Primitive boreosphenidan mammal (?Deltatheroida) from the Early Cretaceous of Oklahoma

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We describe a new boreosphenidan mammal, *Atokatheridium boreni* gen. et sp. n., from the Early Cretaceous of Oklahoma, based on an upper molar and a tentatively referred lower molar. The upper molar is characterized by a small protocone and unwinged conules, broad stylar shelf, paracone taller than metacone, and lack of pre- and postcingula. Comparisons with relevant Early and Late Cretaceous boreosphenidans suggest closest similarity to Deltatheroida, including one character (extreme development of the distal stylar shelf, which projects labially and lacks cusps) interpreted as derived. The tentatively attributed lower molar shows similarity to *Deltatheridium* and the ?aegialodontid genus *Kielantherium* in having the paraconid higher than the metaconid, but differs from *Kielantherium* in having a differently shaped talonid. From *Aegialodon* it differs in having a vertically oriented (rather than semi-procumbent) paraconid and a larger talonid. We figure also two isolated trigonids, differing in size, which show some resemblance to that of ?*Atokatheridium*. Deltatheroidans, despite their generally primitive dental morphology, are otherwise surely known only from the Late Cretaceous, and are largely restricted to the Old World. If a deltatheroidan, the new taxon implies a significant temporal range extension for the group, and provides another biogeographic link between Cretaceous mammals of Asia and North America.

Key words: Boreosphenida, Deltatheroida, Aegialodontidae, Early Cretaceous, Oklahoma.

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Introduction

Boreosphenidans (eutherians, metatherians, and proximal relatives with tribosphenic molars, see Luo *et al.* 2001) have long been known from the Late Cretaceous, where they are represented by large collections and, in many cases, rather complete specimens. By contrast, they are very poorly known from the Early Cretaceous, where their record is largely based on isolated teeth. Differentiation of Metatheria and Eutheria based on fossils is best recognized by dental formula, tooth replacement, degree of premolar molarization, and cranial morphology. Many poorly known therians from the Early Cretaceous, of which the dental formulae and other characters are not known, are referred to as 'Theria of metatherian-eutherian grade' (Patterson 1956) or 'tribotheres' (Butler 1978).

Boreosphenidans of undoubted Early Cretaceous age have been reported from only two stratigraphic units in North America: the Trinity Group (including the Antlers Formation) of Texas (Patterson 1956; Slaughter 1971; Butler 1978; Jacobs *et al.* 1989) and Oklahoma (Cifelli 1997), and the Cloverly Formation of Wyoming and Montana (Cifelli 1999). We omit a diverse fauna from the Cedar Mountain Formation, Utah, which appears to lie on the Albian–Cenomanian boundary (Cifelli *et al.* 1997). Also omitted are occurrences of mammals whose affinities are highly uncertain (Prothero 1983; Sarjeant & Thulborn 1986).

With a few exceptions (Slaughter 1971; Cifelli 1999), all North American, Early Cretaceous Boreosphenida are known by isolated teeth, and collectively include seven named and one unnamed genera: *Pappotherium* Slaughter, 1965; *Holoclemensia* Slaughter, 1968; *Kermackia* Slaughter; 1971; *Slaughteria* Butler, 1978; *Trinititherium* Butler, 1978; *Comanchea* Jacobs *et al.*, 1989, *Montanalestes* Cifelli, 1999; and Boreosphenida family and genus indet. (described by Cifelli 1997 and referred to hereafter as the 'Oklahoma molar'). Of these, only four (*Pappotherium*, *Holoclemensia*, *Comanchea*, and the 'Oklahoma molar') are certainly known by upper molars and invite formal, direct comparison with the new taxon described below; however, tentatively referred lower molars permit additional, hypothetical comparisons.

Somewhat older boreosphenidans, also represented by isolated teeth, are known from western Europe and northern Africa. The geologically oldest of these are two lower molar talonids, from the Purbeck Limestone Group (Berriasian) of England (Sigogneau-Russell & Ensom 1994). The celebrated *Aegialodon dawsoni* Kermack *et al.*, 1965 is known by a lower molar from the slightly younger (Valanginian) Wealden Group, England (Kermack *et al.* 1965). Two taxa are known from the Berriasian of Morocco: *Tribotherium* Sigogneau-Russell, 1991, known by upper and (tentatively referred) lower molars; and *Hypomylos* Sigogneau-Russell, 1992, known by lower molars only (see Sigogneau-Russell 1994).

To date, Asia has yielded the best record of Early Cretaceous Boreosphenida. The most complete specimens come from Guchin Us, Mongolia, of presumed Aptian–Albian age. These fossils represent the primitive therian *Kielantherium* Dashzeveg, 1975, known by a dentary with four molars and numerous antemolar alveoli (see Dashzeveg & Kielan-Jaworowska 1984); and the eutherian *Prokennalestes* Kielan-Jaworowska & Dashzeveg, 1989, whose species *P. trofimovi* and *P. minor* are represented by numerous upper and lower jaws with teeth (Kielan-Jaworowska & Dashzeveg 1989; Sigogneau-Russell *et al.* 1992). This genus was also reported from the possibly older (Barremian–Aptian) Murtoi Formation, Transbaikalia, Russia. Subsequently Averianov & Skutschas (2001) erected for *Prokennalestes abramovi* a new monotypic genus *Murtoilestes*, represented by isolated upper and lower molars. Finally, the eutherian *Bobolestes* Nessov, 1985, is known by two upper molars from the late Albian of Uzbekistan (see Nessov *et al.* 1994). *Endotherium* Shikama, 1947, is represented by a dentary fragment with three molars. The original figure (Shikama 1947: fig. 4) is poor and almost certainly inaccurate. We concur with Clemens *et al.* (1979: p. 28) that *Endotherium* 'remains only an ambiguous example of an early eutherian mammal,' and consider it a *nomen dubium*.

Institutional abbreviations. — OMNH, Oklahoma Museum of Natural History, Norman, Oklahoma, USA; SMP-SMU, Shuler Museum of Paleontology, Southern Methodist University, Dallas, Texas, USA.

Terminology

Dental nomenclature follows Van Valen (1966: fig. 1A), with the additional terms 'groove for the protoconid' (Crompton & Kielan-Jaworowska 1978) and 'preparastyle' (Kielan-Jaworowska & Dashzeveg 1989). The measurements were taken following the scheme of Lillegraven & Bieber (1986: fig. 1).

We introduce two indices for comparing proportions of upper molars in early boreosphenidan mammals (Fig. 1): width factor (WF), width of the distal stylar shelf relative to total tooth width (w2/w1); and length factor (LF), length of the protocone relative to total tooth length (l2/l1).

Systematic paleontology

Order ?Deltatheroida Kielan-Jaworowska, 1982

Family indet.

Genus *Atokatheridium* gen. n.

Type species by monotypy: *Atokatheridium boreni* gen. et sp. n.

Derivation of the names: *Atoka*, for Atoka County, Oklahoma, source of the only known specimen(s); *theridium* (from the Greek *theridion*, a small beast). The species is named for David L. Boren, in recognition of his support for the OMNH.

Atokatheridium boreni gen. et sp. n.

Figs. 1, 2B, 4B.

Holotype: OMNH V61623, right upper molar.

Type horizon and locality: Aptian or Albian Antlers Formation; OMNH locality V706, Atoka County, Oklahoma (see Cifelli 1997).

Material. — The holotype represents a mesial right upper molar, complete except for the labial roots. The enamel appears to be somewhat water-worn, so that cristae are possibly less sharp than originally. OMNH 61624, a left lower molar of uncertain position, is tentatively referred to the species, but formally excluded from the hypodigm and diagnosis (see below).

Generic and specific diagnosis. — Small boreosphenidan mammal with upper molars characterized by numerous plesiomorphies (small protocone, small, unwinged paraconule, metaconule marked only as a swelling, broad stylar shelf, paracone taller than metacone, and lack of pre- and postcingula). The tooth is 1.26 mm long, its anterior width is 1.67, while posterior width is 1.70 mm. Similar to Deltatheroida and differs from *Holoclemensia*, *Tribotherium*, and early eutherians and marsu-

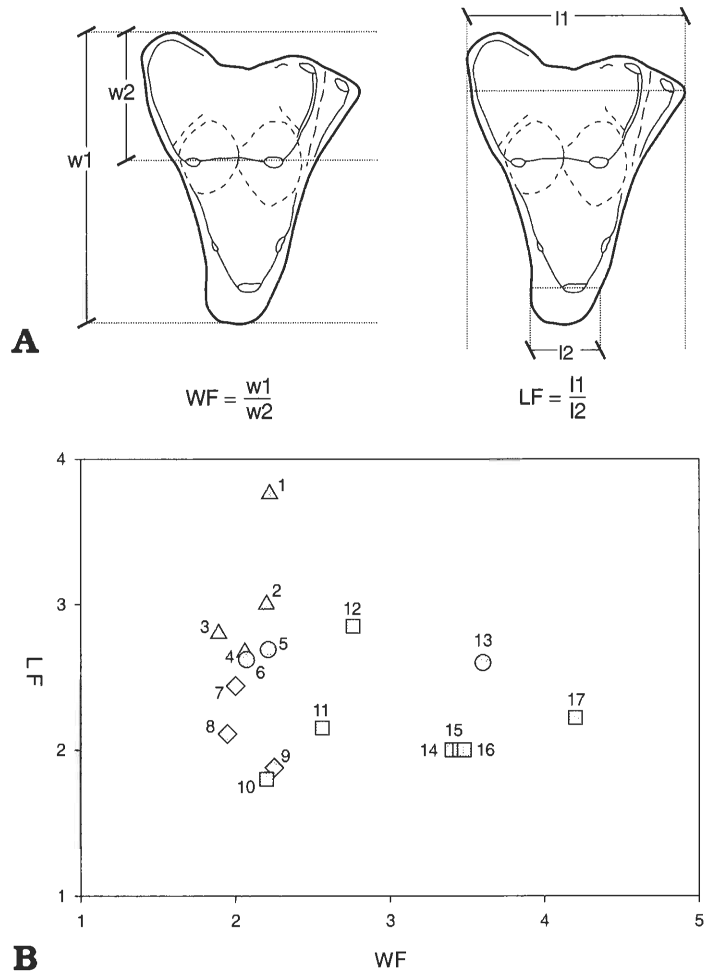

Fig. 1. **A**. Upper molar of *Atokatheridium boreni*, showing measurements on which length (**LF**) and width (**WF**) ratios are based. **B**. Plot of LF vs. WF for upper molars of various Cretaceous boreosphenidans. High values on the X-axis reflect a narrow distal stylar shelf; those on the Y-axis reflect an anteroposteriorly short protocone. Triangles, *Atokatheridium* and Deltatheroida; circles, 'tribotheres'; diamonds, marsupials; squares, eutherians. 1, *Deltatheridium* (M2); 2, *Atokatheridium* (Mx); 3, *Sulestes* sp. (M2); 4, unnamed ?deltatheroidan from Scollard Formation (Maastrichtian), Canada (Mx); 5, *Potamotelses* (Mx); 6, cf. *Kermackia* or *Trinititherium* (Mx); 7, *Kokopellia* (M3); 8, *Eodelphis* sp. (M3); 9, *Eodelphis* sp. (M2); 10, *Cimolestes cerberoides* (M1); 11, *C. cerberoides* (M2); 12, *Murtoilestes* (M2); 13, *Pappotherium* (Mx); 14, *Prokennalestes* (M1); 15, *Bobolestes* (M2); 16, *Prokennalestes trofimovi* (M2); 17, *Kennalestes gobiensis* (M2).

pials in extreme development of the distal stylar shelf, which projects labially and lacks cusps. Differs from all early boreosphenidans except *Tribotherium* in the lesser development of conules, particularly the metaconule. Differs from early eutherians, marsupials, *Holoclemensia*, and the 'Oklahoma molar' in lesser mesiodistal expansion of the protocone. Differs from *Pappotherium* in lesser development of the parastylar region, smaller stylar cusps, less prominent cristae, shallower groove for the protoconid, and less height differential between paracone and metacone. Differs from *Holoclemensia* in lacking a mesostyle, having a deep ectoflexus, and lesser development of the parastylar region. Differs from *Comanchea* in having broader parastylar region and in the presence of an ectoflexus.

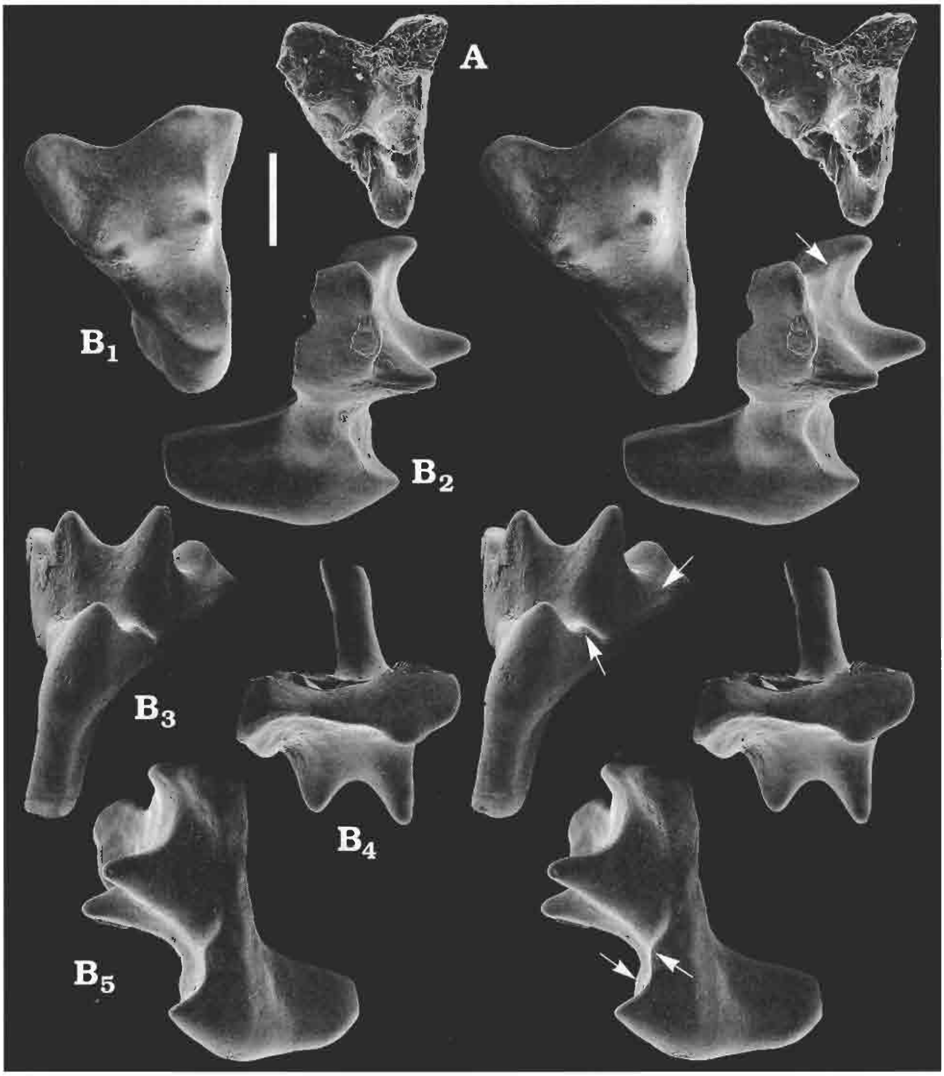

Fig. 2. **A**. Cf. *Kermackia* or *Trinititherium* sp. (SMP-SMU 62402, Butler Farm, Antlers Formation, Texas), right Mx; occlusal stereopair. **B**. *Atokatheridium boreni* gen. et sp. n. (OMNH locality V706, Antlers Formation, Oklahoma). Right Mx (OMNH 61623, holotype) in occlusal (**B_1**), distal (**B_2**), lingual (**B_3**), labial (**B_4**), and mesial (**B_5**) views. Arrow in B_2 points to incipient third cusp in parastylar region. Lower arrow in B_3 and right arrow in B_5 point to paraconule. Upper arrow in B_3 points to shallow groove for protoconid. Left arrow in B_5 points to slight swelling, rather than cusp, in metaconular region. SEM stereomicrographs. Scale bar 0.5 mm.

?*Atokatheridium boreni* gen. et sp. n.

Figs. 3A, 5B.

Material. — A left lower molar, OMNH 61624, from the same formation and locality as the holotype of *A. boreni*, is tentatively referred to ?*A. boreni* on the basis of its small size, occurrence at the same locality as the holotype specimen, morphological appropriateness, and distinctiveness from all other lower molars of boreosphenidan mammals known from the Trinity Group of both Texas and Oklahoma.

Description. — OMNH 61624 is complete except for the tip of the protoconid and some loss of enamel fragments on the precingulid. The tooth is 1.28 mm long, trigonid width is 0.86, and the talonid width 0.49 mm. The precingulid extends to the lingual margin of the tooth, forming a small, mesiolingual projection at the base of the paraconid. The paracristid is heavily worn; there is little wear to the metacristid and talonid, though major shearing surfaces (see Crompton 1971) are clear and well developed. The paraconid and metaconid are well separated, so that the trigonid angle is rather obtuse compared to that seen in ?*Pappotherium, Holoclemensia,* and primitive members of Marsupialia and Eutheria. The paraconid is much taller and more robust than the metaconid, slightly slanting anteriorly, which, however, may be an artifact of preservation. A distal metacristid (see Fox 1975) extends distolabially from the apex of the metaconid. The talonid is much lower and narrower than the trigonid and has a very small, shallow basin that is open lingually. Two cusps, hypoconid and hypoconulid, are present; despite the presence of some wear on the rim of the talonid, it is clear that no entoconid was ever present.

Family & gen. indet., sp. A.

Fig. 3B.

Material. — Isolated right trigonid OMNH 61642, from Aptian or Albian Antlers Formation; OMNH locality V706, Atoka County, Oklahoma.

Description and comparisons. — OMNH 61642 is a trigonid with a tiny fragment of the talonid; the trigonid length is 0.92 mm, the width 0.80. All three trigonid cusps are completely preserved and shaped as regular vertical cones. The protoconid is much taller and wider than the two remaining cusps, of which the paraconid is slightly higher than the metaconid. The paraconid and metaconid are well separated at their bases. The precingulid is not prominent, semilunar in occlusal view, situated in the middle of the mesial wall of the trigonid. It differs from ? *A. boreni* in being slightly larger and having a more obtuse trigonid (longer in proportion to width). The difference between the heights of the protoconid and metaconid is probably less, and the precingulid is more labially placed. From OMNH 61643 (described below) it differs in being smaller, in having the trigonid generally lower (lesser distance between the bottom of the paraconid/metaconid embrasure and the base of roots), and in having the paraconid and metaconid more separated at the base.

Family & gen. indet., sp. B.

Fig. 3C.

Material. — Isolated right trigonid OMNH 61643, from Aptian or Albian Antlers Formation; OMNH locality V706, Atoka County, Oklahoma.

Description and comparisons. — OMNH 61643 is a complete, well preserved, relatively large trigonid, 1.02 mm long and 1.16 mm wide, with a broken tiny fragment of the talonid. The trigonid is very high, and the distance between the base of the roots and the bottom of the embrasure between the paraconid and metaconid measures 0.8 mm, whereas it is only 0.36 mm in OMNH 61642 (unknown in ?*Atokatheridium boreni* because of the state of preservation). The difference between the height of the protoconid and the two other cusps is probably less than in OMNH 61642. The paraconid is higher than the metaconid and the difference between their heights is slightly greater than in OMNH 61642. The bases of the paraconid and metaconid almost touch one another, while in the two other taxa they are more widely separated. Shares with ?*Atokatheridium. boreni* a less obtuse trigonid than in OMNH 61642, and differs from ?*A. boreni* and OMNH 61643 in having the precingulid only developed lingually (in front of the paraconid).

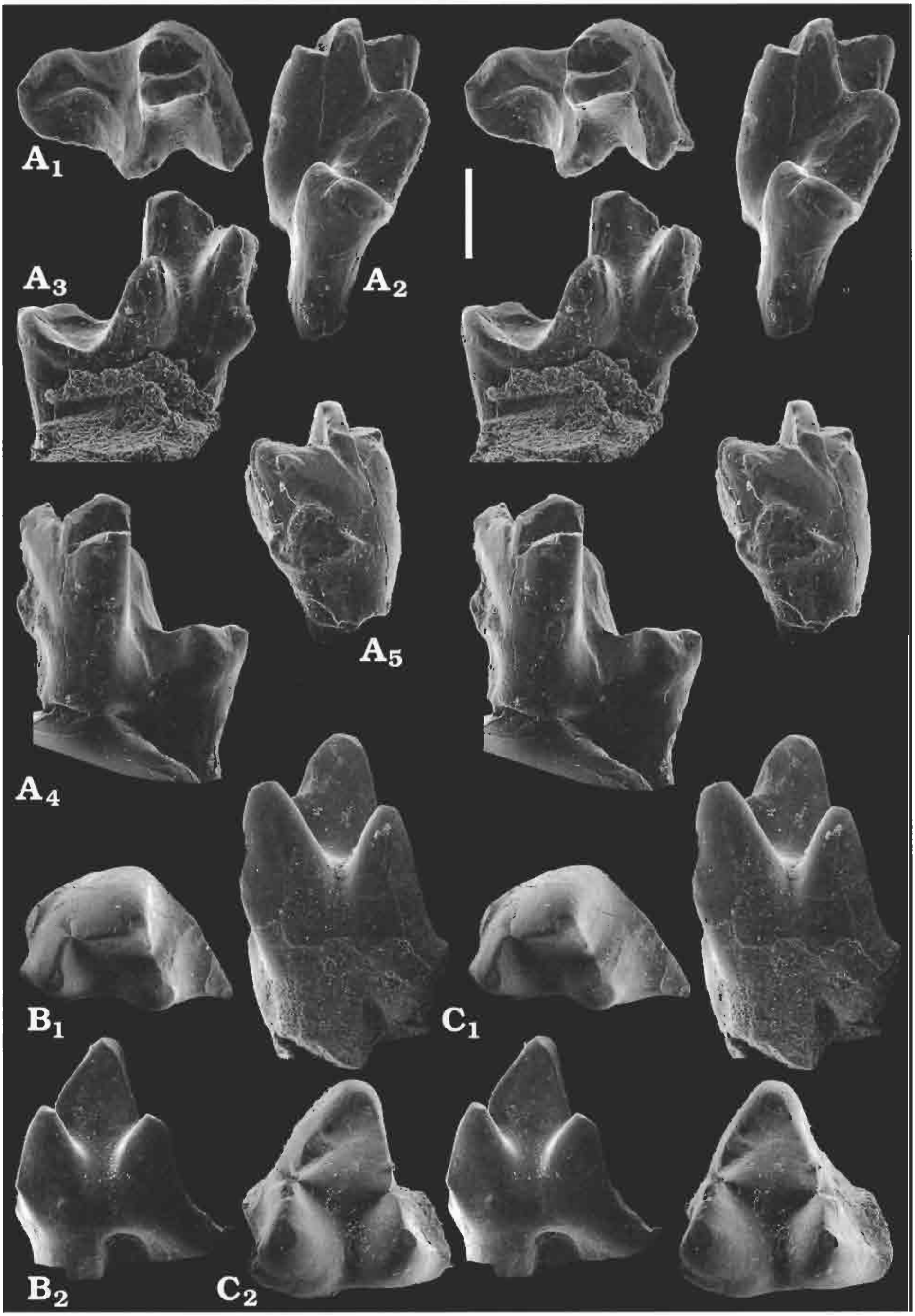

Fig. 3. **A**. ?*Atokatherikdium boreni* gen. et sp. n., left mx (OMNH 61624; OMNH locality V706, Antlers Formation, Oklahoma)) in occlusal (**A_1**), distal (**A_2**), lingual (**A_3**), labial (**A_4**), and mesial (**A_5**) views. **B**. ?Deltatheroida, family & gen. indet., sp. A., right trigonid, OMNH 61642, same horizon and locality, occlusal view (**B_1**), lingual view (**B_2**). **C**. ?Deltatheroida, family & gen. indet., sp. B, right trigonid, OMNH 61643, same horizon and locality. Lingual view (**C_1**), occlusal view (**C_2**). SEM stereomicrographs. Scale bar 0.5 mm.

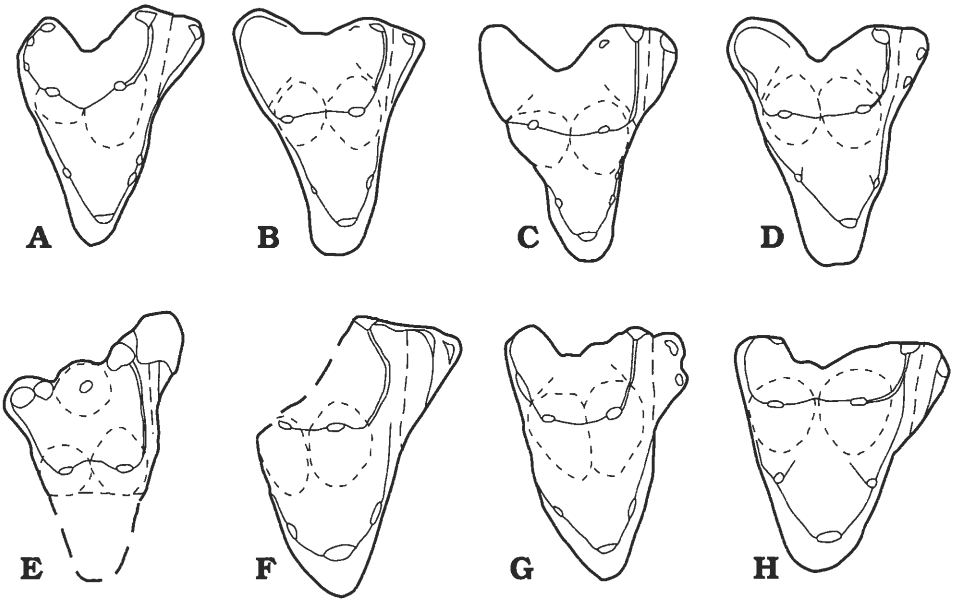

Fig. 4. Diagrammatic comparison of Early Cretaceous tribosphenic upper molars and Late Cretaceous *Deltatheridium* in occlusal view, rendered to approximately the same width and reversed as needed. **A**. *Pappotherium* (penultimate M). **B**. *Atokatheridium* (Mx). **C**. *Deltatheridium* (M2). **D**. *Murtoilestes* (M2). **E**. *Holoclemensia* (?penultimate M). **F**. 'Oklahoma molar' (Mx). **G**. *Prokennalestes* (M2). **H**. *Bobolestes* (M2). Based on original specimens, casts, and photographs. Not to scale.

Discussion

***Atokatheridium* and other Trinity therians**. — Could *Atokatheridium boreni* represent a known taxon that is based on lower molars? *Kermackia* (Fig. 5D) and *Trinititherium*, from the Antlers Formation of Texas, invite comparison as they are also small and rather primitive. Upper molars have not been formally referred to either, but Butler (1978) considered it likely that SMP-SMU 62402 (Fig. 2A) belongs to one or the other. Among upper molars from the North American Early Cretaceous, this specimen is morphologically most similar to *Atokatheridium boreni*. SMU-SMP 62402 is significantly smaller than the holotype of *A. boreni* (Fig. 2B) and bears a deeper ectoflexus (which could be a positional variation). The most important difference lies in the conules, both of which are well developed in SMP-SMU 62402. In *Atokatheridium*, the paraconule is very small, and a metaconule as such is lacking, with only a faint swelling in this region.

The tentatively referred lower molar (Figs. 3A, 5B) is of interest in evaluating both proximal and more general relationships of *Atokatheridium*. ?*A. boreni* clearly differs from lower molars of advanced 'tribotheres' (e.g., ?*Pappotherium* and *Holoclemensia*), Marsupialia, and Eutheria in a number of respects, such as the great height and width differential between trigonid and talonid, obtuse trigonid angle, presence of a distal metacristid and only two talonid cusps, not to mention other features (e.g., Cifelli 1993). Accordingly, we limit our comparisons mainly to structurally similar boreosphenidans, including primitive 'tribotheres' and Deltatheroida.

?*A. boreni* is, in general features, broadly similar to lower molars of *Kermackia* and *Trinititherium*, primitive boreosphenidans from the Antlers Formation of northern Texas, but is clearly distinct from both. It has been suggested by Clemens (in Butler 1978) that the sole known specimen of *Trinititherium slaughteri* represents a distal lower molar of *Kermackia texana*. We consider this likely, but tentatively retain them as distinct. ?*A. boreni* differs from lower molars of these taxa in having a lingually extended precingulid (represented by a small, median knob in *Kermackia* and *Trinititherium*), in height differential between paraconid and metaconid (paraconid much taller than metaconid in ?*A. boreni*, whereas the reverse is true of *Kermackia*; the cusps are subequal in height in *Trinititherium*, but the metaconid is the more robust of the two); and a smaller talonid (broader and longer in *Kermackia* and *Trinititherium*). Lower molars of *Kermackia* have a peculiar, 'flexed' appearance whereby the talonid appears to be bowed labially with respect to the trigonid; this feature is lacking in ?*A. boreni*. An entoconid, lacking on ?*A. boreni*, is present on lower molars of *Kermackia*. The talonid is damaged on the only known specimen of *Trinititherium*. Like ?*A. boreni*, an entoconid is clearly lacking, but it differs in having what appears to have been a much taller hypoconid.

Broader comparisons and affinities of *Atokatheridium*. — *A. boreni* appears to generally retain more plesiomorphies than lower molars referred to *Potamotelses aquilensis*, from the early Campanian of Canada (Fox 1972). On the other hand, it is clearly more advanced in most features than lower molars of *Hypomylos phelizoni*, from the Berriasian of Morocco (Sigogneau-Russell 1992, 1994). *Hypomylos* differs from ?*A. boreni* in having a taller metaconid than paraconid; a small, labially placed, knob-like precingulid, a much more obtuse trigonid angle; and a narrower, shorter talonid that is not as distinctly basined. *Potamotelses* differs from ?*A. boreni* in having a precingulid that does not extend to the lingual margin of the tooth; subequal paraconid and metaconid; a relatively lower trigonid; and a broader, longer talonid with three distinct cusps.

?*A. boreni* (see Fig. 5) is structurally similar to lower molars of the deltatheroidans *Sulestes* sp., from the Coniacian of Uzbekistan (Kielan-Jaworowska & Nessov 1990) and *Deltatheridium pretrituberculare*, from the Campanian of Mongolia (Kielan-Jaworowska 1975). A noteworthy similarity is the strong development of the paraconid and the weak metaconid. Lower molars of *Deltatheridium* and *Sulestes* are of more robust construction than ?*A. boreni*, reflecting their much larger size. In *Sulestes*, the talonid is somewhat broader than that of ?*A. boreni*, from which it further differs in having three cusps. The talonid of lower molars in *Deltatheridium* is comparable in proportions to that of ?*A. boreni*, but differs in the variable presence of a weak entoconid. Fox (1976) reports that an 'anterointernal cusp' is present in Deltatheridiidae, as it is in ?*A. boreni*. Available lower molars of *Deltatheridium* apparently lack the anterolingual cingular cusp, but it is present in the deltatheroidans *Deltatherus* and *Sulestes* (Nessov 1997).

Closest comparison appears to be with *Kielantherium gobiensis*, a primitive boreosphenidan that may be closely related to Deltatheroida (see Dashzeveg 1975; Dashzeveg & Kielan-Jaworowska 1984; Marshall & Kielan-Jaworowska 1992; Cifelli 1993). Relative development of the talonid and of the lingual trigonid cusps vary according to tooth locus in *Kielantherium*. However, the paraconid is more strongly developed than the metaconid, a feature shared with Deltatheroida. In general, ?*A. boreni*

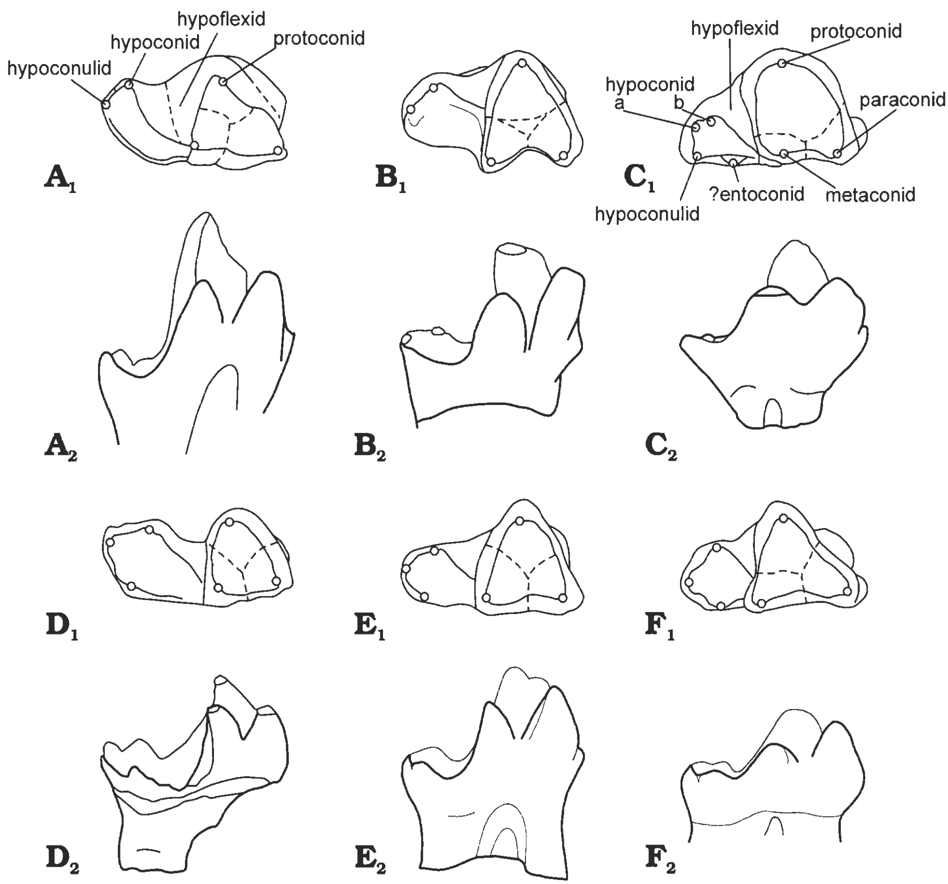

Fig. 5. Diagrammatic comparison of lower molars. **A**. *Kielantherium* (?m2). **B**. ?*Atokatheridium* (mx). **C**. *Aegialodon* (mx). **D**. *Kermackia* (mx). **E**. *Deltatheridium* (m2). **F**. *Sulestes* (m1). $\mathbf{A_1}$–$\mathbf{F_1}$ in occlusal, $\mathbf{A_2}$–$\mathbf{F_2}$ in lingual views. Based on original specimens, casts, and photographs. Not to scale.

appears to be more advanced than lower molars of *Kielantherium* in having a slightly greater differential between paraconid and metaconid, and a broader, more basined talonid. Notably, the precingulid extends to the lingual margin of the tooth in *Kielantherium*, forming a peculiar anterolingual projection at the base of the paraconid, as it does in ?*A. boreni*.

Dashzeveg (1975) assigned *Kielantherium* to Aegialodontidae, a referral followed by Butler (1978, 1990), Kielan-Jaworowska *et al.* (1979), Dashzeveg & Kielan-Jaworowska (1984) and many others. Butler (1978) erected for the Aegialodontidae, Kermackiidae, Deltatheridiidae, and *Potamotelses*, the order Aegialodontia, within his new infraclass Tribotheria. Subsequently, however, he (Butler 1990) withdrew his infraclass Tribotheria, and restricted Aegialodontia to *Aegialodon* and *Kielantherium*. The distinction of these two genera has been questioned by Fox (1976), whose suggestion that *Kielantherium* should be considered a junior synonym of *Aegialodon* has been followed recently by McKenna & Bell (1997). Comparison of the single known lower molar of *Aegialodon* with lower molars of *Kielantherium* (Fig. 5) shows important differences between the two genera. *Aegialodon* differs from *Kielantherium* in having a semi-procumbent (oriented obliquely antero-dorsally) rather than dorsally oriented paraconid, while the protoconid is relatively more robust with respect to the paraconid and metaconid. Further differences concern the structure of the talonid, which in *Aegialodon* is roughly triangular in occlusal view, rather than very narrow and rectangular, as in *Kielantherium*. Because of the poor state of preservation, the number of talonid cusps in *Aegialodon* cannot be established with any certainty, but three talonid cusps cannot be excluded. Other than *Aegialodon*, semi-procumbency of the paraconid occurs only in *Slaughteria* Butler, 1978 among Early Cretaceous 'tribotheres'. The metaconid is incomplete in *Aegialodon*, and its height with respect to the paraconid cannot be determined. ?*A. boreni* is more similar to *Kielantherium* than to *Aegialodon* (Fig. 5) in lacking procumbency of the paraconid, in having a relatively less robust protoconid, and in having a roughly rectangular talonid with only two cusps. All three have a lingually extended precingulid; the polarity and significance of this feature is uncertain.

Among known Cretaceous boreosphenidans, both upper (Figs. 2, 4) and (tentatively referred) lower molars of *Atokatheridium* (Figs. 3, 5) are most comparable to Deltatheroida. Many points of similarity (e.g., small protocone and conules, presence of distal metacristid, the latter not observable with certainty in all Deltatheroida; great height and width differential between trigonid and talonid) are presumably plesiomorphies. A broad stylar shelf is also generally interpreted as a primitive feature (e.g., Clemens & Lillegraven 1986). As the preparacrista is interpreted to be one of the primary shearing crests of the tribosphenic upper molar (Patterson 1956), it is reasonable to predict that the mesial part of the stylar shelf was broad ancestrally. Interpreting the ancestral condition for the distal stylar shelf is less clear, and depends in part on cusp homologies (see, e.g., Crompton 1971). It is instructive to note that the oldest boreosphenidan known by upper molars, *Tribotherium*, has a narrow distal stylar shelf (Sigogneau-Russell 1994: fig. 1A). Deltatheroidans and *Atokatheridium* have an unusually broad distal stylar shelf (Figs. 1, 3), which we tentatively recognize as a derived feature. The situation is somewhat less ambiguous for the lower molar of ?*A. boreni*: the greatly enlarged paraconid, and strong wear on the paracristid shearing surface, are quite probably derived conditions that are also seen in Deltatheroida. These features of the upper and lower molars are associated, and are related to emphasis on postvallum–prevallid shearing (Muizon & Lange-Badré 1997).

Is *Atokatheridium* a deltatheroidan? The issue is complicated by consideration of *Kielantherium*, which closely resembles *Atokatheridium* in structure of lower molars. The paraconid is also taller than the metaconid in *Kielantherium*, but its affinities are problematic: referral to Deltatheroida poses conflict in other characters (Cifelli 1993), such as premolar count (*Kielantherium* has at least four premolars, while there are three in Deltatheroida). In view of these uncertainties, we consider *Atokatheridium* to possibly be a deltatheroidan, but do not formally refer it to the group. In this context, it is instructive to note that the combination of a short protocone (presumed plesiomorphy) and a broad distal stylar shelf (tentatively regarded as an apomorphy) serve to distinguish upper molars of undoubted Deltatheroida from those of 'tribotheres', eutherians, and marsupials, and that in this respect the upper molar of *Atokatheridium* falls among Deltatheroida (Fig. 1B).

In addition to the upper molar of *A. boreni*, and tentatively attributed lower molar referred to as ?*A. boreni*, we describe and figure two other taxa from the same formation and locality, referred to as ?Deltatheroida, family & gen. indet., sp. A and sp. B (Figs. 3B and C respectively). Both are represented by isolated trigonids, which show typical deltatheroidan-like structure in having the paraconid higher than the metaconid. The distal metacristid appears to be present on both. Both appear too large to be counterparts of the upper molar of *Atokatheridium boreni*. As long as the talonids of both of them remain unknown, it is impossible to venture an opinion as to whether they possessed an entoconid (as characteristic of typical Late Cretaceous Deltatheroida) or rather retained a two-cusped, primitive talonid, as characteristic of *Kielantherium and ?Atokatheridium boreni*. If deltatheroidans, they show that this group was already diversified in the Early Cretaceous.

The oldest undoubted deltatheroidans are *Sulestes* and *Deltatherus*, from the Coniacian of Uzbekistan (Kielan-Jaworowska & Nessov 1990; Nessov 1997), though questionable records extend back to the Cenomanian (Nessov *et al.* 1994). North American deltatheroidans are poorly known. Isolated upper and lower molars closely similar to those of *Deltatheroides* have been described from the Maastrichtian on this continent (Fox 1974). Recent work (Rougier *et al.* 1998) has shown, contrary to earlier opinions (Gregory & Simpson 1926; Kielan-Jaworowska *et al.* 2000) that *Deltatheridium* has four molars, so the differences between the two genera are smaller than previously thought. Kielan-Jaworowska *et al.* (2000) stated that the differences between the two Mongolian deltatheroidan genera are not clear; however, as they differ in shape of M3, we regard them as separate genera pending further findings. The only other North American record comes from the Turonian of Utah, represented by a fragmentary lower molar (Cifelli 1990). If a deltatheroidan, *Atokatheridium* would thus be the oldest member of the group and one of the only ones known from North America.

Another Early Cretaceous mammal inviting a comparison with *Atokatheridium* is *Murtoilestes*, classified by its authors as a eutherian (Averianov & Skutschas 2001). *Murtoilestes* resembles the undoubted eutherian *Prokennalestes* in the presence of a preparastyle and a protoconal region that is similar in proportions, but differs in having a broader, longer stylar shelf, in this respect resembling *Atokatheridium* and Deltatheroida. However, the conules are stronger and bear small wings in *Murtoilestes*. Finally, *Atokatheridium* (and ?*Atokatheridium*) may be compared with stagodontid marsupials, which also have a broad distal stylar shelf, narrow protocone, and in lower molars the paraconid enlarged with respect to the metaconid. In every other aspect of upper and lower molar morphology (e.g., presence of strong, winged conules, anteroposteriorly elongate protocone, labially extended protocristae, lingually placed paraconid, labial postcingulid), however, even the earliest stagodontid *Pariadens* is structurally more advanced in features typical of Marsupialia (Eaton 1993), and is dissimilar to *Atokatheridium*.

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Prymitywny ssak z podgromady Boreosphenida (?Deltatheroida) z wczesnej kredy Oklahomy

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Streszczenie

W pracy opisano nowy gatunek i rodzaj prymitywnego ssaka o zębach trybosfenicznych – *Atokatheridium boreni*, z wczesnej kredy stanu Oklahoma w Stanach Zjednoczonych. Nowy takson oparty jest na dobrze zachowanym górnym zębie trzonowym i na dolnym trzonowcu, zaliczonym z zastrzeżeniem. *Atokatheridium* został zaliczony do podgromady Boreosphenida, obejmującej ssaki o zębach trybosfenicznych, które powstały na Półkuli Północnej zapewne we wczesnej kredzie. Do Boreosphenida należą wszystkie współcześnie żyjące ssaki właściwe – torbacze i łożyskowce, ich kopalni przedstawiciele, oraz formy wymarłe o zębach trybosfenicznych, których stanowisko systematyczne jest nieustalone. *Atokatheridium* jest jednym z najstarszych znanych przedstawicieli boreosfenidów. Górny trzonowiec nowego taksonu charakteryzuje się małym protokonem, konulami pozbawionymi skrzydełek, bardzo szeroką półką stylarną, oraz brakiem przednich i tylnych wałeczków (cingulum). Porównanie z zębami wczesno- i późnokredowych boresosfenidów wskazuje, że *Atokatheridium* najbardziej jest zbliżony do przedstawicieli późnokredowego rzędu Deltatheroida, który należy do Metatheria i stanowi grupę siostrzaną torbaczy. Cechą wspólną jest obecność bardzo rozszerzonej części dystalnej półki stylarnej, która wystaje w kierunku dowargowym i jest pozbawiona guzków stylarnych. Z drugiej strony, dolny trzonowiec zaliczony z zastrzeżeniem do *Atokatheridium* wykazuje podobieństwo zarówno do trzonowców deltateroidów, jak i do słabo poznanej grupy wczesnokredowych boreosfenidów – egialodontów, szczególnie do rodzaju *Kielantherium*.

W pracy zilustrowano także dwa niekompletne dolne trzonowce (trygonidy) pochodzące z tej samej formacji co *Atokatheridium*, które wykazują pewne podobieństwo do trzonowca zaliczonego z zastrzeżeniem do *Atokatheridium*. Rząd Deltatheroida, który charakteryzuje się ogólnie prymitywną budową zębów i ma wzór zębowy taki jak torbacze, znany był dotąd tylko z późnej kredy i tylko z Półkuli Północnej. Jeżeli *Atokatheridium* należy rzeczywiście do Deltatheroida, to wskazywałoby to że deltateroidy pojawiły się we wczesnej kredzie.