

NEW TRIBOSPHENIC MAMMALS FROM THE MUSSENTUCHIT LOCAL FAUNA (CEDAR MOUNTAIN FORMATION, CENOMANIAN), UTAH, USA

RICHARD L. CIFELLI, JOSHUA E. COHEN, and BRIAN M. DAVIS

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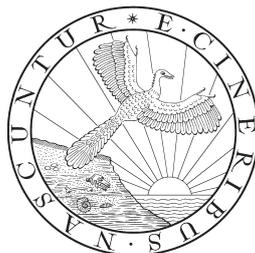
Herein we describe two new tribosphenic mammals from the Cedar Mountain Formation of Emery County, Utah, USA. The fossils occur in a narrow stratigraphic interval near the top of the unit (Mussentuchit Member) and date to approximately the Early–Late Cretaceous boundary (early Cenomanian, ~97 Mya). The specimens were recovered from screen-washing bulk rock samples. Both taxa are based on isolated teeth; from the limited morphology represented, both lack obvious specializations of the two major therian groups, Metatheria and Eutheria, and for present purposes they are regarded as basal tribosphenidans. *Dakotadens pertritus* sp. n. is the more abundant of the two and is closely related to a previously known species from the overlying (upper Cenomanian) Naturita Formation. *Culicolestes kielanae* gen. et sp. n. is notable in its large size (similar to *Pariadens mckennai* from the same fauna) relative to most other pre-Campanian tribosphenidans. The mammals of the Mussentuchit Local Fauna, now fully described on the basis of available fossils, represent one of the most diverse assemblages known from the Mesozoic, including some 22 taxa. Tribosphenidans, however, are neither abundant nor diverse, and include only six recognized species; most Late Cretaceous assemblages of North America include twice as many. Four of these are marsupialiforms and the remaining two, described herein, are considered basal tribosphenidans. Both eutherians and deltatheroidans, known from earlier and later faunas on the continent, are lacking. Triconodontids (Eutriconodonta) and spalacotheriids (basal Trechnotheria) make up nearly a third of mammalian diversity in the Mussentuchit Local Fauna, and account for about 40% of mammalian fossils identified to species level. Spalacotheriids (four taxa) are particularly abundant relative to both older (Albian) and younger (late Cenomanian onward) assemblages, suggesting some taphonomic or paleoecologic bias.

Key words: Cretaceous, Mammalia, Tribosphenida, Cedar Mountain Formation.

Richard L. Cifelli [rlc@ou.edu] and Joshua E. Cohen [jecohen@ou.edu], Sam Noble Museum and Department of Biology, University of Oklahoma, Norman, OK 73072, USA.

Brian M. Davis [bm.davis@louisville.edu], Department of Anatomical Sciences and Neurobiology, University of Louisville, 511 S. Floyd St. Room 111, Louisville, KY 40202, USA; and Sam Noble Museum, 2401 Chautauqua Ave., Norman, OK 73072, USA.

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INTRODUCTION

The record of Cretaceous mammals in North America, long notorious for its patchiness and extended hiatuses (*e.g.*, Clemens *et al.* 1979), has improved substantially in recent decades (Kielan-Jaworowska *et al.* 2004). Notably, sampling from the Albian has increased (see Davis and Cifelli 2011; Cifelli and Davis 2015, and references therein), and the early part of the Late Cretaceous (late Cenomanian–Santonian) is now represented by several assemblages from southern Utah (see Eaton 1993, 1995, 2013 and references therein). Lying in between and approximating the Lower–Upper Cretaceous boundary, the uppermost unit (Mussentuchit Member of Kirkland *et al.* 1997) of the Cedar Mountain Formation has yielded a diverse suite of vertebrates, the Mussentuchit Local Fauna (Cifelli *et al.* 1999). The fauna is notable in that it includes a number of elements characteristic of later Cretaceous assemblages, together with surviving members of archaic clades (Cifelli *et al.* 1997). Mammals, for example, include such early-appearing clades as plagiaulacidan multituberculates, spalacotheriid “symmetrodonts”, and triconodontids, as well as cimolodontan multituberculates and some of the earliest representatives of Marsupialiformes, which dominate Campanian–Maastrichtian assemblages of North America (Eaton and Nelson 1991; Eaton 1993; Cifelli and Madsen 1998, 1999; Eaton and Cifelli 2001; Cifelli 2004).

Herein we describe two new tribosphenidans from the Mussentuchit Local Fauna, completing the mammalian assemblage as based on available fossils. Though they are represented by fragmentary remains (isolated teeth, often incomplete) and are of uncertain affinities, the new tribosphenidans increase known taxonomic and morphologic diversity of the mammalian assemblage from the Mussentuchit Local Fauna, and prompt comparisons with earlier and later faunas.

Institutional abbreviations. — MNA, Museum of Northern Arizona, Flagstaff, Arizona, USA; OMNH, Oklahoma Museum of Natural History, Norman, Oklahoma, USA; UALVP, University of Alberta Laboratory of Paleontology, Edmonton, Alberta, Canada; URBAC, Uzbek/Russian/British/American/Canadian Joint Palaeontological Expeditions (currently housed at San Diego State University, San Diego, California, USA).

Acknowledgments. — First and foremost, RLC and BMD extend our most heartfelt thanks to the late Zofia Kielan-Jaworowska for the opportunities and guidance she gave us as we began our way up the steep learning curve for Mesozoic mammals. She was a role model without equal, and although she is no longer with us, she continues to be a source of inspiration. We thank the many individuals who helped in field and laboratory activities, principal among them the Judd family (Castle Dale, Utah, USA), Elizabeth M. Larson (Tulsa, Oklahoma, USA), Scott K. Madsen (Salt Lake City, Utah, USA), Randall M. Nydam (Midwestern University, Glendale, Arizona, Utah, USA), Cynthia L. Gordon (University of Oklahoma, Norman, Oklahoma, USA), and Kent S. Smith (Oklahoma State University, Tulsa, Oklahoma, USA). We are grateful to Jeff Eaton (Natural History Museum of Utah, Salt Lake City, Utah, USA) for his advice and help through the years. Partial support for this research was provided by grants to RLC from the National Geographic Society (4761-91, 5021-92) and the National Science Foundation (BSR 8906992, DEB 9401994). We are grateful to the Price Field Office, Bureau of Land Management, for facilitating access to the field area and permission to collect fossils on Federal lands. Finally, we thank Eaton, Alyson Brink (Texas Tech University, Lubbock, Texas, USA) and Gloria Cuenca-Bescós (Zaragoza University, Zaragoza, Spain) for their insightful comments on an earlier version of the manuscript.

METHODS, TERMINOLOGY, AND CONVENTIONS

All specimens described herein were obtained through underwater screen-washing and associated fossil recovery techniques (Cifelli *et al.* 1996). Scanning electron micrographs of specimen casts were obtained at the OMNH using a Denton Vacuum Desk II sputter coater (Denton Vacuum LLC, 1259 North Church Street Building 3, Moorestown, New Jersey 08057, USA) and a LEO 1450VP SEM (Carl Zeiss NTS LLC, One Corporation Way, Peabody, Massachusetts 01960, USA). Tooth measurements (all in millimeters) were taken with a Reflex Microscope (see MacLarnon 1989, Consultantnet Ltd, 94 High Street, Linton, Cambridge, CB21 4JT, UK), as defined by Lillegraven and McKenna (1986). Dental terminology (Fig. 1) mainly follows Kielan-Jaworowska *et al.* (2004, p. 412, fig. 11.1); where necessary, we provide references illustrating other

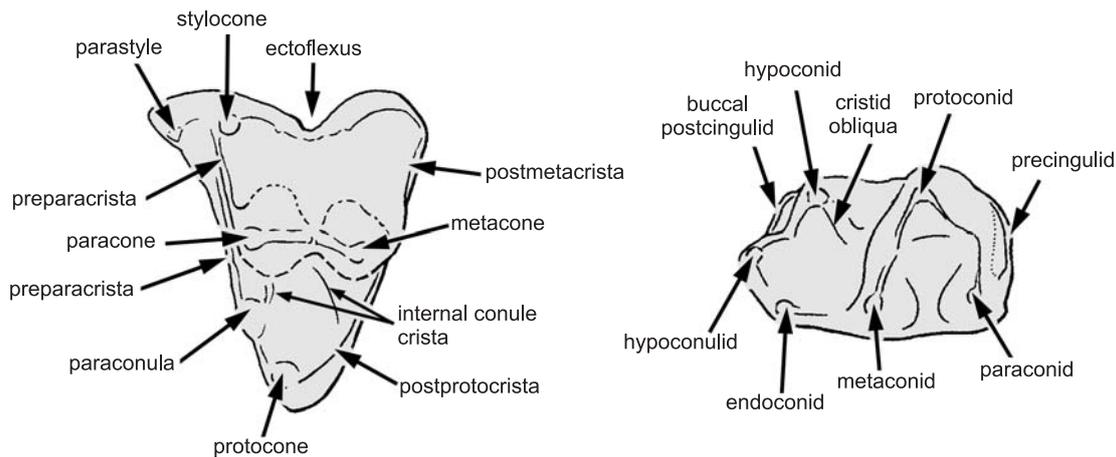


Fig. 1. Terminology for mammalian molars, based on the marsupialiform *Kokopellia juddi* (from Cifelli 2004).

structures and introduce new terms in the text. Unless otherwise specified, our implicitly comparative descriptions refer to basal tribosphenidan morphology, as approximated by taxa such as *Aegialodon* (Kermack *et al.* 1965), *Kielantherium* (Dashzeveg and Kielan-Jaworowska 1984; Lopatin and Averianov 2006), *Kermackia* (Slaughter 1971), and *Potamotelses* (Fox 1972).

We recognize Tribosphenida (McKenna 1975; = Boreosphenida of Luo *et al.* 2001; see Rougier *et al.* 2007; Davis 2011a) in a restricted sense, and exclude australosphenidans, which may have independently evolved a similar molar pattern (Luo *et al.* 2001, 2002; Martin and Rauhut 2005; Luo 2007; Davis 2011b). The taxa described herein join a growing roster of Cretaceous mammals having tribosphenic molars (*sensu* Simpson 1936) but lacking obvious apomorphies of living therian groups. Bryan Patterson, first to recognize this primitive structural grade, coined the accurate (but long-winded) moniker “therian mammals of uncertain infraclass affinities but of metatherian-eutherian grade” (Patterson 1956, p. 13) to describe them. Later, Butler (1978) formally placed then-known taxa in the Tribotheria, a paraphyletic assemblage. Though he later abandoned the name (Butler 1990), the term “tribotherian” has survived (*e.g.*, Sigogneau-Russell 1995; Kielan-Jaworowska *et al.* 2004). In order to avoid unwanted taxonomic implications, we refer to these taxa as basal tribosphenidans. Within Tribosphenida, we follow Vullo *et al.* (2009) in recognizing Marsupialiformes as a stem-based group including fossil taxa more closely related to crown Marsupialia than to Deltatheroidea. With reference to other mammals of the Mussentuchit Local Fauna, we follow Gaetano and Rougier (2011) in restricting Eutriconodonta Kermack *et al.*, 1973 to taxa more closely related to *Triconodon* than to Cladotheria McKenna, 1975; and we refer to spalacotheriid “symmetrodonts” as basal trechnotherians (*e.g.*, Li and Luo 2006).

Our original descriptions and formal proposal of new scientific names, below, constitute nomenclatorial acts governed by the International Commission on Zoological Nomenclature (ICZN) Code of Nomenclature. Accordingly, we have registered this paper and contained nomenclatorial acts in ZooBank, the official registry designated by ICZN. The identifiers for the publication and taxa carry a “LSID” prefix and appear following the citation for this paper (above) and each new name (below), respectively. ZooBank can be accessed at <http://zoobank.org/>.

Measurement abbreviations. — ANW, anterior (mesial) width (trigonid width of lower molars); AP, anteroposterior (mesiodistal) length; POW, posterior (distal) width (taloid width of lower molars).

GEOLOGIC SETTING AND AGE

Specimens described herein were collected in the course of a long-term, large-scale microvertebrate collecting program in the Cedar Mountain Formation between 1990 and 2002. The fossils were recovered from OMNH localities V213, V234, V235, V239, V240, V695, V794, and V868 (Fig. 2). Stratigraphic positions for the sites are given in Cifelli *et al.* (1999). All are on public lands administered by the US Bureau of Land

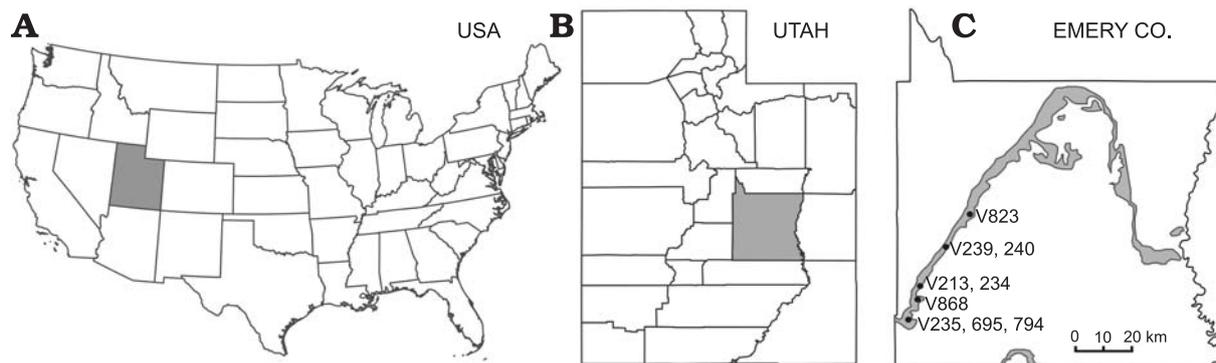


Fig. 2. Study area in Emery County, Utah, USA, showing outcrop of the Cedar Mountain Formation and approximate positions of fossil localities. Maps of USA (A) and Utah with counties (B) from FreeVectorMaps.com; outcrop belt and locality positions (C) after Cifelli *et al.* (1999).

Management, which also manages locality data associated with the fossils. The sites, which include representation of several different depositional facies (Goldberg 2000), are closely spaced geographically and lie in a restricted stratigraphic interval near the top of the Cedar Mountain Formation. Multiple, concordant radiometric dates indicate that the Mussentuchit Local Fauna dates to about 97 Mya (Cifelli *et al.* 1997; Cifelli *et al.* 1999; see also Garrison *et al.* 2007) and is of early Cenomanian age, close to the Albian–Cenomanian (Early–Late Cretaceous) boundary, which is currently placed at 100.5 Mya (Gradstein *et al.* 2012; Cohen *et al.* 2013).

SYSTEMATIC PALEONTOLOGY

Mammalia Linnaeus, 1758

Tribosphenida McKenna, 1975

Family incertae sedis

Genus *Dakotadens* Eaton, 1993

Type species: *Dakotadens morrowi* Eaton, 1993.

Referred species. — The type, and *Dakotadens pertritius* sp. n.

Distribution. — Cenomanian, Utah.

Dakotadens pertritius sp. n.

(Figs 3, 4, Table 1)

LSID urn:lsid:zoobank.org:act:879DE202-E0DA-4D75-BB50-5F2772A86C86

Holotype: OMNH 33247, left upper molar lacking the protocone.

Etymology: *Pertritius*, Latin, very worn, in allusion to the heavy occlusal and apical wear that characterizes known molars of the species.

Type locality: OMNH locality V695, Emery County, Utah, USA.

Type horizon: Mussentuchit Member, Cedar Mountain Formation (97.0 ± 0.1 Ma, Cifelli *et al.* 1999; see Garrison *et al.* 2007).

Referred material. — OMNH 25617 (OMNH locality V235), distobuccal corner of left Mx; 27641 (OMNH locality V794), left Mx lacking mesiobuccal corner; 25813 (OMNH locality V239), left last upper

Table 1. Dental measurements (in mm) of *Dakotadens pertritius* sp. n. (*, holotype).

Specimen	Tooth	AP	ANW	POW
OMNH 33247*	Mx	2.42	–	–
OMNH 25798	mx	2.4	1.41	1.29
OMNH 27544	m1	2.54	1.22	1.17
OMNH 33997	m1?	–	1.28	–
OMNH 30588	mx	–	–	1.38
OMNH 24148	mx	–	–	1.4
OMNH 25803	mx	–	–	1.26

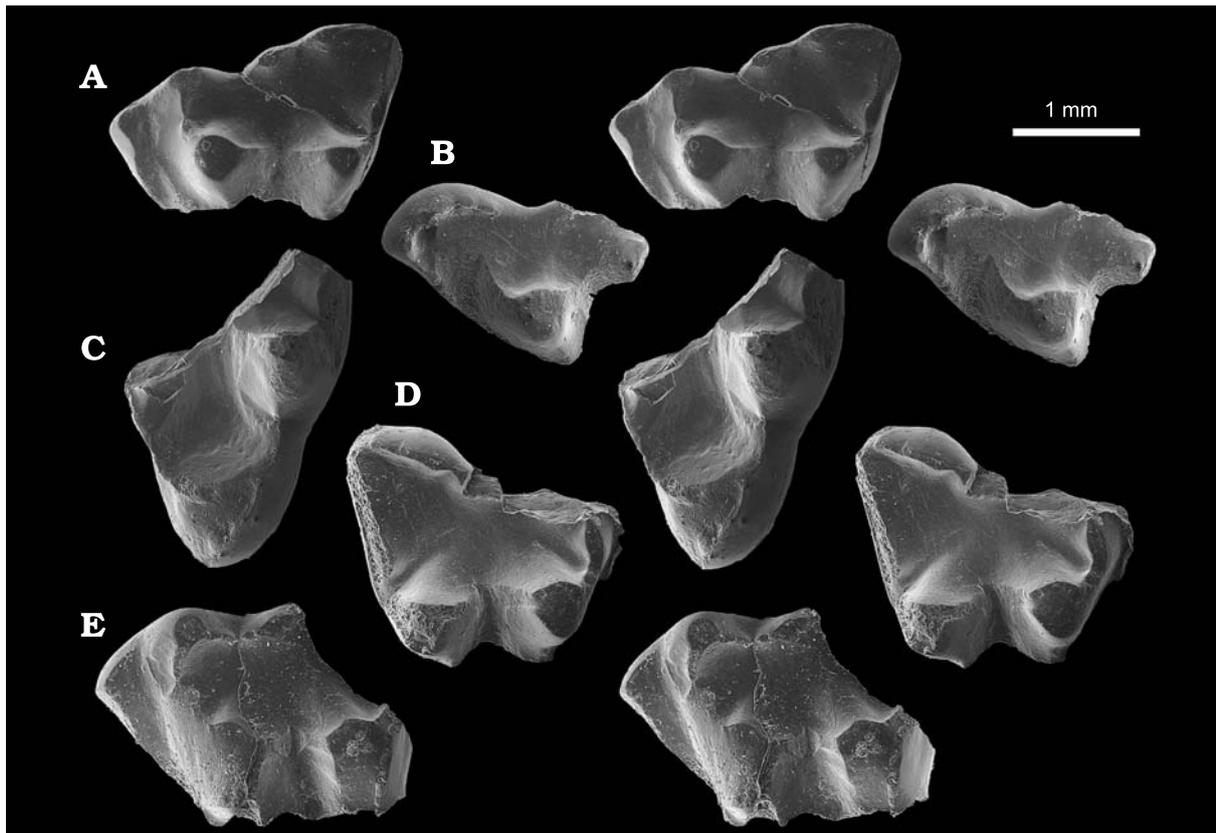


Fig. 3. *Dakotadens pertritius* sp. n., upper molars. All specimens are from the Mussentuchit Member, Cedar Mountain Formation (Cenomanian), Emery County, Utah, USA. **A.** OMNH 33247 (holotype), OMNH locality V695, LMx lacking the protocone in occlusal stereopair. **B.** OMNH 25813, OMNH locality V239, left last upper molar lacking the protocone in occlusal stereopair. **C.** OMNH 27641, OMNH locality V794, LMx lacking the mesiobuccal corner in occlusal stereopair. **D.** OMNH 27640, OMNH locality V794, RMx lacking the protocone and mesiobuccal corner in occlusal stereopair. **E.** OMNH 27644, OMNH locality V794, LMx lacking the protocone and distobuccal corner in occlusal stereopair.

molar lacking the protocone; 27640 (OMNH locality V794), right Mx lacking the protocone and mesiobuccal corner; 27509 (OMNH locality V695), mesiobuccal corner of right Mx; 27644 (OMNH locality V794), left Mx lacking the protocone and distobuccal corner; 26731 (OMNH locality V695), fragment of Mx; OMNH 25798 (OMNH locality V239), left ?last lower molar; 27544 (OMNH locality V695), left m1; 33998 (OMNH locality V794), talonid of right mx; 25627 (OMNH locality V234), talonid of left mx; 33997 (OMNH locality V794), trigonid of right m1?; 30588 (OMNH locality V794), talonid of right mx; 24148 (OMNH locality V213), talonid of right mx; 25803 (OMNH locality V239), talonid of right mx.

Diagnosis. — Similar to *D. morrowi*, but smaller with higher molar crowns. The paracone and metacone are closer together than in *D. morrowi*, with the centrocrista V-shaped in buccal view; protocone mesiodistally shorter. The stylocone is the largest stylar cusp when present (lacking on the last upper molar); differs from *D. morrowi* in that cusps in the C and D positions are less developed. The postmetacrista has a distinct notch at the base of the metacone; this notch is poorly developed or lacking in *D. morrowi*. Lower molars have a greater talonid/trigonid height differential, with relatively narrower talonid, and the protoconid is significantly taller than the metaconid and paraconid; cusp f is less developed, not forming a strong precingulid as seen in *D. morrowi*. All cusps of upper and lower molars show a distinctive pattern of heavy apical and occlusal wear.

Description. — Upper molars (Fig. 3) generally have short, robust cusps with heavy apical and occlusal wear. The paracone and metacone are subequal in height; the former cusp is slightly more voluminous and more heavily worn, suggesting that it may have been slightly taller than the metacone when unworn. The paracone is wider than the metacone, both mesiodistally and buccolingually. The metacone is more angular (*i.e.*, it has a pyramidal appearance, with planar faces, in occlusal view) than the paracone, which is more rounded and bulbous; both cusps have well-defined keels on their lingual faces, owing to wear. The

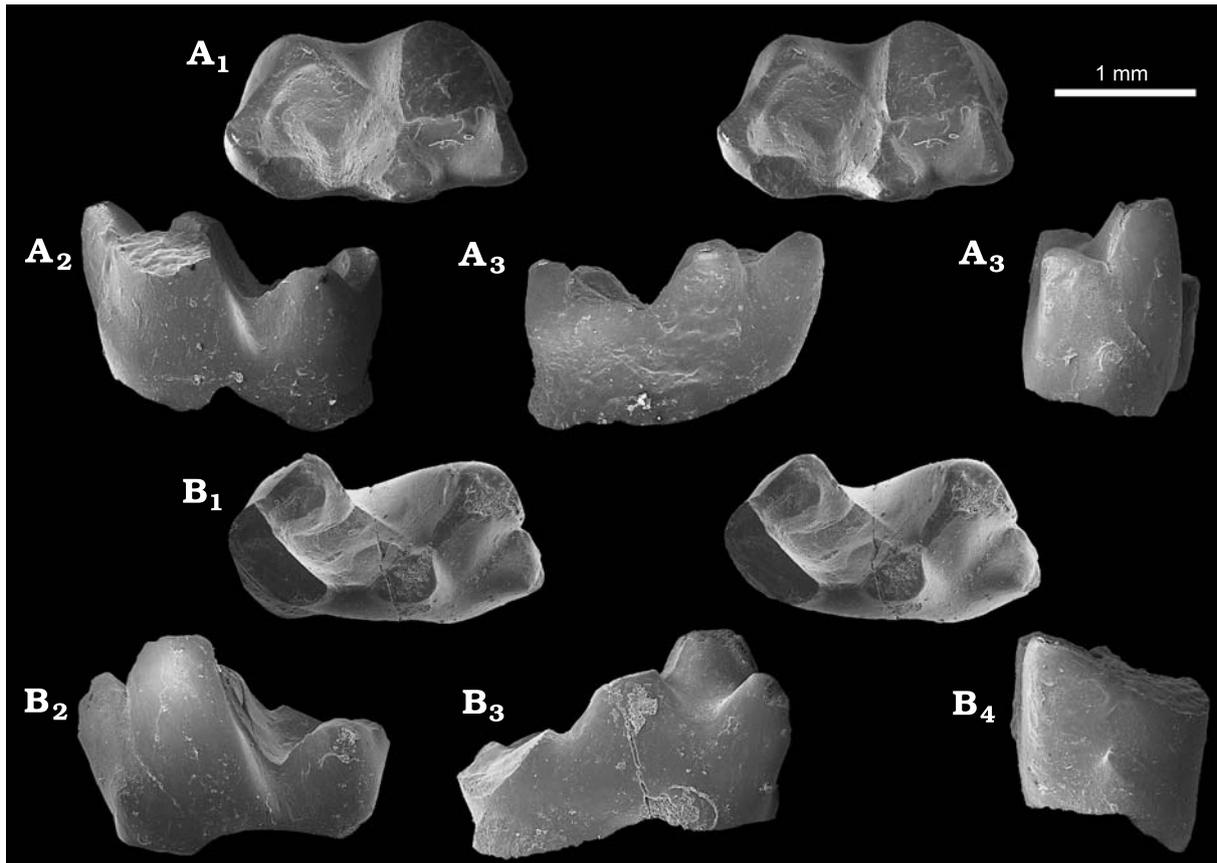


Fig. 4. *Dakotadens pertritrus* sp. n., lower molars. All specimens are from the Mussentuchit Member, Cedar Mountain Formation (Cenomanian), Emery County, Utah, USA. **A.** OMNH 25798, OMNH locality V239, Lmx in occlusal stereopair (A₁), buccal (A₂), lingual (A₃), and mesial (A₄), views. **B.** OMNH 27544, OMNH locality V695, Lm1 in occlusal stereopair (B₁), buccal (B₂), lingual (B₃), and mesial (B₄) views.

paracone and metacone have separate bases and are slightly inclined mesially and distally, respectively; the centrocrista (crest joining the apices of paracone and metacone; Davis 2007, p. 219, fig. 2A) shows light wear. A stylocone is present directly buccal to the paracone except for the last upper molar (OMNH 25813, Fig. 3B), which bears instead a series of cusplules in the position of the stylocone. The stylocone is inflated and bulbous, with heavy apical wear; it is connected to the paracone by a preparacrista that bears a weak notch. In OMNH 25813, the preparacrista fades out and terminates halfway between the paracone and parastyle. A parastyle is present directly mesial to the stylocone position (the photos shown in Fig. 3B are rotated counterclockwise from anatomical position, such that the parastyle appears to lie lingual to the stylocone), and is lingually connected to a mesial cingulum, which is presumably the buccal extension of the preprotocrista. The parastylar lobe of the stylar shelf is about half the width of the metastylar lobe. A weak ectoflexus is developed distal to the stylocone and mesial to stylar cusp C. Stylar cusps C and D (Clemens 1979, p. 200, fig. 11-1) are present but are variable in their development. Stylar cusp C is distal to the deepest point of the ectoflexus, and cusp D is directly buccal to the metacone. Both stylar cusps C and D are situated along the buccal edge of the stylar shelf. Stylar cusps C and D are small but distinct, roughly equivalent in size, bulbous, and joined by a faint ridge in OMNH 33247 (Fig. 3A); they appear to be similar but slightly weaker on OMNH 27640 (Fig. 3D; cusp C is broken on this specimen). As with all the cusps, stylar cusps C and D tend to show apical wear, despite the fact that they do not directly occlude with opposing structures on the lower molars (see discussion in Clemens 1979). The postmetacrista is notched at its junction with the metacone. This notch extends buccomesially across the stylar shelf, giving the metastylar region the appearance of a pennant extending backward and outward from the mesial part of the stylar shelf.

OMNH 27641 (Fig. 3C), a left upper molar lacking the paracone and most of the stylar shelf, is noteworthy because it preserves the protoconal region. The protocone is rounded lingually and has a steep buccal surface, forming the lingual face of a deep trigon basin. No metaconule per se is present, although there is a faint notch

where the postprotocrista terminates at the metacone. A somewhat better though still questionable case can be made for the presence of a paraconule, represented by a swelling and buccally-extending keels lingual to the paracone. Much of the damage to the tooth crown evidently occurred postmortem, though it is clear that occlusal wear is present. Notably, the presence of a deep and extensive facet on the postmetacrasta suggests strong reliance on postvallum-prevallid shear (supported also by the length and development of the postmetacrasta on OMNH 27640, Fig. 3D). The protocone of OMNH 27641 differs from those on non-ultimate molars referred to *D. morrowi* (Eaton 1993, p. 108, fig. 4A, B, D, E) in being shorter mesiodistally.

Lower molars, like the uppers, are characterized by short, robust cusps and typically show heavy apical wear. The trigonid/talonid height differential exceeds that of *D. morrowi* but is less than in comparable taxa such as *Kielantherium*, and the talonid is broad, being subequal to the trigonid in width. The paraconid and metaconid are most broadly separated and weakest on OMNH 27544 (Fig. 4B), suggesting that it is a first molar. The trigonid is more mesiodistally compressed on OMNH 25798 (Fig. 4A). The paraconid is not lingually displaced, as is typically the case for Late Cretaceous marsupials (Clemens 1979), nor is it appressed to the metaconid, as often occurs among early eutherians (e.g., Kielan-Jaworowska *et al.* 1979, 2004). The paraconid and metaconid are subequal in height and volume, though the metaconid is more severely worn in available specimens. The cristid obliqua originates below the notch in the protocristid (the crest connecting protoconid and metaconid; Kielan-Jaworowska *et al.* 2004, p. 412, fig. 11.1B), and a distal metacristid (Fox 1975, p. 424, fig. 4) is lacking. The talonid basin is bowl-like and deep. The hypoconulid differs in development, orientation and placement, as a result of either individual or positional variation. In some cases (e.g., OMNH 25798) it appears to be slightly displaced lingually; in others (e.g., OMNH 30588) it is more centrally placed. No buccal postcingulid is present. Near the mesial base of the crown, cusp f is variable in its development, either as a small knob (OMNH 27544) or as a ridge that extends buccally along the base of the protoconid (OMNH 25798).

Comments. — Although nowhere abundant, *Dakotadens pertritus* is among the more cosmopolitan of species from the upper Cedar Mountain Formation, being known from six different sites (see discussion in Goldberg 2000). Its molars are notable in the robust construction of cusps and strong apical wear, suggesting a divergence in diet from most other early tribosphenidans.

In addition to the hypodigm of *D. morrowi*, Eaton (1993) mentioned two additional upper molars referable to the genus, as *Dakotadens* sp. We identify both of these as ultimate molars. Neither is surely conspecific with MNA V6318, the ultimate upper molar Eaton (1993, p. 108, fig. 4G) referred to *D. morrowi*: MNA V6025 (Eaton 1993, p. 108, fig. 4O) apparently has a much smaller parastylar region (that of MNA V6318 is broken) and a more rounded protocone; while MNA V5345 (Eaton 1993, p. 108, fig. 4N) is considerably larger, with a more mesiodistally expanded protocone. The only one of these to preserve the mesiobuccal part of the crown more-or-less intact is MNA V6025, in which the parastyle is much shorter than that of OMNH 25813, described above as a partial ultimate upper molar of *D. pertritus*. MNA V5345 appears to be too large to belong to *D. pertritus*; MNA V6318 and OMNH 25318 (ultimate upper molars referred to *D. morrowi* and *D. pertritus*, respectively) are comparable, but known parts do not overlap sufficiently for comparison. We provisionally agree with Eaton (1993) that at least two (and perhaps three) species of *Dakotadens* (or close relative[s]) are present in the Naturita Formation (previously considered to be the Dakota Formation; see Young 1960; Carpenter 2014).

Genus *Culicolestes* gen. n.

LSID urn:lsid:zoobank.org:act:00D3168A-523D-40FC-A92A-9FBEBF4B948E1

Type species: *Culicolestes kielanae* sp. n., monotypic.

Etymology: Culico- (*Culex*, Latin, gnat or midge), for species of *Culicoides* (commonly called “cedar gnats”), the unforgettable companions to field parties working in the study area during mid-May–early-July; and -lestes (Greek, meaning robber or plunderer, a commonly-used suffix for genera of small predatory mammals).

Distribution. — As for the type and only species.

Diagnosis. — As for the type and only species.

Culicolestes kielanae gen. et sp. n.

(Fig. 5)

LSID urn:lsid:zoobank.org:act:4FF5387E-2377-4E1B-BD21-CDF580FD01F0

Holotype: OMNH 25809, left upper molar missing the distal stylar shelf and some cusp apices.

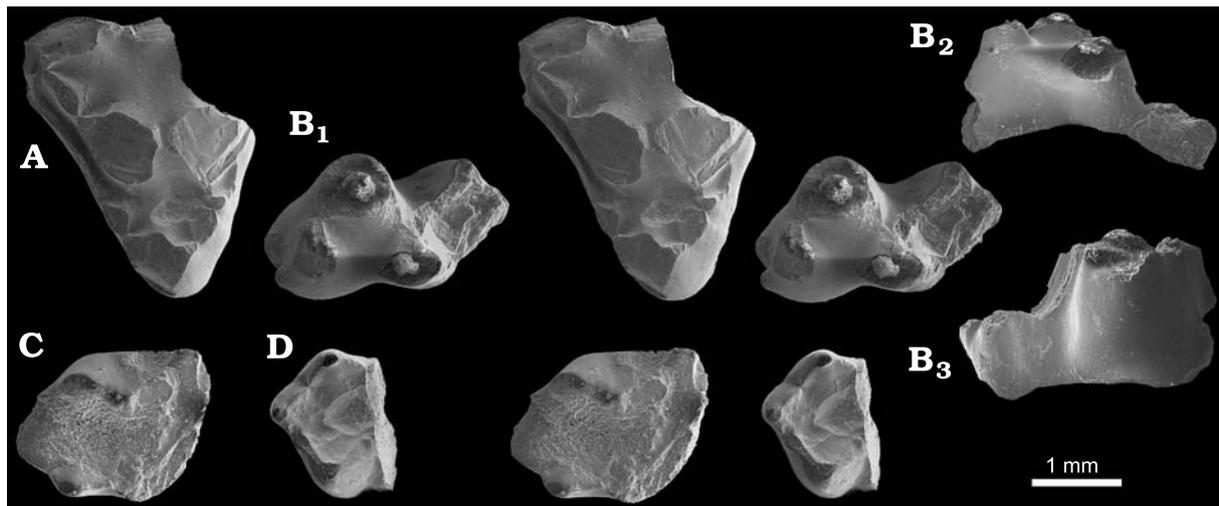


Fig. 5. *Culicolestes kielanae* gen. et sp. n. All specimens are from the Mussentuchit Member, Cedar Mountain Formation (Cenomanian), Emery County, Utah, USA. **A.** OMNH 25809 (holotype), OMNH locality V239, LMx missing distal stylar shelf and cusp apices in occlusal stereopair. **B.** OMNH 26727, OMNH locality V695, Rmx missing lingual part of talonid in occlusal stereopair (B₁), lingual (B₂), and buccal (B₃) views. **C.** OMNH 26441, OMNH locality V235, talonid of Lmx in occlusal stereopair. **D.** OMNH 25625, OMNH locality V234, talonid of Rmx in occlusal stereopair.

Etymology: For the late Zofia Kielan-Jaworowska (1925–2015), in recognition of her contributions to knowledge of Cretaceous mammals.

Type locality: OMNH locality V239, Emery County, Utah, USA.

Type horizon: Mussentuchit Member, Cedar Mountain Formation (97.0 ± 0.1 Ma, Cifelli *et al.* 1999; see Garrison *et al.* 2007).

Referred material. — The type, and OMNH 26727 (OMNH locality V695), right lower molar missing lingual part of the talonid; OMNH 25625 (OMNH locality V234), talonid of right lower molar; and 26441 (OMNH locality V235), talonid of left lower molar.

Tentatively-referred specimens. — OMNH 25830 (OMNH locality V240), talonid of right lower molar; and OMNH 25802 (OMNH locality V239), talonid of left lower molar.

Diagnosis. — Most similar to *Dakotadens* among comparable taxa, differing in: larger size; upper molars with preparacrista extending mesially, toward the parastyle (rather than buccally, toward the stylocone, as in *Dakotadens* and most other basal tribosphenidans); conules and internal cristae more distinct (presumed apomorphies); paracone and metacone share a common base; trigon basin not as deep; stylar shelf wider (mesially, at least). Lower molars are larger than and distinct from those of *Dakotadens* in having a strong, cusp-like f (developed as a narrow ridge in *Dakotadens*), a strong e cusp (weak or absent in *Dakotadens*), and a greater trigonid/talonid height differential.

Description. — The single known upper molar, OMNH 25809 (Fig. 5A) is battered and incomplete: the paracone and metacone are broken off near their bases and the metastylar region is missing. The tooth is distinctive in the fauna by virtue of its large size (ANW = 3.71) and robust construction. The mesial part of the stylar shelf, at least, is broad, suggesting that the specimen represents a tooth in the middle of the molar series. The bases of the paracone and metacone are well joined, and judging from the bases, the cusps may have been subequal. The preparacrista is deeply notched near the base of the paracone and again at its mesiobuccal termination, mesial to the stylocone and nearly at the mesiobuccal corner of the tooth, which is broken (the development of a parastyle is uncertain). Judged by its base, the stylocone was robust and developed mesiodistally; it forms a noticeable bulge on the buccal side of the crown. The ectoflexus appears to have been shallow. The inflection of enamel in the ectoflexus suggests that a low cusp was likely present in the C position. The protocone is small (both mesiodistally and buccolingually) relative to the condition generally seen in Late Cretaceous marsupialiforms (Clemens 1979; Kielan-Jaworowska *et al.* 2004). The preprotocrista extends mesiobuccally past the base of the paracone and terminates at the broken mesiobuccal corner of the tooth. The extent of the postprotocrista is uncertain owing to breakage, but it appears to have terminated near the break, approximately in mesiodistal alignment with the paracone and metacone. Both paraconule and metaconule are present near the bases of paracone and metacone, respectively; the specimen is worn but internal conular cristae can be distinguished. The trigon basin is well marked but not as deep as in *Dakotadens*.

Lower molars are referred to *Culicolestes kielanae* on the basis of size, similar construction (robust cusps) to the upper molar, and morphological appropriateness (small protocone on upper molars with corresponding open trigonid and narrow, small talonid on lowers). The most complete specimen, OMNH 26727 (ANW = 1.71; Fig. 5B), preserves most of the crown except the lingual part of the talonid; major cusp apices are broken. The trigonid is open lingually, with the paraconid placed well mesial to (and distinct from) the metaconid. No determination can be made as to the relative height of paraconid and metaconid. The paraconid is slightly buccal to the metaconid. Its mesiolingual face forms a keel that terminates in a pronounced cusp e, which in turn overlies a concavity that presumably fit with the hypoconulid of the preceding tooth. Buccally, a prominent cusp f is present adjacent to the concavity and below the level of cusp e (cusps e [mesiolingual] and f [mesiobuccal] are variably-developed, basal cuspules on lower molars of early mammals and close relatives; see Crompton and Jenkins 1968, p. 432, fig. 2B, C).

The distal wall of the trigonid bears a distal metacristid that is continuous with the cristid obliqua. The talonid appears to have been somewhat narrower than the trigonid (as also seen in OMNH 26441; Fig. 5C), and the trigonid was elevated well above the level of the talonid.

Comments. — *Culicolestes kielanae*, known only by a few fragmentary teeth, is notable in its large size, in this respect rivaling *Pariadens mckennai* (also poorly known), the largest marsupialiform in the Mussentuchit Local Fauna (Cifelli 2004). The species are otherwise dissimilar: lower molar cusps of *C. kielanae* are low, rounded, and rapidly reduced by apical and occlusal wear; those of *P. mckennai* are tall, sharp, and support well-developed shearing crests. *P. mckennai* further differs in its greater height of the paraconid and metaconid; better-differentiated, taller talonid cusps; and (as in other marsupialiforms) the presence of a buccal postcingulid. Upper molars of *P. mckennai* are not known, but those of closely-related *P. kirklandi* from the Naturita Formation (Eaton 1993, p. 119, fig. 8A–D) differ from *Culicolestes* in having a much larger (buccolingually and mesiodistally) protocone and in having well separated paracone and metacone (bases of the two cusps are united in *Culicolestes*).

Gen. et sp. indet.

(Fig. 6)

Included specimens. — Upper molariforms and parts thereof: OMNH 26449, protocone (OMNH locality V235); OMNH 26729, buccal portion of tooth, preserving paracone and metacone, and the metastylar lobe (OMNH locality V695); OMNH 30532, also buccal part of a tooth crown with paracone, metacone, and metastylar lobe (original fossil lost in quarrying; specimen preserved as a natural mold and casts made from that mold; OMNH locality V695); OMNH 33238, complete except for metacone (OMNH locality V695); and OMNH 33052, in which paracone and metacone are broken at their bases and the distal stylar shelf is missing.

Description. — These specimens vary in size and morphology and probably represent multiple taxa. They are described together because we are uncertain as to their identity and because they share fundamental points of similarity: the protocone is small, the mesial part of the stylar shelf is developed as a crest or cingulum only, and the stylocone is lacking or, when present, is placed mesial (rather than buccal) to the paracone.

OMNH 33238 (Fig. 6A) is the most complete of these teeth. The metacone is broken, but judging from the size of the base, the paracone was clearly much larger than the metacone. Their cusp bases are well joined, forming a united mound in the center of the crown. The paracone is conical and virtually unworn, save for minor apical wear, with a keel present only on the distal face (postparacrista; a preparacrista is absent). A small parastyle is developed mesial to the paracone. No stylocone is present; a faint cingulum runs along the buccal wall of the paracone, and is developed into a minute cuspule at the distobuccal base of that cusp. Distally, the stylar shelf is broad, with a well-developed metastylar region. The postmetacrista is oriented distobuccally at an angle less than 135° (from a horizontal passing through the approximated positions of the apices of paracone and metacone) and is incompletely preserved, but it was notched near its junction with the metacone; distobuccal to this, a faint swelling is present near the metastylar angle of the crown. The protocone is remarkable for its weak development, both mesiodistally and buccolingually. It forms a salient point, with its buccal face being virtually planar (a trigon basin as such is not developed) and sloping deeply toward the bases of the paracone and metacone. A very faint bulge hints at the presence of a paraconule, but the metaconule is absent and the protoconal cristae end at the bases of the paracone and metacone.

OMNH 26729 (Fig. 6B) is similar but smaller. Although it is less complete than OMNH 33238, it adds some morphological details. The metacone is significantly shorter than the paracone and the postmetacrista

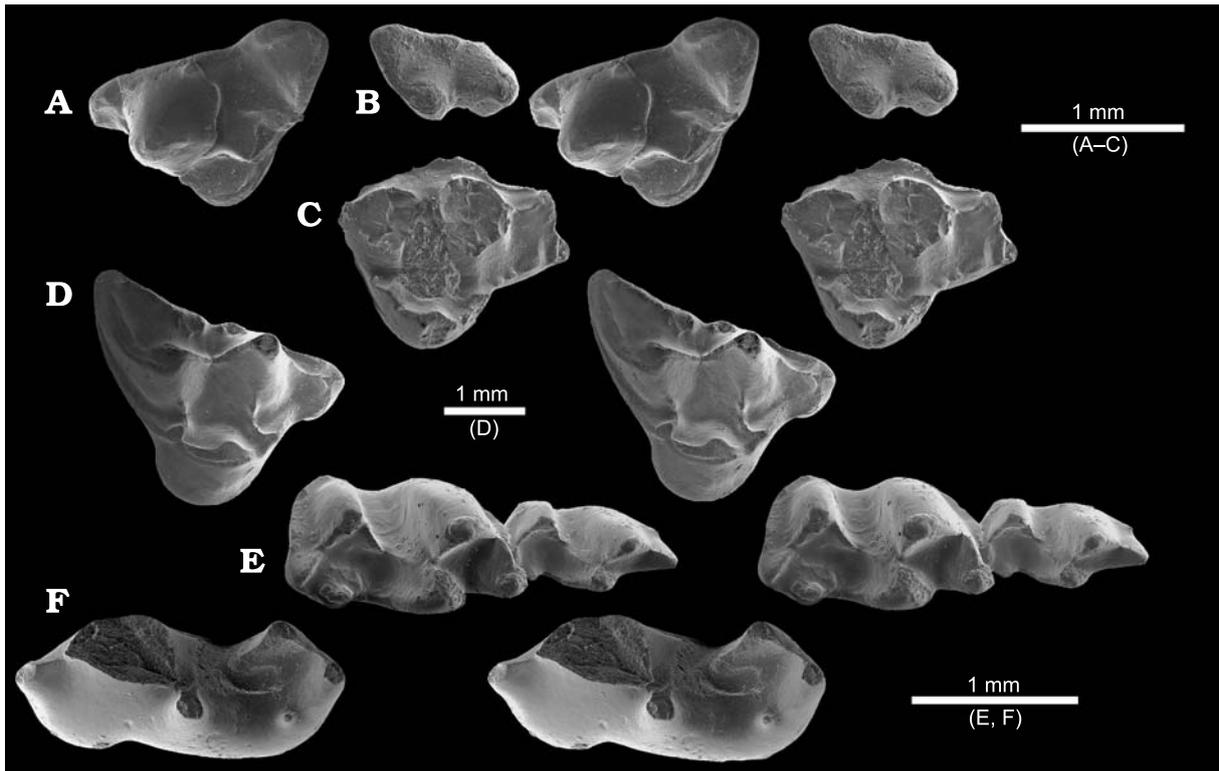


Fig. 6. Theria incertae sedis (A, B), and Marsupialiformes (C–F). A–C and F are from the Mussentuchit Member, Cedar Mountain Formation (Cenomanian), Emery County, Utah, USA; units and localities for D–E are listed below. A. OMNH 33238, OMNH locality V695, left upper molariform, occlusal stereopair. B. OMNH 26729, OMNH locality V695, right upper molariform fragment, missing protocone and mesial stylar shelf, occlusal stereopair. C. cf. *Sinbadelphys schmidti*, OMNH 33082, OMNH locality V868, right DP3, occlusal stereopair. D. *Protolambda florencae*, OMNH 68824, OMNH locality V1209, Hell Creek Formation (Maastrichtian), Carter County, Montana, USA, right dp3, occlusal stereopair. E. *Alphadon eatoni*, OMNH 27380, OMNH locality V798, North Horn Formation (Maastrichtian), Emery County, Utah, USA, left dp3–m1, occlusal stereopair. F. cf. *Kokopellia juddi*, OMNH 33972, OMNH locality V868, right dp3, occlusal stereopair.

is oriented somewhat more buccally than is the case in OMNH 33238. Light apical wear is present on both paracone and metacone; occlusal wear is evident on the postmetacrista and centrocrista, but the enamel is lightly frosted and occlusal wear cannot be definitively established elsewhere. A faint rim is present along the buccal margin of the stylar shelf in the metastylar region; as with OMNH 33238, a weak cusplule is present distobuccal to the base of the paracone.

Comments. — The striking features of these specimens (paracone much larger than metacone, small protocone, conules weak or lacking, mesial stylar shelf and stylocone lacking) are reminiscent of *Picopsis*, described by Fox (1980), and *Tirotherium*, described by Montellano-Ballesteros and Fox (2015), both from the Santonian Milk River Formation of southern Alberta. A similar specimen is also described by Davis *et al.* (2016, this volume) from the coeval Eagle Formation of northern Montana, and we offer complementary comments here. (In the text that follows, we collectively refer to these upper molariforms as “*Picopsis*-like”.) Yet in these same features, these fossils resemble deciduous premolars, in particular, DP3 of metatherians. Fox (1980) made point-by-point comparisons between the holotype upper molariform of *Picopsis pattersoni* Fox, 1980 (UALVP 15100) and DP3 of marsupials, regarding the former as distinct and as representing a permanent molar. Like the upper molariforms of *Picopsis* and *Tirotherium*, the specimens described under this heading do show some differences when compared with DP3 of “typical” Late Cretaceous marsupialiforms such as *Protolambda florencae* (Clemens, 1966) (Fig. 6D; see Clemens 1966 for illustrations of other taxa). For example, in *P. florencae*, the protocone is relatively larger and the protoconal cingula extend past the metacone and paracone, respectively; conules and internal conular cristae are present; the paracone and metacone are more nearly equal in size; the postmetacrista is oriented distobuccally; and a crest descends along the mesial face of the paracone, terminating at the parastyle. On this basis, we recognize at least one marsupialiform DP3, OMNH 33082 (perhaps belonging to *Sinbadelphys schmidti* Cifelli, 2004), from the

Mussentuchit Member of the Cedar Mountain Formation (Fig. 6C). Yet this does not prove, nor even suggest by default, that the specimens described under this heading, as well as upper molariforms referred to *Picopsis* and *Tirotherium*, are permanent teeth (molars). Knowledge of deciduous teeth belonging to early marsupialiforms and basal tribosphenidans is poor; among other metatherians, DP3 of the deltatheroidan *Sulestes karakshi* Nesso, 1985 (URBAC 04-149, Averianov *et al.* 2010, p. 307, fig. 2C, D), at least, departs from the pattern typical of North American marsupialiforms. More broadly, great morphological disparity among deciduous teeth of Cretaceous tribosphenidans is suggested by *Slaughteria eruptens*, regardless of how many deciduous teeth the holotype contains (contrast Winkler *et al.* 2011 with Davis 2011a). Based on their size, the upper molariforms referred to *Tirotherium aptum* Montellano-Ballesteros *et al.* 2015 are reasonably interpreted as DP3 of the two species of *Aquiladelphis* from the same fauna (Fox 1971; Davis 2007).

The principal concern with recognition of *Picopsis*-like teeth as representing upper molars is that, in our opinion, there are no plausible lower molars (which tend to be much more abundant than uppers in fossil assemblages) from any of the assemblages in which the uppers have been found. In our view, the trigonid ascribed to *Picopsis pattersoni* (UALVP 15101, Fox 1980, p. 1491, fig. 1F–J) and the lower molariforms referred to *Tirotherium aptum* (UALVP 29423, 29417, 29422, Montellano-Ballesteros and Fox 2015, p. 80, fig. 2) can be readily identified as marsupialiform dp3 by their low, poorly formed, and widely separated paraconid and metaconid; and by the strongly developed talonid, which is broader than the trigonid and which bears three distinct cusps (hypoconid, hypoconulid, and entoconid) enclosing a well-formed talonid basin. An example from the Cedar Mountain Formation is OMNH 33972 (Fig. 6F), which we provisionally refer to *Kokopellia juddi*. In most features, it is similar to dp3 of Late Cretaceous marsupialiforms such as *Alphadon eatoni* (Fig. 6E). If, as Montellano-Ballesteros and Fox (2015) propose, *Picopsis*-like teeth represent upper molars specialized for carnivory, emphasizing postvallum-prevallid shearing (see Muizon and Lange-Badré 1997), then upper molars with a reduced protocone, reduced stylocone, and hypertrophied postmetacrista should co-occur with lowers that have a strongly developed paracristid (the crest connecting paraconid to protoconid; Kielan-Jaworowska *et al.* 2004, p. 412, fig. 11.1B), with a large paraconid (compared to metaconid) and a small, narrow talonid. This is well illustrated by specimens referred to the North American deltatheroidan *Nanocuris improvida* Fox, Scott, and Bryant, 2007 (see Wilson and Riedel 2010). We know of no such lower molars from units in which *Picopsis*-like teeth have been reported.

Summing up, *Picopsis*-like upper molariforms show some differences from known marsupialiform DP3. Yet there remains ambiguity as to whether these molariforms are deciduous or permanent, and that ambiguity will remain until more informative specimens come to light (some alternative affinities, such as molariform eutherian premolars, are explored elsewhere in this volume, Davis *et al.* 2016). We regard the specimens as indeterminate, and we regard the taxa based on them (*Picopsis pattersoni* and *Tirotherium aptum*) as nomina dubia.

DISCUSSION

This paper completes alpha-level systematic treatment of mammals from the Mussentuchit Local Fauna, as based on specimens now in hand (6680 specimens cataloged to date in the OMNH collection, 1586 of which are referable to Mammalia). The mammalian assemblage includes three triconodontids, nine multituberculates, four spalacotheriid trechnotherians, and six tribosphenidans, for a total of 22 recognized taxa (Table 2). Although many species (for example, the two described herein) are poorly known, it is reasonable to conclude that the assemblage is well sampled (also see Goldberg 2000): mammalian diversity exceeds that of virtually all other Mesozoic faunas known. Of those from the Cretaceous of North America, for example, diversity easily eclipses that of the most completely-sampled Judithian assemblages (15–17 species), and rivals the best-known local faunas of Lancian age (23–33 species, data from Kielan-Jaworowska *et al.* 2004). Taxon-by-taxon comparisons to other faunas are limited by the fact that multituberculates, which are dominant elements in Cretaceous faunas of North America (*e.g.*, Clemens and Kielan-Jaworowska 1979; Kielan-Jaworowska *et al.* 2004; Wilson *et al.* 2012), have not yet been fully described from Early Cretaceous (Albian) faunas of the continent. At the genus level, two taxa are shared with Albian assemblages (the triconodontids *Astroconodon* and *Corviconodon*, Cifelli *et al.* 1998; Cifelli and Madsen 1998) and seven (the multituberculates *Mesodma*, *Bryceomys*, *Cedaromys*, and *cf. Paracimexomys*; the basal trechnothere

Table 2. Mammals of the Mussentuchit Local Fauna. Unidentified taxa are included where they appear to represent unnamed species.

Eutriconodonta Kermack <i>et al.</i> , 1973
Triconodontidae Marsh, 1887
<i>Astroconodon delicatus</i> Cifelli <i>et Madsen</i> , 1998
<i>Corviconodon utahensis</i> Cifelli <i>et Madsen</i> , 1998
<i>Jugulator amplissimus</i> Cifelli <i>et Madsen</i> , 1998
Multituberculata Cope, 1884
?Plagiaulacidae Gill, 1872
Gen. <i>et sp. indet.</i>
Neoplagiaulacidae Ameghino, 1890
? <i>Mesodma</i> sp. Jepsen, 1940
Family incertae sedis
<i>Janumys erebos</i> Eaton <i>et Cifelli</i> , 2001
cf. <i>Paracimexomys perplexus</i> Eaton <i>et Cifelli</i> , 2001
<i>Dakotamys robisoni</i> (Eaton <i>et Nelson</i> , 1991)
<i>Bryceomys intermedius</i> Eaton <i>et Cifelli</i> , 2001
<i>Cedaromys bestia</i> (Eaton <i>et Nelson</i> , 1991)
<i>Cedaromys parvus</i> Eaton <i>et Cifelli</i> , 2001
<i>Ameribaatar zofiae</i> Eaton <i>et Cifelli</i> , 2001
Trechnotheria McKenna, 1975
Spalacotheriidae Marsh, 1887
<i>Spalacolestes cretulablatta</i> Cifelli <i>et Madsen</i> , 1999
<i>Spalacolestes inconcinnus</i> Cifelli <i>et Madsen</i> , 1999
<i>Spalacotheridium noblei</i> Cifelli <i>et Madsen</i> , 1999
?Spalacotheriidae Marsh, 1887
Gen. <i>et sp. indet.</i>
Tribosphenida McKenna, 1975
Family incertae sedis
<i>Dakotadens pertritus</i> sp. n.
<i>Culicolestes kielanae</i> gen. <i>et sp. n.</i>
Metatheria Huxley, 1880
?Stagodontidae Marsh, 1889
<i>Pariadens mckennai</i> Cifelli, 2004
Family incertae sedis
<i>Adelodelphys muizoni</i> Cifelli, 2004
<i>Kokopellia juddi</i> Cifelli, 1993
<i>Sinbadelphys schmidti</i> Cifelli, 2004

Spalacotheridium; the basal tribosphenidan *Dakotadens*; and the marsupialiform *Pariadens*) with younger faunas (Cifelli and Madsen 1999; Eaton and Cifelli 2001; Cifelli 2004).

At higher taxonomic levels, tribosphenidans of the Mussentuchit Local Fauna differ from Albian assemblages in being dominated by marsupialiforms. This is consistent with the pattern in younger Cretaceous faunas of North America, although the Mussentuchit assemblage lacks the remarkable morphologic and taxonomic diversity seen among marsupialiforms of the Campanian–Maastrichtian (Cifelli 2004). And, although negative evidence must be interpreted cautiously, it is worth noting that eutherians and deltatheroidans, known from both older and younger faunas in North America (Kielan-Jaworowska *et al.* 2004; Davis and Cifelli 2011; Cifelli and Davis 2015), have not been identified among tribosphenidans of the Mussentuchit Local Fauna. Lastly, molars of the two tribosphenidans described herein, *Dakotadens pertritus* and *Culicolestes kielanae*, as well as previously-described *Pariadens mckennai*, depart from the primitive pattern common among Early Cretaceous taxa (*e.g.*, the “Trinity therians”, Davis and Cifelli 2011) in being larger, with more robust construction and more rounded cusps, suggesting exploitation of different food resources. One poorly-known species from the Cloverly Formation, *Argaliatherium robustum*, is similar, suggesting that such diversification had begun by the Albian (Cifelli and Davis 2015). Numerous mammals in this size range (for present purposes, arbitrarily defined as having molars with an AP of ≥ 2.5 mm) and having robust, rounded cusps are encountered among marsupialiforms of Aquilan–Lancian faunas of North America (Kielan-Jaworowska *et al.* 2004).

Given the relatively large numbers of mammalian fossils and species recovered from the upper Cedar

Mountain Formation, tribosphenidans cannot be regarded as either abundant or diverse: the total of six recognized species (which account for only 11% of mammalian fossils identified to species level) is comparable to diversity from the more poorly sampled Albian faunas of North America (five species from the Cloverly Formation, Wyoming and Montana, and eight from the Trinity Group, Texas and Oklahoma, Cifelli and Davis 2015); and is less than typically seen among Late Cretaceous assemblages, such as the Santonian–Campanian Milk River fauna (some 14 species, Kielan-Jaworowska *et al.* 2004). A major factor at play with regard to the Mussentuchit Local Fauna involves archaic groups, the triconodontids (eutriconodontans) and spalacotheriids (basal trechnotheres). These persisted into the Santonian–Campanian, as rare occurrences of one or two species (Fox 1969, 1976; Cifelli and Madsen 1986; Eaton 2013; Eaton and Cifelli 2013). In the Mussentuchit Local Fauna, by contrast, triconodontids and spalacotheriids collectively make up almost a third (seven of 22) of mammalian species, and the spalacotheriids (which are rare in Albian faunas of North America) account for almost 40% of mammalian fossils identified to species level. These differences suggest some taphonomic or paleoecologic bias. Further data, including better sampling of younger (Turonian) faunas (currently under study by JEC) and systematic treatment of North America’s Albian multituberculates, will be required to address the issue.

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