1. Earliest Evidence of Deltatheroida (Mammalia: Metatheria) from the Early Cretaceous of North America

Brian M. Davis*
Sam Noble Oklahoma Museum of Natural History
Department of Zoology
University of Oklahoma
2401 Chautauqua Ave.
Norman, OK 73072, USA
bmdavi@ou.edu

Richard L. Cifelli
Sam Noble Oklahoma Museum of Natural History
Department of Zoology
University of Oklahoma
2401 Chautauqua Ave.
Norman, OK 73072, USA
rlc@ou.edu

Zofia Kielan-Jaworowska
Instytut Paleobiologii PAN
ul. Twarda 51/55
PL-00-818 Warszawa
Poland
zkielan@twarda.pan.pl

1.1 Introduction

Deltatheroida are small therian mammals known only from the Cretaceous of Asia and North America. As fossils, they are represented mainly by isolated teeth and dentigerous jaws, though rostra, a petrosal, and the calcaneus, at least, have been described for the best known genus, Asiatic *Deltatheridium* (Rougier et al., 1998; Horovitz, 2000). Aside from two dubious forms: *Oxlestes* (Nessov, 1982) and *Khuduklestes* (Nessov et al., 1994), Deltatheroida are unambiguously represented by only four genera (*Deltatheridium, Deltatheroides, Deltatherus*, and *Sulestes*), all Asiatic in distribution and all placed in the family Deltatheridiidae (see Kielan-Jaworowska et al., 2004). The Asian record of Deltatheridiidae ranges from Coniacian to late Campanian. In North America, one genus, Aptian-Albian *Atokatheridium*, has been tentatively referred to Deltatheroida (Kielan-Jaworowska and Cifelli, 2001). Other records of the group on this continent consist of poorly represented, unnamed taxa from the Turonian (Cifelli, 1990a), late Campanian, and late Maastrichtian (Fox, 1974).

The dentition of deltatheroidans has beguiled mammalian systematists since the first specimens were found some 80 years ago, the main problem areas being molar structure and dental formula. It has long been generally agreed that the molars are characterized by a number of plesiomorphies: Gregory and

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*Address for correspondence: bmdavi@ou.edu

E.J. Sargis and M. Dagosto (eds.), *Mammalian Evolutionary Morphology: A Tribute to Frederick S. Szalay*, 3–24.

Simpson (1926, p. 2), for example, described them as exhibiting a "pretritubercular stage of evolution" (in the sense of Osborn, 1907), and they lack certain apomorphies common to eutherians and metatherians (Cifelli, 1993a). Combined with this primitiveness (for example, the small protocone, broad stylar shelf, and weak conules on upper molars; small, poorly basined talonid, often with only hypoconid and hypoconulid, on lower molars), however, are certain specializations suggestive of carnivory (Butler, 1990a, b). Most significant in this regard is the hyperdevelopment of postvallum-prevallid shearing, as indicated by a salient, elongate postmetacrista on upper molars and enlarged paraconid-paracristid on lowers. This functional complex is associated with carnivory in living mammals and has been identified in various fossil forms: in addition to Deltatheroida, three groups of marsupials and as many as three groups of eutherians are characterized by the hypertrophied postvallum-prevallid shearing system (Muizon and Lange-Badré, 1997). Reduction of crushing and grinding function often accompanies hypertrophy of postvallum-prevallid shearing in molars of mammalian carnivores (MacIntyre, 1966; Muizon and Lange-Badré, 1997). This leaves open the door for interpretation of certain features of deltatheroidan molars (e.g., small protocone and small talonid) as correlates of carnivorous specialization, rather than plesiomorphies. The general consensus, however, seems to be the interpretation that deltatheroidans represent the first therians specialized for carnivory; and that otherwise, their molar structure is exceedingly primitive (e.g., Szalay, 1994). In any event, molar structure has proven to be of limited use in assessing broader relationships of Deltatheroida (however, Rougier et al. (2004) have identified several informative molar characteristics in deltatheroidans).

Interpretation of the postcanine dental formula in deltatheroidans has changed through the years, with significant implications for higher relationships of the group. Gregory and Simpson (1926) found the molar structure to be structurally antecedent to that of creodonts and certain insectivores, a view that attained wide acceptance (Matthew, 1928; Simpson, 1928, 1945). The first specimens to be described are poorly preserved; that of *Deltatheridium* preserved six upper and lower postcanine loci, and that of *Deltatheroides* preserved seven upper molar loci. Gregory and Simpson (1926) interpreted the specimens as preserving P/p1–3, M/m1–3 and P/p1–4, M/m1–3, respectively: that is, a eutherian (four premolars and three molars) or eutherian-derived pattern, rather than the count seen in marsupials (three premolars and four molars). This interpretation, based on poorly preserved specimens then available, was to lead mammalian systematists astray for nearly 50 years. Van Valen (1966) erected the order Deltatheridia to include creodonts and certain insectivores; and this view, or minor variants thereof, attained some general acceptance in the late 1960s and early 1970s (McKenna et al., 1971; Szalay and McKenna, 1971; McKenna, 1975). Based on new, more numerous, and better preserved specimens, Butler and Kielan-Jaworowska (1973; see also Kielan-Jaworowska, 1975) documented the presence of three premolars and four molars in *Deltatheroides* and the lower jaw of *Deltatheridium*; the existence of a fourth upper molar in *Deltatheridium* was later reported by Rougier et al. (1998). Despite this similarity to marsupials, deltatheroidans were for a time relegated to the taxonomic *Erebus* of "Theria of metatherian-eutherian grade" (Kielan-Jaworowska, 1975; Kielan-Jaworowska et al., 1979) or "tribotheres" (Butler, 1978; Clemens and Lillegraven, 1986). A metatherian relationship for Deltatheroida was first championed by Kielan-Jaworowska and colleagues (Kielan-Jaworowska and Nessov, 1990; Kielan-Jaworowska, 1992; Marshall and Kielan-Jaworowska, 1992), in part based on perceived similarities to Stagodontidae (North American, Cretaceous marsupials) and/ or Borhyaenoidea (South American, Cenozoic marsupials). More substantial support for this hypothesis has come from newly collected specimens of *Deltatheridium* from Mongolia, which show marsupial similarities in the pattern of tooth replacement, structure of the dentary, and aspects of cranial anatomy (Rougier et al., 1998). Nonetheless, the position of Deltatheroida as basal Metatheria remains precarious, differing even in some studies conducted by the same authors (e.g., Luo et al., 2002; Luo et al., 2003).

Though higher-level relationships of Deltatheroida are not directly relevant to the present paper (except, perhaps, in our conclusions as to molar count), we accept deltatheroidans as a stem group of Metatheria. This provides us with an excellent opportunity to link our chapter thematically with the purpose of this book: to honor Fred Szalay. Fred has worn many hats during his long, magnificently productive scientific career as a student of mammalian evolution. Lest physical anthropology attempt to lay proprietary claim on Fred Szalay, we point out that he is widely recognized for his seminal contributions on the evolutionary radiations of metatherian mammals. Szalay was the first to recognize fundamental, adaptively important differences in the ankle of metatherians and eutherians (Szalay, 1984), is the progenitor of a once-radical but now universally accepted hypothesis that South American microbiotheres are closely related to Australian marsupials (Szalay, 1982), and is the co-describer of the first Cretaceous marsupial from Asia (Trofimov and Szalay, 1994; Szalay and Trofimov, 1996). Szalay and Sargis (2001) reconstructed the early adaptive radiation of marsupials in South America based on form-function analysis, and tested hypotheses of marsupial relationships using the same data. In this context, it is also relevant to mention that Fred is author of a widely-cited book on the evolutionary history of marsupials (Szalay, 1994). We are pleased to offer this small contribution as a tribute to Fred Szalay, who has added so much to understanding of metatherian history.

1.1.1 Conventions and Abbreviations

We follow the general practice of abbreviating molars and premolars with the letters "M" and "P", respectively; teeth belonging to the lower dentition are indicated with a lower case letter. Right and left are abbreviated "R" and "L", respectively. Molar terminology follows that of Bown and Kraus (1979). Standards of measurement are illustrated in Figure 1.1, and measurements of all described specimens are listed in Table 1.1.

Institutional abbreviations: FMNH, Field Museum of Natural History, Chicago, Illinois; OMNH, Oklahoma Museum of Natural History, Norman, Oklahoma; SMP-SMU, Shuler Museum of Paleontology, Southern Methodist University, Dallas, Texas.

1.1.2 Historical Background

Of the many significant scientific advances made by the American Museum Central Asiatic Expeditions (Andrews, 1932), the discovery of Cretaceous mammals clearly ranks among the most groundbreaking. Mesozoic mammals had, of course, been known to science as early as the first half of the nineteenth century (Broderip, 1828); and both Cope (1882, 1892) and Marsh (1889a, b, 1892) described a number of Late Cretaceous taxa from western North America. These, however, were based on scant remains: jaws, or – more commonly – bits and pieces thereof. It thus came as a welcome surprise when skulls were reported from the Djadokhta Formation, in the Mongolian part of the Gobi Desert (Gregory and Simpson, 1926). Three of the five genera described by Gregory and Simpson were placed in the then new family Deltatherididae: *Deltatheridium*, known by two rostral parts of the skull and associated dentaries; *Deltatheroides*, known by a partial rostrum preserving partial crowns for the last four postcanine teeth; and *Hyotheridium*, represented by a snout with the upper and lower tooth rows interlocked. Of these, *Hyotheridium* is so poorly known as to be indeterminate (it may be a eutherian); we follow Kielan-Jaworowska et al. (2004) in considering the type and only species, *H. dobsoni*, as a *nomen dubium*. As noted above, Gregory and Simpson (1926) accorded Deltatherididae a basal position among Eutheria, an interpretation that was to remain unchallenged until new, more complete fossils were described in the 1970s.

The first record of deltatheroidans from North America is that of Fox (1974), who reported several *Deltatheroides*-like isolated teeth from Campanian and Maastrichtian horizons (units follow current stratigraphic nomenclature): an upper molar from the Scollard Formation, Alberta; a lower molar and a trigonid of another from the Lance Formation, Wyoming; and a talonid from the Dinosaur Park Formation, Alberta. Subsequently, Cifelli (1990a) described another fragmentary specimen (a lower molar trigonid) from the Smoky Hollow Member of the Straight Cliffs Formation (Turonian), Utah, referring the fossil to Deltatherididae, indet.

Returning to Asia, Kielan-Jaworowska (1975) had, in the meantime, described new material from the Gobi Desert, Mongolia, assembled by the Polish-Mongolian Palaeontological Expeditions. Recovered from both the Djadokhta and Baruungoyot formations, these fossils include five specimens (three rostra with dentaries, a maxilla, and a dentary) of *Deltatheridium* and a dentary assigned to *Deltatheroides*.

The geographic range of Deltatheroida was extended to middle Asia by Nessov (1985), who described *Sulestes karakshi* from the Bissekty Formation (Coniacian) of Uzbekistan. The holotype is a maxillary fragment with M1–2; Nessov (1987) later referred an isolated lower molar to the genus. In recognition of its distinctness from *Deltatheridium* and *Deltatheroides*, Nessov (1985) placed *Sulestes* in its own subfamily, Sulestinae. Kielan-Jaworowska and Nessov (1990) elaborated on the systematics of the group by removing *Deltatheroides* and some unnamed taxa to their own family, Deltatheroididae. Subsequent authors (McKenna and Bell, 1997; Kielan-Jaworowska et al., 2004; Rougier et al., 2004) have abandoned formal subdivision of Deltatheroida, recognizing (as we do herein) the single family Deltatherididae. A second deltatheroidan from the Bissekty Formation of Uzbekistan was initially described by Nessov (1993) as *Deltatheroides kizylkumensis* and later (Nessov, 1997) transferred to its own genus, *Deltatherus. D. kizylkumensis* is known by two lower molars and an edentulous fragment of a maxilla. A more recent record of a Mongolian deltatheroidan genus in the Cretaceous of middle Asia was provided by Averianov (1997), who named *Deltatheridium nessovi* from the Darbasa Formation (Campanian) of Kazakhstan. *D. nessovi* is known only by the labial part of an upper molar, perhaps M2.

Several significant fossils from Mongolia have been reported in recent years. Two new specimens of *Deltatheridium pretrituberculare*, represented by partial skulls with well-preserved upper and lower dentition and postcranial fragments, were collected in the Gobi Desert at the Ukhaa Tolgod locality, Nemegt Basin, by members of the Mongolian Academy of Sciences–American Museum of Natural History Expeditions. The most significant details of these specimens were published by Rougier et al. (1998) and Horovitz (2000). The nearby locality of Kholbot (Red Rum) yielded to the same field parties a maxilla of *Deltatheroides cretacicus*, including all four molars in a good state of preservation. As a result, this hitherto poorly understood taxon is incomparably better known (Rougier et al., 2004). For the sake of completeness, several other Asiatic taxa deserve passing mention: an undescribed specimen known as the "Gurlin Tsav skull", first thought to represent a deltatheroidan (Kielan-Jaworowska and Nessov, 1990) but now considered to be more closely related to stagodontid marsupials (Rougier et al., 1998; Rougier et al., 2004); and *Oxlestes* and *Khuduklestes*, each based on an isolated axis vertebra (see Nessov, 1982; and Nessov et al., 1994, respectively) and, for all intents and purposes, indeterminate (Kielan-Jaworowska et al., 2004).

Atokatheridium boreni was described by Kielan-Jaworowska and Cifelli (2001) on the basis of a single upper molar from the Antlers Formation of southern Oklahoma (a lower molar was regarded as probably representing the species but was not formally referred to *A. boreni*). This taxon, of possible reference to Deltatheroida as suggested by Kielan-Jaworowska and Cifelli (2001), is notable in its occurrence: *Atokatheridium* is of Aptian-Albian age, significantly older than the Asiatic taxa securely referred to the group. Tentative placement of *Atokatheridium* in Deltatheroida was subsequently adopted by Kielan-Jaworowska et al. (2004) and was provisionally supported by the preliminary cladistic analysis of Rougier et al. (2004). Herein we describe additional fossils of *Atokatheridium boreni*, together with those representing a new but allied species. These new specimens allow us to refer both taxa to Deltatheroida, family Deltatheridiidae, with some confidence, to present morphological comparisons among relevant genera, and to make preliminary faunal comparisons between the classic "Trinity therian" sites of Texas and the Antlers Formation of Oklahoma.

1.1.3 Geological Context

The specimens described herein were collected from the Antlers Formation in extreme southeast Atoka County, Oklahoma (Figure 1.1). The Antlers Formation is a terrigenous unit comprised of sandstones, together with variegated siltstones and mudstones that were deposited under deltaic, fluvial, and strandplain systems, not far from the paleocoastline (Hobday et al., 1981). In Oklahoma, the Antlers Formation crops out as a narrow band extending westward from the Arkansas border across the southeastern part of the state, turning southward into northcentral Texas. From there it extends southward and westward into central Texas, where its lateral equivalent, the Trinity Group, can be subdivided into three formations on the basis of an interposed marine unit, not present in northcentral Texas or Oklahoma. These three units are, in ascending order, the Twin Mountains, Glen Rose, and Paluxy formations; the Glen Rose being a nearshore limestone of marine origin (see detailed discussion of stratigraphy in Winkler et al., 1990), famous for its dinosaur trackways (Bird, 1985). Invertebrates from the Glen Rose Formation and marginal marine facies of the Twin Mountains Formation show the latter unit to be Aptian in age, and that the basal Albian lies near the bottom of the Glen Rose Formation. The marine Walnut Formation of the Fredericksburg Group, together with data from the Glen Rose Formation, suggest that the Paluxy Formation correlates with the lower Albian (Jacobs and Winkler, 1998). Many sites in the Trinity Group of Texas and Oklahoma have yielded fossil vertebrates, mainly fishes and reptiles (e.g., Langston, 1974; Thurmond, 1974).

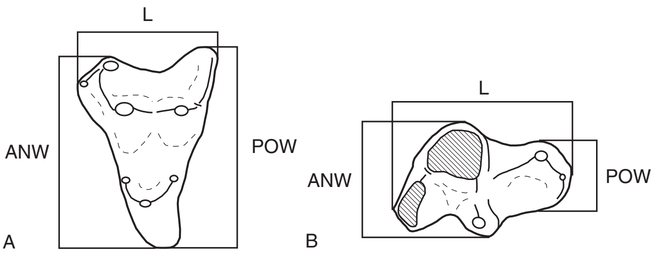

FIGURE 1.1. Standards of measurement for upper (A) and lower (B) molars. ANW, anterior width; L, length; POW, posterior width. Line drawings based on *Atokatheridium boreni*.

The Twin Mountains and Paluxy formations are lithologically similar, so that they cannot be distinguished northward and eastward of the pinchout of the Glen Rose Formation, where they are laterally represented by the Antlers Formation. As such, the undifferentiated Antlers Formation is simply regarded as being of Aptian-Albian age (e.g., Winkler et al., 1990; Jacobs and Winkler, 1998). Most of the published mammals from the Trinity Group of Texas are from sites north of the Glen Rose pinchout, and hence are placed in the Antlers Formation. Most notable among these sites are Greenwood Canyon, worked by Bryan Patterson and associates in the early 1950s (Patterson, 1951, 1955, 1956), and Butler Farm, worked by Bob Slaughter and associates in the 1960s (e.g., Slaughter, 1965, 1968a, b, 1969, 1971). Both of these sites are close to the top of the Antlers Formation, suggesting that they may lie within the younger part of the age range for the unit, perhaps around 108 Ma (Jacobs and Winkler, 1998, Figure 1.2).

The Antlers Formation thins northward and eastward into Oklahoma and it is estimated (Rennison, 1996) to be about 150 m thick in the vicinity of OMNH locality V706, which yielded the specimens reported herein. Correlation with parts of the Trinity Group in Texas, including sites that have yielded mammals there, is hampered by a number of factors, including lateral variability in lithology and lack of intercalated marine units. Based on data from a nearby well hole (Hart and Davis, 1981), OMNH V706 appears to lie near the local middle of the Antlers Formation (Cifelli et al., 1997; see Brinkman et al., 1998 for more complete discussion of stratigraphy, sedimentology, and age of the Antlers Formation at OMNH locality V706). This was corroborated by Rennison (1996) who, based on ratios of stable carbon isotopes, proposed two possible correlations of the lower to middle part of the Antlers Formation in Oklahoma: with the middle part of the Twin Mountains Formation and/or the lower to middle part of the Glen Rose Formation. Summarizing the limited and somewhat equivocal data now available, OMNH locality V706 (1) lies within the Antlers Formation of Oklahoma; (2) probably correlates with the upper Aptian to lowest Albian; and (3) appears to be older than the most productive mammal sites in the Antlers Formation of Texas, Greenwood Canyon and Butler Farm.

Given this possible difference in age of important mammal sites, together with some obvious faunal differences among vertebrate-bearing sites of the Antlers Formation and Trinity Group (see below) in general, we believe that it is no longer appropriate to recognize a collective, generalized "Trinity fauna." Meticulous studies by L. L. Jacobs, D. A. Winkler, and others at Southern Methodist University, Dallas, have

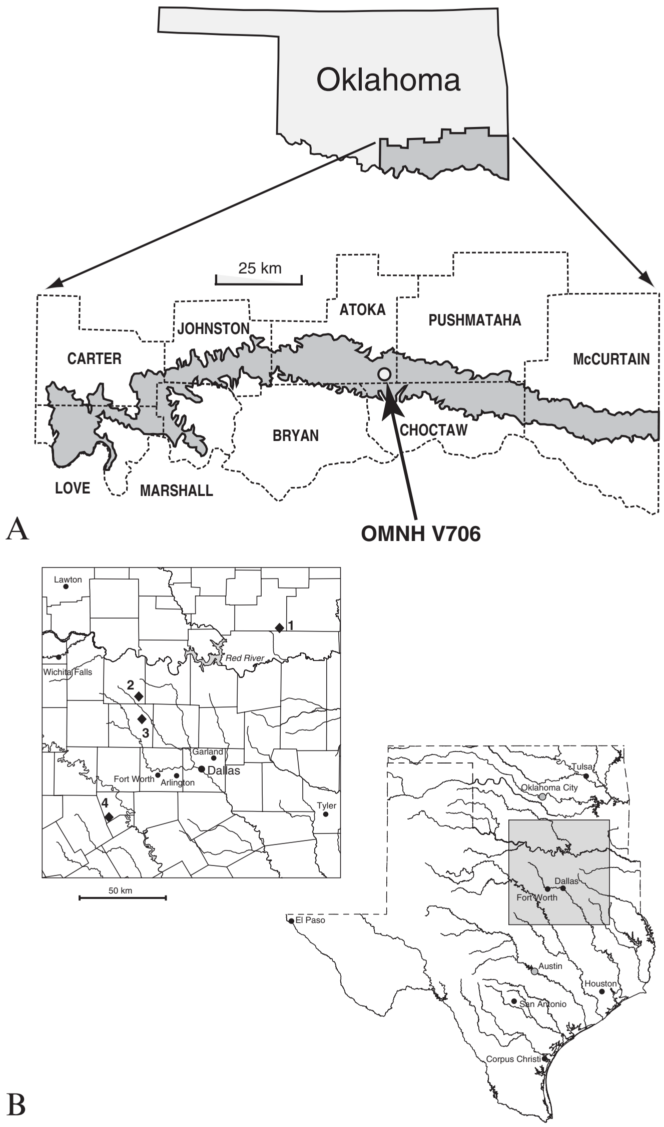

FIGURE 1.2. Early Cretaceous mammal localities, Trinity Group, Texas and Oklahoma. A, Map detailing outcrop of Antlers Formation (shaded) in southeastern Oklahoma. McLeod Honor Farm (OMNH microvertebrate locality V706) indicated by dot. B, Map detailing mammal-bearing microvertebrate localities from 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).

resulted in the discovery of many new sites in the Trinity and overlying groups, with recognition of important faunal changes within the sequence (e.g., Winkler et al., 1990; Jacobs and Winkler, 1998). To promote comparisons (both geographically and stratigraphically) and precision of usage, we herein introduce the term Tomato Hill local fauna in referring to the vertebrate assemblage from OMNH locality V706. A list of the 42 vertebrate taxa (including eight mammalian varieties) currently recognized from the Tomato Hill local fauna is given in Table 1.1.

TABLE 1.1. Measurements of described specimens. Numbers in brackets indicate estimates due to breakage. Standards of measurement illustrated in Figure 1.1.

	ID	Locus	L	ANW	POW
Oklatheridium szalayi					
	62411	LM1	1.4	[1.3]	[1.6]
	62410	LM2	1.5	[1.7]	[1.8]
	61180	LM2	[1.5]	[1.7]	[1.8]
	63727	RM3	[1.5]	[2.2]	[1.6]
	33945	Lm1	–	1.0	–
	33940	Rm2 or 3	–	1.0	–
cf. Oklatheridium sp.					
	33455	LMx	[1.6]	1.9	[2.1]
Atokatheridium boreni					
	61151	LM1	[0.9]	1.1	1.3
	61623	RM2	1.2	1.6	1.7
	63725	LM3	[1.5]	[2.0]	[2.0]
	61624	Lmx	1.3	0.8	0.5
	61181	Lmx	–	0.8	–

Tomato Hill is the local name for the immediate vicinity of OMNH locality V706, which lies on the flank of the first major terrace above the Muddy Boggy River and on the grounds of the Howard McLeod Corrections Center, operated by the Department of Corrections of the State of Oklahoma. As such, the fossil site was secure from unwanted collecting or other activities, until several years ago, when prison officials determined that landscaping of the area was needed. As a result, the site no longer exists, its former location now lying several meters above current ground level. Vertebrate fossils can occasionally be found in the nearby roadbed, up to 300 m from the former site.

Local exposure of the Antlers Formation at OMNH locality V706 consisted mainly of alternating gray-green and red claystones, together with localized, intermittent lenses of poorly consolidated sandstones and occasional horizons with small limonitic carbonate nodules, suggesting the presence of paleosols. There were two fossil horizons at OMNH V706, the upper of which represented a mass death assemblage, consisting of numerous, mostly articulated dinosaur skeletons. Most of these belong to the basal iguanodontian *Tenontosaurus tilletti* (see Ostrom, 1970; Forster, 1990), representing a wide variety of growth stages. At least one partial skeleton of the maniraptoran *Deinonychus antirrhopus* was also recovered from this horizon (Brinkman et al., 1998). Both of these species are otherwise known only from the Cloverly Formation, Wyoming and Montana (Ostrom 1969, 1970).

The lower fossil horizon at Tomato Hill, located immediately adjacent to and approximately 1.5 m below the dinosaur assemblage, lay in a dark gray, mottled mudstone with numerous localized, thin sandstone lenses, often bearing small mud clasts. Limonitic carbonate nodules were also abundant in this horizon. Fossils from this horizon, which include those described herein, consist mainly of microvertebrate remains, together with dinosaur and crocodile teeth, as well as small fragments of larger bone (e.g., turtle carapace). Preservation of the bone varies from excellent to abraded and rolled; some of the mammal teeth are lacking the enamel and have an etched appearance, suggesting that their owners had become meals and had passed through digestive tracts. The accumulation of vertebrate fossils at this horizon has been interpreted as lag formed within a fluvial overbank deposit, probably laid down in a localized depression on a floodplain (Cifelli, 1997).

TABLE 1.2. Vertebrate fauna of the Tomato Hill Local Fauna (OMNH locality V706), Antlers Formation, Atoka County, Oklahoma. References are given in footnotes.

- Chondrichthyes
  - Hybodontiformes
    - Hybodontidae
      - *Hybodus butler*[1]
      - ?*Hybodus* sp.[1]
    - Polyacrodontidae
      - *Lissodus anitae*[1]
- Osteichthyes
  - ?Semionitiformes
    - ?Semionotidae
      - gen. and sp. indet.[1]
  - ?Lepisosteiformes
    - ?Lepisosteidae
      - gen. and sp. indet.[1]
  - Pycnodontiformes
    - Pycnodontidae
      - ?*Palaeobalistum* sp.[1]
      - *Gyronchus dumblei*[1]
  - Amiiformes
    - ?Amiidae
      - gen. and sp. indet.[1]
  - Order and family indet.
      - gen. and sp. indet.[1]
- Lissamphibia
  - Allocaudata
    - Albanerpetontidae
      - *Albanerpeton arthridion*[2]
  - ?Caudata, family indet.
      - gen. and sp. indet.[1]
  - Anura, family indet.
      - gen. and spp. (2) indet.[1]
- Reptilia
  - Testudines
    - Family indet.
      - gen. and sp. indet.[1]
    - Pleurosternidae
      - *Naomichelys* sp.[1]
    - Glyptopsidae
      - ?*Glyptops* sp.[1]
  - Squamata
    - ?“Paramacellodidae”
      - *Atokasaurus metarsiodon*[3]
    - Teiidae
      - *Ptilotodon wilsoni*[3]
      - gen. and sp. indet.[3]
    - ?Scincomorpha
      - gen. and spp. indet. (2)[3]
    - ?Anguimorpha
      - gen. and sp. indet.[3]
  - Crocodylia
    - Bernissartiidae
      - *Bernissartia* sp.[1]
    - ?Atoposauridae
      - gen. and sp. indet.[1]
    - ?Goniopholididae
      - gen. and sp. indet.[1]
    - ?Pholidosauridae
      - gen. and sp. indet.[1]
  - Ornithopoda
    - Family *incertae sedis*
      - *Tenontosaurus tilletti*[5]
  - Sauropoda
    - Brachiosauridae
      - *Astrodon* sp.[1]
  - Theropoda
    - Carcharodontisauridae
      - *Acrocanthosaurusatokensis*[1]
    - Dromaeosauridae
      - *Deinonychus antirrhopus*[4]
  - ?Aves
    - Order and family indet.
      - gen. and sp. indet.[1]
- Mammalia
  - Eutriconodonta
    - Triconodontidae
      - *Astroconodon denisoni*[6]
  - Multituberculata
    - Family *incertae sedis*
      - ?*Paracimexomys crossi*[7]
      - gen. and spp. (2) indet.
  - “Stem Cladotheria”
    - Spalacotheriidae
      - ?*Spalacotheroides* sp.[8]
  - Boreosphenida, order uncertain
    - Holoclemensiidae
      - *Holoclemensia texana*[8]
    - Pappotheriidae
      - ?*Pappotherium* sp.[8]
    - Family uncertain
      - gen. and spp. (3) indet.[8]
  - Deltatheroida
    - Deltatheridiidae
      - *Atokatheridium boreni*[10]
      - *Oklatheridium szalayi*[9]

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[1] Cifelli et al. (1997).
[2] Gardner (1999).
[3] Nydam and Cifelli (2002).
[4] Brinkman et al. (1998).
[5] Werning (2005).
[6] Turnbull and Cifelli (1999).
[7] Cifelli (1997).
[8] RLC, unpublished data.
[9] This study.
[10] Kielan-Jaworowska and Cifelli (2001).

1.2 Systematic Paleontology

Infraclass Metatheria Huxley, 1880
Cohort Deltatheroida Kielan-Jaworowska, 1982
Family Deltatheridiidae Gregory and Simpson, 1926

Included genera: *Deltatheridium* Gregory and Simpson, 1926, type genus; *Atokatheridium* Kielan-Jaworowska and Cifelli, 2001; *Deltatheroides* Gregory and Simpson, 1926; *Deltatherus* Nessov, 1997; *Oklatheridium* gen. nov.; *Sulestes* Nessov, 1985; and taxa left in open nomenclature (Fox, 1974; Cifelli, 1990a).

Distribution: See Kielan-Jaworowska et al. (2004).

Diagnosis: See Kielan-Jaworowska et al. (2004).

Comments: Additional characters used to define Deltatheroida can be found in Appendix 3 of Rougier et al. (2004). *Atokatheridium* (Kielan-Jaworowska and Cifelli, 2001) and *Oklatheridium* gen. nov. are referred to the Deltatheridiidae based primarily on the presence of hypertrophied shearing crests (postmetacrista and paracristid) and an enlarged paraconid, which are apomorphies relative to the condition in basal Boreosphenida. *Sulestes* has been demonstrated to be phylogenetically removed from the core of the family in recent analyses (Luo et al., 2003; Rougier et al., 2004), and is clearly derived in a separate direction from the rest of the Deltatheroida. As noted, however, we follow recent studies (Rougier et al., 1998, 2004; Kielan-Jaworowska et al., 2004) and include *Sulestes* in Deltatheridiidae, without subdividing the family. *Khudukulestes* (Nessov et al., 1994) and *Oxlestes* (Nessov, 1982), known only by isolated axis vertebrae, have been referred to the Deltatheroida based on their large size with respect to contemporaneous mammals; however, this element is unknown from and non-comparable to most other Mesozoic mammals, leaving no support for their inclusion in the cohort.

Type species: *Oklatheridium szalayi* sp. nov., type species by monotypy.

Etymology: *Okla-*, in reference to the state of Oklahoma, where specimens belonging to the taxon were discovered, and *–theridium*, from the Greek *theridion*, meaning small beast, a common suffix for Cretaceous mammals; *szalayi*, in honor of Frederick S. Szalay, for his invaluable contributions to our understanding of mammalian paleobiology, and especially for his work on the Metatheria.

Holotype: OMNH 62410, a LM2 lacking the protoconal region of the crown (Figure 1.3B).

Referred specimens: OMNH 62411, LM1; OMNH 61180, LM2; OMNH 63727, RM3; OMNH 33945, Lm1; OMNH

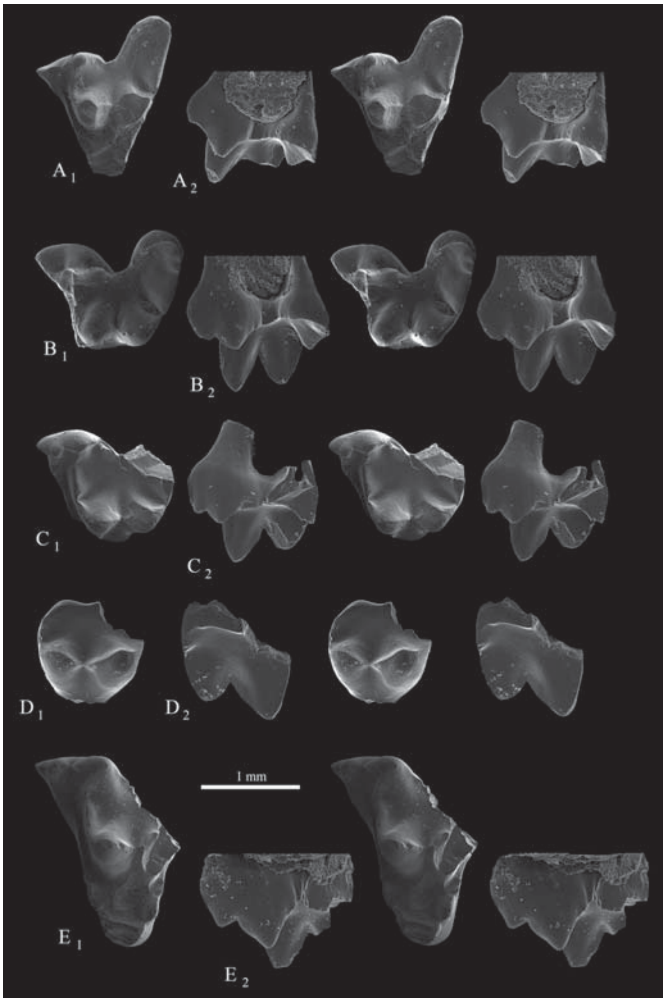

FIGURE 1.3. Upper molars of *Oklatheridium szalayi* gen. et sp. nov. (A–D) and *?Oklatheridium* sp. (E) OMNH locality V706, Antlers Formation (Aptian–Albian), Atoka County, Oklahoma. A, OMNH 62411, LM1, in occlusal (A_1) and labial (A_2) views; B, OMNH 62410 (holotype), LM2, in occlusal (B_1) and labial (B_2) views; C. OMNH 61180, LM2, in occlusal (C_1) and lingual (C_2) views; D, OMNH 63727, RM3, in occlusal (D_1) and lingual (D_2) views; E, OMNH 33455, LM2 or 3, in occlusal (E_1) and labial (E_2) views.

61643, Rm2 or 3; OMNH 33940, Rm2 or 3; OMNH 63728, Rm2 or 3; OMNH 63730, Lm2 or 3.

Distribution: OMNH locality V706, Antlers Formation (Aptian–Albian), Atoka County, Oklahoma.

Diagnosis: Moderate-sized deltatheroidan, larger than *Atokatheridium* but smaller than other taxa, and distinctive from all other deltatheroidans in having a deeper ectoflexus, larger and more anteriorly placed parastyle, stronger and more inflated stylocone (*Sulestes* might have had a stylocone of similar size, though breakage prevents direct comparison), taller, more labially oriented postmetacrista, and well developed conular cristae (all presumed apomorphies). Differs from all deltatheroidans except *Sulestes* in less height differential between the paracone and metacone, metacone somewhat broader than the paracone, portion of the preprotocrista labial to paraconule strong and broad, protoconal region anteroposteriorly expanded, and conules well developed (all presumed apomorphies). Differs specifically from *Sulestes* in greater width of the protoconal region (plesiomorphy), and lack of marginal cuspules on the metastylar lobe of the stylar shelf (polarity uncertain). Differs from all deltatheroidans except *Deltatheridium* in strong suppression of the metastylar lobe on M3. Differs from *Pappotherium* in stronger development of the metastylar lobe, less height differential and less divergence between metacone and paracone, stronger postmetacrista, and weaker developed postprotocrista terminating at the base of the metacone. Differs from *Holoclemensia* in less development of the parastylar lobe and greater development of the metastylar lobe, and absence of cusp "C" and other stylar cusps.

Description: Three upper molar loci are known for *Oklatheridium szalayi*. It is unknown whether or not this taxon possessed four molars, as is the case in *Deltatheridium* and *Deltatheroides*, but a reasonable case in the affirmative may be made based on other close morphological similarities between these deltatheroidans (see the Morphological Comparisons section of the Discussion). The upper dentition of *O. szalayi* is based on five isolated molars, all incomplete. Two specimens, OMNH 62411 and 62410 (Figures 1.3A, B; LM1 and LM2, respectively) are very similar in terms of wear patterns, relative morphology, preservation, and breakage and almost certainly belong to the same individual. The specimens were also found in relatively close association, though both are isolated teeth.

The M1, represented by one specimen (OMNH 62411; Figure 1.3A), is the most complete, lacking only the protocone. The parastylar lobe is significantly narrower than the metastylar lobe, giving the crown an asymmetrical outline. The stylocone is large, occupies the entire surface of the parastylar lobe, and is positioned directly labial to the paracone. The stylocone is roughly conical, though somewhat transversely compressed, and stands approximately one-half the height of the paracone (an exact comparison is impossible due to slight breakage at the apex of the paracone). The stylocone is connected via a weak crest to the parastyle, which is positioned lower on the crown and slightly more lingually. The parastyle is closely appressed to the stylocone, and situated at the terminal end of a moderately well developed preprotocrista. Both this crest and the parastyle are heavily worn, presumably due to occlusion with the protoconid of the opposing lower molar. There are no other stylar cusps present, though the labial margin is rimmed by a strong crest. The metastylar lobe is relatively narrow and runs obliquely to the long axis of the crown. The occlusal surface is occupied almost entirely by the slope of the postmetacrista, which is very tall and sharp. The ectoflexus is somewhat shallow due to the size difference between the parastylar and metastylar lobes. The paracone and metacone are conical, closely appressed, and roughly equal in size at their bases.

The cusps were presumably divergent (most of the metacone is missing due to breakage), since the paracone leans anteriorly. The bases of both cusps are equal in lingual extent. The apices of the paracone and stylocone are connected via a short, salient, and somewhat weakly developed preparacrista. The crest dips low in the middle, forming a weak notch. The centrocrista is straight and very weak. The postmetacrista is extremely well developed, with a deep carnassial notch present near the base of the metacone. The crest runs posterolabially. The protoconal region of the crown is small, comparable in width to that of *Atokatheridium*. This region is considerably better developed than in most other deltatheroidans (except *Sulestes*). The protocone itself is entirely missing. The conules are well developed, approximately equal in size, and possess weak internal cristae (the postparaconular crista is slightly the better developed of the two). The paraconule is positioned more labiad relative to the metaconule. The preprotocrista is continuous from the paraconule to the parastyle, creating a narrow shelf on the anterior margin of the crown. The postprotocrista extends past the metaconule only to the base of the metacone before terminating. The trigon basin is very small and restricted.

The M2 is represented by two specimens (OMNH 62410 (holotype) and 61180; Figure 1.3B, C, respectively). Both specimens are missing the protoconal region of the crown; OMNH 61180 additionally lacks the metastylar lobe and the tip of the metacone. From what is present, the M2 was larger than the M1. The parastylar lobe on M2 is much wider than on M1, though still not as wide as the metastylar lobe. The stylocone is similar in all relative dimensions to M1, though this cusp is much taller on OMNH 62410 than on OMNH 61180. The parastyle is positioned somewhat more labially than on M1. The ectoflexus is very deep on the type specimen, though the stylar shelf is rather broad centrally on OMNH 61180, indicating a shallower ectoflexus (breakage prevents determination of the actual depth on this specimen). The metastylar lobe is very broad and similar to that of M1 in all respects. There are no stylar cusps present posterior to the stylocone, though both specimens exhibit a small cuspule positioned on the posterior margin of the stylocone. The paracone and metacone are somewhat more transversely compressed than on M1. The paracone is taller than the metacone, but both cusps are approximately equally long in labial view. They share a significant portion of their bases and are somewhat divergent. The preparacrista is similar to that of M1, though the crest OMNH 61180 is significantly sharper and more deeply notched. The centrocrista is sharp and straight. The postmetacrista on M2 is very strong, sharp, and deeply notched, even more so than on M1. The crest runs much more directly labially than on M1. The preprotocrista is relatively narrow but still complete. Both specimens are broken labial to the conules, but OMNH 61180 shows evidence of a sharp crest running up the lingual surface of the paracone, likely representing an internal crista from the paraconule. This feature is absent on OMNH 62410, and shows a different orientation of the postparacrista from the condition on M1. The postprotocrista is similar to that of M1 in that it terminates at the base of the metacone.

The M3 is represented by one fragmentary specimen (OMNH 63727; Figure 1.3D), preserving only the paracone, metacone, and metastylar lobe. Based solely on the central portion of the crown, the M3 was larger still than the M2, falling in line with the typical deltatheroidan molar size progression of M1<M2<M3>?M4 (M4 is not known for this taxon, but it is reasonable to assume that the tooth at this locus would have been smaller than the M3). The metastylar lobe is strongly reduced relative to M1 and M2, consisting of a narrow, flat, gently rounded shelf. A slight concavity exists at the posterolabial corner of the metastylar lobe, which could have fit the parastylar lobe of a succeeding molar. This feature provides possible evidence for the presence of four molars in *Oklatheridium szalayi*. The parastylar lobe appears to have broken away at the deepest point of the ectoflexus, which was apparently very shallow. The paracone and metacone are closely appressed at their bases and strongly divergent, with the paracone significantly taller than the metacone, which is very short relative to the metacone on the other loci. Both cusps are somewhat transversely compressed, with nearly flat labial faces. The preparacrista is preserved from the apex of the paracone to its base, and is relatively strong and sharp. The centrocrista is straight and sharper than in the other loci. The postmetacrista, however, is very low and weak, though a small carnassial notch is still present at the base of the metacone. No trace of a postprotocrista is present on the base of the metacone, implying that it terminated more lingually, if it progressed past the metaconule.

The lower dention of *Oklatheridium szalayi* is based on six isolated molars, all of which preserve only the trigonid. These trigonids can be confidently referred to the upper molars based on expected size and morphology; it is also noteworthy that upper and lower molars referred to *O. szalayi* achieve the highest frequency of tribosphenic specimens in the collection from this locality. The trigonid is tall; though the talonid is missing, the trigonid cusps are much higher than the break that roughly indicated the position of the talonid. All three trigonid cusps are strong, with the protoconid being the tallest. The paraconid is taller and anteroposteriorly longer than the metaconid. As in other deltatheroidan taxa, this height difference appears to increase posteriorly through the molar series. *O. szalayi* differs from other deltatheroidans in having a more “closed” trigonid, with the bases of the paraconid and metaconid contacting each other. Both cusps support sharp crests with carnassial notches; however, the paracristid is much stronger than the protocristid, as would be expected in a dentition specialized for postvallum-prevallid shear. A well-developed wear facet is present on the anterior surface of the paracristid (facet 2 of Crompton, 1971). The lower molars are primitive in retaining well developed cusps e and f on the anterior surface of the trigonid. A short, strong precingulid runs nearly vertically, associated with cusp f, but is restricted to the anterior surface of the paraconid lingual to the paracristid notch (primitively, cusp f is placed more anterolabially on the molar, as is the case in the aegialodontid *Kielantherium*). Additionally, *O. szalayi* possesses a distal metacristid (see Section 1.3 for comments regarding the interpretation of this feature), though it appears to be variable in strength between specimens. This feature is shared by many early tribosphenic mammals, as a vertical continuation of the cristid obliqua from the talonid.

Though only trigonids are preserved, the morphology of the break where the talonid was connected does shed light on what the talonid would be expected to look like. The morphology of the break where the talonid was connected suggests the talonid was smaller than the trigonid (OMNH 33945 and 33940; Figure 1.4). Though its length cannot be assessed, it was likely narrower than the trigonid (though it could have been expanded posteriorly, in a "flexed" manner similar to that of *Kermackia*, cf. Butler, 1978: Figure 1.3K). All deltatheroidans possess a small talonid relative to the trigonid. However, the upper molars of *Oklatheridium szalayi* possess relatively well developed protocone and conules, so it would be expected that the talonid of this taxon would also be broader and better developed than is typical of Deltatheroida (*Sulestes*, which has the best developed talonid among previously known Deltatheroida, also has a strong protocone and conules on the upper molars. See Kielan-Jaworowska and Nessov, 1990: Figures 1.1–1.4). Confirmation of these speculations must, however, await discovery of more complete material.

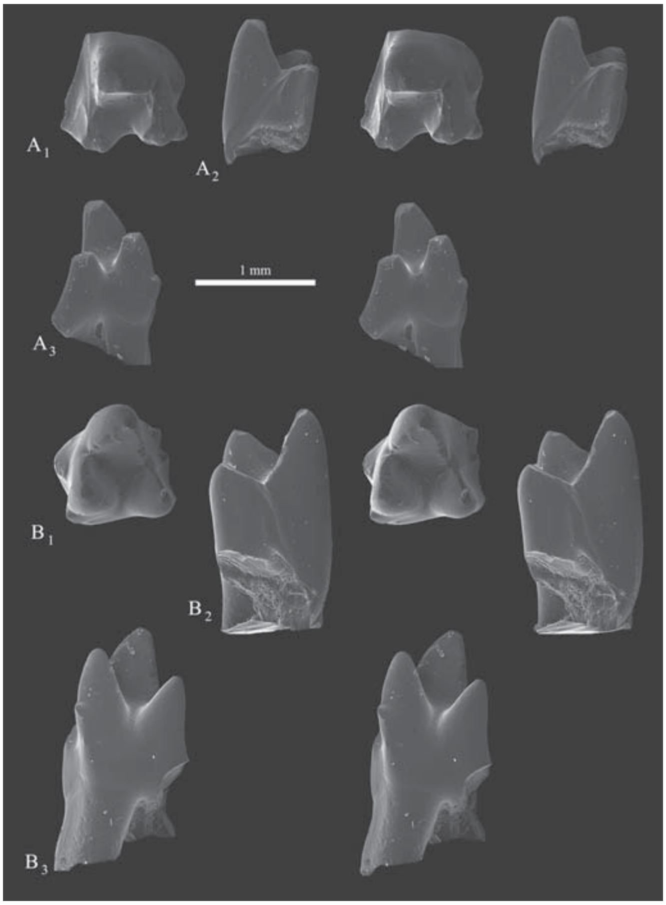

FIGURE 1.4. Lower molars of *Oklatheridium szalayi* gen. et sp. nov. OMNH locality V706, Antlers Formation (Aptian–Albian), Atoka County, Oklahoma. A, OMNH 33945, Lm1, in occlusal (A_1), posterior (A_2), and lingual (A_3) views; B, OMNH 33940, Rm2 or 3, in occlusal (B_1), posterior (B_2), and lingual (B_3) views.

Despite the lack of knowledge concerning talonid morphology, the lower molars of *Oklatheridium szalayi* compare favorably with those of deltatheroidan mammals. However, a number of features are common to other early tribosphenic mammals, prompting comparisons to non-deltatheroidan taxa. *Kielantherium* is similar in having a relatively taller paraconid than metaconid, but *O. szalayi* differs in having a lesser height differential between protoconid and paraconid, less separation of paraconid and metaconid (presumed apomorphies), and a more lingual placement of cusp f and the precingulid (polarity uncertain). Molars of *O. szalayi* differ from the stem boreosphenidan *Potamotelses* (Fox, 1975) in being generally higher-crowned (even on m1), in having a relatively taller paraconid and a transversely wider trigonid, and in retaining a stronger cusp e (presumed plesiomorphy). *O. szalayi* differs from all "Trinity therians" in the fact that the paraconid is substantially taller and more robust than the metaconid. However, it is similar to both *Pappotherium* and *Holoclemensia* in the degree of development of strong shearing crests on both the anterior and posterior edges of the trigonid.

The molar loci of *Oklatheridium szalayi* are defined on the basis of general morphological trends present in most primitive tribosphenic mammals (and specifically the resemblance of the lower molar specimens to equivalents in deltatheroidans where tooth locus can be established with certainty), as one moves posteriorly through the molar series. The m1 (represented by one specimen, OMNH 33945; Figure 1.4A) is smaller than the posterior molars. The tooth is also relatively lower crowned, with the protoconid slightly recumbent posteriorly. The posterior margin of the trigonid (most notably the posterolingual margin) slopes gently posteriorly down toward the talonid (or where the talonid would be in a complete molar). Without a dentary with associated teeth or at least a larger sample of isolated teeth that includes complete lower molars, it is unclear whether the remaining trigonids (OMNH 33940, 61643, 63728, and 63730; Figure 1.4B) represent the second or third molar locus. In *Deltatheridium*, the m2 is the largest molar, though this difference is not as clear in *Deltatheroides*. In both taxa, however, the occlusal outline of m1 is preserved on m2, while the m3 has a somewhat broader trigonid. In occlusal outline, the four trigonids designated m2 or m3 are all very similar to the specimen designated as m1, hence by analogy it is possible that they all represent m2. However, due to difficulties in differentiating between the second and third molar loci without a better sample, the specimens are assigned as m2 or 3. These trigonids are somewhat larger in all dimensions than m1. The crown is higher, and there is a greater size difference between the paraconid and metaconid. The two cusps are nearly subequal on m1, but on m2 or 3 the paraconid is noticeably taller and longer than the metaconid. One of these trigonids (OMNH 61643) was described briefly by Kielan-Jaworoska and Cifelli (2001) as "Family et gen. indet., sp. B".

Comments: Upper molars of *Oklatheridium szalayi* exhibit features typical of primitive boreosphenidans, such as a paracone taller than the metacone and a relatively small protocone. However, they are derived in a number of important features. In most early tribosphenic taxa, prevallum/postvallid shearing is dominant (Crompton, 1971; Clemens and Lillegraven, 1986). *O. szalayi*, as well as some other taxa (e.g., *Sulestes, Pappotherium*, and *Potamotelses*), possesses an enlarged shelf-like preprotocrista in addition to a strong preparacrista that would allow second-rank or *en echelon* shear along the anterior margin of the upper molar (Fox, 1975). However, *O. szalayi* departs from most other early tribosphenic mammals in also possessing an hypertrophied postmetacrista which, coupled with a tall, sharp paracristid on the lower molars, would have provided strong postvallum-prevallid shearing capability.

Referred specimen: OMNH 33455, RM2 or M3 (Figure 1.3E).

Distribution: OMNH locality V706, Antlers Formation (Aptian–Albian), Atoka County, Oklahoma.

Description: (from Cifelli, 1997, p. 10) "Judged by the relatively wide stylar shelf labial to the paracone and the elongate preparacrista, OMNH 33455 (Figure 1.3) appears to be a penultimate tooth, M2 or 3, depending on whether three or four molars were present in the dentition (see Fox, 1975 for discussion). The posterolabial corner of the tooth and the metacone are missing; the tip of the protocone is also broken (Figure 1.3A). Damage precludes some standard measurements; ANW is 1.96 mm; protocone width and length (as defined by Butler, 1990a) are 0.64 and 0.79, respectively. Stylar cusps A and B (terminology follows Clemens, 1979) are prominent, the latter being nearly as tall as the paracone. A well-marked preprotocrista extends labially from the protocone to stylar cusp A; this crest is uninterrupted in the region of the paracone (Figure 1.3A, B), such as in primitive marsupials and eutherians. By contrast, the postprotocrista extends only to the base of the metacone. Both conules are well developed and project slightly beyond the occlusal margin of the tooth. The paraconule is positioned about halfway between protocone and paracone and bears a small postparaconular crista that terminates at the base of the paracone; the metaconule is placed distinctly closer to the protocone and its internal crista is weak or lacking."

Comments: OMNH 33455 is similar to upper molars of *Oklatheridium szalayi* in terms of general outline and morphology (Figure 1.3), such as the shape and proportions of the stylocone and paracone, but it is distinct in a number of important ways. As mentioned above, the locus represented by OMNH 33455 cannot be confidently determined, primarily due to loss of the metastylar lobe, so direct comparisons with other specimens must be approached cautiously. For example, OMNH 33455 is larger than the type specimen of *O. szalayi* (OMNH 62410), an M2, though it appears to be smaller than the M3 (OMNH 63727) in some dimensions. But for present purposes, morphological similarities suggest the most appropriate comparisons are with the M2 of *O. szalayi* (OMNH 62410).

The cusps on OMNH 33455 are more robust than in *O. szalayi* (likely due to its larger size). The parastyle is better separated from the stylocone and positioned lower and more labially. The preparacrista is sharper and more distinct, and the preprotocrista is substantially wider and stronger in OMNH 33455. These differences leave some doubt as to the association of this specimen with *Oklatheridium*, but given the nature of the specimens in the Tomato Hill Local Fauna, it is most likely that the similarities between OMNH 33455 and *Oklatheridium* indicate the specimen represents a similar, related taxon. However, breakage of the metastylar lobe on OMNH 33455 prevents us from referring this specimen confidently or placing it elsewhere.

Holotype: OMNH 61623, RM2 (Figure 1.5B).

Newly referred specimens: OMNH 61151, LM1; OMNH 63725, LM3; OMNH 61624, Lmx; OMNH 61181, Lmx; OMNH 34905, Rmx.

Distribution: OMNH locality V706, Antlers Formation (Lower Cretaceous: Aptian–Albian), Atoka County, Oklahoma.

Revised diagnosis: Small deltatheroidan differing from all other deltatheroidans in smaller size, weaker stylocone, shallower ectoflexus, slightly narrower parastylar lobe, trend of increasing width of metastylar lobe posteriorly through molar series (excluding the unknown but hypothesized M4), greater height differential between the paracone and metacone, extremely weak development of conules, lack of conular cristae, transversely wider protoconal region, and a taller protocone. Differs from *Oklatheridium* and *Sulestes* in weaker conules. Differs from *Oklatheridium* in slightly narrower metastylar lobe and more posteriolabially oriented postmetacrista on M2, and in retention of a wide metastylar lobe on M3.

Description: Three upper molar loci are known with some confidence in *Atokatheridium boreni*. Each locus is represented by a single specimen; two are complete, but all three are rather worn (Figure 1.5). The M1 (OMNH 61151), despite being heavily worn, is confidently referred based on numerous general morphological similarities between it and the M2 (OMNH 61623). The M3 (OMNH 63725), however, is both broken and heavily worn or digested, making its referral somewhat more tentative.

The M1 (Figure 1.5A) is very small, though its original size is impossible to determine due to loss of nearly all the enamel. The parastylar lobe is very narrow and bears a small stylocone. The parastyle is small and closely approximated to the stylocone, though placed considerably lower on the crown.

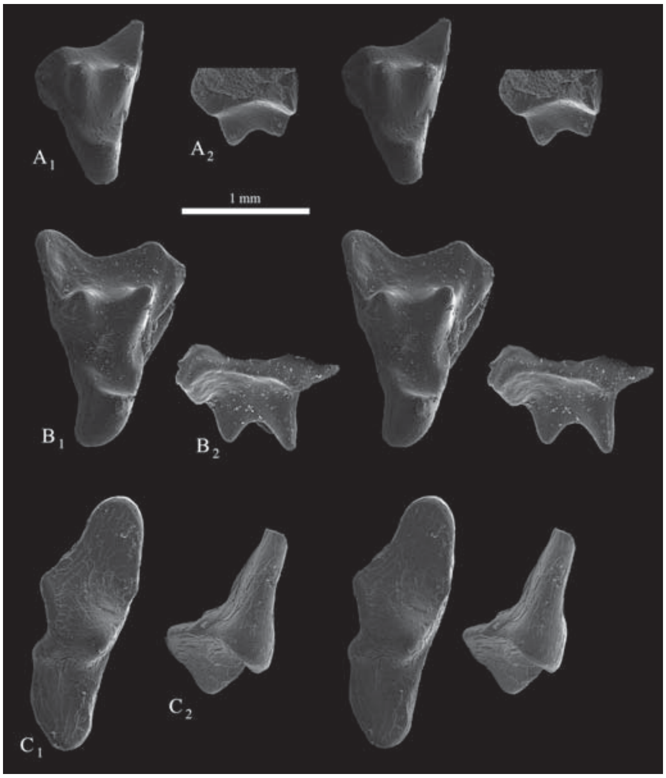

FIGURE 1.5. Upper molars of *Atokatheridium boreni* Kielan-Jaworowska and Cifelli, 2001. OMNH locality V706, Antlers Formation (Aptian–Albian), Atoka County, Oklahoma: A, OMNH 61151, LM1, in occlusal (A_1) and labial (A_2) views; B, OMNH 61623 (holotype), RM2, in occlusal (B_1) and labial (B_2) views; C, OMNH 63725, LM3, in occlusal (C_1) and labial (C_2) views.

The ectoflexus is nearly absent, despite the metastylar lobe being significantly wider than the parastylar lobe. No cusps or cuspules appear to have been present posterior to the stylocone, and no evidence of a cingulum along the labial edge of the stylar shelf is preserved. The paracone is taller than the metacone, though it cannot be determined how great the original difference was. The cusps are connate, share a large part of their bases, and are divergent. A short, low preparacrista runs from the apex of the paracone directly to the stylocone. The centrocrista appears to have been straight. The postmetacrista, though also worn, is still very tall and strong. The crest runs posterolabially from the apex of the metacone, and bears a strong carnassial notch near the base of the metacone. The entire surface of the metastylar lobe slopes anteriolabially from the postmetacrista. The protoconal region of the crown is short but transversely wide (relative to other deltatheroidans), and shallowly basined. Given the apparent amount of wear, the protocone is very tall and procumbent. No evidence of conules remains, though they were likely present since they occur on the type specimen. The preprotocrista runs uninterrupted to the parastyle and is not particularly well developed. The postmetacrista terminates at the base of the metacone.

The M2 (OMNH 61623; Figure 1.5B) is strongly similar to M1 in almost every respect, though its improved preservation provides more information (though the tooth is still somewhat abraded). The M2 is considerably larger than the M1, though enamel loss on the M1 makes direct size comparison difficult. The parastylar lobe is wider than on M1, though the stylocone is still small. The ectoflexus is slightly deeper, and a weak cingulum rims the labial margin of the crown. The metastylar lobe is wider than on M1. The paracone is significantly taller than the metacone, and both cusps are spire-like and strongly divergent. Conules are present as weak bulges along the pre- and postprotocristae, approximately equidistant between the bases of the paracone and metacone and the protocone.

The M3 (OMNH 63725; Figure 1.5C) is missing the paracone and parastylar lobe, and what remains of the molar is heavily abraded, with a melted appearance. The M3 is larger still than the M2, and much of the size difference is due to the presence of a significantly wider metastylar lobe on the M3. In both these respects, the relationships between the M2 and the presumed M3 of *Atokatheridium* are strikingly similar to those seen in *Deltatheroides cretacicus* (see Section 1.3.1 for further discussion). Though the entire parastylar lobe is missing, the ectoflexus was likely very deep, in sharp contrast with the preceding molars (however, a relatively narrow parastylar lobe would result in a shallower, short ectoflexus, less of a departure from the morphology of the M1 and M2). The metastylar lobe is very wide, nearly as wide as the portion of the crown from the metacone to protocone. No trace of a rimming cingulum or stylar cusps remains. The metacone is short and stout, and was closely appressed to the paracone. The postmetacrista is tall and deeply notched, running much more directly labiad than on M1 or M2. The protoconal region is very wide and short, but worn almost smooth. No evidence of conules is present, but their small size on the M2 makes it unlikely that they would be preserved on a tooth as worn as OMNH 63725. The protocone is heavily worn, so height cannot be determined. The preprotocrista is broken not far from the protocone, but the postprotocrista terminates in a similar spot as on the M2, posterolingual to the base of the metacone.

The lower dentition of *Atokatheridium boreni* is represented by one complete molar and two trigonids (Figure 1.6). The only lower molar specimen bearing a talonid was described by Kielan-Jaworoska and Cifelli (2001, p. 382) in the initial publication of *Atokatheridium boreni*, though it was referred to ?*A. boreni*: "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 is 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; the protocristid and talonid also show wear, though major shearing surfaces (see Crompton, 1971) are clear and well developed. The paraconid and metaconid are well separated,

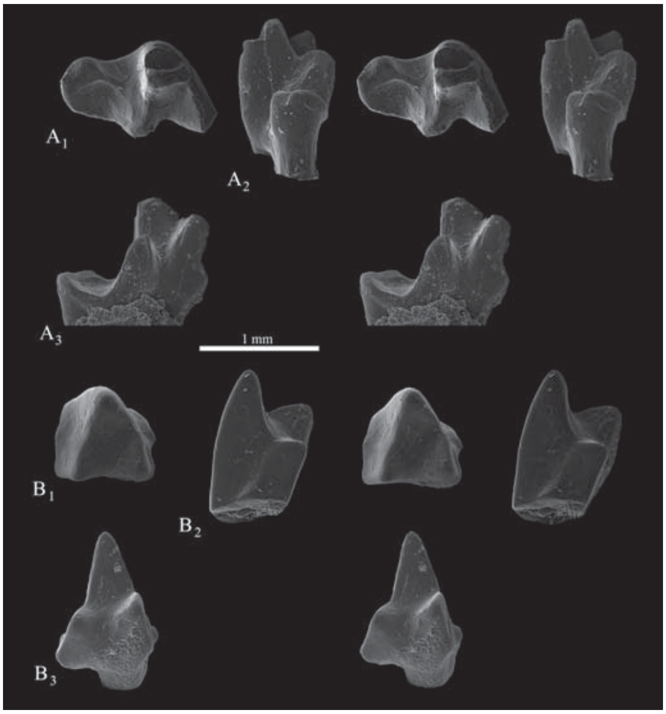

FIGURE 1.6. Lower molars of *Atokatheridium boreni* Kielan-Jaworowska and Cifelli, 2001. OMNH locality V706, Antlers Formation (Aptian–Albian), Atoka County, Oklahoma: A, OMNH 61624, Lmx, in occlusal (A_1), posterior (A_2), and lingual (A_3) views; B, OMNH 61181, Lmx, in occlusal (B_1), posterior (B_2), and lingual (B_3) views.

so that the trigonid angle is rather obtuse compared to that seen in *Pappotherium, Holoclemensia*, and early members of Marsupialia and Eutheria. The paraconid is much taller and more robust than the metaconid and appears to slant anteriorly, though this appearance 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 no entoconid was ever present." This specimen is referred to the upper molars based on deltatheroidan characteristics, such as a paraconid much taller than the metaconid and a small, poorly-developed talonid; and to *Atokatheridium* specifically because of its small size (*Atokatheridium* is considerably smaller than *Oklatheridium*). In comparison with *Deltatheridium*, OMNH 61624 compares most favorably with the m3 based on the angle formed by the trigonid cusps, but the talonid is considerably better developed in *Atokatheridium*. This is plausible, since the protoconal region on the M3 is the widest of the molar series, and if the protocone was as tall on that tooth as it is on the M2, one would expect a more discernable talonid on the m3 compared to taxa such as *Deltatheridium*.

Both of the isolated trigonids (OMNH 34905 and OMNH 61181) compare very well with the trigonid of OMNH 61624 in both size and morphology. Both are complete, but virtually all the enamel is missing except for two small chips still attached to the anterior and posterior surfaces of OMNH 34905, so the full height of the trigonid cusps is still difficult to evaluate. OMNH 61181 likely represents the same locus as OMNH 61624. The protoconid is spire-like, and is by far the tallest cusp. The metaconid is strongly reduced in size, with the paraconid higher and slightly anteriorly projecting. The trigonid is open lingually. The paracristid is sharp and notched, though not as strongly as in *Oklatheridium*. A distal metacristid is present, running steeply posteriorly from the metaconid. OMNH 34905 is identical in morphology, but it preserves chips of enamel on the anterior base of the paraconid and the posterior surface of the protoconid.

Comments: With the description of *Oklatheridium szalayi*, the large majority of tribosphenic lower molar specimens from the Tomato Hill Local Fauna are partitioned into two morphological groups; this allows a more confident assignment of OMNH 61624 to *Atokatheridium boreni* than was made by Kielan-Jaworoska and Cifelli (2001).

1.3 Discussion

1.3.1 Morphological Comparisons

Both the age (Early Cretaceous) and generally plesiomorphic nature of the molars of *Oklatheridium* and *Atokatheridium* invite comparison with primitive boreosphenidan taxa (such as *Aegialodon, Kielantherium*, and *Potamotelses*). The lower molars of the Tomato Hill taxa resemble those of early boreosphenidans in a number of ways (Figure 1.7). Cuspule e is present, situated on the anterolingual margin of the paraconid (see Appendix 1 of Luo et al., 2002 for distribution of this character), and cuspule f is cuspate on most trigonids. A distal metacristid is present on the posterior aspect of the trigonid, running ventrolabially from the metaconid, and similarly developed as in the Trinity therians (see Patterson, 1956; Turnbull, 1971; Butler, 1978) but much weaker than in *Aegialodon* or *Kielantherium*. Our observations suggest that the distal metacristid is a true crest and not a wear feature, despite the fact that both the preparacrista and preprotocrista are expected to produce separate facets on the posterior wall of the trigonid (Crompton, 1971). In *Aegialodon*, the paraconid is taller than the metaconid, but the height difference is greater in the Tomato Hill taxa, as it is in other deltatheroidans. The talonid is shallow, open lingually, and poorly developed relative to the trigonid; only two cusps are present (hypoconid and hypoconulid). The trigonid/talonid proportions of *Atokatheridium* (a talonid is not known for *Oklatheridium*) are certainly primitive. The talonid is better developed than in *Aegialodon*, much

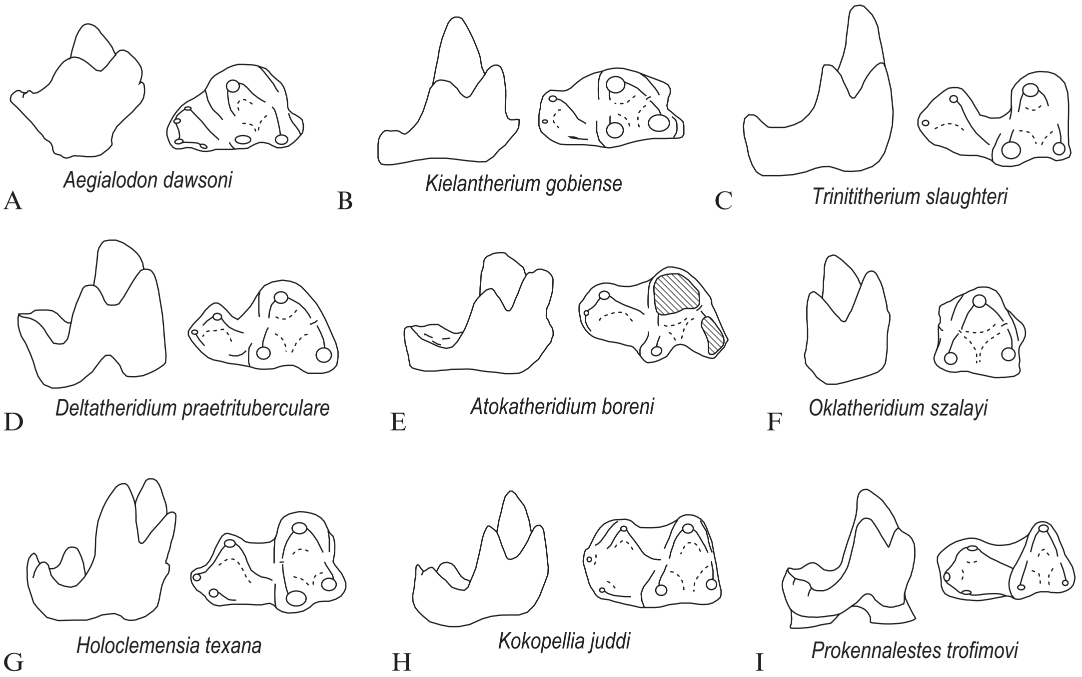

FIGURE 1.7. Lower molar comparisons (lingual and occlusal views): A, *Aegialodon dawsoni;* B, *Kielantherium gobiense* (reversed); C, *Trinititherium slaughteri,;* D, *Deltatheridium praetrituberculare;* E, *Atokatheridium boreni;* F, *Oklatheridium szalayi* (reversed); G, *Holoclemensia texana;* H, *Kokopellia juddi;* I, *Prokennalestes trofimovi*. (A modified from Kermack et al. 1965; B–I original.) Line drawings not to scale.

less developed than in *Potamotelses*, but of similar structural grade as *Kielantherium. Atokatheridium* is also similar to stem boreosphenidans in lacking a postcingulid.

The lower molars of the Tomato Hill taxa possess a few characters that serve to distance them somewhat from the primitive boreosphenidan condition. Most notable is the hypertrophy of the paraconid and paracristid. The paraconid is significantly taller than the metaconid (somewhat similar to *Kielantherium*), projecting somewhat anteriorly and supporting a very strong crest and carnassial notch (this shearing surface is particularly well developed on trigonids referred to *Oklatheridium*). Notably, the paraconid of both taxa lacks the distinct mesiolingual keel present in *Kokopellia* and more derived metatherians (Luo et al., 2002). Additionally, the trigonid basin is somewhat more closed in *Oklatheridium* compared to primitive taxa and *Atokatheridum*, due to a swelling of the bases of the paraconid and metaconid.

The upper molars of *Oklatheridium* and *Atokatheridium* provide strong support for a molar count of four, though only three loci are represented in each taxon. It should be noted, however, that in some early taxa the upper and lower molar counts are not equal (*Sinodelphys*, for example, has four upper molars but only three lower molars, see Luo et al., 2003). Though the ancestral boreosphenidan molar count is unknown, all stem taxa with a known (or at least surmised) dentition suggest four molars were present. The aegialodontid *Kielantherium gobiense*, initially described on the basis of a single lower molar (Dashzeveg, 1975), is known by a dentary preserving four molars (Dashzeveg and Kielan-Jaworowska, 1984). The "Trinity therians" *Holoclemensia* and *Pappotherium* were reconstructed by Butler (1978) as having four upper molars (but see Fox, 1975 for contrasting interpretation of *Pappotherium*). Additionally, the deltatheridiids *Deltatheroides cretacicus* and *Deltatheridium pretrituberculare* have been demonstrated to possess four molars (Gregory and Simpson, 1926; Rougier et al., 1998), though the ultimate upper molar is tiny and was assumed absent in early descriptions (Butler and Kielan-Jaworowska, 1973; Kielan-Jaworowska, 1975; Rougier et al., 1998). Though an ultimate molar is not known for either of the Tomato Hill taxa, one is assumed to have been present based on morphological similarities at the third molar locus between these taxa and the two aforementioned deltatheridiids. Additionally, the slight concavity on the posterolabial margin of the metastyle of the M3 of *Oklatheridium* might suggest an interlocking mechanism with the parastyle of an M4 (however, it should be noted that this feature is absent on the M3 of *Atokatheridium*). Figure 1.8 shows the molar series of both *Oklatheridium* and *Atokatheridium* with a hypothetical M4. The large metastylar lobe on M3 of *Atokatheridium* suggests its M4 (if present) was large compared with that of

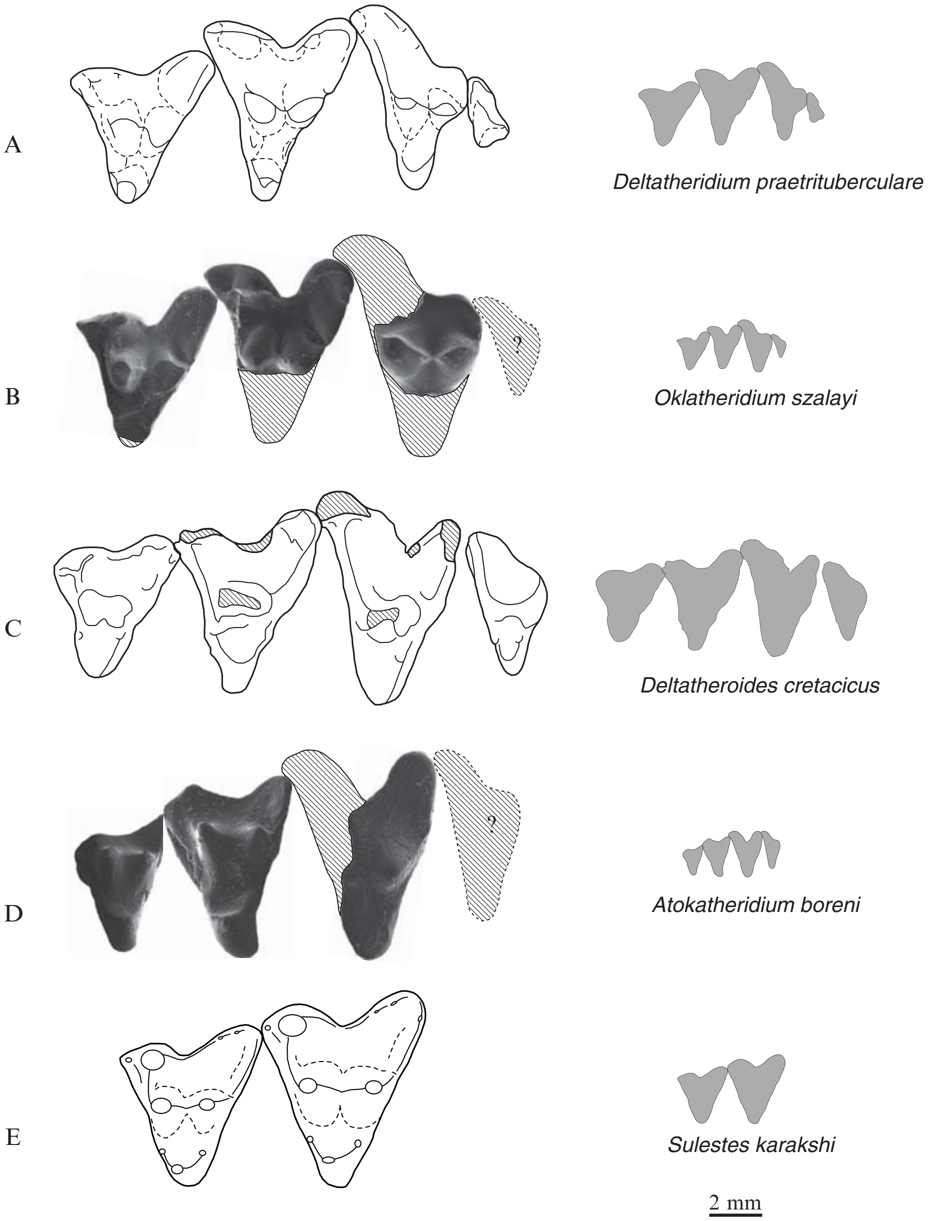

FIGURE 1.8. Upper molar series comparisons: A, *Deltatheridium praetuberculare;* B, *Oklatheridium szalayi;* C, *Deltatheroides cretacicus;* D, *Atokatheridium boreni;* E, *Sulestes karakshi*. (A and C from Rougier et al. 2004; B, D, and E original.) Line drawings resized for comparison; scale bar applies only to silhouettes.

other deltatheroidans (as is the case in *Deltatheroides*), where reduction of the posterolabial portion of M3 correlates with strong overall reduction of the fourth molar (as is the case in *Deltatheridium*).

The primitive condition for the protoconal region is well illustrated by the recently-described upper molar of the aegialodontid *Kielantherium* (Lopatin and Averianov, 2006, see our Figure 1.9A). The protocone is very small and situated on a short, narrow shelf, and the conules are lacking. The postprotocrista is very short, though the preprotocrista provided double-rank shearing on the anterior margin of the molar. The protoconal region differs significantly between the two Tomato Hill taxa. The protocone is tall and transversely wide in *Atokatheridium*, but the conules are virtually absent. In *Oklatheridium*, the entire width of the protoconal region is uncertain, but it was likely nearly as wide and longer still than in *Atokatheridium*. The conules in *Oklatheridium* are relatively large compared to those of stem boreosphenidans, deltatheroidans, or other contemporaneous taxa, providing another point of contrast. All considered, the protoconal region of *Atokatheridium* shows a blend of primitive and advanced features, while *Oklatheridium* is generally

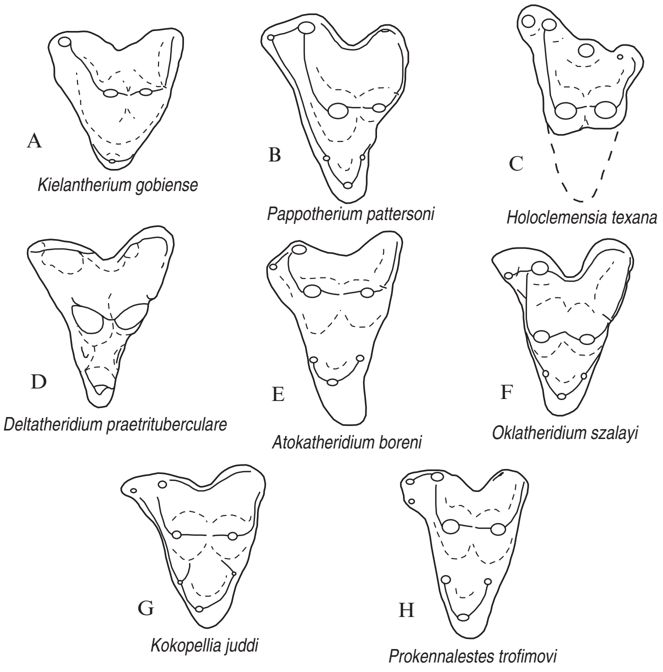

FIGURE 1.9. Upper molar comparisons: A, *Kielantherium gobiense* (reversed); B, *Pappotherium pattersoni* (reversed); C, *Holoclemensia texana* (reversed); D, *Deltatheridium praetrituberculare*; E, *Atokatheridium boreni* (reversed); F, *Oklatheridium szalayi* (lingual half reconstructed); G, *Kokopellia juddi*; H, *Prokennalestes trofimovi*. (A from Lopatin and Averianov 2006; B modified from Slaughter 1965; C modified from Slaughter 1968; D from Rougier et al. 2004; E–F original.) Line drawings not to scale.

more advanced. The protocone of both taxa is much better developed than the tiny, poorly developed protocone of *Kielantherium* and *Picopsis* (Fox, 1980), and is more similar to that of *Holoclemensia*.

Upper molars of the Tomato Hill taxa exhibit primitive morphology in a number of other features (Figure 1.9). The postprotocrista terminates just slightly around the base of the metacone; though the crest is somewhat better developed than in *Potamotelses*, it is equal to or less developed than in *Pappotherium*. The paracone and metacone also show some primitive features, such as the sharing of a significant portion of their bases and height. The cusps are connate at their bases and divergent, with the notch occupied by the centrocrista straight but shallow. The paracone is taller than the metacone, as in other early boreosphenidans, but the height difference is less in *Oklatheridium* (and thus more advanced). The parastylar lobe is generally primitive in the Tomato Hill taxa. The stylocone is large, with a much smaller and closely appressed parastyle situated basally on a small anterior projection of the shelf. It should be noted that this anterior projection in *Oklatheridium* is somewhat larger (advanced) than in *Atokatheridium*. Finally, the absence of any stylar cusps posterior to the stylocone can be interpreted as primitive, though as Clemens and Lillegraven (1986, p. 77), wisely observed, “evolution of stylar cusps in the region between the stylocone and metastylar corner of the crown poses vexatious questions.” Posterior stylar cusps (with the exception of non-homologous cuspules) are absent in *Peramus*, most stem boreosphenidans, all deltatheroidans, and basal metatherians. However, a stylar cusp in the “D” position is present in the “tribotheres” *Pappotherium, Holoclemensia*, and *Comanchea*, and the basal eutherian *Paranyctoides*, suggesting some degree of homology, or raising the possibility of some functional importance of this portion of the stylar shelf.

There are a number of advanced features present in the upper molars of the Tomato Hill taxa, though the two taxa differ somewhat in many of these. The protocone is wide and well developed, especially in *Oklatheridium* (coupled with strong conules). The preprotocrista is moderately developed but continuous from the paraconule to the parastyle, a feature present in *Pappotherium* but absent in *Holoclemensia*. The metacone is relatively taller in *Oklatheridium* than in all other early taxa, approaching (though still shorter than) the paracone in height. Most notably, the metastylar lobe and postmetacrista are much more strongly developed than in any contemporaneous taxa.

The main features that serve to differentiate the Tomato Hill taxa from stem boreosphenidans such as *Aegialodon, Kielantherium*, and *Potamotelses* are those commonly associated with adaptations for carnivory. The primary shearing surfaces (in this case, the postmetacrista and paracristid) are hypertrophied. It should be noted that these features appear independently multiple times through evolution, for example, in the Late Cretaceous Stagodontidae as well as the South American “dog-like” marsupials, the Borhyaenidae (see Muizon and Lange-Badré, 1997). Additionally, the protocone is better developed than in some early boreosphenidans. Significance of the relatively large protocone is unclear; it appears that the protocone became enlarged independently in later metatherians, eutherians, and perhaps among the “Trinity therians”. In the context of Early Cretaceous mammals, the Tomato Hill taxa are unique in possessing such an advanced suite of characters, such as a large protocone and specializations for carnivory, especially given their small body size.

The only tribosphenic mammals with both geographic and temporal proximity to the Tomato Hill taxa hail from stratigraphically younger horizons in the Trinity Group of northern Texas. The “Trinity therians”, traditionally referred to as “Theria of metatherian-eutherian grade” (Patterson, 1956; Kielan-Jaworowska et al., 1979) because their affinities to the two higher groups of mammals are debatable, are a motley group of six described taxa that vary widely in size and morphology (Patterson, 1956; Slaughter, 1965, 1968a, b, 1971; Turnbull, 1971; Butler, 1978, 1990a; Jacobs et al., 1989). Direct comparison of lower molars between these taxa and the Tomato Hill taxa yields only a few similarities, mainly with the larger and more advanced *Pappotherium* (Figure 1.7). No “Trinity therian” has cusp proportions that approach the height differential between the paraconid and metaconid seen in either *Oklatheridium* or *Atokatheridium*. However, both *Pappotherium* and *Holoclemensia* have well developed shearing crests on the trigonid (due to the size of the metaconid, *Holoclemensia* shows emphasis on the protocristid as opposed to the paracristid). The talonid of *Atokatheridium* is much less developed than that of any described "Trinity therian", in that it is very small relative to the trigonid and it bears only two cusps (*Trinititherium* has been described as having an incipient entoconid (Butler, 1978), but no evidence of any entoconid is present in *Atokatheridium*). The talonid of *Atokatheridium* is very primitive, but the trigonids of the Tomato Hill taxa are advanced and clearly divergent from any forms seen among the "Trinity therians".

The differences among upper molars of the Tomato Hill taxa and the "Trinity therians" are more striking (Figure 1.9). *Pappotherium* is more generally primitive than either, with a narrower metastylar lobe, smaller metacone, and poorly developed protocone. *Holoclemensia*, on the other hand, is oddly derived. It differs from the Tomato Hill taxa in having a very large cusp in the mesostylar position (absent on all other contemporaneous taxa), a narrow metastylar lobe, a small stylocone, and a very small metacone. However, the protocone is about as well developed as in *Oklatheridium*.

The Tomato Hill taxa differ from basal Eutheria in a number of features (Figures 1.7, 1.9). The oldest North American eutherian, *Montanalestes keeblerorum* (Cifelli, 1999), from the Aptian–Albian Cloverly Formation, is derived in having a well developed, three-cusped talonid; it retains a vestige of a distal metacristid on the first molar only. Upper molars from early eutherians (such as *Murtoilestes*) differ from the Oklahoma taxa in having a smaller stylocone and a larger protocone and conules. Neither *Atokatheridium* nor *Oklatheridium* compares well with any basal eutherian.

There are also important differences between basal metatherians and the Tomato Hill taxa (Figures 1.7, 1.9). Disregarding *Sinodelphys szalayi* (Luo et al., 2003) (for which little occlusal morphology is known), *Kokopellia juddi* (Cifelli, 1993b; see also Cifelli and Muizon, 1997) is the oldest uncontested metatherian. It differs from the Tomato Hill taxa in having subequal paraconid and metaconid; a well developed, three-cusped talonid; some approximation of entoconid and hypoconulid; and presence of a postcingulid. Upper molars have a similarly developed protocone (though the conules are weaker in *Kokopellia* than in *Oklatheridium*), but differ in having a subequal paracone and metacone and subequal parastylar and metastylar lobes.

Comparison of *Oklatheridium* and *Atokatheridium* to *Kokopellia* is noteworthy in that the Deltatheroida have often been placed basally within Metatheria (Rougier et al. 1998, 2004; Kielan-Jaworowska et al. 2004; a trend followed in this paper). The inclusion of the Tomato Hill taxa in Deltatheroida indicates that the group was already morphologically diverse and distinctive by the end of the Early Cretaceous, in turn implying that diversification of Metatheria was already well under way by that time.

Atokatheridium and *Oklatheridium* compare favorably with other deltatheroidans. Lower molars (Figure 1.7) are very similar, sharing a tall paraconid and strong, sharp paracristid. The height difference between the paraconid and metaconid is the least in *Oklatheridium* and the greatest in *Atokatheridium* (the full height of the metaconid is unknown in *Sulestes* due to breakage). The trigonid is open lingually in *Atokatheridium*, as in *Deltatheridium* and *Sulestes*, though it is more closed in *Oklatheridium*. A distal metacristid is present in all deltatheroidans. The small, low talonid preserved in *Atokatheridium* is very similar to that of *Deltatheridium*. Both have a shallow, open talonid basin and only two cusps (hypoconid, hypoconulid) are present in the majority of specimens belonging to *Deltatheridium pretrituberculare*, as is the case for the only known lower molar of *Atokatheridium boreni*. The talonid in *Sulestes*, however, is somewhat stronger and possesses three equally developed cusps. The height difference between the trigonid and talonid is less in *Sulestes* than in other deltatheroidans, though it is likely that the only known lower molar referred to this genus is an m1, and in *Deltatheridium* the m1 has the relatively lowest trigonid.

The upper molars of the Tomato Hill taxa share a number of similarities with other deltatheroidans (Figures 1.8, 1.9), most notably retention of a large stylocone, emphasis on the postmetacrista, and a taller paracone that shares a significant portion of its base with the metacone. The general outline of the M2 of *Atokatheridium* is very similar to that of *Deltatheroides*. However, *Atokatheridium* has a significantly narrower stylar shelf and wider protoconal region, with a taller protocone. *Atokatheridium* differs similarly from *Deltatheridium*, but also has a shallower ectoflexus and shows less emphasis on prevallum shear, with a reduced preparacrista. Conversely, *Oklatheridium* has the deepest ectoflexus among deltatheroidans, as well as the greatest width disparity between the parastylar and metastylar lobes. The postmetacrista is very strongly developed, as in other deltatheroidans, but the crest is oriented more directly labiad. The metacone in *Oklatheridium* is lower than the paracone, but the height difference is relatively much less than in other taxa. The protocone and conules of *Oklatheridium* are much better developed than in any other deltatheroidan; though *Sulestes* has strong conules, the protoconal region is relatively narrow.

The third upper molar locus of each of the Tomato Hill taxa suggests the presence of a fourth molar, as noted earlier, but in each taxon the expected morphology of that fourth molar is quite distinct (Figure 1.8). The M3 referred to *Oklatheridium* shows strong reduction of the metastylar lobe, leaving only a rim labial to the metacone. This condition is seen in other taxa in which the fourth molar is heavily reduced, with the third molar assuming the morphology typical of the ultimate molar. The unique Late Cretaceous (Lancian) marsupial *Glasbius* exhibits this condition, with a tiny fourth molar present; this condition is also seen in *Deltatheridium*, where the presence of the fourth upper molar remained undocumented until exceptionally complete material became available (Rougier et al., 1998). The size of the M3 referred to *Oklatheridium* indicates that a succeeding molar was present; morphology of the M3 suggests that the last molar was strongly reduced. In this respect, the most appropriate model for restoration of the tooth row is *Deltatheridium* (Figure 1.8A, B). By contrast, the M3 assigned to *Atokatheridium* possesses a very wide metastylar lobe and a deep ectoflexus that is distinct from the anterior molars. Morphology indicates that an M4 was certainly present in this taxon as well. Though loss of the anterior half of the tooth makes direct comparison with the other loci impossible, the relative strength of the metastylar lobe suggests a much larger M4 than would have been present in *Oklatheridium*, perhaps more similar to the condition seen in *Deltatheroides* (Figure 1.8C, D; see Rougier et al., 2004).

1.3.2 Faunal Comparisons

Vertebrates of the Tomato Hill local fauna are listed in Table 1.1. Many of the 42 taxa known thus far are only identified to higher taxonomic level, reflecting incompleteness of the fossils, the fact that many groups remain to be studied, and the poor state of knowledge regarding Early Cretaceous terrestrial vertebrates in general. Among mammals, for example, only the triconodontid *Astroconodon* (see Turnbull and Cifelli, 1999) and the deltatheroidans (Kielan-Jaworowska and Cifelli, 2001, this study) have received treatment to date, with the remainder being currently under study. With these caveats, a few general comments on mammals of the Tomato Hill local fauna may be made.

The most obvious comparison lies with the two main mammal-yielding sites in the Trinity Group of Texas, both of which are in reasonably close geographic (and possibly stratigraphic) proximity (Figure 1.1): Greenwood Canyon (Montague County) and Butler Farm (approximately 20 km to the south, in Wise County). As noted under "Geological Context", above, both of these sites (which, like OMNH V706, no longer exist) lay within the local uppermost part of the Antlers Formation, and mammals collected from them are probably somewhat geologically younger than those of the Tomato Hill local fauna. A minimum of some eight mammalian varieties is known from Greenwood Canyon, which is reasonably close to the estimate for the Tomato Hill local fauna. Similarly, published reports suggest the presence of at least eight mammalian taxa at Butler Farm, though the actual number may be closer to six, if the synonymies suggested in Table 1.3 are verified by further study. The Greenwood Canyon and Butler Farm faunas are strikingly similar to each other, even at the species level: the triconodontid *Astroconodon denisoni* is present in both, as are the stem boreosphenidans *Kermackia texana, Pappotherium pattersoni*, and *Holoclemensia texana*. Indeed, if (as we suspect)

TABLE 1.3. Mammals from Greenwood Canyon (Montague County) and Butler Farm (Wise County), upper Antlers Formation, northern Texas. References and comments are given in footnotes.

Greenwood Canyon	Butler Farm
Eutriconodonta	Eutriconodonta
Triconodontidae	Triconodontidae
Astroconodon denisoni[1]	*Astroconodon denisoni*[1]
Multituberculata	Multituberculata
Family uncertain	Family uncertain
gen. and sp. indet. (2)[2]	gen. and sp. indet. (2)[2]
"Stem Cladotheria"	
Spalacotheriidae	
Spalacotheroides bridwelli[3]	
Boreosphenida, Order uncertain	Boreosphenida, Order uncertain
Family uncertain	Kermackiiidae
gen. and sp. indet.[4,5]	*Kermackia texana*[7]
Kermackiidae	[*Trinititherium slaughteri*][8]
Kermackia texana[4]	Pappotheriidae
Pappotheriidae	*Pappotherium pattersoni*[9]
Pappotherium pattersoni[4]	[*Slaughteria eruptens*][10]
Holoclemensiidae[6]	Holoclemensiidae
Holoclemensia texana[4]	*Holoclemensia texana*[11]

[1] Patterson (1951), Slaughter (1969), Turnbull and Cifelli (1999).

[2] Krause et al. (1990).

[3] Patterson (1955, 1956).

[4] Butler (1978).

[5] Passing mention should be made of a partial edentulous dentary, FMNH PM 583, described as an unidentified therian by Patterson (1956, Figures 10, 11), and later designated as the holotype and only known specimen of *Adinodon pattersoni* by Hershkovitz (1995), who placed it in his marsupial family "Marmosidae". We follow Cifelli and Muizon (1997) in regarding this as a *nomen dubium* and, like Patterson, consider the specimen to represent an interesting but presently unidentifiable "therian of metatherian-eutherian grade" (i.e., stem boreosphenidan).

[6] Family erected by Aplin and Archer (1987), who followed Slaughter (e.g., 1968a, b, 1971) in regarding *Holoclemensia* to be marsupial. Butler (1978) placed the genus in the Pappotheriidae, within his suprafamilial group (infraclass) Tribotheria, a collocation of basal tribosphenic mammals. Most subsequent workers (e.g., Kielan-Jaworowska et al., 1979; McKenna and Bell, 1997; Kielan-Jaworowska et al., 2004; but see Fox, 1980; Luo et al., 2003) have followed Butler in excluding *Holoclemensia* from Metatheria, but a formal revision remains in the future, and for present purposes we provisionally recognize Aplin and Archer's monotypic family Holoclemensiidae.

[7] Slaughter (1971).

[8] We follow W. A. Clemens (cited in Butler, 1978: 11) in considering the holotype and only known specimen of *T. slaughteri*, a posterior lower molar (SMP-SMU 61728), to probably represent a positional variant of *Kermackia texana*, also known only by a lower molar, though we do not formally synonomize them.

[9] Slaughter (1965, 1971).

[10] The holotype and only known specimen of *Slaughteria eruptens*, a fragment of dentary bearing four teeth (SMP-SMU 61992), was originally described and illustrated by Slaughter (1971, pl. 9) as *Pappotherium pattersoni*. Butler (1978) erected the new genus and species *Slaughteria eruptens* for the specimen, partly on the strength of Slaughter's 1971: 137) observation (based on X-rays) that no unerupted teeth were present in the specimen. Slaughter (1971) considered the first molariform tooth of SMP-SMU 61992 to be a molarized last premolar (and therefore evidence of eutherian affinities), whereas Butler (1978) supposed it to be a first molar. Subsequent study using ultra high-resolution X-ray computed tomography shows that both interpretations were incorrect: the tooth in question is the last deciduous premolar (Kobayashi et al., 2002). We follow Slaughter (1971) and Kobayashi et al. (2002) in regarding the specimen as probably belonging to *Pappotherium pattersoni*, but do not formally sink *Slaughteria eruptens* into synonymy.

[11] Slaughter (1968a, b, 1971).

the boreosphenidans *Slaughteria eruptens* and *Trinititherium slaughteri* (both from Butler Farm) are junior subjective synonyms of *Pappotherium pattersoni* and *Kermackia texana*, respectively, then the two mammalian assemblages are identical, with one exception: the stem cladotherian *Spalacotheroides bridwelli*, which is known only from Greenwood Canyon. Whether or not this is a significant difference is difficult to judge, especially in light of the tiny, fragile nature of spalacotheriid fossils, and the small sample sizes in general. Based on published reports (Patterson, 1956; Slaughter, 1971; Turnbull, 1971; Butler, 1978), the most characteristic feature of the Greenwood Canyon–Butler Farm assemblages appears to be the great abundance of the stem boreosphenidans *Holoclemensia* and, to a lesser extent, *Pappotherium*.

By comparison, current data show that the mammalian assemblage of the Tomato Hill local fauna is quite different. The triconodontid *Astroconodon denisoni* is shared with Greenwood Canyon and Butler Farm. However, this species has a considerable stratigraphic range, as it is also known from Paluxy Church, one of the stratigraphically lowest vertebrate sites known in the Twin Mountains Formation (Winkler et al., 1990, p. 102). In a broader context, occurrence of the genus *Astroconodon* is widespread, both geographically and stratigraphically: it is also known from the?Aptian–Albian of the Cloverly Formation, Wyoming and Montana (Cifelli et al., 1998), and from near the Albian–Cenomanian (Early–Late Cretaceous) boundary in the Cedar Mountain Formation, Utah (Cifelli and Madsen, 1998).

Two other mammalian varieties possibly shared between the Tomato Hill local fauna and the Texas sites are the aforementioned *Spalacotheroides* (a stem cladotherian) and *Pappotherium* (a stem boreosphenidan), both of which are tentatively identified by rare, incomplete fossils from OMNH locality V706. Unfortunately, the holotype of *Spalacotheroides bridwelli* (the only species known for the genus), which consists of a dentary fragment bearing an incomplete molar (FMNH PM 933, see Patterson, 1955, Figure 145), is not particularly diagnostic, owing to recent discovery of a number of other spalacotheriids with similar lower molars (see review by Cifelli and Madsen, 1999). Identification of *Pappotherium* in the Tomato Hill local fauna is based on a heavily worn, incomplete upper molar, and should be regarded as tentative.

The most important difference between the mammalian assemblages from Butler Farm and Greenwood Canyon on one hand, and the Tomato Hill local fauna on the other, concerns the presence and relative abundance of boreosphenidans. Whereas the Butler farm and Greenwood Canyon faunas are dominated by *Holoclemensia* (especially) and *Pappotherium*, these are rare at Tomato Hill, where most of the boreosphenidan fossils are referable to the two deltatheroidans *Atokatheridium boreni* and *Oklatheridium szalayi*. Given the limited data at hand, the source(s) of these faunal differences (geological age, paleoecology, or both) cannot be identified at present.

1.3.3 Deltatheroida In Space and Time

1.3.3.1 North America

With the exception of a few fossils from the Neocomian Lakota Formation of South Dakota (Cifelli and Gordon, 2005), no mammals older than Aptian–Albian age are known from the Early Cretaceous of North America. Hence, *Atokatheridium* and *Oklatheridium* are, by default, the oldest deltatheroidans known from the continent. Among boreosphenidans, the Aptian–Albian record from North America otherwise consists of "tribotheres" (e.g., *Holoclemensia, Pappotherium, Kermackia*, see Butler, 1978 and comments above) and a single eutherian, *Montanalestes* (Cifelli, 1999). Beginning at the Early–Late Cretaceous boundary, North American assemblages became dominated by marsupials (Cifelli and Davis, 2003; Cifelli, 2004), with occasional "tribotheres" also present (e.g., Fox, 1972, 1976, 1980, 1982; Clemens and Lillegraven, 1986); eutherians did not reappear until the late Santonian or early Campanian (Fox, 1984), and did not diversify appreciably until the late Maastrichtian (e.g., Lillegraven, 1969). Following the Aptian–Albian, the next possible deltatheroidan is from the Turonian part of the Straight Cliffs Formation, southern Utah, represented by a relatively large but incomplete lower molar (Cifelli, 1990a). The only other specimens of deltatheroidans from the Cretaceous of North America were reported by Fox (1974), who identified an upper molar (Scollard Formation, late Maastrichtian, Alberta) and three lowers or parts thereof (Oldman Formation, late Campanian, Alberta; Lance Formation, late Maastrichtian, Wyoming) as cf. *Deltatheroides* sp. Rougier et al. (2004) considered the upper molar, at least, unidentifiable to genus, and we follow their judgment. In a strict consensus tree resulting from the analysis of Rougier et al. (2004), this upper molar came out as part of an unresolved tetrachotomy with *Atokatheridium, Deltatheridium*, and *Deltatheroides*; the four collectively forming a sister taxon to *Sulestes* within Deltatheroida.

1.3.3.2 Asia

The geologically oldest boreosphenidans of Asia come from the Barremian of Liaoning Province, China. The two best known are *Eomaia scansoria* and *Sinodelphys szalayi*, referred to Eutheria and Metatheria, respectively (Ji et al., 2002; Luo et al., 2003). Through the remainder of the Cretaceous, the boreosphenidan fauna of Asia was dominated by eutherians, and in this respect it differs markedly from North American assemblages for this time interval (e.g., Lillegraven, 1974; Cifelli, 2000; Cifelli and Davis, 2003).

The antiquity of Deltatheroida in Asia is debatable. Excluding *Kielantherium* (see above), which is from the ?Aptian–Albian "Höövör Beds", Mongolia (Dashzeveg and Kielan-Jaworowska, 1984), the next geologically oldest taxa that have been referred to Deltatheroida are of Cenomanian age. Both of these, *Oxlestes grandis* (from the Khodzhakul Formation, Uzbekistan, see Nessov, 1982; Nessov et al.,

1994) and *Khuduklestes bohlini* (Gansu Province, China, geological unit unknown see Nessov et al., 1994), are based on axis vertebrae and were referred to Deltatheroida on the basis of their relatively large size. Neither of these constitutes a verifiable record of the group, and we follow Rougier et al. (2004) in dismissing them from further consideration.

The geologically oldest, generally accepted records of deltatheroidans in Asia come from Coniacian strata in the Bissekty Formation at Dzharakuduk, Uzbekistan. *Sulestes* (represented by *S. karakshi* Nessov 1985 and *Sulestes* sp., see Kielan-Jaworowska and Nessov, 1990), known by a maxilla fragment with M1–2 and a referred lower molar, is relatively advanced, despite its geological age; as noted, Rougier et al. (2004) place it as sister taxon to remaining deltatheroidans. *Deltatherus kizylkumensis* was initially placed in *Deltatheroides* by Nessov (1993), but later transferred to its own genus (Nessov, 1997). The only informative specimens are two lower molars, one of which was illustrated by Kielan-Jaworowska et al. (2004, Figure 12.7C). We accept *Deltatherus* as a deltatheroidan and included it within the family Deltatheridiidae, but cannot comment further on its affinities. Finally, the geologically youngest and incomparably best known deltatheroidans come from beds of probable Campanian age in Asia. These are *Deltatheroides*, from the? early Campanian (and possibly younger strata) in Mongolia (Gregory and Simpson, 1926; Kielan-Jaworowska, 1975; Rougier et al., 2004); and *Deltatheridium*, known from the? early through? late Campanian of Mongolia (*D. pretrituberculare*, Gregory and Simpson, 1926; Kielan-Jaworowska, 1975; Rougier et al., 1998) and the Campanian of Kazakhstan (*D. nessovi*, see Averianov, 1997).

1.3.3.3 Origin and Dispersal of Deltatheroida

Ever since Deltatheroida were given ordinal status and recognized as being a monophyletic clade (Kielan-Jaworowska, 1982), they have been recognized as a mainly Asiatic group. Given the perceived similarity of *Deltatheroides*-like fossils described by Fox (1974) to the Mongolian form, presence of the group in North America could be reasonably explained by immigration from Asia, probably not long before first occurrence of relevant fossils. Though specimens from the Gobi Desert remain indisputably the most complete and abundant, the waters have become considerably murkier with the discoveries of the past 2 decades. Summing up evidence then available, Cifelli (2000) concluded that Deltatheroida dispersed twice between North America and Asia. A significant result of the analysis by Rougier et al. (2004) is that known distribution of the group may be explained by a single dispersal between the two continents.

Where did Deltatheroida originate? Data at hand are insufficient for anything more than speculation: the answer may be summarized as “source unknown”. If pressed to speculate, however, we are inclined to favor a North American origin for deltatheroidans, as suggested by Rougier et al. (2004). This group of elegant little carnivores first appeared in North American Aptian–Albian, antedating their appearance in Asia. New data presented above also show that there was some morphological diversity, at least, among deltatheroidans in the Aptian–Albian of Oklahoma.

Though rare and poorly represented, Deltatheroida appear to have been continuously present in North America from the Aptian–Albian until nearly the end of the Cretaceous, and in Asia from the Coniacian through the ?late Campanian, at least. Hence, the minimum age constraint for dispersal to Asia is Coniacian. Occurrences of several other boreosphenidan groups are germane here, though they provide little in the way of clarification. Stratigraphic distributions suggest the following examples: marsupials (stem-based definition, see Kielan-Jaworowska et al., 2004) appeared in North America no later than the Albian–Cenomanian boundary (Cifelli, 2004) and appeared in Asian no later than Coniacian (Averianov and Kielan-Jaworowska, 1999); Ungulatomorpha were present in Asia by the Cenomanian or Turonian (Setoguchi et al., 1999), were diverse on the continent by the Coniacian (Nessov et al., 1998), and had appeared in North America by the late Campanian (Cifelli, 2000) or, perhaps, as early as Santonian (Nessov et al., 1998); and the ?nyctitheriid lipotyphlan *Paranyctoides* appears to have been present in Asia by the Coniacian (Nessov, 1993; Archibald and Averianov, 2001), whereas its first appearance in North America is late Santonian or early Campanian (Fox, 1984; Cifelli, 1990b). Though these distributions do not provide much in the way of constraints, they do suggest the working hypothesis that a mammalian dispersal event between North America and Asia may have occurred sometime between the Early–Late Cretaceous boundary and the Coniacian, and that Deltatheroida may have dispersed between the continents during this interval.

Acknowledgments. We would first like to thank Drs. Eric Sargis and Marian Dagosto for inviting us to contribute to this volume, and for their supreme patience during the preparation of this manuscript. We also thank Dr. Cynthia Gordon for her role in initial collection and curation of the described specimens, and Dr. Cyprian Kulicki for his assistance with the SEM at the Instytut Palaeobiologii, Polska Akademia Nauk, Warsaw. Funding for this project was provided in part by grants from the American Chemical Society, the National Science Foundation (RLC), and Instytut Paleobiologii (ZK-J).

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