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TAXONOMIC REVISION OF TRIBOSPHENIC MAMMALS FROM THE LOWER CRETACEOUS ANTLERS FORMATION OF TEXAS AND OKLAHOMA, USA

A.O. Averianov^{1,2}

¹Zoological Institute of the Russian Academy of Sciences, Universitetskaya Emb. 1, 199034 Saint Petersburg, Russia; e-mail: dzharakuduk@mail.ru

²Department of Sedimentary Geology, Geological Faculty, Saint Petersburg State University, 16 Liniya VO 29, 199178 Saint Petersburg, Russia

ABSTRACT

There are five taxa of tribosphenic mammals in the Early Cretaceous Antlers Formation of Texas and Oklahoma, USA: a basal stem therian (*Kermackia texana*), stem therians near the eutherian-metatherian dichotomy (*Holoclemensia texana* and *Pappotherium pattersoni*), and stem marsupials (*Atokatheridium boreni* and *Oklatheridium szalayi*). *K. texana* has a primitive therian postcanine formula with three molars, replacement of p5, M3 with low protocone and no conules, lower molars with a large trigonid angle, oblique protocristid, paraconid smaller than metaconid (except m3), strong distal metacristid, narrow talonid, small talonid basin, and small entoconid (absent on m3). *H. texana* also has replacement in the fifth premolar locus and three molars. It is more derived in having a larger protoconal region with higher protocone and conules present, lack of distal metacristid, smaller trigonid angle, transverse protocristid, and wide talonid with larger talonid basin. It is similar to Eutheria by having M1 with reduced ectoflexus, semimolariform p5, and low trigonid angle with transverse protocristid. *Holoclemensia* cannot be referred to Eutheria because of the lack of the second rank postvallum/prevallid shear and unwinged conules. *P. pattersoni* (= *Slaughteria eruptens*) has replacement in the fifth premolar position, premolariform p5, and three molars (symplesiomorphies for Theria). It is more derived than *Holoclemensia* in having a wider and shorter talonid. *Pappotherium* is similar to Eutheria in having a low trigonid angle, transverse protocristid, and the cristid obliqua labial to the protocristid notch. It cannot be attributed to the Eutheria because of the narrow protoconal region, low protocone, small conules lacking internal cristae, postprotocrista not extending labially past the metacone base, and a small talonid basin. *Atokatheridium boreni* and *Oklatheridium szalayi* (= *O. minax*, syn. nov.) have four molars and emphasis on the postvallum/prevallid shear (large metacone on M2, strong postmetacrista, paraconid higher than metaconid). These taxa cannot be attributed to the Deltatheroidea because of large protoconal region with winged conules. *Oklatheridium* is further different from the Deltatheroidea in having a wider talonid and better developed entoconid.

Key words: Antlers Formation, Early Cretaceous, evolution, Mammalia, North America, Theria

ТАКСОНОМИЧЕСКАЯ РЕВИЗИЯ ТРИБОСФЕНИЧЕСКИХ МЛЕКОПИТАЮЩИХ ИЗ НИЖНЕМЕЛОВОЙ ФОРМАЦИИ АНТЛЕРС ТЕХАСА И ОКЛАХОМЫ, США

A.O. Аверьянов^{1,2}

¹Зоологический институт Российской академии наук, Университетская наб. 1, 199034 Санкт-Петербург, Россия; e-mail: dzharakuduk@mail.ru

²Кафедра осадочной геологии, Геологический факультет, Санкт-Петербургский университет, 16 линия ВО 29, 199178 Санкт-Петербург, Россия

РЕЗЮМЕ

Установлено присутствие 5 таксонов трибосфенических млекопитающих в раннемеловой формации Антлерс в Техасе и Оклахоме, США: базальное стволовое териевое млекопитающее (*Kermackia texana*), стволые таксоны териевых млекопитающих вблизи дивергенции сумчатых и плацентарных (*Holoclemensia*

texana и *Pappotherium pattersoni*), и стволые таксоны сумчатых млекопитающих (*Atokatheridium boreni* и *Oklatheridium szalayi*). *K. texana* характеризуется примитивной для териев формулой щечных зубов с тремя молярами, сменой зубов в пятом премолярном локусе, МЗ с низким протоконом без конулей, нижние моляры с большим углом тригониды, косым протокристом, параконид меньше метакониды (кроме мЗ), сильно выраженным дистальным метакристом, узким талонидом, маленьким бассейном талониды, маленьким энтоконидом (отсутствует на мЗ). У *H. texana* также была смена в пятом премолярном локусе и три моляра. Этот таксон более продвинул по наличию более крупного протокона с конулями, отсутствием дистального метакристы, меньшим углом тригониды, поперечным протокристом, и широким талонидом с большим бассейном. Близок к *Eutheria* по строению М1 с редуцированным эктофлексусом, полумоляриформным р5, и небольшим углом тригониды с поперечным протокристом. Однако *Holoclemensia* не может быть отнесена к *Eutheria* из-за отсутствия дополнительных режущих кромок на коренных зубах и внутренних гребней конулей. Для *P. pattersoni* (= *Slaughteria eruptens*) была характерна смена пятого премоляра, премоляриформный р5 и три моляра (симплезиоморфии для Theria). Этот таксон более продвинул, чем *Holoclemensia* по наличию более широкого и короткого талониды. *Pappotherium* близок к *Eutheria* по небольшому углу тригониды, поперечному протокристу, и положению бокового кристы лабиальнее бороздки протокристы. Этот таксон не относится к *Eutheria* из-за узкого и низкого протокона, маленьких конулей без внутренних крист, короткой постпротокристы, и небольшого бассейна талониды. *Atokatheridium boreni* и *Oklatheridium szalayi* (= *O. minax*, *sup. nov.*) характеризуются четырьмя молярами и усиленными режущими кромками метакониды и паракониды. Эти таксоны не относятся к *Deltatheroidea* из-за крупного протокона и наличием внутренних гребней конулей. *Oklatheridium* также отличается от *Deltatheroidea* более широким талонидом и лучше развитым энтоконидом.

Ключевые слова: формация Антлерс, ранний мел, эволюция, Mammalia, Северная Америка, Theria

INTRODUCTION

Isolated teeth and jaw fragments of tribosphenic mammals from the Lower Cretaceous (Aptian-Albian) Antlers Formation in northern Texas, USA, collectively called “Trinity therians”, are among the most hard-won paleontological finds. An “accidental” discovery of two triconodontan jaw fragments and an indeterminate mammalian humerus in 1949 by R.H. Denison in the “Trinity Sand” (now Antlers Formation of Trinity Group) at Greenwood Canyon near Forestburg (Zangerl and Denison 1950; Patterson 1951), followed by extensive prospecting and processing of fossiliferous matrix in the Forestburg area. This work resulted in discovery of two new mammal localities, while the original Greenwood Canyon was the most productive. During four field seasons about 46 tons of matrix were screen-washed, which produced approximately 300 mammalian specimens (Patterson 1955, 1956). Among these only 34 specimens were referable to therian mammals (Patterson 1956). This is 11% of the whole mammalian sample, dominated by multituberculates and triconodontans, and about 1.35 tons of matrix per each therian specimen. Discovery of Early Cretaceous mammals in Texas was spectacular because Early Cretaceous mammals were not known previously in

North America and only one mammal locality of that age was known elsewhere (the rich Purbeck fauna from the Berriasian of England was considered Late Jurassic in age by that time). Moreover, the Early Cretaceous is the time when divergence and early evolution of two major groups of modern mammals, *Eutheria* and *Metatheria*, occurred. The “Forestburg therians” allowed for the first study of this problem utilizing fossils (Patterson 1956). The Trinity mammal localities were destroyed because of subsequent urbanization of the Forestburg area. However, a new productive microvertebrate locality with tribosphenic mammals was discovered within the Antlers Formation in neighboring Oklahoma (Cifelli 1997; Kielan-Jaworowska and Cifelli 2001; Davis et al. 2008; Davis and Cifelli 2011).

The Trinity therians are most interesting because they are close phylogenetically to the metatherian-eutherian dichotomy. But because of this the morphology of their dentition is mostly plesiomorphic. This, coupled with the scarcity and fragmentary nature of the specimens, caused a great controversy in interpretation of the Trinity therians in the past (see “review of the previous work” below). Davis and Cifelli (2011) provided the last comprehensive taxonomic revision of these mammals. However, my study of all available specimens in US museums led

to considerable different results, which are discussed in this article. The discussion about attribution of the specimens is present in the “comments” section of the respective taxa under “systematic paleontology.”

Institutional abbreviations. CNHM, Chicago Natural History Museum (Field Museum), Chicago, USA; OMNH, Oklahoma Museum of Natural History, Norman, USA; SMP–SMU, Shuler Museum of Paleontology, Southern Methodist University, Dallas, USA.

REVIEW OF THE PREVIOUS WORKS

The first scientific treatment of Forestburg therians was published by Patterson (1956). He intentionally did not apply taxonomic names because of the fragmentary nature of the material. Patterson provided detailed descriptions and illustrations of 14 molars or molar fragments and one edentulous dentary fragment in the CNHM collection (Greenwood Canyon locality). He recognized two morphological types of upper molars and three types of lower molars. Patterson (1956: 13) classified these specimens as “therian mammals of uncertain infraclass affinities but of metatherian-eutherian grade.” This concept of therians of “metatherian-eutherian grade” persisted for a long time in the literature (Kielan-Jaworowska et al. 1979). Based on new materials, Patterson (1956) provided a thorough discussion of the evolution of mammalian molar teeth. In particular, he introduced the term stylocone for the large stylar cusp of the upper molars and proposed that the lingual cusp of the upper molars of “pantotherians,” identified previously as a protocone, is homologous with the paracone of tribosphenic molars. According to Patterson (1956), some of the Forestburg therians may represent the group from which Eutheria and Metatheria arose.

Mills (1964: fig.6D) published a diagram showing occlusal relationships of upper and lower molars of a Forestburg therian, based on CNHM PM 884 (upper) and CNHM PM 1005 (lower) from Greenwood Canyon locality. In CNHM PM 884 the protocone is missing and Mills mistook the small preserved paracone for the protocone. Hence this Forestburg therian, in Mill’s interpretation, is only slightly more derived compared with *Peramus* in having paracone and metacone of equal size and somewhat larger protocone (lacking altogether in *Peramus*).

The first named taxon of Trinity therians was *Pappotherium pattersoni* Slaughter, 1965, referred

to the new family Pappotheriidae Slaughter, 1965 within Theria incertae sedis, based on a maxillary fragment with the two last molars (SMP–SMU 61725) from Butler Farm locality (Slaughter 1965). Slaughter identified in the material from Butler Farm three types of lower molars, types 4–6, additional to the types 1–3 described by Patterson (1956) from Greenwood Canyon. Slaughter assumed that one of the upper molar types, recognized by Patterson (1956), corresponds to the molars of *Pappotherium*. Slaughter described also two premolars, a lower (SMP–SMU 61730) and an upper (SMP–SMU 61731). These premolars were later referred to a triconodontan (Butler 1978: 14). According to Slaughter (1965: 18) “*Pappotherium* and Patterson’s forms from Greenwood Canyon [...] apparently are very near the point of divergence of placentals and marsupials from a common ancestor – either just before, just after, or during this event.” Thus the first interpretation of Trinity therians (Patterson 1956; Slaughter 1965; Clemens 1966, 1968, 1970; Hopson and Crompton 1969; Lillegraven 1969; Butler 1977, 1990, 1992) was, in modern usage, placement of them within the stem group of Theria, but not attributable to the crown groups Marsupialia or Placentalia.

The next described taxon was *Holoclemensia texana* Slaughter, 1968 based on an upper molar missing the protocone (SMP–SMU 61997, holotype), ultimate upper molar (SMP–SMU 62009), and lower molar (SMP–SMU 62131) from Butler Farm (Slaughter 1968b, c). The new taxon was referred to the marsupial family Didelphidae and was considered the earliest known marsupial. The referral to Metatheria was based on “large stylar cusp C, increased size of metacone, and accompanying incipient twinning of the hypoconulid and entoconid” (Slaughter 1968b: 255). The attribution to Didelphidae was explained by the similarity to *Alphadon*, a Late Cretaceous stem marsupial referred at that time to Didelphidae (Clemens 1979). According to the modern phylogenetic nomenclature, this classification implies that *H. texana* belongs to the crown group Marsupialia.

The same year Slaughter (1968a) published two premolars from Butler Farm, SMP–SMU 61948, an upper penultimate premolar with a purported protocone, and SMP–SMU 61947, a lower ultimate premolar with a small metaconid. Slaughter interpreted the morphology of these premolars as submolariform. Because submolariform premolars are not known in

marsupials, he considered these specimens as evidence of eutherians in the Butler Farm locality.

In a review on origin and early differentiation of therian mammals McKenna (1969) placed *Pappotherium* and *Holoclemensia* at the roots of Eutheria and Metatheria, respectively. In modern usage this means that *Pappotherium* is a stem placental and *Holoclemensia* is a stem marsupial.

The first revision of all tribosphenic mammals from Butler Farm locality was published by Slaughter (1971). The previously identified type 6 of Trinity lower molars, represented by a single specimen (SMP–SMU 61728), was considered as belonging to a taxon morphologically intermediate between “pantotherians” and therians. It has a complete distal metacristid and incipient entoconid, but the entocristid is lacking. Another lower molar (SMP–SMU 62398) with a complete distal metacristid and entocristid was referred to a new taxon, *Kermackia texana* Slaughter, 1971. *K. texana* was viewed as a taxon intermediate between the previous one (molar type 6) and *Holoclemensia* and *Pappotherium*. The metatherians were represented by *H. texana* with three specimens originally referred to that taxon (Slaughter 1968b). The eutherians were represented by more numerous specimens. Among these there are three submolariform premolars, two of which were reported previously (Slaughter 1968a) and one new tooth, SMP–SMU 62399, a lower ultimate premolar with a metaconid and a single-cusped talonid with an incipient talonid basin. *P. pattersoni* was also referred to Eutheria, as well as a smaller pappotheriid represented by an upper molar (SMP–SMU 62402). A dentary specimen with four cheek teeth, first of which is an erupting premolar (SMP–SMU 61992), was tentatively referred to *Pappotherium* based on size and occlusal relationships. The dentition of this specimen was interpreted as two simple premolars, a molariform ultimate premolar, and first molar, as in eutherians. X-rays of this specimen show no erupting teeth other than the first premolar. A back-to-front replacement sequence has been reconstructed for this specimen (see also Slaughter et al. 1974). The previously recognized Trinity molar type 4 (SMP–SMU 61726), a dentary fragment with canine (SMP–SMU 62400), and an upper incisor (SMP–SMU 62401) were also referred to Eutheria.

Turnbull (1971) reviewed the Trinity therians from Greenwood Canyon with special emphasis on their bearing to marsupial evolution. He identi-

fied four taxa in this material: *Holoclemensia* cf. *texana* (uppers: CNHM PM 1000, 1004, 1238; lowers: CNHM PM 1005), *Holoclemensia* sp. (uppers: CNHM PM 886, 1015; lowers: CNHM PM 660, 887, 930, 948, 965, 966, 1119, 1249), *Pappotherium* cf. *pattersoni* (uppers: CNHM PM 884, 999, 1075; lowers: CNHM PM 922, 1046, 1120, 1245), and *Pappotherium* sp. (upper: CNHM PM 1287). Turnbull considered both *Pappotherium* and *Holoclemensia* as stem therians (order Tribosphenata nov. and cohort Tribosphenata nov. within Theria).

Crompton (1971: fig.3) reconstructed occlusal relationships and wear facet for *Pappotherium* based on the penultimate upper molar of the holotype and referred lower molar from Butler Farm locality (SMP–SMU 61726). He noted absence of internal conular cristae (second rank shearing surfaces 3b and 4b) and weak development of shearing surfaces 5 and 6 on a small protocone in this taxon. The external conular cristae duplicated the shearing surfaces of the preparacrista and postmetacrista, thus providing a second rank of cutting edges. A new reconstruction of wear facets on *P. pattersoni* upper molar, without wear on protocone, has been published by Kielan-Jaworowska (1975: fig. 8) and Crompton and Kielan-Jaworowska (1978: fig. 4).

The molar structure of Trinity therians was revised by Fox (1975). *Pappotherium* and *Holoclemensia* are more derived than primitive therians (exemplified by *Aegialodon*, *Kermackia*, and *Potamotelses*) in having double-rank prevallum-postvallid shear and loss of contact between the paracone and distal metacristid. Fox argued that *Pappotherium* has three molars and *Holoclemensia* – four molars. The main argument was that in *Holoclemensia* both ultimate upper molars have a similar morphology, with a reduced metastylar lobe, while in *Pappotherium* only ultimate molar have this morphology. In *Deltatheroides* with four molars the metastylar lobe is reduced on both ultimate and penultimate molars. Butler (1977: 243) considered that this argument is “based on a misinterpretation of the evidence,” but did not provide further explanation in that paper. Later he noted that the case with *Deltatheroides* is not typical because the last molar is in the state of reduction in this taxon and a variety of Late Cretaceous metatherians have the penultimate molar with a well-developed metastylar lobe (Butler 1978: 21). Because of the supposed dental formula and other dental characters, Fox followed Slaughter (1971) in referring *Pappotherium* and *Holoclemensia*

to stem Placentalia and Marsupialia, respectively. Fox also noted the presence of new taxa among undescribed specimens of Trinity therians.

A new interpretation of Trinity therians based on revision of the whole sample from Greenwood Canyon and Butler Farm localities was presented by Butler (1978). According to this revision, there are at least five or six taxa of Trinity therians: *Pappotherium pattersoni*, *Holoclemensia texana*, *Kermackia texana*, *Trinititherium slaughteri* Butler 1978, and *Slaughteria eruptens* Butler, 1978. *Pappotherium* and *Holoclemensia* are the most common taxa; both have four molars, as in marsupials, and complex premolars, as in placentals. Both are referred to the Pappotheriidae, which cannot be attributed to either Marsupialia or Placentalia but represents a separate evolutionary lineage (new order Pappotherida). The two smaller forms, *Kermackia* and *Trinititherium*, have lower molars more primitive than in Pappotheriidae and were placed in a new family Kermackiidae (new order Aegialodontia). *Trinititherium slaughteri* is based on a single lower molar (SMP–SMU 61728), the molar type 6 of Slaughter (1965). A small upper molar (SMP–SMU 62402) could belong to either *Kermackia* or *Trinititherium*. *Slaughteria eruptens* is based on a dentary fragment with four cheek teeth (SMP–SMU 61992), which was referred previously to *P. pattersoni* by Slaughter (1971). Butler considered it unlikely that this specimen has a molariform premolar because of its Early Cretaceous age and interpreted its dentition as the last two premolars and the first two molars. It was placed provisionally in Kermackiidae. Orders Aegialodontia (Aegialodontidae, Kermackiidae, Deltatheriidae, and *Potamotelses*) and Pappotheriidae constitute the new subclass Tribotheria. Tribotherians are mammals with tribosphenic molars that are not classifiable as marsupials or placentals.

Fox (1980) placed Kermackiidae (*Kermackia* and ?*Trinititherium*) in Tribotheria, incertae sedis. *Holoclemensia* was referred to the recent order Marsupicarnivora, incertae sedis, and Pappotheriidae (*Pappotherium* and *Slaughteria*) to the extinct suborder Proteutheria of recent Insectivora.

Slaughter (1981) criticized Butler's reconstruction of cheek dentitions for *Pappotherium* and *Holoclemensia*. He thought that *Holoclemensia* has not a molariform premolar and that *Pappotherium* has three molars and a molariform ultimate premolar. This interpretation allows referral of *Holoclemensia*

to the stem Marsupialia and *Pappotherium* to the stem Placentalia.

HersHKovitz (1982) restudied CNHM PM 583, and the edentulous dentary fragment from Greenwood Canyon described by Patterson (1956). After immersion of the specimen in oil of anise, he found that the alveolus of the third incisor is "staggered" between the i2 and i4 alveoli, as in modern didelphid marsupials. Butler (1978) thought that this specimen possible belongs to either *Holoclemensia* or *Pappotherium*. Later HersHKovitz (1995) erected a new taxon, *Adinodon pattersoni* HersHKovitz, 1995, referred to a new subfamily Adinodontinae within the modern didelphimorphian family Marmosidae (=Didelphidae), for CNHM PM 583. Thus, according to HersHKovitz at least one of Trinity therians belongs to the crown group Marsupialia.

Archer (1984) proposed the supercohort Proto-delfhia to contain *Holoclemensia*. Later Aplin and Archer (1987) erected the monotypic family Holoclemensiidae for the latter genus. *Holoclemensia* was viewed by these authors a stem marsupial.

Jacobs et al. (1989) described *Comanchea hilli* Jacobs et al., 1989 based on a fragmented upper molar (SMP–SMU 71848) from the Pecan Valley Estates locality within the Paluxy Formation in Central Texas, a lateral equivalent of the upper section of the Antlers Formation in North-Central Texas, USA (Winkler et al. 1990). The new taxon was referred to Aegialodontia. SMP–SMU 71848 is similar to the hypothetically reconstructed upper molar of *Aegialodon* (Crompton 1971) in having a small protocone but has an unexpectedly derived stylar region, with the stylar shelf reduced mesially and well-developed stylar cusps. Later this specimen was considered a molar, premolar, or deciduous tooth (Winkler et al. 1990). Jacobs et al. (1989) concluded that *Holoclemensia* is not a marsupial because a stylar cusp C could be developed independently, as in *Comanchea*, and the degree of twinning of entoconid and hypoconulid is not the same as in Late Cretaceous metatherians. According to these authors, the Trinity therians represent two evolutionary grades, aegialodontids (*Comanchea*, *Kermackia*, and *Trinititherium*) and pappotheriids (*Pappotherium*, *Holoclemensia*, and *Slaughteria*). Jacobs et al. (1989) and Winkler et al. (1990) also published an edentulous dentary fragment with alveoli for five double-rooted premolars (SMP–SMU 62006) from the Paluxy Church locality within the Twin Mountains Formation, a lateral

equivalent of the lower section of the Antlers Formation. This specimen may belong to either *Pappotherium* or *Holoclemensia*.

Marshall and Kielan-Jaworowska (1992) considered only *Slaughteria* among Trinity therians referable to Eutheria, because of a supposedly molariform ultimate premolar.

Cifelli (1993a) published the first phylogenetic analysis that included Trinity therians. This analysis resulted in an unresolved position of *Kermackia*, *Trinititherium*, and *Slaughteria* at the root of the tree before the split of Metatheria and Eutheria, while *Kielantherium* with more plesiomorphic tribosphenic molars was included in Metatheria. *Comanchea* was grouped together with “Picopsidae” in a sister taxon to Theria. This is not surprising because all these taxa, as was found later, are based on deciduous teeth (Averianov et al. 2010; Davis and Cifelli 2011). *Pappotherium* and *Holoclemensia* were included in Eutheria.

Turnbull (1995) presented in a poster form an attempt to attribute edentulous dentary fragments from the Antlers Formation to the described taxa. In particular, he was inclined to refer the holotype of *Adinodon pattersoni* (CNHM PM 583) to *Holoclemensia*.

Cifelli and Muizon (1997) did not confirm the presence of a “staggered” lower incisor in CNHM PM 583 or in any Late Cretaceous metatherian. According to these authors, this character first appeared only in the Paleocene South American marsupials. Consequently, *Adinodon pattersoni* was considered a nomen dubium.

Cifelli (1997) announced discovery of Early Cretaceous mammals in a new microvertebrate locality McLeod 2 within the Antlers Formation in Oklahoma, USA. This locality is gone now (Davis et al. 2008). Among two first mammal specimens from this locality, one was an upper tribosphenic molar (OMNH 33455). This specimen is more derived than *Pappotherium* and *Holoclemensia* in having a taller protocone, and more developed and more labially placed conules, with internal crista at least on the paraconule. It was considered as representing a possible new taxon, which was not named. Cifelli proposed that the first molariform tooth in the holotype of *Slaughteria eruptens* is a deciduous premolar. Based on this, he questioned validity of this taxon, which may be synonymous with *P. pattersoni*. He also questioned reference of *Slaughteria* to Kermackiidae, which was based on possible presence of a distal meta-cristid in *S. eruptens*, but otherwise the latter taxon,

having a larger talonid basin and strong entoconid, is similar with Pappotheriidae. Cifelli concurred with Slaughter (1971) that presence of molariform premolars in the Antlers Formation of Texas strongly suggests that eutherians were present in North America during the Early Cretaceous.

Analyses of the metatherian relationships following discovery of new specimens of deltatheroidans from the Late Cretaceous of Mongolia (Rougier et al. 1998, 2004), identified *Holoclemensia* as a basal metatherian, at a trichotomy with Deltatheroidea and a clade of all other metatherians. The same result was repeated by Wible et al. (2001). However, adding of *Atokatheridium* and *Nanocuris* to the same data matrix resulted in the position of Deltatheroidea as the sister taxon for the clade *Holoclemensia* + all other metatherians (Wilson and Riedel 2010).

In a phylogenetic analysis presented by Averianov and Skutschas (1999) *Pappotherium* is a stem placental, *Holoclemensia* is a stem therian, and *Kermackia* and *Slaughteria* are unresolved sister taxa to the group *Holoclemensia* + Theria. *Comanchea* was clustered with *Picopsis*, as in Cifelli (1993b).

Novacek (1999: fig. 7) presented a cladogram of major clades of therians showing *Holoclemensia* as a stem marsupial.

Four additional specimens of tribosphenic mammals from the McLeod 2 locality have been described by Kielan-Jaworowska and Cifelli (2001). The upper molar (OMNH 61623) with a small protocone and unwinged conules is the holotype of *Atokatheridium boreni* Kielan-Jaworowska and Cifelli, 2001. This taxon was tentatively referred to Deltatheroidea because of extreme development of stylar shelf, considered as a derived character. A lower molar (OMNH 61624) with obtuse trigonid angle, distal metacristid, and only two talonid cusps, was questionably referred to *A. boreni*. Two lower molar trigonids (OMNH 61642 and 61643) have been identified as ?Deltatheroidea indet. Placement of *Atokatheridium* within Deltatheroidea has been confirmed in the phylogenetic analysis by Rougier, Wible et al. (2004).

Kobayashi et al. (2002) used X-ray CT scanning of SMP-SMU 61992, the holotype of *Slaughteria eruptens*. They found a germ of a replacement tooth under the first molariform tooth, showing that this tooth is a deciduous premolar, as was suggested previously by Cifelli (1997). The erupted teeth in this specimen have been identified as p2, p3, dp4, and m1, assuming that this animal had four premolars. The

reconstructed eruption sequence is (dp3?) → dp4 → m1/p3 → p2 → p4. Different interpretations of the eruption sequence in this specimen were presented by Luo et al. (2004), Archibald and Averianov (2012), and Davis (2011b). Kobayashi et al. (2002) noted that it is possible that *Slaughteria* is a juvenile of *Pappotherium*, as was originally suggested by Slaughter (1971). Kobayashi et al. (2002) also suggested that SMP–SMU 62398, the holotype of *Kermackia texana*, could be a deciduous premolar.

In the analysis by Luo et al. (2003) *Holoclemensia* is a basal metatherian forming a trichotomy with *Sinodelphys* and a clade of remaining metatherians. *Atokatheridium* clustered with *Deltatheridium*. In the analysis of a modified version of this dataset presented by Luo and Wible (2005) *Holoclemensia* is clustered with *Sinodelphys* in a taxon sister to the remaining metatherians. Deltatheroidea is not monophyletic and *Atokatheridium* forms a trichotomy with *Deltatheridium* and the clade containing remaining metatherians. In a subsequent analysis of the same matrix Luo et al. 2011 the phylogenetic position of discussed taxa is the same as in Luo et al. (2003).

In a now classical book on Mesozoic mammals (Kielan-Jaworowska et al. 2004) classified Trinity therians as “tribotherians,” or stem “boreosphenidans.” The term Boreosphenida is redundant (Rougier et al. 2007; Davis 2011b) and here I use the traditional concept of Tribosphenida (McKenna 1975). Three families, not referred to any order, have been recognized: Kermackiidae (*Kermackia* and *Trinititherium*), Pappotheriidae (*Pappotherium*), and Holoclemensiidae (*Holoclemensia*). The difference between the holotypes of *K. texana* and *T. slaughteri* are slight and may represent positional variation in teeth. *Slaughteria* was not referred to any family and its potential synonymy with *Pappotherium* has been noted. *Atokatheridium* was referred to Deltatheroidea, family incertae sedis. *Adinodon pattersoni* was omitted from classification because it is indeterminate.

Davis et al. (2008) described a considerably improved sample of tribosphenic molars from McLeod 2 locality (Tomato Hill local fauna). The deltatheroidan *Oklatheridium szalayii* Davis et al., 2008 is based on the holotype upper molar (OMNH 62410) and eight referred upper and lower molars. The latter included OMNH 61643 was referred to ?Deltatheroidea indet. by Kielan-Jaworowska and Cifelli (2001). The upper molars represent three molar loci (M1–4) but authors did not exclude the possibility of a fourth

molar. All lower molars are represented by the trigonid only and do not help to establish a dental formula for this taxon. *O. szalayii* is larger than *A. boreni* but considerably smaller than Late Cretaceous Asiatic deltatheroidans. *O. szalayii* differs from other deltatheroidans by well-developed conular cristae. OMNH 33455, the upper molar described previously by Cifelli (1997), has been identified as ?*Oklatheridium* sp. Davis et al. (2008) also added five new molars to *A. boreni*, two uppers and three lowers. Their hypothesized dental formula was four molars for this taxon, although the referred specimens documented only M1–3 loci. Attribution of the lower molar (OMNH 61624) to *A. boreni* (Kielan-Jaworowska and Cifelli 2001) was more confidently confirmed. The authors followed W.A. Clemens, cited in Butler (1978: 11), in considering SMP–SMU 61728, the holotype of *Trinititherium pattersoni*, as a positional variant of *Kermackia texana*. They also agreed with Slaughter (1971) and Kobayashi et al. (2002) in considering the holotype of *Slaughteria eruptens* as possibly belonging to *Pappotherium pattersoni* but did not synonymize these taxa formally.

In a phylogenetic analysis performed by Vullo et al. (2009), *Holoclemensia* appeared as a stem therian.

Describing new specimens of the Late Cretaceous Asiatic deltatheroidan *Sulestes*, Averianov et al. (2010) commented on several taxa of Trinity therians. OMNH 63725, identified as M3 of *A. boreni* by Davis et al. (2008) is considerably larger than other upper molars of this species and differs in having a distinctly wider stylar shelf. This specimen was referred to *Oklatheridium*. This referral resulted in placement of *Atokatheridium* among stem therians rather than deltatheroidans in the phylogenetic analysis. In this analysis *Pappotherium* is a stem therian and *Holoclemensia* a stem placental. On the their cladogram (Averianov et al. 2010: fig. 8) and in the list of synapomorphies, clade 10 was erroneously designated as Eutheria, while it should have been clade 9, including *Holoclemensia*. Averianov et al. (2010: fig. 9) published a reconstruction of the upper cheek teeth of *Holoclemensia* with three molars.

During the reanalysis of the CT scans of SMP–SMU 61992 made by Kobayashi et al. (2002), Davis (2011b) found a small partially calcified tooth germ under the last preserved molariform tooth in this specimen, implying that it had two molariform deciduous teeth, dp4 and dp5, a pattern not known in any extinct or extant therian. Winkler et al. (2011), used

higher resolution CT scans of SMP–SMU 61992 and concluded that the conjectural structure below the last preserved molariform tooth is posteriorly open and resembles neither the cap nor bell stage of a developing tooth. Here we accept the replacement pattern for SMP–SMU 61992 suggested by Kobayashi et al. (2002) and Winkler et al. (2011). Winkler et al. (2011) also used the size comparison for attribution of lower molars to the taxa based on upper molars, *Holoclemensia* and *Pappotherium*. They formally synonymized *Slaughteria eruptens* and *Pappotherium pattersoni*.

Davis and Cifelli (2011) presented a thorough revision of all Trinity therians. In this paper the McLeod 2 locality was considered in the context of the Tomato Hill local fauna. *Atokatheridium boreni* (Deltatheriidae) is represented by eleven molars from Tomato Hill locality – three uppers and eight lowers. M4 is still unknown but hypothesized. The interpretation of *Oklatheridium* was changed, with two species now recognized, *O. szalayii* and *O. minax* Davis and Cifelli, 2011. Only upper molars were attributed to the named species, while lower molars were identified as *Oklatheridium* sp. The sample of *O. szalayii* includes five molars, three M1, one M2, and one M3. All but one of these molars comes from Tomato Hill locality, the exception being CNHM PM 1238, which is from the Greenwood Canyon locality. The holotype of *O. minax* (OMNH 33455) is a tooth (M2) from Tomato Hill locality described by Cifelli (1997) and identified as ?*Oklatheridium* sp. in Davis et al. (2008). Two other upper molars have been referred to this species: CNHM PM 884 (M1) from Greenwood Canyon locality and OMNH 63727 (RM3) from Tomato Hill locality. *Pappotherium pattersoni* was provisionally referred to the Metatheria based on presumed presence of four molars. Except the holotype, five upper molars and five lower molar trigonids from Greenwood Canyon and Tomato Hill localities have been referred to this species. *Holoclemensia texana*, placed in Eutheria incertae sedis, is known from five upper and eleven lower molars from the Butler Farm, Greenwood Canyon, and Tomato Hill localities. Also one upper premolar (P4, SMP–SMU 61948), one lower premolar (p5, SMP–SMU 62399), and a deciduous upper premolar (DP5, SMP–SMU 71848, holotype of *Comanchea hillii* from Pecan Valley Estates locality) have been tentatively referred to *H. texana*. In spite of this referral being only tentative, *C. hillii* was unquestionably synony-

mized with *H. texana*. One lower molar (SMP–SMU 61726) from Butler Farm locality has been identified as *Holoclemensia* sp. One lower premolar (p5, OMNH 67134), and seven lower molars, including SMP–SMU 61728, the holotype of *Trinititherium slaughteri*, have been referred to *Kermackia texana* (Kermackiidae, Tribosphenida incertae sedis). One upper molar (SMP–SMU 62402) was referred to *K. texana* tentatively. These specimens come from the Butler Farm, Greenwood Canyon, and Tomato Hill localities. *Slaughteria eruptens* (Tribosphenida, family incertae sedis) includes, except the holotype, a lower premolar (p5, CNHM PM 1098), and two fragmented lower molars (OMNH 63726 and 63721). Thus this taxon is also known from the three localities mentioned above. Two specimens from the Greenwood Canyon locality, an upper ultimate molar (CNHM PM 1075) and lower molar (CNHM PM948), were identified as Tribosphenida incertae sedis.

As the above review shows, considerable controversy surrounds interpretations of the Trinity therians. This is undoubtedly caused by the fragmentary nature of most specimens and their largely plesiomorphic morphology. The postulated phylogenetic position of these taxa is heavily influenced by their taxonomic interpretation, association of upper and lower dentitions, identification of the molar positions, and hence the dental formula. In the next section I present a view on the classification of Trinity therians. All numerical indices mentioned in the text are based on the measurements provided by Davis and Cifelli (2011).

SYSTEMATIC PALEONTOLOGY

Mammalia Linnaeus, 1758

Tribosphenida McKenna, 1975

Stem group of Theria Parker and Haswell, 1897

Kermackia texana Slaughter, 1971

(Fig. 1)

Theria indet.: Patterson (1956: fig. 4A).

Trinity lower molar type 3: Patterson (1956: fig. 9B); Winkler et al. (2011: fig. 10).

Trinity lower molar type 6: Slaughter (1965: fig. 4); Slaughter (1971: pl. 1); Fox (1975: fig. 7A).

Kermackia texana: Slaughter (1971: 133, pl. 2); Fox (1975: fig. 7B); Butler (1978: fig. 3K); Kielan-Jaworowska et al. (2004: fig. 11.4D); Davis and Cifelli (2011: fig. 8C–G).

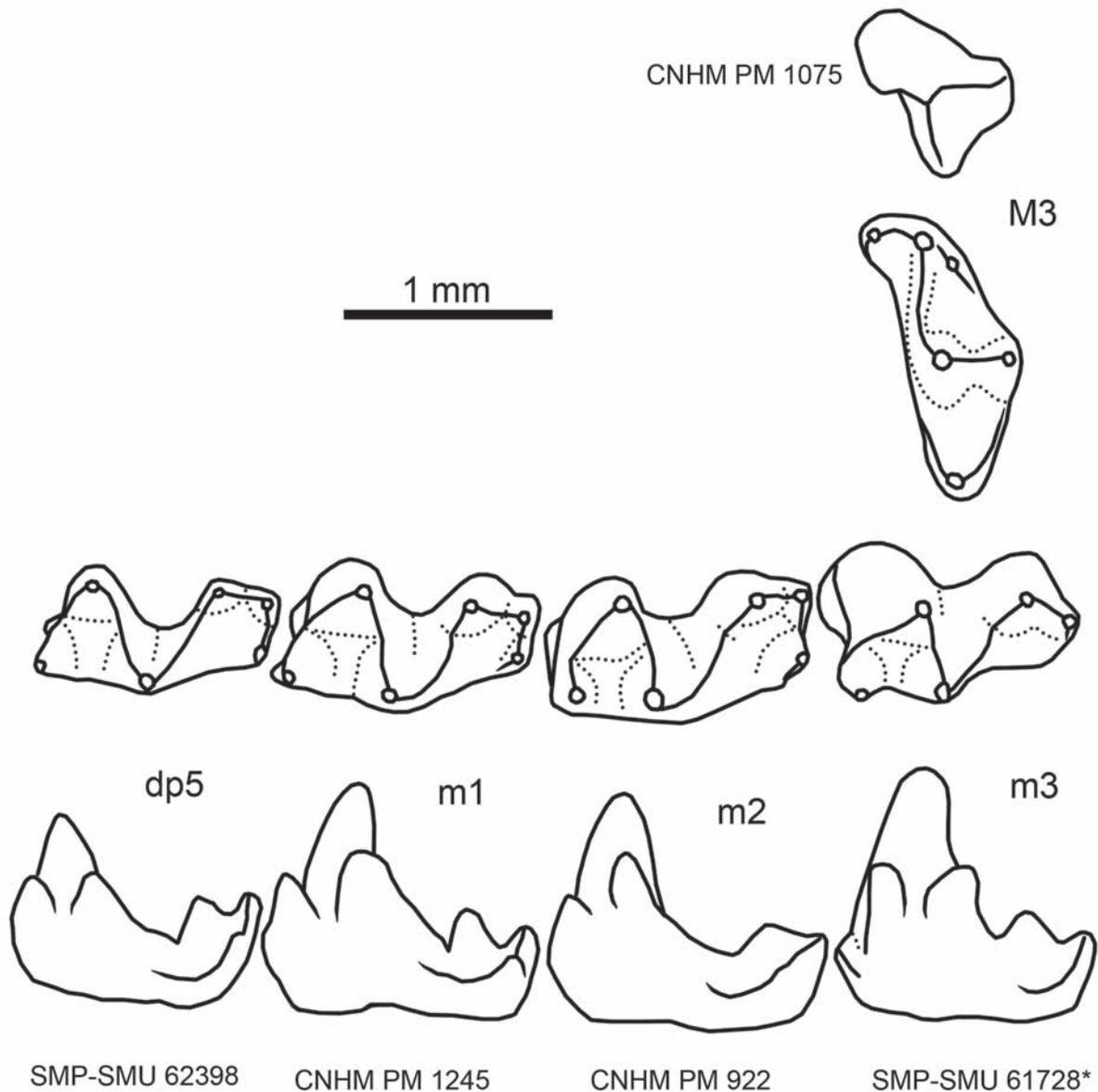


Fig. 1. The stem therian *Kermackia texana* from the Early Cretaceous Antlers Formation of Texas and Oklahoma, USA. Upper teeth are in labial and occlusal views, lower teeth – in occlusal and lingual views. Worn cusps and crests are reconstructed. Mesial end is to the left. Asterisk denotes reversed image at the collection number. Scale bar = 1 mm.

Pappotherium cf. *pattersoni*: Turnbull (1971: figs. 3C, 6D–F).

Trinititherium slaughteri: Butler (1978: 10, fig. 3T); Kielan-Jaworowska et al. (2004: 419, fig. 11.4E).

Kermackia or *Trinititherium*: Butler (1978: fig. 2c).

Tribosphenida indet.: Davis and Cifelli (2011: fig. 10A).

Holotype. SMP–SMU 62398, right dp5.

Type locality and horizon. Butler Farm locality, Wise County, Texas, USA; Antlers Formation, Lower Cretaceous (Aptian–Albian).

Referred specimens. Type locality: SMP–SMU 61728, left dentary fragment with m3 and alveoli for m2 (holotype of *Trinititherium slaughteri* Butler, 1978).

Greenwood Canyon locality: CNHM PM 1075, left M3. CNHM PM 1245, right m1. CNHM PM 922, right m2. CNHM PM 1046, left mx trigonid. Possible also the lost mx trigonid (CNHM PM 1065) mentioned by Butler (1978: 10).

Tomato Hill locality: OMNH 61178, right mx trigonid. OMNH 63893, left mx trigonid. OMNH 63731, left mx talonid.

Differential diagnosis. A stem therian different from Metatheria by replacement in fifth premolar locus, three molars, and paraconid smaller than metaconid (except on m3). Differs from Metatheria and Eutheria by small and low protocone, lack of conules, strong distal metacristid, narrow talonid, and small entoconid, lacking on m3. Additionally differs from Eutheria by keel-like vertical crest on paraconid. Differs from the Trinity stem therians *Holoclemensia* and *Pappotherium* by lack of conules, greater trigonid angle, paraconid and metaconid separated by lingual groove, oblique protocristid, distal metacristid present, narrow talonid, and keel-like vertical crest of paraconid. Among other stem therians differs from *Aegialodon*, *Kielantherium*, and *Hypomylos* by larger talonid with entoconid, from *Juramaia* by lack of conules, and from *Tribactonodon* by having keel-like vertical crest of paraconid instead of mesiolingual cuspule e. Differs also from *Aegialodon* and *Kielantherium* by paraconid smaller than metaconid. Differs from a premetatherian stem therian *Montanalestes* by distal metacristid present, paraconid smaller than metaconid, and paraconid and metaconid separated by lingual groove.

Description. CNHM PM 1075 is an ultimate upper molar, M3 based on the dental formula inferred from the lower molars (see below). The crown is dominated by a large paracone, which occupies a central position, with the parastylar lobe and protoconal region almost equal in width. The metacone is strongly reduced and the metastylar lobe is lacking. The preprotocrista is long and strong. It connects the relatively large stylocone. The parastyle is somewhat smaller than the stylocone. There is a prominent ectocingulum on the parastylar lobe, with a minute stylar cusp. The protocone is very low and narrow mesiodistally. There are no conules. The preprotocrista connects the parastyle. The postmetacrista terminates at the base of the metacone.

There are four complete lower molars and several fragments. Among complete molars, SMP–SMU 62398 is the smallest and CNHM PM 922 is the

largest. The ultimate molar in a dentary fragment (SMP–SMU 61728) is somewhat smaller than the latter tooth. These size differences between the specimens may reflect a size trend within the molar series: gradual increase towards the penultimate molar and decrease on the ultimate molar. Two alternative interpretations of this trend are possible: these teeth are m1–4 or an ultimate deciduous premolar and m1–3. The second alternative is preferred here because SMP–SMU 62398 is 7% shorter than CNHM PM 1245, while in stem therians with four molars m1 and m2 have a similar length (Dashzeveg and Kielan-Jaworowska 1984). Moreover, on SMP–SMU 62398 the precingulid is very faint and the mesiolingual cuspule e is lacking. These features are common for the deciduous ultimate premolar abutting the simple deciduous penultimate premolar. The m1 contacts with the ultimate permanent premolar, which has a developed talonid heel, and thus it possesses an elaborated precingulid and mesiolingual cuspule e for the interlocking with p5. Thus *Kermackia* likely had three molars (see also Davis and Cifelli 2011).

SMP–SMU 61728 is a posterior dentary fragment with m3 and alveoli for m2. The broken base of the coronoid process can be seen just posterior to the m3 (Davis and Cifelli 2011: fig. 8G3). The specimen is likely not mature because the coronoid process closely approximates the unworn last molar and the retromolar space is not developed. The difference between the mesial and distal alveoli in m2 is less pronounced compared with m3. This suggests that m2 had a larger talonid. The lingual alveolar border is sharp and higher than the labial alveolar border. This is correlated with the unequal height of the molar crown, which is deeper on the labial side.

All molariform teeth (dp5 and m1–3) are similar in having a low and labially deflected talonid, long talonid isthmus, and prominent distal metacristid. The protoconid is heavily worn on dp5 but apparently was lower compared with the molars. The trigonid angle is ~52° (dp5), ~54° (m1), ~46° (m2), and ~48° (m3). The protoconid is the highest on m3. The protocristid is oblique on dp5 and m1 but more transverse on m2–3. The protocristid usually lacks the protocristid notch (present on trigonid fragments from the Tomato Hill locality). The metaconid is robust, about half the height of the protoconid. On m3 the metaconid is greatly reduced and similar in height with the paraconid. The paraconid is small, spike-like, and placed somewhat labial to the metaco-

nid. It is pointed vertically, parallel to the metaconid. These cusps are separated by a small gap allowing the trigonid basin to open lingually. All molars have a well-developed precingulid (mesiolabial cuspule f). On dp5 the precingulid is very faint. On m1–2 there is a slight vertical keel on the mesiolingual slope of the paraconid representing the mesiolingual cuspule e. There is a strong distal metacristid extending from the metaconid tip towards the base of the hypoconid where it is separated from the cristid obliqua by a distinct notch. Slaughter (1971) and Butler (1978) noted an additional cusp on the distal metacristid on m3. This is a preservation artifact caused by chipping of this crest in SMP–SMU 61728.

The talonid is narrower than the trigonid. The talonid width to trigonid width ratio is 0.77 (dp5), 0.74 (m1), 0.81 (m2), and 0.68 (m3). The talonid isthmus opposite the hypoflexid is very long, compatible in length with the remaining part of the talonid. The hypoconid is the highest cusp, about twice higher than the hypoconulid. The small entoconid is present on dp5 and m1–2 and lacking on m3 (Butler's (1978) identification of the rudimentary entoconid on this tooth cannot be confirmed). The talonid basin is small and sloping lingually. The entocristid is hardly discernable on m1–2, and lacking on dp5 and m3. Thus the talonid basin is open lingually.

Comments. Davis and Cifelli (2011) refereed SMP–SMU 62402, an isolated upper molar from Butler Farm, to *K. texana*. This specimen is identified here as dp5 of *Pappotherium pattersoni* (see below). These authors also referred to *K. texana* a lower ultimate premolar, OMNH 67134 (Davis and Cifelli 2011: fig. 8B) because of characteristic notch on the crest between the trigonid and the talonid cusp. This notch has been considered as serially homologous with the notch between the distal metacristid and the cristid obliqua of the lower molars in *Kermackia*. This notch cannot be homologous because on the premolar it is on the crest between the protoconid and hypoconid (talonid cusp), while on molars it is on the crest between the metaconid and hypoconid. Moreover, it is highly improbable that such a primitive tribosphenic taxon had a semimolariform premolar. A similar notch is present on p5 referred to *Holoclemensia texana* (SMP–SMU 61947). Otherwise OMNH 67134 is very similar with p5s of *Holoclemensia* and it is referred here to that taxon. It differs by somewhat smaller size, but the lower molars of *Holoclemensia* from the Tomato Hill locality are also distinctly

smaller than those from the Butler Farm locality (see comments to *Holoclemensia*).

Holoclemensia texana Slaughter, 1968 (Fig. 2)

Theria indet.: Patterson (1956: figs. 3B, 5, 6); Clemens (1966: fig. 13b).

Trinity lower molar type 2: Patterson (1956: fig. 8B).

Forestburg molar: Mills (1964: fig. 6D).

Trinity lower molar type 4: Slaughter (1965: fig. 2); Slaughter (1971: pl.10C, D).

Trinity lower molar type 5: Slaughter (1965: fig. 3).

Eutheria indet.: Slaughter (1968a: fig. 1); Slaughter (1971: pls. 5, 6, 7D–G).

Clemensia texana [preoccupied generic name]: Slaughter (1968b: 254, fig. 1).

Holoclemensia texana: Slaughter (1968c: 1306); Slaughter (1971: pls. 3, 4); Fox (1975: fig. 2B); Butler (1978: figs. 1H, 2k-o, 3H, 4g, h, 5H); Kielan-Jaworowska et al. (1979: fig. 10–4C–F); Kielan-Jaworowska et al. (2004: fig. 11.5E); Averianov et al. (2010: fig. 9); Davis and Cifelli (2011: figs. 6A–G, 7A–E).

Unidentified lower molar: Crompton (1971: fig. 3).

Holoclemensia cf. *texana*: Turnbull (1971: figs. 2A, C, 5C).

Holoclemensia sp.: Turnbull (1971: figs. 2D, 5A, B); Davis and Cifelli (2011: fig. 7F).

Pappotherium pattersoni: Butler (1978: fig. 4f).

Comanchea hilli: Jacobs et al. (1989: 4992, figs. 1, 2); Winkler et al. (1990: fig. 10); Kielan-Jaworowska et al. (2004: fig. 11.6B).

Kermackia texana: Davis and Cifelli (2011: fig. 8B).

Holotype. SMP–SMU 61197, right M2 missing protocone.

Type locality and horizon. Butler Farm locality, Wise County, Texas, USA; Antlers Formation, Lower Cretaceous (Aptian-Albian).

Referred specimens. Type locality: SMP–SMU 61948, left P4. SMP–SMU 62009, right M3. SMP–SMU 61947, left p5 (the specimen is now heavily damaged). SMP–SMU 62399, left p5. SMP–SMU 62722, right m1 (Davis and Cifelli (2011) indicated that this specimen has only talonid preserved, possible because of broken cast at their disposal). SMP–SMU 61726, left m1. SMP–SMU 62131, left m1. SMP–SMU 61727, left m2. SMP–SMU 62721, right m3.

Greenwood Canyon locality: CNHM PM 1000, left M1 missing protocone. CNHM PM 1004, right M1 missing protocone and parastylar and metastylar lobes. CNHM PM 886, right M2 missing protocone and parastylar lobe. CNHM PM 1005, right m1.

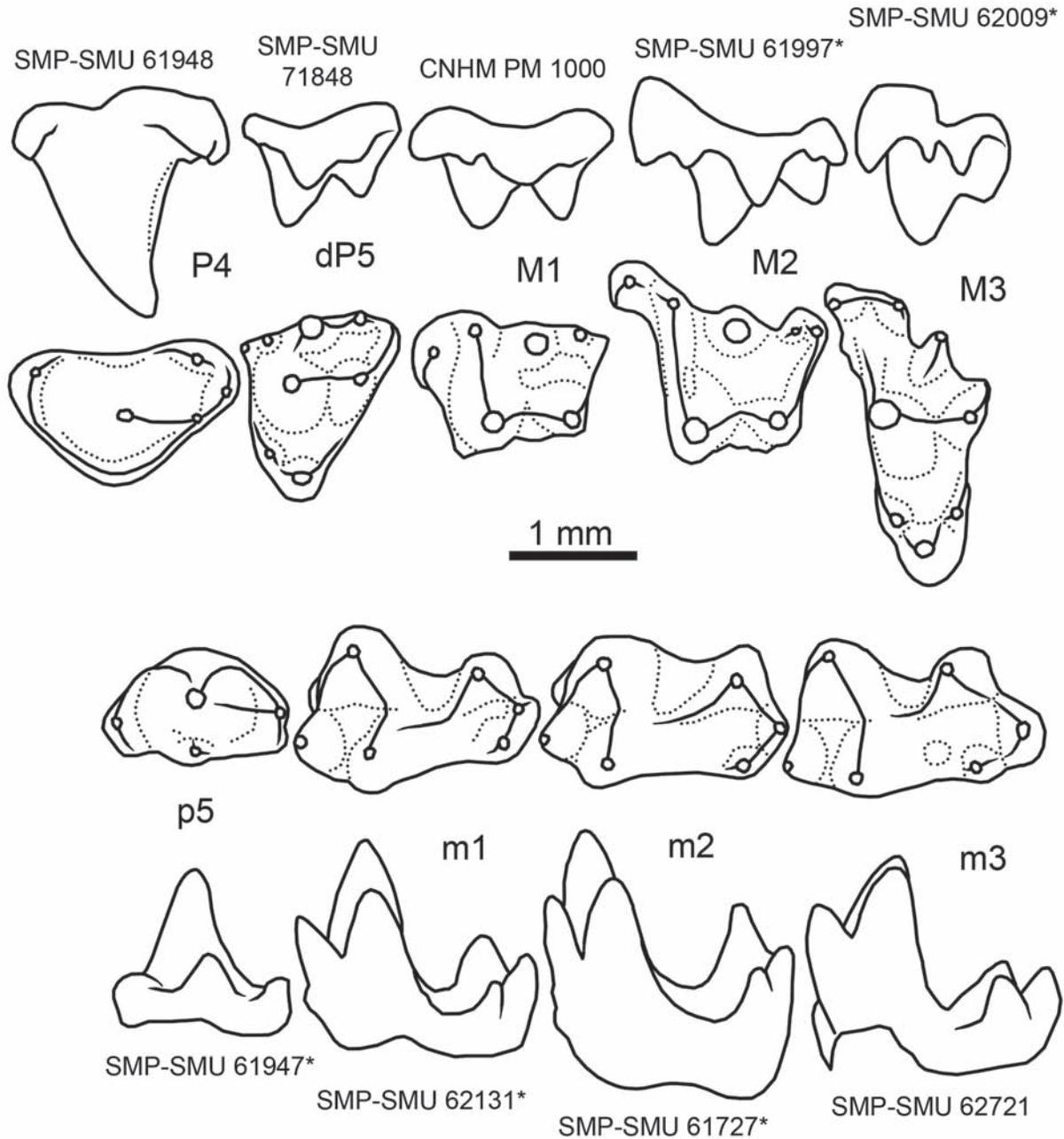


Fig. 2. The stem therian *Holoclemensia texana* from the Early Cretaceous Antlers Formation of Texas, USA. Upper teeth are in labial and occlusal views, lower teeth – in occlusal and lingual views. Worn cusps and crests are reconstructed. Mesial end is to the left. Asterisk denotes reversed image at the collection number. Scale bar = 1 mm.

CNHM PM 887, right mx trigonid. CNHM PM 3877, right mx trigonid.

Tomato Hill locality: OMNH 67134, right p5. OMNH 62412, heavily worn right mx. OMNH 62414, left mx talonid. OMNH 63894, right mx talonid.

Pecan Valley Estates locality: SMP–SMU 71848, left dP5 (holotype of *Comanchea hillii*).

Differential diagnosis. A stem therian different from Metatheria by replacement in fifth premolar locus, three molars, and paraconid smaller than

metaconid. Similar with Eutheria and different from other stem therians by M1 with reduced ectoflexus, semimolariform p5, and low trigonid angle with transverse protocristid. Differs from Eutheria by postprotocrista not extending labially past metacone base and conules lacking internal cristae. Differs from *Kermackia* by conules present, smaller trigonid angle, transverse protocristid, paraconid and metaconid bases not separate, distal metacristid lacking, wider talonid, and larger entoconid. Differs from *Pappotherium* by large stylar cusp C, larger protocone and conules, and cristid obliqua lingual to protocristid notch. Differs from a premetatherian stem therian *Montanalestes* by paraconid smaller than metaconid.

Description. The SMP–SMU 61948 is the penultimate upper premolar (P4) referable to *H. texana* (Butler 1978; Averianov et al. 2010; Davis and Cifelli 2011). The main cusp is tall and trenchant. Its tip is somewhat deflected distally. The mesial side of the main cusp is rounded, while along the distal side there is a sharp ridge connecting the distal cingulum. On the labial side of the crown, closer to the mesial end, there is a shallow ectoflexus. There is a distinct mesial cingulum with small mesial cusp at the base of the crown. The distal end of the crown is more transversely expanded, and bears three cusps. The distolabial cusp is the largest. It is placed on the distolabial cingulum which is disrupted from the distal cingulum. Slaughter (1981) identified the distolabial cusp in this specimen as a stylar cusp C, but it is more corresponding to the position of the stylar cusp E on molars. A somewhat smaller distal cusp is on the distal cingulum which continues into the lingual cingulum. A third minute cusp is just an eminence on the meeting of the distal cingulum and the crest from the main cusp. The lingual cingulum was apparently present on the broken area between the mesial and distal cingula. Possible a small protoconal bulge was present there, but not a true protocone, as was suggested previously by Slaughter (1968a) and Butler (1978). Certainly there is no root supporting the protocone mentioned by Slaughter (1981: 682). The premolar has two roots.

The dP5 (SMP–SMU 71848) is a triangular tooth with a mesiodistally wide and transversely short protoconal region. The paracone is the largest cusp. The metacone is distinctly smaller and separated from the latter. The labial margin of the tooth is skewed mesially, with the stylar shelf mesially reduced, as typical for the dP5. I cannot discern the

preparacrista described by Davis and Cifelli (2011). The parastyle and stylocone are poorly differentiated and almost non-existent. The large stylar cusp C is similar in size to the metacone. It is connected to a smaller stylar cusp D by a strong ridge. The metastyle is not differentiated. The postmetacrista is relatively long and straight. The protocone is low, more than twice smaller than the paracone. There is a relatively large paraconule without internal crista. The preprotocrista terminates at the base of the paracone. The metaconule region is damaged.

All upper molars except M3 (SMP–SMU 62009) have the protoconal region broken. The M1 is represented by two fragments, one heavily worn (CNHM PM 1000) and another missing the parastylar and metastylar lobes (CNHM PM 1004). In the latter specimen the paracone is broken but it has a larger base compared with the metacone and certainly was a highest labial cusp. In CNHM PM 1000 the height differential between the labial cusps is decreased by substantial wear. Butler's (1978: 5) observation that on CNHM PM 1000 "the metacone is farther from the buccal edge than the paracone" is not correct. In all upper molars of *Holoclemensia*, as well as in other stem therians, the metacone is slightly labial to the paracone. The preprotocrista is incompletely preserved (CNHM PM 1004) or eliminated by wear (CNHM PM 1000). Evidently it was short and extending to a small stylocone. The parastylar lobe protrudes mesially and only little labially. The parastyle was likely larger than stylocone and separated from the latter by the parastylar groove. The metastylar lobe is very small, with short and weak postmetacrista. It does not project labially beyond the labial extent of the parastylar lobe. The stylar cusp C (=mesostyle of Davis and Cifelli 2011) is very large and occupies a position between the paracone and metacone. In both specimens there is a minute stylar cusp in D position distal to the cusp C. The labial extent of preprotocrista is not certain because of wear in CNHM PM 1000. Fox (1975: 420) considered that in this specimen the preprotocrista extended mesial to the paracone. The postprotocrista terminates at the base of the metacone (CNHM PM 1004).

The M2 is represented by two labial fragments, the holotype and CNHM PM 886. On the holotype the paracone and metacone are almost totally eliminated by wear. In CNHM 886 these cusps are little worn, with metacone lower and somewhat labially placed. The preparacrista is long and low, extending

labially towards a very small stylocone. At the labial base of the paracone, just distal to the preparacrista, there is a peculiar furrow. This furrow, although less developed, can be seen in another M2 (CNHM PM 886) and on M1 (CNHM PM 1004). This character might be diagnostic for *Holoclemensia*. The parastylar lobe is very narrow and projects mesiolabially to a great extent. The parastyle is about twice larger and higher than the stylocone, not equal in size to the stylocone, as was described by Davis and Cifelli (2011: 452). The parastylar groove is almost vertical. The metastylar lobe is small, but larger than on M1. It projects labially as far as the stylar cusp C. The latter is somewhat smaller than in M1 and have a similar central position. It is not as high as the metacone. On the holotype there are two cusps on the metastylar lobe, the distal metastyle and the mesial cusp which is likely corresponds to the cusp D of M1. In CHNM PM 886 this cusp is represented by a minute enamel swelling. The postmetacrista is short and low, as in M1. The labial extent of the preprotocrista is obscured by intensive wear facet 1b on the holotype. According to Slaughter (1968b: 254) the preprotocrista extends from the protoconal region to the parastyle. According to Fox (1975: 420) there is no preprotocrista (=anterior cingulum) mesial to the paracone. The latter observation might be correct because the preprotocrista is interrupted at the paracone on an unworn M3 (see below).

The single known M3 (SMP–SMU 62009) is almost complete, except missing the lingual portion of the protocone. The metacone is more than twice smaller than the paracone and the metastylar lobe is reduced, as typical for ultimate molars. The preprotocrista extends labially, but terminates before the parastyle. The parastylar lobe is large and projects labially. The parastyle is large and more than twice larger than the stylocone. The cusp C is distinctly smaller than in M2. It is little higher than the stylocone and spire-like. The protocone is relatively high, about two-thirds the height of the paracone. The conules lack internal cristae and are close to the protocone. The preprotocrista is interrupted mesial to the paracone. The postprotocrista does not extend labially beyond the base of the metacone.

There are three ultimate lower premolars (p5) referred to *H. texana* (SMP–SMU 62399 lacks the paraconid and OMNH 67134 has a broken labial side). There are some minor differences between the specimens caused by individual variation. The p5

has a fully developed trigonid with high protoconid, small metaconid appressed to the latter, and low cingular paraconid. The metaconid is variably developed. It is approximately one-third of the protoconid height. The protocristid is a low ridge not elevated above the cusps' surface. The talonid is single-cusped and not basined. The protoconid and talonid cusp (hypoconid) are connected by two ridges, a straight ridge in the middle of the crown and an arcuate ridge along the labial crown side. There is a notch on the median ridge at the base of the talonid cusp (this ridge is heavily worn in OMNH 67134). A third, less pronounced ridge, is also along the labial crown side and connects the protoconid with the mesial cingulid. The two roots are similar in size and widely spaced.

There are six more or less complete lower molars and two trigonids referable to *H. texana*. According to Davis and Cifelli (2011: 453) the m1 is characterized “by less inflation of the metaconid relative to the other loci, and less height and transverse width differential between the trigonid and talonid.” However, the single complete molar identified as m1 by these authors (SMPU–SMU 61727) has the largest value of talonid width to trigonid width ratio (0.85). In the four molars identified here as m1 this ratio is 0.63–0.75, $M=0.71\pm 0.03$. SMPU–SMU 61727 is considered here as the single known m2. SMP–SMU 62721, with the talonid width to trigonid width ratio of 0.80 and distinctly short talonid is considered here as m3. The trigonid fragments cannot be identified as to tooth locus.

In all lower molars the trigonid is more than twice higher than the talonid, except the m2 which has a high hypoconid. The metaconid is robust and only slightly smaller than the protoconid; in one m1 (SMP–SMU 62131) and m3 both cusps are of nearly equal height. The paraconid is a spike-like and procumbent cusp, which is about twice smaller than the metaconid, and placed labial to the metaconid apex. The paraconid is smallest in SMP–SMU 62722 (m1) and largest on m3. The bases of paraconid and metaconid are confluent. The trigonid angle is 32–42° in m1 and 30° in m3. The protocristid is transverse with a deep carnassial notch. On the mesial side of the trigonid there is a long oblique precingulid (mesiolabial cuspule f). The mesiolingual cuspule e is present only in SMP–SMU 62131. There is no distal metacristid, but there is a faint ridge along the distolingual corner of the metaconid connecting the tip of metaconid with the entocristid.

The talonid is distinctly narrower transversely compared with the trigonid on m1. On m2–3 the talonid is more transversely expanded but still narrower than the trigonid. The deep hypoflexid widely separates the trigonid and the talonid has a narrow mesial end. This narrowed mesial part of the talonid is longer on m2 compared the m1, except one m1 (SMP–SMU 61726), where it is as long as in m2. Because of a deep hypoflexid, the cristid obliqua is located lingual to the protocristid notch, not below this notch, as was described by Davis and Cifelli (2011). Only in SMP–SMU 62131 does the cristid oblique extend along the metaconid wall above the protocristid notch; in other molars it terminates lower. The talonid cusps are pointed and vertical. The hypoconid is the biggest cusp, the entoconid is the smallest. The bases of the entoconid and hypoconulid are approximated or separated by a small gap. On the m3 the hypoconulid is more projecting distally than in other molars. The talonid basin is sloping lingually, with the deepest point on the talonid isthmus. The entocristid is distinctly lower compared with the cristid obliqua.

Comments. The lost upper premolar CNHM PM 931 (Patterson 1956: fig. 2A; Butler 1978: fig. 4d) was identified as P5 of *H. texana* by Averianov et al. (2010: fig. 9). However, this tooth, with length 1.31 and width 0.73 (Patterson 1956: 28), appears to be too small for this species. The size of CNHM PM 931 is suitable for *Pappotherium* or *Atokatheridium*. It is considered here as *Theria* indet.

CNHM PM 583, a dentary fragment with alveoli for i1–4, single-rooted, possibly not fully erupted canine, and double-rooted p1–4 (Patterson 1956: figs. 10, 11; Hershkovitz 1982: fig. 5; Hershkovitz 1995: fig. 9), the holotype of *Adinodon pattersoni* Hershkovitz, 1995, may belong to *H. texana* based on suitable size, as was previously suggested by Butler (1978) and Turnbull (1995). This, however, should be confirmed by discovery of jaws with dentition.

OMNH 62412, the heavily worn lower molar from the Tomato Hill locality, was identified as m3 of *H. texana* (Davis and Cifelli 2011: fig. 7E). In the structure of the trigonid it agrees with the lower molars of *H. texana*, but it is distinctly smaller. The cristid obliqua extends to the level of the protocristid notch approximately at the middle of the metaconid transverse width. The talonid is almost eliminated by wear. Two other specimens from the Tomato Hill locality (OMNH 62414 and 63894) referred

to *H. texana* are talonid fragments. OMNH 67134, a p5 from the Tomato Hill locality, is also definitely smaller than p5s of *Holoclemensia* from the Butler Farm locality. A distinct taxon, closely related to *Holoclemensia*, may be present in the Tomato Hill fauna. Similarly, a single specimen from the Pecan Valley Estates locality (dP5, SMP–SMU 71848) may belong not to *H. texana* (there are no dP5's from the type locality) but to a similar taxon. However, all these taxonomic issues cannot be resolved without additional specimens. In particular, new taxa similar to *Holoclemensia* should be based on upper molars.

Pappotherium pattersoni Slaughter, 1965

(Fig. 3)

Pappotherium pattersoni: Slaughter (1965: 4, fig. 1); Crompton (1971: fig. 3); Slaughter (1971: pls. 7A, B, 8D–F, 9); Fox (1975: fig. 1); Kielan-Jaworowska (1975: fig. 8); Butler (1978: figs. 1P, 2a, d, 5P); Kielan-Jaworowska et al. (1979: fig. 10–4A, B); Kielan-Jaworowska and Cifelli (2001: fig. 4A); Kielan-Jaworowska et al. (2004: fig. 11.5D); Davis and Cifelli (2011: fig. 5D).

Pappotheriidae indet.: Slaughter (1971: pl. 7C).

Slaughteria eruptens: Butler (1978: 12, fig. 3S); Kobayashi et al. (2002: figs. 1, 2); Kielan-Jaworowska et al. (2004: figs. 3.24C, 11.4F); Luo et al. (2004: fig. 4C); Davis (2011b: figs. 1A, 2); Davis and Cifelli (2011: fig. 9D, E); Winkler et al. (2011: figs. 1–4).

Kermackia or *Trinititherium*: Butler (1978: fig. 2j).

Cf. *Kermackia* or *Trinititherium* sp.: Kielan-Jaworowska and Cifelli (2001: fig. 2A).

Kermackia texana: Davis and Cifelli (2011: fig. 8A).

Holotype. SMP–SMU 61725, right maxilla fragment with M2–3.

Type locality and horizon. Butler Farm locality, Wise County, Texas, USA; Antlers Formation, Lower Cretaceous (Aptian–Albian).

Referred specimens. Type locality: SMP–SMU 62402, right dP5. SMP–SMU 61992, left dentary fragment with p3, p4, p5 in crypt, dp5, and m1 (holotype of *Slaughteria eruptens* Butler, 1978).

Differential diagnosis. A stem therian differing from Metatheria in replacing the fifth premolar locus, three molars, and paraconid smaller than metaconid. Similar to Eutheria and differing from other stem therians in having a low trigonid angle with a transverse protocristid. Differs from Eutheria by postprotocrista not extending labially past metacone base and conules lacking internal cristae. Differs from *Kermackia* in possessing conules, a smaller trigonid

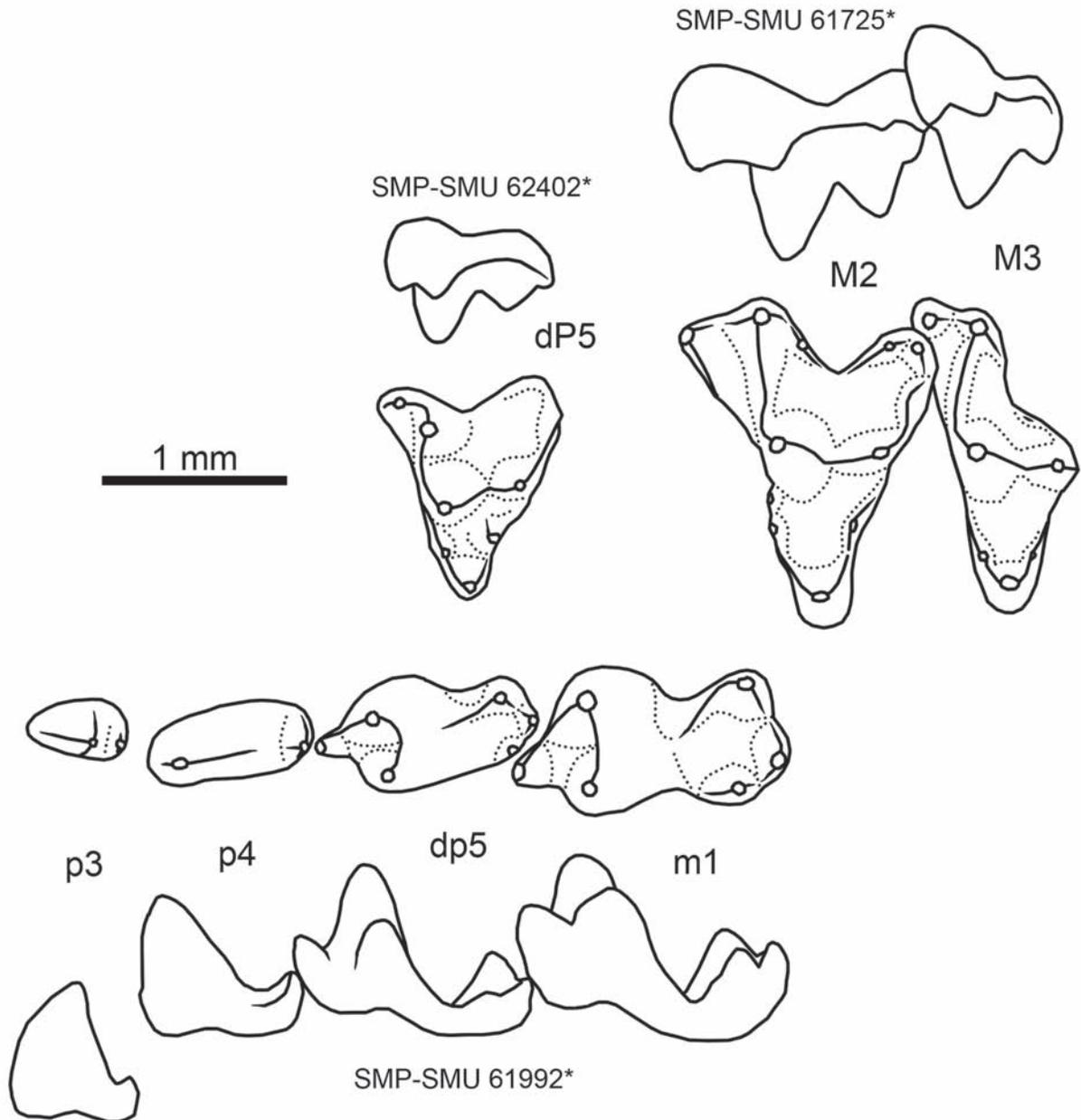


Fig. 3. The stem therian *Pappotherium pattersoni* from the Early Cretaceous Antlers Formation of Texas, USA. Upper teeth are in labial and occlusal views, lower teeth – in occlusal and lingual views. Worn cusps and crests are reconstructed. Mesial end is to the left. Asterisk denotes reversed image at the collection number. The protoconal region of M3, now broken, is based on Slaughter (1965: fig. 1C) and (Butler 1978: fig. 1P). Scale bar = 1 mm.

angle, a transverse protocristid, paraconid and metaconid conjoined lingually, a distal metaconid lacking, a wider talonid, and a larger entoconid. Differs from *Holoclemensia* in lacking large styler cusp C, in having smaller protocone and conules, and cristid

obliqua labial to protocristid notch. Differs from the premetatherian stem therian *Montanalestes* in having paraconid smaller than metaconid.

Description. The DP5 is very similar in the structure and proportions to the M2 of the holotype

but significantly smaller. The parastylar lobe is destroyed (reconstructed on Fig. 3) and likely was less expanded compared with M2. According to Davis and Cifelli (2011: 454) “the stylocone appears to have been very large and closely appressed to the paracone.” This is likely a characteristic of dP5, which usually has a short preparacrista and mesially reduced stylar shelf. The protocone region is small so the paracone and metacone are placed closer to the lingual side of the crown. These cusps are high and have deep vertical lingual walls. The metacone is smaller and lower than the paracone and labially placed compared with the latter. The tips of the labial cusps, especially the paracone, are heavily worn. The postmetacrista is relatively short and cusp-like. The protocone is very low, only about half of the paracone height, and narrow mesiodistally. The preprotocrista and postprotocrista do not extend labially past the bases of the paracone and metacone, respectively. The conules are very small. The metaconule likely had a short premetaconule crista while the paraconule is not winged. The paraconule is somewhat closer to the protocone compared with the metaconule.

On M2 the parastylar lobe is larger and more labially projecting compared with the metastylar lobe. The parastylar lobe is expanded distally, with a large stylocone and parastyle, while the metastylar lobe is pointed terminally. The stylocone and the parastyle are of similar size but the latter cusp is placed lower on the crown. The ectoflexus is deep and pointed. The stylar shelf, a flat area between the labial margin and the bases of labial cusps, is relatively wide. There is a faint ectocingulum along the ectoflexus, interrupted in the deepest point of the latter. The ectocingulum bears two additional cingular cusps. One is very small and placed on the distal slope of the stylocone. The other is just mesial to the metastyle and likely corresponds to the stylar cusp D. The paracone and metacone are placed in the center of the crown and have deep, vertical lingual walls. The paracone is a massive cusp, highest on the crown. The metacone is about twice lower than the paracone, significantly compressed labio-lingually, and pointed distoventrally. The centrocrista is straight and extends down the crown less the half of the paracone height, so the paracone and the metacone are connate at their bases. The preparacrista is a strong and relatively long crest between the paracone and the stylocone. The postmetacrista is slightly shorter, with a central postmetacrista cusp. The protoconal region is less than

half of the crown width and narrow mesiodistally. The protocone is very low, less than half of the paracone height. The conules are small and lack internal cristae. The larger paraconule is about midway between the protocone and the base of paracone. There is a minute additional cusp on the preprotocrista just labial to the paraconule (Crompton 1971: fig. 3A). The metaconule is almost undistinguishable and slightly more distant from the protocone compared with the paraconule. The preprotocrista extends labially towards the parastyle according to the earlier illustrations (now this region is heavily damaged). The postprotocrista terminates at the base of the metacone.

On M3 the parastylar lobe extends labially to the same extent as on M2, but less expanded terminally. The stylocone and parastyle are similar in size and somewhat smaller than on M2. The parastyle is more labially placed compared to the M2 and appressed to the metastyle of M2. The metastylar lobe is completely reduced. There is a short ectocingulum labial of the centrocrista notch as well as a short segment extending distally from the stylocone. The paracone is lower than on M2 but has a mesiodistally wider base on the expense of the metacone, which is small but still a distinct cusp. The preparacrista is longer than on M2 and also extends towards the stylocone. The protoconal region is now missing on this specimen. According to the earlier illustrations it was similar to that of M2 except the conules, if present, were even smaller. These illustrations show the preprotocrista of M3 extending labially towards the parastyle. This cannot be confirmed based on the study of the specimen and cast. This is unlikely because the preparacrista of M3 closely appressed the postmetacrista of M2 leaving no space for an additional crest (preprotocrista) between them. The M3 had a labiolingual width similar to that of M2. There is a terminal part of the postprotocrista preserved at the lingual base of the metacone.

The single known dentary fragment (SMP–SMU 61992) is twice deeper at the posterior end compared with the anterior end. The posterior mental foramen is located between the dp5 and m1. I cannot confirm presence of the Meckelian groove, suggested by Davis (2011b: 677).

The lower dentition is known from a single specimen (SMP–SMU 61992) with p3, p4, p5 in crypt, dp5, and m1 (for an alternative interpretation, not followed here, see Davis 2011b; Davis and Cifelli 2011). On p3 the main cusp is blade-like, convex anteriorly

and straight posteriorly. The apex of the crown occurs dorsally midway between the roots. There is a small distal cusp on p3 revealed by CT scans. On p4 the apex of the main cusp is above the mesial root. The mesial side of the main cusp is vertical; the distal side is gradually sloping towards the distal cusp. The p3 and p4 are similar in size. The unerupted p5 is distinctly larger than p4 and its main cusp is similar to that in p3, except the tip is distally tilted. There is no mesial cusp on either known premolar, although on p5 it could be added later in ontogeny. On p4 there is a very faint mesial cingulid. The size of distal cusp increases from p3 to p5.

The dp5 is distinctly narrower than m1 and has a wide trigonid angle ($\sim 74^\circ$) and the talonid which is narrower than the trigonid (talonid width to trigonid width ratio is 0.66). The protocristid is slightly oblique. The tips of the protoconid and metaconid are heavily worn. The metaconid is about twice smaller than the protoconid. The paraconid is little worn and smaller than the metaconid. It is widely separated from the metaconid and placed mesially so the entire cusp is completely mesiolingual to the protoconid. There is a very faint precingulid below the paracristid notch. There is no distal metacristid on dp5, as well as on m1. The talonid is almost as long as the trigonid, with a long talonid isthmus opposite to the hypoflexid. The talonid cusps are relatively small. The hypoconid is the largest and the entoconid is the smallest. The hypoconulid is equidistant from the other talonid cusps. Almost all the talonid basin is filled by the bases of the talonid cusp, with a small flat area near the talonid isthmus. The cristid obliqua is short, does not extend vertically on the metaconid wall, and terminates labial to the protocristid notch. Some part of the cristid obliqua might be eliminated by wear. The roots are well separated. The distal root is about twice longer mesiodistally than the mesial root.

The m1 agrees in morphology with dp5 except the trigonid is mesiodistally compressed, with trigonid angle of $\sim 36^\circ$, and the talonid is shorter and wider (talonid width to trigonid width ratio is 0.94). The protoconid is broken and the tips of paraconid and metaconid are worn. In occlusal view the protoconid occupies almost half of the trigonid. The bases of the paraconid and metaconid are conjoined, leaving a very small trigonid basin. The paraconid is placed entirely mesial to the protoconid, as in dp5. The protocristid is more transverse than on dp5. There are a strong cusp-like precingulid (mesiolabial cuspule f)

and a very faint mesiolingual cuspule e separated by a depression for the dp5's hypoconulid. The talonid is similar in most respects to that of dp5, except the entoconid is higher than the hypoconulid. Because of expanded hypoconid, the hypoconulid is closer to the entoconid. The talonid basin is very small, as in dp5. The cristid obliqua is similarly short and terminates labial to the protocristid notch. The distal root is slightly longer mesiodistally compared with the mesial root.

Comments. Davis and Cifelli (2011) referred ten isolated teeth or tooth fragments from Greenwood Canyon and Tomato Hill localities to *P. pattersoni*.

CNHM PM 999 and 1749 have been identified as M1 and M2 of *P. pattersoni* by Davis and Cifelli (2011). Because these teeth are structurally different from the ultimate and penultimate molars in the holotype of *P. pattersoni*, it was supposed that this taxon had four upper molars. I refer CNHM PM 999 and 1749 to *Atokatheridium* and *Oklatheridium*, respectively. Consequently, there is no basis for inference of the four molars dental formula for *P. pattersoni*.

The protoconal region CNHM PM 1325 (Turnbull 1971: fig. 3E; Butler 1978: fig. 2g; Davis and Cifelli 2011: fig. 5C) has been identified as M2 of *P. pattersoni*. It is considerably larger than the protocone of M2 of the *P. pattersoni* holotype.

The trigonids CNHM PM 930 (Patterson 1956: fig. 8C; Turnbull 1971: fig. 6A; Davis and Cifelli 2011: fig. 5G), CNHM PM 1119 (Turnbull 1971: fig. 5F), CNHM PM 1249 (Turnbull 1971: fig. 5E; Davis and Cifelli 2011: fig. 5I), OMNH 61219 (Davis and Cifelli 2011: fig. 5J), and OMNH 63729 (Davis and Cifelli 2011: fig. 5H) are not referable to *P. pattersoni* because of their larger size, trigonid not compressed mesiodistally, and paraconid not reduced.

An incomplete lower premolar with two talonid cusps, CNHM PM 1098 (Butler 1978: fig. 4b; Davis and Cifelli 2011: fig. 9A), referred to *Slaughteria eruptens* (Davis and Cifelli 2011), is similar in size with dp5 of *Pappotherium pattersoni*. It cannot be p5 of this taxon because its p5, as revealed by CT-scans, is not molariform, with single large talonid cusp.

The lower molar OMNH 63726 with a damaged talonid (Davis 2011b: fig. 1B; Davis and Cifelli 2011: fig. 9B), referred to *Slaughteria eruptens*, is similar in size with the m1 on the holotype of *S. eruptens* but differs in having uncompressed trigonid and unreduced paraconid, which is somewhat higher than the metaconid.

The talonid OMNH 63721 (Davis 2011b: fig. 1C; Davis and Cifelli 2011: fig. 9C), referred to *Slaughteria eruptens*, is similar in size and proportions of the talonid cusps with m1 of the *S. eruptens* holotype, but has a distinctly shorter talonid isthmus lingual to the hypoflexid.

Stem group of Marsupialia Illiger, 1811

Atokatheridium boreni Kielan-Jaworowska and Cifelli, 2001

(Fig. 4)

Theria indet.: Patterson (1956: fig. 3A); Butler (1978: fig. 2b).

Holoclemensia sp.: Turnbull (1971: fig. 2E).

Pappotherium cf. *pattersoni*: Turnbull (1971: fig. 3B).

Pappotherium pattersoni: Butler (1978: figs. 2h, 5P); Davis and Cifelli (2011: fig. 5A, E, F).

Atokatheridium boreni: Kielan-Jaworowska and Cifelli (2001: 379, figs. 2B, 4B); Kielan-Jaworowska et al. (2004: fig. 12.7D); Rougier et al. (2004: fig. 6E); Davis et al. (2008: figs. 1.5A, B, 1.6A, B, 1.9E); Davis and Cifelli (2011: fig. 2A, B, D, E).

Atokatheridium boreni?: Kielan-Jaworowska and Cifelli (2001: figs. 3A, 5B); Kielan-Jaworowska et al. (2004: fig. 12.7E).

Holotype. OMNH 61623, right M2.

Type locality and horizon. Tomato Hill locality, Atoka County, Oklahoma, USA; Antlers Formation, Lower Cretaceous (Aptian-Albian).

Referred specimens. Type locality: OMNH 61151, left dP3. OMNH 61185, right M3. OMNH 61624, left m4. OMNH 34905, right mx trigonid. OMNH 61181, left mx trigonid. OMNH 63724, left mx trigonid.

Greenwood Canyon locality: CNHM PM 999, right M1 missing protocone. CNHM PM 1015, left M3 missing protocone.

Differential diagnosis. A stem marsupial different from stem therians and Eutheria in possessing four molars and paraconid higher than metaconid. Differs from premetatherian stem therian *Montanalestes* in having four molars, and paraconid and metaconid separated by lingual groove. Differs from stem marsupial *Oklatheridium* by parastylar lobe reduced, small styelar cusp C present at least in some specimens, paraconid with keel-like vertical crest, and distal metacristid better developed. Differs from Deltatheroidea by larger protoconal region with better developed winged conules. Differs from stem

marsupial *Kokopellia* in having conules with shorter internal cristae, paraconid higher than metaconid, and lack of labial postcingulid.

Description. The single known dP3 (OMNH 61151) is heavily worn and chemically eroded, with most of the enamel gone. This tooth has been interpreted previously as M1 (Davis et al. 2008; Davis and Cifelli 2011). However, it is distinctly smaller than M2 and smaller than the expected size of M1 for this taxon. Davis et al. (2008) explained the considerable size differences between OMNH 61623 (M2) and 61151 (M1) by the enamel loss in the latter. However, both specimens are abraded in a similar extent. This size differences are more appropriately found between an M2 and dP3, which is accepted here. More importantly, it has the styelar shelf reduced mesially, a distinct character of deciduous upper premolars in stem marsupials and placentals (Averianov et al. 2010; Archibald and Averianov 2012; Gheerbrant and Astibia 2012). The stylocone and parastyle cannot be recognized. These cusps are likely removed by abrasion (the stylocone is reconstructed on Fig. 4). The paracone and metacone are connate at their bases and divergent. The paracone is somewhat higher than the metacone. The preparacrista is short and low. The postmetacrista is tall and almost labially directed. The protocone is relatively tall, similar in height to the metacone, and mesiodistally wide. There are no conules but according to Davis et al. (2008) they were likely present before abrasion because they are present on the M2. More likely, only a paraconule was present, or both conules were absent, as in deciduous upper premolars of stem marsupials exemplified by the "*Picopsis*" morphotype (Fox 1980; Cifelli 1990; Averianov et al. 2010). The preprotocrista extends to the parastylar region, while the postprotocrista terminates at the base of the metacone.

The M1 is represented by a single incomplete specimen, CNHM PM 999. This tooth has been referred previously to *Pappotherium* (Turnbull 1971; Butler 1978; Davis and Cifelli 2011). Before this, Slaughter (1965: 12, 14) mentioned a notable difference of this specimen from *Pappotherium*: "the parastyle is small, low and poorly demarcated from the stylocone, whereas the parastyle in *Pappotherium* [M2] is almost as large as the stylocone and separated by a deep V-shaped notch." This difference cannot be related to the position variation, as on M1 the parastylar lobe is expected to be larger than on M2. The construction of the parastylar lobe in CNHM PM

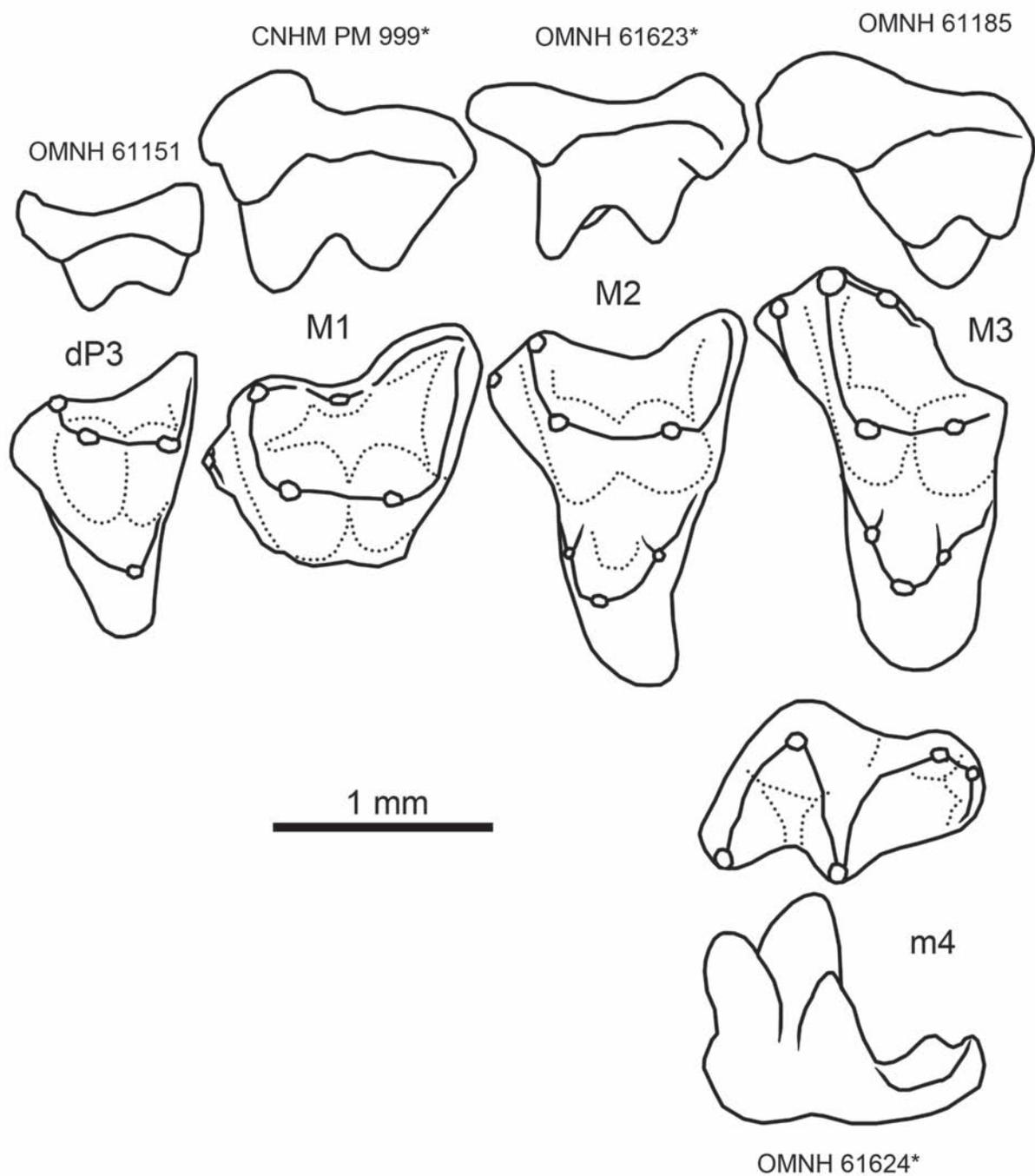


Fig. 4. The stem marsupial *Atokatheridium boreni* from the Early Cretaceous Antlers Formation of Texas and Oklahoma, USA. Upper teeth are in labial and occlusal views, lower teeth – in occlusal and lingual views. Worn cusps and crests are reconstructed. Mesial end is to the left. Asterisk denotes reversed image at the collection number. The dP3 and M2 are based on heavily abraded molars which may lose some structural details. The damaged metastylar region of M3 is restored from CNHM PM 1015. Scale bar = 1 mm.

999 agrees more with the holotype M2 of *Atokatheridium boreni*. The parastylar lobe is distinctly narrower labiolingually than the metastylar lobe, which is a positional character of M1. However, the parastylar lobe does not expand mesially, as in *Juramaia* or *Prokennalestes* (Kielan-Jaworowska and Dashzeveg 1989; Luo et al. 2011). The parastyle is a low small cusp. The preparacrista is short and concave mesially in occlusal view. It is a low ridge depressed between the bases of the paracone and stylocone. The stylocone has a wide base but the cusp is not as high as in *Oklatheridium*. Both Patterson (1956) and Butler (1978) noted a slight enamel elevation in the position of the stylar cusp C. There is a slight ectocingulum distal to this elevation. The postmetacrista is a strong and long ridge, notched at the base of the metacone. The protoconal region is missing. The preprotocrista extends labially to the parastyle. The postprotocrista terminates at the base of the metacone.

The holotype M2 (OMNH 61623) is modified by chemical abrasion that led to loss of all enamel and some dentine. In particular, large portions of the surface of labial cusps has been removed by abrasion, giving them a peculiar spire-like appearance. The parastylar lobe is only slightly narrower compared with the metastylar lobe. The ectoflexus is shallow and symmetrical. The labial cingulum if were present, is completely gone by abrasion. The paracone and metacone are connate at the base and divergent. The metacone is distinctly shorter than the paracone. The preparacrista is short and terminates at the stylocone, which is rather small, even if the abrasion is considered. The protocone is similar in height to the metacone, and mesiodistally wider than the paracone. There are winged conules, which are slightly closer to the protocone than to the apices of the labial cusps. The size and position of the conules are likely affected by the abrasion.

The M3 is known from two specimens, OMNH 61185 and CNHM PM 1015, both worn and the latter missing the protocone. Both specimens are similar in size and morphology, except the metacone, which is more reduced in OMNH 61185. Davis and Cifelli (2011) identified both these teeth as the penultimate teeth (M3 in their interpretation) of *Pappotherium*. The metastylar lobe was considered by these authors as missing in both specimens. This region is damaged in OMNH 61185, but intact in CNHM PM 1015 (pers. obs.; see also interpretation in Butler 1978: fig. 2b). The peculiar morphology of these teeth, having

a reduced metastylar lobe but relatively large metacone and protoconal region suggests that these are indeed penultimate molars, as was suggested by Davis and Cifelli (2011). However, these teeth are not referable to *Pappotherium* because the penultimate molar in that taxon has unreduced metastylar lobe. The paracone is distinctly larger than the metacone. In CNHM PM 1015 the metacone has a short postmetacrista, which is totally absent in ONHM 61185. The parastylar lobe is prominent, with strong and long preparacrista, which is almost labially directing. The stylocone is small and separated from a somewhat smaller parastyle by a distinct parastylar groove. Distal to the stylocone there is a small stylar cusp. Butler (1978: 5) was uncertain if this cusp is equivalent to the stylar cusp C. Certainly it is not homologous with the large stylar cusp C in *Holoclemensia*. The protocone, known only in OMNH 61185, is heavily worn and its original height cannot be estimated. It is relatively wide mesiodistally. In this specimen there are winged conules, which are close to the paracone than to the labial cusps.

OMNH 61624 is a single complete lower molar referable to *Atokatheridium boreni*. This tooth was first questionably (Kielan-Jaworowska and Cifelli 2001; Kielan-Jaworowska et al. 2004) and later confidently referred to this taxon (Davis et al. 2008; Davis and Cifelli 2011). The tooth is similar to deltatheroidans in having the paraconid much higher than the metaconid and a small two-cusped talonid. The protoconid is partially broken. The paracristid is heavily worn. The paraconid is inclined mesially. The protocristid is almost transverse. The trigonid angle is $\sim 50^\circ$. The bases of paraconid and metaconid are separated by a vertical groove. At the base of the paraconid there is a distinct vertical keel-like ridge representing the mesiolingual cuspule e. It is separated by an embayment for the hypoconulid of the preceding molar from the short precingulid (mesiolabial cuspule f). Both these structures have been described as precingulid in Kielan-Jaworowska and Cifelli (2001). The distal metacristid is almost completely eliminated by wear against the mesial side of the protocone (wear facet 5). In any case it cannot be characterized as strong. The talonid is about twice narrower and somewhat shorter than the trigonid. The hypoconid is low. The hypoconulid is about twice smaller. Both cusps are heavily worn. There is no entoconid. The talonid basin is small and slopes lingually.

The position of OMNH 61624 within the molar series has been considered uncertain in earlier publications (Kielan-Jaworowska and Cifelli 2001; Davis et al. 2008; Davis and Cifelli 2011). Based on trigonid angle, it was compared with m3 (penultimate molar) of *Deltatheridium* (Davis et al. 2008). Later was found that this tooth might represent the m4, but significant differences with m4s of deltatheroidans have been noted (Davis and Cifelli 2011). OMNH 61624 is considered here the ultimate molar (m4) because of reduction of metaconid and talonid, and a relatively great trigonid angle. The presence of four molars is inferred from the morphology of the upper molars.

Two (Kielan-Jaworowska and Cifelli 2001; Davis et al. 2008) and subsequently seven (Davis and Cifelli 2011) isolated trigonids from the Tomato Hill locality have been referred to *Atokatheridium boreni* (OMNH 34095, 61181, 63724, 63889, 63890, 63891, and 63892). These trigonids vary in size and morphology. In all specimens, except OMNH 63892, the paraconid is higher than the metaconid at a various extent. In three specimens (OMNH 34905, 61181, and 63724) there is a faint cristid obliqua, which reaches the metaconid apex only in OMNH 34905. These three specimens are similar with OMNH 61624 in the structure of the precingulid and a keel-like vertical cuspule e. Only these three specimens are here attributed to *A. boreni*. In OMNH 63889 and 63890 there is no distal metacristid but there is a cristid obliqua extending on the distal trigonid wall towards a point below the protocristid notch. OMNH 63724 has been identified as m1 based on larger trigonid angle (~70°) and relative cusp heights after comparison with deltatheroidans (Davis and Cifelli 2011).

Comments. The previous interpretation of *Atokatheridium* as a deltatheroidan was based on a mixed sample of upper molars, including one specimen of *Oklatheridium* (OMNH 63725), and on deltatheroidan-like morphology of a lower molar (OMNH 61624) and referred trigonids. Attribution of OMNH 63725 to *Atokatheridium* has been disputed by Averianov, Archibald et al. (2010). In response to this critique, Davis and Cifelli (2011: 444) noted that referral of *Atokatheridium* to the Deltatheroida is based on “both upper and lower molar morphology at all known loci.” However, the holotype upper molar (OMNH 61623) has no specific similarities with deltatheroidans. It has narrower stylar shelf and a larger protocone with winged conules. The postmetacrista

is less pronounced. Reference to the work of Rougier et al. (2004) as supporting the deltatheroidan affinities of *Atokatheridium* is misleading because this, as well as other successive publications, used a chimeric association of *Atokatheridium* and *Oklatheridium* in the phylogenetic analysis. *Atokatheridium* is considered here as a stem marsupial (see the next section).

***Oklatheridium szalay* Davis, Cifelli et Kielan-Jaworowska, 2008**
(Fig. 5)

Theria indet.: Patterson (1956: figs. 2B, 4B); Vandebroek (1961: fig. 37); Mills (1964: fig. 6D); Butler (1978: fig. 2p).

Trinity lower molar type 2: Patterson (1956: figs. 7, 8A, 9A); Winkler et al. (2011: figs. 8, 9).

Holoclemensia cf. *texana*: Turnbull (1971: fig. 2B).

Pappotherium cf. *pattersoni*: Turnbull (1971: fig. 3A).

Pappotherium sp.: Turnbull (1971: fig. 3D).

Holoclemensia sp.: Turnbull (1971: figs. 5D, 6B, C).

Pappotherium pattersoni: Butler (1978: figs. 2e, f, i, 3P, 5H); Davis and Cifelli (2011: fig. 5B).

Tribosphenida indet.: Cifelli (1997: fig. 3); Davis and Cifelli (2011: fig. 10B).

Deltatheroida? indet.: Kielan-Jaworowska and Cifelli (2001: fig. 3B, C).

Oklatheridium szalay: Davis et al. (2008: figs. 1.3A–C, 1.4, 1.7F, 1.8B, 1.9F); Davis and Cifelli (2011: fig. 3A–E).

Oklatheridium? sp.: Davis et al. (2008: fig. 1.3E).

Atokatheridium boreni: Davis et al. (2008: fig. 1.5C); Davis and Cifelli (2011: fig. 2C).

Oklatheridium minax: Davis and Cifelli (2011: 444, fig. 3F–G).

Oklatheridium sp.: Davis and Cifelli (2011: fig. 4).

Holotype. OMNH 62410, left M2 missing protocone.

Type locality and horizon. Tomato Hill locality, Atoka County, Oklahoma, USA; Antlers Formation, Lower Cretaceous (Aptian-Albian).

Referred specimens. Type locality: OMNH 62411, left M1 with broken protocone. OMNH 61180, left M2 missing protocone. OMNH 63725, left M2 with abraded crown and missing parastylar region. OMNH 33455, left M3 missing metastylar lobe (holotype of *Oklatheridium minax* Davis and Cifelli, 2011). OMNH 63986, right M3 missing protocone. OMNH 61642, right dp3 trigonid. OMNH 33945, left m4 trigonid. OMNH 33940, right mx trigonid. OMNH 61643, right mx trigonid. OMNH 63728, right mx trigonid. OMNH 63730, left mx trigonid. OMNH 66771, right mx trigonid.

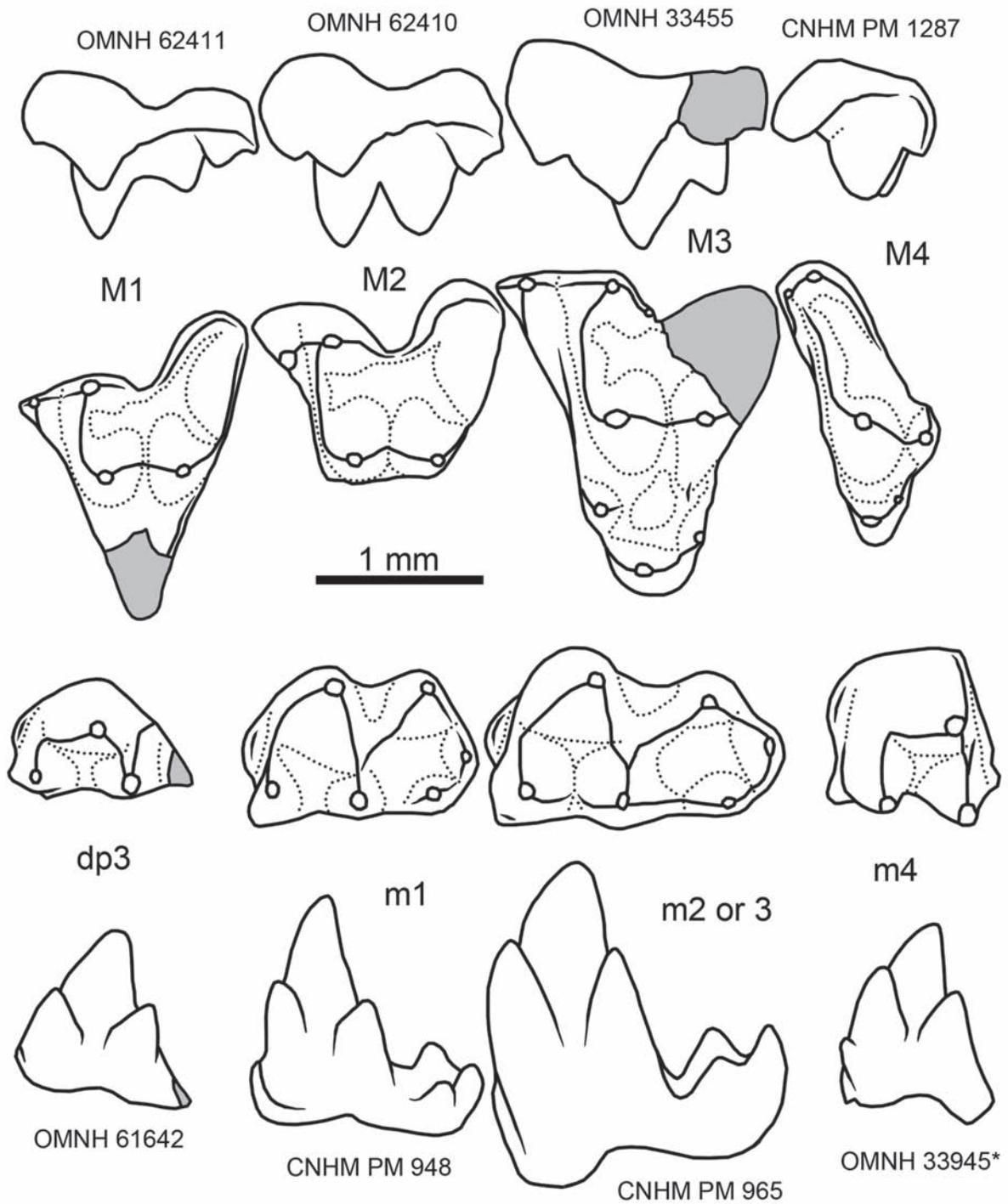


Fig. 5. The stem marsupial *Oklatheridium szalayi* from the Early Cretaceous Antlers Formation of Texas and Oklahoma, USA. Upper teeth are in labial and occlusal views, lower teeth – in occlusal and lingual views. Worn cusps and crests are reconstructed. Mesial end is to the left. The broken parts of M1 and M3 are shown in grey. Asterisk denotes reversed image at the collection number. Scale bar = 1 mm.

Greenwood Canyon locality: CNHM PM 884, left M1 missing protocone and metastylar lobe. CNHM PM 1238, left M1 missing protocone and parastylar lobe. CNHM PM 1749, left M2 missing protocone and metastylar lobe. CNHM PM 1287, left M4. CNHM PM 948, right m1. CNHM PM 965, right mx. CNHM PM 660, right mx trigonid.

Differential diagnosis. A stem marsupial different from stem therians and Eutheria in having four molars and paraconid higher than metaconid. Differs from premetatherian stem therian *Montanalestes* in having four molars, paraconid and metaconid separated by lingual groove, and longer cristid obliqua. Differs from stem marsupial *Atokatheridium* in having parastylar lobe larger, parastyle with keel-like vertical crest, stylar cusp C absent, paraconid without with keel-like vertical crest, and distal metacristid lacking in most specimens. Differs from Deltatheroidea in having larger protoconal region with better developed winged conules and, wider talonid, and well-developed entoconid. Differs from stem marsupial *Kokopellia* in having conules with shorter internal cristae, paraconid higher than metaconid, lack of keel-like vertical crest of paraconid, longer cristid obliqua, and lack of labial postcingulid.

Description. Four upper molar positions can be identified (M1–4). The M1 is interpreted here as unreplaced dP5. The M1 (OMNH 62411, CNHM PM 1238) has distinctly smaller size compared with M2–3, and reduced anteriorly stylar shelf, a character also found in ultimate deciduous premolars. The CNHM PM 884, identified as M1 because of short preparacrista, is somewhat larger than other M1s, which is interpreted as individual variation. The OMNH 33455 has been identified as M2 (Davis et al. 2008; Davis and Cifelli 2011). However, it has the preparacrista distinctly longer than in the specimens identified as M2 (OMNH 61180, 62410, CNHM PM 1749) but compatible in length with the preparacrista in M3 (OMNH 63986). Thus OMNH 33455 is identified here as M3. The M4 is represented by a single specimen (CNHM PM 1287).

The M1 has reduced parastylar lobe and short preparacrista, while the metastylar lobe is long, labially projecting, and with a long postmetacrista. On M2 the parastylar and metastylar lobes are of similar size. On M3 the parastylar lobe is longer and the metastylar lobe is broken on both known specimens (OMNH 33455, 63986). The nature of the breakage suggests that the metastylar lobe was unreduced

on M3. The metastylar lobe is absent on M4. The metacone is lower than the paracone but somewhat broader at least on M2. According to Davis et al. (2008) the height differential between the paracone in metacone in *Oklatheridium* is smaller than in any other Trinity therian. On M4 the metacone is much smaller than the paracone. On M4 the parastylar lobe constitutes the half of the tooth transverse width. The preparacrista connects the stylocone on M1–3, except OMNH 63986 (M3), where it turns abruptly towards the parastyle. On the M4 the preparacrista terminates before the reduced stylocone and parastyle. The parastyle is a prominent cusp with a peculiar sharp mesial keel extending towards the base of the crown, except the M4, where it is considerably reduced. The stylocone is distinctly higher than the parastyle. There are no other stylar cusps, except a small cuspule immediately distal to the stylocone present in some specimens (CNHM PM 1749, M2, and OMNH 63986, M3). Davis and Cifelli (2011: 446) described this cuspule also for OMNH 61180 (M2), but in this specimen it is an artifact of ectocingulum breakage in a more distal position. The ectocingulum is sharp and prominent, especially on the metastylar lobe on M1–3. On M4 the ectocingulum is prominent along the parastylar lobe but absent opposite to the metacone. The stylar shelf, a flat area between the ectocingulum and the bases of paracone and metacone, is distinctly narrower compared with deltatheroidans. The preprotocrista extends labially towards the parastyle. The postprotocrista terminates at the base of the metacone. The protoconal region is present only in OMNH 33455 (M3) and CNHM PM 12867 (M4). On OMNH 33455 the protocone is broken and its height cannot be estimated. The paraconule is heavily worn. A small metaconule is placed closer to the protocone. The premetaconule crista is not present. Davis and Cifelli (2011: 446) found no evidence of internal cristae in OMNH 33455. However, the postparaconule crista was likely present but obliterated by wear. On the M4 there is a very small unwinged metaconule and a small crenulation of the preprotocrista on the place of the paraconule. The protocone is small, more than twice lower and mesiodistally shorter compared with the paracone.

The lower molars are represented by two complete specimens (CNHM PM 948 and 985) and several trigonid fragments. Both CNHM PM 948 and 985 has been identified as belonging to the same

molar type 2 by Patterson (1956). Davis and Cifelli (2011) referred the first specimen to *Oklatheridium* sp. and the second to *Tribosphenida* indet. CNHM PM 948 identified here as m1 of *O. szalayii* because of paraconid higher than metaconid and short trigonid. This specimen has a peculiar lingual cingulid at the paraconid (Davis and Cifelli 2011), which is accounted here as individual variation. A crest within the talonid basin on this specimen described by Davis and Cifelli (2011) is likely a preservation artifact. One small trigonid (OMNH 61642), identified previously as m1 (Davis and Cifelli 2011), is likely dp3. In transversely narrow crown and widely open trigonid (75°) it is similar with dp3 in the Late Cretaceous stem marsupials (Cifelli and Muizon 1998: fig. 3B). Another small trigonid (OMNH 33945) with the smallest metaconid may be m4. The other specimens are either m2 or m3.

On all specimens the paraconid is higher than the metaconid. The protoconid is the highest trigonid cusp. The paracristid is strong, with a deep carnassial notch. The protocristid is weaker and transverse. The trigonid angle is 75° in dp3, 51° in m1, 45–51° in m2–3, and 52° in m4. The bases of paraconid and metaconid are separated and the trigonid basin is open lingually via a small gap. The precingulid (mesiolabial cuspule f) is long and oblique, separated by a depression from the variable developed mesiolingual cuspule e. In CNHM PM 948 the cuspule e continues lingually as a cingulid at the base of the paraconid. The cristid obliqua connects the protocristid notch or somewhat lingual to it (CNHM PM 948, 965). In two specimens (OMNH 61642 and 61643) it extends to the metaconid apex or near so and formally can be called the distal metacristid. Along the distolingual edge of the metaconid there is a faint crest connecting the entocristid.

The talonid is known only in CNHM PM 948 (m1) and 965 (m2 or 3). It is narrower than the talonid. The talonid width to trigonid width ratio is 0.91 (m1) or 0.80 (m2–3). The talonid is distinctly shorter on m1 compared with the middle molar. On CNHM PM 948 the talonid cusps are damaged. On CNHM PM 965 the hypoconid and hypoconulid are of similar size. The entoconid is somewhat smaller. The hypoconulid is equidistant from other talonid cusps and somewhat projecting distally. The talonid basin is horizontal and closed lingually by the entocristid.

Comments. The CNHM PM 884 has been considered as M2 of *Pappotherium* by Butler (1978). The

OMNH 63727, missing the protocone and metastylar lobe, has been identified as M3 of *O. szalayii* (Davis et al. 2008: fig. 1.3D) or *O. minax* (Davis and Cifelli 2011: fig. 3H). This tooth is remarkable in having a completely reduced metastylar lobe combined with relatively unreduced metacone, which is half the height of the paracone. It is distinctly larger than any other upper molar referred here to *Oklatheridium* and it is considered here as *Tribosphenida* indet.

Originally *Oklatheridium* has been identified as a deltatheroidan (Davis et al. 2008; Davis and Cifelli 2011). However, it differs from the Deltatheroidea in a number of important characters (Table 1, characters 5, and 9–12): the protoconal region is larger, with better developed conules, the protocristid is more transverse, there is no distal metacristid, and the talonid is much wider, with unreduced entoconid. *Oklatheridium* is considered here as a stem marsupial (see the next section).

PHYLOGENETIC POSITION OF TRINITY THERIANS

Historically the interpretation of the Trinity therians underwent three phases (see review of the previous work for details and references):

- 1) Both placentals and marsupials have been identified based on molar count, submolariform premolars, and development of stylar cusps on upper molars;
- 2) All taxa have been referred to the “Theria of metatherian-eutherian grade,” i.e. stem therians in modern usage;
- 3) Some taxa have been included in the numerical phylogenetic analyses, which showed conflicting results.

The inconsistent position of Trinity therians on cladograms has been caused by incompleteness of the materials and different interpretation of the content of the taxa. With two exceptions, the Trinity therians are represented by isolated teeth or tooth fragments. Table 2 summarizes the dental synapomorphies for the major therian clades proposed in the recent phylogenetic analyses focused on the interrelationships of Mesozoic therians. The characters relevant to the Trinity therians are discussed hereinafter.

Upper incisors. SMP–SMU 62401 from the Butler farm locality has been identified as eutherian upper incisor (Slaughter 1971: 138, fig. 1B, pl. 10A). The crown is spatulate and bicusuate, with a strong

Table 1. Proposed synapomorphies for Deltatheroidea.

#	Character	References
1	Size of molars increases markedly posteriorly	Rougier et al. 1998, 2004
2	Stylar cusp D absent	Luo et al. 2003
3	Metacone and paracone bases adjoined	Averianov et al. 2010
4	Strongly developed salient postmetacrista with paraconid enlarged and metaconid reduced	Rougier et al. 1998, 2004
5	Protocone small with distinct trigon basin	Rougier et al. 1998, 2004
6	Trigonid open, with anteromedial paraconid	Rougier et al. 2004
7	Paraconid taller than metaconid	Rougier et al. 1998, 2004
8	Paraconid and metaconid aligned	Rougier et al. 1998, 2004
9	Protocristid oblique to jaw axis	Rougier et al. 2004
10	Distal metacristid present	Rougier et al. 2004
11	Talonid very narrow, subequal to base of metaconid, developed lingually	Rougier et al. 1998; Averianov et al. 2010
12	Entoconid absent*	Luo et al. 2003

*Present in *Sulestes* (Averianov et al. 2010).

distal cusp, and median ridge on the lingual side. The root is rounded, while the upper incisors of therians should have transversely compressed root (Table 2, character 2). This tooth could be a lower incisor of the alticonodontid triconodontan *Astroconodon densoni* Patterson, 1951 known from the Butler Farm locality (Patterson 1951; Slaughter 1969; Turnbull and Cifelli 1999). A single spatulate lower incisor is characteristic for the Alticonodontidae (Cifelli and Madsen 1998).

CNHM PM 1100 from the Greenwood Canyon locality is a small incisor with spatulate crown, which is about twice wider than the transversely compressed root. There is a distinct lingual cingulum. This tooth could be an upper incisor of a therian (Table 2, character 2), but its attribution to any known taxon of Trinity therians is problematic.

Lower incisors. The now lost specimen SMP–SMU 62400 from the Butler Farm locality has been attributed to Eutheria by Slaughter (1971: 138, fig. 1A, pl. 10B). It is a dentary fragment with a simple peg-like procumbent tooth and alveoli for a double-rooted tooth behind. The dentary is very shallow, with a large mental foramen posterior to the preserved tooth. Slaughter (1971) and Butler (1978: 16) considered this tooth as a canine followed

by double-rooted p1. However, it is more likely that these teeth are the last incisor and double-rooted canine. The procumbent posterior lower incisor is characteristic for the Cimolestidae and Zalambdalestidae among Mesozoic Eutheria (Wible et al. 2009: character 21). By size this specimen is suitable for *Pappotherium pattersoni*.

An edentulous dentary fragment CNHM PM 583 from the Greenwood Canyon locality, attributable to *Holoclemensia texana* by size (see comments to that taxon above), preserves alveoli for the four incisors. Hershkovitz (1982, 1995) identified five incisors in this specimen, third of which is “staggered” between the two adjacent incisors. However, the “staggered” condition of the incisor in this specimen cannot be verified (Cifelli and Muizon 1997). The absence of i4 (Table 2, character 6) is not a eutherian synapomorphy, because i4 is present in *Prokennalestes* and Zhlestidae (Sigogneau-Russell et al. 1992; Archibald and Averianov 2012). The two other purported eutherians with four lower incisors, *Eomaia* and *Juramaia* (Ji et al. 2002; Luo et al. 2011), are likely stem therians O’Leary et al. 2013. Thus, if CNHM PM 583 indeed belongs to *H. texana*, the presence of four lower incisors will not preclude attribution of this taxon to Eutheria.

Table 2. Proposed dental synapomorphies for the major therian clades. Theria is a crown group including Metatheria and Eutheria. Metatheria is the total clade for Marsupialia (crown group) plus stem marsupials. Eutheria is the total clade for Placentalia (crown group) plus stem placentals.

#	Character	Clade	References
Incisors			
1	Five upper incisors	Eutheria	Luo et al. 2003, 2011
2	Upper incisors root transversely compressed	Theria	O'Leary et al. 2013
3	I1 orthodont	Theria	O'Leary et al. 2013
4	I4 rhomboidal	Theria	O'Leary et al. 2013
5	Staggered lower incisor present	Metatheria	Wible et al. 2007, 2009; Averianov et al. 2010
6	i4 absent	Eutheria	O'Leary et al. 2013
Canines			
7	Deciduous canine absent	Metatheria	Rougier et al. 1998, 2004
8	Upper canine single rooted	Metatheria	Rougier et al. 1998, 2004; Averianov et al. 2010
9	Lower canines divergent	Metatheria	O'Leary et al. 2013
Cheek teeth general			
10	Seven postcanine loci	Metatheria	Rougier et al. 1998, 2004; Wible et al. 2007, 2009
Premolars general			
11	Three premolars	Metatheria	Cifelli 1993a, b; Rougier et al. 1998, 2004; Averianov and Skutschas 1999; Wible et al. 2007, 2009
12	Replacement of dP1/dp1 and dP2/dp2 absent	Metatheria	Rougier et al. 1998, 2004
13	Only ultimate premolar replaced	Metatheria	Averianov and Skutschas 1999
Upper premolars			
14	Procumbent first upper premolar separated by diastema	Metatheria	Rougier et al. 1998, 2004
15	P2 crown with two or more clearly defined cusps	Theria	O'Leary et al. 2013
16	P2 position replacement absent	Metatheria	O'Leary et al. 2013
17	P2 somewhat smaller than M1 (=M2)	Metatheria	O'Leary et al. 2013
18a	Tall trenchant premolar in penultimate position	Eutheria	Rougier et al. 1998, 2004; Wible et al. 2007, 2009; Averianov et al. 2010
18b	Tall trenchant premolar in penultimate position	Marsupialia*	Luo et al. 2003
18c	P4 height greater than P5 height	Theria	O'Leary et al. 2013
19	Penultimate premolar parastylar lobe absent or small	Placentalia	Wible et al. 2007, 2009

Table 2. *Continued*

#	Character	Clade	References
20	P4 metacone absent	Metatheria	O'Leary et al. 2013
21	P4 metastyle (stylar cusp E) distolabial to paracone or metacone	Eutheria	O'Leary et al. 2013
22a	Penultimate premolar with protoconal bulge	Eutheria	Rougier et al. 1998, 2004; Wible et al. 2007, 2009; Luo et al. 2011
22b	P4 protocone present	Eutheria	O'Leary et al. 2013
23	P5 position replacement absent	Metatheria	O'Leary et al. 2013
24a	Ultimate premolar with protocone or protoconal swelling	Eutheria	Luo et al. 2003, 2011
24b	Ultimate premolar protocone smaller than paracone	Eutheria	Wible et al. 2007, 2009
25	Ultimate premolar molariform	Eutheria	Rougier et al. 1998, 2004
Lower premolars			
26	Five lower premolars	Eutheria	Luo et al. 2011
27a	First premolar oblique	Metatheria	Wible et al. 2007, 2009
27b	p1 mesial root labial to distal root	Metatheria	O'Leary et al. 2013
28	p2 position replacement absent	Metatheria	O'Leary et al. 2013
29	p2 talonid present	Theria	O'Leary et al. 2013
30	p3 absent	Theria*	O'Leary et al. 2013
31	p5 position replacement absent	Metatheria	O'Leary et al. 2013
32	Ultimate premolar symmetrical	Eutheria	Luo et al. 2003, 2011
33	Ultimate premolar paraconid distinctive but low	Eutheria	Wible et al. 2007, 2009
34	Ultimate premolar with paraconid enlarged	Eutheria	Luo et al. 2003, 2011
35	Ultimate premolar complex, with a partial trigonid and/or talonid	Eutheria	Averianov et al. 2010
36	Ultimate premolar mesiolingual cingulid absent	Placentalia	Wible et al. 2007, 2009
Molars general			
37a	Three molars	Eutheria	Rougier et al. 1998, 2004
37b	Three molars	Metatheria*	Vullo et al. 2009
38	Four molars	Metatheria	Cifelli 1993a; Averianov et al. 2010
39	Size of molars increases posteriorly	Metatheria	Rougier et al. 2004; Wible et al. 2007, 2009
40	Size of molars does not increase posteriorly	Eutheria	Rougier et al. 1998
Upper molars			
41	Molars interlock absent	Eutheria	O'Leary et al. 2013
42	M1 has three roots	Theria	O'Leary et al. 2013
43	Parastylar groove well developed	Theria	Averianov and Skutschas 1999
44a	Stylar shelf slightly reduced labial to paracone	Marsupialia	Rougier et al. 1998

Table 2. *Continued*

#	Character	Clade	References
44b	M1 stylar shelf labial to paracone narrower than stylar shelf labial to metacone	Theria	O'Leary et al. 2013
45	Preparastyle present	Eutheria	Luo et al. 2011
46	Stylar cusp A (parastyle) small to indistinct	Marsupialia	Rougier et al. 1998
47	M2 stylar cusp A (parastyle) subequal to larger than B (stylocone)	Theria	Wible et al. 2007, 2009
48	Stylar cusp C absent	Theria	Averianov and Skutschas 1999
49	Stylar cusp D present	Metatheria	Luo et al. 2003
50	Stylar cusp E poorly developed or absent	Eutheria	Luo et al. 2003
51	Deep ectoflexus on penultimate and preceding molar	Metatheria	Rougier et al. 1998, 2004
52	Metacone slightly smaller than paracone	Metatheria	Rougier et al. 1998, 2004; Luo et al. 2003
53a	Metacone enlarged	Metatheria	Cifelli 1993b
53b	M1 (=M2) metacone taller than paracone	Metatheria	O'Leary et al. 2013
53c	M2 (=M3) metacone taller than paracone	Metatheria	O'Leary et al. 2013
54a	M1 (=M2) metacone more lingual than paracone	Metatheria	O'Leary et al. 2013
54b	M2 (=M3) metacone more lingual than paracone	Metatheria	O'Leary et al. 2013
55a	Centrocrista V-shaped	Marsupialia	Luo et al. 2003
55b	M2 (=M3) premetacrista mesiolabial	Metatheria	O'Leary et al. 2013
56	Postmetacrista cusp absent	Eutheria	Averianov and Skutschas 1999
57a	Postmetacrista strongly developed, with paraconid enlarged and metaconid reduced on lower molars	Metatheria	Averianov et al. 2010
57b	M1 (=M2) postmetacrista long	Metatheria	O'Leary et al. 2013
58	M2 postparacrista and postmetacrista subequal	Eutheria	O'Leary et al. 2013
59	Preprotocrista extends labially past the base of paracone	Theria	Rougier et al. 1998, 2004
60a	Postprotocrista extends labially past base of metacone	Theria	Cifelli 1993a, b
60b	Postprotocrista extends labially past base of metacone	Eutheria	Rougier et al. 1998, 2004; Luo et al. 2011
60c	Postprotocrista extends labially past base of metacone	Metatheria	Vullo et al. 2009
70a	Protocone broadened	Metatheria	Cifelli 1993b
70b	Protocone slightly expanded in its apical half	Eutheria	Luo et al. 2011
71a	M1 (=M2) protocone larger than paracone	Metatheria	O'Leary et al. 2013
71b	M2 (=M3) protocone larger than paracone	Metatheria	O'Leary et al. 2013
72	Conules absent	Marsupialia	Rougier et al. 1998; Luo et al. 2003
73	Metacingulum and metaconule present in addition to postprotocrista	Theria	Luo et al. 2011

Table 2. *Continued*

#	Character	Clade	References
74	Conules well developed, trenchant, and bearing cristae	Theria	Cifelli 1993b
75	M2 paraconule prominent, midway or closer to paracone	Theria	Wible et al. 2007, 2009
76	M2 metaconule prominent, midway or closer to protocone	Theria	Wible et al. 2007, 2009
77a	Distance between conules 31–50% of total tooth length	Eutheria	Luo et al. 2003, 2011
77b	M2 conular region moderate, 31–50% of total tooth length	Theria	Wible et al. 2007, 2009
78	M2 postcingulum present, extending to labial margin	Placentalia	Wible et al. 2007, 2009
Lower molars			
79	Interlocking mechanism between adjacent molars absent	Placentalia	O'Leary et al. 2013
80	m1 smaller than succeeding molars	Metatheria	Cifelli 1993a
81a	Height differential between trigonid and talonid reduced	Metatheria	Cifelli 1993a, b
81b	Trigonid less than twice higher than talonid	Eutheria	Vullo et al. 2009
82a	Trigonid angle acute	Theria	Rougier et al. 2004
82b	Trigonid angle less than 35°	Eutheria	Luo et al. 2003
83	m2 trigonid mesiodistally compressed, less than 50% of total tooth length	Eutheria	Wible et al. 2007, 2009
84	Prevallid shearing facets strongly developed and transverse	Theria	Luo et al. 2003
85	Paracristid with deep carnassial notch	Eutheria	Vullo et al. 2009
86a	m1 paracristid not notched	Eutheria	O'Leary et al. 2013
86b	m2 paracristid not notched	Eutheria	O'Leary et al. 2013
87	Protocristid transverse	Theria	Rougier et al. 2004
88	m2 protocristid complete but depressed protoconid and metaconid stands above depressed central section of protocristid	Eutheria	O'Leary et al. 2013
89	m1 (=m2) protocristid discontinuous and deeply notched	Metatheria	O'Leary et al. 2013
90	m1 (=m2) postenocristid present	Metatheria	O'Leary et al. 2013
91	m2 metaconid subequal to protoconid, 80–100% of its height	Eutheria	O'Leary et al. 2013
92a	dp5 (=m1) paraconid forming vertical keel	Metatheria	O'Leary et al. 2013
92b	m1 (=m2) paraconid forming vertical keel	Metatheria	O'Leary et al. 2013
92c	m2 (=m3) paraconid forming a vertical keel	Metatheria	O'Leary et al. 2013
93a	Paraconid shorter than metaconid	Theria	Rougier et al. 1998, 2004
93b	m2 paraconid lower than metaconid	Theria	O'Leary et al. 2013
93c	Paraconid reduced	Eutheria	Averianov and Skutschas 1999

Table 2. *Continued*

#	Character	Clade	References
94	Paraconid and metaconid subequal in height, or paraconid slightly smaller	Eutheria	Vullo et al. 2009
95	Posterior molars with lingual crests in trigonid	Eutheria	Vullo et al. 2009
96	dp5 (=m1) trigonid distal wall weakly inclined	Metatheria	O'Leary et al. 2013
97	Talonid 40–70% of trigonid width	Theria	Luo et al. 2003
98	Talonid broadened	Metatheria	Cifelli 1993a, b
99	dp5 (=m1) wear present in bottom of talonid basin	Metatheria	O'Leary et al. 2013
100	dp5 (=m1) talonid notched lingually but not open	Metatheria	O'Leary et al. 2013
101	Distal metacristid absent	Eutheria	Luo et al. 2003
102a	dp5 (=m1) cristid obliqua strong trenchant	Metatheria	O'Leary et al. 2013
102b	m1 cristid obliqua very strong trenchant	Theria	O'Leary et al. 2013
103	Cristid obliqua contacts trigonid at protocristid notch	Eutheria	Luo et al. 2003
104	m2 (=m3) cristid obliqua contact to midpoint between protoconid and metaconid in vicinity of protoconid	Metatheria	O'Leary et al. 2013
105a	dp5 (=m1) talonid distolabial side angular	Metatheria	O'Leary et al. 2013
105b	m1 (=m2) hypoconid distolabial side angular	Metatheria	O'Leary et al. 2013
105c	m2 (=m3) hypoconid distolabial side angular	Metatheria	O'Leary et al. 2013
106	Hypoconid/protoconid height ratio between 40–60%	Eutheria	Luo et al. 2003, 2011
107	m1 (=m2) hypoconid-hypoconulid crest weak	Metatheria	O'Leary et al. 2013
108	Entoconid present, with slight approximation to hypoconulid	Metatheria	Luo et al. 2003
109	m2 entoconid smaller than hypoconid and/or hypoconulid	Theria	Wible et al. 2007, 2009
110	Wear facet 5 and 6 differentiated on labial face of entoconid	Eutheria	Luo et al. 2003, 2011
111a	Hypoconulid “twinned” with entoconid	Metatheria	Cifelli 1993b
111b	m2 (=m3) hypoconulid twinned to entoconid	Metatheria	O'Leary et al. 2013
112	Strong labial postcingulid present	Metatheria	Cifelli 1993a, b
113	Penultimate molar longest	Eutheria	Luo et al. 2011
114	m3 shorter than m1 (50–90%)	Theria	O'Leary et al. 2013
115	Ultimate molars rotates during eruption	Metatheria	Rougier et al. 1998, 2004
116	Ultimate molar hypoconulid short and erect	Marsupialia	Rougier et al. 1998; Luo et al. 2003
117	Ultimate molar hypoconulid tall and sharply recurved	Theria	Wible et al. 2007, 2009

*Possible typographic error or miscoding artifact.

Canines. The likely upper double-rooted canine CNHM PM 1124 (Butler 1978: fig. 4e) is too small to be assigned to *Holoclemensia* or *Oklatheridium*, but is of right size for *Atokatheridium*. If attributed to the latter taxon, this would advocate against its metatherian affinities (Table 2, character 8).

The large canine alveolus in CNHM PM 583 is likely for the erupting permanent canine which could be double rooted.

There are two isolated canines from the Greenwood Canyon locality with small crown and subdivided root, which are likely lower canines (CNHM PM 982 and 1070). Attribution of these specimens to the Theria is not certain.

Postcanine dental formula. A large suite of synapomorphies is related to the postcanine dental formula (Table 2, characters 10–13, 16, 18, 23, 26, 28, 30, 31, 37, 38, and 80). The current consensus is that the primitive dental formula for the Theria includes five premolars and three molars (Averianov et al. 2010; O’Leary et al. 2013). In eutherian lineage P3/p3 has been reduced (Archibald and Averianov 2012) and lost in Placentalia (O’Leary et al. 2013). O’Leary et al. (2013) listed absence of p3 (Table 2, character 30) as a synapomorphy for the Theria, which is an obvious mistake. The metatherians evolved four molars via non replacement of the ultimate deciduous premolar, dP5/dp5 (O’Leary et al. 2013). Metatherians also lost one premolar position, P1/p1 (Averianov et al. 2010) or P3/p3 (O’Leary et al. 2013), which, together with transferal of the fifth premolar position to the molars, resulted in three premolars in this group. Only the last of these premolar positions, P3/p3, homologues to P4/p4 of primitive therian form, is replaced (Luckett 1993; Rougier et al. 1998; Luo et al. 2004). *Pappotherium* (= *Slaughteria*) displays replacement at least in two premolar positions, a primitive therian condition, used previously to prove attribution of this taxon to the Eutheria (Slaughter 1971, 1981). Among Trinity therians, *Kermackia*, *Holoclemensia*, and *Pappotherium* are interpreted as having three molars. *Holoclemensia* might also have five premolars, if SMP–SMU 62006 (Jacobs et al. 1989: fig. 4; Winkler et al. 1990: fig. 11C, D) belongs to that taxon. These characters exclude all the three taxa from the Metatheria and *Holoclemensia* from the Placentalia, but not from the Eutheria. The four molar positions can be reconstructed for *Atokatheridium* and *Oklatheridium*, which suggests attribution of these taxa to the Metatheria (table 1, character 38).

Tall trenchant upper premolar. It has long been accepted that the tall trenchant upper premolar is in the ultimate position in metatherians and in the penultimate position in eutherians (Table 2, character 18). Now it is clear that this character is correlated with the change in the postcanine dental formula. In stem therians, as exemplified by *Peramus* (Clemens and Mills 1971; Averianov et al. 2010), and in eutherians the tallest upper premolar is the penultimate tooth (P4). In metatherians this tooth becomes the ultimate premolar because of lack of replacement in the fifth premolar locus. A tall trenchant upper premolar attributed to *Holoclemensia* (SMP–SMU 61948) is identified as P4, following Davis and Cifelli (2011), because a primitive therian – eutherian dental formula is inferred for this taxon.

Penultimate upper premolar parastylar lobe. In stem therians, such as *Peramus* and *Juramaia* (Clemens and Mills 1971; Luo et al. 2011), as well as in basal eutherians such as *Prokennalestes* and Zhelestidae (Kielan-Jaworowska and Dashzeveg 1989; Archibald and Averianov 2012), there is no parastylar lobe on the penultimate upper premolar (P4). A small mesial cusp and/or mesial cingulum can be present there. This condition is also present in SMP–SMU 61948, the P4 referred to *Holoclemensia*. Wible et al. (2007, 2009) listed the parastylar lobe of the penultimate upper premolar absent or small as a synapomorphy for the Placentalia (Table 2, character 19). This is likely an artifact of taxon sampling and/or coding.

Penultimate upper premolar protoconal bulge. Presence of a protocone or protoconal bulge has been cited as a synapomorphy for the Eutheria (Table 2, character 22). A small protoconal bulge, but not a true protocone, might be present in P4 of *Holoclemensia* (SMP–SMU 61948). This specimen likely had a complete lingual cingulum. In *Peramus* there is no lingual cingulum on P4 (Clemens and Mills 1971). On P4 of *Juramaia* there is a complete lingual cingulum but no a protocone swelling. The protocone swelling is present on P4 in *Prokennalestes* and Zhelestidae (Kielan-Jaworowska and Dashzeveg 1989; Archibald and Averianov 2012). This character seems to be a good synapomorphy for the Eutheria. If indeed present in *Holoclemensia*, it would suggest attribution of this taxon to the Eutheria.

Ultimate lower premolar submolariform. There are several proposed synapomorphies related to the molarization of the ultimate lower premolar (Table 2, characters 32–35). The submolariform lower pre-

molars from the Butler Farm locality (SMP–SMU 61947 and 62399) have been used to prove presence of Eutheria in the Trinity fauna (Slaughter 1968a, 1971, 1981). Later these premolars have been referred to *Pappotherium* (SMP–SMU 62399) and *Holoclemensia* (SMP–SMU 61947), classified as stem therians (Butler 1978). Davis and Cifelli (2011) referred SMP–SMU 62399 to *Holoclemensia* and a similar tooth from the Tomato Hill locality (OMNH 67134) to *Kermackia*. *Holoclemensia* is a eutherian and *Kermackia* is a stem therian according to these authors. Here all these three specimens referred to *Holoclemensia*. As described in the previous systematic section, there is some size and structural variation between these specimens. These premolars have a trigonid with low cingular paraconid and variable developed metaconid, which is from one third to one half of the protoconid height. The protocristid is a low ridge. The talonid is single cusped and not basined. Among the stem therians the ultimate lower premolar is known for *Amphitherium*, *Nanolestes*, *Arguimus*, *Mozomus*, *Peramus*, *Juramaia*, and *Eomaia* (Clemens and Mills 1971; Butler and Clemens 2001; Ji et al. 2002; Martin 2002; Li et al. 2005; Lopatin and Averianov 2006; Luo et al. 2011). In all these taxa it is a simple premolariform tooth. Davis and Cifelli (2011) maintain that m1 of *Arguimus* is a molariform ultimate premolar but gave no arguments in support of their view. The p5 is premolariform in the eutherians *Prokennalestes*, *Paranyctoides*, *Maelestes*, and Asioryctitheria, in spite that P5 is submolariform, with fully developed protocone, in these taxa (Kielan-Jaworowska and Dashzeveg 1989; Sigogneau-Russell et al. 1992; Archibald and Averianov 2006; Wible et al. 2009; Averianov and Archibald 2013). The p5 is premolariform also in the Early Cretaceous eutherians *Acristatherium* and *Sasayamamylos*, for which the structure of P5 is uncertain or unknown (Hu et al. 2010; Kusuhashi et al. 2013). Among zhelestids the p5 is premolariform in the Cenomanian – early Turonian taxa and has a variable developed small metaconid in the late Turonian taxa (Averianov and Archibald 2005; Archibald and Averianov 2012). The p5 is submolariform, with a well-developed metaconid, in a Cenomanian eutherian *Bobolestes* and the Turonian-Campanian Zalambdalestidae (Archibald and Averianov 2003; Wible et al. 2004; Averianov and Archibald 2005; Zan et al. 2006). Apparently, molarization of p5 developed independently in different eutherian lin-

eages. This undermines significance of this character as a eutherian synapomorphy and an argument for attributing of *Holoclemensia* to that group.

Upper molars stylar cusps. A number of purported synapomorphies describe development of the stylar cusps on the upper molars (Table 2, characters 45–50). Noteworthy, presence of a large stylar cusp C in *Holoclemensia* have long been used as an argument for reference of this taxon to the Metatheria (see review of the previous work). Among Trinity therians, a much smaller stylar cusp C is variable present in *Atokatheridium*. As was discussed by Davis and Cifelli (2011), the early metatherians lack the stylar cusp C and thus it was acquired by *Holoclemensia* independently from the Metatheria. Wible et al. (2007, 2009) cited the parastyle subequal to larger than the stylocone as a therian synapomorphy (Table 2, character 47). Similarly, Davis and Cifelli (2011) considered reduced stylocone of *Holoclemensia* as a eutherian character. The significance of this character is not certain. In some stem therians, such as *Nanolestes*, *Peramus*, and *Kielantherium*, the parastyle is larger than the stylocone (Clemens and Mills 1971; Martin 2002; Lopatin and Averianov 2007). In the stem therian *Juramaia* and basal eutherians *Prokennalestes* and *Murtoilestes* the stylocone is slightly larger than the parastyle (Kielan-Jaworowska and Dashzeveg 1989; Averianov and Skutschas 2001; Luo et al. 2011). Among the Trinity therians the stylocone is larger than the parastyle in *Atokatheridium* and *Oklatheridium*. In *Holoclemensia* and *Pappotherium* there is a stylar cusp in D position. The upper molar stylar cusps have no occlusal relationships with the lower molar structures and their function is uncertain. Apparently development of these cusps has little if any phylogenetic significance (Clemens and Lillegraven 1986).

Penultimate and antepenultimate upper molars deep ectoflexus. A deep ectoflexus on penultimate and preceding molar has been proposed as a metatherian synapomorphy (Table 2, character 51). These molars are M1–2 in the stem therians and eutherians and M2–3 in the metatherians. In metatherians this condition is best exemplified by deltatheroidans (Rougier et al. 2004; Averianov et al. 2010). However, this condition is present also in stem therians (*Peramus*, *Juramaia*), and basal eutherians (*Prokennalestes*, *Murtoilestes*, *Kulbeckia*) (Clemens and Mills 1971; Kielan-Jaworowska and Dashzeveg 1989; Averianov and Skutschas 2001; Archibald and

Averianov 2003; Luo et al. 2011). In zhelestids the ectoflexus on the antepenultimate upper molar (M1) is greatly reduced to absent (Nesov et al. 1998; Averianov and Archibald 2005; Archibald and Averianov 2012). Among the Trinity therians this character is developed in *Oklatheridium* and, to a lesser extent, in *Atokatheridium* (condition for *Pappotherium* is unknown). A derived condition, with reduced ectoflexus on the antepenultimate upper molar (M1), is present in *Holoclemensia*. This is another, possibly independently acquired, eutherian-like characteristic of that taxon.

Postmetacrista cusp. The absence of the postmetacrista cusp has been suggested as a eutherian synapomorphy (Table 2, character 56), while earlier Slaughter (1971) considered this cusp as a character supporting eutherian affinities for *Pappotherium*. In addition to *Pappotherium*, this cusp is present in *Kielantherium*, *Juramaia*, *Prokennalestes*, and *Murtoilestes* (Kielan-Jaworowska and Dashzeveg 1989; Averianov and Skutschas 2001; Lopatin and Averianov 2007; Luo et al. 2011). This character is likely a plesiomorphy for the stem therians and basal eutherians.

Prevallum and postvallum shear. The main shearing surfaces of the upper and lower tribosphenic molars, preparacrista – protocristid and postmetacrista – paracristid, are unequally developed in eutherians and metatherians. In eutherians there is an emphasis on the preparacrista – protocristid (prevallum/postvallid) shear, while in metatherians – on the postmetacrista – paracristid (postvallum/prevallid) shear. This is manifested, in particular, in better development of the paracone and metaconid in eutherians and the metacone and paraconid in metatherians (Table 2, characters 52–54, 57, 84, 93, and 94). In derived therians, this system of the first-rank shearing surfaces has been enhanced by additional, double-rank shearing surfaces: preprotocrista – protocristid (prevallum/postvallid) and postprotocrista – paracristid (postvallum/prevallid) (Table 2, characters 59, 60, and 73). The Early Cretaceous aegialodontid *Kielantherium* already has an emphasis on the postvallum/prevallid shear, with strong postmetacrista and paraconid higher than the metaconid (Lopatin and Averianov 2007). This metatherians-like characteristic was possibly acquired by *Kielantherium* independently from the metatherians, as well as its dental formula with four molars, which was suggested previously by Davis and Cifelli (2011). This is likely because a number of stem therians also have

paraconid higher than metaconid: *Amphibetulimus*, *Peramus*, *Mozomus*, and *Arguimus* (Averianov et al. in press). In *Kielantherium* there is a fully developed second-rank prevallum/postvallid shear, with the preprotocrista extending labially towards the parastylar region. The second-rank postvallum/prevallid shear is not developed, however. The postprotocrista terminates at the base of the metacone. The acquisition of the second-rank postvallum/prevallid shearing surface has been postulated as a synapomorphy for Theria, Eutheria, or Metatheria (Table 2, character 60). It is present in a stem therian *Juramaia* and basal eutherians *Prokennalestes*, *Murtoilestes*, and *Bobolestes*, where the postprotocrista terminates near the labial end of the metacone (Kielan-Jaworowska and Dashzeveg 1989; Averianov and Skutschas 2001; Averianov and Archibald 2005; Luo et al. 2011). The primitive condition, exemplified by *Kielantherium*, is characteristic for all Trinity therians. Two taxa of Trinity therians (*Atokatheridium* and *Oklatheridium*) have emphasis on the postvallum/prevallid shear, with strong postmetacrista and paraconid higher than metaconid. This apparently suggests metatherians affinity for these taxa. In other Trinity therians (*Kermackia*, *Holoclemensia*, and *Pappotherium*), the paraconid is smaller than metaconid.

Upper molars protocone size. The mesiodistal expansion of the protocone has been suggested as a eutherian or metatherian synapomorphy (Table 2, characters 70, 71). In *Kermackia* and *Holoclemensia* the protoconal region is known only for the ultimate molars (M3) where it can be reduced compared with the preceding molars. On M2 of *Pappotherium* the protocone is extremely narrow mesiodistally. This has been used as an argument for deltatheroidan affinities of this taxon (Davis and Cifelli 2011). However, more likely, it is retention of the primitive therian condition. The protocone of *Pappotherium* is very low, paralleling the condition of stem therians *Kielantherium* and *Juramaia* (Lopatin and Averianov 2007; Luo et al. 2011). In basal eutherians, such as *Prokennalestes* and *Murtoilestes*, the protocone is significantly higher (Kielan-Jaworowska and Dashzeveg 1989; Averianov and Skutschas 2001). The protoconal region in *Atokatheridium* (preserved in M2–3) and *Oklatheridium* (M3) is more expanded mesiodistally compared with deltatheroidans. The protoconal region was likely narrow on M1 of *Oklatheridium* where it is incompletely preserved. The wide protoconal region of M3 in *Oklatheridium* correlates with the wide talonid of

the middle lower molar (m2 or 3) attributed to that taxon. This character advocates against close relationships of *Oklatheridium* and deltatheroidans.

Upper molar conules. In *Kielantherium* the protocone is a single cusp in the protoconal region (Lopatin and Averianov 2007). In more derived therians one or two cusps (conules) have been added on the protoconal cristae (Table 2, characters 74–76), while Rougier et al. (1998) and Luo et al. (2003) cited lack of conules as a marsupial synapomorphy (Table 2, character 72). The conules are totally lacking on M3 of *Kermackia* and the same is likely true for the other upper molars in that taxon which are not known. In *Pappotherium* the conules are very small and lack internal cristae; the metaconule is absent on M3. This condition is similar to that of a stem therian *Juramaia* Luo et al. 2011. In *Holoclemensia* the protoconal region is known only for M3. Both conules are present there; they are distinctly larger than in *Pappotherium*, but still lack the internal cristae. In *Atokatheridium* there are small conules with short internal cristae on M2 and M3 (protoconal region is unknown for M1 and M4). In *Oklatheridium* there is a large paraconule with postparaconule crista and a smaller, likely unwinged, metaconule on M3. On M4 there is only small and unwinged metaconule (protoconal region is unknown for M1–2). The development of the conules in *Atokatheridium* and *Oklatheridium* is more similar to that in basal eutherians *Prokennalestes* and *Murtoilestes* (Kielan-Jaworowska and Dashzeveg 1989; Averianov and Skutschas 2001) than to condition of deltatheroidans, where conules are small and lack internal cristae (Averianov et al. 2010).

Lower molars trigonid angle and protocristid orientation. In stem therians and some basal eutherians and metatherians the trigonid of lower molars is more open lingually and the protocristid is more oblique to the dentary axis compared with more derived taxa (Table 2, characters 82, 83, and 87). In *Kermackia* the trigonid angle of lower molars is 46–54° and the protocristid is oblique. In *Atokatheridium* there is a single complete lower molar (m4) with trigonid angle 50° and oblique protocristid. In *Oklatheridium* the trigonid angle is 45–52° and the protocristid is more transverse. Both *Holoclemensia* and *Pappotherium* have a smaller trigonid angle (30–42°) and a transverse protocristid. These are relatively derived characters, present in a few basal eutherians, such as *Sasayamamylos* or *Bobolestes* (Averianov and Archibald 2005; Kusuhashi et al. 2013).

Lower molars paraconid vertical crest. A keel-like mesiolingual edge of the lower molars paraconid, which corresponds to the mesiolingual cuspule e, has long been considered as a metatherian feature (Table 2, character 92), although it is present also in a basal eutherian *Murtoilestes* (Averianov and Skutschas 2001). Among Trinity therians this character present in *Kermackia* and *Atokatheridium*. Davis et al. (2008) thought that this crest is absent in *Atokatheridium*. At least for the latter taxon this character may suggest metatherian affinities.

Lower molars talonid width. In the early tribosphenic mammals, like *Kielantherium*, talonid was narrow, about half of the trigonid width (Dashzeveg and Kielan-Jaworowska 1984; Lopatin and Averianov 2007). With the further development of the protoconal region, the talonid becomes wider, approaching or exceeding the trigonid in width (Table 2, characters 97, 98). Among Trinity therians *Kermackia* has the low talonid to trigonid width ratio (0.68–0.81), which is consistent with the phylogenetic position of this taxon as a stem therian. *Holoclemensia* has similar values of this ratio; it varies individually and between the tooth positions from 0.63 to 0.85. In *Oklatheridium* the talonid is only slightly narrower than the trigonid, with the talonid to trigonid width ratio of 0.80–0.91. This is markedly different from the condition of deltatheroidans, where the talonid is very narrow. *Pappotherium* is the most derived among Trinity therians in this respect, with the talonid with to trigonid width ratio of 0.94 for m1.

Lower molars distal metacristid and cristid oblique. The distal metacristid is a crest connecting the metaconid with the hypoconid, which shears against the paracone (Fox 1975). It is present in stem therians that have the paracone the largest cusp of the upper molars and the protocone absent or small. With further development of the protocone it starts to shear against the metaconid (wear facet 5), which led to disconnection of the distal metacristid from the metaconid (Crompton 1971; Davis 2011a). Davis (2011b: 677) redefined distal metacristid “as an oblique crest on the posterior face of the metaconid, but not necessarily reaching the apex of the cusp.” However, in this definition the distal metacristid would not differ from the cristid obliqua. Here I follow the definition of the distal metacristid by Fox (1975) as a continuous crest between the metaconid apex and the hypoconid. The disrupted crest, not reaching the metaconid apex, is the cristid obliqua. Several purported synapomorphies

are related to the distal metacristid and orientation of the cristid obliqua (Table 2, characters 101–104). Among Trinity therians the distal metacristid is well-developed in the stem therian *Kermackia*. *Atokatheridium* and *Oklatheridium* show a transitional stage where some teeth still have a faint distal metacristid while in other teeth it is disconnected from the metaconid apex (cristid obliqua). In this respect both taxa are different from deltatheroidans which have the distal metacristid. The next stage is exemplified by *Holoclemensia*, where the cristid obliqua is rarely ascending on the trigonid wall above the protocristid notch. *Pappotherium* has the most derived condition, with short cristid obliqua, although this could be accentuated by the wear of the single known specimen. In *Holoclemensia* the cristid obliqua terminates lingual to the protocristid notch which is correlated with the narrow talonid relative to the trigonid. In *Pappotherium*, which have the talonid nearly equal to the trigonid in width, this crest terminates labial to the protocristid notch (some labial shift of this crest could be caused by the wear of the single known specimen). The cristid obliqua contacting the trigonid at the protocristid notch or more labial has been cited as a synapomorphy for either Eutheria or Metatheria (Table 2, characters 103, 104). Evidently this trait was developed independently in these lineages in correlation with the widening of the talonid.

Lower molars hypoconulid and entoconid approximation. In metatherians the hypoconulid and entoconid are closely approximated (“twinned”) (Table 2, character 111). This character has been used as an argument for assigning *Holoclemensia* to the Marsupialia since original description of this taxon (Slaughter 1968b). However, as was shown by Jacobs et al. (1989), in *Holoclemensia* the hypoconulid and entoconid are not as close as in the Late Cretaceous stem marsupials. The approximation of these cusps is correlated with the widening of the talonid and also characteristic for some Late Cretaceous eutherians, including zhelestids (Archibald and Averianov 2012). But none of the Cretaceous eutherians show a peculiar metatherian condition, with the hypoconulid and entoconid almost aligned mesiodistally.

CONCLUSIONS

There are five tribosphenic taxa in the vertebrate fauna of the Antlers Formation of Texas and Oklahoma, USA (Table 3). The most primitive

taxon is a stem therian *Kermackia texana*, which has primitive therian postcanine formula with three molars, replacement in the fifth premolar position, upper molars with a small protoconal region with low protocone and no conules, lower molars with great trigonid angle, oblique protocristid, paraconid smaller than metaconid (except m3), strong distal metacristid, narrow talonid, small talonid basin, and small entoconid (absent on m3). *Kermackia* has at least one metatherian character – a keel-like vertical crest of the paraconid. *Holoclemensia texana* has such plesiomorphic therian characters as a tall trenchant penultimate upper premolar (P4), replacement in the fifth premolar locus, and three molars. It is more derived compared with *Kermackia* in larger protoconal region with higher protocone and conules present, lack of distal metacristid, smaller trigonid angle, transverse protocristid, and wide talonid with greater talonid basin. *Holoclemensia* has certain similarities with Eutheria: possible protoconal bulge on P4, M1 with reduced ectoflexus, semimolariform p5, and low trigonid angle with transverse protocristid. However, all these traits were likely derived independently in different eutherian lineages. Moreover, it differs from basal eutherians by the postprotocrista not extending labially past the metacone base (lack of the second rank postvallum/prevallid shear) and conules lacking the internal cristae. Therefore *Holoclemensia* is considered here as a stem therian rather than eutherian. A peculiar large stylar cusp C is an autapomorphy of this taxon (Davis and Cifelli 2011). *Pappotherium pattersoni* has the following therian plesiomorphic characters: replacement in the fifth premolar position, premolariform p5, and three molars. It is more derived than *Holoclemensia* in having wider and shorter talonid. By low trigonid angle, transverse protocristid, and the cristid obliqua labial to the protocristid notch (possible wear artifact) *Pappotherium* is similar with Eutheria. It cannot be attributed to the Eutheria because of narrow protoconal region, low protocone, small conules lacking internal cristae, postprotocrista not extending labially past the metacone base, and small talonid basin. *Pappotherium* is considered here as a stem therian. The two remaining taxa, *Atokatheridium boreni* and *Oklatheridium szalayii*, are considered as stem marsupials because of having four molars and emphasis on the postvallum/prevallid shear (large metacone on M2, strong postmetacrista, paraconid higher than metaconid). In *Atokatheridium* a small stylar cusp C

Table 3. Distribution of the tribosphenic mammals in the localities of the Antlers Formation of Texas and Oklahoma, USA.

Taxon	Butler Farm	Greenwood Canyon	Tomato Hill	Pecan Valley Estates
<i>Kermackia texana</i>	+	+	+	–
<i>Holoclemensia texana</i>	+	+	+	+
<i>Pappotherium pattersoni</i>	+	–	–	–
<i>Atokatheridium boreni</i>	–	+	+	–
<i>Oklatheridium szalayi</i>	–	+	+	–

is variable present. These taxa cannot be attributed to the Deltatheroidea because of large protoconal region with winged conules. *Oklatheridium* is further different from Deltatheroidea by wider talonid and better developed entoconid, which is small or reduced in deltatheroidans (Averianov et al. 2010). Condition of these characters is uncertain for *Atokatheridium*, as the single known complete lower molar of this taxon, with narrow talonid and entoconid lacking, is likely a m4 which talonid is supposed to be reduced. The Early Cretaceous Trinity Fauna of North America shows unparalleled diversity of early therian taxa, including a basal stem therian (*Kermackia*), two taxa near the eutherian-metatherian dichotomy (*Holoclemensia* and *Pappotherium*), and two taxa of basal metatherians (*Atokatheridium* and *Oklatheridium*).

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