal Width
<b>P4</b>	3.25		4.05
<b>M1</b>	3.61	4.59	4.82
<b>M2</b>	4.2*	5.09	5.22

#### Garbani Channel localities. Number of specimens shown in parentheses. OR=observed range of variation.

	Length	Mesial Width	Distal Width
<b>P4</b>	2.91 (1)		4.06 (1)
<b>M1</b>	OR 2.55–2.98 (2)	3.27–4.28 (3)	3.51–4.54 (2)
Mean	2.77	3.88	4.03
<b>M2</b>	OR 3.14–4.09 (2)	4.67 (1)	4.76 (1)
Mean	3.62		
<b>M3</b>	OR 2.01 (1)	4.20 (1)	3.32–4.46 (3)
Mean			3.72



**Figure 2.** *Puercolestes* sp. cf. *Pu. simpsoni*, associated P4, M1–M2, UCMP 218933. **A.** Buccal view. **B.** Occlusal view. **C.** Lingual view.

crown of P4 is supported by three roots.

**M1**—The parastylar lobe is positioned mesiobuccal to the paracone (Fig. 2). On most M1s, a small cusp in the position of a stylocone is linked mesially by a low crest to a slightly larger parastyle and lingually to the base of the paracone by a low preparacrista. Distal to the stylocone the ectocingulum is relatively broad with minor crenulations along its buccal margin. In occlusal view, the mesial half of the ectocingulum is slightly expanded; the distal half is broader. In comparison to M2, the ectoflexus of M1 is shallow. The paracone is slightly higher and greater in volume than the metacone. Their bases are merged to approximately one half the height of the paracone. The trigon basin is narrow mesiodistally with the paraconule

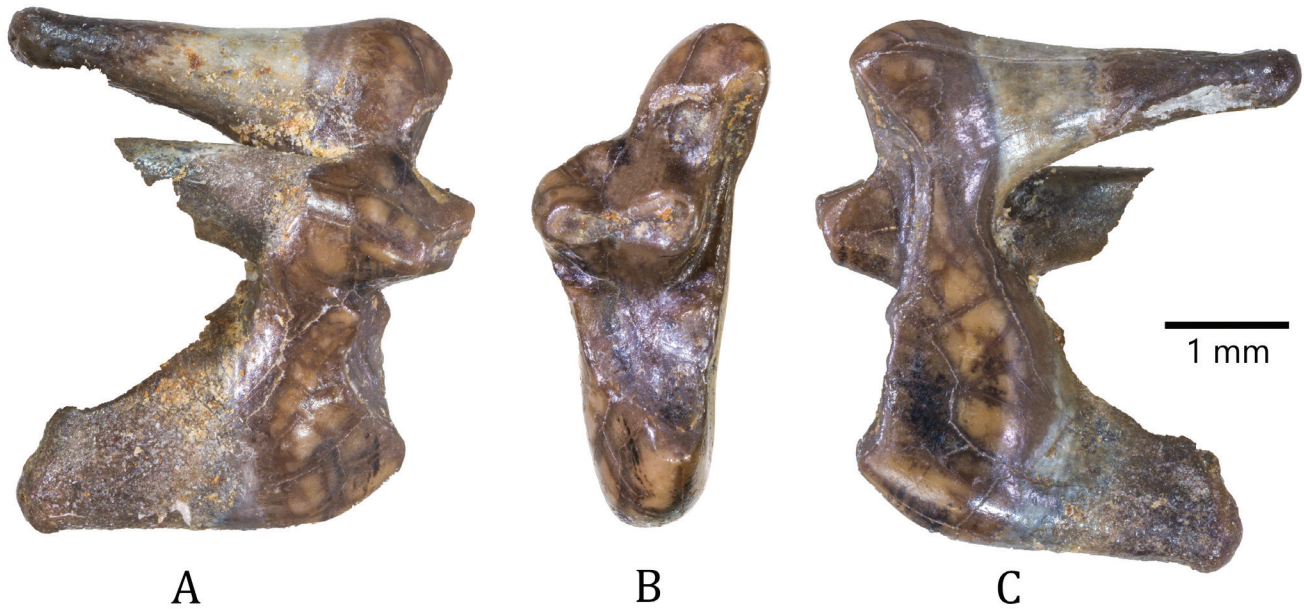
slightly closer to the protocone than the metaconule. The preparaconule crista continues across the mesial side of the paracone to reach the parastylar lobe. By contrast, the postmetaconule crista does not extend as far buccally ending above the apex of the metacone. Neither pre- nor postcingula are present.

**M2**—The parastylar lobe mesial to the preparacrista is similar to that of M1 but slightly more expanded buccolingually (Fig. 2). A small stylocone is present on some teeth. The subequal parastylar and metastylar lobes are separated by a deep ectoflexus, which is distinctly deeper than on M1. In comparison to M1, the paracone and slightly smaller metacone are more closely approximated. A distinct preparaconular crista links the paraconule and parastylar lobe. Changes in slope mark the positions of the postparaconular and premetaconular cristae. The postmetaconular crista flares distally to form a distinct shelf ending above the postmetacrista. The trigon basin is narrow mesiodistally and longer buccolingually. On one tooth (UCMP 258044) the mesial and distal bases of the protocone are slightly inflated but, resembling other M2s, neither distinct pre- nor postcingula are present.

**M3**—On M3s from the GCC localities that are tentatively referred to *Puercolestes* sp. cf. *Pu. simpsoni*, the parastylar lobe is large and carries a small parastyle (Fig. 3). An indistinct crest links this cusp with the paracone. The ectocingulum is narrow with a slight ectoflexus. The paracone is closely approximated to the smaller metacone. The trigon area is narrow and elongated buccolingually. Its mesial margin is distinctly higher than the distal. As a result, the occlusal surface of the trigon is more a distodorsally sloping surface than an enclosed basin. The paraconule is much larger and closer to the protocone than the metaconule. Neither pre- nor postcingula are present.

### Remarks

*Puercolestes simpsoni* was typified on fossils from Pu2 Interval Zone strata of the Nacimiento Formation exposed in the San Juan Basin, New Mexico (Reynolds 1936). The holotype is a fragment of a skull preserving parts of its somewhat damaged postcanine dentition. Williamson et al. (2011, table 1) brought together in the hypodigm of this species nine upper premolars and molars that provided at least one standard dimension of length or width of the crown. Their hypodigm also included ten lower premolars and molars that provided at least one of these dimensions. The sample from Montana representing *Pu. sp. cf. Pu. simpsoni* consists of the associated P4, M1, and M2 (UCMP 218933) from the Kerr



**Figure 3.** *Puercolestes* sp. cf. *Pu. simpsoni*, M3, UCMP 258052. A. Mesial view. B. Occlusal view. C. Distal view.

Ranch locality and 14 isolated upper premolars and molars providing at least one standard dimension of length or width of the crown from localities in the GCC. Other than their somewhat larger size, the teeth preserved in UCMP 218933 (Table 1) do not significantly differ from their counterparts found in the GCC. Given the small size of the available samples, the small differences in their dental dimensions are provisionally interpreted as intraspecific variations.

In their revised diagnosis of *Pu. simpsoni*, Williamson et al. (2011) noted that its dentition is similar in size to that of *Cimolestes incisus* Marsh (1889). This holds true for the teeth referred here to *Pu. sp. cf. Pu. simpsoni*. They also state, “Similar to species of *Cimolestes* and differs from *Batodon* and *Procerberus* in P4 parastylar lobe relatively smaller so that metastylar lobe larger than parastylar lobe (derived character)” (Williamson et al. 2011, p. 164). This relationship in relative proportions of the crowns also characterizes the P4s of *Pu. sp. cf. Pu. simpsoni* from Montana. There is variation in other morphological characters of P4. A small but distinct metacone is present on the P4 of the holotype of *Pu. simpsoni* and the two P4s referred to *Pu. sp. cf. Pu. simpsoni*. However, Williamson et al. (2011) referred two P4s lacking a metacone from the Nacimiento Formation to *Pu. simpsoni*. They also note a difference from the holotype in the smaller size of their protocones. The protocones of the two P4s referred here to *Pu. sp. cf. Pu. simpsoni* are

relatively large resembling the holotype of *Pu. simpsoni*.

In comparison to *Cimolestes incisus* Marsh, 1889, the most obvious distinguishing character cited in the revised diagnosis of *Pu. simpsoni* is the high paraconid on p4 of one of the referred specimens (NMMNH P-34831). Williamson et al. (2011) also tentatively included in *Pu. simpsoni* a p4 (AMNH 59910) whose paraconid is relatively small, similar to premolars of *Ci. incisus* (Fig. 4). AMNH 59910 was informally included in “Genus B” by Van Valen (1966, Plate 7, figs. 6, 7; also illustrated by Williamson et al. 2011, figs. 6C–E). Provisional inclusion of AMNH 59910 in the hypodigm of *Pu. simpsoni* invalidates one if not the most striking morphological difference between *Pu. simpsoni* and *Ci. incisus* cited by Williamson et al. 2011.

If comparisons are limited to the very small samples of P4s and upper molars from Montana and New Mexico, a case might be made to identify the material from Montana as representing a northern population of *Pu. simpsoni*. As discussed below, on the basis of the available samples from Montana, the p4s and lower molars probably referable to *Pu. sp. cf. Pu. simpsoni* and *Bettonia* sp. cf. *Be. tsosia* cannot be distinguished from one another. Until upper and lower dentitions of these two species are found in association and/or criteria are found to distinguish them and reconstruct a major part of the cheek tooth dentition, the P4s and upper molars from Montana are provisionally identified as *Pu. sp. cf.*

*Pu. simpsoni*.

BETONNIA WILLIAMSON, WEIL & STANDHARDT, 2011

BETONNIA TSOSIA WILLIAMSON, WEIL & STANDHARDT, 2011

### Remarks

The genus and species were established on only 11 isolated teeth, many of them fragmentary, from Horizon A (Pu2) and Horizon B (Pu3) of the Nacimiento Formation, New Mexico. Only three upper molars were included in the hypodigm. Of these, the holotype was identified as an M2 missing the parastylar lobe (AMNH 59852). Its distal width, the only dental dimension of an upper molar reported by Williamson et al. (2011, table 3), is 2.50 mm. The two referred upper molars, an M1 (NMMNH P-47221) and M2 (NMMNH P-51583), are incomplete. Eight isolated lower premolars and molars were tentatively referred.

Diagnostic characters of *Be. tsosia* cited by Williamson et al. (2011) are primarily those of the upper molars. The parastylar lobe of M1 is mesiobuccal to the paracone. Pre- and postcingula are present. The mesiodistal width of the molar conular region is greater than 0.51 of the total crown length. Conular cristae are distinct. These characters hold true for the teeth from Montana referred to *Be. sp. cf. Be. tsosia*. Comparison of the values given in Williamson et al. (2011, tables 1, 3) indicates that, with few exceptions, the dental dimensions of teeth referred to *Be. tsosia* are smaller than those referred to *Pu. simpsoni*.

BETONNIA SP. CF. *BE. TSOSIA*  
FIGS. 5–8

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BETONNIA SP. CF. *BE. TSOSIA*  
FIGS. 5–8

**Referred specimens**—Garbani Channel Complex localities. **P4**: UCMP V72129, UCMP 281370; UCMP V73080, UCMP 281372; UCMP V74122, UCMP 281371; UCMP V75194, UCMP 281369. **M1**: UCMP V73080, UCMP 218909; UCMP V74122, UCMP nos. 218911, 218912, 281341; UCMP V99438, UCMP nos. 218904, 218914. **M2**: UCMP V73080, UCMP nos. 218903, 218908; UCMP V74122, UCMP nos. 218920, 218921; UCMP V75193, UCMP nos. 218917, 218918; UCMP V99438, UCMP nos. 218906, 218907, 218915, 218916. **M3**: UCMP V99438, UCMP 281368.

**Basis for association**—Samples of P4s and upper molars of *Betonnia sp. cf. Be. tsosia* from the GCC consist of 21 isolated teeth. Identification of their positions in the dental arcade is based on the assumption that *Be. sp. cf. Be. tsosia* is a cimolestid. Patterns of morphological differentiation distinguishing the P4s and upper molars of *Pu. simpsoni* and latest Cretaceous cimolestids (see Lillegraven 1969, Fox 2015, 2016) provided the basis for determination of their positions in the dental arcade. Dimensions of the P4s and upper molars of *Be. sp. cf. Be.*

**Table 2.** Dental dimensions of *Betonnia sp. cf. B. tsosia*, Garbani Channel localities. Number of specimens shown in parentheses. All dimensions in millimeters. OR=observed range of variation.

		Length	Mesial Width	Distal Width
<b>P4</b>	OR	2.89 (1)		3.10–3.55 (3)
	Mean			3.31
<b>M1</b>	OR	2.27–2.74 (5)	3.28–3.88 (6)	3.61–4.13 (6)
	Mean	2.59	3.59	3.86
<b>M2</b>	OR	2.23–2.76 (8)	3.15–4.02 (8)	3.67–4.29 (10)
	Mean	2.53	3.67	3.98
<b>M3</b>	OR	2.54 (1)	3.81 (1)	3.32 (1)

*tsosia* are given in Table 2.

### Description

*P4*—The parastylar lobe is salient and situated directly mesial to the paracone (Fig. 5). On the available *P4*s, this lobe is damaged, but what remains suggests a parastyle was present. Closely approximated on the distal slope of the paracone is a smaller but distinct metacone. A narrow ectocingulum is present above the metacone. Lingually, the paraconule and metaconule are distinct cusps. The postparaconule and premetaconule cristae delimit the shallow trigon basin. A narrow preparaconule crista extends to the parastylar lobe. Similarly, the postmetaconule crista extends to the distobuccal corner of the crown. The protocone is not as high as the paracone. Pre- and postcingula are narrow, of approximately the same buccolingual extent, and almost meet across the lingual side of the protocone. Like the molars, the crown

is supported by three roots.

*M1*—The large parastylar lobe is directed mesially from the paracone and carries a low but distinct parastyle, which is rarely connected to the paracone by a weak preparamacrista (Fig. 6). Above the paracone, a low ridge extends along the buccal side of the narrow ectocingulum. A shallow ectoflexus separates the mesial section of the ectocingulum from the broader ectocingulum on the metastylar lobe. The paracone is higher and larger than the metacone. Their bases are merged to approximately half the height of the paracone. The paraconule is larger than the metaconule and set farther lingually. Low postparaconule and premetaconule cristae extend toward the bases of the paracone and metacone respectively. The preparaconule crista extends buccally to the parastylar lobe. The postmetaconule crista is broad, flaring distally, and ends dorsal to the apex of the metacone. The talon basin is narrow. The mesiodistal length of the crown

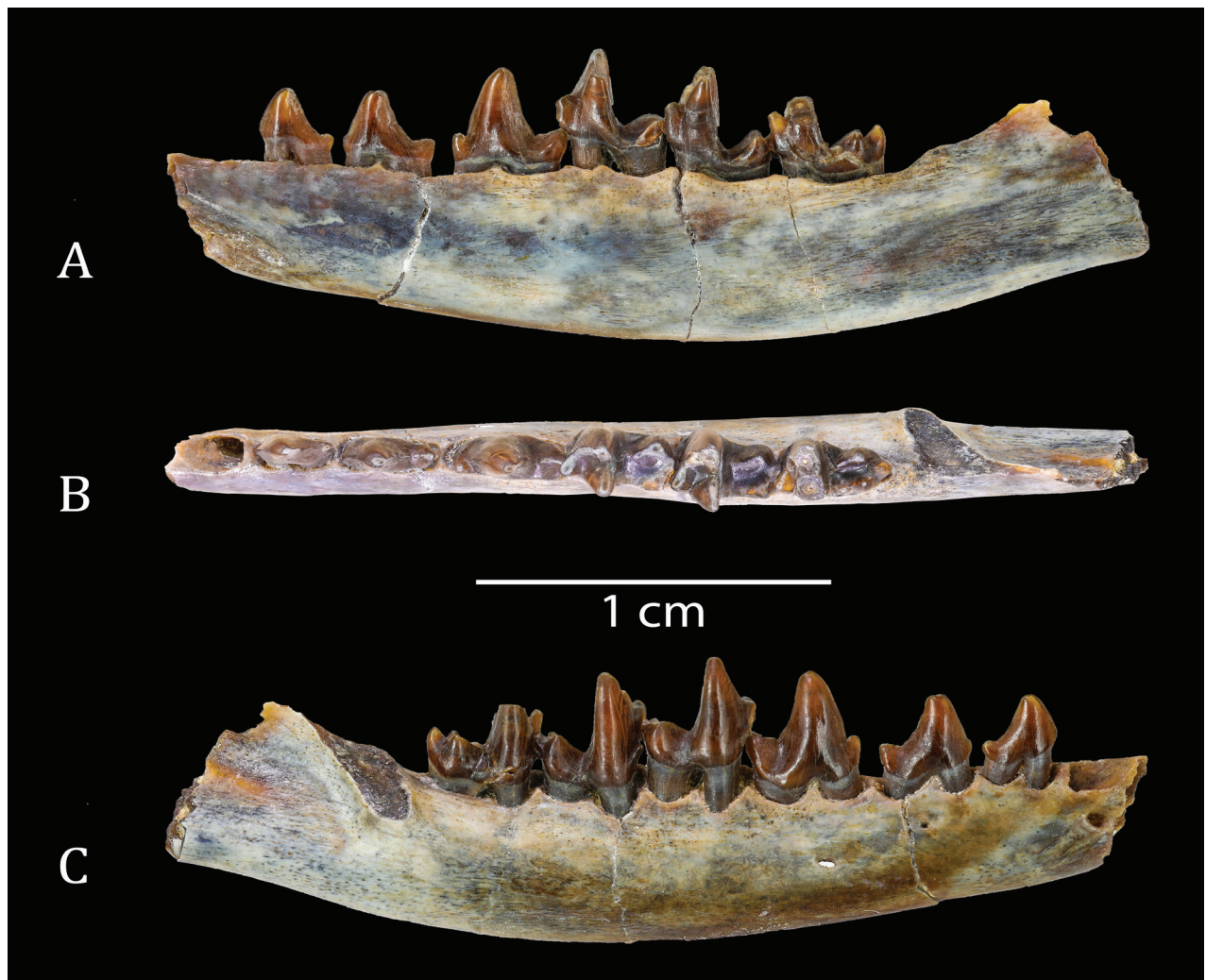
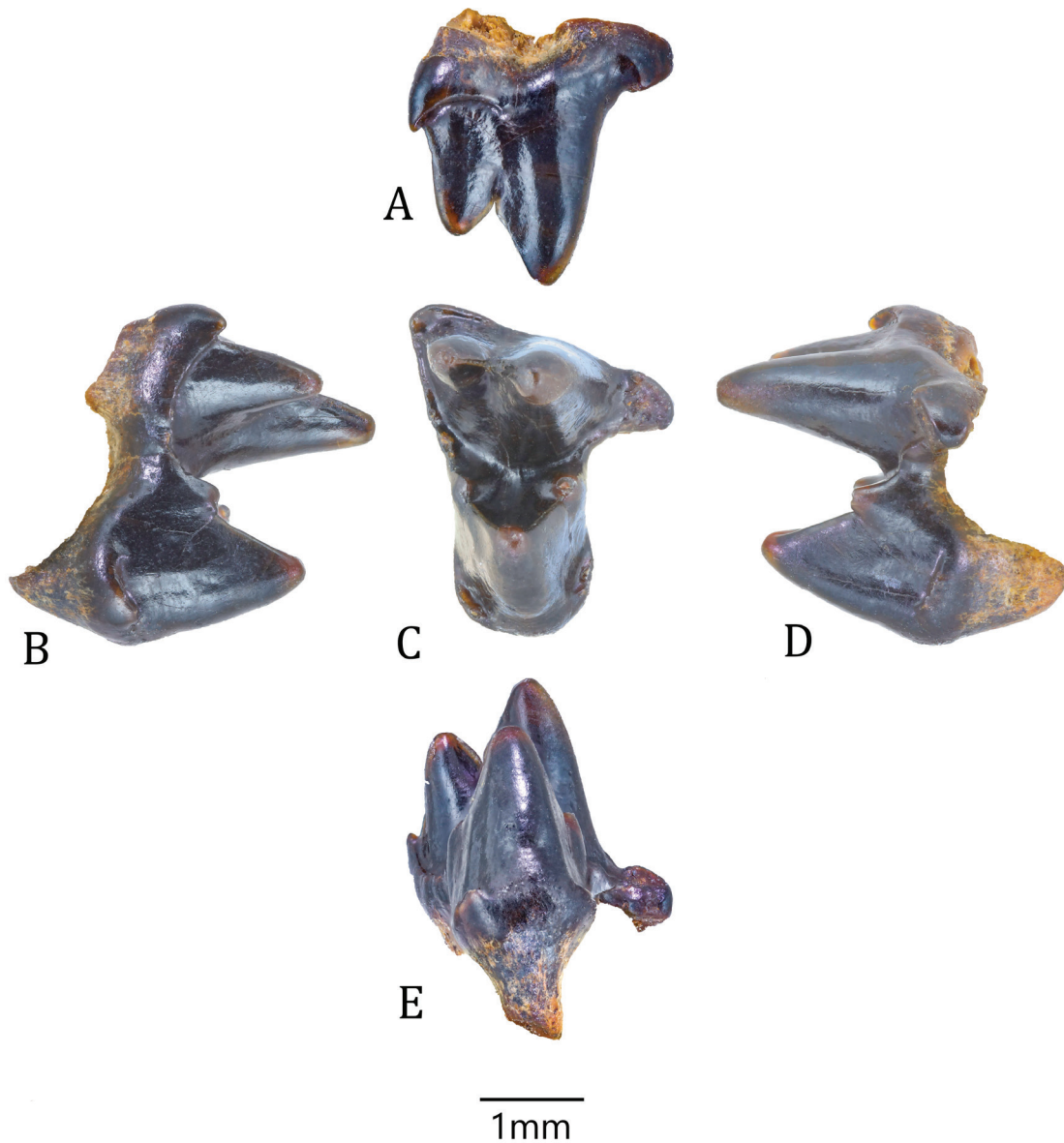


Figure 4. *Cimolestes incisus*, dentary with *p2*–*m3*, UCMP 46874. A. Lingual view. B. Occlusal view. C. Buccal view.



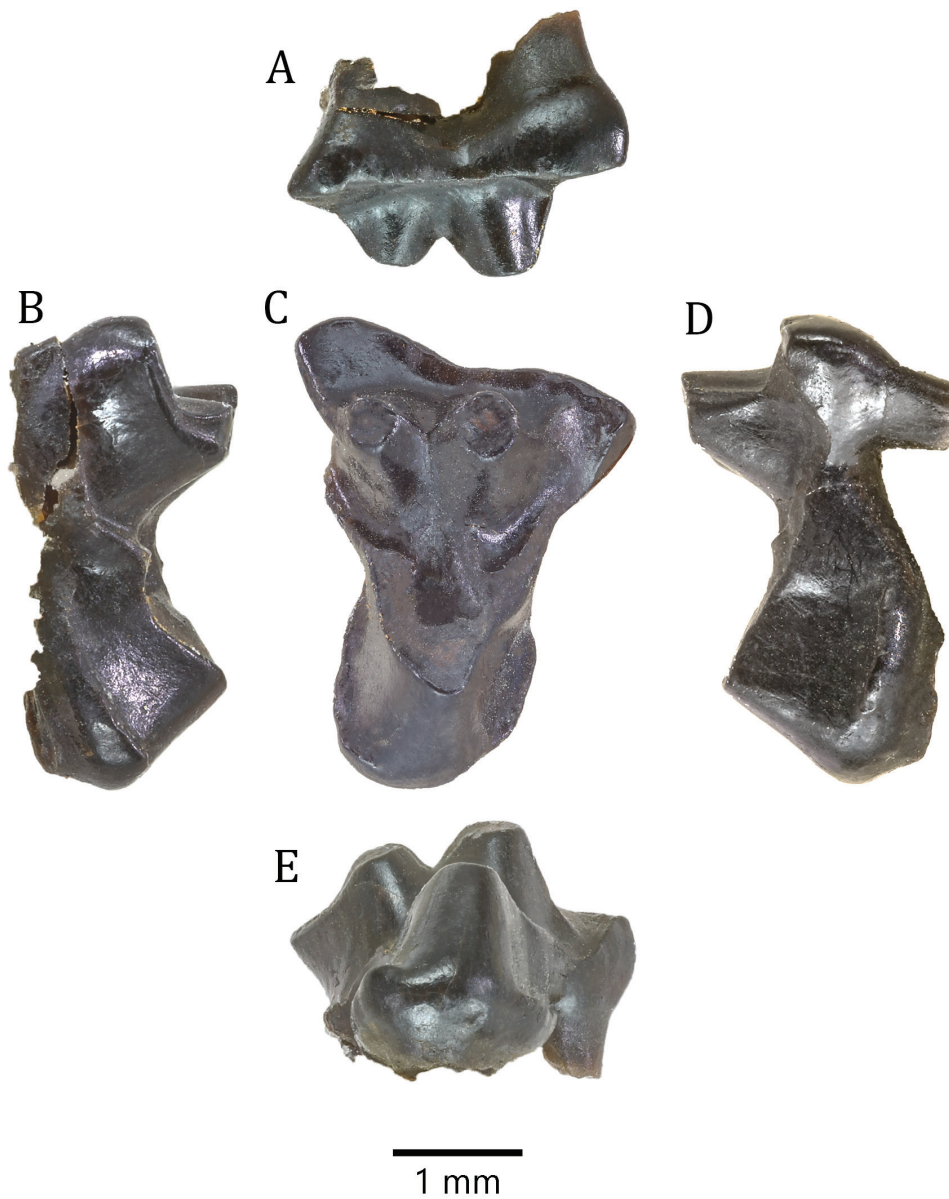
**Figure 5.** *Betonnia* sp. cf. *Be. tsosia*, P4, UCMP 281370. **A.** Buccal view. **B.** Mesial view. **C.** Occlusal view. **D.** Distal view. **E.** Lingual view.

measured across the conules is approximately half the total length of the crown. Lingually the base of the protocone is expanded. Both width and length of the pre- and postcingula are variable. On two of the six M1s in the sample, the cingula are continuous across the lingual side of the protocone. On the others, the precingulum does not extend as far lingually as the postcingulum.

**M2**—Differing from M1, buccal to the paracone the ectocingulum is slightly more convex while the distal part of the ectocingulum is larger and forms a distinct metastylar lobe projecting buccally (Fig. 7). This results

in a more pronounced ectoflexus. The conules are distinct with the paracone somewhat larger and closer to the protocone than the metaconule. On one tooth, UCMP 218915, two small conules are present in the position of the paracone. On one of the ten M2s in the sample, the pre- and postcingula are continuous across the lingual side of the protocone. On the others the precingulum does not extend as far lingually as the postcingulum.

**M3**—The parastylar lobe is large and extends mesio-buccally (Fig. 8). A narrow ectocingulum extends across the paracone and ends dorsal to the apex of the metacone.



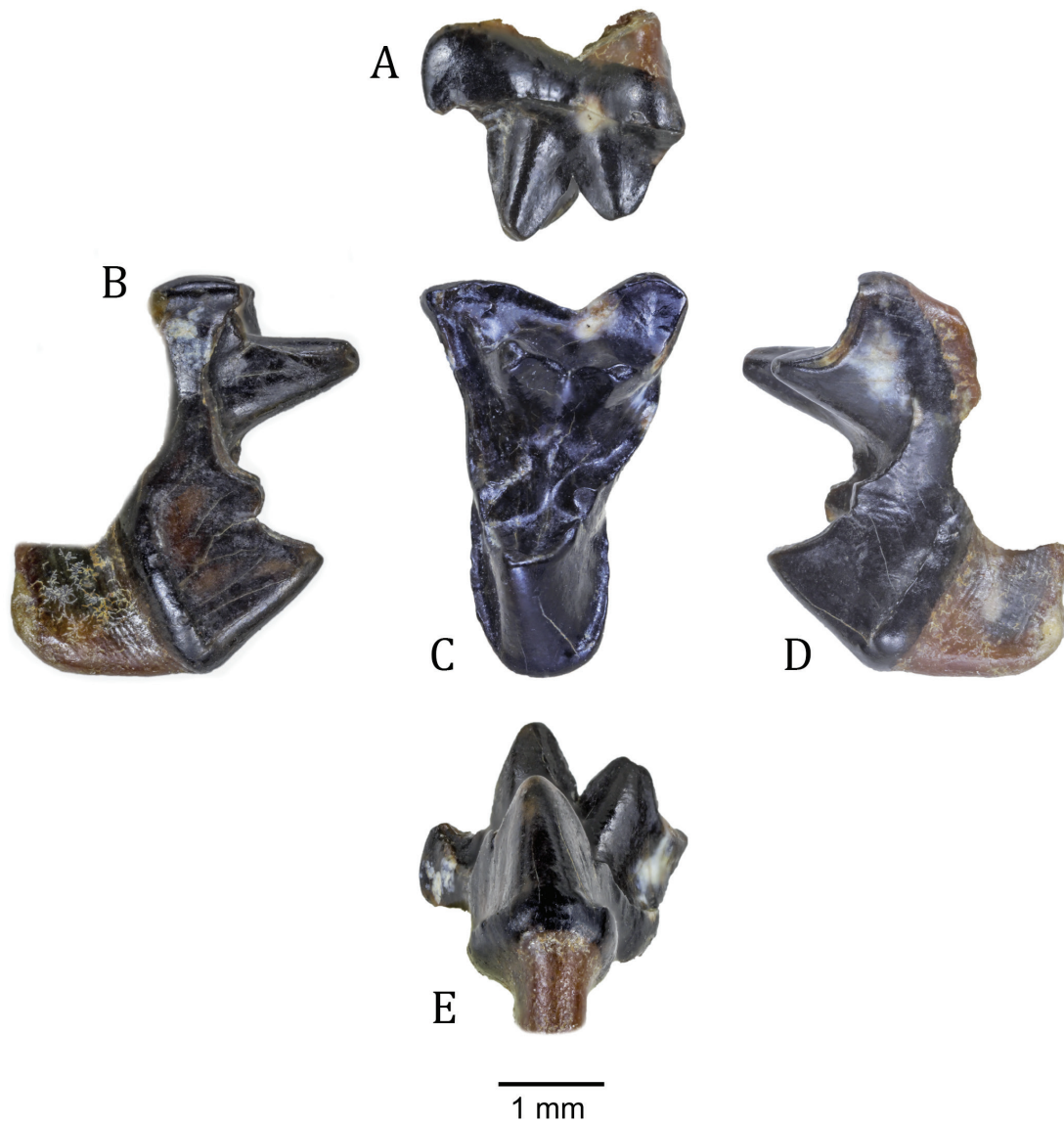
**Figure 6.** *Betonnia* sp. cf. *Be. tsosia*, M1, UCMP 218909. **A.** Buccal view. **B.** Mesial view. **C.** Occlusal view. **D.** Distal view. **E.** Lingual view.

The paracone appears to have been slightly larger than the metacone, but their apices are worn on the one available M3 (UCMP 281368). Forming a trough from the centrocrista to the buccal side of the protocone, the talon basin is narrow mesiodistally, but wide buccolabially. The paraconule is closer to the protocone than the metaconule. A shelf-like preparaconule crista extends to the parastyle. By contrast, the postmetaconule crista is not as broad and shorter ending above the metacone. The precingulum extends from dorsal to the paraconule to the mesial side of the protocone. The postcingulum is shorter

but extends farther lingually than the precingulum.

#### Remarks

To date, only three eutherians with little modified tribosphenic upper dentitions of similar size have been found in Pu3 faunal assemblages of the GCC. They are the subzalambdont (*sensu* Fox 2015) *Betonnia* sp. cf. *Be. tsosia* and *Puercolestes* sp. cf. *Pu. simpsoni*, and *Prodiacodon crustulum* Novacek, 1977. P4s and upper molars of *Be.* sp. cf. *Be. tsosia*, and *Pr. crustulum* can be distinguished from those of *Pu.* sp. cf. *Pu. simpsoni* by the presence of



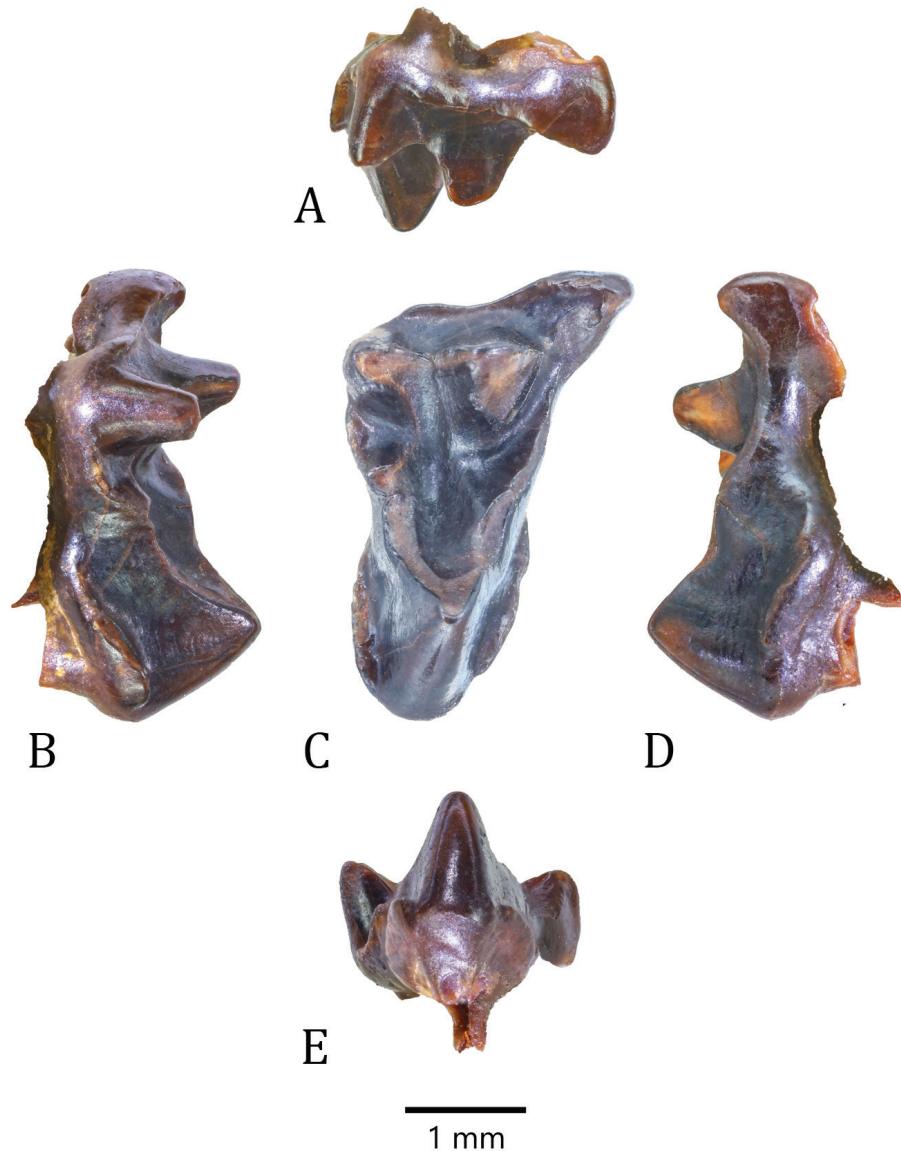
**Figure 7.** *Bettonnia* sp. cf. *Be. tsosia*, M2, UCMP 218917. **A.** Buccal view. **B.** Mesial view. **C.** Occlusal view. **D.** Distal view. **E.** Lingual view.

pre- and postcingula. On P4s and upper molars of *Be. sp. cf. Be. tsosia*, the pre- and postcingula are buccolingually elongate and relatively narrow. On three of the 21 available P4s and upper molars they meet on the lingual side of the protocone. By contrast, on P4s and upper molars of *Pr. crustulum*, which is interpreted to be a leptictid (Clemens 2015), the pre- and postcingula tend to increase in width lingually. On some of the postcingula there is a small but distinct hypocone. On only one of the 21 M1 and M2s of *Pr. crustulum* are the pre- and postcingula continuous across the the lingual side of the protocone.

Size of its M2 and other cheek teeth was one of the characters cited in the diagnosis of *Be. tsosia*. Because of

the small available samples, only limited direct comparisons can be made. The only dimension of an upper post-canine of *Be. tsosia* reported by Williamson et al. (2011) is the distal width of an M2, 2.50 mm. Further, Williamson et al. (2011) made specific comparisons with *Scollardius propalaeoryctes* n. comb Fox, 2015 from Alberta and *Chacopterygus minutus* Williamson et al., 2011 from New Mexico. The distal width of the single available M2 of *S. propalaeoryctes* reported by Lillegraven (1969) is 3.90 mm. The distal width of the single available upper molar, an M1 (NMMNH P-47234) of *Ch. minutus* is 3.10 mm.

The available dimensions of M2s of *Be. sp. cf. Be. tsosia*, *Pu. sp. cf. Pu. simpsoni*, and *Pr. crustulum* from Montana



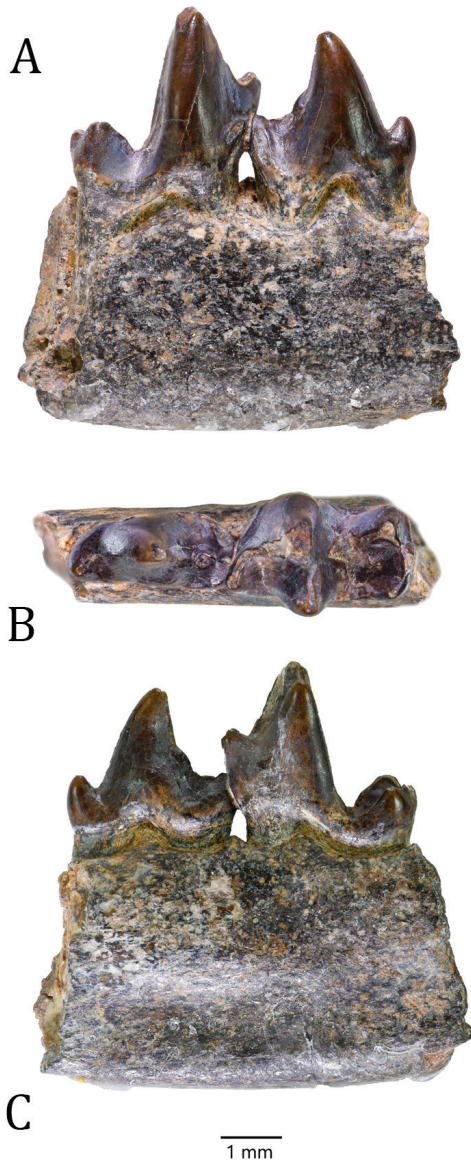
**Figure 8.** *Betonnia* sp. cf. *Be. tsosia*, M3, UCMP 281368. **A.** Buccal view. **B.** Distal view. **C.** Occlusal view. **D.** Mesial view. **E.** Lingual view.

as well as *Pu. simpsoni* and *Be. tsosia* from New Mexico are compared in Table 3. If the one available M2 of *Be. tsosia* is not a small outlier, the upper molars of this species appear to have been distinctly smaller than those of the other species. Stressing that the samples are woefully small, the available data suggests that the dentition of *Be. sp. cf. Be. tsosia* was larger than that of *Be. tsosia*. Additional material might indicate that this difference in size warrants recognition of a new species of *Betonnia* in Montana.

LOWER POSTCANINES (P4, M1-3) PROBABLY REFERABLE TO *PUERCOLESTES* SP. CF. *PUERCOLESTES SIMPSONI* or *BETONNIA* SP. CF. *BETONNIA TSOSIA*

FIGS. 9, 10

**Referred Specimens—p4-m1:** UCMP V75230, UCMP 281342. **m1:** UCMP V72127, UCMP 25805; UCMP V73080, UCMP nos. 218979, 258010, 258014, 258019, 288009; UCMP V73082, UCMP nos. 189519, 258042, 258043; UCMP V74122, UCMP 258035; UCMP V99438, UCMP nos. 258001, 258006, 258007, 281344. **m2:** UCMP V72125, UCMP 281347; UCMP V72128, UCMP 218981; UCMP V72129, UCMP 281348; UCMP V72134, UCMP 258046; UCMP V72137, UCMP 281349; UCMP V73080, UCMP nos. 144457, 186647, 218980, 281351, 281352, 281353, 281354, 281355, 281356, 281373; UCMP V73082, UCMP nos. 192092, 258040; UCMP



**Figure 9.** *Puercolestes* sp. cf. *Pu. simpsoni* or *Betonnia* sp. cf. *Be. tsosia*, fragment of dentary with p4 and m1, UCMP 281342. **A.** Buccal view. **B.** Occlusal view. **C.** Lingual view.

V74122, UCMP nos. 218982, 258032, 258038; UCMP V74126, UCMP nos. 192100, 258030, 281358; UCMP V75194, UCMP nos. 258025, 258026; UCMP V99438, UCMP nos. 192106, 258004, 281359, 281360, 281361. **m3:** UCMP V72129, UCMP nos. 258051, 281364; UCMP V72130, UCMP nos. 258048, 258049; UCMP V72137, UCMP 258045; UCMP V73080, UCMP nos. 258012, 258017, 281362, 281363, 281374; UCMP V74122, UCMP nos. 258031, 258032, 258034, 258036, 258037; UCMP V75193, UCMP 258027; UCMP V99438, UCMP 281365.

**Basis for association**—The basis for identification of the 61 isolated cimolestid lower molars and a fragment

**Table 3.** Comparison of dental dimensions of M2. All dimensions in millimeters. Number of specimens shown in parentheses. \*=estimated value.

New Mexico	Length	Mesial width	Distal width
<i>Puercolestes simpsoni</i> <sup>1</sup>	2.70–3.20+ (2)	4.50 (1)	4.70 (1)
<i>Betonnia tsosia</i> <sup>1</sup>			2.50 (1)
Montana			
<i>Puercolestes</i> sp. cf. <i>P. simpsoni</i>	3.14–4.2* (3)	4.67–5.09 (2)	4.76–5.22 (2)
<i>Betonnia</i> sp. cf. <i>B. tsosia</i>	2.23–2.76 (8)	3.15–4.02 (8)	3.67–4.29 (10)
<i>Prodiacodon crustulum</i> , M1–M2 combined <sup>2</sup>	2.35–2.86 (21)	3.25–3.96 (21)	3.57–4.12 (21)

<sup>1</sup> Dimensions from Williamson et al. (2011)

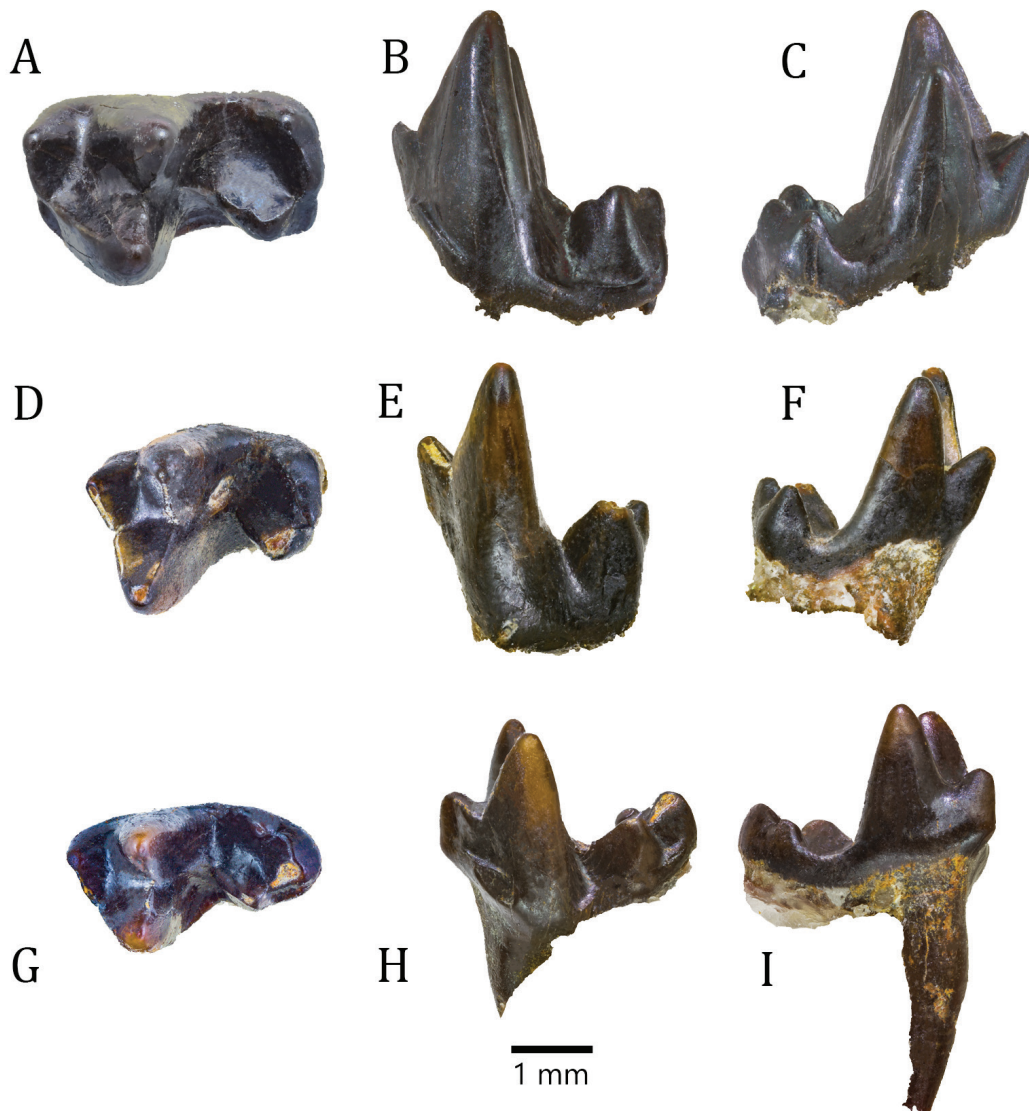
<sup>2</sup> Dimensions from Clemens (2015)

of dentary preserving p4 and m1 (UCMP 281342) from the GCC included here is discussed after description of the material. A summary of their dental dimensions is given in Table 4. Identification of their positions in the dental arcade is based on comparisons with dentaries of *Puercolestes simpsoni* (NMMNH P-34831 and P-55408 as well as KU 9411) from the Nacimiento Formation (Williamson et al. 2011), a dentary of *Cimolestes incisus* (Fig. 4) from the Lance Formation, Wyoming, and dentaries of other Late Cretaceous cimolestids (see Lillegraven 1969, Fox 2015, 2016).

### Description

**p4**—A p4 and m1 are preserved in association in a fragment of dentary, UCMP 281342 (Fig. 9, Table 5). On p4 a small, low paraconid is slightly offset buccally at the mesial end of the crown. In lateral view, the mesial slope of the protoconid, the highest cusp, is slightly convex. Its distal slope is straighter, shorter, and vertical in orientation. This slope ends in a bulbous area. A small cusp links this area with the hypoconulid to form the crest of the talonid. Buccally, a slight depression slopes from this crest to the base of the crown. A metaconid is not present.

**m1**—The trigonid is more than twice the height of the narrower talonid (Figs. 9, 10A–C, Tables 4, 5). Only minor rugosities or a short, narrow precingulid are present on the mesial side of the trigonid. The paraconid, the lowest cusp of the trigonid, is well separated from the higher



**Figure 10.** *Puercolestes* sp. cf. *Pu. simpsoni* or *Betonnia* sp. cf. *Be. tsosia*, **m1**, UCMP 189519 in: **A.** Occlusal view. **B.** Buccal view. **C.** Lingual view. **m2**, UCMP 258025 in: **D.** Occlusal view. **E.** Buccal view. **F.** Lingual view. **m2**, UCMP 258025 in: **D.** Occlusal view. **E.** Buccal view. **F.** Lingual view. **m3**, UCMP 25803 in: **G.** Occlusal view. **H.** Buccal view. **I.** Lingual view.

metaconid, and the trigonid basin is open lingually. A carnassial notch is present at the lowest point of the protoconid, which links the metaconid to the higher protoconid. The talonid is slightly narrower than the trigonid. Of the cusps forming the distal margin of the talonid, the hypoconid is the highest. The hypoconulid, which projects only slightly distally, is lower than the hypoconid but higher than the entoconid. The cristid obliqua extends mesially to reach the trigonid below the carnassial notch in the protoconid. Although there can be minor rugosities in the hypoflexus, a high, continuous

entocristid is not present, and the talonid basin opens lingually. Rarely, a weak postcingulid extends from the hypoconulid to the base of the crown where it joins a weak basal cingulid.

*m2*—Differs from *m1* in the buccal position and closer approximation of the paraconid to the metaconid and consequent reduction in the size of the trigonid basin (Fig.10D–F). Also, the difference in height of the paraconid and metaconid is less than that found on *m1*s. None of the *m2*s in the sample have a postcingulid or buccal basal cingulids. Otherwise the morphologies of *m1* and

**Table 4.** Dental dimensions of cimolestid lower molars from Garbani Channel localities. All dimensions in millimeters. OR=Observed range of variation. N=number of teeth

		Length	Trigonid width	Talonid width
<b>m1</b>				
	OR	2.36–3.97	1.57–2.81	1.29–2.48
	Mean	3.18	2.17	1.78
	N	15	15	15
<b>m2</b>				
	OR	2.14–3.71	1.54–3.00	1.02–2.41
	Mean	2.78	2.35	1.68
	N	29	30	29
<b>m3</b>				
	OR	2.60–3.63	1.34–2.98	1.03–1.65
	Mean	3.14	2.11	1.38
	N	16	15	14

m2 are similar.

m3—In comparison to the preceding molars, the difference in height of the trigonid and talonid is less (Fig. 10G–I). Resembling m2, the paraconid is in a buccal position and approximated to the metaconid. A striking difference from the preceding molars is the narrower, mesiodistally elongated talonid ending in a salient

**Table 5.** Comparison of p4 dimensions. All dimensions in millimeters.

San Juan Basin, New Mexico, p4s			
	Length	Width	
<i>Puercolestes simpsoni</i> <sup>1</sup>			
NMMNH P-34831	3.30	1.80	
AMNH 59910	2.55	1.30	
<i>Betonnia tsosia</i> <sup>1</sup>			
NMMNH 44347	1.75	1.05	
Garbani Channel locality, Montana			
UCMP 281342, associated p4 and m1			
	Length	Mesial width	Distal width
<b>p4</b>	2.90	1.83	
<b>m1</b>	3.35	2.49	1.57

<sup>1</sup> Dimensions from Williamson et al. (2011)

hypoconulid. The hypoconulid is the highest cusp. The hypoconid and entoconid are smaller than the hypoconulid, but their relative heights vary. On some m3s, minor cuspules are present along the low entocristid. The distal root is distinctly larger than the mesial.

## Remarks

*Betonnia* sp. cf. *Be. tsosia*, *Puercolestes* sp. cf. *Pu. simpsoni*, and *Prodiacodon crustulum* are the only eutherians with little modified tribosphenic upper dentitions of similar size that have been identified in Pu3 faunal assemblages found in the GCC. It is assumed that the lengths of their m1–m2s and M1–M2s are similar. Of the little modified tribosphenic lower molars from the GCC localities, lower molars of *Pr. crustulus* were identified by their size, high trigonids relative to their talonids, mesiodistal approximation of paraconid and metaconid resulting in a distinct distal angulation of the paracristid, and broader talonids relative to trigonids on m1 and m2 (Clemens 2015). Identification of these lower molars left 61 isolated cimolestid lower molars and a fragment of dentary preserving p4 and m1 (UCMP 281342) that are possibly referable to *Be. sp. cf. Be. tsosia* or *Pu. sp. cf. Pu. simpsoni*,

Williamson et al. (2011) argued that the morphology of p4 provided a significant character for differentiation of the lower dentitions of *Pu. simpsoni* and *Be. tsosia*. Three p4s from the Nacimiento Formation were cited in their study. The p4 in a partial lower dentition of *Pu. simpsoni* (NMMNH P-34831) has a strikingly high paraconid, a character cited in the revised diagnosis of the species. In the hypodigm of this species, Williamson et al. (2011) also included an isolated p4 (AMNH 59910) with a smaller paraconid. They noted that it resembles p4s of species of *Cimolestes*, but they provisionally interpreted the morphological differences as a product of individual variation. Finally, a distinctly smaller isolated p4 (NMMNH P-44347) was referred to *Be. tsosia* (Table 5). Its protoconid is high and bulbous, and the paraconid is small and low. The talonid is a simple crest ending at a small cusp.

The p4 in the fragment of dentary from the GCC, UCMP 281342 (Fig. 9), has a small, low paraconid that differs from the high paraconid of the p4 in NMMNH P-34831. UCMP 281342 is larger than the isolated p4 (NMMNH 44347) referred to *Be. tsosia* (Table 5) and lacks a bulbous protoconid. The closest similarity in morphology is with the isolated, *Cimolestes*-like p4 (AMNH 59910) that was referred to *Pu. simpsoni* by Williamson et al. (2011).

Turning to the m1 preserved in UCMP 281342, its

dental dimensions fall within the observed ranges of variation in the sample of 15 isolated m1s from the GCC localities (Tables 4, 5). Length of its crown and width of its trigonid fall above the means for the GCC sample; talonid width is smaller than the mean. Comparisons of the dimensions in small samples of P4 and M1–M3 of *Pu. sp. cf. Pu. simpsoni* and *Be. sp. cf. Be. tsosia* suggest the dentition of *Pu. sp. cf. Pu. simpsoni* was somewhat larger (Tables 1, 2).

In summary, although tenuous, similarity in morphology, particularly to the paraconid of p4 (AMNH 59910), and size of the associated m1, suggest that UCMP 281342 might be referable to *Pu. sp. cf. Pu. simpsoni*. No distinctive differences in size or morphology were found among the lower molars from the GCC local faunas that provide bases for clearly distinguishing elements of the lower dentitions of *Pu. sp. cf. Pu. simpsoni* from those of *Be. sp. cf. Be. tsosia*. In this study, no attempt has been made to distinguish the p4s or lower molars of these two species.

#### DISCUSSION

Local faunas in the GCC and other Pu3 Interval Zone deposits document an early phase in the recovery of the terrestrial fauna of the North American Western Interior after the mass extinction at the K-Pg boundary. Some species of metatherians and eutherians in these faunal assemblages have been described and analyzed in previous publications (Clemens 1974, 2004, 2006, 2011, 2013, 2015, 2017a, 2017b, Clemens and Wilson 2009). In a series of faunal lists, Wilson (2014) cataloged the Pu1 and the Pu2/Pu3 undifferentiated local faunas of the Tullock Member of the Fort Union Formation. Clemens (2017b) reviewed the Pu1 record from this member and recognized the presence of *Procerberus formicarum* Sloan and Van Valen, 1965 and *Pr. sp. cf. Pr. grandis* Middleton and Dewar, 2004. In what were then considered Pu2/Pu3 undifferentiated local faunas, Wilson (2014) recognized the presence of two cimolestids: *Cimolestes cf. Ci. simpsoni* and *Procerberus sp. A*. Subsequent research indicates that these faunal assemblages are correlatives of the Pu3 Interval Zone and existed within an interval of approximately 375 to 850 ka after the K-Pg boundary (Sprain et al. 2018).

On the basis of the fossils then available, Clemens (1973) argued that at the generic level *Puercolestes* could not be distinguished from *Cimolestes*, and recognized *Ci. simpsoni*. With additional material, Williamson et al. (2011) provisionally concluded that *Puercolestes* was distinguishable. *Pu. simpsoni* is recognized here in Pu2

and Pu3 of the Nacimiento Formation. An associated P4, M1, and M2 and 14 isolated upper cheek teeth from Pu3 localities in the Tullock Member are identified as *Pu. sp. cf. Pu. simpsoni*. On the basis of this sample of upper cheek teeth, an unqualified reference to *Pu. simpsoni* might be warranted. However, because this sample is small and the lower dentition of *Pu. sp. cf. Pu. simpsoni* cannot be clearly identified, restraint is warranted.

*Cimolestes incisus* is recognized in the Lancian, and *Pu. simpsoni* as well as *Pu. sp. cf. Pu. simpsoni* in the Puercan. In their phylogenetic analysis, Williamson et al. (2011) supported the interpretation that *Ci. incisus* and *Pu. simpsoni* were closely related and that *Pu. simpsoni* was a North American survivor taxon across the K-Pg boundary. Although limited, the morphology of the available dental material supports the hypothesis that *Pu. sp. cf. Pu. simpsoni* was a member of this lineage.

The P4s and upper molars from the Tullock Member identified as *Betonna sp. cf. Be. tsosia* clearly differ from those of *Pu. sp. cf. Pu. simpsoni* in the presence of pre- and postcingula and the mesiodistal breadth of the conular regions of the crowns of M1 and M2. The hypodigm of *Be. tsosia* from the Nacimiento Formation consists of only 11 isolated teeth, many fragmentary (Williamson et al. 2011). The limited number of dental dimensions currently available suggests that *Be. tsosia* was distinctly smaller than *Pu. simpsoni*. Similarly, P4s and upper molars of *Be. sp. cf. Be. tsosia* appear to have been smaller than those of *Pu. sp. cf. Pu. simpsoni*, but the difference in size does not appear to be as great. If additional material substantiates this difference in size, recognition of a separate species in Montana might be warranted.

On the basis of isolated molariforms, Williamson et al. (2011) recognized *Chacopterygus minimus*, as well as a group of small cheek teeth simply dubbed “Cimolestidae, gen. et sp. undet.” The hypodigm of *Ch. minimus* consists of only three isolated upper cheek teeth that differ in their very small size and relatively large parastylar region. No lower cheek teeth were referred to *Chacopterygus* Williamson et al., 2011. The genus has not been recognized in the sample from the Tullock Member. Small molariform teeth similar in size to those identified as “Cimolestidae, gen. et sp. undet.” by Williamson et al. (2011) have been found in the Tullock Member and will be described in another study.

The phylogenetic relationships of Lancian and Puercan cimolestids are poorly understood. As discussed by many authors, the Family Cimolestidae as currently recognized probably is polyphyletic (e.g. Archibald 1982, Strauss

2006, 2007, Williamson et al. 2011, Fox 2015). In part, this is a product of the rarity of fossils and the limited number of characters that can be considered. Williamson et al.'s (2011) phylogenetic analysis was a step forward. Fox (2015) constructively addressed the problem of use of the genus *Cimolestes* as a composite taxon that did not recognize the morphological diversity of the species included in the genus by Lillegraven (1969). A thorough analysis of the taxonomic diversity and phylogenetic relationships of North American Lancian and Puercan cimolestids is beyond the scope of this study and remains a challenge for future research.

#### ACKNOWLEDGEMENTS

I gratefully acknowledge the contributions of members of the University of California Museum of Paleontology field parties and other colleagues who over more than four decades have helped collect fossils and geological data presented here. I thank the Engdahl family (particularly Bob, and Jane), the Kerr family, as well as many other landowners in Garfield County who not only provided access to their ranches but extended help and hospitality to our field crews. Special thanks to the late Harley Garbani and Richard Farrand for discovery of fossils on which this study is based. The Bureau of Land Management, Charles M. Russell National Wildlife Refuge, and U.S. Corps of Engineers provided permits for research on lands under their jurisdiction. Thanks to Dave Strauss who took the images and skillfully formatted Figures 2 to 10. In the course of this research I benefited greatly from discussions with P. Holroyd and G.P. Wilson. J.J. Eberle, P. Holroyd, and T.E. Williamson provided helpful reviews of the manuscript. Also, I thank D.M. Erwin for her extensive editorial help. Financial and other support was provided by the National Science Foundation (most recently EAR 9505841), the Hell Creek Project III, and the University of California Museum of Paleontology. This is University of California Museum of Paleontology Contribution No. 2091.

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