Reappraisal of the tribosphenidan mammals from the Trinity Group (Aptian–Albian) of Texas and Oklahoma

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The Trinity therians have long been the focus of attempts to reconstruct the evolutionary history of higher mammals, especially in the context of the development of tribospheny. In this paper, we update the taxonomy of the tribosphenidan taxa known from the Trinity Group and establish with more confidence the premolar/molar count in each. Many isolated specimens can be referred to a specific tooth locus. Additional diversity is revealed within the Deltatheroida, with the description of an additional species of *Oklatheridium*; *Pappotherium* is here considered a likely metatherian based on the inferred presence of four molars, while *Holoclemensia* is a basal eutherian (the opposite of some traditional interpretations). The remainder of the genera, *Kermackia* and *Slaughteria*, cannot be allied with either of the living groups of tribosphenidan mammals using the available data. We identify strong morphological diversity within this assemblage of stem taxa, including modifications to the traditional tribosphenic occlusal pattern in *Kermackia*. Mammalian evolution at the base of the tribosphenidan radiation was complex, and this underscores the need for caution when interpreting the morphology and relationships of taxa known by incomplete material.

Key words: Tribosphenida, Metatheria, Eutheria, Deltatheroida, Trinity Group, Early Cretaceous.

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Introduction

Mammalian faunas during the Cretaceous document the rapid, global diversification of tribosphenic mammals (sensu McKenna 1975). Early Cretaceous taxa were already hinting at the considerable breadth of morphology demonstrated by Maastrichtian groups; however, the relationships of early tribosphenidans are poorly understood. This is largely due to the fragmentary and generally plesiomorphic nature of their remains—high-level taxonomic assignments are typically based on derived molar features (often absent) or dental formula from relatively complete specimens (usually unknown).

The first Early Cretaceous mammals from North America were discovered in 1949 (Zangerl and Denison 1950; Patterson 1951) from the Trinity Sands near Forestburg in north-central Texas, now regarded as a part of the Trinity Group, specifically the Antlers Formation (see Winkler et al. 1989, 1990; Davis et al. 2008 for a summary of the regional geology). Since then, small but hard-won collections have been deposited at the Field Museum in Chicago, the Shuler Museum of Paleontology at Southern Methodist University (Dallas, Texas), and the Sam Noble Oklahoma Museum of Natural History at the University of Oklahoma (Norman, Oklahoma). The most abundant mammal to date in the fauna is the triconodontid *Astroconodon denisoni* Patterson, 1951, though most of the multituberculate fossils have yet to be de-

scribed. The therian (here more appropriately referred to as tribosphenidan) material consists of isolated teeth and tooth fragments, with only a couple of more complete specimens known. Two localities in Texas, Greenwood Canyon and Butler Farm, are of particular historic importance and have yielded the vast majority of specimens, though a diverse local fauna is also known from southeastern Oklahoma (see Davis et al. 2008: table 1.2, and references therein) (Fig. 1).

Although he formally named no taxa, initial description of the Trinity mammalian fauna was made by Bryan Patterson (1956), and his work still stands as one of the most important contributions to Mesozoic paleomammalogy. Subsequent work by Bob Slaughter (1965, 1968a, b, 1969, 1971, 1981), William Turnbull (1971, 1995, 1999), and Percy Butler (1978), among others, led to the erection of eight monotypic genera of tribosphenidan mammals: *Pappotherium pattersoni* Slaughter, 1965, *Holoclemensia texana* (Slaughter, 1968b), *Kermackia texana* Slaughter, 1971, *Trinititherium slaughteri* Butler, 1978, *Slaughteria eruptens* Butler, 1978, *Comanchea hilli* Jacobs, Winkler, and Murray, 1989, *Atokatheridium boreni* Kielan-Jaworowska and Cifelli, 2001, and *Oklatheridium szalayi* Davis, Cifelli, and Kielan-Jaworowska, 2008. The age and generally primitive nature of these taxa made them a template for discussions of the evolution of higher mammals. The "eupantotherians" that dominated the well sampled Late Jurassic Morrison Formation and the earliest Cretaceous Purbeck Group were generally thought to hold the
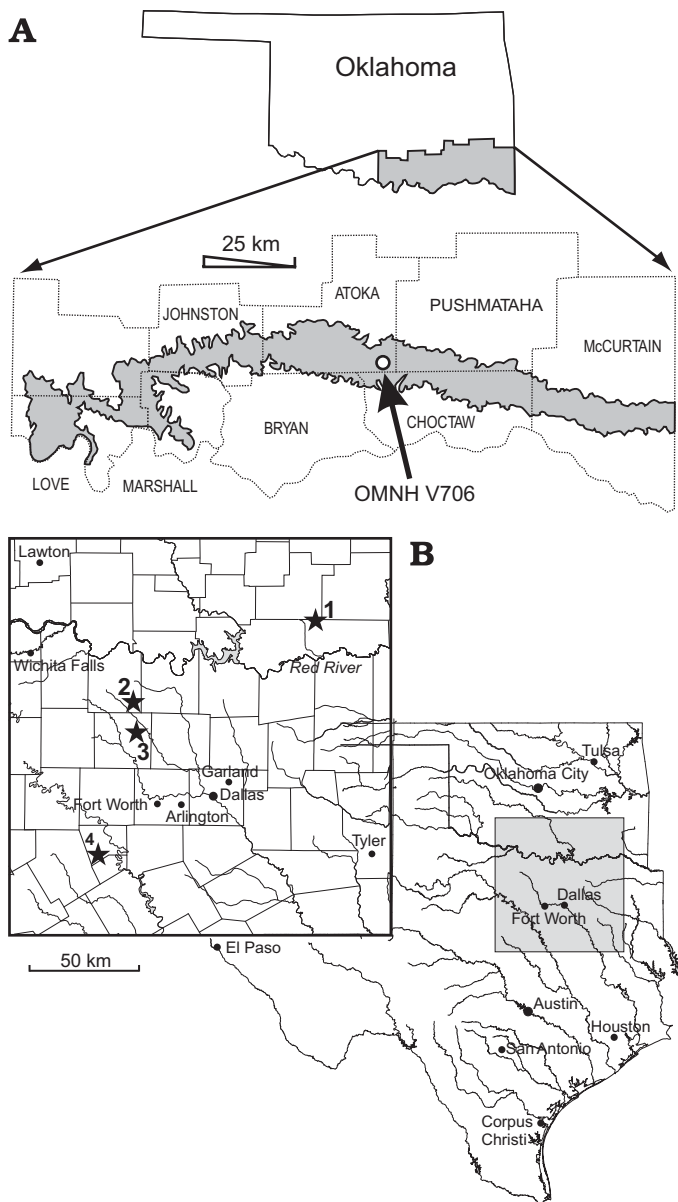
Fig. 1. Early Cretaceous mammal localities, Trinity Group, Texas and Oklahoma. **A**. Map detailing outcrop of Antlers Formation (shaded) in southeastern Oklahoma. McLeod Honor Farm (OMNH microvertebrate locality V706) indicated by open circle. **B**. Map detailing mammal-bearing microvertebrate localities from the Trinity Group (Aptian–Albian): 1, McLeod Honor Farm; 2, Greenwood Canyon; 3, Butler Farm (all Antlers Formation); 4, Paluxy Church (Twin Mountains Formation, late Aptian). From Davis et al. (2008).

origin of tribosphenic mammals; metatherians and eutherians were abundant and diverse in the Late Cretaceous Lance and Hell Creek formations, temporally and morphologically bracketing the Aptian–Albian Trinity Group taxa. Breakthroughs that would define and influence all later work on fossil mammals were made with reference to these taxa as transitional—Patterson's (1956) concepts of molar cusp homology and Crompton's (1971) functional model of tribosphenic evolution are two examples.

Attempts were also made to recognize the Metatheria-Eutheria divergence within or just prior to the Trinity Group fauna. *Holoclemensia* was initially described as a metatherian (Slaughter 1968b), and has been subsequently retained at the base of that clade in reference to similarities with later taxa such as *Alphadon* (see Discussion). *Pappotherium* was referred early on to the Eutheria (Van Valen 1967), and the presence of semi-molariform premolars in the sample was also cited as evidence documenting the presence of eutherians in the Trinity fauna (Slaughter 1968a, 1971). Later finds in Asia would claim an earlier divergence of these groups (in the Barremian; Ji et al. 2002; Luo et al. 2003), and it would become clear that other taxa of a similar evolutionary grade to those from the Trinity Group would persist into the Late Cretaceous (at least in North America; e.g., Fox 1972, 1980; Cifelli 1994). The historical discussions of the tribosphenidans from the Trinity Group, put into a modern context by more recent fossil discoveries, provide a framework for the revision we present below.

Institutional abbreviations.—FMNH and PM, Field Museum of Natural History, Chicago, USA; OMNH, Sam Noble Oklahoma Museum of Natural History, Norman, USA; SMP-SMU, Shuler Museum of Paleontology, Southern Methodist University, Dallas, USA.

Other abbreviations.—ANW, anterior (mesial) width; AP, anteroposterior (mesiodistal) length; POW, posterior (distal) width.

Material and methods

We have included material from the entire known sample of tribosphenidan mammals from the Trinity Group of Texas and Oklahoma, housed in the FMNH, OMNH, and SMP-SMU. PM specimens are from Greenwood Canyon (north-central Texas), SMP-SMU specimens are from Butler Farm (north-central Texas), and OMNH specimens are from Tomato Hill (southeastern Oklahoma). The material consists almost entirely of isolated teeth—though some dentigerous fragments are known, they preserve very limited portions of the dentition, making referral of many isolated specimens difficult. Consequently, the portion of the sample treated herein is restricted to molars, as well as any ultimate premolars which are modified in such a way to make them uniquely identifiable. Scanning electron micrographs of specimens were obtained at the OMNH; some specimens were imaged using a Keyence Digital Microscope VHX1000E at the SMP-SMU. Measurements (in millimeters) for all specimens are provided in Tables 1–9; some measurements were taken from photographs, while all others were taken with a Reflex Microscope (Consultantnet Ltd, 8A The Grip, Linton, Cambridge, CB21 4NR, UK), as defined by Lillegraven and Bieber (1986).
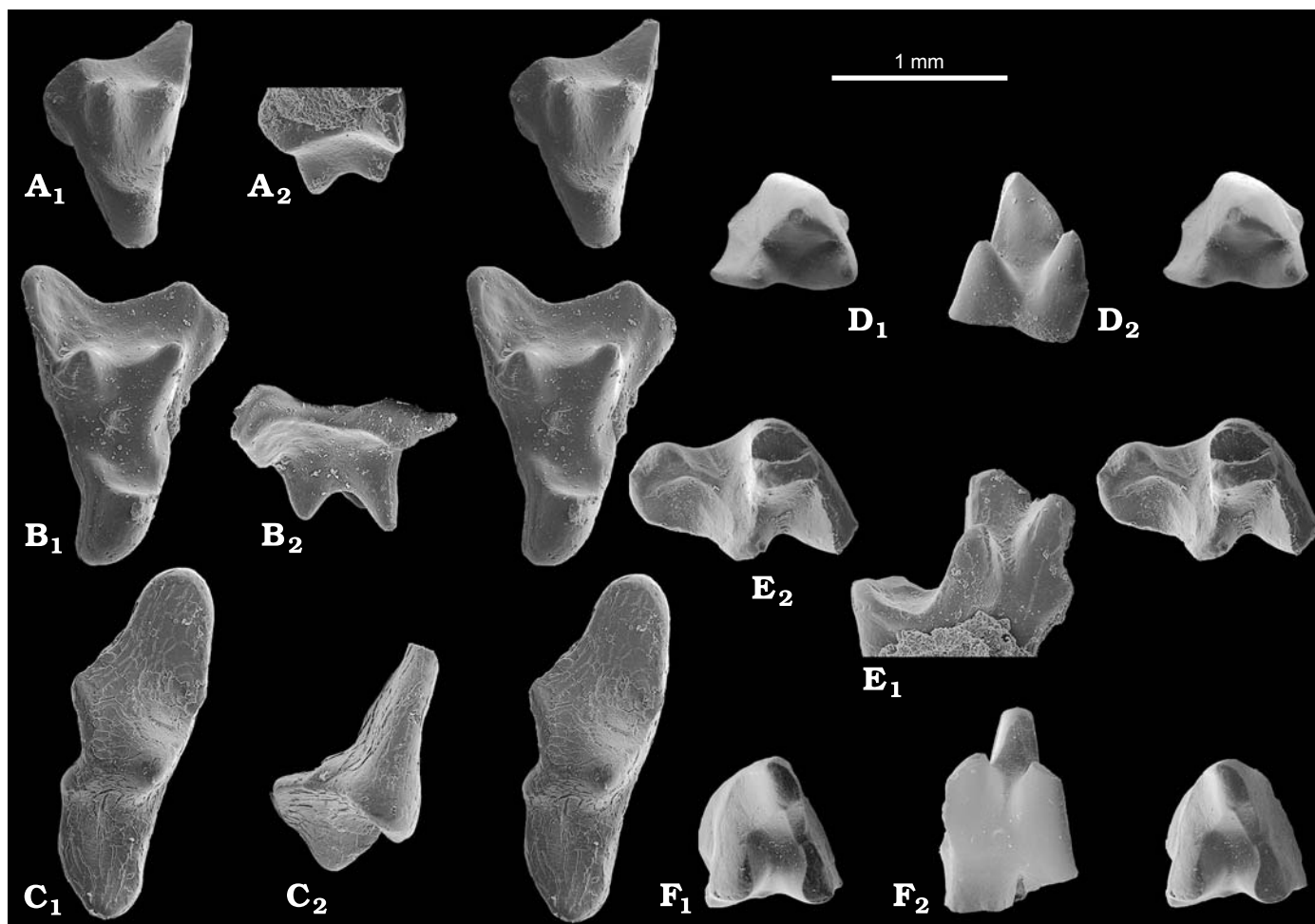
Fig. 2. The deltatheroidan *Atokatheridium boreni* Kielan-Jaworowska and Cifelli, 2001 from the Early Cretaceous of Oklahoma. **A**. OMNH 61151, LM1 in occlusal (A_1) and buccal (A_2) views. **B**. OMNH 61623, RM2 (holotype) in occlusal (B_1) and buccal (B_2) views. **C**. OMNH 63725, LM3 in occlusal (C_1) and buccal (C_2) views. **D**. OMNH 63724, Lm1 in occlusal (D_1) and lingual (D_2) views. **E**. OMNH 61624, Lmx in occlusal (E_1) and lingual (E_2) views. **F**. OMNH 63891, Rmx in occlusal (F_1) and lingual (F_2) views.

Systematic paleontology

Subclass Tribosphenida McKenna, 1975

Infraclass Metatheria Huxley, 1880

Cohort Deltatheroida Kielan-Jaworowska, 1982

Family Deltatheridiidae Gregory and Simpson, 1926

Genus *Atokatheridium* Kielan-Jaworowska and Cifelli, 2001

Type species: *Atokatheridium boreni* Kielan-Jaworowska and Cifelli, 2001, Tomato Hill (OMNH V706), middle Antlers Formation (Aptian–Albian).

Atokatheridium boreni Kielan-Jaworowska and Cifelli, 2001

Fig. 2, Table 1.

Holotype: OMNH 61623, RM2.

Type locality: Tomato Hill (OMNH V706), southeastern Oklahoma, USA.

Type horizon: Middle Antlers Formation (Aptian–Albian).

Referred material.—OMNH 61151, LM1; 63725, LM3; 63724, Lm1; 63889, Rm1; 63890, Rm1; 34905, Rmx; 61181, Lmx; 61624, Lmx; 63891, Rmx; 63892, Lmx (all from the type locality).

Emended diagnosis.—Small deltatheroidan differing from all other deltatheroidans in smaller size, weaker stylocone, shallower ectoflexus on mesial molars, slightly narrower parastylar lobe, trend of increasing width of metastylar lobe distally through molar series (excluding the unknown but hypothesized M4), greater height differential between the paracone and metacone, transversely wider protoconal region, and a taller protocone. Differs from *Oklatheridium* and *Sulestes* in weaker conules. Differs from *Oklatheridium* in slightly narrower metastylar lobe on M2, and in less reduction of the metastylar lobe on M3.

Description

Detailed descriptions of the molars of *Atokatheridium boreni* can be found in Davis et al. (2008), and will not be repeated here (with the exception of lower molars which can be re-

Table 1. Measurements (in mm) of the deltatheroidan *Atokatheridium boreni* Kielan-Jaworowska and Cifelli, 2001 from the Early Cretaceous of Oklahoma. Abbreviations: AP, anteroposterior (mesiodistal) length; ANW, anterior (mesial) width; POW, posterior (distal) width.

Locus	Specimen number	AP	ANW	POW
M1	OMNH 61151	0.97	1.10	1.36
M2	OMNH 61623	1.35	1.62	1.75
M3	OMNH 63725	–	–	2.03
m1	OMNH 63724	–	0.63	–
	OMNH 63889	–	0.73	–
	OMNH 63890	–	0.56	–
mx	OMNH 34905	–	0.71	–
	OMNH 61181	–	0.80	–
	OMNH 61624	1.32	0.81	0.50
	OMNH 63891	–	0.82	–
	OMNH 63892	–	0.69	–

ferred with confidence to the first molar locus, described below). However, the morphology is summarized to facilitate comparisons between the various tribosphenidan taxa described in this paper.

Upper molars: The three referred upper molars of *Atokatheridium boreni* (Fig. 2A–C) are all to a greater or lesser extent abraded, so some morphological details may be lost or understated. The molars are transversely wide, with a wide stylar shelf (especially the metastylar lobe of the M3). The paracone is larger and taller than the metacone, and the postmetacrista is strong and deeply-notched at the base of the metacone as in other deltatheroidans. The stylocone is well developed but not as large as in *Oklatheridium* or *Pappotherium*. The preparacrista is weak, but this could be a factor of preservation. The protoconal region of the crown is mesiodistally compressed and wide. The conules are distinct but weak, and there is faint evidence of an internal crista on the paraconule. The preprotocrista extends to the parastyle, but the postprotocrista ends at the base of the metacone.

Lower molars: *A. boreni* is known by a single complete but abraded isolated lower molar and several fragmentary molars preserving only the trigonid (Fig. 2E). Given the poor preservation of the sample, it is not possible to confidently identify most specimens to locus. OMNH 61624 has a very tall trigonid relative to the small talonid, and a very prominent, projecting paraconid that is much taller than the metaconid. These features suggest that this specimen might represent the m4, but there are some substantial differences between it and preserved m4s of other deltatheroidans. In *Deltatheridium* and *Sulestes*, the trigonid is extremely obtuse-angled, and in the former the metaconid is completely absent (Rougier et al. 1998; Averianov et al. 2010). While the low, small talonid in *A. boreni* is open lingually and lacks an entoconid (comparing in some ways favorably with the basal tribosphenidan *Kielantherium*; Dashzeveg and Kielan-Jaworowska 1984), the trigonid has a high, wall-like paracristid, reinforcing deltatheroidan affinities for this taxon. A strong distal metacristid is present. The remainder of the re-

ferred lower molars (with the exception of those identified as m1s, see below) generally agree with OMNH 61624 in morphology, though they are all either too heavily worn or poorly preserved to add anything new.

OMNH 63724 (Fig. 2D) is identified as an m1 on the basis of a somewhat more open trigonid and on relative cusp heights. Only the trigonid is preserved, and it is transversely compressed and lingually open relative to the other referred lower molars. The paraconid is slightly taller than but not as robust as the metaconid; the paraconid is not inclined, as would be expected if the specimen were a deciduous premolar. A distal metacristid is present. The paracristid is strong and notched, and this specimen can be excluded from the other deltatheroidan in the fauna, *Oklatheridium*, based on size. The relative size and proportions of this specimen in reference to the rest of the referred sample agree well with the distal trend in morphology of the molar series seen in *Deltatheridium* (Rougier et al. 1998), and it is on this basis that it is excluded from the other tribosphenidans of the Trinity Group.

Comments.—*Atokatheridium* was referred with confidence to the Deltatheroida by Davis et al. (2008) based on the combination of a strong upper molar postmetacrista on all upper molar loci and a tall lower molar paraconid (well-developed postvallum/prevallid shear, which is typical of all deltatheroidans). Averianov et al. (2010: 318) disputed the deltatheroidan nature of this taxon, claiming that the referral "...was heavily influenced by interpretation of a relatively large incomplete [M3]..." and concluding that *Atokatheridium* was a stem tribosphenidan. Justification for the referral of OMNH 63725 to *Atokatheridium* (not *Oklatheridium* as suggested by Averianov et al. 2010) and of the taxon to the Deltatheroida was given in detail by Davis et al. (2008: 13: fig. 1.8), and draws from both upper and lower molar morphology at all known loci. Other recent work on the group (e.g., Rougier et al. 2004) has supported this position, and we feel no further validation is necessary.

Stratigraphic and geographic range.—Middle Antlers Formation (Aptian–Albian), southeastern Oklahoma, USA.

Genus *Oklatheridium* Davis, Cifelli, and Kielan-Jaworowska, 2008

Type species: *Oklatheridium szalayi* Davis, Cifelli, and Kielan-Jaworowska, 2008, Tomato Hill (OMNH V706), middle Antlers Formation (Aptian–Albian).

Included species: *Oklatheridium minax* sp. nov.

Emended diagnosis.—Moderate-sized deltatheroidan differing from all other deltatheroidans in relatively larger talonid; differs from all other deltatheroidans except *Atokatheridium* in narrower stylar shelf; differs from other deltatheroidans except *Sulestes* in less height differential between paracone and metacone, metacone broader than paracone, prominent conules, mesiodistally broad protocone, and presence of entoconid; differs from *Atokatheridium* in larger size, larger stylocone, and relatively larger metaconid; differs from

Sulestes in wider protoconal region; differs from *Deltatheroides* in stronger reduction of metacone and metastylar lobe on M4.

Oklatheridium szalayi Davis, Cifelli, and Kielan-Jaworowska, 2008

Fig. 3A–E, Table 2.

Holotype: OMNH 62410, LM2 missing the protoconal region of the crown.

Type locality: Tomato Hill (OMNH V706), southeastern Oklahoma, USA.

Type horizon: Middle Antlers Formation (Aptian–Albian).

Referred material.—OMNH 62411, LM1 (missing the protocone); PM 1238, LM1 (missing the protoconal region); OMNH 61180, LM1 (missing the protoconal region); OMNH 63986, RM3 (missing the metastylar lobe and protoconal region).

Emended diagnosis.—Species of *Oklatheridium* differing from *O. minax* in smaller size, relatively smaller stylocone, and greater relative size difference between M1 and M2.

Description

Detailed descriptions of the molars of *Oklatheridium szalayi* can be found in Davis et al. (2008), and will not be repeated here. However, the identification of a second species of *Oklatheridium* based on upper molars (*O. minax* sp. nov.) has led to the removal of all lower molars from the hypodigm of *O. szalayi*. These specimens are here referred to *Oklatheridium* sp. (see below). The upper molar morphology of *O. szalayi* is summarized to facilitate comparisons between the various tribosphenidan taxa described in this paper.

Upper molars: The upper molars of *O. szalayi* are in many ways similar to those of *Pappotherium*, and are distinguished primarily by relative proportions of the paracone and metacone. In both species of *Oklatheridium*, there is less height differential between these cusps than in *Pappotherium*, and the metacone is slightly broader than the paracone (the opposite is true in *Pappotherium*). The parastylar lobe increases substantially in width between the M1 and the M3, and the parastyle is prominent. The metastylar lobe is long
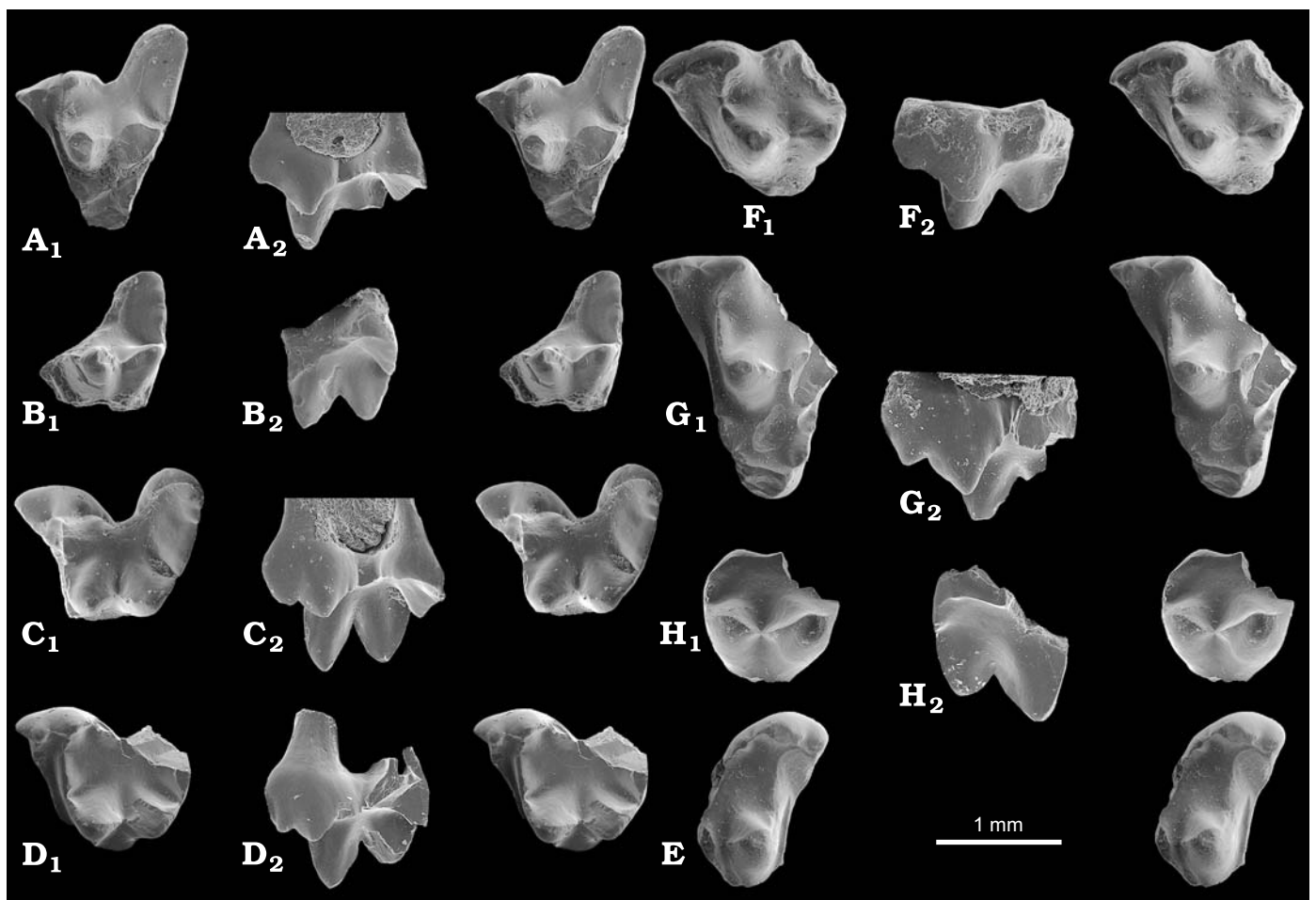

Fig. 3. The deltatheroidans *Oklatheridium szalayi* Davis, Cifelli, and Kielan-Jaworowska, 2008 (**A–E**) and *O. minax* sp. nov. (**F–H**) from the Early Cretaceous of Oklahoma and Texas. **A**. OMNH 62411, LM1 in occlusal (A_1) and buccal (A_2) views. **B**. PM 1238, LM1 in occlusal (B_1) and buccal (B_2) views. **C**. OMNH 62410, LM2 (holotype) in occlusal (C_1) and buccal (C_2) views. **D**. OMNH 61180, LM2 in occlusal (D_1) and buccal (D_2) views. **E**. OMNH 63986, RM3 in occlusal (E_1) and buccal (E_2) views. **F**. PM 884, LM1 in occlusal (F_1) and buccal (F_2) views. **G**. OMNH 33455, LM2 (holotype) in occlusal (G_1) and buccal (G_2) views. **H**. OMNH 63727, RM3 in occlusal (H_1) and buccal (H_2) views.

Table 2. Measurements (in mm) of the deltatheroidan *Oklatheridium szalayi* Davis, Cifelli, and Kielan-Jaworowska, 2008 from the Early Cretaceous of Oklahoma and Texas. Numbers in brackets indicate estimates. Abbreviations: AP, anteroposterior (mesiodistal) length; ANW, anterior (mesial) width; POW, posterior (distal) width.

Locus	Specimen number	AP	ANW	POW
M1	OMNH 62411	1.27	1.4	1.76
	PM 1238	[1.12]	–	–
M2	OMNH 61180	1.45	–	–
	OMNH 62410	1.51	–	–
M3	OMNH 63986	[1.45]	–	–

and bears a very strong, notched postmetacrista. There is some variation in the depth of the ectoflexus, but it is quite deep on the holotype (similar to that seen in the M2 of *Deltatheridium*). The stylocone is the only stylar cusp (typical of deltatheroidans, despite the variable presence of cuspules or crenulations in *Sulestes*; see Averianov et al. 2010), but there is a small cuspule present immediately distal to the stylocone on one M2 (OMNH 61180) and the referred M3 (OMNH 63986).

The M3 originally referred to *O. szalayi* by Davis et al. (2008), OMNH 63727, appears to belong instead to *O. minax* sp. nov. (see below). A different specimen, OMNH 63986 (Fig. 3E), is a better match for M3 of *O. szalayi*, in terms of size. This molar is fragmentary, preserving only the paracone, parastylar lobe, and the mesial base of the metacone. The stylocone is large and well separated from the paracone; the parastylar lobe is much wider than any specimen referred to *Pappotherium* (see below). There is a prominent cuspule along the ectocingulum immediately distal to the stylocone, and the ectocingulum appears to have been strong, as in other specimens of this taxon.

Comments.—The presence of *Oklatheridium* in the Greenwood Canyon sample, a taxon otherwise only known from Tomato Hill, was originally suggested by Alexander Averianov (personal communication to BMD, 2007) in reference to PM 1238, a LM1 originally referred to *Pappotherium* by Butler (1978).

Stratigraphic and geographic range.—Greenwood Canyon (Triconodont Gully), upper Antlers Formation (Aptian–Albian), north-central Texas, USA; Tomato Hill (OMNH V706), middle Antlers Formation (Aptian–Albian), southeastern Oklahoma, USA.

Oklatheridium minax sp. nov.

1997 Tribosphenida indet.; Cifelli 1997: fig. 3
2008 ?*Oklatheridium* sp.; Davis, Cifelli, and Kielan-Jaworowska 2008: fig. 1.3

Fig. 3F–H, Table 3.

Etymology: From the Latin for "threatening", in reference to the strongly-developed shearing crests in this taxon, and its larger size compared to the other deltatheroidans of the Trinity Group.

Holotype: OMNH 33455, LM2 missing the metacone and metastylar lobe.

Type locality: Tomato Hill (OMNH V706), southeastern Oklahoma, USA.

Type horizon: Middle Antlers Formation (Aptian–Albian).

Referred material.—PM 884, LM1 (missing the protoconal region); OMNH 63727, RM3 (missing the parastylar lobe and protoconal region).

Diagnosis.—Species of *Oklatheridium* differing from *O. szalayi* in overall larger size, relatively heavier stylocone, and in less relative size difference between M1 and M2.

Description

Upper molars: PM 884 (Fig. 3F) is a large, somewhat abraded molar with a very heavy stylocone. The relatively narrow parastylar lobe and shallow ectoflexus indicate this to be an M1. The metacone is lower and broader than the paracone, features consistent with *Oklatheridium*. The paracone and stylocone are connected by a strongly notched preparacrista. The parastyle is large and positioned slightly lingual to the stylocone. While this molar is substantially larger than the M1 referred to *O. szalayi* (Table 2), it is still smaller than the M2 of *O. minax* and is therefore referred to that species.

OMNH 33455 (Fig. 3G) was initially described by Cifelli (1997: 10), and referred to ?*Oklatheridium* sp. by Davis et al. (2008). Comparisons with the proportions of the M2 of *O. szalayi* suggest that this specimen represents the M2 (as proposed by Davis et al. 2008). The stylocone is very large and separated from the parastyle by a strong notch. The protoconal region is broad, bearing large conules. The paraconule is more buccally positioned than the metaconule, and there is no evidence of internal cristae. The paracone is mostly broken, but it appears to have been much heavier than in all other deltatheroidans.

The M3 of *O. minax*, OMNH 63727 (Fig. 3H), was originally referred to *O. szalayi* by Davis et al. (2008). However, it appears to be too large for that species (as is evident from comparisons between the M2 and M3 of the morphologically similar *Deltatheridium*; see Davis et al. 2008: fig. 1.8). The parastylar lobe of this specimen is broken but the remaining portion suggests that it would likely have been very wide; the metastylar lobe is reduced in width but still retains a prominent shelf. The metacone is much lower than the paracone but is only slightly shorter mesiodistally. The centrocrista is formed by very sharp crests. The pattern of breakage suggests that the protoconal region would have been large, comparable to but slightly smaller than that in OMNH 33455 (see hypothetical restoration in Davis et al. 2008: fig. 1.8).

Table 3. Measurements (in mm) of the deltatheroidan *Oklatheridium minax* sp. nov. from the Early Cretaceous of Oklahoma and Texas. Numbers in brackets indicate estimates. Abbreviations: AP, anteroposterior (mesiodistal) length; ANW, anterior (mesial) width; POW, posterior (distal) width.

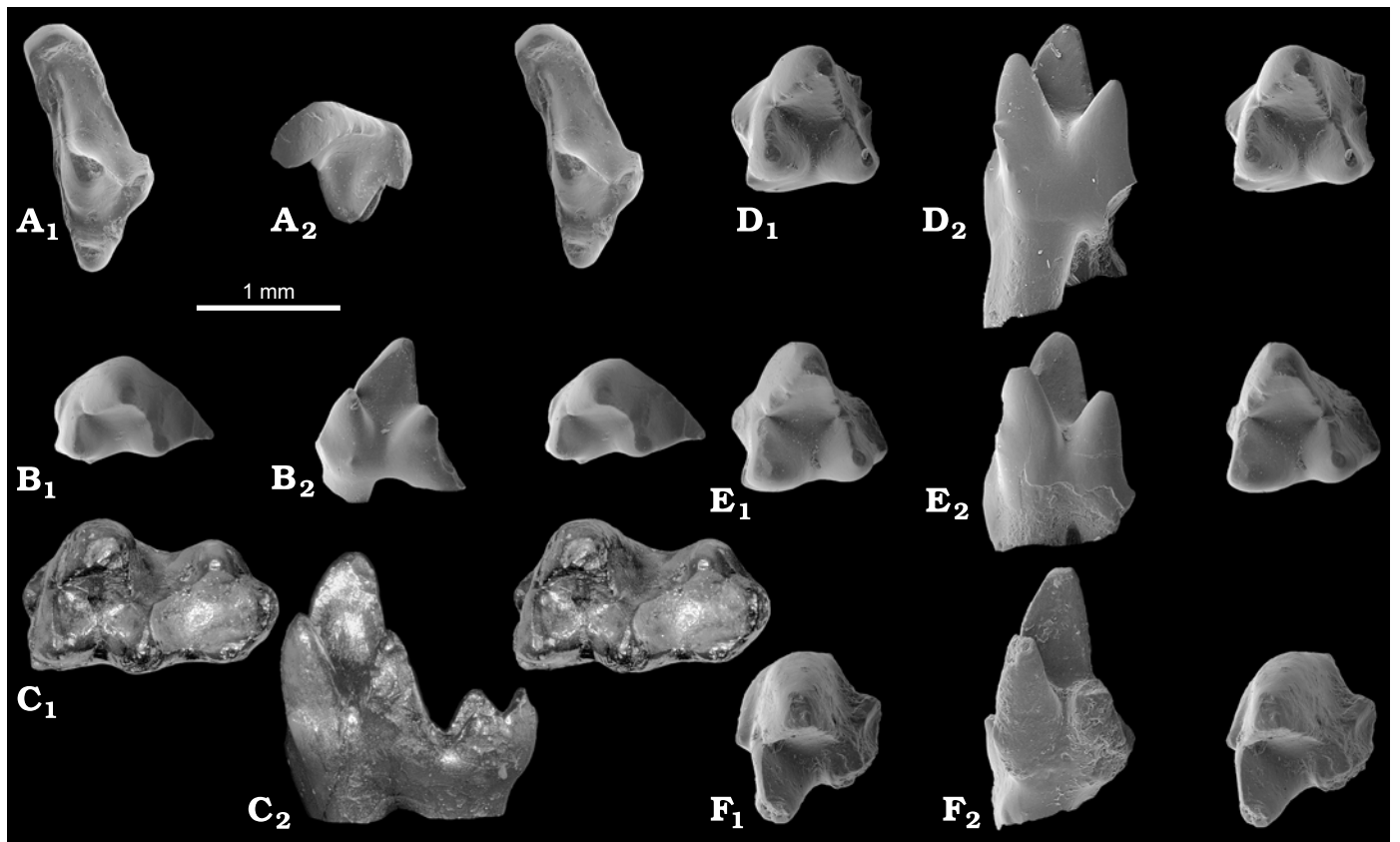| Locus	Specimen number	AP	ANW	POW
M1	PM 884	[1.63]	–	–
M2	OMNH 33455	[1.68]	–	–
M3	OMNH 63727	[1.33]	–	–

Fig. 4. Molars referred to the deltatheroidan *Oklatheridium* sp. from the Early Cretaceous of Oklahoma and Texas. **A**. PM 1287, LM4 in occlusal (A_1) and buccal (A_2) views. **B**. OMNH 61642, Rm1 in occlusal (B_1) and lingual (B_2) views. **C**. PM 965, Rmx in occlusal (C_1) and lingual (C_2) views. **D**. OMNH 33940, Rmx in occlusal (D_1) and lingual (D_2) views. **E**. OMNH 61643, Rmx in occlusal (E_1) and lingual (E_2) views. **F**. PM 660, Rmx in occlusal (F_1) and lingual (F_2) views.

Stratigraphic and geographic range.—Greenwood Canyon (Triconodont Gully), upper Antlers Formation (Aptian–Albian), north-central Texas, USA; Tomato Hill (OMNH V706), middle Antlers Formation (Aptian–Albian), southeastern Oklahoma, USA.

Oklatheridium sp.
Fig. 4, Table 4.

Referred material.—PM 1287, LM4; OMNH 61642, Rm1 (trigonid only); OMNH 33940, Rmx (trigonid only); OMNH 33945, Lmx (trigonid only); OMNH 61643, Rmx (trigonid only); OMNH 63728, Rmx (trigonid only); PM 660, Rmx (trigonid only); PM 965, Rmx.

Description

Upper molar: PM 1287 was originally illustrated in Patterson (1956: fig. 4B; Fig. 4A). This specimen was referred to *Pappotherium* sp. by Turnbull (1971), though Butler (1978) did not believe it could belong to either that genus or *Holoclemensia*, and must represent the ultimate molar of something different. In their interpretation of the molar series of the Tomato Hill deltatheroidans, Davis et al. (2008: fig. 1.8) speculated that the M4 of *Oklatheridium* would be heavily reduced, much like the condition in the larger but morpho-

logically similar *Deltatheridium*. PM 1287 retains a large paracone, stylocone, and preparacrista (characters of the mesial molars of *Oklatheridium*), while the metacone and metastylar lobe are strongly reduced (a trend beginning with the M3; Fig. 3E, H). Such strong reductions in ultimate molar proportions are not expected in Early Cretaceous lineages other than deltatheroidans. The ultimate molar of the other deltatheroidan in the sample, *Atokatheridium* (hypothesized

Table 4. Measurements (in mm) of specimens referred to the deltatheroidan *Oklatheridium* sp. from the Early Cretaceous of Oklahoma and Texas. Abbreviations: AP, anteroposterior (mesiodistal) length; ANW, anterior (mesial) width; POW, posterior (distal) width.

Locus	Specimen number	AP	ANW	POW
M4	PM 1287	1.15	1.56	0.91
m1	OMNH 61642	–	0.71	–
mx	OMNH 33940	–	1.04	–
	OMNH 33945	–	0.99	–
	OMNH 61643	–	1.05	–
	OMNH 63728	–	0.98	–
	OMNH 63730	–	1.03	–
	OMNH 66771	–	0.94	–
	PM 660	–	1.07	–
	PM 965	1.77	1.08	0.86

by Davis et al. 2008: fig. 1.8), probably would bear a proportionately larger protocone. This is the basis for referral of this specimen to *Oklatheridium*; however, the absence of a more completely preserved molar series precludes specific assignment of this M4 within the genus.

Lower molars: Davis et al. (2008) referred a number of lower molars (all represented by trigonids) to *Oklatheridium szalayi*. However, the recognition of a second species of *Oklatheridium* necessitates reconsideration of all lower molar material. The fragmentary nature of these specimens (with the exception of PM 965, described below) makes it difficult to differentiate between size and morphological differences that are attributable to positional variation, and differences which relate to interspecific variation. A conservative approach is warranted, and all lower molars are here referred to *Oklatheridium* sp.

One specimen is complete (PM 965; Fig. 4C) and allows the talonid morphology of this genus to be described. This molar bears a very large and prominent paraconid, with a tall, deeply notched paracristid. The metaconid is much lower than the paraconid. In occlusal view, the trigonid cusps form a roughly equilateral triangle. Cusp f is prominent but not shelf-like, and is positioned below the paracristid notch. A very small cusp e is located slightly higher but at the mesiolingual margin of the paraconid. A distinct distal metacristid is present, meeting the cristid obliqua at its mesial terminus below the protocristid notch. The highly developed prevallid shear evidenced by this specimen clearly points to deltatheroidan affinities, and it shares much of its trigonid morphology with the other specimens referred to *Oklatheridium*. However, the most striking feature of this molar is the size of the talonid. While smaller in area than the trigonid, it is still substantially larger, in a relative sense, than in all other known deltatheroidans. The hypoconid is the largest cusp, and is conical except for a flat internal face. The hypoconulid is as tall as the hypoconid, but is elongate and somewhat ridge-like. The hypocristid between these cusps is long enough to have accommodated a relatively large metacone, which also supports referral of this specimen to *Oklatheridium*. The entoconid is lower than the other cusps but is still very prominent and broad, and the entocristid is notched. The talonid basin is well enclosed and deep, and the three cusps are evenly spaced. In all, the talonid is not as predicted by Davis et al. (2008) for *Oklatheridium*, especially in that it is much larger than the preserved talonid in *Atokatheridium* (Fig. 2E). The pattern of breakage on other trigonids referred to *Oklatheridium* does not preclude this sort of talonid morphology, and PM 965 is on the large end of the size range for the sample, which suggests it may represent *O. minax*. This species has a much larger protoconal region than other deltatheroidans, which should reflect an accompanying large talonid.

Of the remainder of the sample, only the trigonid of an m1 is readily identifiable. OMNH 61642 (Fig. 4B) is markedly different from OMNH 33945, incorrectly identified as an m1 by Davis et al. (2008), in being lower crowned, much narrower transversely, and in having widely spaced paraconid

and metaconid. It is proportionally very similar to the m1 of *Atokatheridium*, differing only in larger size and a somewhat proportionally larger paraconid.

Stratigraphic and geographic range.—Greenwood Canyon (Triconodont Gully), upper Antlers Formation (Aptian–Albian), north-central Texas, USA; Tomato Hill (OMNH V706), middle Antlers Formation (Aptian–Albian), southeastern Oklahoma, USA.

Infraclass ?Metatheria Huxley, 1880

Family Pappotheriidae Slaughter, 1965

Genus *Pappotherium* Slaughter, 1965

Type species: *Pappotherium pattersoni* Slaughter, 1965, Butler Farm, upper Antlers Formation (Aptian–Albian).

Pappotherium pattersoni Slaughter, 1965

Fig. 5, Table 5.

Holotype: SMP-SMU 71725, a right maxillary fragment preserving the M3 and M4.

Type locality: Butler Farm, north-central Texas, USA.

Type horizon: Upper Antlers Formation (Aptian–Albian).

Referred material.—PM 999, RM1 (missing protoconal region); PM 1749, LM2 (missing metastylar lobe and protoconal region); PM 1325, LM2 (protoconal region only); OMNH 61185, RM3 (missing metastylar lobe); PM 1015, LM3 (missing metastylar lobe and protoconal region); OMNH 61219, Lmx (trigonid only); OMNH 63729, Rmx (trigonid only); PM 930, Rmx (trigonid only); PM 1119, Rmx (trigonid only); PM 1249, Lmx (trigonid only).

Emended diagnosis.—Putative metatherian differing from other basal metatherians (such as *Kokopellia*) in lack of twinning between hypoconid and hypoconulid, absence of buccal postcingulid, and presence of distal metacristid on lower molars; differs from deltatheroidans in subequal paraconid and metaconid on lower molars; differs from *Holoclemensia* in inferred presence of four molars, larger

Table 5. Measurements (in mm) of the tribosphenidan *Pappotherium pattersoni* Slaughter, 1965 from the Early Cretaceous of Oklahoma and Texas. Numbers in brackets indicate estimates. Abbreviations: AP, anteroposterior (mesiodistal) length; ANW, anterior (mesial) width; POW, posterior (distal) width.

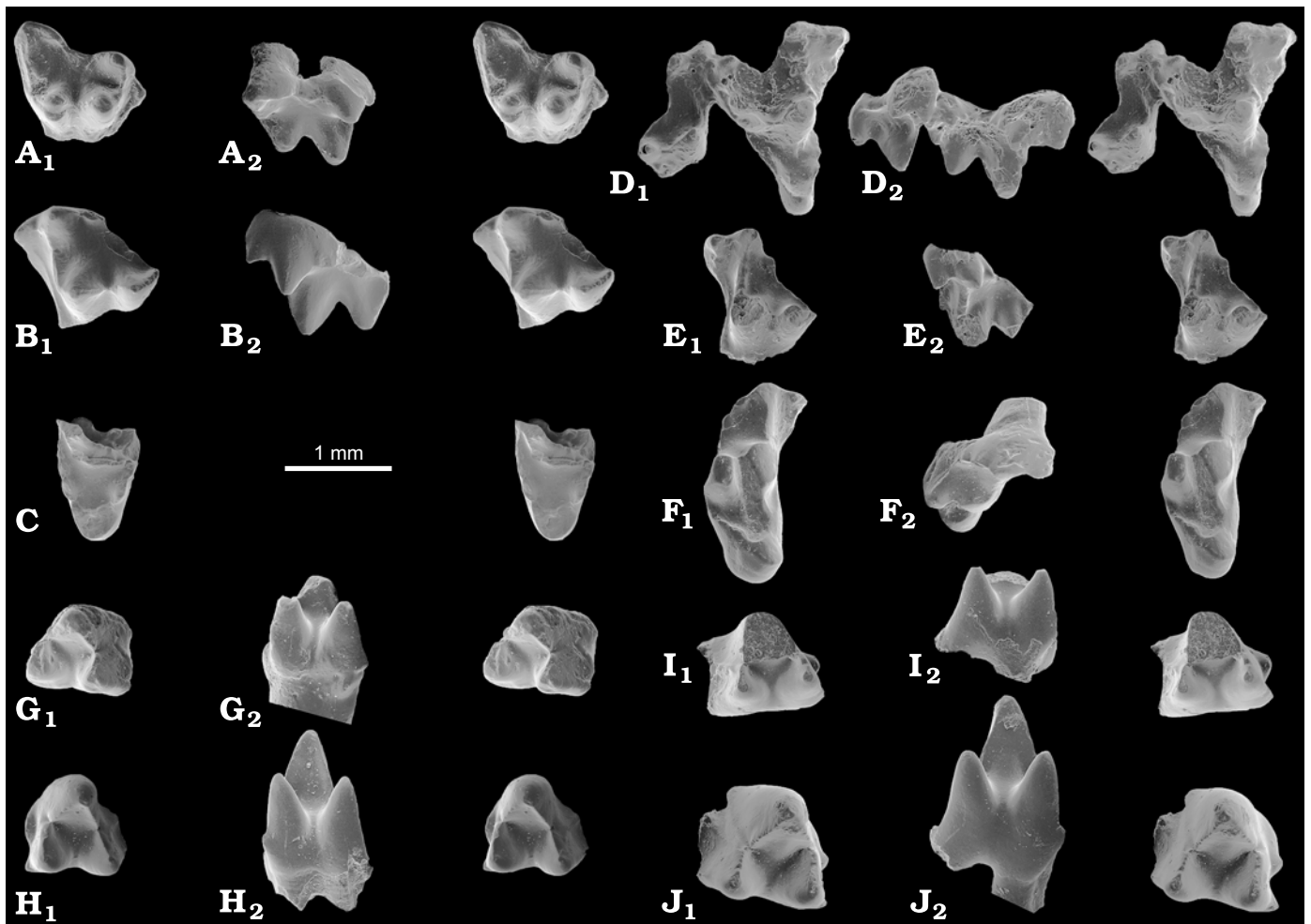| Locus	Specimen number	AP	ANW	POW
M1	PM 999	1.26	–	–
M2	PM 1749	[1.49]	–	–
M3	OMNH 61185	[1.43]	1.89	–
	PM 1015	[1.25]	–	–
	SMP-SMU 61725	1.38	1.84	1.66
M4	SMP-SMU 61725	0.86	–	–
mx	OMNH 61219	–	1.16	–
	OMNH 63729	–	1.00	–
	PM 930	–	0.90	–
	PM 1119	–	0.92	–
	PM 1249	–	0.95	–

Fig. 5. The metatherian *Pappotherium pattersoni* Slaughter, 1965 from the Early Cretaceous of Oklahoma and Texas. **A**. PM 999, RM1 in occlusal (A_1) and buccal (A_2) views. **B**. PM 1749, LM2 in occlusal (B_1) and buccal (B_2) views. **C**. PM 1325, LM2 in occlusal view. **D**. SMP-SMU 61725, right maxillary fragment with M3 and M4 (holotype) in occlusal (D_1) and buccal (D_2) views. **E**. PM 1015, LM3 in occlusal (E_1) and buccal (E_2) views. **F**. OMNH 61185, RM3 in occlusal (F_1) and buccal (F_2) views. **G**. PM 930, Rmx in occlusal (G_1) and lingual (G_2) views. **H**. OMNH 63729, Rmx in occlusal (H_1) and lingual (H_2) views. **I**. PM 1249, Lmx in occlusal (I_1) and lingual (I_2) views. **J**. OMNH 61219, Lmx in occlusal (J_1) and lingual (J_2) views.

stylocone, absence of mesostyle, deeper ectoflexus, closer approximation of paracone and metacone, mesiodistally longer trigonid, subequal paraconid and metaconid, and presence of distal metacristid; differs from *Slaughteria* in larger size, inferred presence of four molars, and weaker paracristid.

Description

Upper molars: The M1 of *Pappotherium pattersoni* is represented by a single worn and broken specimen (PM 999; Fig. 5A). The width of the parastylar lobe and the position of the parastyle support the locus assignment of this molar. The paracone is much taller and slightly broader than the metacone. The paracone is closely approximated with and connected to the large stylocone by a strong and slightly notched preparacrista. The parastyle is low and situated between the other two cusps. Though the metastylar lobe is wide, the ectoflexus is shallow. There is a weak ectocingulum but no evidence of any other stylar cusps. The postmetacrista is strong and notched, but less so than in deltatheroidans. The

crown is broken lingual to the paracone and metacone. The preprotocrista is wide and continuous to the parastyle, but the postprotocrista ends at the base of the metacone.

The M2 (Fig. 5B) is less worn than the M1 but also less complete. The paracone and metacone are both large and strong, but the paracone is again taller and broader. The stylocone is a large cusp, but the parastylar lobe is much wider than on the M1. The parastyle is more prominent and positioned more directly mesial to the stylocone. A broken chip of enamel indicates the presence of a small cuspule distal to the stylocone, and connected to it by a weak crest. The remainder of the stylar shelf is missing (beyond the deepest point of the ectoflexus), and it appears that the stylar shelf was quite wide on this specimen. The postmetacrista was likely strong. The tip of the protocone is broken from the second referred M2 (Fig. 5C), but it does preserve distinct conules positioned relatively close to the protocone. No internal cristae are present, and it appears that the postprotocrista ended at the base of the metacone. The preprotocrista is very wide, becoming more of a shelf.

The M3 is represented by three specimens, all in differing states of preservation (Fig. 5D–F). All are smaller than the M2. The holotype bears a complete M3, but the specimen is heavily coated in glue and appears to have lost much of its enamel. In all three specimens, the parastylar lobe is very wide, and the metacone is much smaller than the paracone. The stylocone is large but relatively smaller than on the M1–2. The parastyle is also large and is well-separated from the stylocone. The preparacrista is strong. There is some evidence of a small cuspule similar to that on the M2. The ectoflexus is much deeper than on the mesial molars, and where preserved (the holotype only), the metastylar lobe is slightly narrower than the parastylar lobe. The protoconal region on OMNH 61185 is heavier than on SMP-SMU 61725, and while this is not likely due to preservation, there are some possible geographic differences (relating mostly to size) among the Trinity Group samples (see Discussion). The conules are distinct and positioned close to the protocone (the metaconule appears to be absent from the holotype M3, but there is breakage in that region).

A single M4 is known, preserved along with an M3 as part of the holotype (SMP-SMU 61725; Fig. 5D). The metacone and metastylar lobe are strongly reduced relative to the M3, while the paracone and parastylar lobe are wide and very prominent. The preparacrista runs to the stylocone. The protoconal region is missing from this specimen, so no other information is available.

Lower molars: Only trigonids are preserved of all lower molars referred to *P. pattersoni* (Fig. 5). While there is some variation in size, none of the differences typically attributable to position are evident. The trigonid is roughly equilateral in occlusal view, with a prominent protoconid and subequal paraconid and metaconid. The paracristid is somewhat stronger and more heavily notched than the protocristid, but not to the degree seen in deltatheroidans. Cusp f is prominent and nearly vertical, while cusp e is much smaller though still distinct. From what is preserved, the cristid obliqua appears to have met the trigonid beneath the protocristid notch, and a distal metacristid is present.

Stratigraphic and geographic range.—Greenwood Canyon (Triconodont Gully, Turtle Gully), upper Antlers Formation (Aptian–Albian), north-central Texas, USA; Tomato Hill (V706), middle Antlers Formation (Aptian–Albian), southeastern Oklahoma, USA.

Infraclass Eutheria Gill, 1872

Order incertae sedis

Family Holoclemensiidae Aplin and Archer, 1987

Genus *Holoclemensia* (Slaughter, 1968b)

Type species: *Holoclemensia texana* Slaughter, 1968b, Butler Farm, upper Antlers Formation (Aptian–Albian).

Holoclemensia texana Slaughter, 1968b

Figs. 6, 7, Table 6.

1989 *Comanchea hilli* Jacobs, Winkler, and Murry, 1989: 4992, fig. 1.

Holotype: SMP-SMU 61997, RM2 missing the protoconal region.

Type locality: Butler Farm, north-central Texas, USA.

Type horizon: Upper Antlers Formation (Aptian–Albian)

Referred material.—PM 1000, LM1 (missing protoconal region); PM 1004, RM1 (missing paracone, parastylar lobe, and protoconal region); PM 886, RM2 (missing paracone, parastylar lobe, and protoconal region); SMP-SMU 62009, RM3; SMP-SMU 61727, Lm1; PM 887, Rm1 (trigonid only); PM 966, Lm1 (trigonid only); PM 1005, Rm2; PM 3877, Lm2 (trigonid only); SMP-SMU 62131, Lm2; SMP-SMU 62721, Rm2; OMNH 62412, Rm3; OMNH 62414, Lmx (talonid only); OMNH 63894, Rmx (talonid only); SMP-SMU 62722, Rmx (talonid only).

Tentatively referred material.—SMP-SMU 61948, LP4; SMP-SMU 71848, LDP5 (holotype of *Comanchea hilli*); SMP-SMU 62399, Lp5.

Emended diagnosis.—Basal eutherian mammal differing from all other basal eutherians in presence of a very large central stylar cusp (= mesostyle); differs from stem tribosphenidans in very small size of stylocone, the presence of a very large mesostyle, relatively narrow metastylar lobe at all loci, a prominent, flange-like parastylar lobe on mesial molars, very tall, bulbous metaconid on lower molars, and highly mesiodistally compressed trigonid; differs from deltatheroidans in presence of three molars, relatively weak postmetacrista, small stylocone, and small, inclined paraconid; differs from *Slaughteria* in larger size, presence of metaconid on p5, metaconid taller than paraconid on molars, and absence of distal metacristid; differs from *Pappotherium* in

Table 6. Measurements (in mm) of the eutherian *Holoclemensia texana* Slaughter, 1968b from the Early Cretaceous of Oklahoma and Texas. Numbers in brackets indicate estimates. Abbreviations: AP, anteroposterior (mesiodistal) length; ANW, anterior (mesial) width; POW, posterior (distal) width.

| Locus	Specimen number	AP	ANW	POW
P4	SMP-SMU 61948	1.8	1.04	–
DP5	SMP-SMU 71848	1.25	1.25	1.45
M1	PM 1000	1.52	–	–
	PM 1004	[1.67]	–	–
M2	PM 886	[1.71]	–	–
	SMP-SMU 61997	1.67	–	–
M3	SMP-SMU 62009	1.26	2.43	1.65
p5	SMP-SMU 62399	1.43	0.90	–
m1	PM 887	–	1.30	–
	PM 966	–	1.20	–
	SMP-SMU 61727	1.94	1.30	1.10
m2	PM 1005	1.91	1.38	1.03
	PM 3877	–	1.34	–
	SMP-SMU 62131	1.90	1.21	0.85
	SMP-SMU 62721	2.05	1.48	1.19
m3	OMNH 62412	1.49	1.09	0.70
mx	OMNH 62414	–	–	1.01
	OMNH 63894	–	–	0.97
	SMP-SMU 62722	–	–	1.04
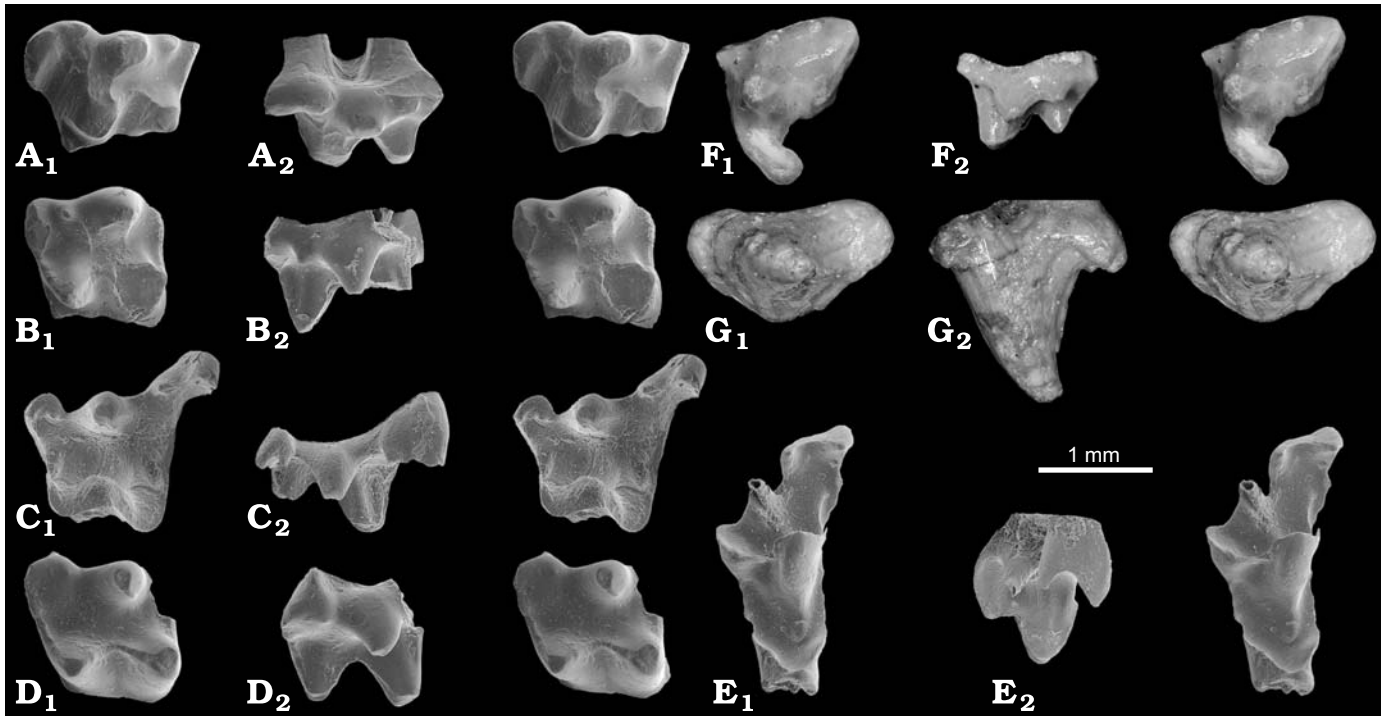
Fig. 6. The basal eutherian *Holoclemensia texana* Slaughter, 1968b from the Early Cretaceous of Oklahoma and Texas. **A**. PM 1000, LM1 in occlusal (A_1) and buccal (A_2) views. **B**. PM 1004, RM1 in occlusal (B_1) and buccal (B_2) views. **C**. SMP-SMU 61997, RM2 (holotype) in occlusal (C_1) and buccal (C_2) views. **D**. PM 889, RM2 in occlusal (D_1) and buccal (D_2) views. **E**. SMP-SMU 62009, RM3 in occlusal (E_1) and buccal (E_2) views. **F**. SMP-SMU 71848 (holotype of *Comanchea hilli* Jacobs et al., 1989), LDP5 in occlusal (F_1) and buccal (F_2) views. **G**. SMP-SMU 61948, LP4 in occlusal (G_1) and buccal (G_2) views.

presence of three molars, shallower ectoflexus, more separated paracone and metacone, narrower metastylar lobe, metaconid taller than paraconid, and absence of distal metacristid.

Description

Upper premolars: Two upper premolars are tentatively referred to *Holoclemensia texana*. SMP-SMU 61948 (Fig. 6G) is a very large, trenchant premolar, complete except for some minor breakage along the lingual margin. Both Slaughter (1968{a,b?}: 135) and Butler (1978: 14) interpreted this breakage to indicate the presence of a small protocone on this specimen; whether this was indeed the case or if simply a lingual cingulum was present is impossible to judge. Separate mesiobuccal and distobuccal cingula each bear a small cuspule (the distal one is larger). The size and morphology of the principal cusp on this specimen strongly suggest that it is a p4 (see the discussion of serial homology in Davis 2011). *H. texana* is the largest tribosphenidan known from the Trinity Group, and the only taxon appropriate in size for referral of this specimen. However, the possibility that another larger, unknown taxon was present in the fauna cannot be excluded.

SMP-SMU 71848 (Fig. 6F) is a worn and fragmentary upper molariform tooth, established as the holotype of *Comanchea hilli* by Jacobs et al. (1989), who implicitly regarded it to be a molar. However, it possesses features that are more consistent with a deciduous premolar, especially in light of the upper molar morphology of *H. texana*. The paracone is large and swollen, and the metacone is very small and well separated from the paracone. A very weak preparacrista connects to a very small parastyle, which is the first in a line of four stylar cusps. An equally small stylocone is immediately distal to the parastyle, and it is followed by a very large mesostyle (equal in size to the metacone), positioned distobuccal to the paracone. A weak ridge connects the mesostyle with a smaller cusp (possibly equivalent to stylar cusp D). The protoconal region is transversely narrow but somewhat long mesiodistally; a distinct but small paraconule is present. This specimen compares well with the morphology of the upper molars of *H. texana*, except in ways that are characteristic of deciduous premolars (Cifelli 1999a): the parastylar and protoconal regions are reduced, and the paracone is large and swollen relative to the metacone. Considering how strongly molariform this specimen is and how much smaller it is than the referred P4, it is most likely a DP5.

Upper molars: All specimens except for the M3 are missing the protoconal region of the crown. The M1s (Fig. 6A, B) are heavily worn, but together they provide morphology for the entire buccal half of the crown. The paracone was clearly larger than the metacone. The preparacrista appears to have been low, but observation is difficult due to wear and breakage. The postmetacrista is much weaker than in *Pappotherium* or deltatheroidans. The stylocone is small and positioned at the buccal margin of a wide, wing-like parastylar lobe which projects beyond the buccal extent of the metastylar lobe (in a similar fashion to but to a greater extent than
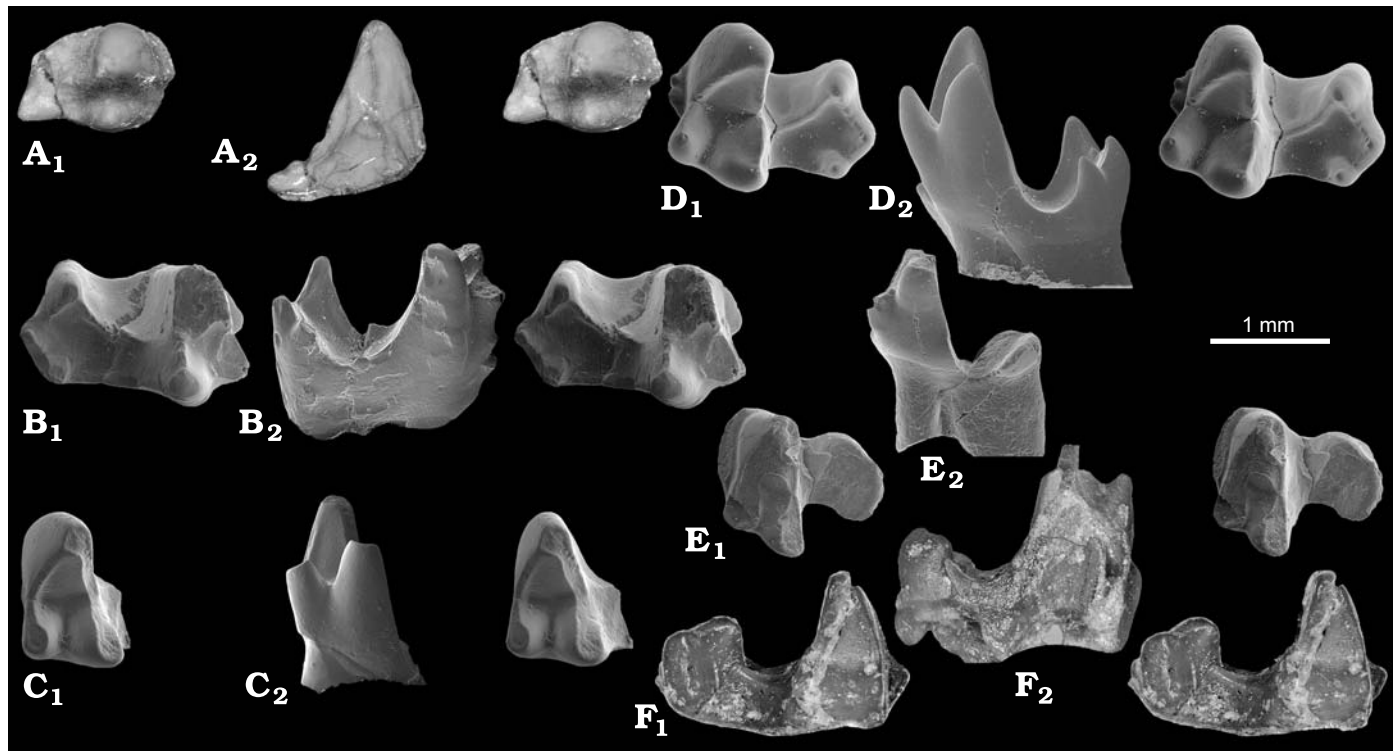
Fig. 7. The basal eutherian *Holoclemensia texana* Slaughter, 1968b from the Early Cretaceous of Oklahoma and Texas (A–E). **A**. SMP-SMU 62399, Lp5 in occlusal (A_1) and lingual (A_2) views. **B**. SMP-SMU 61727, Lm1 in occlusal (B_1) and lingual (B_2) views. **C**. PM 887, Rm1 in occlusal (C_1) and lingual (C_2) views. **D**. PM 1005, Rm2 in occlusal (D_1) and lingual (D_2) views. **E**. OMNH 62412, Rm3 in occlusal (E_1) and lingual (E_2) views. **F**. SMP-SMU 61726, Lmx referred to *Holoclemensia* sp. in occlusal (F_1) and lingual (F_2) views.

in *Prokennalestes*; see Kielan-Jaworowska and Dashzeveg 1989). The mesostyle is much larger than the stylocone but not as tall as the metacone, and is positioned at or just mesial to the middle of the centrocrista; a low bulge just distal to it indicates the presence of another stylar cusp (in the position of stylar cusp D). An ectoflexus is lacking. The preprotocrista is obliterated by wear in PM 1000, but it probably participated in the large parastylar lobe. The postprotocrista does not extend buccally past the base of the metacone.

The M2 (Fig. 6C, D) is larger than the M1. The paracone is taller than the metacone and relatively well separated from it, and the preparacrista, postmetacrista, and centrocrista are all low. The stylocone is very small (equal in size to the parastyle), and positioned mid-way on a wide, mesiobuccally projecting parastylar lobe; it anchors the preparacrista. The mesostyle is large and centrally positioned, as on the M1. The metastylar lobe is much narrower than the parastylar lobe, but relatively wider than on the M1. There is weak evidence of a small cuspule on the distal stylar shelf, and an ectocingulum is absent. The postprotocrista has the same extent as on the M1.

SMP-SMU 62009 (Fig. 6E) represents the M3 and is the most complete upper molar, missing only the lingual portion of the protocone. The crown is transversely wide and mesiodistally compressed, with substantial reduction to the metacone and metastylar lobe, as is typical for ultimate molars. The paracone is large and dominant, while the metacone is

low and thin; the preparacrista is oriented toward the parastyle, but terminates prior to reaching it. The parastylar lobe is short and wide, with a large, sharp parastyle and a much smaller stylocone. The mesostyle is delicate and spire-like as compared to the other molars. The protocone is also tall, about two-thirds the height of the paracone, and is flanked by a small paraconule and metaconule. The conules are closely appressed to the protocone. The preprotocrista is interrupted for a brief stretch mesial to the paracone.

Lower premolar: SMP-SMU 62399 (Fig. 7A) is a semi-molariform premolar. The protoconid is rounded much like that on a typical molar, and a low but distinct metaconid is present directly lingual to the protoconid. The mesialmost portion of the crown is broken, but there is no evidence that a paraconid was present. A weak ridge runs down the distal face of the metaconid, parallel to a stronger crest from the protoconid, bounding a wide trough; the crests meet at a single, very low heel cusp. The heel bends slightly lingually (in occlusal view); the distobuccal portion of the crown is basally expanded, and bears a very small isolated cuspule. While it agrees well morphologically with the expected p5 for *H. texana*, it is considerably mesiodistally shorter than the referred lower molars; its referral to this taxon is therefore tentative. An additional premolar from Butler Farm, SMP-SMU 61947 (see Butler 1978: fig. 4G), may also represent the p5 for *H. texana* (Alexander Averianov personal communication, 2011). This specimen is better preserved than SMP-SMU

62399, but it does not differ appreciably in morphology and was unavailable for study at the time of this project.

Lower molars: Specimens representing all three lower molar loci are known for *H. texana*. In general, all share a mesiodistally compressed trigonid bearing a large metaconid and a much smaller, somewhat procumbent paraconid. The m1 (Fig. 7B, C) is characterized by less inflation of the metaconid relative to the other loci, and less height and transverse width differential between the trigonid and talonid. The hypoconid is very prominent (it would likely have been taller than the paraconid), while the other two talonid cusps are subequal in size. The talonid basin is deep but not well enclosed mesiolingually due to the absence of a prominent entocristid.

The trigonid of the m2 (Fig. 7D) is much taller than the talonid, and it is transversely much wider than mesiodistally long. The metaconid is heavy and inflated (more obvious in lingual view). The paraconid is small, slightly inclined, and set somewhat buccal to the metaconid. The protocristid is more prominent and more strongly notched than in *Pappotherium*. The morphology (and presence) of the e and f cusps are variable; cusp e is either absent or represented by two very tiny cuspules on the mesiolingual base of the paraconid. Cusp f is much more prominent, and varies from a strong, oblique ridge to a short flange. The cristid obliqua meets the trigonid below the protocristid notch, and a distal metacristid is absent. The three talonid cusps are evenly spaced, though the hypoconid is again by far the tallest cusp. The entoconid is slightly smaller than the hypoconid, and lacks a strong entocristid.

One heavily worn and abraded specimen is referred to the m3 (OMNH 62412; Fig. 7E). In trigonid morphology, it clearly represents *Holoclemensia* but it demonstrates typical trends in distal molar loci, and resembles what would be appropriate for an ultimate molar of this taxon. The crown is smaller overall than the other specimens. The trigonid is more strongly mesiodistally compressed than the other loci, and while the major cusps are largely broken it is clear that the metaconid was very large and the paraconid was much smaller and set buccally. The protocristid was strong and notched. Cusp e is apparently absent (breakage of the paraconid could have removed it), and cusp f is represented by a strong, worn cingulid that occupies the entire mesial face of the trigonid and extends to the buccal side of the protoconid. The talonid is heavily worn such that no individual cusps can be discerned. The basin is, however, open mesiolingually as in the other referred specimens (due to a weak entocristid).

Stratigraphic and geographic range.—Butler Farm, upper Antlers Formation (Aptian–Albian), north-central Texas, USA; Greenwood Canyon (Triconodont Gully, Turtle Gully), upper Antlers Formation (Aptian–Albian), north-central Texas, USA; Pecan Valley Estates (SMP-SMU locality 157), Paluxy Formation (Albian); Tomato Hill (OMNH V706), middle Antlers Formation (Aptian–Albian), southeastern Oklahoma, USA; Willawalla, upper Antlers Formation (Aptian–Albian), north-central Texas, USA.

Holoclemensia sp.

Referred material.—SMP-SMU 61726, Lmx.

Description.—SMP-SMU 61726 (AP: 2.06, ANW: 1.43, POW: 0.90; Fig. 7F) is a complete but heavily fractured lower molar. It is referable to *Holoclemensia* in trigonid proportions—the trigonid is wide and mesiodistally compressed, the paraconid was much shorter than the metaconid (broken) and positioned somewhat buccally, and a distal metacristid is absent. However, the talonid is elongate and curled, in a manner similar to *Kermackia*. The cristid obliqua meets the trigonid more lingually than in specimens of *H. texana*, and the entoconid is relatively much larger (subequal to or larger than the hypoconid). This specimen is too poorly preserved to be of any other taxonomic use.

Stratigraphic and geographic range.—Butler Farm, upper Antlers Formation (Aptian–Albian), north-central Texas, USA.

Infraclass incertae sedis
Family Kermackiidae Butler, 1978
Genus *Kermackia* Slaughter, 1971

Type species: *Kermackia texana* Butler, 1971, Butler Farm, upper Antlers Formation (Aptian–Albian).

Kermackia texana Slaughter, 1971
Fig. 8, Table 7.

1978 *Trinititherium slaughteri* Butler, 1978: 10, fig. 3.
Holotype: SMP-SMU 62398, Rmx.
Type locality: Butler Farm, north-central Texas, USA.
Type horizon: Upper Antlers Formation (Aptian–Albian).

Referred material.—OMNH 67134, Rp5 (missing the mesiobuccal corner); OMNH 63731, Lmx (talonid only); OMNH 63893, Lmx (trigonid only); PM 922, Rmx; PM 1046, Lmx (trigonid only); PM 1245, Rmx; SMP-SMU 61728, a left dentary fragment preserving m3 (the holotype of *Trinititherium slaughteri* Butler, 1978).

Tentatively referred material.—SMP-SMU 62402, RM1 (missing the mesiobuccal corner).

Table 7. Measurements (in mm) of the tribosphenidan *Kermackia texana* from the Early Cretaceous of Oklahoma and Texas. Numbers in brackets indicate estimates. Abbreviations: AP, anteroposterior (mesiodistal) length; ANW, anterior (mesial) width; POW, posterior (distal) width.

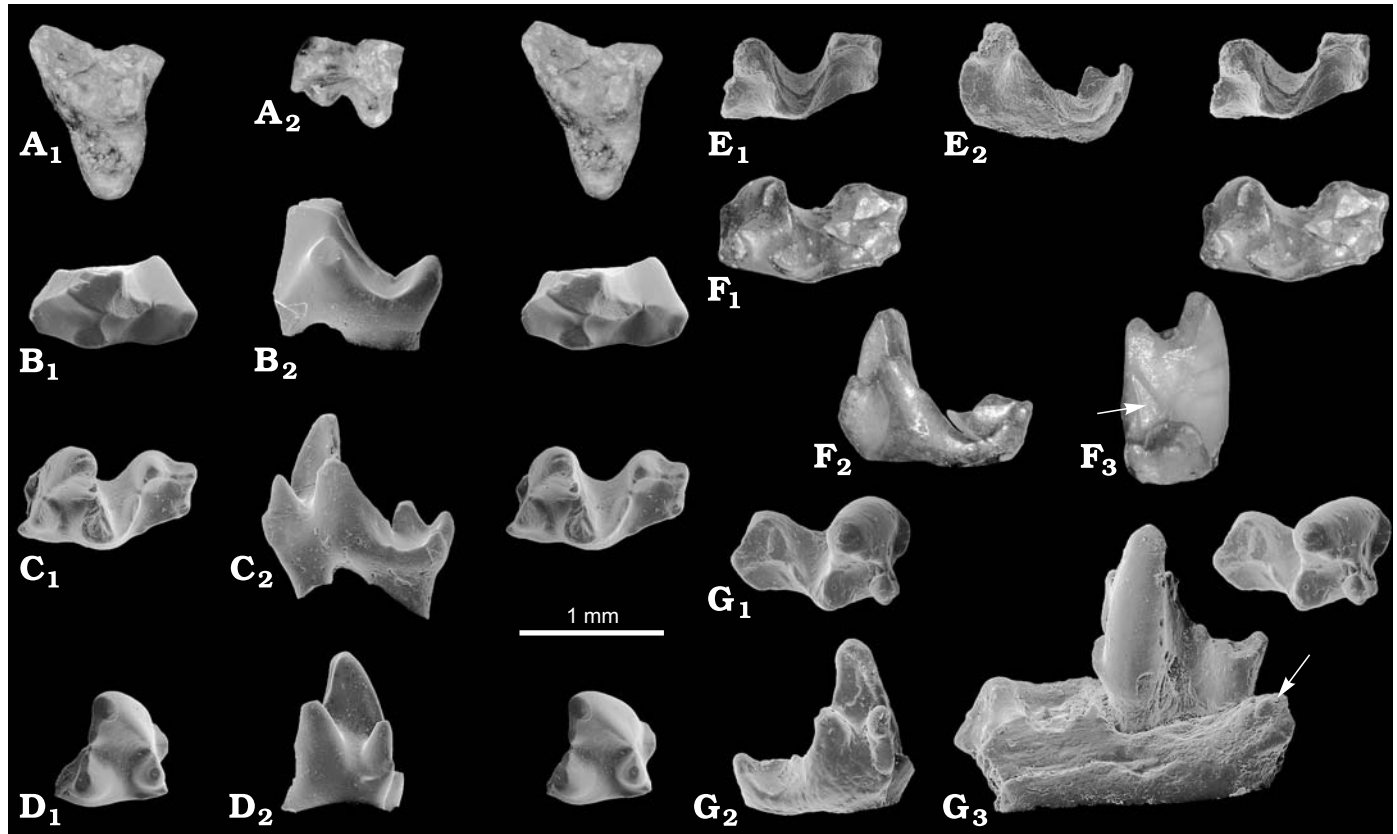| Locus	Specimen number	AP	ANW	POW
M1	SMP-SMU 62402	0.93	1.12	1.28
p5	OMNH 67134	[1.27]	–	–
m3	SMP-SMU 61728	1.25	0.77	0.52
mx	OMNH 61178	–	0.83	–
	OMNH 63731	–	–	0.57
	OMNH 63893	–	0.73	–
	PM 922	1.30	0.72	0.58
	PM 1046	–	0.57	–
	PM 1245	1.25	0.70	0.52
	SMP-SMU 62398	1.16	0.57	0.44

Fig. 8. The tribosphenidan *Kermackia texana* Slaughter, 1971 from the Early Cretaceous of Oklahoma and Texas. **A**. SMP-SMU 62402, RM1 in occlusal (A_1) and buccal (A_2) views. **B**. OMNH 67134, Rp5 in occlusal (B_1) and lingual (B_2) views. **C**. PM 1245, Rmx in occlusal (C_1) and lingual (C_2) views. **D**. OMNH 63893, Lmx in occlusal (D_1) and lingual (D_2) views. **E**. SMP-SMU 62398, Rmx (holotype) in occlusal (E_1) and lingual (E_2) views. **F**. PM 922, Rmx in occlusal (F_1), lingual (F_2), and distal (F_3) views (arrow indicates the presence of wear facet 5, sensu Crompton 1971). **G**. SMP-SMU 61728, left dentary fragment with m3 (holotype of *Trinititherium slaughteri* Butler, 1978) in occlusal (G_1), lingual (G_2), and buccal (G_3) views (arrow indicates mesial base of ascending ramus, suggesting that the ultimate molar is preserved).

Emended diagnosis.—Very small tribosphenidan characterized by the following unique combination of characters: lower molars with a very large, broad metaconid (much larger than the paraconid), distal metacristid hypertrophied such that it meets the cristid obliqua at a notch immediately mesial to the hypoconid (instead of at the base of the trigonid), and large, inflated upper molar paracone.

Description

Upper molar: SMP-SMU 62402 (Fig. 8A) is tentatively referred to *Kermackia texana* on the basis of size and occlusal fit; the only other taxon from the sample of equivalent size is *Slaughteria*, but the lower molar morphology of *K. texana* (described below) suggests that its upper molars are somewhat modified as represented by SMP-SMU 62402. The paracone is very large and inflated, while the metacone is substantially smaller and positioned slightly buccally with respect to the paracone. The postmetacrista is only moderately developed. The parastylar lobe is largely broken, but from the pattern of breakage the stylocone appears to have been very large and closely appressed to the paracone. The ectoflexus was moderately deep, and the parastylar lobe was probably narrower than the metastylar lobe. There is no evi-

dence of stylar cusps other than the stylocone. The protoconal region is well developed (the protocone is as tall as the metacone) and bears both conules. The metaconule is situated close to the protocone, while the paraconule is equidistant from the protocone and paracone. The tooth is heavily abraded, obscuring any other features (including wear facets). This specimen is considered to be a first molar based on the width of the metastylar lobe (tends to be reduced on ultimate molars), and the inferred approximation of the stylocone to the paracone (the parastylar lobe is typically wider on second molars). *Kermackia* is interpreted to have had three molars (see below).

Lower premolar: OMNH 67134 (Fig. 8B) is a small, semi-molariform premolar broken obliquely at about the midline of the protoconid. The main cusp is large but with heavy apical wear; it is flanked lingually by a mesiodistally broad metaconid. The two cusps are connected by a weak crest. Two additional crests descend distally from the protoconid and meet a crest running mesially from a large heel cusp. A strong notch is present at this juncture; a very similar (and probably serially homologous) notch is found in lower molars of *Kermackia texana* (see below). The talonid is otherwise undeveloped, except for a faint, low rim enclosing the

lingual margin. The small overall size, broad metaconid, and strongly notched heel crest support referral of this specimen to *K. texana*. The absence of any molarization of the talonid indicates that this premolar is from the adult series, and the presence of a prominent metaconid suggests it is the ultimate premolar. Without material to suggest otherwise, *Kermackia* is interpreted to possess the primitive tribosphenidan condition of five premolars and three molars (see Davis in press, and references therein).

Lower molars: The lower molars of *Kermackia* are highly distinctive (Fig. 8C–G), but the limited preservation of the current sample precludes identification of any specimens to locus except the ultimate (interpreted as m3; see below). In occlusal view, the entire crown appears to bow lingually, due to the small size of the paraconid on the mesial end, the poorly-developed lingual margin of the talonid on the distal end, and the hypertrophied distal metacristid on the prominent metaconid in the middle. The trigonid is taller than the talonid and bears a high protoconid and a lower but large, broad metaconid. The paraconid is by far the smallest trigonid cusp and varies from being delicately constructed to low and robust (this likely reflects some positional or intraspecific variation). Cusp f is developed as a shelf but it is limited to the mesial base of the trigonid. Cusp e is present as a distinct ridge projecting from the mesiolingual corner of the paraconid, resembling the keel-like structure characteristic of marsupials (Cifelli 2004: 70, footnote 2).

The distal metacristid, as defined by Fox (1975) and modified by Davis (in press), typically descends from the apex of the metaconid to the point at which the cristid obliqua meets the distal wall of the trigonid, typically below the protocristid notch. In *Kermackia*, however, the distal metacristid is modified into a very strong ridge that projects from the apex of the metaconid and descends to meet a foreshortened cristid obliqua immediately mesiolingual to the hypoconid; a well developed notch is present where the two crests meet. The rationale for this interpretation (and the functional implications) is discussed later in the text. As a consequence of the long, ridge-like distal metacristid, the talonid is set much farther distally than would be expected for its small size and degree of development. The hypoconid is the largest cusp, followed by the hypoconulid which is slightly larger than the entoconid. The cusps are evenly spaced, but the entoconid lacks an entocristid so the shallow talonid basin is open lingually (there is substantial space between the entoconid and the trigonid).

The holotype of *Trinititherium* (SMP-SMU 61728; Fig. 8G) comprises a small dentary fragment bearing a single molar posterior to two alveoli. It also preserves a small portion of the ascending ramus, visible distobuccal to the talonid of the molar. This suggests that the single preserved tooth is the ultimate molar, and accompanying features such as a reduction in the height of the metaconid and a decrease in the size of the talonid (and absence of the entoconid) can account for any differences between this specimen and those otherwise referred to *Kermackia*. *Trinititherium* is therefore a junior

synonym of *Kermackia*, and this specimen represents the m3.

Comments.—William Clemens proposed that *Trinititherium* may be a distal molar of *Kermackia* (personal communication in Butler 1978: 11), and this view is supported here (see the description).

Stratigraphic and geographic range.—Butler Farm, upper Antlers Formation (Aptian–Albian), north-central Texas, USA; Greenwood Canyon (Triconodont Gully), upper Antlers Formation (Aptian–Albian), north-central Texas, USA; Tomato Hill (OMNH V706), Antlers Formation (Aptian–Albian), southeastern Oklahoma, USA.

Family incertae sedis
Genus *Slaughteria* Butler, 1978

Type species: *Slaughteria eruptens* Butler, 1978, Butler Farm, upper Antlers Formation (Aptian–Albian).

Slaughteria eruptens Butler, 1978
Fig. 9, Table 8.

Holotype: SMP-SMU 61192, a left dentary fragment preserving the p2, p3, dp4 and dp5 (partially developed and unerupted replacement teeth at the p4–5 are visible in CT; Fig. 9E).

Type locality: Butler Farm, north-central Texas, USA.

Type horizon: Upper Antlers Formation (Aptian–Albian).

Referred material.—PM 1098, Rp5 missing the mesial half of the protoconid; OMNH 63726, Rmx missing portions of the talonid, and OMNH 63721, Rmx (talonid only).

Emended diagnosis.—Very small tribosphenidan characterized by strongly molariform dp4 and dp5; permanent p5 premolariform but with an expanded talonid; differs from *Pappotherium* in smaller size, presumed presence of three molars, stronger paracristid; differs from *Holoclemensia* in absence of metaconid on p5, subequal paraconid and metaconid, presence of distal metacristid, and relatively smaller talonid; differs from *Kermackia* in absence of a metaconid on p5, subequal paraconid and metaconid, weaker distal metacristid, relatively taller trigonid, and relatively mesiodistally shorter talonid; differs from deltatheridiids in presence of five lower premolars and three molars, subequal paraconid and metaconid, and possession of entoconid.

Table 8. Measurements (in mm) of the tribosphenidan *Slaughteria eruptens* Butler, 1978 from the Early Cretaceous of Oklahoma and Texas. Numbers in brackets indicate estimates. Abbreviations: AP, anteroposterior (mesiodistal) length; ANW, anterior (mesial) width; POW, posterior (distal) width.

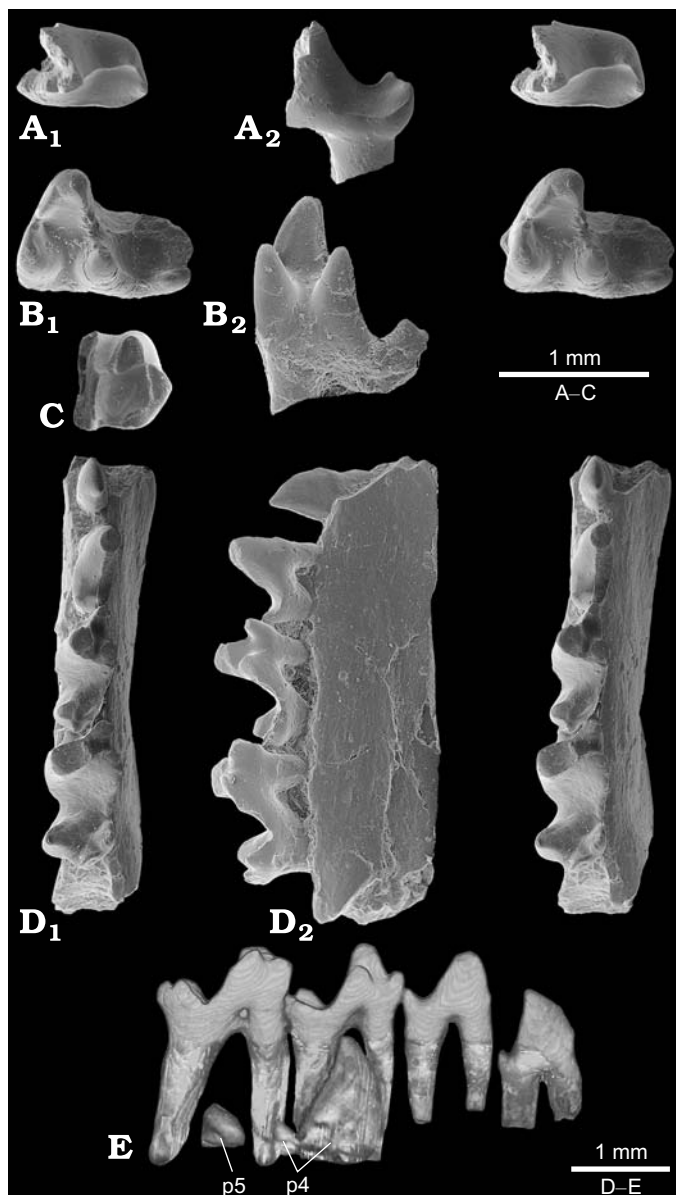| Locus	Specimen number	AP	ANW	POW
p2	SMP-SMU 61192	0.63	0.33	–
p3	SMP-SMU 61192	0.94	0.42	–
dp4	SMP-SMU 61192	1.25	0.62	0.51
dp5	SMP-SMU 61192	1.45	0.73	0.72
p5	PM 1098	[1.07]	0.59	–
mx	OMNH 63721	–	–	0.65
	OMNH 63726	1.23	0.77	0.52

Fig. 9. The tribosphenidan *Slaughteria eruptens* Butler, 1978 from the Early Cretaceous of Oklahoma and Texas. **A**. PM 1098, Rp5 in in occlusal (A$_1$) and lingual (A$_2$) views. **B**. OMNH 63726, Rmx in occlusal (B$_1$) and lingual (B$_2$) views. **C**. OMNH 63721, Rmx in occlusal (C$_1$) and lingual (C$_2$) views. **D**. SMP-SMU 61992, left dentary fragment with p2, p3, dp4, and dp5 (holotype) in occlusal (D$_1$) and lingual (D$_2$) views. **E**. 3-D reconstruction of SMP-SMU 61992 from CT data (in lingual view, bone removed), with developing p4 and p5 indicated (modified from Davis 2011).

Description

Detailed descriptions of the holotype and referred molar material of *Slaughteria eruptens* can be found in Davis (in press), and will not be repeated here. However, an additional premolar is herein referred, and the morphology of the rest of the hypodigm is summarized to facilitate comparisons between the various tribosphenidan taxa described in this paper.

Lower premolars: The holotype of *S. eruptens* (SMP-SMU 61192; Fig. 9D–E) was interpreted by Davis (in press)

to preserve the p2, p3, dp4, and dp5. Both deciduous premolars are strongly molariform but have low trigonids bearing a small, procumbent, and buccally positioned paraconid as well as a relatively broad, well developed talonid. CT data revealed the presence of two permanent premolars developing within the jaw (Kobayashi et al. 2002; Davis [in press]. The permanent p4 is large and trenchant with a single small heel cusp, while only the tip of the principal cusp of the p5 is calcified. PM 1098 (Fig. 9A) is an ultimate lower premolar missing the mesial half of the principal cusp. This cusp was tall and conical; because of damage the presence or absence of a metaconid or paraconid cannot be ascertained. A crest descends the main cusp to meet a small but prominent heel cusp. This cusp is situated on the buccal side of the talonid, and is connected by a weak crest to an additional, distolingually positioned cusp. A faint ridge encloses the lingual margin of the talonid. This specimen agrees well in size with *S. eruptens*, and is most likely a p5 based on its semimolariform morphology (the p4 should have a much taller, trenchant principal cusp).

Lower molars: OMNH 63726 (Fig. 9B) is a mostly complete lower molar, missing only portions of the talonid. The trigonid is tall and equilateral, with subequal paraconid and metaconid. The paracristid is high and strongly notched, and a distal metacristid is present. The talonid was somewhat narrower than the trigonid, is well basined, and bears a distinct entoconid.

Stratigraphic and geographic range.—Greenwood Canyon (Triconodont Gully), upper Antlers Formation (Aptian–Albian), north-central Texas, USA; Tomato Hill (OMNH V706), middle Antlers Formation (Aptian–Albian), southeastern Oklahoma, USA.

Family indet.

Gen. et sp. indet.
Fig. 10, Table 9.

Material.—PM 1075, L ultimate upper molar; PM 948, Rmx.

Description

There is nothing to suggest that these two specimens necessarily belong to the same taxon, and they are described here under the same heading for convenience.

Upper molar: PM 1075 (Fig. 10A) is an ultimate upper molar. The metacone and metastylar lobe are very strongly reduced; the parastylar lobe and protoconal region are of equal width. The preparacrista is strong and meets the stylocone, which is subequal to the parastyle. No ectoflexus is

Table 9. Measurements (in mm) of specimens referred to Tribosphenida indet. from the Early Cretaceous of Texas. Abbreviations: AP, anteroposterior (mesiodistal) length; ANW, anterior (mesial) width; POW, posterior (distal) width.

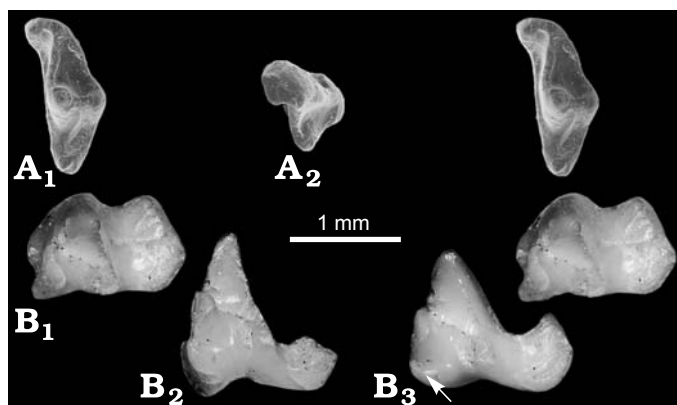| Locus	Specimen number	AP	ANW	POW
M4	PM 1075	0.85	1.36	0.85
mx	PM 948	1.41	0.95	0.86

Fig. 10. Tribosphenida indet. from the Early Cretaceous of Oklahoma and Texas. **A**. PM 1075, LM4 in occlusal (A_1) and buccal (A_2) views. **B**. PM 948, Rmx in occlusal (B_1), lingual (B_2), and oblique lingual (B_3) views (arrow indicates lingual cingulid).

present. The protocone is low but distinct, and no conules are evident. The preprotocrista is wide and continuous to the parastyle. This molar is superficially similar to the M4 of *Pappotherium pattersoni*, except that the distal portion of the crown is more reduced. It cannot be determined from the data on hand if PM 1075 is an M4, which are typically reduced in the larger taxa from the Trinity Group (such as *Pappotherium* and *Oklatheridium*), or an M3 from a smaller taxon (such as *Kermackia* or *Slaughteria*).

Lower molar: PM 948 (Fig. 10B) is a complete but slightly damaged lower molar. The trigonid is much taller than the talonid; the protoconid is the dominant cusp, but the metaconid is broken at its base so relative heights are impossible to judge. The paraconid does not appear to be particularly small (as in *Holoclemensia*) or large (as in deltatheroidans), and it supports a strong, notched paracristid. The cusps are evenly spaced. Cusp f is a wide, oblique ridge. Interestingly, cusp e begins as a small mesiolingual projection but extends around the entire lingual base of the paraconid as a cingulid (much as in the "peramuran" *Minimus* (Sigogneau-Russell 1999) and the enigmatic, non-tribosphenic australosphenidans from Gondwana (see Luo et al. 2001; Rougier et al. 2007). A distal metacristid is present. The talonid is mesiodistally short but as wide as the trigonid. The cusps are leveled by abrasion, but the hypoconid was clearly the largest. A small ring of enamel indicates the position of the hypoconulid, which is situated a substantial distance from the hypoconid, placing it much closer to the entoconid. The entoconid was very small and elongate. A crescentic swath of abrasion covers the entire distal and lingual margins of the talonid, delimited internally by what appears to be a separate crest that is concentric with the hypoconulid, entoconid, and entocristid. The talonid basin is developed between this crest and the cristid obliqua, which is low and meets the trigonid below the protocristid notch. The pattern of wear on the talonid of this specimen is interesting, as well. Wear facets 3 and 5 are developed (sensu Crompton 1971), but facet 4 is not evident. The occlusal surface of the talonid bears evidence of strong apical wear. The combination

of these features and the lingual cingulid on the paraconid indicate that this specimen represents a separate taxon from those described above, one which possibly possessed a different occlusal relationship between upper and lower molars.

Stratigraphic and geographic range.—Greenwood Canyon (Triconodont Gully), upper Antlers Formation (Aptian–Albian), north-central Texas, USA.

Discussion

***Holoclemensia* as a eutherian**.—There have been several attempts to assign some of the tribosphenidan taxa from the Trinity Group to either the Metatheria or Eutheria (e.g., Slaughter 1968a, b, 1971; Fox 1975), based largely on molar count and molarization of premolars. Most recent workers have, however, adopted Patterson's (1956) original conservative concept of "Theria of Metatherian-Eutherian Grade", choosing to informally affiliate these taxa as stem tribosphenidans (though taxonomic sampling in phylogenetic analyses is usually limited to either *Holoclemensia* or *Pappotherium*). A trove of well-preserved material described in the past decade or so has led to the identification of several Early Cretaceous metatherians and eutherians (Cifelli 1999b; Ji et al. 2002; Luo et al. 2003; Hu et al. 2010)—metatherians are less ambiguous in a number of respects that are exhibited even in the poorly preserved teeth and (rarely) jaw fragments that predominate the record (e.g., twinning of the hypoconulid and entoconid, presence of a buccal postcingulid, inflected angular process), but the identification of early eutherians presents, in our opinion, more of a challenge.

The principal features generally used to define early eutherians, a postcanine dental formula comprising four or more premolars and three molars, together with a semi-molariform ultimate premolar (e.g., Kielan-Jaworowska et al. 1979; Fox 1984; Kielan-Jaworowska and Dashzeveg 1989), are more plausibly interpreted as plesiomorphies inherited from an earliest tribosphenidan (or even pre-tribosphenidan) ancestor. These characters are present in Cretaceous taxa recognized as eutherians, such as *Prokennalestes*, *Maelestes*, and zhelestids (Sigogneau-Russell 1992; Wible et al. 2009a), but also in the most appropriate non-tribosphenic sister taxon, *Peramus* (Clemens and Mills 1971) (while the P5 of *Prokennalestes* is molariform, the p5 lacks a metaconid; Signogeau-Russell et al. 1992). The stem zatherian *Arguimus* (see Lopatin and Averianov 2006a) also possesses five premolars, the ultimate of which is semi-molariform (we interpret the tooth identified as the m1 by Lopatin and Averianov 2006a as the p5). It would seem, therefore, that other characters need to be identified to separate early eutherians from stem tribosphenidans.

We argue that the earliest fossil eutherians cannot be identified solely on the basis of dental formula or characters derived from the lower dentition; these features may serve to differentiate eutherians from metatherians, but they do not

reflect any departure from the presumed primitive tribosphenidan morphology (see review in Davis 2011). There are, however, upper molar characters that are shared across early eutherians: reduction in the size of the stylocone and a wide, flange-like parastylar lobe on mesial molars. In this regard, *Holoclemensia* is considered a eutherian—it retains the primitive tribosphenidan postcanine dental formula and semi-molariform ultimate premolar, but it has upper molars that are structurally similar to and share the above features with early eutherians such as *Bobolestes*, *Murtoilestes*, *Paranyctoides*, and *Prokennalestes* (Fig. 11; see Kielan-Jaworowska et al. 2004: fig. 13.19).

Our interpretation of the upper molar morphology of *Holoclemensia* provides additional evidence removing it from the basal metatherian position it has occupied in recent analyses (e.g., Rougier et al. 2004; Luo et al. 2007). Historically, this taxon has been allied with marsupials based predominantly on the presence of a large central stylar cusp, or by the presumed presence of four upper molars (Slaughter 1968b; Fox 1975). Among Late Cretaceous taxa (which were the closest references available at the time), eutherians tend to have a reduced stylar shelf lacking major stylar cusps. Marsupials such as *Alphadon* have a suite of well developed stylar cusps on a wide shelf, with the centralmost (cusp C) often being the largest. However, a number of older, more primitive metatherians have been described in recent decades (e.g., *Iqualadelphis* Fox, 1987, *Kokopellia* Cifelli, 1993, *Aenigmadelphys* Cifelli and Johanson, 1994), and it is now clear that the primitive metatherian and eutherian conditions are probably the same—the stylar shelf was wide, and stylar cusps other than the stylocone are either lacking or represented by a small, distal cusp (cusp D). The large mesostyle in *Holoclemensia* represents a curious apomorphy and is immaterial to its broader relationships. The identification of *Holoclemensia* as a eutherian is significant in that it becomes the oldest representative from North America for which portions of both the upper and lower dentitions are known, and demonstrates that a wider diversity of eutherians was likely present in North America in the Early Cretaceous than previously thought. Our results corroborate the recent analysis of Averianov et al. (2010), who refer specimens to *Holoclemensia* in the same manner and are the only others to place this taxon at the base of the Eutheria. The only point in which our reconstructions of the upper postcanine series for *Holoclemensia* differ concerns the presence or absence of a protocone on the P5. Averianov et al. (2010: fig. 9) base the P5 on PM 931, a specimen which lacks a protocone but is now unfortunately lost. Our hypothetical reconstruction (Fig. 11C) is based on comparisons with morphologically similar basal eutherians, such as *Prokennalestes* and *Paranyctoides*.

***Pappotherium* as a metatherian**.—The holotype of *Pappotherium pattersoni* preserves two upper molars, the distal of which has a strongly reduced metacone and metastylar lobe (Fig. 5D). This association provides more insight than usual into the reconstruction of the number of upper molars in a fragmentary Cretaceous therian, and has fueled debate about this taxon. Early authors described the two preserved molars as the M2 and M3 (Slaughter 1965; Crompton 1971), and a more thorough analysis was performed by Fox (1975). Using comparisons of occlusal outlines between the deltatheroidan *Deltatheroides*, the stem tribosphenidan *Potamotelses*, and Cretaceous eutherians, Fox (1975) concluded that *Pappotherium* had three upper molars. His argument centered on the retention of a relatively wide metastylar lobe on the mesial molar of the holotype, and that it agreed with the M2 of deltatheroidans and eutherians (Fox 1975 argued that, for the specimen to represent the M3 and M4, there must be strong distal reduction of both molars). Butler (1978) countered that the penultimate upper molar in Late Cretaceous marsupials (the M3) has a very wide metastylar lobe, and that distal suppression of the penultimate molar could correlate with evolution toward loss of the M4, with no bearing on the condition in *Pappotherium*. Butler (1978) counted four molars in *Pappotherium*, based on his interpretation of the morphology of the holotype and the referral of other isolated upper molars in the sample to mesial loci.

Our revision of the sample from the Trinity Group largely corroborates Butler's (1978) specimen referrals, and tentatively supports the presence of four upper molars in *Pappotherium*. The penultimate upper molar of the holotype (interpreted by us as the M3) differs markedly from the referred M1 in the width of the parastylar lobe, a character which varies predictably through the molar series in metatherians (Fig. 5). This strongly suggests the presence of an intermediate molar locus, though we lack complete material to confirm our assignments. Moreover, the discovery of a much better preserved specimen of *Deltatheroides* (Rougier et al. 2004) disputes Fox's (1975) favorable comparison between this taxon and *Pappotherium*; instead, the M3 and M4 of each seem to agree very closely. Recent analyses that have included *Pappotherium* are non-committal on the number of molars in this taxon (Rougier et al. 2004; Ji et al. 2006; Averianov et al. 2010). Unfortunately, there are no data bearing on premolar count in *Pappotherium*; the presence of three premolars (as in deltatheroidans and other metatherians) or four (as in the aegialodontid *Kielantherium* or the putative stem metatherian *Sinodelphys*; Dashzeveg and Kielan-Jaworowska 1984; Luo et al. 2003) cannot be established. Assuming that deltatheroidans are basal metatherians (and the evidence is strong; see Rougier et al. 2004), the molar features typically used to characterize Late Cretaceous metatherians are absent at the base of the clade; deltatheroidans lack twinning of the hypoconid and hypoconulid, and a buccal postcingulid. As noted above, postcanine dental formula is a poor character for uniting the Eutheria, but it appears that the development of four molars among tribosphenidans is rare enough to be of some utility alone in establishing relationships with the Metatheria. Talonid morphology is unknown in *Pappotherium*, but it shares the presence of four molars (and a larger, more derived protocone) with only deltatheroidans and other metatherians. It is most parsi-

monious to assume, as a working hypothesis, that *Pappotherium* represents a basal metatherian. Also worth noting are similarities between *Pappotherium* and deltatheroidans (Butler and Kielan-Jaworowska 1973). In occlusal outline and general structure, upper molars of *Pappotherium* differ from deltatheroidans only in some proportions of the paracone and metacone (see Figs. 2, 3, 5). Upper molars of *Pappotherium* suggest that postvallum/prevallid shearing was well developed, as in deltatheroidans. However, this is not reflected in relative development of trigonid cusps and shearing crests on lower molars. It is conceivable that *Pappotherium* is a stem deltatheroidan, but present evidence is permissive, not indicative, of such a relationship.

The aegialodontid *Kielantherium* retains the primitive postcanine tooth count (eight; McKenna 1975) but is derived in the possession of four molars and four premolars. This taxon presents either an early exemplar of the metatherian tooth formula (prior to loss of a premolar), or an independent suppression of replacement at the ultimate premolar locus (generally accepted as the most likely mechanism for the increase in molar count in marsupials; see Luckett 1993). The absence of any other metatherian characters in *Kielantherium*, coupled with highly plesiomorphic upper molar morphology (Lopatin and Averianov 2006b) lend support for the latter hypothesis. Therefore, while the affinities of *Kielantherium* appear to lie with taxa near the base of the tribosphenidan radiation, other taxa with a definitive molar count of four are most likely metatherians. A molar count of four in *Potamotelses* was hypothesized by Fox (1975); if additional material demonstrates this to be the case, it is likely that this taxon can be referred to the Metatheria. Evaluation of its affinites are, however, beyond the scope of this paper.

Diversity within the Deltatheroida.—The description of the talonid morphology for *Oklatheridium* (Fig. 4) and the identification of a second species, *O. minax* (Fig. 3), increase known taxonomic and morphological diversity within the Deltatheroida. While all deltatheroidans share particular features such as very strongly developed postvallum-prevallid shear (resulting in a large paraconid and paracristid), in other ways the genera form a continuum. *Deltatheridium*, *Deltatheroides*, and *Atokatheridium* all retain a relatively poorly developed protoconal region and a corresponding small talonid, lacking an entoconid (despite the interpretation by Averianov et al. (2010) that *Atokatheridium* is a basal tribosphenidan and not a deltatheroidan, a view which is not supported here; see Comments under Systematic paleontology, above). On the other end of the spectrum, the species of *Oklatheridium* have a much larger protoconal region with strong conules, and the referred complete lower molar bears a large, well enclosed talonid suggesting that substantial grinding function was either emphasized or retained in this genus (depending on polarity). *Sulestes* is somewhat intermediate; it possesses strong conules, a broad protoconal region, and an entoconid, but none approach the development in *Oklatheridium*.
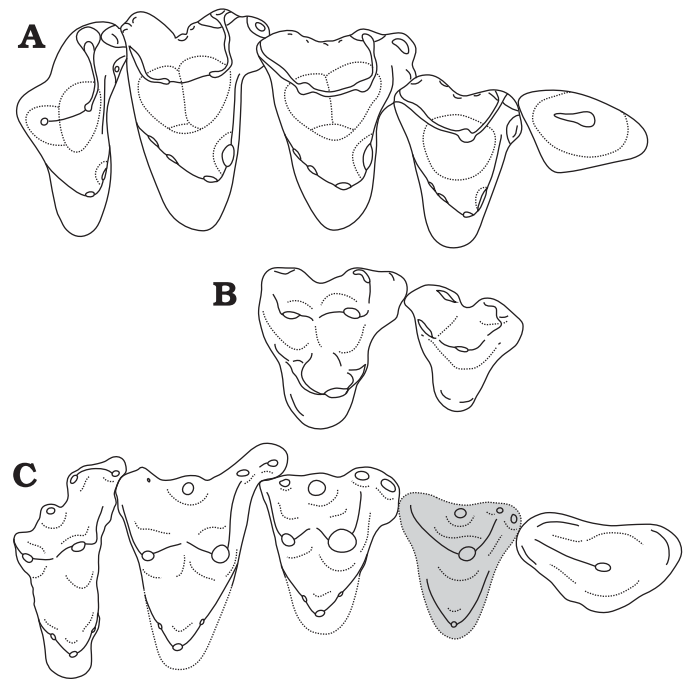

Fig. 11. Upper dentitions of Cretaceous eutherians. **A**. *Prokennalestes* (P4–M3), Early Cretaceous of Mongolia. **B**. *Paranyctoides* (P5–M1), Late Cretaceous of Uzbekistan, Alberta, and Utah. **C**. *Holoclemensia* (P4–M3, with some reconstruction indicated by dashed outlines, and P5 hypothetical and shaded grey), Early Cretaceous of Oklahoma and Texas. Note the flange-like parastyle on M1 and reduced stylocone on all molars, shared characteristics of early eutherians. Not to scale. A, modified from Kielan-Jaworowska and Dashzeveg (1989); B modified from Kielan-Jaworowska et al. (2004).

The wide range of differences in the protoconal/talonid regions of deltatheroidan molars reflects variation probably attributable to the familial (or at least subfamilial) level. The relatively poor material referable to the North American taxa does hamper comparisons (the Asiatic taxa are known by substantially better specimens; see Rougier et al. 1998; Averianov et al. 2010), as do uncertainties regarding the ancestry of the group (and the resulting polarity of their molar specializations). However, resolution of the suprageneric relationships of the various deltatheroidan taxa is beyond the scope of this paper.

The uneven distribution of deltatheroidans between the local faunas in Oklahoma and Texas is worth noting. These taxa are abundant at Tomato Hill but are rare in the Texas localities; based on the known material *Atokatheridium* is absent entirely from Texas, while *Oklatheridium* is represented in that state by only five specimens. The samples from the Trinity Group as a whole are relatively small, so future collecting efforts may provide additional data on possible stratigraphic or geographic trends regarding these taxa.

Molar function in *Kermackia*.—The lower molars of *Kermackia* are very distinctive (Fig. 8), and are likely indicative of specialized occlusal function divergent from the basic

tribosphenic pattern. The most prominent feature of the lower molar is the hypertrophied distal metacristid, which is developed into a strong ridge and descends from the apex of the metaconid nearly to the hypoconid. A short cristid obliqua meets the distal metacristid well distal to the trigonid wall, and a strong notch is developed at this junction. Elongation of the distal metacristid creates a wide embrasure to accept the upper molar paracone during occlusion, with the broad buccal surface of the distal metacristid serving as the primary structure for guiding and shearing against both the lingual and distal surfaces of the paracone as the jaws close. The hypocristid is comparatively very short, and in many specimens the hypoconulid is set almost directly distal to the hypoconid instead of at an oblique angle. The shallow and comparatively small contact surface for the metacone suggests that this cusp was substantially smaller and buccally offset relative to the paracone.

Despite being somewhat small and rotated relative to the long axis of the tooth, the talonid has a well developed basin and cusps. This simply suggests that *Kermackia* is derived from a typical tribosphenic morphology—the entoconid and the talonid basin are positioned more distally than in other taxa, displaced by the area devoted to the paracone (defined by the distal metacristid and cristid obliqua). On one specimen (PM 922; Fig. 8F) there is a distinct, triangular wear facet developed on the distal face of the distal metacristid, in the position of facet 5; this typically results from contact with the mesial surface of the protocone (Crompton 1971). The facet begins at the lingualmost extent of the distal metacristid and widens downward, but it ends abruptly before invading the talonid basin. The referred upper molar, SMP-SMU 62402 (Fig. 8A), has a wide protoconal region with a strong paraconule; though the specimen is too abraded to preserve wear features, the requisite morphology is present to account for the pattern observed on PM 922.

While there is clear occlusal contact with the mesial surface of the upper molar protoconal region, no wear is evident within the talonid basin or on the inner face of the entoconid (facet 6; Crompton 1971) on any specimens, suggesting that the basin and distolingual portion of the talonid have no occlusal function in *Kermackia*. This region is positioned in such a way that an upper molar structure would have to be present directly lingual to the metacone in order to contact it. While the referred upper molar does bear a broad protoconal region, it does not appear to have been expansive enough to occlude with both the distal metacristid and the entoconid. The strongly developed notch at the base of the distal metacristid (a feature not found in any other Mesozoic mammal) is evidence of the importance of shear in this taxon. However, more complete material (especially upper molars) is necessary to fully understand the function of the derived morphology in *Kermackia*.

"Theria of Metatherian-Eutherian Grade".—The molar count for all the described tribosphenidans from the Trinity Group can be reconstructed with some confidence. The deltatheroidans *Atokatheridium* and *Oklatheridium* likely shared the basal metatherian count of three premolars and four molars demonstrated in closely allied forms from Asia (see Rougier et al. 1998; Rougier et al. 2004). *Pappotherium* also had four molars, and we tentatively place it within the Metatheria. In addition to *Holoclemensia*, both *Slaughteria* and *Kermackia* likely possessed five premolars and three molars. While upper molar morphology is unknown in *Slaughteria* (making high-level relationships difficult to establish), the aberrant lower molar morphology and referred upper molar of *Kermackia* are very different from those of early eutherians. Shared postcanine dental formula across basal eutherians, unallocated stem tribosphenidan taxa, and proximal outgroups (e.g., *Peramus*) suggests that this is a poor character on which to base relationships. The absence of any characters definitively supporting either eutherian or metatherian affinities for some tribosphenidan taxa supports the utility of retaining an informal stem group at least until more complete mateiral is known. It also serves to underscore the importance of utilizing character suites in making taxonomic referrals, instead of relying on single features which might be symplesiomorphic.

Conclusions

The sample of tribosphenidans from the Trinity Group of Texas and Oklahoma, though fragmentary, stands in a place of historic importance for the development of modern paleomammalogy. While the available data suggest that the metatherian-eutherian split occurred in Asia at or prior to the Jurassic–Cretaceous boundary (see review in Cifelli and Davis 2003; Wible et al. 2009b), at least some members of each group had dispersed to North America by the Aptian–Albian as demonstrated by eutherians such as *Holoclemensia* and *Montanalestes* (from the contemporaneous Cloverly Formation; Cifelli 1999b), and the ?metatherian *Pappotherium*. The Deltatheroida were morphologically diverse early in the history of the group, as evident by the two genera from the Trinity fauna. Other tribosphenidans show evidence of a substantial radiation while still providing key insights into the transition from their non-tribosphenic ancestors—*Kermackia* possesses molars which are clearly divergent in form and function from the primitive tribosphenic bauplan, while *Slaughteria* presents direct evidence of premolar count and tooth replacement pattern in a basal taxon. This fresh look at the Trinity Group taxa at once helps to improve our understanding of tribosphenidan evolution during the Early Cretaceous of North America, while also begging for better preserved material to address a number of unresolved questions; namely, the biogeographic role North America played in the early evolution and distribution of basal metatherians and eutherians, and the nature of the persistence of stem tribosphenidan taxa well into the Cretaceous.

Acknowledgements

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