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THE EVOLUTION OF EARLY TRIBOSPHENIC MAMMALS

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ABSTRACT

The history of paleomammalogy stretches back to the beginning of paleontology as a scientific discipline; though with far less fanfare, early fossil mammals were discovered alongside the iconic dinosaurs that would capture the imagination of the world. Their small size and generally poor preservation limited the data which could be gleaned from fossil mammals, until advances in collection and study techniques in the middle of the 20th Century sparked a revolution in our understanding of mammalian character evolution. Recent fossil discoveries, most notably from poorly-sampled regions such as China and the southern continents, have led to further reevaluation of the complex nature of early mammalian evolution; in particular, the relationships between the living groups of mammals and the arrangement of the major fossil lineages have been thrown into question.

This dissertation utilizes the most recent concepts of mammalian evolution and relationships to take a fresh look at some historically and scientifically important faunas. The overall aim is to thoroughly evaluate the transition to tribospheny from amongst a cloud of lineages, each bearing a particular blend of archaic and derived dental and mandibular features. Of particular note are three groups: the Australosphenida, which have been regarded either as relatives of living insectivores or an endemic Gondwana radiation with a deep history; the Peramura, which are generally viewed as the sister-group to the clade containing most living mammals; and the Trinity therians, which have been cited as representing the earliest divergence between marsupials and placentals, and which were fundamental to our modern ideas of molar evolution.

While some new taxa are described and the contents of high-level taxa are reorganized, the principal results of these studies provide a new interpretation of character evolution in early fossil mammals. Tribosphenic mammals (the Tribosphenida) are a monophyletic group with a likely Laurasian origin, or at least an initial Laurasian radiation. The Australosphenida are structurally but not functionally similar, and represent a separate clade entirely; their relationship to monotremes is unclear. The Peramura are the best known sister-group to the Tribosphenida, and present a clear transitional morphotype. The tribosphenidan mammals from the Trinity Group illustrate the dynamic radiation and dispersal of advanced mammals that had already occurred by the Early Cretaceous; early eutherians and metatherians are represented, as well as taxa which, though curiously derived, are best left unallocated.

PREFACE

This dissertation was intended as a collection of four independent, publishable papers, centrally focused on the evolution of tribosphenic mammals. At the time of this writing (April, 2011), the chapters are in various stages of submission/publication. Chapter 1, “A novel interpretation of the tribosphenidan mammal *Slaughteria eruptens* from the Lower Cretaceous Trinity Group, and implications for dental formula in early mammals”, will be published in the third issue of the *Journal of Vertebrate Paleontology* and may be cited as:

Davis, B.M. 2011. A novel interpretation of the tribosphenidan mammal *Slaughteria eruptens* from the Early Cretaceous Trinity Group, and implications for dental formula in early mammals. *Journal of Vertebrate Paleontology* 31: 1-8.

Chapter 2, “Evolution of the tribosphenic molar pattern in early mammals, with comments on the “Dual-Origin” hypothesis”, is currently in review for the *Journal of Mammalian Evolution*. Chapter 3, “Reappraisal of the tribosphenidan mammals from the Trinity Group (Aptian-Albian) of Texas and Oklahoma”, is currently in review for *Acta Palaeontologica Polonica*. Chapter 4, “Micro-computed tomography reveals a diversity of peramuran mammals from the Purbeck Group (Berriasian) of England”, is being prepared for submission to *Palaeontology*.

INTRODUCTION

Modern mammals can be characterized as far more active than other living vertebrate groups (with the exception of birds), possessing a very high basal metabolic rate (BMR). Mammals have a set of physiological advantages as a result, most notably the ability to remain very active at night when abient temperatures are lower, as well as other developmental and reproductive advantages tied to high growth rates. However, a high BMR is energetically expensive and mammals must constantly forage. Therefore, there should be strong selective pressure on structures which help support a mammalian BMR; mammals are unique among living vertebrates in their ability to mechanically process food through mastication, which allows the extraction of maximum nutrition. The complex cheek teeth and precise occlusion that set mammals apart were highly instrumental in their adaptive success; our understanding of the evolution of this functional complex has come into focus only in recent decades, and there remains much debate about the origin of the modern mammalian tooth pattern and its implications for the high-level relationships of both fossil and living clades. Regardless, the advantage modern mammals have over other living vertebrates is their ability to slice and crush food in a single chewing stroke, using a multi-functional molar complex. The exploration of this particular character is the focus of this dissertation.

Historical interpretations of the evolution of mammalian molars suffered from the poor fossil record at the close of the 19th Century; derived and relatively modern-like faunas were known from the Late Cretaceous and early Paleogene of the American Western Interior, but the next point of comparison were the substantially older faunas of the Late Jurassic/earliest Cretaceous Morrison Formation and Purbeck Group.

Consequently, in the absence of good transitional morphotypes a modern molar pattern was thought to have been derived directly from a "symmetrodont"-style, reversed-triangle configuration. The Cope-Osborn Theory of Trituberculy was established on the premise that the original non-mammalian, single-cusped cheek tooth developed mesial and distal accessory cusps (elaborated in triconodontans), which then underwent rotation around the main central cusp (buccally on upper molars, lingually on lower molars). The resulting reversed, tritubercular molars would serve as the starting point from which all manners of living mammalian feeding strategies would arise, through modification or addition to the original design. Advances in the understanding of ontogeny at the turn of the 20th Century would discard some portions of the Theory of Trituberculy, notably the notion of cusp rotation. On upper molars, the large lingual cusp (called the protocone by Osborn, based on his surmise that it represented the original, singular cusp around which the other molar cusps rotated) was determined to be a secondary acquisition, with the paracone being the first cusp to mineralize as the molar developed in the jaw. Cusp homology in older, more primitive lineages (such as dryolestids) was revised, since the large lingual cusp in these taxa was homologous not with the protocone but with the paracone, lending support to the in-situ development of the buccal half of modern upper molars and the importance of the protocone as a derived feature of modern mammals.

The functional significance of the basic modern mammalian molar pattern was given a name by G. G. Simpson in 1936, when he coined the term "tribosphenic". This described the new crushing function (*tribos*) of modern mammals, which combines with the original shearing portion of the crown (*sphene*) to thoroughly process food during chewing. Discovery of the oldest tribosphenic mammals, from Early Cretaceous rocks of the Trinity Group in northern Texas in the 1950s, helped to fill an enormous temporal and morphological gap in the known fossil record. Studies of tribosphenic function through paired wear features on upper and lower molars (particularly those by Fuzz Crompton in the 1970s) allowed topological features to be tracked through more primitive morphotypes, and demonstrated definitive support for homology through the transition to tribospheny. An increasing complexity of shearing surfaces can be recognized through the Jurassic and into the Cretaceous, with the development of functional occlusal overlap occurring in tribosphenic mammals. This trend demonstrates a possible functional response to selective pressure in early mammals towards improved mastication, in support of a high mammalian BMR.

However, an additional pattern becomes clear—the adaptive advantage of a tribosphenic molar pattern was great enough that numerous convergences can be recognized in early mammalian history. One group, the docodonts, likely evolved a functionally similar molar pattern from outside therian ancestry. Another group, shuotheriids, derived strikingly similar molar morphology from a probable "symmetrodont" ancestor. A third group is more complicated. The discovery of mammals with very tribosphenic-like lower molars from the Early Cretaceous of Australia in the 1990s, followed by discoveries of much older but morphologically similar taxa from other parts of Gondwana, raised questions about the timing and place of the origin of modern clades. Disputes about the nature of occlusal function in these taxa led to the establishment of a "Dual-Origin" hypothesis of tribosphenic patterns; living marsupials and placentals, as well as their fossil relatives, represented a lineage with a Laurasian origin and initial dispersal (the Boreosphenida), while the Gondwanan taxa form a separate, endemic radiation (named the Australosphenida) which is possibly represented today by living monotremes. However, molar function and relationships among australosphenidans is far from settled.

An updated review of the progression of mammalian molar morphotypes through the Jurassic and earliest Cretaceous, leading to the development of tribospheny, is a central topic in this dissertation. The dynamics just prior to the appearance of tribosphenic mammals (in a morphological not temporal sense) is of particular significance, as the groundwork for the major features of advanced mammals (the protocone and talonid basin) can be seen in their most likely sister-group, the peramurans. Also of prime importance is a discussion of molar function in australosphenidans, and their relationships to living mammal clades. The adaptive significance of the tribosphenic molar pattern is clear both in terms of helping to explain the success of living mammals in invading nearly every dietary niche on the planet, and in recognizing patterns of morphological evolution among early fossil mammals. The energetic costs of a high BMR in mammals can be supported in part through efficient mechanical processessing of food, a task accomplished by complex cheek teeth with an evolutionary origin deep in the fossil past.

A novel interpretation of the tribosphenidan mammal *Slaughteria eruptens* from the Lower Cretaceous Trinity Group, and implications for dental formula in early mammals

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RH: DAVIS—REINTERPRETATION OF *SLAUGHTERIA*

ABSTRACT

Published CT data from the holotype of the early tribosphenidan *Slaughteria eruptens* were reanalyzed to test a new hypothesis of dental formula in this taxon. Results indicate that *Slaughteria* had a premolar count of five, and that erupted (or erupting) teeth of the holotype all represent premolar loci—the p2, p3, dp4, dp5 (a partially calcified p5 is identified below the dp5). This dental formula is supported by serial homology of cheek teeth between eutherians and metatherians and the pre-tribosphenic mammal *Peramus*. The presence of five premolars in *Slaughteria* provides additional evidence that this tooth count is primitive for tribosphenidans as a whole. *Slaughteria* also presents an undocumented mode of tooth replacement, with a mixed alternating and sequential pattern. This pattern may represent the condition in other taxa with five premolars, such as *Peramus* and some early eutherians, with potential bearing on the polarity of tooth replacement at the base of the Tribosphenida.

INTRODUCTION

In 1956, Bryan Patterson published arguably one of the most influential papers in the past century on the study of Mesozoic mammals. In it, he highlighted a fledgling and fragmentary but highly significant collection of isolated teeth from the Lower Cretaceous Trinity Group of north-central Texas. These mammals linked the relatively well-sampled but temporally and morphologically disparate faunas of the Late Jurassic and Late Cretaceous, forming a continuity that Patterson would use to develop a new interpretation of the evolution of the mammalian dentition.

Work on the Trinity fauna intensified during the 1960s, leading to the eventual description of nearly one dozen species of mammals, eight of which are monotypic tribosphenic genera (Slaughter, 1965, 1968a, 1971; Butler, 1978; Jacobs et al., 1989; Kielan-Jaworowska and Cifelli, 2001; Davis et al., 2008). The specimens collected remained almost entirely isolated teeth, hampering consistent suprageneric allocation of the taxa, which largely lack synapomorphies that characterize groups present later in the Cretaceous (Slaughter, 1968a, b; Fox, 1975; Kielan-Jaworowska et al., 1979). Of the more complete material, Slaughter (1971) described a partial dentary preserving two premolariform and two molariform teeth (SMP-SMU 61192), referring it to *Pappotherium pattersoni* and assigning the taxon to the Eutheria. He based this assignment largely on diphyodonty of the anterior premolars (the first premolariform tooth in the specimen is erupting, and marsupials replace only the ultimate premolar). Slaughter noticed more wear on the second molariform tooth than on the first, implying it erupted earlier and that these two teeth represented the p4 and the m1 (the p4 having had a deciduous predecessor; x-ray photographs of the specimen, though unpublished, were cited as showing no evidence of replacement teeth within the jaw). Molarization of the penultimate erupted tooth (p4 according to Slaughter's identification) also lent support for eutherian affinities, and he interpreted the jaw to contain the p2, p3, p4, and m1.

In his re-evaluation of the Trinity fauna, Butler (1978) removed the specimen from *Pappotherium* and erected a new taxon, *Slaughteria eruptens*, with SMP-SMU 61192 as the holotype. He doubted that any taxon, even a eutherian, would have developed a fully molarized (molariform) premolar by the Early Cretaceous. Because Slaughter (1971: 137) stated that no unerupted teeth were present, Butler (1978) made the reasonable inference that the two molariform teeth represent molars (the m1 and m2). Butler did not comment on which particular loci were represented by the two premolariform teeth, though he would have likely assigned them to the p3 and p4. He placed *Slaugheria* in a new family, the Kermackiidae, which was removed from the extant infraclasses along with the rest of the described tribosphenic taxa from the Trinity Group. These and other, similar taxa have since been relegated to a grey area variably called “therians of eutherian-metatherian grade” (Patterson, 1956), “tribotherians” (Butler, 1978), and “stem boreosphenidans” (Kielan-Jaworowska et al., 2004). It should be noted that the rank Boreosphenida, erected by Luo et al. (2001), is here abandoned for the more familiar term Tribosphenida (as defined by McKenna, 1975). Boreosphenida was established to house Laurasian taxa with tribosphenic molars to the exclusion of the Australosphenida (an enigmatic Gondwanan clade with functionally but not necessarily homologous tribosphenic molars, possibly also including the monotremes). The Boreosphenida do not differ in contents from the Tribosphenida, though the latter is more clearly a node-based clade. Competing hypotheses (e.g., Rich et al., 2002; Woodburne, 2003) dramatically affect the composition of the clades proposed by Luo et al. (2001), so it is preferable to use a name with equal utility but more stability.

A CT scan of SMP-SMU 61192, obtained by Kobayashi et al. (2002), demonstrated the presence of a replacement premolar below the first molariform tooth. This provided definitive evidence that the erupted tooth at this locus is a molariform deciduous premolar instead of a member of the permanent dentition (the p4 following Slaughter, 1971; or the m1 following Butler, 1978). They interpreted the specimen to preserve the p2, p3, dp4 (underlain by a developing p4), and m1. This is essentially the same formula determined by Slaughter (1971), differing only in the identification of a successional premolar developing underneath the first molariform tooth (apparently missed by Slaughter in his x-ray photograph). The last preserved tooth in the jaw was deemed less worn than the dp4 (contra Slaughter, 1971) and no replacement tooth was detected below, so it was identified as the m1.

Interpretation of the morphology preserved in *Slaughteria* has been in flux since its original description. This specimen is significant in that it is one of very few Cretaceous higher mammals for which tooth replacement is observable. Replacement of cheek teeth is somewhat variable among living groups but is believed to be fundamental to the success of mammals as a clade (see the review in Luo et al., 2004). This has a direct impact on our understanding of the early stages of modern mammal evolution, and the events during the Early Cretaceous that would give rise to the huge diversity of mammals by the beginning of the Cenozoic. For this study, I have reinterpreted the original CT data from Kobayashi et al. (2002) and identified additional specimens from the Trinity Group that are referable to *Slaughteria*. Renderings were done in VGStudio Max v.2.1 (Volume Graphics, Heidelberg, Germany).

Institutional Abbreviations—FMNH, Field Museum of Natural History, Chicago, U.S.A.; **OMNH**, Sam Noble Museum, Norman, U.S.A.; **SMP-SMU**, Shuler Museum of Paleontology, Southern Methodist University, Dallas, U.S.A.

SYSTEMATIC PALEONTOLOGY

Subclass Tribosphenida McKenna, 1975

Order and Family INCERTAE SEDIS

SLAUGHTERIA ERUPTENS Butler, 1978

(Figs. 1, 2)

Pappotherium pattersoni Slaugher, 1965: Slaughter, 1971:136, pl. 8, 9 (original description).

Slaughteria eruptens Butler, 1978:12, fig. 12 (established new taxon).

Holotype—SMP-SMU 61192, a left dentary fragment interpreted here to preserve the p2, p3, dp4, and dp5 (Fig. 1A).

Type locality and horizon—Butler Farm (SMP-SMU), upper Antlers Formation (?Albian), north-central Texas, U.S.A.

Referred material—OMNH 63726, a right lower molar (Fig. 1B); OMNH 63721, a fragmentary right lower molar preserving only the talonid (Fig. 1C).

Tentatively referred material—OMNH 63889, a fragmentary right lower molar preserving only the trigonid.

Other locality—Tomato Hill (V706), middle Antlers Formation (Aptian-Albian), southeastern Oklahoma, U.S.A.

Emended diagnosis—Very small tribosphenidan mammal characterized by possession of five lower premolars, strongly molariform dp4 and dp5, and large, trenchant p4; molars differentiated from *Pappotherium* by smaller size, stronger paracristid, and relatively shorter talonid; differentiated from *Holoclemensia* by subequal paraconid and metaconid, and relatively smaller talonid; differentiated from *Kermackia* by subequal paraconid and metaconid, weaker distal metacristid, relatively taller trigonid, and relatively shorter talonid; differentiated from deltatheridiids by subequal paraconid and metaconid, and possession of five premolars; differentiated from *Montanalestes* in relative proportions of paraconid and metaconid (paraconid somewhat larger in *Slaughteria*, though still subequal to metaconid in height), presence of distal metacristid, and lack of precingulid (developed from cusp f in *Montanalestes*).

Description

The holotype of *Slaughteria eruptens*, a left dentary fragment (SMP-SMU 61192), preserves four erupted postcanine teeth, two of which are premolariform and two of which are molariform (Fig. 1A). Based on observations outlined below, I interpret the preserved teeth in SMP-SMU 61192 to represent p2, p3, dp4, and dp5. The specimen also preserves a portion of an additional alveolus for a tooth posterior to those present. The dentary tapers dorsoventrally at a relatively steep angle, suggesting that the preserved teeth were near the front of the jaw. As pointed out by Kobayashi et al. (2002), a mental foramen is present below the anterior alveolus of the dp5 (equals their m1). It is possible that Meckel's groove is present, terminating under the dp4 (there is some crushing of the lingual wall of the dentary, which could instead explain this feature).

The p2 is in the process of erupting, and is still slightly reclined such that the small, simple heel is below the alveolar margin. The crown has a strongly convex anterior margin, with a very slight, almost imperceptible bulge in the position of a basal anterior cusp. It is estimated to be subequal in height to the p3 (prior to apical wear of the latter). The roots of the p2 are subequal, very stout, and originate deep in the dentary (Fig. 2). A thin ridge of bone spans the width of the jaw between the roots.

The p3 is much less convex anteriorly, though apical wear has removed the tip of the main cusp. It shows a similar very slight bulge instead of a distinct anterior basal cusp. The talonid of the p3 is substantially larger than on the p2, resulting in an anteroposteriorly longer crown. There is a very small cuspule labial to and set lower than the principal talonid cusp. The roots of the p3 are subequal and do not extend as deeply into the jaw as do those of the p2. The entire space between the roots is filled with bone, and the absence of a crypt indicates this tooth is part of the adult dentition.

The dp4 is molariform with a fully developed trigonid. The paraconid is small, inclined, and positioned more on the anterior margin of the crown than at the anterolingual corner. This, combined with the broad talonid (as wide as the trigonid), are general features of deciduous premolars (see Cifelli, 1999a). Significant apical wear of the trigonid has removed the apices of the cusps, but the protoconid was by far the tallest cusp, and the crown was approximately as tall as the p3. The metaconid is broad at its base. At the anterior base of the crown, a very small f cusp is developed, but there is no evidence of cusp e (typically present at the anterolingual corner of the paraconid). There is heavy wear on the posterior face of the trigonid. A strong ridge runs down the extreme lingual margin of the crown from the metaconid to the entoconid, and a distal metacristid is discernable (here defined as an oblique crest on the posterior face of the metaconid, but not necessarily reaching the apex of the cusp—a slight reinterpretation of the original definition by Fox, 1975). The talonid is broad and deeply basined and, while substantially lower than the trigonid, had an approximately equal footprint. There is some apical wear on the talonid cusps, but the hypoconid appears to have been the largest, with the entoconid and hypoconulid subequal to each other in size. The three cusps are evenly spaced. The cristid obliqua meets the trigonid below the protocristid notch. The posterior root is larger than the anterior root, which is undergoing resorption (Fig. 2).

The CT data collected from SMP-SMU 61192 by Kobayashi et al. (2002) revealed the presence of a replacement premolar below the dp4 (Fig. 2). The underlying p4 is incompletely calcified, and the talonid is only barely connected to the main part of the crown. The p4 is developing in a lingual position (relative to the dp4) and is oriented obliquely within the crypt. The crown is very tall and trenchant, much taller than any other tooth present in the jaw. The principal cusp is strongly laterally compressed and symmetrical, with a simple but tall single-cusped talonid (Fig. 2). The size of the p4 relative to the other postcanines suggests several different scenarios regarding dental formula in this taxon and identification of the posteriormost preserved tooth in the specimen (see Discussion).

The last preserved tooth in the specimen is interpreted here as the dp5 instead of the m1. The crown resembles the dp4 in general proportions; though the paraconid is set closer to the metaconid (resulting in a more acute trigonid), the cusp is still very low and strongly inclined, and the talonid is as broad as or even slightly broader than the trigonid (Fig. 1A). These features suggest that the tooth is a molariform deciduous premolar instead of a molar. The original heights of the trigonid cusps are impossible to determine due to breakage and wear, but the protoconid was likely the tallest cusp, followed by the relatively broad metaconid. The dp5 differs from the dp4 in the presence of a very faint cusp e and a much larger cusp f, which create an embrasure for the hypoconulid of the preceding tooth. The crown of the dp5 is more worn than the dp4 (in accord with observations by Slaughter, 1971 and contra Kobayashi et al., 2002). The posterior trigonid wall is worn so heavily that the surface has been rendered concave. No evidence remains of a distal metacristid. Though the original height of the trigonid is hard to discern, the talonid appears to have been relatively tall as compared with other early tribosphenic mammals (e.g., *Montanalestes* Cifelli, 1999b). The talonid is also heavily worn; there is substantial apical wear on the hypoconid, and the cristid obliqua has been obliterated. The talonid cusps are more or less evenly spaced. The entoconid is substantially larger than on the dp4 and bears some evidence of wear on the internal face. A wear facet is present on the postcristid. There is a small scar on the posterior face of the hypoconulid indicating embrasure by the e and f cusps of the m1. The posterior root of the dp5 is only slightly larger than the anterior root.

Kobayashi et al. (2002) identified the dp5 as an m1 on the basis of the absence of a replacement tooth, though no bone infill is present below the crown (infill has formed below the p3 and appears to be forming below the p2); they ascribed objects in the bottom of the crypt to fragments of the dentary forced into the space due to breakage. The dentary is indeed broken at the posterior end of the specimen, but the location and morphology of one particular object are inconsistent with a bone fragment. This object is here interpreted as the calcifying tip of the principal cusp of a developing replacement tooth, the p5 (Fig. 2). This tooth was developing lingual to the roots of the dp5, as would be expected, and is triangular in lateral outline. It is isolated in the crypt: it is virtually free from contact with the inner medial surface of the dentary, and maintains only brief contact with the inner labial surface (the developing p4 also has labial contact with the dentary). The thickness of the dentary in coronal section does not change substantially below the dp5, nor does it deviate inward (which would indicate crushing); there is no evidence that the specimen was damaged sufficiently in this region to produce this particular object. The p5 is also separate from smaller objects which are more likely to represent bone fragments from the ventral margin of the dentary. The anterior portion of the p5 is solid and heavy, but it is open posterolabially in transverse section, demonstrating the development of a pulp cavity (Fig. 2A). This semilunate shape is consistent with a developing tooth crown and is difficult to imagine as a stray bone fragment. The tooth looks like it would have been much more blunt than the p4, but very little of the crown is calcified so the final height and morphology is impossible to judge.

OMNH 63726 is a mostly complete right lower molar (missing only portions of the enamel on the talonid) referred to *Slaughteria eruptens*, though the exact locus is unknown (Fig. 1B). The proportions of the trigonid (notably its acuteness and height relative to the talonid) make it unlikely that it represents an m1. Referral is based on crown size and inferred proportions of the talonid, in reference to the collection of therian molars from the Butler Farm (FMNH), Greenwood Canyon (SMP-SMU), and Tomato Hill (OMNH) localities (it is more likely that the specimen represents a previously-described taxon than something new; it does not resemble any other known taxon but agrees with what would be expected for the molars of *Slaughteria*). The protoconid is symmetrical and is the tallest cusp; the paraconid and metaconid are subequal to each other in proportions. The paracristid is strongly developed and notched, to a similar degree as in the deltatheroidans known from the same locality (*Atokatheridium* and

Oklatheridium; see Davis et al., 2008). There is only a very faint bulge in the position of cusp e, and a modest cusp f is developed. The trigonid shows moderate occlusal wear, and a strong distal metacristid is present. The talonid is substantially lower than the trigonid, and the entoconid is the only talonid cusp preserved; this cusp is not as proportionally large as in the dp5, but is somewhat broad. The cristid obliqua meets the trigonid below the protocristid notch. Despite breakage, it appears that the talonid was shorter and narrower than the trigonid.

OMNH 63721 is a broken right lower molar preserving only the talonid (Fig. 1C). It matches in size and proportions to what remains of the talonid on OMNH 63726, though it might be slightly shorter than what is suggested by the breakage on the more complete specimen. OMNH 63721 is shorter than it is wide, and shows significant apical wear on the talonid cusps, which are evenly distributed. The hypoconid was the largest cusp, followed closely by the hypoconulid and lastly by the low but broad entoconid.

OMNH 63889, a broken right lower molar preserving only the trigonid, is tentatively referred to *Slaughteria* based on size and relative proportions of the cusps, though most of the enamel appears to be missing. The paraconid and metaconid are equally developed, but the strong paracristid gives the impression that the paraconid is larger in occlusal view. The trigonid cusps are low overall, suggesting that this specimen may represent the m1. However, the fragmentary nature of the tooth and the absence of most enamel preclude a more confident assignment.

DISCUSSION

Identification of tooth loci in *Slaughteria*

The current study builds on the CT data and observations of the previous work on *Slaughteria* (see Introduction). Personal evaluation of the CT data from Kobayashi et al. (2002) and study of published and unpublished material from the Antlers Formation led to a novel conclusion regarding the identification of the tooth loci represented in SMP-SMU 61192. I follow the interpretation of Slaughter (1971) and Kobayashi et al. (2002) in regarding the first three teeth as p2–4 (with the dp4 underlain by the developing p4), but the last tooth is here identified as the dp5 instead of the m1. The general proportions of the crown, especially the inclination of the trigonid cusps and relative height and width of the talonid, are indicative of a deciduous premolar (Fig. 1A). An open crypt is present underneath the tooth and the calcifying tip of a replacement tooth can be identified within (see Description, above; Fig. 2); if accepted, this confirms the identification of this locus as the p5. This is coupled with the discovery of OMNH 63726, an isolated lower molar that is appropriate for referral to *Slaughteria* on the basis of size and morphology (Fig. 1). This molar is slightly smaller than the dp5, and differs in talonid proportions (see a similar comparison, for example, between molariform deciduous premolars and molars in Lillegraven, 1969: fig. 27.2-3).

Strong support for the identification of the loci preserved in *Slaughteria* is also provided by serial homology. Owen (1868) first suggested homology of the seven cheek teeth of living eutherian and marsupial mammals. McKenna (1975) later proposed that eight is the primitive number of cheek teeth for tribosphenic mammals (with loss of a premolar in eutherians, and loss of a premolar with suppressed replacement of a molariform deciduous premolar in marsupials). These two hypotheses were synthesized by Luckett (1993); he proposed homology specifically of the posterior five cheek teeth of eutherians and metatherians. The fifth position from the posterior end of the dental series is occupied by a large, trenchant premolar (typically the tallest postcanine crown) in most Cretaceous tribosphenidans where the morphology is known (Fig. 3). This corresponds to the p3 in metatherians and the penultimate premolar in eutherians. Outgroup comparison shows the same condition; the penultimate premolar in *Peramus* (the p4) is large and trenchant (illustrated recently by Averianov et al., 2010:fig. 9). In *Slaughteria*, this describes the developing p4 (a large, trenchant premolariform) and implies that it, too, is the penultimate premolar. Identification of this locus as the p4 (instead of the p3) is supported by the nature of the premolar situated two positions forward in the jaw; it is in the process of erupting, leaving considerable doubt that it can represent the p1—though the dp1 is known to be replaced in some Mesozoic taxa, such as dryolestids (Martin, 1997), the condition is unknown in more proximal outgroups and is known not to occur in the vast majority of living tribosphenidans (Ziegler, 1971). Therefore, the best supported conclusion is that SMP-SMU 61192 preserves the p2, p3, dp4, and dp5. The referred lower molar (OMNH 63726) cannot be confidently assigned to locus, so the number of molars in *Slaughteria* remains unknown but was likely three (where known among tribosphenidans, only some eutherians share a premolar count of five). It should be noted that australosphenidans also share five premolars and three molars (Luo et al., 2002); however, the relationships of this clade are highly uncertain, so they are not considered here. Other interpretations of dental formula in *Slaughteria* are rejected as follows:

p2-p3-dp4-m1—The last tooth in SMP-SMU 61192 is more worn than the dp4 (as pointed out in Slaughter, 1971, and contra the observations in Kobayashi et al., 2002; Fig. 1A); both the anterior and posterior faces of the trigonid are heavily worn such that a concave surface is developed posteriorly, obliterating the distal metacristid and the cristid obliqua. A higher degree of wear implies this tooth erupted before the dp4, and as molars do not begin development until the ultimate premolar has nearly begun calcifying (Luckett, 1993), it is more likely this tooth represents the dp5. Additional lines of evidence against this interpretation are outlined above and in the Description section.

p1-p2-dp3-dp4—This interpretation can be rejected on the basis that it is very unlikely that the first preserved premolar represents the p1, as discussed above. This tooth is still erupting, implying it has either been replaced or is extremely delayed in development. While replacement of the dp1 does occur in dryolestids (Martin, 1997), it is not known to occur in any Cretaceous tribosphenidan and occurs only in a handful of Tertiary genera and one Recent genus (Simpson, 1945; Ziegler, 1971).

p1-p2-dp3-m1—Problems with the identification of the fourth tooth as a molar are discussed above, but the serial homology of the trenchant replacement premolar with the p3 of metatherians is attractive (this dental formula would imply *Slaughteria* is a metatherian, or that it represents the only known Cretaceous parallelism for this character). However, the p1 in all metatherians is a very small tooth, much smaller than the p2 (these teeth are subequal in *Slaughteria*; Fig. 1A). The first premolariform in SMP-SMU 61192 is still erupting; it is either a successional tooth (demonstrating replacement at this locus), or a substantially delayed primary tooth. The first two premolars in metatherians are considered the dp1 and dp2 because successors do not develop at these loci (Luckett, 1993), and while the dp1 is the last premolar to develop, the amount of wear present on the other teeth would be consistent only with extremely delayed eruption (unlikely).

Implications for dental formula and tooth replacement in basal Tribosphenida

It has been previously suggested that the possession of five premolars is primitive for tribosphenidans (McKenna, 1975; Novacek, 1986; but see Luckett, 1993), despite the general presence in living marsupial and placental mammals of three and four premolars, respectively. Data from basal taxa are largely equivocal, and complete postcanine dentitions are known in very few instances. Five premolars are present in the basal eutherians *Eomaia* (Ji et al., 2002), and *Prokennalestes* (Sigogneau-Russell et al., 1992) (and possibly also in *Montanalestes* Cifelli, 1999b). Many Late Cretaceous eutherians have four premolars, but it has become clear that this is likely secondary reduction through loss of the p3 locus—five premolars are variably present in some taxa (e.g., *Gypsonictops*, Lillegraven, 1969; *Kennalestes*, Kielan-Jaworowska, 1981), and others such as *Bobolestes*, *Maelestes*, and the zhelestids unequivocally possess five (e.g., Averianov and Archibald, 2005; Wible et al., 2009). Basal metatherians have either four premolars (*Sinodelphys* Luo et al., 2003) or three (*Kokopellia* Cifelli, 1993; deltatheroidans Rougier et al., 1998). The aegialodontid *Kielantherium* is interesting in that it possesses four molars while also showing evidence of at least four premolars, with an additional anterior alveolus preserved for either another premolar or the canine (Dashzeveg and Kielan-Jaworowska, 1984). However, the majority of described Early

Cretaceous tribosphenidans are known only by isolated teeth, providing no data regarding dental formula.

The most appropriate outgroup comparison is with the non-tribosphenic taxon *Peramus* from the Purbeck Group of England. *Peramus* has three molars and five premolars, the ultimate of which is partially molariform (McKenna, 1975). Where known, five premolars are also present in all stem zatherians (sensu McKenna, 1975; Martin, 2002), such as *Amphitherium* (Butler and Clemens, 2001), *Arguimus* (Lopatin and Averianov, 2006), and *Nanolestes* (Martin, 2002). McKenna (1975) proposed serial homology of the large penultimate premolar of *Peramus* (the p4), the p3 of marsupials, and the penultimate premolar of eutherians such as *Kennalestes* and *Zalambdalestes* (the p3) (Fig. 3). Following McKenna's hypothesis, the large, developing p4 of *Slaughteria* is the penultimate premolar, giving it a premolar count of five. *Slaughteria* can be added to a growing number of Early Cretaceous taxa for which five premolars are known, lending more support to five as the primitive count for the Tribosphenida. Loss of one premolar is necessary to derive the typical eutherian count of four, and it is generally accepted that reduction occurred at the third locus (based largely on the premolar at the p3 or pc locus in *Gypsonictops*; Lillegraven, 1969; Clemens, 1973; McKenna, 1975; Fox, 1977). Following the five-premolar hypothesis, the metatherian count of three is also a derived condition, possibly through loss of one anterior premolar locus (see hypothesis of Ziegler, 1971, though direct evidence of loss from transitional taxa is lacking; the diastema between the p1 and p2 in *Sinodelphys* is notable but of unknown significance, Luo et al., 2003, but see differing interpretation in Averianov et al., 2010) and suppression of replacement at the ultimate premolar locus. The last premolar in marsupials becomes developmentally indistinguishable from a molar, and is assimilated into the molar series in terms of both function and terminology (Luckett, 1993; see also Averianov et al., 2010 for discussion of the derived metatherian dental formula, and see Järvinen et al., 2008 for discussion of a possible mechanism for suppression of replacement in the Recent shrew *Sorex*). When considering a primitive premolar count of five, problems with consistent locus numbering arise. Serial homology supports correlation of the large, trenchant premolar (Fig. 3); however, this locus is labeled the p4 in *Peramus*, the p3 in marsupials, and either the p3 or p4 in eutherians (depending on how many premolars are present in the taxon). The application of alternate terms could provide clarification (Clemens, 1973; Cifelli, 2000), but these would need to apply to all taxa (even non-tribosphenic ones) for which homology can be established (attempted recently by Giallombardo et al., 2010).

Diphyodonty of the antemolar dentition is a fundamentally mammalian character (though some early mammals show replacement at molariform loci, see Luo et al., 2004 and references therein). Among living mammals, marsupials are unique in replacement of only the ultimate premolar (but see Archer, 1974), while eutherians replace all antemolar teeth except the first premolar (as discussed above). The sequence of replacement in mammals is variable, proceeding in either direction and sequentially or in an alternating fashion. Replacement in the Trechnotheria (the clade containing spalacotheriid “symmetrodonts”, dryolestoids, and crown therians, sensu McKenna, 1975) proceeds posteriorly in an alternating pattern (Martin, 1997; Luo et al., 2004). This also holds for *Slaughteria*, as established by Kobayashi et al. (2002), though some modification is necessary per the results of this study. A replacement pattern of dp3 – dp2 – dp4 is generally accepted as primitive for trechnotherians with four premolars (Luo et al., 2004).

However, until this study direct evidence of tooth replacement in taxa with five premolars was unknown. Developmental study in living mammals shows that the posterior-most premolar locus is the first to develop, and that the posterior-most molariform premolar is the last locus to be replaced (Luckett, 1993). If we accept that the dp4 in eutherians with four premolars is homologous with the dp5 in *Slaughteria* (supported by serial homology—in both instances this locus follows a large, trenchant premolar in the adult; see Discussion, Figs. 1A, 3), the dp5 would be the last tooth replaced, resulting in a replacement pattern of dp3 – dp2 – dp4 – dp5 for *Slaughteria*. This pattern is unknown in any other mammal, so fossils of other taxa possessing five premolars and preserving a partial juvenile dentition are necessary to validate this hypothesis. This result has obvious implications for the polarity of postcanine tooth replacement at the base of the Tribosphenida.

The suprafamilial relationships of *Slaughteria* are still unclear; eutherians show a general trend toward molarization of the ultimate (and sometimes penultimate) premolar, but the morphology of the p5 in *Slaughteria* is unknown and the developing p4 is premolariform. *Slaughteria* lacks any features consistent with the Metatheria (i.e., dental formula, twinning of the entoconid and hypoconulid, presence of a labial postcingulid), but it cannot confidently be allied with the Eutheria, either (as a dental formula of five premolars and three molars is likely primitive for the Tribosphenida and not alone indicative of eutherian relationships). Either the characters necessary to allocate *Slaughteria* and other early tribosphenidans into one of the major infraclasses remain elusive, or a wide diversity of stem taxa were in existence at the beginning of the Cretaceous, from which the Eutheria and Metatheria would later evolve.

CONCLUSIONS

Reinterpretation of the CT data in Kobayashi et al. (2002) and study of material from the Lower Cretaceous Antlers Formation led to a novel interpretation of the tooth loci represented in the holotype of *Slaughteria eruptens*. The specimen is considered here to preserve four premolars, the p2, p3, dp4, and dp5. A dominant, trenchant p4 is developing in the jaw—locus identification is based on less occlusal wear of the dp4 relative to the dp5 in SMP-SMU 61192, and serial homology across tribosphenidans and earlier zatherian groups. The calcified tip of the p5 is identified in the crypt below the dp5. An isolated, nearly complete lower molar and isolated talonid (OMNH 63726 and 63721, respectively) are referred to *Slaughteria* on the basis of size and morphology, along with tentative referral of an isolated trigonid (which might represent the m1). This taxon cannot be confidently assigned to either the Eutheria or Metatheria based on the known material. *Slaughteria* is one of the few Early Cretaceous tribosphenidans for which any evidence of postcanine tooth formula exists. *Slaughteria* is also interpreted to present a previously unknown pattern of tooth replacement: dp3 – dp2 – dp4 – dp5. The possession of five premolars (and possibly the interpreted pattern of tooth replacement in *Slaughteria*, given its premolar count) is likely a primitive character among the Tribosphenida, though more complete fossils are necessary to shed light on the transition to the derived postcanine dental formulae of living marsupials and eutherians.

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Figure Captions

FIGURE 1. SEM images of the stem tribosphenidan *Slaughteria eruptens* Butler, 1978 from the Antlers Formation (Aptian-Albian) of Oklahoma and Texas, U.S.A. **A**, SMP-SMU 61192 (holotype), a left dentary fragment preserving p2, p3, dp4, and dp5, in lingual (A_1) and occlusal (A_2, stereo pair) views; **B**, OMNH 63726, a right lower molar, in occlusal (B_1, stereo pair), lingual (B_2), anterior (B_3), and posterior (B_4) views; **C**, OMNH 63729, a right lower molar preserving only the talonid, in occlusal view. [stereo pairs; print exact size]

FIGURE 2. 3-D renderings of the holotype (SMP-SMU 61192) of *Slaughteria eruptens* Butler, 1978, from data collected by Kobayashi et al. (2002). **A**, horizontal section of the jaw in dorsal view, showing position and morphology of developing p4 and p5; **B**, sagittal section of the jaw in lingual view, showing developing p4 and p5; **C**, lingual view with bone removed, showing developing p4 and p5. [planned for page width]

FIGURE 3. Illustration of serial homology of the large, trenchant premolar at the fifth tooth position from the back of the tooth row (shaded gray) among lower dentitions of various lineages. **A**, the basal marsupial *Kokopellia* (p3); **B**, the asioryctithere

Kennalestes (p3); **C**, the basal eutherian *Prokennalestes* (p4); **D**, the stem tribosphenidan *Slaughteria* (p4); **E**, the “peramuran” *Peramus* (p4). A, modified from Cifelli, 1993; B, modified from Kielan-Jaworowska, 1969; C–D, original. Not to scale. [planned for column width]

Figure 1

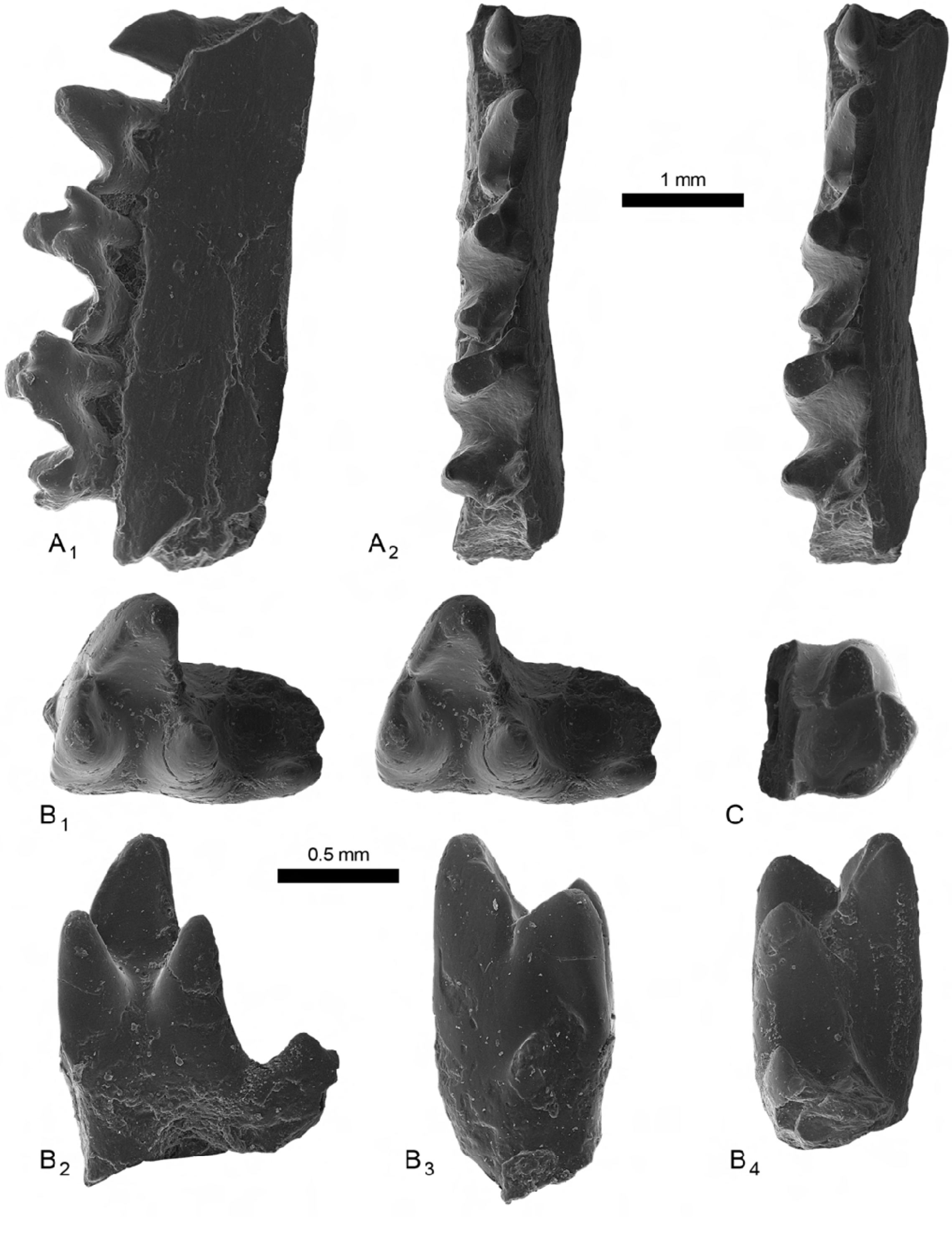


Figure 2

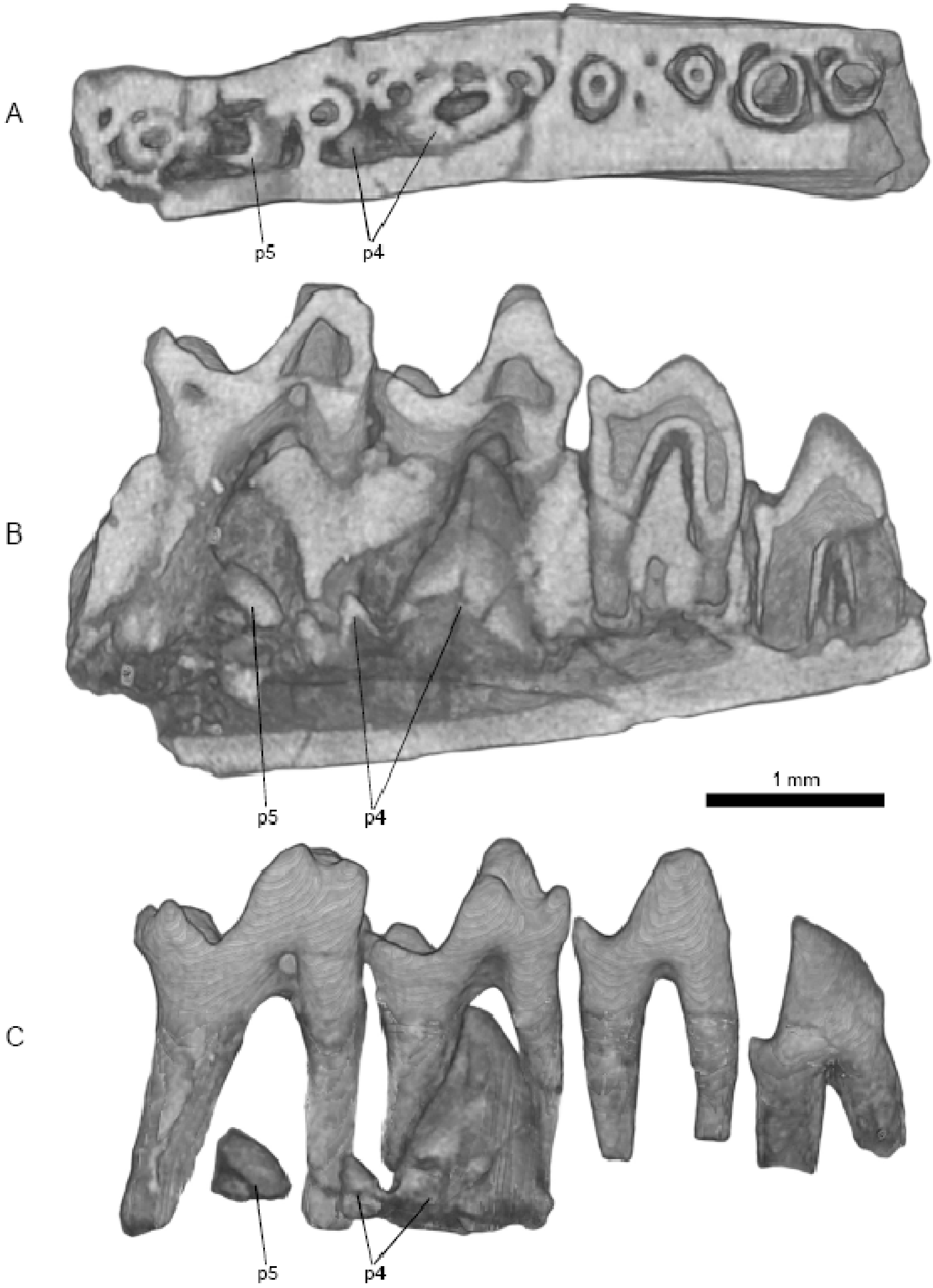
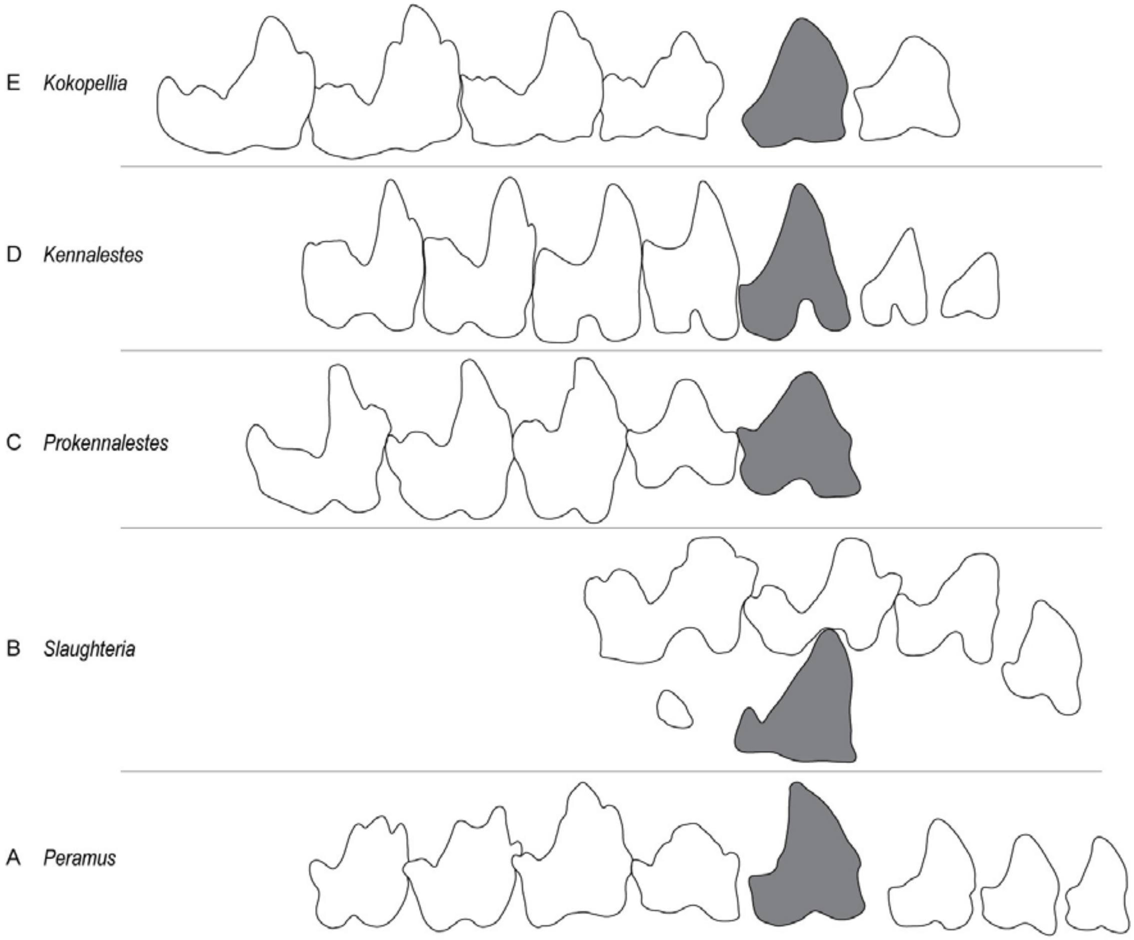


Figure 3


E Kokopellia
D Kennalestes
C Prokennalestes
B Slaughteria
A Peramus

Evolution of the Tribosphenic Molar Pattern in Early Mammals, with Comments on the "Dual-Origin" Hypothesis

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RH: EVOLUTION OF EARLY TRIBOSPHENIC MAMMALS

Abstract

Development of the tribosphenic molar was a fundamental event leading to the rise of modern mammals. This multi-functional complex combined shearing and grinding in a single chewing stroke and provided the raw morphology for the later evolution of the myriad dietary adaptations employed by mammals today. Here I present a series of morphotypes that represent stepwise acquisition of characters that led to the elaboration of the molar crown, and help establish homology of important cusps in pre- and early tribosphenic mammals. This is accomplished by evaluation of wear features that provide direct evidence of occlusal function, and mapping these features on molars of the various morphotypes demonstrates their utility in determining homology. The original singular lower molar talonid cusp is homologous with the hypoconid, and upper molar cusp C in early mammals is homologous with the metacone (cusp "C" is a neomorph with variable occurrence). The lingual translation of the metacone (best demonstrated in *Peramus*) creates an embrasure for the lower molar hypoconid, and is accompanied by the development of the hypoconulid and a new shearing surface. Lastly, the Gondwanan radiation of tribosphenic-like mammals, the Australosphenida (including monotremes) is determined to be functionally non-tribosphenic. The Tribosphenida are otherwise monophyletic, with a Laurasian origin at or just prior to the Jurassic-Cretaceous boundary.

Key words: Mammalia; Tribosphenida; Australosphenida; Mesozoic; molar occlusion, homology

Introduction

Discussion of the evolution of early mammalian dentitions has been ongoing since the discovery of the first Mesozoic mammal nearly 200 years ago (Broderip 1828). Early descriptions allied all fossil taxa with living groups (either the Insectivora or the Marsupialia), even morphologically divergent groups such as the multituberculates (e.g., Owen 1871; Cope 1884; Osborn 1888a; Gregory 1910; separated at the level of subclass by Granger 1915; Simpson 1929). Marsh (1880) gave specific treatment to the majority of then-known Jurassic mammals (dominated by members of the Dryolestidae) through erection of the order Pantotheria (later reorganized into the "Eupantotheria" by Kermack and Mussett 1958). Molars of "eupantotheres" are primitive in many respects, but they are structurally more similar to modern forms than are those of multituberculates or eutriconodontans, and the group would later be placed variably under the Placentalia (Osborn 1907a) and Metatheria (Gregory 1910). It is clear that "eupantotheres" occupy an important position in deciphering the evolutionary history of modern mammalian dentitions (see, for example, Butler 1939).

Attempts at establishing molar homology between "eupantotheres" and known Late Cretaceous and early Cenozoic mammals gained traction in light of better fossils, such as the diverse therian fauna from the Trinity Group of north Texas (Patterson 1956) and the discovery of the upper dentition of the pre-tribosphenic mammal *Peramus* (Clemens and Mills 1971), as well as advances in knowledge of tooth occlusion (Mills 1966; Crompton and Hiiemae 1970; Crompton 1971). But with the advent of cladistic techniques allowing exploration of character evolution across the whole of the Mammalia (e.g., Rowe 1988; Luo et al. 2002), and the discovery of enigmatic taxa from Gondwana (Archer et al. 1985; Flynn et al. 1999; Rich et al. 2001; Rauhut et al. 2002; Rougier et al.

2007), the waters have been muddied and the development of the modern mammalian dentition (as well as the interrelationships of pre- and early tribosphenic groups) is due a reappraisal.

The term “tribosphenic” was coined by Simpson (1936) to replace the awkward monikers developed in the Cope-Osborn theory of trituberculy (e.g., Osborn 1907b). Simpson intended the term to be a functional as well as homologous starting point for all groups of marsupial and placental mammals (historically treated together to the exclusion of the monotremes), but it is becoming clear that monotremes are also derived from taxa with complex cheek teeth resembling those of early crown therians (Archer et al. 1985; Rowe et al. 2008) (to say nothing of other attempts at a similar morphology by groups such as docodonts and shuotheriids). It is therefore worth examining what it means to be “tribosphenic”, and reconcile the available evidence for three scenarios: 1, tribosphenic morphology, as defined by Simpson (1936), evolved once and all mammals with a tribosphenic dentition (therians and monotremes) are monophyletic; 2, the morphology is homoplastic within the crown Mammalia, i.e., acquired independently by the ancestors of monotremes and crown therians; or 3, monotremes and their purported fossil relatives (grouped as the Australosphenida in some phylogenies; Luo et al. 2001) lack the characteristic features of tribospheny and are functionally distinct from other modern mammals. In evaluating these competing hypotheses, it is vital to first establish homology (if possible) between topologically corresponding regions of the molars of the various groups in question. This is crucial to consistent coding of morphology in phylogenetic analyses. Homology cannot be assumed, it must be demonstrated—otherwise, discussion of character evolution may potentially be meaningless.

Conventions

To avoid confusion, the term “tribosphenic” is used herein as a functional instead of phylogenetic concept. Molar terminology follows traditional designations, as illustrated in Kielan-Jaworowska et al. (2004: fig. 11.1). Where cusp homologies are uncertain or debated, the sequential lettering system proposed by Crompton and Jenkins (1968) is used. Wear facets developed by molar occlusion are numbered following Crompton (1971), though the coloring scheme used in the figures of the present paper is different. Definitions of higher taxonomic ranks follow McKenna and Bell (1997) and Kielan-Jaworowska et al. (2004), unless otherwise stated. The term Boreosphenida, erected by Luo et al. (2001) to contain the Laurasian radiation of tribosphenic mammals, is replaced by the older and more familiar term Tribosphenida McKenna, 1975. The terms have equivalent meanings—see recent critiques in Rougier et al. (2007) and Davis (in press).

Morphological Background

Reversed, interlocking, and roughly triangular molars are widely regarded as the precursors to higher mammal dentitions (Fig. 1). The principal cusps support crests which shear past an opposing set during occlusion to mechanically process food. In some lineages, such as dryolestids and spalacotheriids, simple orthal shear was elaborated by very acute triangulation and an increase in the number of molars, effectively elongating the functional area of the tooth row (see reviews of these groups in Kielan-Jaworowska et al. 2004). Other groups improved shearing function through the expansion of portions of the individual molars, specifically in the development of the lower molar talonid. This involved the internal structures of the molars in occlusion, increasing functional area by allowing occluding molars to overlap instead of restricting shear to the anterior and posterior margins of the crown. In modern groups, the lower molar talonid provides a grinding surface for the multifunctional tribosphenic dentition through occlusion with the upper molar protocone (Fig. 1B, D), achieved through the addition of transverse jaw movement during mastication (Crompton and Hiiemae 1970). However, the talonid region of the crown has its origins among stem mammaliaforms and substantially predates the evolution of the protocone. Originally, it provided a stop for the tall central upper molar cusp during occlusion (cusp A of Crompton and Jenkins 1968), and supported some minor shearing (Fig. 1A: cusp d, facet 3). The talonid of stem mammaliaforms such as *Kuehneotherium*, as well as basal trechnotherians (the clade containing the last common ancestor of spalacotheriid “symmetrodonts”, crown Theria, and its descendents; McKenna 1975) has a single small posterior cusp (traditionally referred to as cusp d; Crompton and Jenkins 1968) which serves as the distal terminus of a short shearing crest that is functionally equivalent to if not homologous with the cristid obliqua in therians (Fig. $1A_2$, B_2). Most non-tribosphenic trechnotheres (“symmetrodonts”, dryolestoids, and stem zatherians as defined by Martin 2002) retain this single-cusped talonid, while “peramurans” and some basal tribosphenidans have two cusps. Other stem tribosphenidans, as well as full-fledged metatherians and eutherians (the clades containing marsupials and placentals, respectively), possess three individual talonid cusps distributed around a central basin.

Historically, there have been differing interpretations as to the homology of the talonid structure across early mammals. Following his concept that primitive mammalian molars were of a tritubercular-tuberculosectorial design, Osborn (1888b) coined the term ‘hypoconid’ to identify the singular talonid cusp in early mammals (equals the cusp which persists alone in all forms more plesiomorphic than the “peramuran” *Peramus*), as a correlate of the upper molar hypocone of derived placental mammals. This was later tied to topological and functional comparisons with more derived taxa. Mills (1964) suggested homology between cusp d and the hypoconid based on occlusal relationships of the talonid in *Amphitherium* (from the Bathonian Stonesfield Slate). He interpreted the existence of wear on both faces of the talonid cusp, leading him to infer the presence of a functional metacone on the upper molars of that taxon (Mills 1964: fig. 4). As the posterior face of the hypoconulid typically has no occlusal contact with the upper molar, Mills concluded that the singular talonid cusp in *Amphitherium* must represent the hypoconid. Freeman (1976) followed this interpretation during his description of the contemporaneous and morphologically similar *Palaeoxonodon* from the Bathonian Forest Marble, by identifying an incipient hypoconulid and entoconid on the holotypic lower molar. A number of later authors would continue to support homology of the hypoconid with cusp d (Prothero 1981; Butler 1990; Martin 2002; Lopatin and Averianov 2006a).

Alternately, Gregory (1910) and Simpson (1928) equated the primitive talonid cusp with the entoconid, based on its position at the posterolingual edge of the crown in “symmetrodonts” and dryolestids. This interpretation, however, has since lost support. Lastly, homology of cusp d could lie with the hypoconulid. Cusp d is situated at the posterior end of the crown and directly contacts the succeeding molar, so comparisons with the hypoconulid of derived taxa give support for this conclusion. Butler (1939) was an early advocate of this interpretation, and many subsequent workers agreed (Patterson 1956; Kermack et al. 1968; Crompton 1971; Bown and Kraus 1979; Kielan-Jaworowska et al. 2004; Rougier et al. 2007; and to a lesser extent Simpson 1928).

From the above, two plausible hypotheses can be presented as to the homology of the primitive talonid cusp (Fig. 2). First, cusp d is homologous with the hypoconid. The primitive talonid cusp first appears situated centrally on the posterior crown, and must have migrated labially to its modern position as the talonid elongated in derived taxa. A neomorphic hypoconulid must have later been added posterior and somewhat lingual to the hypoconid (Fig. 2A). Alternately, cusp d is homologous with the hypoconulid. A neomorphic hypoconid was later added along the cristid obliqua as the talonid lengthened, followed by a labial deflection of both the anterior portion of this crest and the hypoconid to achieve a modern configuration (Fig. 2B). In taxa with a complex talonid, the hypoconulid is typically in a central or lingual position and is the posterior-most talonid cusp, serving to interlock the molar with the succeeding tooth. The hypoconid is usually situated on the labial margin of the talonid and serves to anchor the principal shearing crest, the cristid obliqua (equivalent to the posterior shearing crest of stem mammaliaforms such as *Kuehneotherium*; see Fig. 1A_2, B_2). The single-cusped talonid found in plesiomorphic taxa occupies both of these roles.

Upper molar morphology changed to match elaboration of the talonid through a general rearrangement of the internal cusps and shearing surfaces. As compared with a stem mammaliaform morphotype such as that represented by *Kuehneotherium*, the elongated cristid obliqua in lower molars of amphitheriids is coupled with an increase in the functional area on the posterior face of the paracone (facet 3; Fig. 3A, B). Aside from the development of the unquestionably neomorphic protocone and the accompanying lingual expansion of the crown, the most significant difference between pre-tribosphenic and tribosphenic upper molars concerns the position of the metacone. Among advanced forms, the metacone is situated immediately posterior to the paracone and the two cusps are more or less subequal (Fig. $1B_1$). The morphology of the basal tribosphenidan *Kielantherium* suggests that the metacone was likely relatively much smaller in primitive taxa (see Lopatin and Averianov 2006b: fig. 1C), which leads to two competing hypotheses: either the metacone is a neomorph (originally suggested by Gregory and Simpson 1926 and furthered by Crompton 1971), or homology can be established with one of the existing cusps in early pre-tribosphenic taxa (as suggested by Butler 1939; Hopson 1997). Upper and lower molar morphology must have evolved in synchrony as a functional complex, so the exploration of character evolution and homologies of cusp d and the metacone will be discussed together. Consequently, the major lineages of pre- and basal tribosphenic mammals will be represented in this paper by taxa known by both upper and lower molars, presented as a progressive series of morphotypes without implication of actual ancestry. Support will be drawn not only from cusp and crest topology and configuration, but also from wear facets left as direct evidence of occlusal relationships. The australosphenidans, currently known by lower dentition alone (except for derived Cenozoic taxa), will be treated separately at the end.

Kuehneotherium *as structurally ancestral*

A case can be made that *Kuehneotherium* represents a good primitive morphotype to serve as a starting point for a discussion of tribosphenic molar evolution. It is known from very old rocks—isolated teeth and dentary fragments have been recovered from British fissure fills dated to the Late Triassic-Early Jurassic (Kermack et al. 1968; Fraser et al. 1985). It is derived relative to stem mammaliaforms with a “triconodont” molar configuration (i.e., three principal cusps arranged in a row, such as *Morganucodon*) in that its molars exhibit an obtuse-angled triangulation, but plesiomorphic relative to all trechnotheres in this same character. *Kuehneotherium* also possesses a relatively large and distinct cusp d, situated near the midline of the crown (Fig. $1A_2$). Other obtuse-angled “symmetrodonts”, such as *Tinodon* from the Late Jurassic of the USA and Early Cretaceous of Britain (includes *Eurylambda*, Prothero 1981), are possibly derived in the reduction of cusp d and the morphology of the anterior portion of the upper molar (but see Rougier et al. 2003 for an argument to the contrary).

A thorough description of the molars of *Kuehneotherium* can be found elsewhere (e.g., Kermack et al. 1968), so it will not be repeated here. However, it is useful to briefly cover features that are necessary for a discussion of homology. As noted above, *Kuehneotherium* possesses molars which are weakly triangulated. A broad wear facet occupies the entire anterior surface of the upper molar (facet 1 of Crompton 1971; Fig. $1A_1$). Facet 2 extends from the metastylar corner to the posterior face of cusp C (= metacone, as originally proposed by Kermack et al. 1968; see discussion in next section on homology of this cusp). Lower molars have a similar occlusal outline, but with a distinct but low cusp d situated posteriorly at the mid-point of the crown. This cusp had some role in molar interlocking, as well as providing a stop for cusp A (paracone) during occlusion, resulting in a small amount of shear as indicated by the presence of facet 3 (Fig. 1A). The apex of cusp d is connected to the base of cusp c (metaconid) by a weak, short crest which is topologically and functionally equivalent to the cristid obliqua in later taxa, as it is also associated with facet 3.

Elongation of the talonid: the Amphitheriidae

Some major lineages of Jurassic and Early Cretaceous mammals, such as the Dryolestidae and Spalacotheriidae, reduced emphasis on the role of the talonid and instead emphasized the primitive shearing portion of the crown (the trigon and trigonid). Acute triangulation of the molars provided room in the jaw to increase the number of molars, resulting in a continuous shearing surface that is functionally similar to pinking shears. Stem members of the Zatheria, on the other hand, experienced elongation of the talonid. *Amphitherium*, from the Middle Jurassic Stonesfield Slate of England, was included as a stem zatherian in a monotypic Amphitheriidae by Martin (2002). It is unfortunately only represented by several dentaries (Mills 1964; Butler and Clemens 2001), so details of the upper dentition are unknown. As it is important to consider upper and lower molar morphology together as a functional complex, a taxon other than *Amphitherium* is more useful.

Palaeoxonodon, from the Forest Marble of England (also Middle Jurassic), is known by a large number of isolated upper and lower molars (Freeman 1976; Sigogneau-Russell 2003). Its affinities are somewhat contentious; the variable presence of a cuspule along the cristid obliqua and an “incipient basin” on the talonid of some specimens of

Palaeoxonodon was used to loosely ally this taxon with *Peramus* in the “Peramura”, to the exclusion of *Amphitherium* (Freeman 1976, 1979; maintained in Kielan-Jaworowska et al. 2004). However, *Palaeoxonodon* possesses a single principal talonid cusp (plesiomorphy) and upper molars that are generally primitive relative to *Peramus*, in that the metacone is labially positioned (no embrasure for the hypoconid) and a lingual cingulum is lacking (Fig. 3). In terms of lower molar morphology, at least, it is of the same structural grade as *Amphitherium*. I tentatively follow Sigogneau-Russell (2003) in placing *Palaeoxonodon* within the Amphitheriidae as a stem zatherian instead of allying it with *Peramus*, which is clearly derived in upper and lower molar morphology (see next section). Therefore, *Palaeoxonodon* will be used to represent the amphitheriid morphotype in this discussion.

The talonid of *Palaeoxonodon* is long and crescentic relative to that seen in *Kuehneotherium* or dryolestids, arcing labially to a single cusp situated posterior to the protoconid. This cusp is positioned labial to and in-line with the protoconid, and it denotes the posterior margin of wear facet 3, which occupies the anterolabial face of the cristid obliqua (Fig. 3B_2). The single talonid cusp in amphitheriids is therefore both topologically and functionally equivalent to the hypoconid of tribosphenic taxa, and should be considered homologous (as outlined in the scenario illustrated in Fig. 2A). The upper molar paracone shears anteriorly against the distal metacristid and the protocristid, and posteriorly against the elongate cristid obliqua; consequently, facet 3 on the upper molar is broad relative to that in *Kuehneotherium* (apomorphy)(Fig. 3A_1, B_1). There is no upper molar embrasure for the hypoconid (see next section) and no additional wear features are developed at this morphological stage, as amphitheriid upper molars do not differ markedly from those of dryolestids. It should be noted that Mills (1964) described the presence of a minute facet 4 on the lower molars of *Amphitherium*, but there is no mention of the facet by Butler and Clemens (2001) and personal observations failed to identify it (it is possible it has been obscured by additional preparation). Though there is evidence for an increase in the number of molars from *Kuehneotherium* to *Amphitherium* (Butler and Clemens 2001), it is clear that amphitheriids achieved improved shearing through changes in the molar crown itself, instead of by solely elongating the molar row (as demonstrated by the overlap between adjacent molars; see Mills 1964).

Homology of the posterior upper molar cusps of early mammals has traditionally been contentious, but the morphology and wear features in *Palaeoxonodon* (and subsequently *Peramus*; see next section) provide key evidence. As previously noted in *Kuehneotherium*, wear facet 2 extends from the metastylar corner of the crown to the large posterior cusp (traditionally labeled cusp C, but called the metacone by Kermack et al. 1968; Fig. $3A_1$). In more derived taxa (e.g., dryolestids, stem zatherians, some tribosphenidans), there is at least one additional cusp present along the posterior margin of the tooth, labial to the cusp typically labeled the metacone (Fig. $3B_1$, C_1). Crompton (1971) proposed that this cusp may be homologous with cusp C in basal mammals, and that the metacone is a neomorph. He tentatively labeled this cusp “c” (replaced with “C” for consistency by Kielan-Jaworowska et al. 2004: 350–351). In *Palaeoxonodon,* facet 2 extends from the metastylar corner to the posterior face of the metacone, lingual to cusp “C” (Fig. $3B_1$). In fact, in all relevant taxa (*Kuehneotherium* and all trechnotheres) facet 2 always extends to the lingual-most cusp on the posterior upper molar crest (cusp C in *Kuehneotherium* and the metacone in all derived taxa), implying that this specific cusp maintains a consistent occlusal relationship with the lower molar (postvallum/prevallid shear). It follows that the metacone is homologous with cusp C, and that the labial cusp labeled cusp “c” (or “C”) is a neomorph with variable occurrence (see *Nanolestes* for an extreme example; Martin 2002).

The “peramuran” stage

The general trend towards tribospheny involves (1) an increase in the length of shearing surfaces through added complexity of the molar crown; and (2) addition of crushing/grinding function through opposition between a neomorphic lingual upper molar cusp, the protocone, and a lingually-expanded basin on the talonid of lower molars. The primitive reversed-triangle design, perpetuated by spalacotheriids and dryolestids, was modified in amphitheriids through elongation of the cristid obliqua and resulting expansion of shearing surface 3 (Fig. 3). This increased occlusal overlap and began to take advantage of crests within the crown instead of relying solely on the embrasure shear afforded by the principal crests at the anterior and posterior margins. The next level of complexity involved the repositioning and elaboration of structures inside the occlusal outline of the molar crown to accommodate a new cusp and shearing surface, allowing more functional area to fit within a given space.

This transition is best exhibited by *Peramus* from the Early Cretaceous (Berriasian) Purbeck Group of England. The lower molar talonid has at least two cusps, which are easily correlated with cusps of fully tribosphenic taxa—a hypoconid placed labially behind the protoconid, and a hypoconulid set posterolingually at the midpoint of the talonid. Wear facet 3 occupies the same area as in the Amphitheriidae, but an additional facet, set at approximately a right angle, faces posterolabially between the two talonid cusps along the hypocristid (facet 4). Thus, the shearing surfaces of the lower molar run in alternating directions (Fig. 3D). This can only be accomplished by the presence of an upper molar embrasure for the hypoconid, created by a new inflected shearing surface. The upper dentition of *Peramus*, described by Clemens and Mills (1971), includes molars with a well-developed, individualized, and lingually-placed metacone (Fig. 3C_1). The shift in position of this cusp (from a posterolabial position in *Palaeoxonodon*) allows the hypoconid to fit between the paracone and metacone at the end of occlusion, with facet 3 forming in the same manner as in earlier taxa. The anterior face of the metacone developed a special role in occlusion by shearing against the new surface on the posterior face of the hypoconid, creating facet 4. Migration of the metacone to a functional position directly posterior to the paracone logically must be coupled with the appearance of a new wear feature on the opposing lower molar, specifically by the addition of a second talonid cusp (the hypoconulid) to support facet 4 (proposed also by Clemens and Mills 1971: 103–104).

Facet 2 on the upper molars of *Peramus* agrees well with that of *Palaeoxonodon* in that it extends from the apex of the metacone to the metastylar corner of the crown, as is also the case in tribosphenic taxa. There are no known taxa with a cusp in the position of the metacone that does not participate in facet 2; this consistent correlation strongly suggests that cusp C of *Kuehneotherium* is homologous with the metacone of derived taxa.

Another notable feature of the upper molars of *Peramus* is the presence of a lingual cingulum (Fig. 3C_1). It does not appear to have been involved in occlusion, and it is incomplete anteriorly and posteriorly. A similar and often stronger structure is present in tinodontid and zhangheotheriid “symmetrodonts”, and it provides a good example of a precursor to a protocone in a pre-tribosphenic mammal. However, there is no functional protocone or protocone-like structure in *Peramus*. Grinding function requires that the talonid must be both lingually expanded and basined, as the anterior surface of the protocone wears against the talonid posterior to the base of the metaconid and lingual to the distal metacristid, creating facet 5 (see next section). This area in *Peramus* is undeveloped, though some specimens do possess a small cuspule corresponding in position to the entoconid. However, the talonid is not basined and a functional protocone is lacking, so the variable presence of this cuspule would likely not have affected occlusion in *Peramus*, and mechanical processing would still have been limited to puncturing and shearing. Structures in this region of the talonid (e.g., the variable presence of an entoconid in *Peramus*, or the variable presence of a lingual rim in *Palaeoxonodon*) may have functioned in a similar manner to the upper molar stylar cusps of later tribosphenidans—they served to provide apical puncturing, or to redirect food back on to the occlusal surface of the molars (as postulated in Crompton 1971).

The major differences between the upper molar morphotypes characterized by *Peramus* and that of the amphitheriids center on the topology of internal molar crown structures. Development of the metacone as a strongly individualized cusp and its translation to a position that is directly posterior to the paracone allows for an embrasure for the hypoconid and creation of the centrocrista (composed of the postparacrista, which bears facet 3, and premetacrista, which bears a new wear feature, facet 4; Fig. 3C$_1$). The shearing surfaces of upper and lower molars are “W” shaped in *Peramus*, through elaboration of internal crests. Placed in the framework outlined above, *Peramus* clearly represents a specific morphotype and demonstrates that individualization and lingual shift of the metacone are directly related to the development of facet 4 on a two-cusped talonid (specifically the presence of the hypoconulid).

Early tribosphenidans: the aegialodontid stage

Molars of stem zatherians and "peramurans" lack a basined talonid and a functional protocone—the hallmark features of tribosphenic mammals—indicating that occlusal function in these taxa was limited to shearing. The earliest tribosphenic taxon, *Tribactonodon*, also from the Berriasian part of the Purbeck Group, England (Sigogneau-Russell et al. 2001), has three well-developed cusps enclosing a well-basined talonid, suggesting the presence of a functional protocone (there are older mammals with tribosphenic-like dentitions—the Australosphenida—but these will be treated separately below). Unfortunately, only a single lower molar is known and it is preserved almost free of wear, making direct interpretation of upper molar morphology impossible. *Aegialodon*, also regarded as fully-tribosphenic, is known from the slightly younger (Valanginian) Wadhurst Formation, but it is also represented by a single lower molar (though much more poorly preserved, Kermack et al. 1965). Though the talonid in *Aegialodon* is relatively much smaller than in *Tribactonodon*, it does provide some evidence of a functional protocone through the presence of wear facet 5 (Fig. 4B). This facet is produced by the anterior slope of the protocone as it occludes on the lingual side of the distal metacristid and finally in the anterior portion of the talonid basin at the end of the chewing stroke.

A number of dentally advanced mammals appeared across Laurasia by the end of the Early Cretaceous: from the Barremian Jehol biota of China, the eutherians *Eomaia* and *Acristatherium* (Ji et al. 2002; Hu et al. 2010) and the purported metatherian *Sinodelphys* (Luo et al. 2003); the eutherians *Montanalestes* from the Cloverly Formation of Montana (Cifelli 1999), and *Prokennalestes* from the Höövör Beds of Mongolia (Kielan-Jaworowska and Dashzeveg 1989), and the diverse fauna from the Trinity Group of northern Texas (Patterson 1956; Slaughter 1971). However, some primitive tribosphenic mammals remained. Of great significance is the aegialodontid *Kielantherium* from the Höövör Beds (Dashzeveg 1975; Dashzeveg and Kielan-Jaworowska 1984), known by three dentulous jaw fragments and an upper molar. The upper molar of this taxon was only recently described (Lopatin and Averianov 2006b, 2007), and it is widely regarded to represent the most plesiomorphic tribosphenidan known (due primarily to protocone structure, see below). *Kielantherium* has been considered synonymous with the considerably older *Aegialodon* (Fox 1976), so it is no surprise that the upper molar is also primitive. Interestingly, it is a very close match to the predicted morphology of Crompton's (1971: fig. 4A) upper molar reconstruction for *Aegialodon*.

Kielantherium has only two talonid cusps, which is plesiomorphic relative to a number of other contemporaneous or even sympatric mammals (such as *Holoclemensia* and *Pappotherium* from the Trinity Group of Texas; and *Prokennalestes*, which, like *Kielantherium*, is from the Höövör Beds of Mongolia). It is parsimonious to assume that *Kielantherium* retained rather than reverted to this primitive morphotype, despite its relatively young age. The hypoconid and hypoconulid are situated close to one another, matching the narrow upper molar embrasure between the closely appressed paracone and metacone (Fig. 4C). While facets 3 and 4 on the lower molar are not much larger than in *Peramus*, widening of the talonid made the talonid angle more acute (defined as the angle between these two shearing surfaces, with the hypoconid at the apex), allowing for a wider draw against the upper molar during occlusion. The protocone is small and low, matching the basined but poorly expanded talonid. Facet 5 is present but small on both the talonid and protocone, providing direct evidence of occlusion and demonstrating what molars of the earliest tribosphenidans may have looked like (Fig. 4C). The posterolingual portion of the talonid does bear a low crest, but there is no evidence of wear to indicate that it fully enclosed the protocone during occlusion, nor that it contacted the posterior face of the protocone. There is, however, wear in the bottom of the talonid basin from contact with the apex of the protocone, continuous with facet 5.

The upper molar of *Kielantherium* closely resembles those of *Peramus* in general outline and proportions, with the obvious addition of a protocone (Fig. $4A_1$, C_1). The first tribosphenidan could have achieved tribospheny through expansion of the lingual cingulum from the condition in *Peramus*, coupled with the development of a cingular cusp to take advantage of and extend the occlusal contact between the anterolingual portion of the upper molar and the posterolingual slope of the lower molar trigonid (facet 5). While no fossils with transitional morphologies are known, the record from the earliest Cretaceous is still very poor. However, *Peramus* fits very well into the morphotypic progression from pre-tribosphenic to fully tribosphenic dentitions.

If upper molars of transitional forms are discovered, it would not be surprising to see some kind of well-developed lingual cingulum bearing one to several substantial cingular cusps. Some amount of lingual expansion of the talonid is seen in stem zatherians and *Peramus*; mechanical support for increased occlusal function in this portion of the lower molar almost necessitates an increase in the size of the posterior root and, in tandem, the area of the crown above it (compare Fig. $3B_2$ and C_2). A lingual talonid shelf, cusps, or crests, as previously discussed, could have functioned like a stylar shelf. Until the expansion of the lingual opposing portions of upper and lower molars had proceeded enough to permit tribosphenic occlusion, a similar set of structures would need to persist in the protoconal region of the upper molar. A protocone-like structure set on a lingual shelf would also function in the same manner as the stylar region on the labial side of the crown, until it and the talonid were large enough to occlude directly.

Advanced Cretaceous tribosphenidans have three principal talonid cusps surrounding a basin. The lingual-most of these, the entoconid, provides a surface for occlusion with the posterior slope of the protocone (or the postprotocrista), as indicated by the presence of facet 6 (Fig. 1B). The entoconid may have also helped close the lingual margin of the talonid basin, keeping food in place during the final stage of occlusion in that region of the crown. This relationship is very important in that it greatly increases the area of the crown involved in grinding or crushing, which was crucial to the later development of durophagy, frugivory, and herbivory in mammals.

While no pre-tribosphenic taxon possesses an entoconid (an incipient cusp is present in the position of the entoconid in some specimens of *Peramus*), the oldest known tribosphenidans do have it, including the earliest recognized members of the Eutheria and Metatheria, *Eomaia* and *Sinodelphys* (respectively), both from the Barremian of China (Ji et al. 2002; Luo et al. 2003). It is unclear why a plesiomorphic two-cusped talonid persists in stem taxa such as *Kielantherium* and *Trinititherium* (Early Cretaceous Trinity Group of Texas) while other early, wide-ranging tribosphenidans have an entoconid. Even the Deltatheroida, which have been placed within the Metatheria in some analyses (i.e., Rougier et al. 2004; Luo et al. 2007), are variable in their expression of this cusp (though perhaps in this case, specialization towards carnivory (Marshall and Kielan-Jaworowska 1992) may have had a role in downplaying the grinding portion of the crown—the oldest deltatheroidans have molars which emphasize shearing at the expense of a simplified talonid; Davis et al. 2008). It is possible that earlier yet undiscovered tribosphenidans lacked an entoconid. Presuming all entoconids are homologous among tribosphenidans (and no evidence to the contrary has been presented), the presence of this feature would provide support for a clade containing the Metatheria and Eutheria as well as stem taxa possessing three talonid cusps, to the exclusion of two-cusped stem taxa (possibly including the Deltatheroida). However, evaluation of this using cladistic methodology is beyond the scope of this paper.

The "dual-origin" of tribosphenic mammals

As discussed above, the definition of "tribosphenic" was originally meant to be both a functional construct and imply homologous morphology (Simpson 1936). At the time, it was generally held that known tribosphenic mammals (marsupials and placentals) had a common origin from somewhere among the Jurassic "eupantotheres". Subsequent discoveries have brought to light taxa which challenge the notion of a monophyletic Tribosphenida (sensu McKenna 1975), as will be discussed below. These imply that "tribosphenic" might better describe a structural grade, as done by Luo et al. (2001).

However, it is first important to note some other lineages which appear to have converged on a dentition that is somewhat functionally equivalent to, though clearly not homologous with, the tribosphenic molar. This serves to demonstrate the complex, often homoplastic nature of mammalian dental evolution and to underscore the need for caution in discriminating between structural homology and functional analogy.

Exercises in pseudotribosphenic molars: the Docodonta and Shuotheriidae

Docodonts are known from the Middle Jurassic through Early Cretaceous, with a Laurasian distribution (for a good review, see Ch. 5 of Kielan-Jaworowska et al. 2004). They are skeletally primitive mammaliaforms (Krusat 1991), but their molars are derived and highly divergent from those of other basal taxa. Docodont upper molars are quadrate or figure-eight shaped, with a large lingual cusp which occluded in a basin formed mainly by an anterior expansion of the lower molars (Fig. 5A). This cusp-on-basin occlusion provides a grinding function, giving docodonts dual-purpose molars. However, their phylogenetic placement is generally near the base of mammals (e.g., Luo et al. 2007).

The molars of docodonts are morphologically very distinctive but functionally similar to those of tribosphenic mammals; a more striking example of functional convergence can, however, be found in the pseudotribosphenic molars of the shuotheriids from the Middle to Late Jurassic. *Shuotherium* is known by a partial dentary from China and several isolated teeth from Britain (Chow and Rich 1982; Sigogneau-Russell 1998; Wang et al. 1998). The original specimen preserved lower molars in situ, so it was clear that the taller, three-cusped trigonid was positioned posterior to a lower, basined structure—the reverse of the condition in otherwise topologically similar tribosphenic molars (Fig. 5B_2). Upper molars referred to *Shuotherium* are remarkably similar to those of geologically younger tribosphenic taxa; they were reconstructed by Chow and Rich (1982) based on the presence of nearly all the corresponding tribosphenic wear facets (sensu Crompton 1971), with the morphology corroborated by the discovery of isolated upper molars referred to *Shuotherium* by Sigogneau-Russell (1998) and Wang et al. (1998) (Fig. 5B_1). The lingual upper molar cusp and anterior lower molar basin were termed the "pseudoprotocone" and "pseudotalonid basin" to highlight their functional but not homologous relationship to these structures in tribosphenic mammals.

The true occlusal relationship between upper and lower molars in shuotheriids was confirmed recently by the discovery of the nearly complete skeleton of *Pseudotribos robustus* from the Middle Jurassic Jiulongshan Formation of China (Luo et al. 2007). This taxon has very similar pseudotribosphenic molars, preserved in occlusion. Primitive features of the shoulder girdle and postdentary region support a basal position of shuotheriids among mammaliaforms, removing them from the ancestry of tribosphenic lineages. Viewed along with the phylogenetic placement and molar morphology of the docodonts, this illustrates that mammals independently arrived at solutions to dual-function molars several times (at least in docodonts, shuotheriids, and tribosphenidans). However, there remains an additional clade with uncertain relationships, the discovery of which led to the proposal of a "dual-origin" of tribosphenic mammals (Luo et al. 2001)—the Australosphenida.

The Australosphenida

In 1985, Archer et al. described the first Mesozoic mammal from Australia, the ornithorhynchid *Steropodon* from the Early Cretaceous Lightning Ridge locality. What was most surprising about this taxon was that the molars of *Steropodon* are highly derived and already resemble the late Oligocene platypus *Obdurodon*, also from Australia (Woodburne and Tedford 1975). Several additional taxa were later recovered from Early Cretaceous rocks in Australia (Flannery et al. 1995; Rich et al. 1997, 1999; Rich et al. 2001), indicating a diverse and unique fauna. Of these, *Kollikodon* and *Teinolophos* have also been allied with the Monotremata (the latter having been formally placed within the Ornithorhynchidae by Rowe et al. 2008). The other known taxa, *Ausktribosphenos* and *Bishops* (united in the Ausktribosphenidae by Rich et al. 1997), superficially resemble in basic morphotype tribosphenic taxa from Laurasian faunas (Fig. 6). They exhibit well developed, basined, and multicusped talonids complete with wear features, and were initially described as primitive placental mammals based primarily on molar count and molarization of the ultimate premolar (Rich et al. 1997; Rich et al. 1998; Rich et al. 2001). The Eutheria were otherwise restricted to northern landmasses until the Maastrichtian.

The discovery of an even older mammal with functionally tribosphenic molars was reported by Flynn et al. (1999) from the Middle Jurassic of Madagascar. *Ambondro* is known by a single dentary fragment preserving three teeth, presumably the ultimate premolar and first two molars (Fig. 7A). It was assigned to the Tribosphenida based on the presence of wear facets in the well-developed talonid that correspond to facets 5 and 6 of Crompton (1971), indicating occlusion by a functional protocone. *Ambondro* was allied to basal tribosphenidans such as *Aegialodon* and *Potamotelses* due to the presence of a strong distal metacristid (not present in ausktribosphenids). This taxon, along with those from the Early Cretaceous of Australia, was proposed as evidence of a Gondwanan origin of tribosphenic mammals, the reverse of the conventional wisdom of the previous century. However, the relatively advanced dentition of ausktribosphenids is juxtaposed with a dentary featuring some very primitive characters, such as the retention of a postdentary trough (unknown in *Ambondro*). This led Kielan-Jaworowska et al. (1998) to question the placental nature of these taxa. These authors, upon parsimony analysis of a large data set, proposed that these taxa (including *Ambondro*) represent a separate Gondwanan radiation which independently acquired a tribosphenic dentition, and erected the Australosphenida to house them plus the monotremes (Luo et al. 2001). Others (e.g., Martin and Rauhut 2005) have also raised questions as to whether the wear in the australosphendian talonid is consistent with the presence of a functional protocone, the absence of which implies that the Australosphenida are not actually tribosphenic (using the term in a strictly functional sense).

The discovery of additional Gondwanan taxa from the Middle Jurassic would fuel the debate about high-level relationships among Mesozoic mammals. The Cañadón Asfalto Formation of Argentina has yielded *Asfaltomylos patagonicus* (Rauhut et al. 2002) and *Henosferus molus* (Rougier et al. 2007; united in the Henosferidae). Henosferids have a complex, basined talonid (Fig. 7), but retain a postdentary trough (unknown in *Ambondro*, which, along with the Henosferidae, represents the basal radiation of the Australosphenida; Rougier et al. 2007). These dentally advanced taxa predate similar forms from Laurasia by at least 20 Ma, raising serious questions about the origin of the tribosphenic molar and modern mammals. Unfortunately, evaluation is hampered by the lack of known upper dentitions for these taxa, so conclusions can only be conjectures.

Australosphenidans with derived molars appear suddenly in the Middle Jurassic, with a wide temporal and morphological gap between them and later tribosphenidans (for example, all australosphenidans have large talonids with highly variable cusp and crest distributions, unlike the earliest tribosphenidans, which invariably have a small, low talonid with two or three predictable cusps). This makes it difficult to resolve topological homology between the two groups, which can lead to inconsistencies when scoring molar morphology in a phylogenetic analysis. There are likely some significant functional differences in talonid occlusion, as indicated by differing wear patterns, and homology cannot be simply assumed for any talonid cusps. Hunter (2004), for example, suggested that only the lingual portion of the talonid in *Ausktribosphenos* is homologous with other therians, the labial cusps and crests having been derived from a cingulid (the cusp or cusps in the position of the entoconid in *Ausktribosphenos* is actually homologous with the hypoconid, citing a similar structure in a specimen referred to the stem zatherian *Nanolestes*). Wear facets were also reinterpreted, with facet 5 combined with facet 1, and facet 6 explained as an expanded facet 3, thus rendering the taxon non-tribosphenic.

Martin and Rauhut (2005) proposed the absence of a functional protocone among the Australosphenida based on the apparent lack of wear within the talonid basin. All wear is instead restricted to the apices of the talonid cusps. It is possible, therefore, that the talonid cusps evolved to occlude directly against cusps or lophs on the upper molar during the transverse portion of the chewing stroke (Martin and Rauhut 2005: fig. 5).

In their description of *Henosferus* from the Middle Jurassic of Argentina, Rougier et al. (2007) generally agree that australosphenidans did not posses tribosphenic molars. They proposed a new scheme for interpreting the molar morphology of the group, in light of what they considered ill-advised attempts at establishing homology based solely on topology or even function, instead relying on the phylogenetic position of the group and features of sister taxa (Rougier et al. 2007: figs. 6B, 9). The anterior wrapping cingulid, used by Luo et al. (2001) to unite australosphenidans (and also monotremes), can be explained as a retained cingulid from a "symmetrodont" origin, which also accounts for the majority of the morphology of the talonid (Rougier et al. 2007: 25, in agreement with Hunter 2004). The talonid in australosphenidans had no occlusal function and lacks any internal wear, similar to (and possibly homologous with) the lower molar cingulids in "symmetrodont" taxa such as *Tinodon* and zhangheotheriids. Using shuotheriids and *Vincelestes* as examples, they feel it is likely that australosphenidans possessed some sort of protocone-like structure on the upper molars, but that it had limited to no occlusal relationship with the lower molars.

I have made personal observations of original material and casts of all non-monotreme australosphenidan taxa except for *Asfaltomylos,* and there is some evidence to support limited occlusal contact by a lingual upper molar structure in some members of this group. Below I describe the wear features of each taxon:

Ausktribosphenos (Fig. 6B)—The molars of this taxon are poorly preserved, and enamel is missing from some important regions of the crown in the holotype. Wear facets 1 and 2 are generally present where observable, but evidence for facet 3 is largely lacking; the cristid obliqua and the anterolabial surface of the hypoconid are slightly convex, a condition not expected given the high degree of wear elsewhere on the teeth (this surface should be worn flat to concave by the action of the posterior surface of the upper molar paracone). The hypoconid is apically worn to a flat surface even with the basin of the talonid. There is no evidence of facet 4 on the posterior surface of the hypoconid. A distal metacristid is absent from the posterior face of the trigonid, and there is no clear lingual demarcation of facet 1; therefore, no clear evidence for facet 5 is present. There is some wear on the inner (labial) surfaces of the cusps situated on the lingual margin of the talonid, but this is most likely due to a transfer of apical wear after the obliteration of the hypoconid. There is no other evidence of wear within the talonid.

Bishops (Fig. 6A)—Most molars assigned to *Bishops* are either unworn or wear is undetectable due to preservation or preparation. Due to very similar molar morphology, it is likely that wear progressed as in *Ausktribosphenos*. The only difference is due to talonid structure; the lingual margin of the talonid in *Bishops* is formed by a heavy rim instead of large cusps, as in *Ausktribosphenos*. Consequently, there is no evidence of any wear on the inner face of this region in *Bishops*, nor in any other region of the talonid.

Ambondro (Fig. 7A)—Wear features on the molars of *Ambondro* differ in important ways from those of ausktribosphenids. Facets 1–4 are present and well developed, but contrary to Martin and Rauhut (2005: 422), there is little evidence of wear on the occlusal surface of the talonid. What these authors interpreted as apical wear is, in my opinion, more attributable to postmortem abrasion. The lingual rim of the talonids on m1 and m2 are formed by thin crests preserved free of wear (though there is breakage on the posterior portion of the m2), and the hypoconid on m1 is still conical, maintaining the shallow but distinct talonid basin. There is no evidence of any wear within the basin, but a small, inverted tear-drop shaped facet is present just lingual to the distal metacristid on the m2, roughly in the position of facet 5 (sensu Crompton 1971). This wear feature is limited to the vertical slope of the trigonid and does not invade the talonid. It provides evidence of a lingual structure on the upper molar of *Ambondro*, but this structure had no occlusal contact with the talonid and cannot be considered a functional protocone (in the tribosphenic sense).

Henosferus (Fig. 7B)—The single molar preserved in the holotype of *Henosferus* is complete but heavily worn. The majority of wear is apical, such that the trigonid is rendered to a flat surface as are the cusps and margin of the talonid. Other specimens show badly fractured but less heavily worn teeth. Facets 1 and 2 are well developed, while facets 3 and 4 are variably developed but present. There is possible presence of a wear facet lingual to the distal metacristid on the m2 on one specimen (same feature as in *Ambondro*); this potential facet was also mentioned by Rougier et al. (2007), but discounted as damaged enamel. The lingual side of the talonid, where preserved, shows no internal wear. It is therefore unclear if a lingual upper molar structure was present in *Henosferus*, but the overall morphology and wear pattern is very similar to that in *Ambondro* so it is likely the two taxa had similar upper molars.

Asfaltomylos (Fig. 7C)—From published descriptions (Martin and Rauhut 2005) wear seems to have progressed in a manner similar to that of *Henosferus*. Martin and Rauhut (2005) were not able to discern either a distal metacristid or wear facet 4, but I suspect both features would be revealed in better preserved specimens of *Asfaltomylos*.

The posterior margin of the talonid (equivalent to the hypocristid) in *Ausktribosphenos* and *Bishops* is oriented at a right angle to the long axis of the crown;

this condition resembles what is seen in toothed monotremes such as *Steropodon* and *Teinolophos* and differs from the Middle Jurassic australosphenidans, which are more similar to tribosphenidans (Fig. 8). *Ambondro* and *Henosferus* have a more typical, obliquely-oriented hypocristid which bears a wear facet on its posterolabial face (facet 4 of Crompton 1971; Fig. 8F–H), presumably caused by action against the anterior slope of the upper molar metacone as in tribosphenidans and *Peramus* (Fig. 4). This facet is absent in lower molars of ausktribosphenids and monotremes; in fact, it is difficult to imagine a metacone (in the traditional sense) occluding in the embrasure between the talonid and succeeding trigonid. The hypoconid in molars of ausktribosphenids is worn flat and there is no evidence of facet 4, yet facet 2 (formed by occlusion against the posterior face of the upper molar) is well developed (Fig. $6B_2$), suggesting that the structure of the upper molars of these taxa is fundamentally different from that of tribosphenic taxa (and presumably the Middle Jurassic australosphenidans, also). This pattern of wear is strikingly similar to that seen in toothed monotremes. Since this appears to be a synapomorphy uniting ausktribosphenids and monotremes to the exclusion of all other mammals, the loph-like "*Monotrematum* Model" proposed by Martin and Rauhut (2005: fig. 5F; Fig. 8E) is the most appropriate hypothesis for upper molar structure in these taxa. The upper molar lophs would abrade directly against the hypoconid and other talonid structures, while the anterior and posterior margins would still function in prevallum/postvallid and postvallum/prevallid shear, producing wear facets 1 and 2. Though this model was originally built to predict the morphology of *Asfaltomylos*, the molars of this taxon, along with *Henosferus* and *Ambondro,* are functionally different from other australosphenidans. It is more likely that henosferids and *Ambondro* possessed an upper molar with a more typically tribosphenic-like protocone, though lacking equivalent occlusal function (thus resembling the condition in shuotheriids). This implies that the Henosferidae + *Ambondro* likely form a clade removed from the ancestry of monotremes, and that ausktribosphenids may represent a stem lineage at the base of the Monotremata (though their actual inclusion within that clade cannot, in my opinion, be resolved with the available data).

Though the phylogenetic analysis of Rougier et al. (2007) as coded did not support inclusion of *Ambondro* in the Henosferidae, I would argue that the differences between the taxa are very slight and the morphological and functional similarities are very strong (Fig. 7). They clearly cluster among australosphenidans to the exclusion of ausktribosphenids—they share premolariform or non-triangulated ultimate premolars (though likely a plesiomophy) and, presumably, a functional upper molar embrasure for the hypoconid, as indicated by the presence of facets 3 and 4 (Fig. 7). In light of this, I propose that *Ambondro* is more closely allied with henosferids than ausktribosphenids, and should be included in the Henosferidae. Ultimate premolar morphology was a principal defining character of the clade (Luo et al. 2001; see henosferid condition in Flynn et al. 1999: fig. 3; Martin and Rauhut 2005: fig. 2; Rougier et al. 2007: fig 4), and it seems likely, based on the above discussion, that upper molars of henosferids were much more similar to shuotheriids and tribosphenidans while ausktribosphenids may have had upper molars resembling the ornithorhynchid *Monotrematum* (Pascual et al. 1992; Fig. 8). However, loph-like monotreme molars could have evolved from a more tribosphenic-like dentition (if present in the Middle Jurassic), as there is a substantial time gap (~50 Ma) between the known records of the two groups.

Ultimately, more complete fossils with upper dentitions are necessary to fully evaluate the role of the australosphenidan talonid during mastication, and their relationships to each other and to northern tribosphenic mammals. However, recent analyses (one of which is simplified in Fig. 9) are in agreement that australosphenidans are not closely related to the Tribosphenida (e.g., Kielan-Jaworowska et al. 2004; Rougier et al. 2007; Ji et al. 2009), and that they represent a separate, Gondwanan radiation (with the exception of the Laurasian shuotheriids, with which they are tentatively allied in some analyses).

Conclusions

A progression of mammalian molar morphotypes is presented, exhibiting changes that reflect stepwise modification of crown structures occurring during the Jurassic and Early Cretaceous:

Kuehneotherium stage: Obtuse-angled "symmetrodonts" were derived relative to the most basal mammaliaforms in triangulation of the three principal molar cusps, increasing the functional area without increasing the length of the crown. The lower molar talonid possessed a single cusp (d) which supported a very short crest (cristid obliqua), functioning to prevent overclosure of the jaws and producing limited shear against the posterior face of the central upper molar cusp (facet 3 on cusp A or paracone).

Amphitheriid stage: Using *Palaeoxonodon* as an example, amphitheriids possessed an elongated talonid with a single, labially-positioned cusp (homologous with the hypoconid). Facet 3 is greatly expanded. The extent of facet 2 on the upper molar in amphitheriids (and all other trechnotherians), from the metastylar corner to the metacone, supports homology of the metacone with cusp C in *Kuehneotherium*.

“Peramuran” stage: The metacone is in a lingual position, directly behind the paracone, in *Peramus*; this creates an embrasure for the hypoconid and produces a new wear surface (facet 4) between the anterior surface of the metacone and the lower molar hypocristid. A second talonid cusp (hypoconulid) occupies the posterior margin of the expanded talonid, securing it between the e and f cusps of the succeeding molar, and anchoring the posterior end of the hypocristid. Wear surfaces of both upper and lower molars are now “W”-shaped as a result of elaboration of internal crown structures. The presence of a lingual cingulum on upper molars may hint at the origin of the protocone.

Basal tribosphenidan stage: Upper and lower molars in aegialodontids (e.g., *Kielantherium*) are expanded lingually, through widening and basining of the talonid and development of the protocone. This allows new occlusal contact on the posterolingual surface of the lower molar trigonid and within the talonid basin itself by a large protocone (facet 5). The addition of grinding function to primitive shearing during a single chewing stroke is the hallmark feature of tribosphenic mammals. Subsequent and matching expansion of the protocone and talonid, along with addition of the entoconid to fully enclose the lingual margin of the basin, created full embrasure for the protocone at the end of the chewing stroke (facet 6).

Other early mammaliaform lineages converged on a similar functional molar morphology, the docodonts and shuotheriids. Both possess expanded anterior structures on the lower molars to accept a large lingual upper molar cusp. It is highly likely that one additional group, the australosphenidans (including monotremes), also developed a molar morphology superficially resembling that of tribosphenidans but lacking a similar grinding function. This clade appears to be highly variable in structure and presumably function, which reflects either separate evolutionary origins within the group or a substantial morphological divergence. Regardless, it is clear that the Tribosphenida, as defined by McKenna (1975), are probably monophyletic to the exclusion of the Australosphenida (as proposed by Luo et al. 2001) and functionally distinct from that group. The balance of evidence supports scenario 3 from the Introduction—mammals with a functional protocone, in the sense of modern metatherians and eutherians and their stem relatives (the Tribosphenida), evolved only once, though there were several convergences on functionally or morphologically similar dentitions (Fig. 9). But as is typically the case with Mesozoic mammals, our understanding of the dynamics of mammalian evolution is hampered by the fragmentary nature of the fossil record. More complete specimens, especially those preserving upper molar morphology, are needed to help complete the picture.

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Figure captions

Fig. 1: Molar terminology and wear facet designation (in occlusal view). A, upper (A_1) and lower (A_2) molars of the archaic "symmetrodont" *Kuehenotherium* (Late Triassic-Early Jurassic of Britain); B, upper (B_1) and lower (B_2) molars of the metatherian *Kokopellia* (Early-Late Cretaceous of USA). Molars are duplicated to show adjacent wear facets, and are not intended to indicate serial loci. Cusp lettering follows Crompton and Jenkins (1968); wear facets follow Crompton (1971). C, schematic of reversed, triangular molar interlocking; D, schematic of tribosphenic molar interlocking. A, modified from Crompton and Jenkins (1968); C, D courtesy of Z.-X. Luo. Anterior is towards the left and labial is towards the top of the page. Not to scale. [planned page width]

Fig. 2: Morphotypic progression of stylized lower molars (in occlusal view), illustrating two hypotheses of talonid cusp evolution discussed in the text: A, cusp d is homologous with the hypoconid, requiring the talonid to arc labially as it elongated, with a neomorphic cusp appearing posterolingually in the position of the hypoconulid; B, cusp d is homologous with the hypoconulid, requiring a neomorphic cusp along the cristid

obliqua to shift labially into the position of the hypoconid as the talonid elongated, with the hypoconulid migrating posterolingually to its derived position. Anterior is towards the left and labial is towards the top of the page. [planned page width]

Fig. 3: Molars and wear facets of the archaic “symmetrodont” *Kuehneotherium*, the amphitheriid *Palaeoxonodon*, and the “peramuran” *Peramus* (in occlusal view). A, upper (A_1) and lower (A_2) molars of *Kuehneotherium* (Late Triassic-Early Jurassic of Britain); B, upper (B_1) and lower (B_2) molars of *Palaeoxonodon* (Middle Jurassic of Britain); C, upper (C_1) and lower (C_2) molars of *Peramus* (Early Cretaceous of Britain); D and E, stylized illustration of the major shearing surfaces in upper (D_1-E_1) and lower (D_2-E_2) molars of *Palaeoxonodon* (D) and *Peramus* (E), showing the alternating orientations of wear features created by the lingual translation of the metacone and appearance of the hypoconulid. Molars are duplicated to show adjacent wear facets, and are not intended to indicate serial loci. Anterior is towards the left and labial is towards the top of the page. Not to scale. [planned page width]

Fig. 4: Molars and wear facets of the “peramuran” *Peramus* and the aegialodontids (basal Tribosphenida) *Aegialodon* and *Kielantherium* (in occlusal view). A, upper (A_1) and lower (A_2) molars of *Peramus* (Early Cretaceous of Britain); B, lower molar of *Aegialodon* (Early Cretaceous of Britain); C, upper (C_1) and lower (C_2) molars of *Kielantherium* (Early Cretaceous of Mongolia). Molars are duplicated to show adjacent wear facets, and are not intended to indicate serial loci. C_1, modified from Lopatin and

Averianov (2006b). Anterior is towards the left and labial is towards the top of the page. Not to scale. [planned page width]

Fig. 5: Molars of the docodont *Haldanodon* and the shuotheriid *Shuotherium* (in occlusal view). A, upper (A_1) and lower (A_2) molars of *Haldanodon* (Late Jurassic of Portugal); B, upper (B_1) and lower (B_2) molars of *Shuotherium* (Middle–Late Jurassic of Britain and China). A, modified from Krusat (1980); B_1, modified from Chow and Rich (1982); B_2 modified from Wang et al. (1998). Anterior is towards the left and labial is towards the top of the page. Not to scale. [planned column width]

Fig. 6: Lower dentition and wear facets of the ausktribosphenids (Australosphenida) *Bishops* and *Ausktribosphenos*, and the insectivoran (Eutheria) *Erinaceus*. A, lower ultimate premolar and m1–3 of *Bishops* (Early Cretaceous of Australia); B, lower ultimate premolar and m1–3 (B_1) and m1–2 (B_2, labial view, reversed) of *Ausktribosphenos* (Early Cretaceous of Australia); C, lower ultimate premolar and m1–3 of *Erinaceus* (Recent of Britain), for comparison in general morphology: note the molariform ultimate premolar, complex, basined talonid, and presence of three molars. A, modified from Rich et al. (2001); B, modified from Rich et al. (1999). All occlusal view except B_2 (labial view, reversed relative to B_1). Anterior is towards the left and labial is towards the top of the page. Not to scale. [planned column width]

Fig. 7: Lower molars and wear facets of the henosferids (Australosphenida) *Ambondro*, *Henosferus*, and *Asfaltomylos* (in occlusal view). A, lower molar of *Ambondro* (Middle

Jurassic of Madagascar); B, lower molar of *Henosferus* (Middle Jurassic of Argentina); C, lower molar of *Asfaltomylos* (Middle Jurassic of Argentina). C, modified from Martin and Rauhut (2005). Anterior is towards the left and labial is towards the top of the page. Not to scale. [planned column width]

Fig. 8: Functional comparisons of lower molar morphology and wear facets of australosphenidans as discussed in the text (in occlusal view). The ausktribosphenids *Ausktribosphenos* and *Bishops* (A, B, respectively, Early Cretaceous of Australia) resemble toothed monotremes such as *Teinolophos* and *Steropodon* (C, D, respectively, Early Cretaceous of Australia) in form and function; E, the "*Monotrematum* Model" (Martin and Rauhut 2005: fig. 5F) as a hypothetical structure of the ausktribosphenid upper molar capable of producing the wear features shown in Fig. $6B_2$. The henosferids *Ambondro* (F, Middle Jurassic of Madagascar) and *Henosferus* (G, Middle Jurassic of Argentina) more closely resemble basal tribosphenidans such as *Kielantherium* (H_2, Early Cretaceous of Mongolia); upper molars of henosferids are most likely to resemble basal tribosphenidans (H_1) or shuotheriids (Fig. $5B_1$). D, modified from Rich et al. (2001); E, modified from Martin and Rauhut (2005); H_1, modified from Lopatin and Averianov (2006b). Anterior is towards the left and labial is towards the top of the page. Not to scale. [planned column width]

Fig. 9: Cladogram (simplified from Rougier et al. 2007) showing molar morphotypes discussed in the text (lower molars on the left, upper molars on the right; in occlusal view). Asterisks denote lineages which evolved molars combining shearing and grinding

in a manner similar to (and including) the Tribosphenida. Numbered nodes indicate major character changes which elaborated internal crown structures and enabled the evolution of true tribospheny: node 1 (Amphitheriidae), elongation of the talonid and expansion of facet 3 (green); node 2 (“Peramura”), lingual translation of metacone, embrasure for hypoconid, development of hypoconulid and facet 4 (orange), lingual expansion of talonid; node 3 (Aegialodontidae), development of functional protocone which sheared lingual to distal metacristid and into talonid basin, creating facet 5 (blue); node 4 (derived tribosphenidans), embrasure for protocone through development of entoconid and facet 6 (purple). For molar illustrations, anterior is towards the left and labial is towards the top of the page. Not to scale.

Figure 1

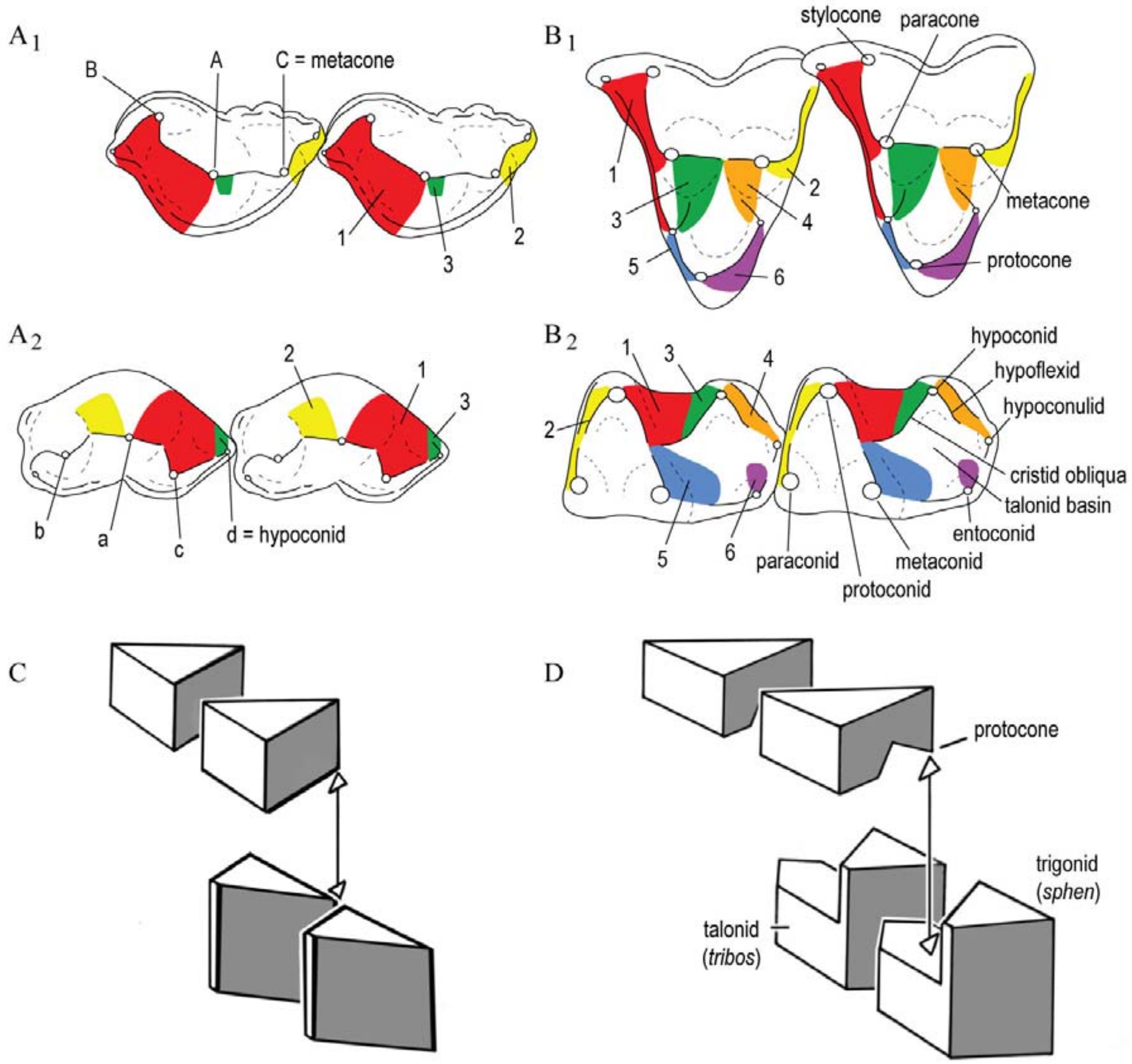

A1
B
A
C = metacone
1
3
2
B1
stylocone
paracone
1
2
3
4
metacone
5
6
protocone
A2
2
1
3
b
a
c
d = hypoconid
B2
1
3
4
2
hypoconid
hypoflexid
hypoconulid
cristid obliqua
talonid basin
entoconid
5
6
paraconid
protoconid
metaconid
C
D
protocone
trigonid
(sphen)
talonid
(tribos)

Figure 2

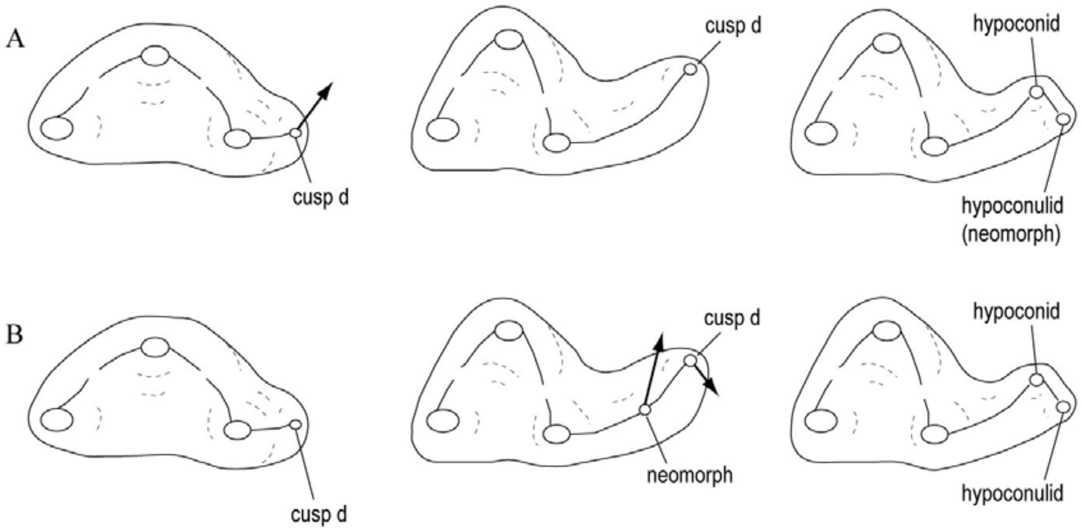
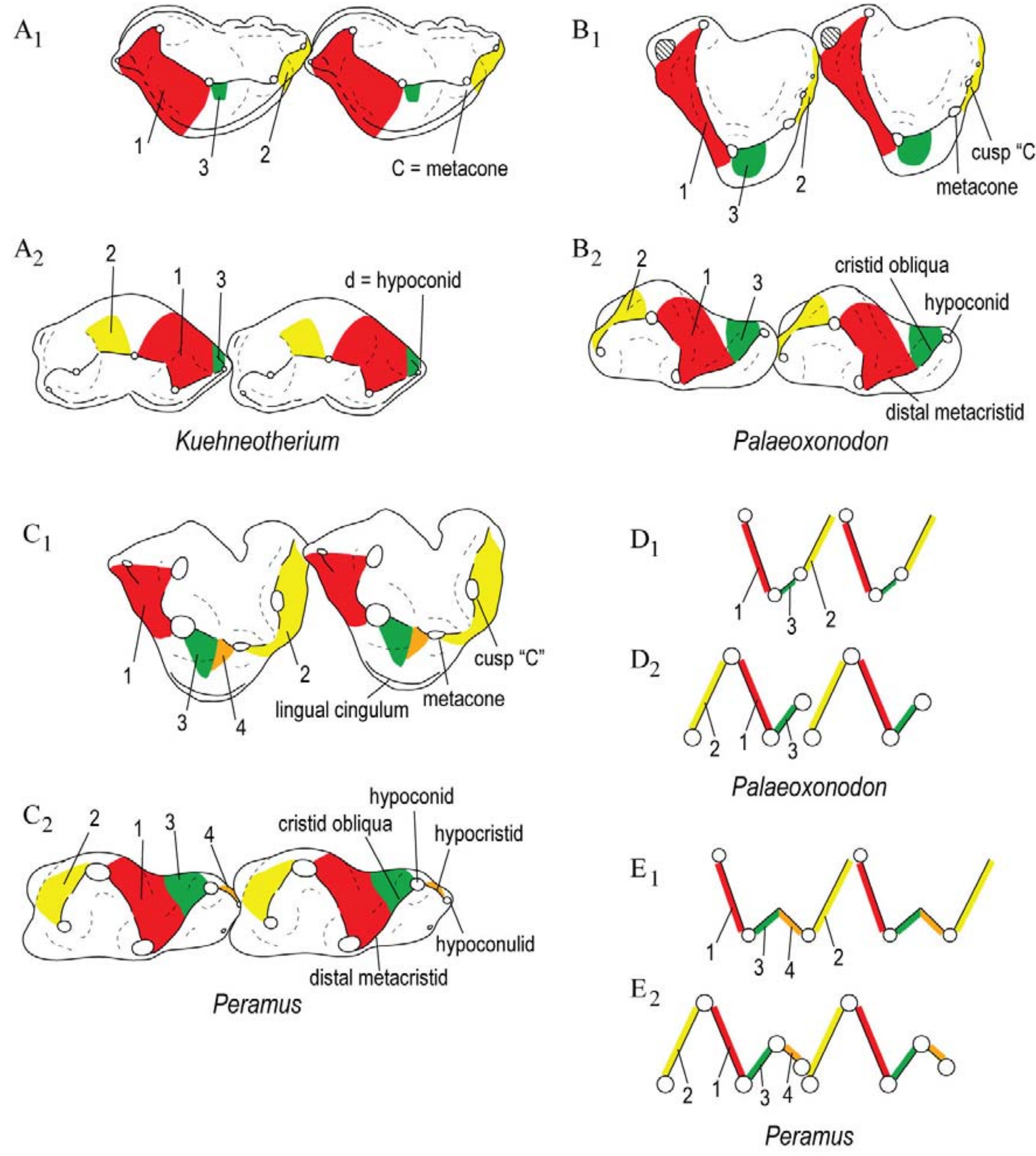

A
cusp d
cusp d
hypoconid
hypoconulid
(neomorph)
B
cusp d
cusp d
neomorph
hypoconid
hypoconulid

Figure 3



A1
1
3
2
C = metacone
B1
1
3
2
cusp "C"
metacone
A2
2
1
3
d = hypoconid
Kuehneotherium
B2
2
1
3
cristid obliqua
hypoconid
distal metacristid
Palaeoxonodon
C1
1
3
4
2
lingual cingulum
metacone
cusp "C"
D1
1
3
2
D2
2
1
3
Palaeoxonodon
C2
2
1
3
4
hypoconid
cristid obliqua
hypocristid
hypoconulid
distal metacristid
Peramus
E1
1
3
4
2
E2
2
1
3
4
Peramus

Figure 4

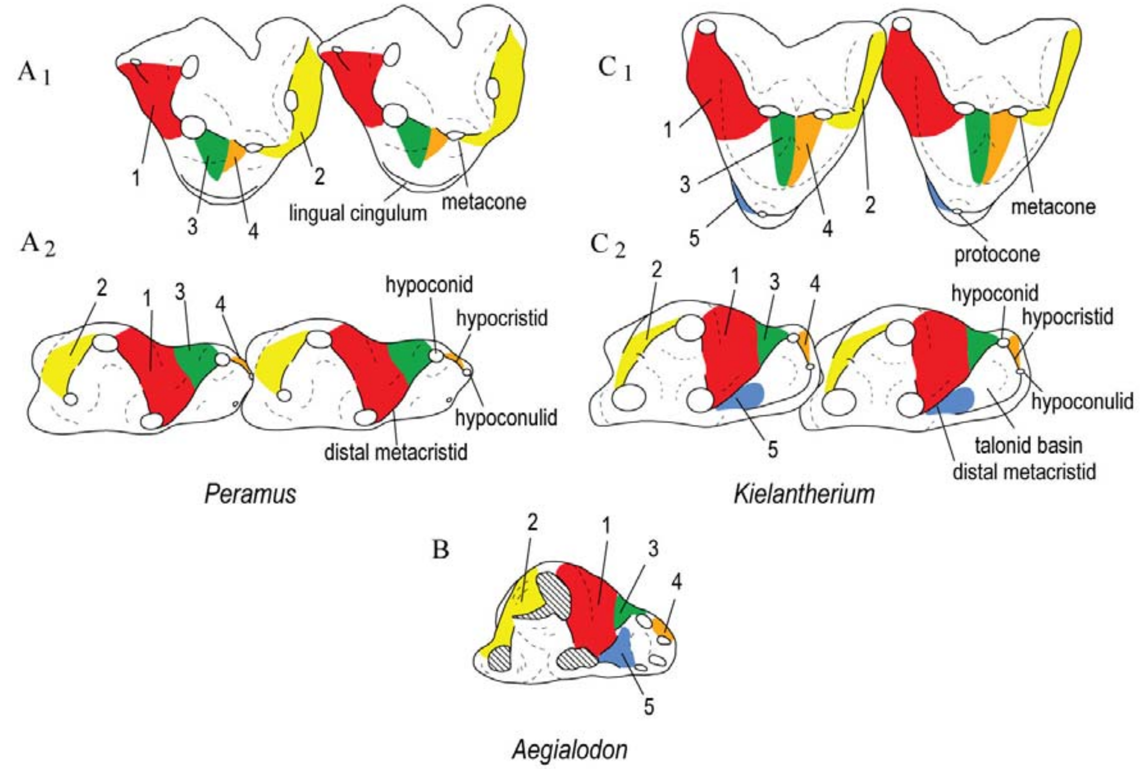

A 1
1
2
3
4
lingual cingulum
metacone
A 2
2
1
3
4
hypoconid
hypocristid
hypoconulid
distal metacristid
Peramus
C 1
1
3
5
4
2
metacone
protocone
C 2
2
1
3
4
hypoconid
hypocristid
hypoconulid
5
talonid basin
distal metacristid
Kielantherium
B
2
1
3
4
5
Aegialodon

Figure 5

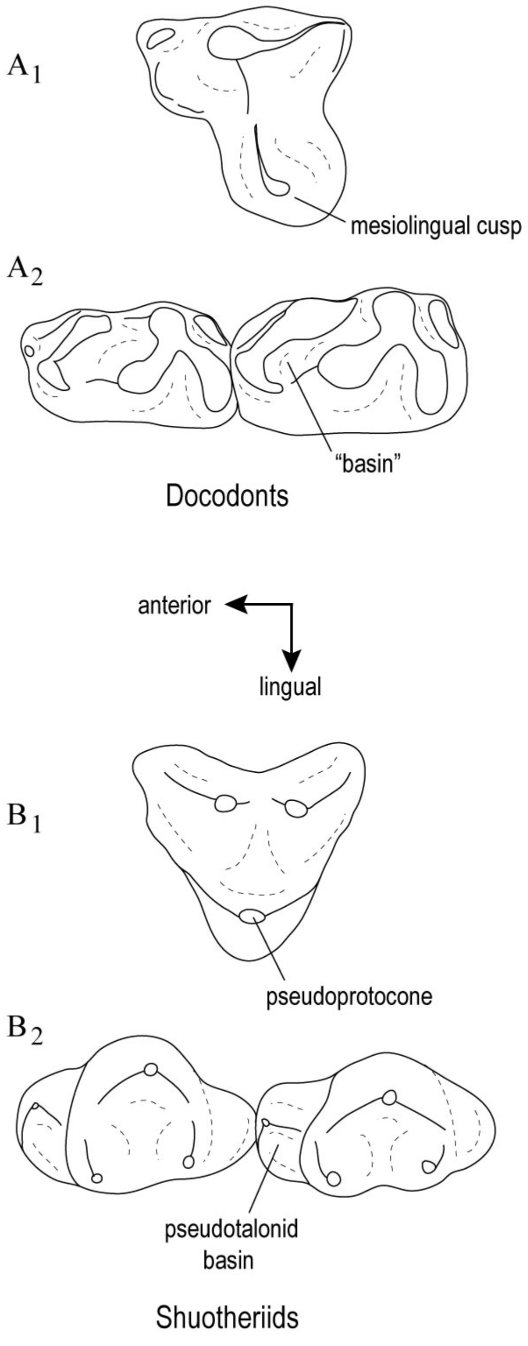

A1
mesiolingual cusp
A2
"basin"
Docodonts
anterior
lingual
B1
pseudoprotocone
B2
pseudotalonid basin
Shuotheriids

Figure 6

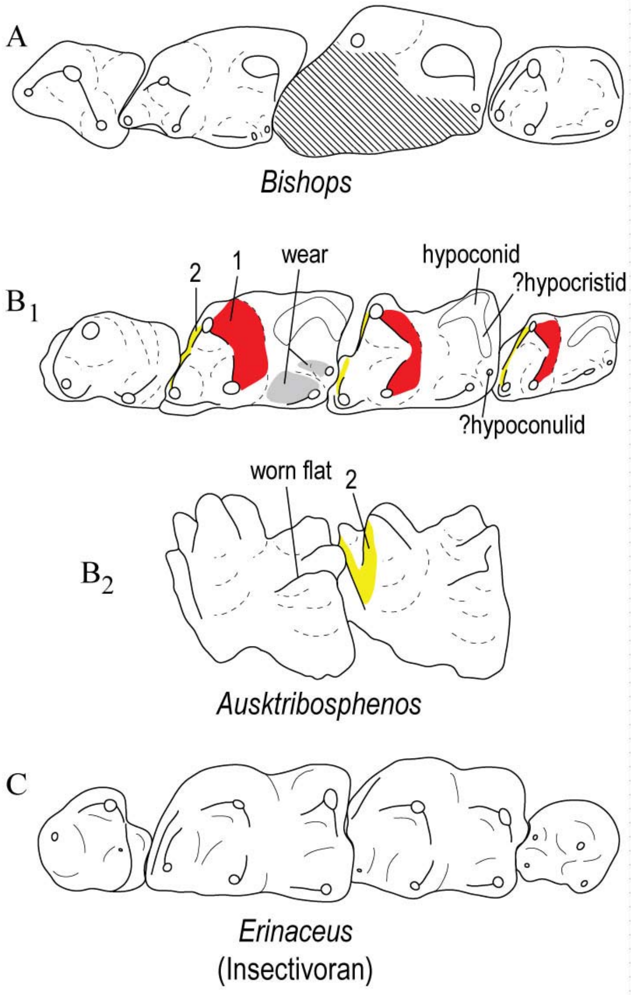
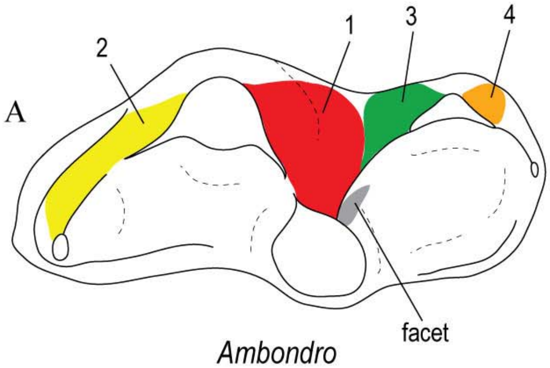
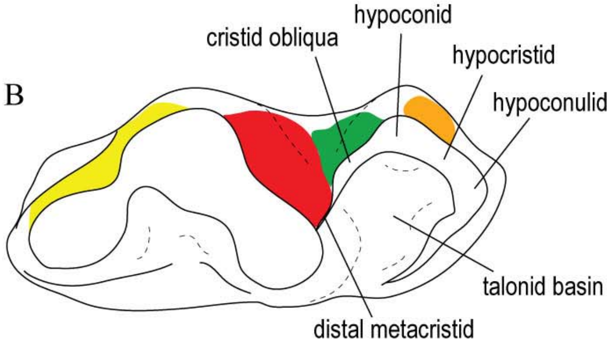

A
Bishops
B1
2
1
wear
hypoconid
?hypocristid
?hypoconulid
worn flat
2
B2
Ausktribosphenos
C
Erinaceus
(Insectivoran)

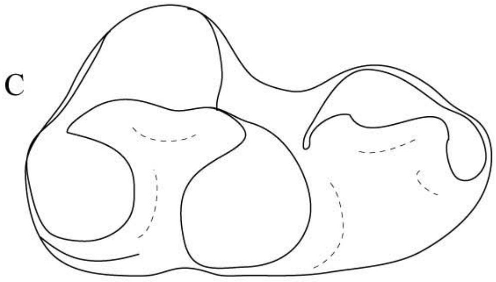
Figure 7



Ambondro



Henosferus



Asfaltomylos

Figure 8

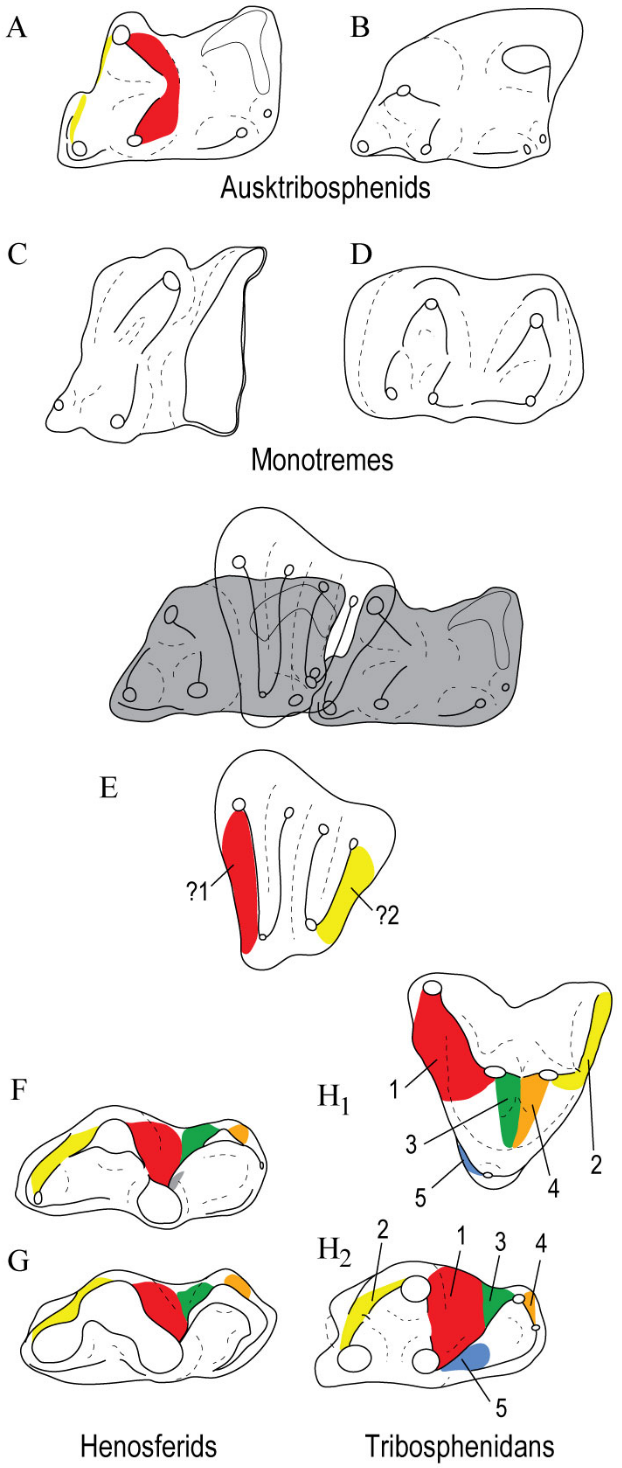
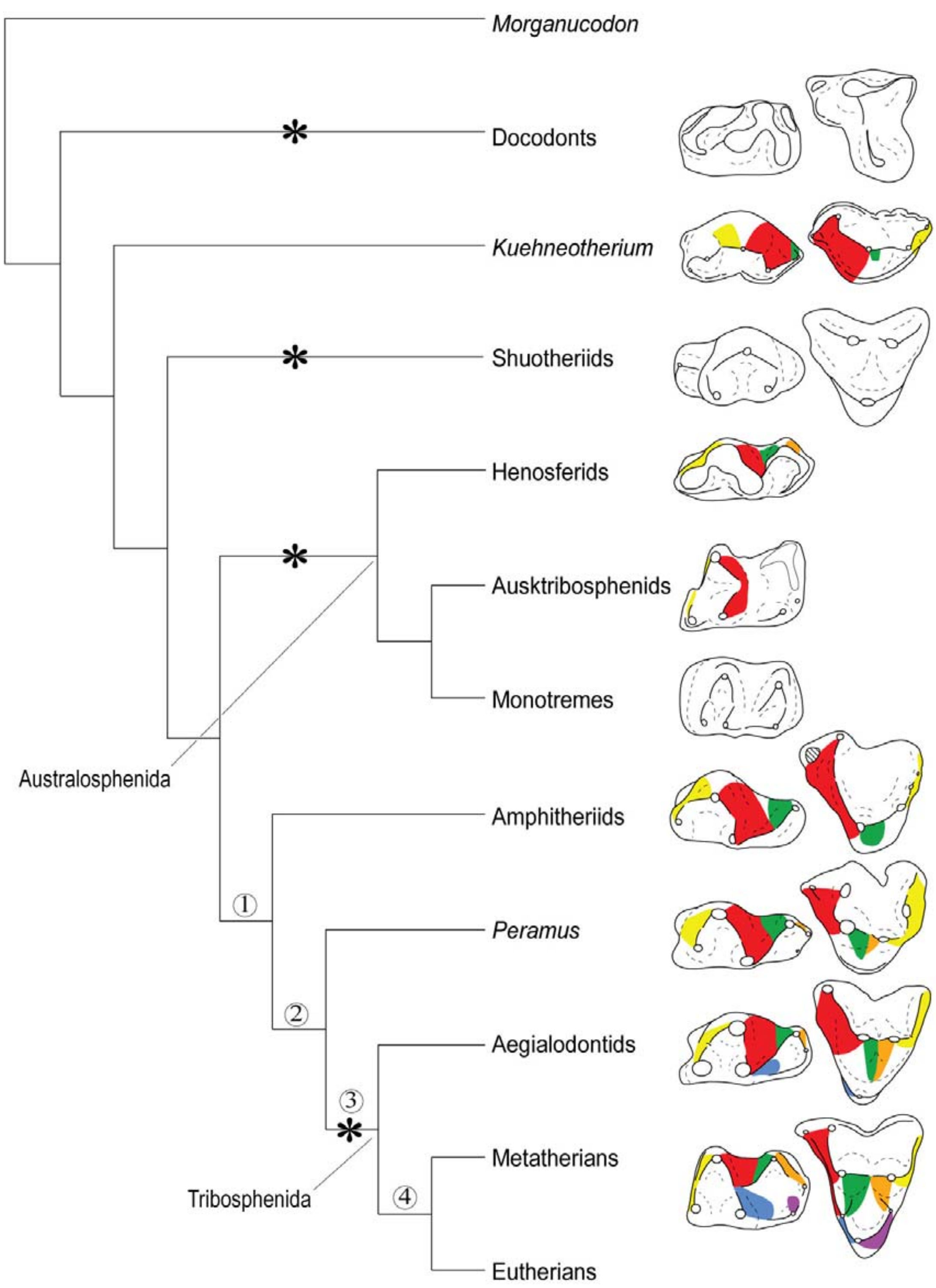

A
B
Ausktribosphenids
C
D
Monotremes
E
?1
?2
F
G
Henosferids
H1
1
3
5
4
2
H2
2
1
3
4
5
Tribosphenidans

Figure 9


Morganucodon
Docodonts
Kuehneotherium
Shuotheriids
Henosferids
Ausktribosphenids
Monotremes
Australosphenida
Amphitheriids
Peramus
Aegialodontids
Metatherians
Eutherians
Tribosphenida
①
②
③
④

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

Brian M. Davis and Richard L. Cifelli

Abstract

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

Keywords: Tribosphenida, Metatheria, Eutheria, Deltatheroida, Trinity Group, Early Cretaceous.

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Introduction

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

The first Early Cretaceous mammals from North America were discovered in 1949 (Zangerl and Denison 1950; Patterson 1951) from the Trinity Sands near Forestburg in north-central Texas, now regarded as a part of the Trinity Group, specifically the Antlers Formation (see Winkler et al. 1989, 1990; Davis et al. 2008 for a summary of the regional geology). Since then, small but hard-won collections have been deposited at the Field Museum in Chicago, the Shuler Museum of Paleontology at Southern Methodist University (Dallas, Texas), and the Sam Noble Oklahoma Museum of Natural History at the University of Oklahoma (Norman, Oklahoma). The most abundant mammal to date in the fauna is the triconodontid *Astroconodon denisoni* Patterson, 1951, though most of the multituberculate fossils have yet to be described. The therian (here more appropriately referred to as tribosphenidan) material consists of isolated teeth and tooth fragments, with only a couple of more complete specimens known. Two localities in Texas, Greenwood Canyon and Butler Farm, are of particular historic importance and have yielded the vast majority of specimens (Fig. 1), though a diverse local fauna is also known from southeastern Oklahoma (see Davis et al. 2008: table 1.2, and references therein).

Although he formally defined no taxa, initial description of the Trinity mammalian fauna was made by Bryan Patterson (1956), and his work still stands as one of the most important contributions to modern paleomammalogy. Subsequent work by Bob Slaughter (1965, 1968a, 1968b, 1969, 1971, 1981), Percy Butler (1978), and William Turnbull (1971, 1995, 1999), among others, led to the erection of eight monotypic genera of tribosphenidan mammals: *Pappotherium pattersoni* Slaughter, 1965, *Holoclemensia texana* (Slaughter, 1968a), *Kermackia texana* Slaughter, 1971, *Trinititherium slaughteri* Butler, 1978, *Slaughteria eruptens* Butler, 1978, *Comanchea hilli* Jacobs et al. 1989, *Atokatheridium boreni* Kielan-Jaworowska and Cifelli, 2001, and *Oklatheridium szalayi* Davis, Cifelli, and Kielan-Jaworowska, 2008. The age and generally primitive nature of these taxa made them a template for discussions of the evolution of higher mammals. The “eupantotherians” that dominated the well sampled Late Jurassic Morrison Formation and the earliest Cretaceous Purbeck Group were generally thought to hold the origin of tribosphenic mammals; metatherians and eutherians were abundant and diverse in the Late Cretaceous Lance and Hell Creek formations, temporally and morphologically bracketing the Aptian-Albian Trinity Group taxa. Breakthroughs that would define and influence all later work on fossil mammals were made with reference to these taxa as transitional—Patterson's (1956) concepts of molar cusp homology and Crompton's (1971) functional model of tribosphenic evolution are two examples.

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

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

Materials

We have included material from the entire known sample of tribosphenidan mammals from the Trinity Group of Texas and Oklahoma, housed in the Field Museum of Natural History (Chicago, USA), the Sam Noble Oklahoma Museum of Natural History (Norman, USA), and the Shuler Museum of Paleontology (Dallas, USA). The material consists almost entirely of isolated teeth—though some dentigerous fragments are known, they preserve very limited portions of the dentition, making referral of many isolated specimens impossible. Consequently, the portion of the sample treated herein is restricted to molars, as well as any ultimate premolars which are modified in such a way to make them uniquely identifiable. Scanning electron micrographs of specimens were obtained at the OMNH; some specimens were imaged using a Keyence Digital Microscope VHX1000E at the SMP-SMU. Measurements (in millimeters) for all specimens are provided in Tables 1–9; some measurements were taken from photographs, while all others were taken with a Reflex Microscope (Consultantnet Ltd, 8A The Grip, Linton, Cambridge, CB21 4NR, UK), as defined by Lillegraven and Bieber (1986).

Systematic paleontology

Subclass Tribosphenida McKenna, 1975

Infraclass Metatheria Huxley, 1880

Cohort Deltatheroida Kielan-Jaworowska, 1982

Family Deltatheridiidae Gregory and Simpson, 1926

Atokatheridium boreni Kielan-Jaworowska and Cifelli, 2001

Fig. 2, Table 1

Holotype: OMNH 61623, RM2.

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

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

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

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

Description

Detailed descriptions of the molars of *Atokatheridium boreni* can be found in Davis et al. (2008), and will not be repeated here (with the exception of lower molars which can be referred with confidence to the first molar locus, described below).

However, the morphology is summarized to facilitate comparisons between the various tribosphenidan taxa described in this paper.

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

Lower molars.—*A. boreni* is known by a single complete but abraded isolated lower molar and several fragmentary molars preserving only the trigonid (Fig. 2E). Given the poor preservation of the sample, it is not possible to confidently identify most specimens to locus. OMNH 61624 has a very tall trigonid relative to the small talonid, and a very prominent, projecting paraconid that is much taller than the metaconid. These features suggest that this specimen might represent the m4, but there are some substantial differences between it and preserved m4s of other deltatheroidans. In *Deltatheridium* and *Sulestes*, the trigonid is extremely obtuse-angled, and in the former the metaconid is completely absent (Rougier et al. 1998; Averianov et al. 2010). While the low, small talonid in *A. boreni* is open lingually and lacks an entoconid (comparing in some ways favorably with the basal tribosphenidan *Kielantherium*; Dashzeveg and Kielan-Jaworowska 1984), the trigonid has a high, wall-like paracristid, reinforcing deltatheroidan affinities for this taxon. A strong distal metacristid is present. The remainder of the referred lower molars (with the exception of those identified as m1s, see below) generally agree with OMNH 61624 in morphology, though they are all either too heavily worn or poorly preserved to add anything new.

OMNH 63724 (Fig. 2D) is identified as an m1 on the basis of trigonid angle and relative cusp heights. Only the trigonid is preserved, and it is transversely compressed and lingually open relative to the other referred lower molars. The paraconid is slightly taller than but not as robust as the metaconid; the paraconid is not inclined, as would be expected if the specimen were a deciduous premolar. A distal metacristid is present. The paracristid is strong and notched, and this specimen can be excluded from the other deltatheroidan in the fauna, *Oklatheridium*, based on size. The relative size and proportions of this specimen in reference to the rest of the referred sample agree well with the distal trend in morphology of the molar series seen in *Deltatheridium* (Rougier et al. 1998), and it is on this basis that it is excluded from the other tribosphenidans of the Trinity Group. Two other isolated trigonids are also referred to the m1 of *Atokatheridium boreni*, OMNH 63889 and 63890.

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

Included species: *Oklatheridium szalayi* Davis, Cifelli, and Kielan-Jaworowska, 2008 (type); *O. minax* sp. nov.

Emended diagnosis.—Moderate-sized deltatheroidan differing from all other deltatheroidans in relatively larger talonid; differs from all other deltatheroidans except *Atokatheridium* in narrower stylar shelf; differs from other deltatheroidans except *Sulestes* in less height differential between paracone and metacone, metacone broader than paracone, prominent conules, mesiodistally broad protocone, and presence of entoconid; differs from *Atokatheridium* in larger size, larger stylocone, and relatively larger metaconid; differs from *Sulestes* in wider protoconal region; differs from *Deltatheroides* in stronger reduction of metacone and metastylar lobe on M4.

Oklatheridium szalayi Davis, Cifelli, and Kielan-Jaworowska, 2008
Fig. 3A–E, Table 2

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

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

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

Referred material.—OMNH 62411, LM1 (missing the protocone); PM 1238, LM1 (missing the protoconal region); OMNH 61180, LM1 (missing the protoconal region); OMNH 63987, RM3 (missing the metastylar lobe and protoconal region).

Other localities.—Greenwood Canyon (Triconodont Gully), upper Antlers Formation (Aptian-Albian), north-central Texas, USA; Tomato Hill (OMNH V706), middle Antlers Formation (Aptian-Albian), southeastern Oklahoma, USA.

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

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

Description

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

Upper molars.—The upper molars of *O. szalayi* are in many ways similar to those of *Pappotherium*, and are distinguished primarily by relative proportions of the paracone and metacone. In both species of *Oklatheridium*, there is less height differential between these cusps than in *Pappotherium*, and the metacone is slightly broader than the paracone (the opposite is true in *Pappotherium*). The parastylar lobe increases substantially in width between the M1 and the M3, and the parastyle is prominent. The metastylar lobe is long and bears a very strong, notched postmetacrista. There is some variation in the depth of the ectoflexus, but it is quite deep on the holotype (similar to that seen in the M2 of *Deltatheridium*). The stylocone is the only stylar cusp (typical of deltatheroidans, despite the variable presence of cuspules or crenulations in *Sulestes*; see Averianov et al.

2010), but there is a small cuspule present immediately distal to the stylocone on one M2 (OMNH 61180) and the referred M3 (OMNH 63987).

The M3 originally referred to *O. szalayi* by Davis et al. (2008), OMNH 63727, appears to belong instead to *O. minax* sp. nov. (see below). A different specimen, OMNH 63987 (Fig. 3E), is a better match for M3 of *O. szalayi*, in terms of size. This molar is fragmentary, preserving only the paracone, parastylar lobe, and the mesial base of the metacone. The stylocone is large and well separated from the paracone; the parastylar lobe is much wider than any specimen referred to *Pappotherium* (see below). There is a prominent cuspule along the ectocingulum immediately distal to the stylocone, and the ectocingulum appears to have been strong, as in other specimens of this taxon.

Oklatheridium minax sp. nov.
Oklatheridium sp.: Davis, Cifelli, and Kielan-Jaworowska 2008: fig. 1.3
Tribosphenida indet.: Cifelli 1997: fig. 3
Fig. 3F–H, Table 3

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

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

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

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

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

Other localities.—Greenwood Canyon (Triconodont Gully), upper Antlers Formation (Aptian-Albian), north-central Texas, USA; Tomato Hill (OMNH V706), middle Antlers Formation (Aptian-Albian), southeastern Oklahoma, USA.

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

Description

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

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

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

Oklatheridium sp.
Fig. 4, Table 4

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

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

Description

Upper molar.—PM 1287 was originally illustrated in Patterson (1956: fig. 4B; Fig. 4A). This specimen was referred to *Pappotherium* sp. by Turnbull (1971), though Butler (1978) did not believe it could belong to either that genus or *Holoclemensia*, and must represent the ultimate molar of something different. In their interpretation of the molar series of the Tomato Hill deltatheroidans, Davis et al. (2008: fig. 1.8) speculated that the M4 of *Oklatheridium* would be heavily reduced, much like the condition in the larger but morphologically similar *Deltatheridium*. PM 1287 retains a large paracone, stylocone, and preparacrista (characters of the mesial molars of *Oklatheridium*), while the metacone and metastylar lobe are strongly reduced (a trend beginning with the M3; Fig. 3E, H). However, the absence of a more completely preserved molar series precludes assignment of this M4 to either of the species of *Oklatheridium*.

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

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

Of the remainder of the sample, only the m1 differs substantially enough to be readily identified. OMNH 61642 (Fig. 4B) is markedly different from the incorrectly referred m1 of Davis et al. (2008) in being lower crowned, much narrower transversely, and in having widely spaced paraconid and metaconid. It is proportionally very similar to the m1 of *Atokatheridium*, differing only in larger size and a somewhat proportionally larger paraconid.

Infraclass ?Metatheria Huxley, 1880

Family Pappotheriidae Slaughter, 1965

Pappotherium pattersoni Slaughter, 1965

Fig. 5, Table 5

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

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

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

Referred material.—PM 999, RM1 (missing protoconal region); PM 1749, LM2 (missing metastylar lobe and protoconal region); PM 1325, LM2 (protoconal region only); OMNH 61185, RM3 (missing metastylar lobe); PM 1015, LM3 (missing metastylar lobe and protoconal region); OMNH 61219, Lmx (trigonid only); OMNH 62427, Lmx (trigonid only); OMNH 63729, Rmx (trigonid only); PM 930, Rmx (trigonid only); PM 1119, Rmx (trigonid only); PM 1249, Lmx (trigonid only).

Other localities.—Greenwood Canyon (Triconodont Gully, Turtle Gully), upper Antlers Formation (Aptian-Albian), north-central Texas, USA; Tomato Hill (V706), middle Antlers Formation (Aptian-Albian), southeastern Oklahoma, USA.

Emended diagnosis.— Putative metatherian differing from other basal metatherians (such as *Kokopellia*) in lack of twinning between hypoconid and hypoconulid, absence of buccal postcingulid , and presence of distal metacristid on lower molars; differs from deltatheroidans in subequal paraconid and metaconid on lower molars; differs from *Holoclemensia* in presence of four molars, larger stylocone, absence of mesostyle, deeper ectoflexus, closer approximation of paracone and metacone, mesiodistally longer trigonid, subequal paraconid and metaconid, and presence of distal metacristid; differs from *Slaughteria* in larger size, presence of four molars, and weaker paracristid.

Description

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

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

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

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

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

Infraclass Eutheria Gill, 1872

Order *incertae sedis*

Family Holoclemensiidae Aplin and Archer, 1987

Holoclemensia texana Slaughter, 1968b

Figs. 6–7, Table 6

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

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

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

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

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

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

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

Description

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

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

Upper molars.—All specimens except for the M3 are missing the protoconal region of the crown. The M1s (Fig. 6A, B) are heavily worn, but together they provide morphology for the entire buccal half of the crown. The paracone was clearly larger than the metacone. The preparacrista appears to have been low, but observation is difficult due to wear and breakage. The postmetacrista is much weaker than in *Pappotherium* or deltatheroidans. The stylocone is small and positioned at the buccal margin of a wide, wing-like parastylar lobe which projects beyond the buccal extent of the metastylar lobe (in a similar fashion to but to a greater extent than in *Prokennalestes*; see Kielan-Jaworowska and Dashzeveg 1989). The mesostyle is much larger than the stylocone but not as tall as the metacone, and is positioned at or just mesial to the middle of the centrocrista; a low bulge just distal to it indicates the presence of another stylar cusp (in the position of stylar cusp D). An ectoflexus is lacking. The preprotocrista is obliterated by wear in PM 1000, but it probably participated in the large parastylar lobe. The postprotocrista does not extend buccally past the base of the metacone.

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

SMP-SMU 62009 (Fig. 6E) represents the M3 and is the most complete upper molar, missing only the lingual portion of the protocone. The crown is transversely wide and mesiodistally compressed, with substantial reduction to the metacone and metastylar lobe, as is typical for ultimate molars. The paracone is large and dominant, while the metacone is low and thin; the preparacrista is oriented toward the parastyle, but terminates prior to reaching it. The parastylar lobe is short and wide, with a large, sharp parastyle and a much smaller stylocone. The mesostyle is delicate and spire-like as compared to the other molars. The protocone is also tall, about two-thirds the height of the paracone, and is flanked by a small paraconule and metaconule. The conules are closely appressed to the protocone. The preprotocrista is interrupted for a brief stretch mesial to the paracone.

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

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

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

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

Holoclemensia sp.
Referred material.—SMP-SMU 61726, Lmx.

Locality.—Butler Farm, upper Antlers Formation (Aptian-Albian), north-central Texas, USA.

Description

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

Infraclass *incertae sedis*

Family Kermackiidae Butler, 1978

Kermackia texana Slaughter, 1971

Fig. 8, Table 7

Trinititherium slaughteri Butler, 1978

Holotype: SMP-SMU 62398, Rmx.

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

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

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

Tentatively referred material.—SMP-SMU 62404, RM1 (missing the mesiobuccal corner).

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

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

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

Description

Upper molar.—SMP-SMU 62404 (Fig. 8A) is tentatively referred to *Kermackia texana* on the basis of size and occlusal fit; the only other taxon from the sample of equivalent size is *Slaughteria*, but the lower molar morphology of *K. texana* (described below) suggests that its upper molars are somewhat modified as represented by SMP-SMU 62404. The paracone is very large and inflated, while the metacone is substantially smaller and positioned slightly buccally with respect to the paracone. The postmetacrista is only moderately developed. The parastylar lobe is largely broken, but from the pattern of breakage the stylocone appears to have been very large and closely appressed to the paracone. The ectoflexus was moderately deep, and the parastylar lobe was probably narrower than the metastylar lobe. There is no evidence of stylar cusps other than the stylocone. The protoconal region is well developed (the protocone is as tall as the metacone) and bears both conules. The metaconule is situated close to the protocone, while the paraconule is equidistant from the protocone and paracone. The tooth is heavily abraded, obscuring any other features (including wear facets). This specimen is considered to be a first molar based on the width of the metastylar lobe (tends to be reduced on ultimate molars), and the inferred approximation of the stylocone to the paracone (the parastylar lobe is typically wider on second molars). *Kermackia* is interpreted to have had three molars (see below).

Lower premolar.—OMNH 67134 (Fig. 8B) is a small, semi-molariform premolar broken obliquely at about the midline of the protoconid. The main cusp is large but with heavy apical wear; it is flanked lingually by a mesiodistally broad metaconid. The two cusps are connected by a weak crest. Two additional crests descend distally from the protoconid and meet a crest running mesially from a large heel cusp. A strong notch is present at this juncture; a very similar (and probably serially homologous) notch is found in lower molars of *Kermackia texana* (see below). The talonid is otherwise undeveloped, except for a faint, low rim enclosing the lingual margin. The small overall size, broad metaconid, and strongly notched heel crest support referral of this specimen to *K. texana*. The absence of any molarization of the talonid indicates that this premolar is from the adult series, and the presence of a prominent metaconid suggests it is the ultimate premolar. Without material to suggest otherwise, *Kermackia* is interpreted to possess the primitive tribosphenidan condition of five premolars and three molars (see Davis in press, and references therein).

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

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

The holotype of *Trinititherium* (SMP-SMU 61728; Fig. 8G) comprises a small dentary fragment bearing a single molar posterior to two alveoli. It also preserves a small portion of the ascending ramus, visible distobuccal to the talonid of the molar. This suggests that the single preserved tooth is the ultimate molar, and accompanying features such as a reduction in the height of the metaconid and a decrease in the size of the talonid (and absence of the entoconid) can account for any differences between this specimen and those otherwise referred to *Kermackia*. *Trinititherium* is therefore a junior synonym of *Kermackia*, and this specimen represents the m3.

Family *incertae sedis*

Slaughteria eruptens Butler, 1978

Fig. 9, Table 8

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

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

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

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

Other localities.—Greenwood Canyon (Triconodont Gully), upper Antlers Formation (Aptian-Albian), north-central Texas, USA; Tomato Hill (OMNH V706), middle Antlers Formation (Aptian-Albian), southeastern Oklahoma, USA.

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

Description

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

Lower premolars.—The holotype of *S. eruptens* (SMP-SMU 61192; Fig. 9D-E) was interpreted by Davis (in press) to preserve the p2, p3, dp4, and dp5. Both deciduous premolars are strongly molariform but have low trigonids bearing a small, procumbent, and buccally positioned paraconid as well as a relatively broad, well developed talonid. CT data revealed the presence of two permanent premolars developing within the jaw (Kobayashi et al. 2002; Davis in press). The permanent p4 is large and trenchant with a single small heel cusp, while only the tip of the principal cusp of the p5 is calcified. PM 1098 (Fig. 9A) is an ultimate lower premolar missing the mesial half of the principal cusp. This cusp was tall and conical, and there is no evidence that it was flanked by a metaconid or paraconid. A crest descends the main cusp to meet a small but prominent heel cusp. This cusp is situated on the buccal side of the talonid, and is connected by a weak crest to an additional, distolingually positioned cusp. A faint ridge encloses the lingual margin of the talonid. This specimen agrees well in size with *S. eruptens*, and is most likely a p5 based on its semi-molariform morphology (the p4 should have a much taller, trenchant principal cusp).

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

Family indet.

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

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

Locality.—Greenwood Canyon (Triconodont Gully), upper Antlers Formation (Aptian-Albian), north-central Texas, USA.

Description

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

Upper molar.—PM 1075 (Fig. 10A) is an ultimate upper molar. The metacone and metastylar lobe are very strongly reduced; the parastylar lobe and protoconal region are of equal width. The preparacrista is strong and meets the stylocone, which is subequal to the parastyle. No ectoflexus is present. The protocone is low but distinct, and no conules are evident. The preprotocrista is wide and continuous to the parastyle. This molar is superficially similar to the M4 of *Pappotherium pattersoni*, except that the distal portion of the crown is more reduced. It cannot be determined from the data on hand if PM 1075 is an M4, which are typically reduced in the larger taxa from the Trinity Group (such as

Pappotherium and *Oklatheridium*), or an M3 from a smaller taxon (such as *Kermackia* or *Slaughteria*).

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

Discussion

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

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

We argue that the earliest fossil eutherians cannot be identified solely on the basis of dental formula or characters derived from the lower dentition; these features may serve to differentiate eutherians from metatherians, but they do not reflect any departure from the presumed primitive tribosphenidan morphology (see review in Davis in press). There are, however, upper molar characters that are shared across early eutherians: reduction in the size of the stylocone and a wide, flange-like parastylar lobe on mesial molars. In this regard, *Holoclemensia* is considered a eutherian—it retains the primitive tribosphenidan postcanine dental formula and semi-molariform ultimate premolar, but it has upper molars that are structurally similar to and share the above features with early eutherians such as *Prokennalestes* and *Paranyctoides* (Fig. 11).

Our interpretation of the upper molar morphology of *Holoclemensia* provides additional evidence removing it from the basal metatherian position it has occupied in recent analyses (e.g., Rougier et al. 2004; Luo et al. 2007). Historically, this taxon has been allied with marsupials based predominantly on the presence of a large central stylar cusp, or by the presumed presence of four upper molars (Slaughter 1968b; Fox 1975).

Among Late Cretaceous taxa (which were the closest references available at the time), eutherians tend to have a reduced stylar shelf lacking major stylar cusps. Marsupials such as *Alphadon* have a suite of well developed stylar cusps on a wide shelf, with the centralmost (cusp C) often being the largest. However, a number of older, more primitive metatherians have been described in recent decades (e.g., *Iqualadelphis* Fox, 1987, *Kokopellia* Cifelli, 1993, *Aenigmadelphys* Cifelli and Johanson, 1994), and it is now clear that the primitive metatherian and eutherian conditions are probably the same—the stylar shelf was wide, and stylar cusps other than the stylocone are either lacking or represented by a small, distal cusp (cusp D). The large mesostyle in *Holoclemensia* represents a curious apomorphy and is immaterial to its broader relationships. The identification of *Holoclemensia* as a eutherian is significant in that it becomes the oldest representative from North America for which portions of both the upper and lower dentitions are known, and demonstrates that a wider diversity of eutherians was likely present in North America in the Early Cretaceous than previously thought. Our results corroborate the recent analysis of Averianov et al. (2010), who refer specimens to *Holoclemensia* in the same manner and are the only others to place this taxon at the base of the Eutheria.

***Pappotherium* as a metatherian.—**The holotype of *Pappotherium pattersoni* preserves two upper molars, the distal of which has a strongly reduced metacone and metastylar lobe (Fig. 5D). This association provides more insight than usual into the reconstruction of the number of upper molars in a fragmentary Cretaceous therian, and has fueled debate about this taxon. Early authors described the two preserved molars as the M2 and M3

(Slaughter 1965; Crompton 1971), and a more thorough analysis was performed by Fox (1975). Using comparisons of occlusal outlines between the deltatheroidan *Deltatheroides*, the stem tribosphenidan *Potamotelses*, and Cretaceous eutherians, Fox concluded that *Pappotherium* had three upper molars. His argument centered on the retention of a relatively wide metastylar lobe on the mesial molar of the holotype, and that it agreed with the M2 of deltatheroidans and eutherians (Fox argued that, for the specimen to represent the M3 and M4, there must be strong distal reduction of both molars). Butler (1978) countered that the penultimate upper molar in Late Cretaceous marsupials (the M3) has a very wide metastylar lobe, and that distal suppression of the penultimate molar could correlate with evolution toward loss of the M4, with no bearing on the condition in *Pappotherium*. Butler counted four molars in *Pappotherium*, based on his interpretation of the morphology of the holotype and the referral of other isolated upper molars in the sample to mesial loci.

Our revision of the sample from the Trinity Group largely corroborates Butler's (1978) specimen referrals, and supports the presence of four upper molars in *Pappotherium*. Moreover, the discovery of a much better preserved specimen of *Deltatheroides* (Rougier et al. 2004) disputes Fox's (1975) favorable comparison between this taxon and *Pappotherium*; instead, the M3 and M4 of each seem to agree very closely. Recent analyses that have included *Pappotherium* are non-committal on the number of molars in this taxon (Rougier et al. 2004; Ji et al. 2006; Averianov et al. 2010). Unfortunately, there are no data bearing on premolar count in *Pappotherium* ; the presence of three premolars (as in deltatheroidans and other metatherians) or four (as in the aegialodontid *Kielantherium* or the putative stem metatherian *Sinodelphys*;

Dashzeveg and Kielan-Jaworowska 1984; Luo et al. 2003) cannot be established. Assuming that deltatheroidans are basal metatherians (and the evidence is strong; see Rougier et al. 2004), the molar features typically used to characterize Late Cretaceous metatherians are absent at the base of the clade; deltatheroidans lack twinning of the hypoconid and hypoconulid, and a buccal postcingulid. As noted above, postcanine dental formula is a poor character for uniting the Eutheria, but it appears that the development of four molars among tribosphenidans is rare enough to be of some utility alone in establishing relationships with the Metatheria. Talonid morphology is unknown in *Pappotherium*, but it shares the presence of four molars (and a larger, more derived protocone) with only deltatheroidans and other metatherians. It is most parsimonious to assume, as a working hypothesis, that *Pappotherium* represents a basal metatherian. Also worth noting are similarities between *Pappotherium* and deltatheroidans (Butler and Kielan-Jaworowska 1973). In occlusal outline and general structure, upper molars of *Pappotherium* differ from deltatheroidans only in some proportions of the paracone and metacone (see Figs. 2, 3, 5). Upper molars of *Pappotherium* suggest that postvallum/prevallid shearing was well developed, as in deltatheroidans. However, this is not reflected in relative development of trigonid cusps and shearing crests on lower molars. It is conceivable that *Pappotherium* is a stem deltatheroidan, but present evidence is permissive, not indicative, of such a relationship.

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

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

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

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

Molar function in *Kermackia*.—The lower molars of *Kermackia* are very distinctive (Fig. 8), and are likely indicative of specialized occlusal function divergent from the basic tribosphenic pattern. The most prominent feature of the lower molar is the hypertrophied distal metacristid, which is developed into a strong ridge and descends from the apex of the metaconid nearly to the hypoconid. A short cristid obliqua meets the distal metacristid well distal to the trigonid wall, and a strong notch is developed at this junction. Elongation of the distal metacristid creates a wide embrasure to accept the upper molar paracone during occlusion, with the broad buccal surface of the distal metacristid serving as the primary structure for guiding and shearing against both the lingual and distal surfaces of the paracone as the jaws close. The hypocristid is comparatively very short, and in many specimens the hypoconulid is set almost directly distal to the hypoconid instead of at an oblique angle. The shallow and comparatively small contact surface for the metacone suggests that this cusp was substantially smaller and buccally offset relative to the paracone.

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

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

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

Conclusions

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

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Table Titles

Table 1: Measurements of the deltatheroidan *Atokatheridium boreni* from the Early Cretaceous of Oklahoma. Abbreviations: AP, anteroposterior (mesiodistal) length; ANW, anterior (mesial) width; POW, posterior (distal) width. Measurements are in millimeters.

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

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

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

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

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

Table 7: Measurements of the tribosphenidan *Kermackia texana* from the Early Cretaceous of Oklahoma and Texas. Numbers in brackets indicate estimates.

Abbreviations: AP, anteroposterior (mesiodistal) length; ANW, anterior (mesial) width; POW, posterior (distal) width. Measurements are in millimeters.

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

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

Figure Captions

Figure 1: Early Cretaceous mammal localities, Trinity Group, Texas and Oklahoma. A, Map detailing outcrop of Antlers Formation (shaded) in southeastern Oklahoma. McLeod Honor Farm (OMNH microvertebrate locality V706) indicated by dot. B, Map detailing mammal-bearing microvertebrate localities from the Trinity Group (Aptian–Albian): 1, McLeod Honor Farm; 2, Greenwood Canyon; 3, Butler Farm (all Antlers Formation); 4, Paluxy Church (Twin Mountains Formation, late Aptian). From Davis et al. 2008.

Figure 2: The deltatheroidan *Atokatheridium boreni* from the Early Cretaceous of Oklahoma. A, OMNH 61151, LM1 in occlusal (A_1) and buccal (A_2) views; B, OMNH 61623, RM2 (holotype) in occlusal (B_1) and buccal (B_2) views; C, OMNH 63725, LM3 in occlusal (C_1) and buccal (C_2) views; D, OMNH 63724, Lm1 in occlusal (D_1) and lingual (D_2) views; E, OMNH 61624, Lmx in occlusal (D_1) and lingual (D_2) views; F, OMNH 63891, Lmx in occlusal (D_1) and lingual (D_2) views.

Figure 3: The deltatheroidans *Oklatheridium szalayi* (A–E) and *O. minax* sp. nov. (F–H) from the Early Cretaceous of Oklahoma and Texas. A, OMNH 62411, LM1 in occlusal (A_1) and buccal (A_2) views; B, PM 1238, LM1 in occlusal (B_1) and buccal (B_2) views; C, OMNH 62410, LM2 (holotype) in occlusal (C_1) and buccal (C_2) views; D, OMNH 61180, LM2 in occlusal (D_1) and buccal (D_2) views; E, OMNH 63987, RM3 in occlusal (E_1) and buccal (E_2) views; F, PM 884, LM1 in occlusal (F_1) and buccal (F_2) views; G, OMNH 33455, LM2 (holotype) in occlusal (G_1) and buccal (G_2) views; H, OMNH 63727, RM3 in occlusal (H_1) and buccal (H_2) views

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

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

Figure 6: The basal eutherian *Holoclemensia texana* from the Early Cretaceous of Oklahoma and Texas. A, PM 1000, Lm1 in occlusal (A_1) and buccal (A_2) views; B, PM 1004, RM1 in occlusal (B_1) and buccal (B_2) views; C, SMP-SMU 61997, RM2 (holotype) in occlusal (C_1) and buccal (C_2) views; D, PM 889, RM2 in occlusal (D_1) and buccal (D_2) views; E, SMP-SMU 62009, RM3 in occlusal (E_1) and buccal (E_2) views; F, SMP-SMU 71848, LDP5 in occlusal (F_1) and buccal (F_2) views; G, SMP-SMU 61948, LP4 in occlusal (G_1) and buccal (G_2) views.

Figure 7: The basal eutherian *Holoclemensia texana* from the Early Cretaceous of Oklahoma and Texas (A–E). A, SMP-SMU 62399, Lp5 (holotype of *Comanchea hilli* Jacobs et al., 1989) in occlusal (A_1) and lingual (A_2) views; B, SMP-SMU 61727, Lm1 in occlusal (B_1) and lingual (B_2) views; C, PM 887, Rm1 in occlusal (C_1) and lingual (C_2) views; D, PM 1005, Rm2 in occlusal (D_1) and lingual (D_2) views; E, OMNH 62412, Rm3

in occlusal (E_1) and lingual (E_2) views; F, SMP-SMU 61726, Lmx referred to *Holoclemensia* sp. in occlusal (F_1) and lingual (F_2) views.

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

Figure 9: The tribosphenidan *Slaughteria eruptens* from the Early Cretaceous of Oklahoma and Texas. A, PM 1098, Rp5 in in occlusal (A_1) and lingual (A_2) views; B, OMNH 63726, Rmx in occlusal (B_1) and lingual (B_2) views; C, OMNH 63721, Rmx in occlusal (C_1) and lingual (C_2) views; D, SMP-SMU 61992, left dentary fragment with p2, p3, dp4, and dp5 (holotype) in occlusal (D_1) and lingual (D_2) views; E, 3-D reconstruction of SMP-SMU 61992 from CT data (in lingual view, bone removed), with developing p4 and p5 indicated (Davis).

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

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

Table 1

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

Table 2

Locus	Specimen Number	AP	ANW	POW
M1	OMNH 62411	1.27	1.4	1.76
	PM 1238	[1.12]	-	-
M2	OMNH 61180	1.45	-	-
	OMNH 62410	1.51	-	-
M3	OMNH 63987	[1.45]	-	-

Table 3

Locus	Specimen Number	AP	ANW	POW
M1	PM 884	[1.63]	-	-
M2	OMNH 33455	[1.68]	-	-
M3	OMNH 63727	[1.33]	-	-

Table 4

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

Table 5

Locus	Specimen Number	AP	ANW	POW
M1	PM 999	1.26	-	-
M2	PM 1749	[1.49]	-	-
M3	OMNH 61185	[1.43]	1.89	-
	PM 1015	[1.25]	-	-
	SMP-SMU 61725	1.38	1.84	1.66
M4	SMP-SMU 61725	0.86	-	-
mx	OMNH 61219	-	1.16	-
	OMNH 62427	-	0.97	-
	OMNH 63729	-	1.00	-
	PM 930	-	0.90	-
	PM 1119	-	0.92	-
	PM 1249	-	0.95	-

Table 6

Locus	Specimen Number	AP	ANW	POW
P4	SMP-SMU 61948	1.8	1.04	-
DP5	SMP-SMU 71848	1.25	1.25	1.45
M1	PM 1000	1.52	-	-
	PM 1004	[1.67]	-	-
M2	PM 886	[1.71]	-	-
	SMP-SMU 61997	1.67	-	-
M3	SMP-SMU 62009	1.26	2.43	1.65
p5	SMP-SMU 62399	1.43	0.90	-
m1	PM 887	-	1.30	-
	PM 966	-	1.20	-
	SMP-SMU 61727	1.94	1.30	1.10
m2	PM 1005	1.91	1.38	1.03
	PM 3877	-	1.34	-
	SMP-SMU 62131	1.90	1.21	0.85
	SMP-SMU 62721	2.05	1.48	1.19
m3	OMNH 62412	1.49	1.09	0.70
mx	OMNH 62414	-	-	1.01
	OMNH 63894	-	-	0.97
	SMP-SMU 62722	-	-	1.04

Table 7

Locus	Specimen Number	AP	ANW	POW
M1	SMP-SMU 62402	0.93	1.12	1.28
p5	OMNH 67134	[1.27]	-	-
m3	SMP-SMU 61728	1.25	0.77	0.52
mx	OMNH 61178	-	0.83	-
	OMNH 63731	-	-	0.57
	OMNH 63893	-	0.73	-
	PM 922	1.30	0.72	0.58
	PM 1046	-	0.57	-
	PM 1245	1.25	0.70	0.52
	PM 1247			
	SMP-SMU 62398	1.16	0.57	0.44

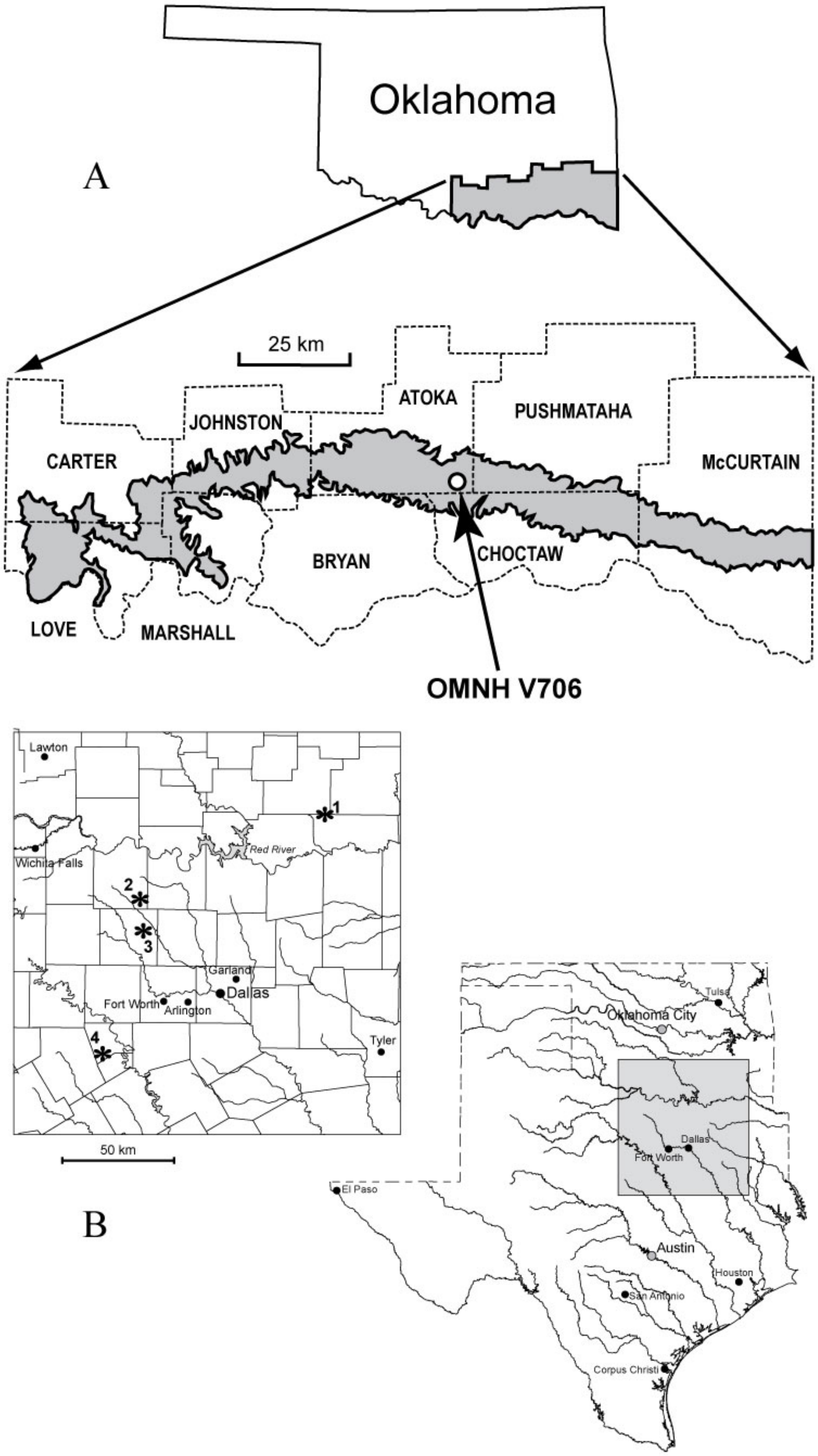
Table 8

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

Table 9

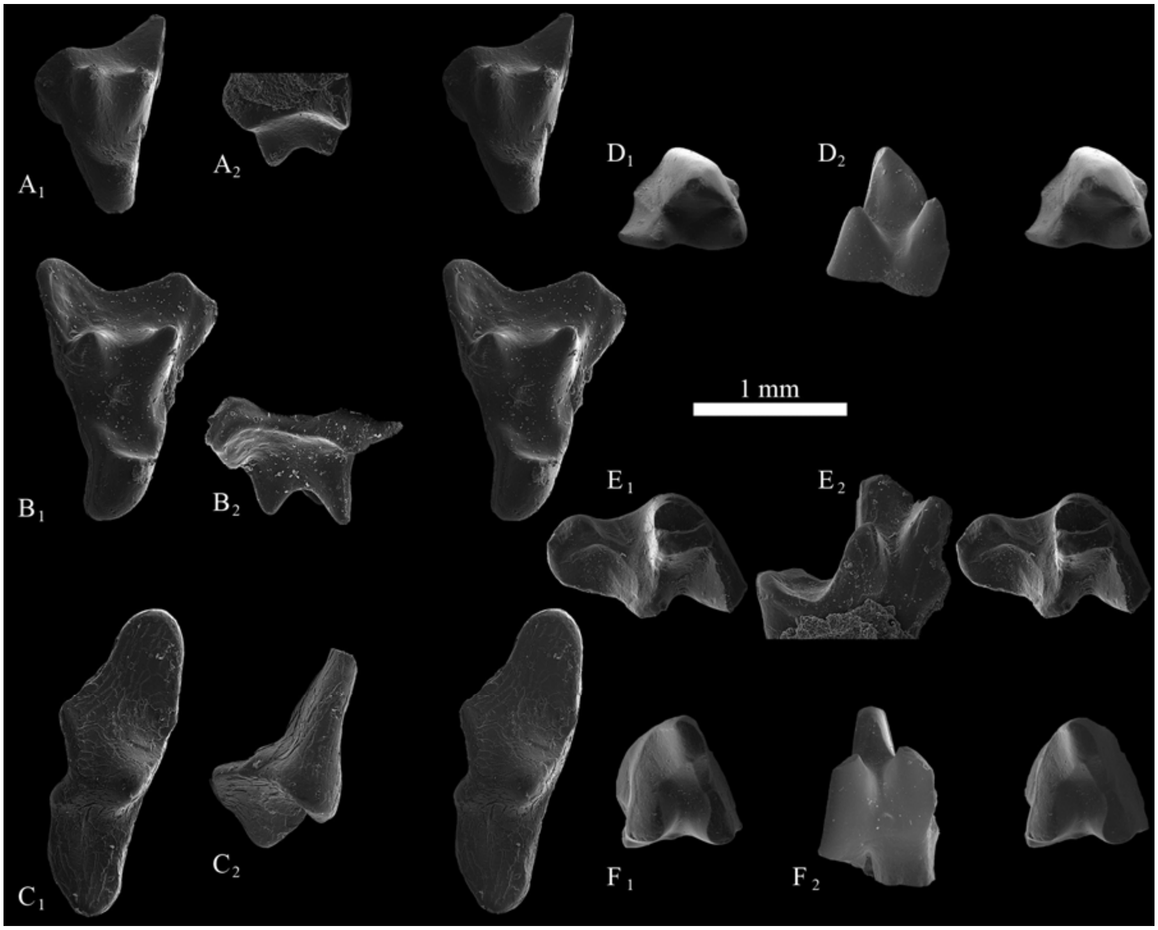
Locus	Specimen Number	AP	ANW	POW
M4	PM 1075	0.85	1.36	0.85
mx	PM 948	1.41	0.95	0.86

Figure 1



A
Oklahoma
25 km
CARTER
JOHNSTON
ATOKA
PUSHMATAHA
McCURTAIN
BRYAN
CHOCTAW
LOVE
MARSHALL
OMNH V706
B
Lawton
Wichita Falls
Red River
1
2
3
4
Garland
Dallas
Fort Worth
Arlington
Tyler
50 km
Tulsa
Oklahoma City
El Paso
Austin
Houston
San Antonio
Corpus Christi

Figure 2



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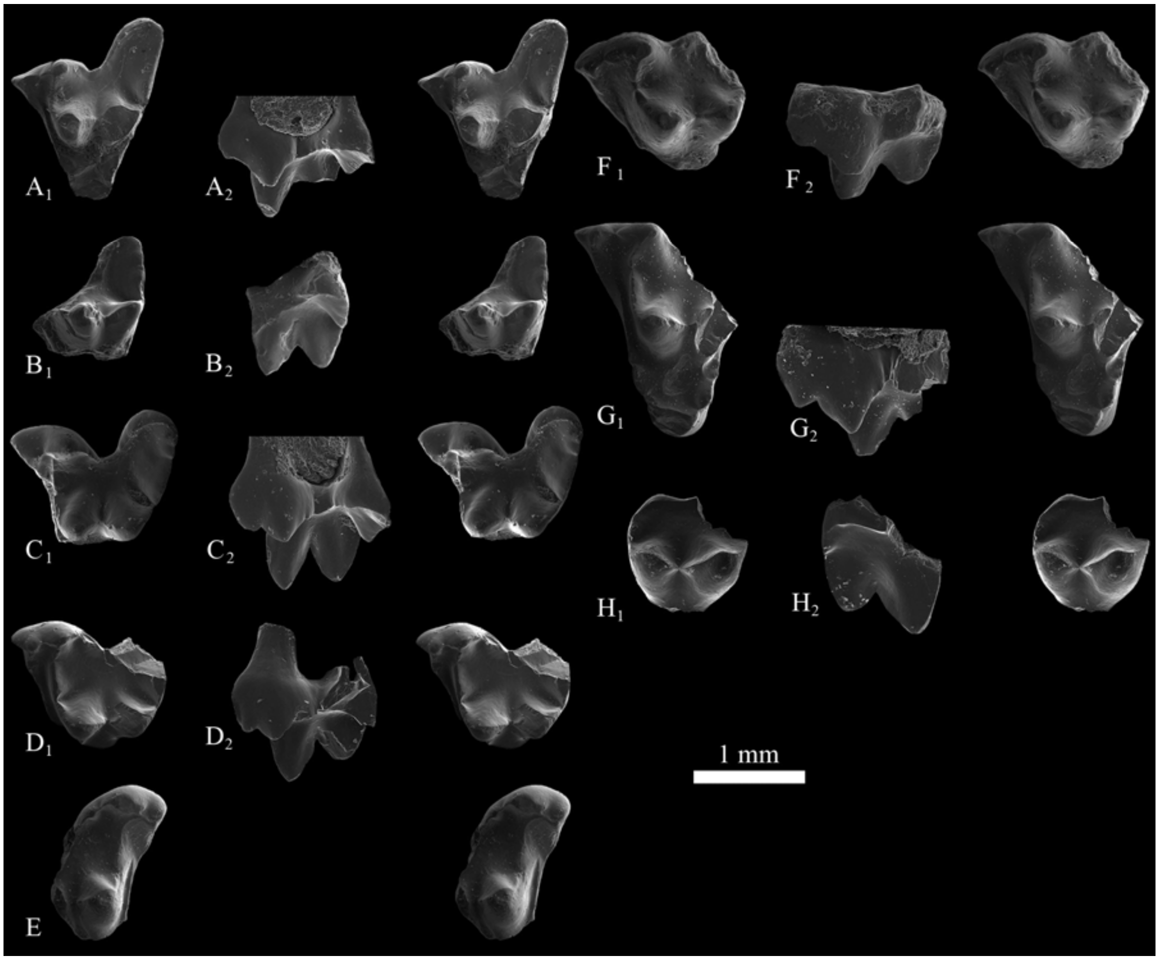

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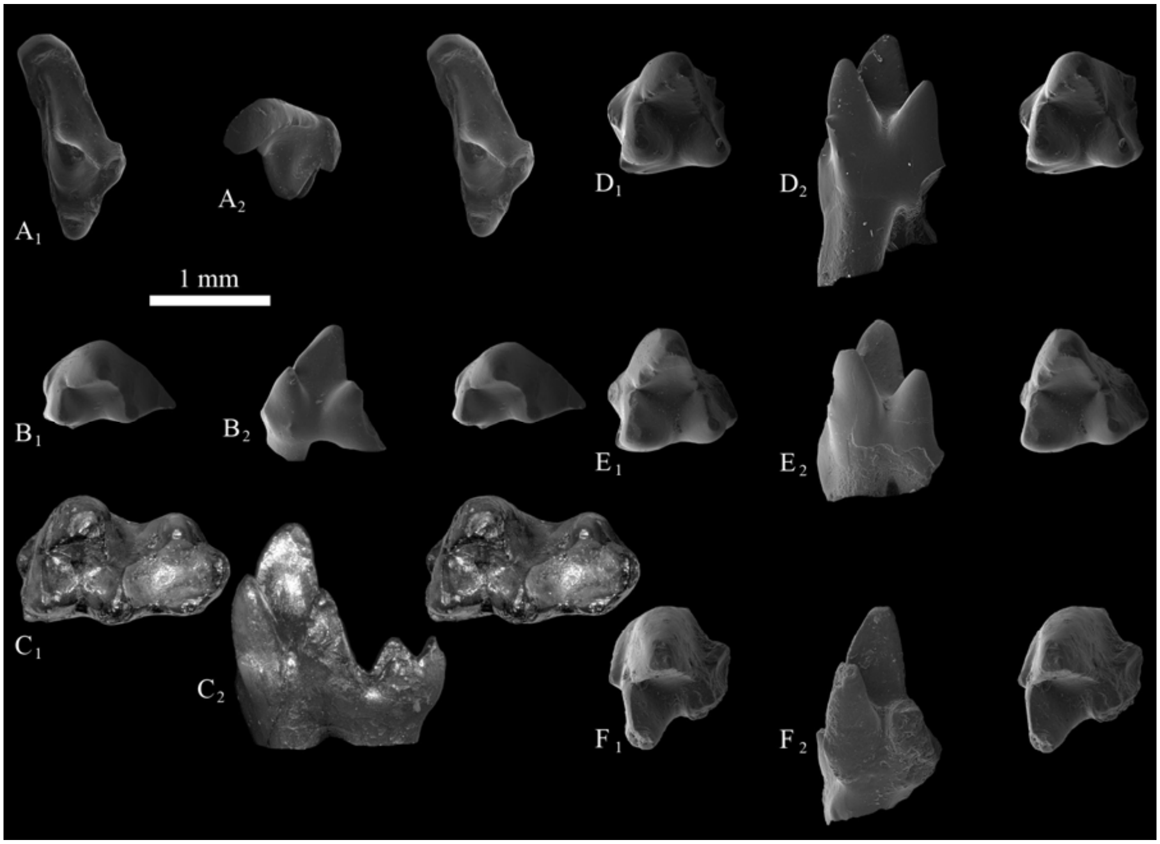


Figure 5

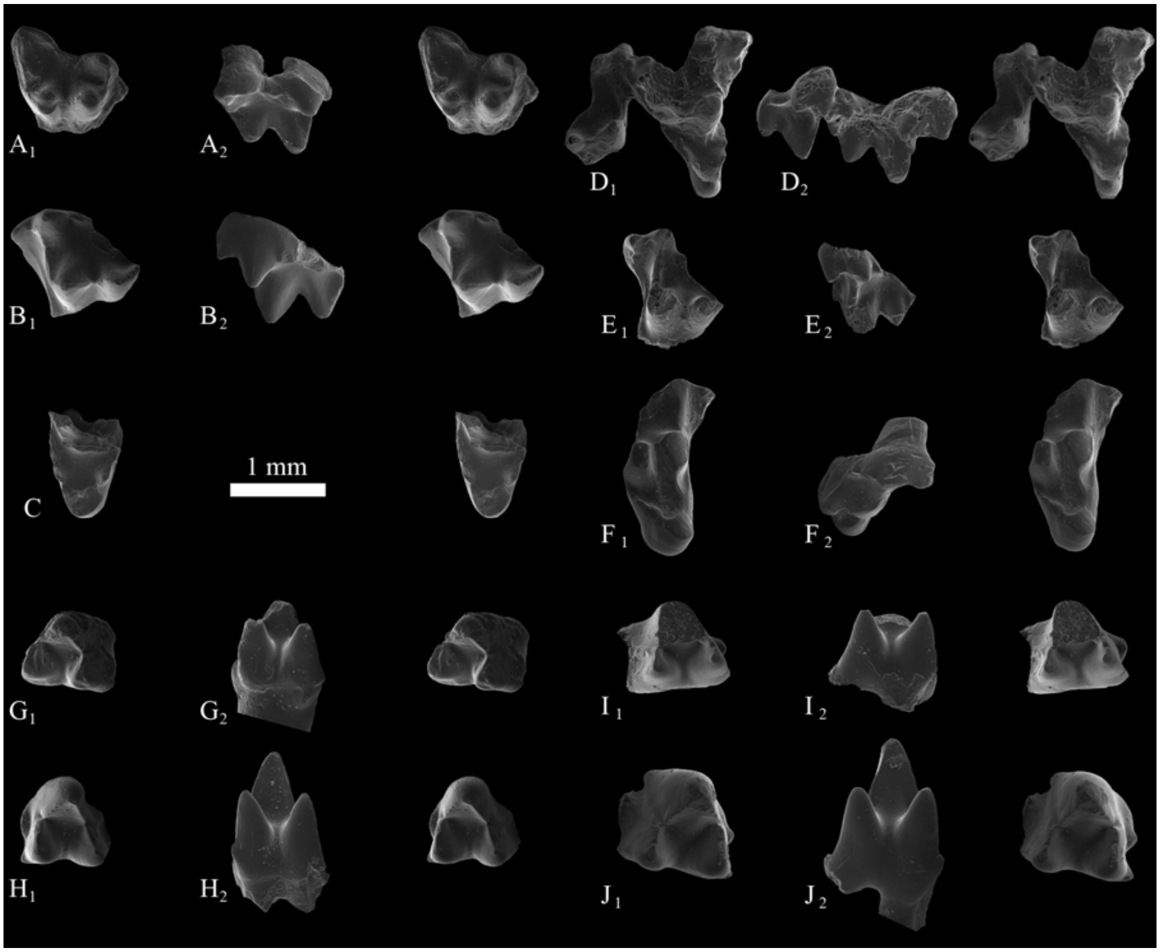


Figure 6

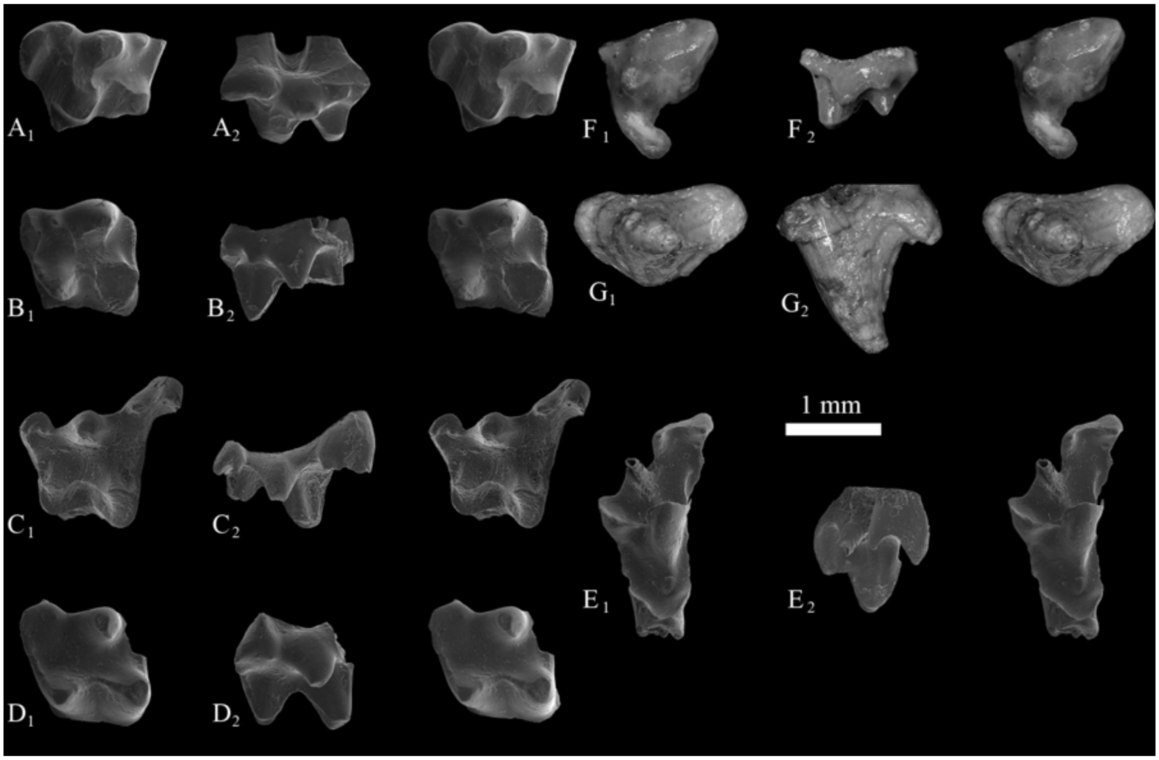


Figure 7

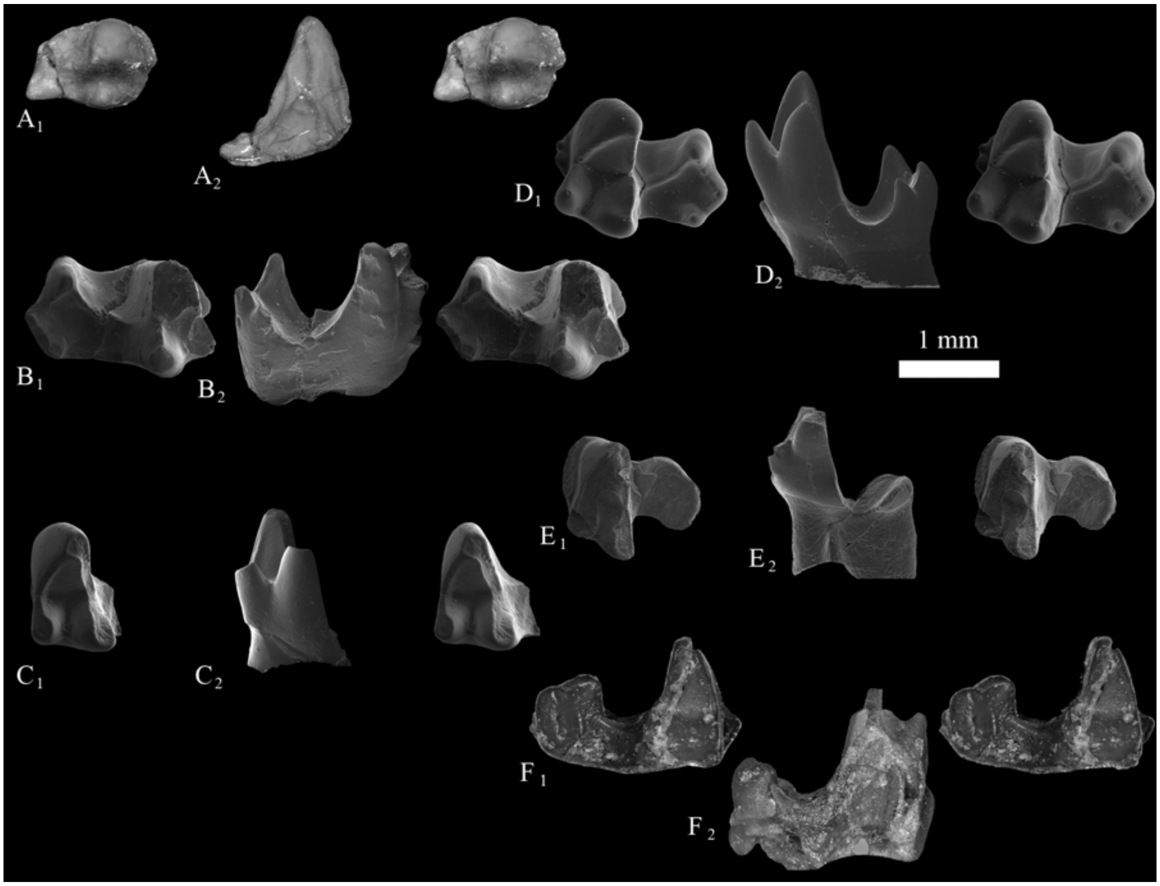


Figure 8

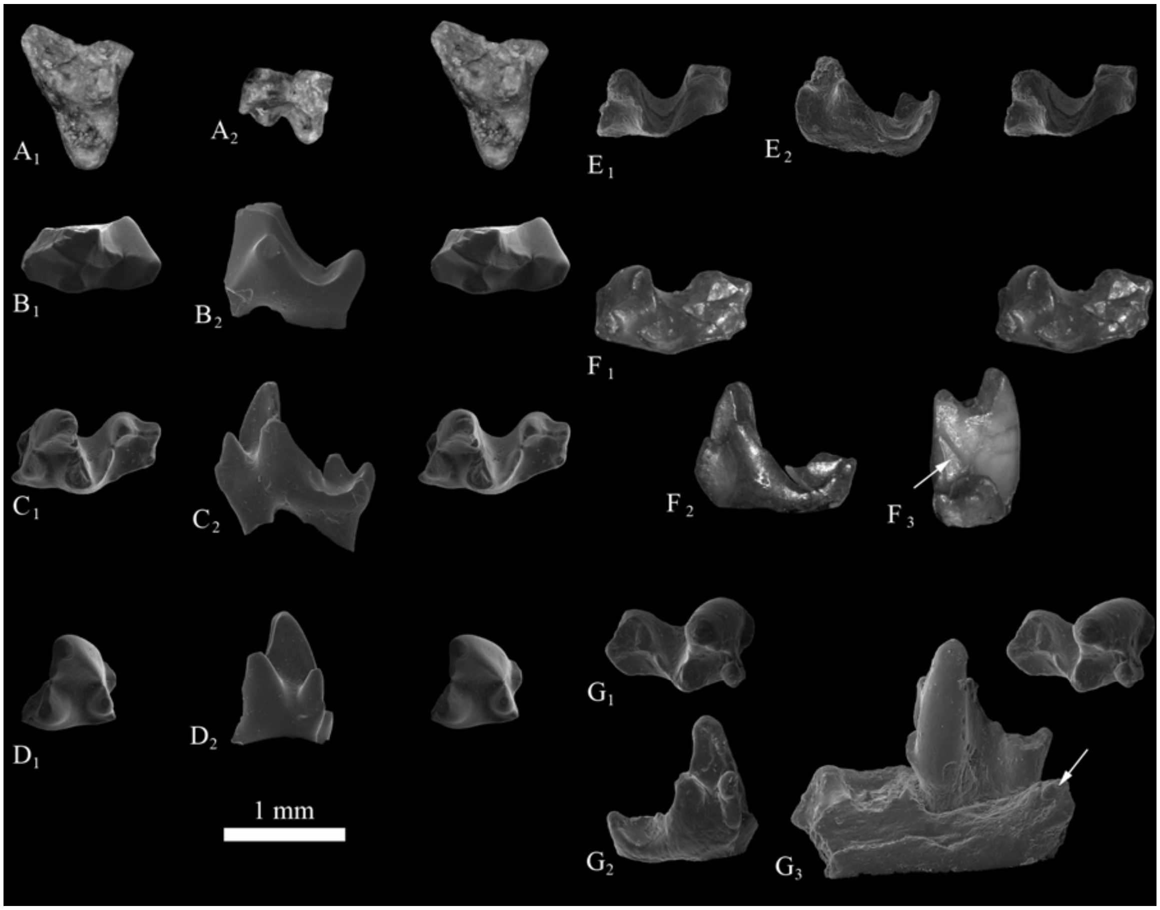


Figure 9

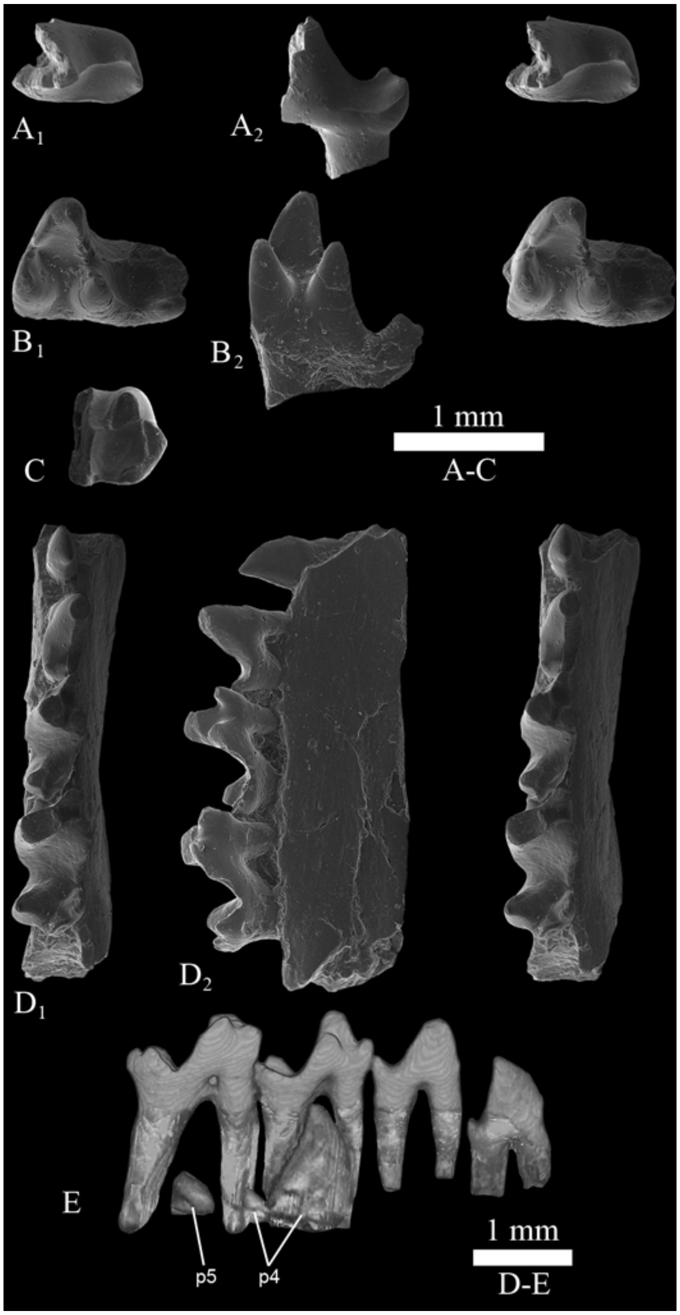


Figure 10

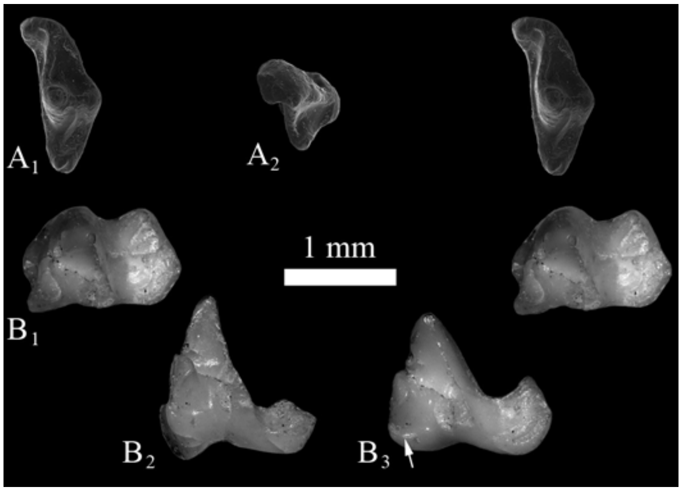
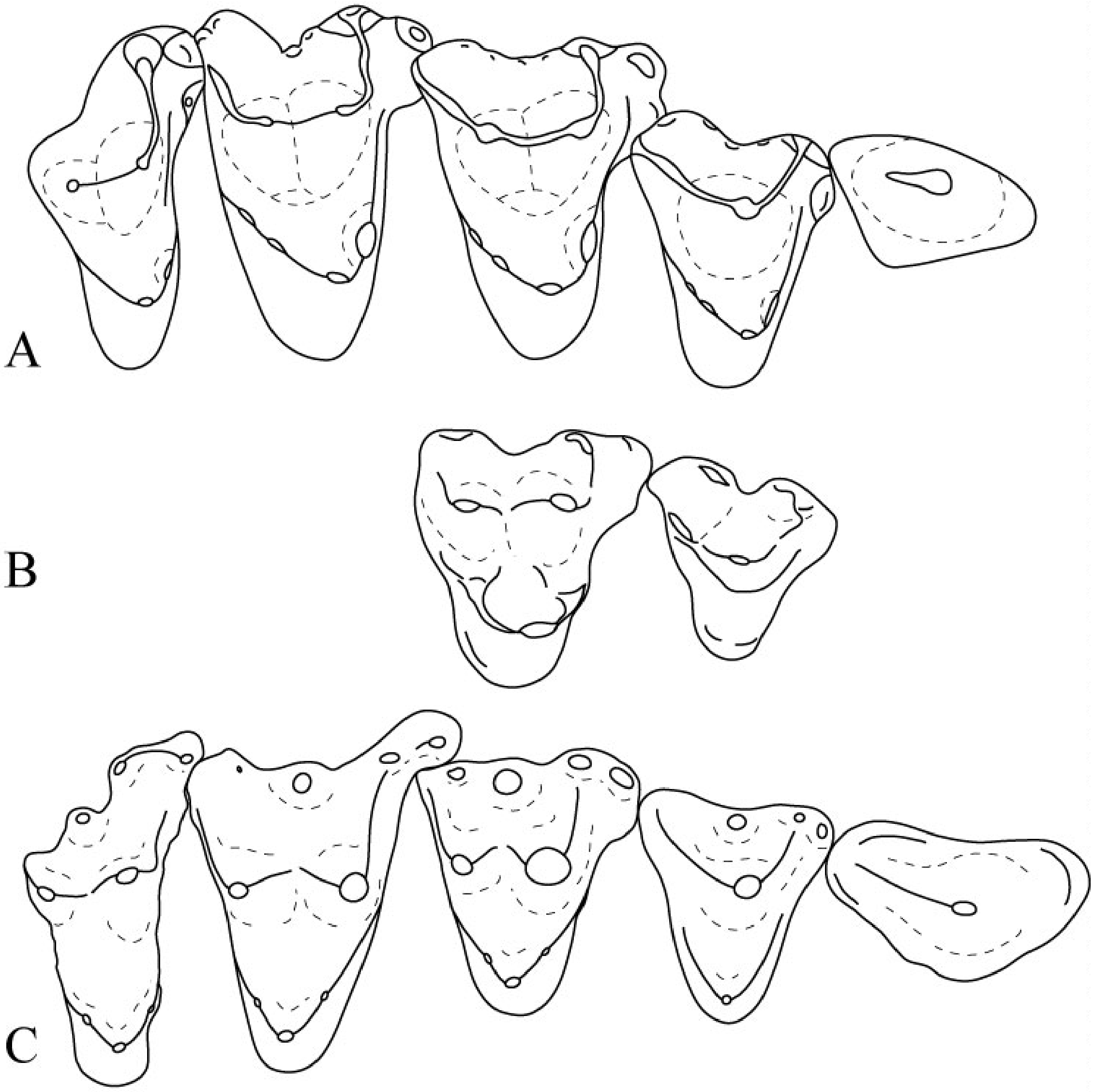


Figure 11



MICRO-COMPUTED TOMOGRAPHY REVEALS A DIVERSITY OF PERAMURAN MAMMALS FROM THE PURBECK GROUP (BERRIASIAN) OF ENGLAND

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Abstract: The known sample of the important pre-tribosphenic mammal *Peramus tenuirostris*, housed in the Natural History Museum (London, UK), was imaged using micro-computed tomography (CT). Substantial morphological diversity was discovered, prompting establishment (and resurrection) of additional taxa from within the original hypodigm of *Peramus tenuirostris*: *Peramus dubius* comb. nov., *Kouriogenys minor* gen. nov., and *Peramuroides tenuiscus* gen. et sp. nov. The Peramura are revised; this group is restricted to taxa with clear evidence of a fully-functional upper molar embrasure for the dominant lower molar talonid cusp (hypoconid), either through development of wear facet 4 or differentiation of a distinct hypoconulid. The Peramura are the most likely sister-taxon to the Tribosphenida (including living marsupials and placentals) and represent a distinct molar morphotype, transitional between primitive lineages characterized by dominant orthal shear (e.g. dryolestoids) and those with modern, multi-functional tribospheny. A very large masseteric foramen is identified in peramurans, but this feature appears to be autapomorphic and of uncertain function.

Keywords: Peramura, Mammalia, tribosphenic, Purbeck Group, Early Cretaceous.

THE HISTORY of modern paleontology can largely be traced back to early 19th century discoveries in England. For example, iconic dinosaurs such as *Megalosaurus* Buckland, 1824 and *Iguanodon* Mantell, 1825 were among the few genera included in the original concept of the Dinosauria by Sir Richard Owen (1842). The study of fossil mammals is also intimately tied to early British work. A half-century before anyone began exploiting the badlands of the American Interior West, W. Broderip (1828) described the first fossil mammals known from Mesozoic rocks, discovered in a quarry near Stonesfield in southern England. In his 1871 monograph, Owen described a highly significant collection of fossil mammals from outcrops of the Lower Cretaceous Purbeck Group (specifically within the Lulworth Formation) at Durlston Bay in the far south of England. His account was updated by G. G. Simpson (1928) to include new ideas on taxonomy and additional specimens subsequently obtained from the collection of Samuel Beckles. Simpson provided a very cogent synthesis of the phylogenetic work done on all the various lineages of Mesozoic mammals known at the time, and settled on a high-level classification which, except for his hypothesis of multiple mammalian origins, largely still stands today.

Of all the known groups of Mesozoic mammals, one taxon, *Peramus*, has a particular relevance to discussions of molar evolution for its generally-accepted transitional morphology between well-known Jurassic groups (such as dryolestoids) and higher mammals. This has not always been the case; early evaluation of *Peramus* was hampered by poor preservation and especially preparation of material. Tiny fossil dentaries were typically left with only the lingual or labial side exposed, so complete knowledge of the morphology of a single specimen was often lacking and referral of specimens known by different views was difficult. Owen (1871) described several taxa from the Purbeck Group which would be merged into *Peramus tenuirostris* by Simpson (1928). *Peramus* was originally placed (though with some uncertainty) in the Paurodontidae (Simpson 1928), and there it would remain until the 1960s, when several specimens were fully freed from matrix by Arthur Rixon and additional specimens were discovered in the NHM collections. A more complete picture of the morphology of the sample became known, and subsequent studies (Mills 1964; Clemens and Mills 1971) revealed that *Peramus* was substantially different from the paurodontids with which it had been historically classified. Mills (1964) allied *Peramus* with *Amphitherium*, which he reconstructed as being functionally very similar, in the Amphitheriidae. The discovery of upper molars, described by Clemens and Mills (1971), led these authors to place *Peramus* in a new family, the Peramuridae (this family was established earlier by Kretzoi 1946, but within the Docodonta, receiving no later support). While removing *Peramus* itself from the direct ancestry of modern mammals, it was proposed that marsupials and placentals were probably derived from peramurids.

In his 1975 classification, McKenna established the Peramura as an infraclass under the Zatheria, with equal rank to the more derived Tribosphenida. The organization and contents within the Peramura have, however, become somewhat unstable in recent decades. Taxa specifically allied with *Peramus* include: *Abelodon* (Brunet *et al.* 1990), *Palaeoxonodon* (Freeman 1979), *Pocamus* (Canudo and Cuenca-Bescós 1996), and *Tendagurutherium* (Heinrich 1998). Of these, *Pocamus* has been synonymized with dryolestid taxa (see Martin 1999; Kielan-Jaworowska *et al.* 2004), and *Abelodon* and

Palaeoxonodon were moved to Zatheria *incertae sedis* by Sigogneau-Russell (1999) (though the latter was retained in the Peramuridae by Martin 2002).

The Peramura (though essentially restricted in practice to *Peramus*) are still widely regarded as the sister-taxon to the Tribosphenida. This study aims to reevaluate the morphology and taxonomy of the historically and scientifically important sample originally referred to *Peramus tenuirostris*. These specimens, along with some fragmentary remains from Africa (see Systematic Palaeontology section), represent a clear transitional step towards the evolution of tribospheny and the rise of modern mammals during the Cretaceous. A more thorough understanding of peramuran morphology and relationships is critical to evaluating their role in the deep evolutionary history of mammals.

Conventions

Identification and numbering of occlusal wear facets follows Crompton (1971), and molar terminology is shown in Text-figure 1. The term Tribosphenida McKenna, 1975 is used in preference over Boreosphenida Luo, Cifelli, and Kielan-Jaworowska, 2001 (see Davis 2011). A postcanine dental formula for *Peramus* of five premolars and three molars, originally established by McKenna (1975), is followed here (see recent summaries of postcanine homology in Averianov *et al.* 2010; Davis 2011). Table 1 lists the classification scheme followed in this paper. Measurements were taken from scan data and are provided in Tables 2–5, and follow Lillegraven and Bieber (1986); depth of the dentary (abbreviated DD) is measured on the lingual side of the dentary below the m2.

Institutional abbreviations

AMNH, American Museum of Natural History, New York, USA; BMNH, Natural History Museum, London, UK; SA (Synclinal d'Anoual), Muséum national d'Histoire naturelle, Paris, France; USNM, United States National Museum, Smithsonian Institution, Washington, USA.

MATERIALS AND METHODS

All specimens described in this paper are housed in the Natural History Museum (London, UK), and were collected from a single locality in the lower part of the Purbeck Group: Durlston Bay (= Durdlestone Bay), Dorsetshire, England, in the Lulworth Formation. Specific details of the discovery within the Natural History Museum collections of some of the specimens treated in this paper, and their subsequent preparation, can be found in Mills (1964) and Clemens and Mills (1971). For more on the history of the mammalian fauna collected from the Purbeck Group, see Kielan-Jaworowska *et al.* (2004: 54) and references cited therein.

All specimens were studied first-hand and imaged using micro-CT. This technology has the advantage of not only providing insights on internal morphology, but also allowing the digital removal of barriers such as preservatives and matrix. However, some features such as wear facets are difficult to discern from CT data, so if unobservable on the original specimen (due to preservation or preparation), these features generally remain so on the renderings. Scanning was performed at the Natural History Museum (London, UK) using a Metris X-Tek HMX ST 225 CT System (Nikon

Metrology, Leuven, Belgium). 3-D renderings of the scan data were done in VGStudio Max v.2.1 (Volume Graphics, Heidelberg, Germany).

SYSTEMATIC PALAEONTOLOGY

Superorder ZATHERIA McKenna, 1975

Order PERAMURA McKenna, 1975 (new rank)

Included families. Peramuridae Kretzoi, 1946 (type family, monotypic).

Definition. All taxa more closely related to *Peramus* than to stem zatherians *sensu* Martin (2002) (e.g. amphitheriids *sensu* Davis in review, *Arguimus*, *Nanolestes*) or tribosphenidans.

Remarks. The Peramura were established at the rank of infraclass by McKenna (1975), but the group is here placed at the ordinal level to emphasize its important role as a structural grade intermediate between stem zatherians and tribosphenidans (see Discussion).

Family PERAMURIDAE Kretzoi, 1946

Included genera. Peramus Owen, 1871 (type genus); *Kouriogenys* gen. nov.; *Peramuroides* gen. nov.; *Tendagurutherium* Heinrich, 1998; and a taxon left in open nomenclature by Sigogneau-Russell (1999).

Tentatively referred genera. *Afriquiamus* Sigongeau-Russell, 1999.

Diagnosis. Differ from stem zatherians and dryolestoids in posterior placement of mandibular foramen, presence of a separate hypoconulid on the m2 (variably present on other molars), and in lingual position of metacone with development of wear facet 4 (*sensu* Crompton 1971) on upper molars; differ from groups other than paurodontids in parallel dorsal and ventral margins of dentary; differ from all taxa (with the possible exception of *Ornithorhynchus*) in presence of a very large masseteric foramen which joins the mandibular canal posterior to or below the molar series.

Remarks. Two taxa from the Berriasian Synclinal d'Anoual of Morocco, each known by a single upper molar (see Sigogneau-Russell 1999 for full descriptions), are here included in the Peramuridae based on shared characters with the upper dentition of *Peramus*. SA 59, left in open nomenclature by Sigogneau-Russell (1999: figs 27–28), is a transversely compressed molar with two roots. It has a lingually positioned metacone with a distinct anterior wear facet (facet 4 of Crompton 1971), suggesting that this taxon had lower molars with a hypoconulid well separated from the hypoconid. In this same paper, a P5 was referred to *Peramus* sp. (SA 37; Sigogneau-Russell 1999: figs 29–30). It does closely resemble the P5 of BMNH M21887 (*Peramus dubius*; see below), but it is equally likely that it belongs to the same taxon as SA 59. *Afriquiamus* is only tentatively placed in the Peramuridae because its metacone is not as lingually positioned as in other peramurids, though it is described as bearing a weak wear facet 4 (Sigogneau-Russell 1999: 120). It also appears from the published photograph that the preparacrista runs to the parastyle instead of the stylocone, suggesting that the stylocone did not participate in shear against the protoconid (see Sigogneau-Russell 1999: fig. 25). Further taxonomic work is postponed until better material from this important unit is known. *Tendagurutherium*, known by a dentary fragment from the Late Jurassic Tendaguru beds of Tanzania (Heinrich 1998), is more confidently included in the Peramuridae. It shares with other peramurans the posterior placement of the mandibular foramen and shows evidence it may have had a large masseteric foramen (it has a deep masseteric fossa which terminates in a pocket; Heinrich 1998: 277). The trigonid of the single known molar has large e and f cusps, but the talonid is damaged. It is described as bearing a single cusp, but with wear on the anterior and posterolabial faces (Heinrich 1998: 279); this suggests the presence of an upper molar embrasure for the hypoconid, as seen in other peramurids, and due to damage the existence of a differentiated hypoconulid cannot be ruled out. A number of other taxa placed as Peramura *incertae sedis* by Kielan-Jaworowska *et al.* (2004) are herein excluded, based on the absence of the peramurid characters listed above (see Discussion).

Distribution. Late Jurassic (Kimmerigian–Tithonian) of Tanzania; Early Cretaceous (Berriasian) of England and Morocco.

Genus Peramus Owen, 1871

Included species. *Peramus tenuirostris* Owen, 1871 (type species); *P. dubius* (Owen, 1871).

Revised diagnosis. Differs from other peramurid genera in presence of strongly-developed hypoconulid embrasure (cusps e and f); differs from *Afriquiamus* in smaller size, more lingually positioned metacone, presence of lingual cingulum, and presence of three roots on upper molars; differs from *Kouriogenys* in two-rooted p1, and p4 anteroposteriorly longer than or equal to p5; differs from *Peramuroides* in larger size, large size difference between p3 and p4, and m1 trigonid angle of 90 degrees; differs from *Tendagurutherium* in absence of evidence for coronoid bone, more ventrally positioned condylar process (even with alveolar margin), and paraconid higher than metaconid; differs from "Gen. et sp. indet." of Sigogneau-Russell (1999) in smaller size, and having transversely wider upper molars with a lingual cingulum and three roots.

Distribution. Purbeck Group, Lower Cretaceous (Berriasian) of England.

Peramus tenuirostris Owen, 1871

Table 2, Text-figures 2, 3A–B, 4

Holotype. BMNH M47742, a left dentary fragment preserving the coronoid and condylar processes, alveoli for the canine and p1–p4, and crowns of the p5 and m1–m3.

Referred material. BMNH M21888, a right dentary fragment preserving broken crowns for the p3–p5 and m1–m3.

Revised diagnosis. Differs from *Peramus dubius* in larger size, greater relative depth of dentary, alveoli for p4 substantially larger than p3, and strong posterior trend in reduction of molar size.

Distribution. As for the genus.

Description

BMNH M47742. M47742 (holotype; Text-fig. 2) represents the largest individual in the sample of peramurans from the Purbeck Group. It is a right dentary fragment broken anterior to the canine alveolus and preserving the rest of the element except for the angular process and the dorsal tip of the coronoid process. Roots of the p1–p4 and crowns of p5 and m1–m3 are preserved. The body of the dentary is parallel-sided and deep through the entire postcanine series. A portion of the symphysis is preserved, beginning below the anterior root of the p2. Two mental foramina are present, one below the anterior root of the p1 and the other below the anterior root of the p5. The masseteric fossa is very deep, with a pronounced anterior pocket. In section, it is unclear if this pocket extends into a foramen in a similar fashion as in other peramuran specimens (Text-fig. 3A; see Discussion for the distribution and relevance of this feature); there is a narrow canal extending anteriorly from the masseteric fossa, separate but parallel to the mandibular canal (similar to the condition in *Ornithorhynchus*; see Discussion). Either this feature was filled after burial, or it was simply much smaller in this specimen. Additionally, the lingual surface of the dentary has been crushed in this region, which could have collapsed the mandibular canal (and possibly also the masseteric foramen, if originally present). The coronoid process is tall and arcs posteriorly towards its tip. The condyle is abraded but appears to have been cylindrical and is positioned slightly above the alveolar margin. Meckel’s groove ends below the m2 and was likely prominent, but the lingual surface of the dentary is damaged below the ascending ramus. If a pterygoid shelf or medial ridge was present, it has been crushed. The mandibular foramen is located far posteriorly, just dorsal to the beginning of the angular process. Only the base of this process is preserved, but it is clearly identifiable by the contour of the ventral surface of the dentary.

Only the roots are preserved for p1–p4. The p4 was probably a very large, heavy tooth judging from the size of the roots and alveoli, which are far larger than any other locus in the specimen. The p5 is premolariform with a somewhat inflated, symmetrical main cusp. There is a prominent, projecting anterior basal cusp positioned slightly anterolingually. The heel is long and bears a single cusp, though there is some evidence for a tiny additional labial cuspule. The anterior cusp and the heel are nearly the same size. The main crests on this tooth were either low or have been abraded.

The m1 is taller than the p5 and has a trigonid angle of 90 degrees. The paraconid is a smaller cusp than the metaconid, but it is set higher on the slope of the protoconid. Cusp e is a small projection from the base of the paraconid, and cusp f is not evident. There is heavy wear in the hypoflexid from the upper molar paracone, and the distal metacristid is prominent. The topology of the talonid is difficult to interpret due to preservation, but at least the hypoconid and hypoconulid were present. There appears to be an additional rise in the center of the talonid, but it is unclear if this represents a "mesoconid" as in M48404 (as interpreted by Butler 1990, and also present in the stem zatherian *Nanolestes*; Martin 2002); this feature is either absent or not preserved on the other molars. There is weak evidence for wear facet 4 on the hypocristid.

The m2 is smaller than the m1, and its trigonid is poorly preserved; the protoconid is leveled and the metaconid is completely missing. The paraconid is complete and somewhat more delicate than on the m1. The trigonid angle is slightly more acute (estimated at 80 degrees). Cusps e and f are better developed and fully embrace the hypoconulid of the m1, but these cusps are still much smaller than on most other specimens of *Peramus*. The hypoconid and hypoconulid are better separated on the m2, and wear facet 4 is more evident. The m3 is substantially smaller and lower crowned than the other two molars. The paraconid is small but high as on the m2, and the metaconid is low and blunt. Cusp e is small as on the m1, and cusp f appears to be absent or represented by a tiny swelling. The talonid is short and lacks a separate hypoconulid. The hypoconid is positioned more lingually than on the other molars.

BMNH M21888. M21888 (Text-fig. 4) is nearly as large as M47742. It is a right dentary fragment broken cleanly anterior to the p3 and posterior to the m3, and preserving broken crowns of all teeth in between. The body is very deep. A mental foramen is present under the anterior root of the p5. There is a groove running on the lingual surface all the way to the p3, but it is poorly delimited and follows some breakage of the dentary; it is unclear if this represents the extent of Meckel's groove. The beginning of the ascending ramus is preserved at the m3, and in section this region reveals a distinct, large masseteric foramen coursing below the tooth row and merging with the mandibular canal below the m1 (Text-fig. 3B). There is a well-defined bony septum separating the two canals.

Very little of the p3 is preserved other than the roots; the crown looks to have been small with a low but distinct heel. The p4 is much larger, though with equally poor preservation. There is a prominent low cusp on the short, wide heel, flanked labially by a small cuspule. The p5 is smaller than the p4, though its main cusp is also completely broken. There is a small cusp that could be interpreted as a metaconid positioned on the midline of the crown, but little else can be said of the premolariform-molariform nature of this tooth. There is a large, conical anterior basal cusp positioned just lingual to the midline of the crown. It is the same size as the single heel cusp, which is separated from the main part of the crown by a transverse trough. There is a faint bulge on the lingual slope of the heel cusp.

The trigonid on the m1 of M21888 is broken. The base of the distal metacristid is evident, and a notch separates it from the cristid obliqua. The hypoconid is the only cusp present and it is set slightly labially to but not far from the midline of the crown. The m2 is better preserved and more typically molariform, with a trigonid angle of 80 degrees. In general morphology, it is very similar to the m2 of M47739 (*Peramus dubius*), differing only in its larger size. The paraconid is positioned high on the protoconid, but both cusps are broken. The metaconid is lower and more lingually positioned. Cusps e and f are large. The distal metacristid is not very distinct, but it appears somewhat worn. The occlusal surface of the talonid is broken, but it was much more expansive than on the m1. The only cusp preserved is an entoconid, which lacks any anterior crest and was likely isolated as in M47739. The m3 looks to have been much smaller than the m2, as in M47742, but the talonid is missing. The trigonid is certainly lower crowned and more acute-angled (70 degrees), with a low, blunt metaconid. The paraconid was likely better separated from the protoconid than on the m2. Cusps e and f are large, and the metaconid bears a distinct distal metacristid.

Peramus dubius (Owen, 1871) comb. nov.

Table 3, Text-figures 3C–E, 5–8

*1871 *Leptocladus dubis* Owen, p. 53, pl. 3, fig. 4.

1871 *Peramus minor* Owen, p. 44, pl. 2, fig. 13.

1928 *Peramus tenuirostris* Owen; Simpson, p. 121, pl. 8, figs 4–5.

1964 *Peramus tenuirostris* Owen; Mills, p. 118, pl. 1.

1971 *Peramus tenuirostris* Owen; Clemens and Mills, p. 9, pl. 1–4.

Holotype. BMNH M47739, a left dentary fragment preserving a portion of the posterior dentary, alveoli for three incisors and the canine, and crowns of the p1–p5 and m1–m3.

Referred material. BMNH M21887, a left maxilla fragment preserving the P1–P5, M1–M2, and a portion of the M3; M47754, a left dentary fragment preserving a portion of the posterior dentary, alveoli for the p1–p4 and m2–m3, and broken crowns of the p5 and m1; M48404, a right dentary fragment preserving roots of the p3 and crowns of the p4–p5 and m1–m3.

Revised diagnosis. Differs from *Peramus tenuirostris* in smaller size, relatively more slender dentary, less substantial size difference between p3 and p4, and m2 and m3 subequal in anteroposterior length.

Distribution. As for the genus.

Description

BMNH M21887. The upper dentition of *Peramus* is represented by a single specimen, M21887 (Text-fig. 5), a left maxilla fragment bearing the entire postcanine dentition (though the M3 is badly damaged). The contact with the jugal is preserved dorsal to the molar row, and what is probably the crushed infraorbital foramen is present above the anterior root of the P4. The posterior margin of a large alveolus is visible anterior to the

P1, representing the single-rooted canine. There is no diastema between these teeth. The P1–P3 are simple, conical and nearly symmetrical crowns lacking well-defined heels. There is no appreciable difference in size. Clemens and Mills (1971) mention the possibility that the P3 is deciduous, based on the relatively wide angle formed by the roots. There is no evidence of a replacement tooth below the P3, the roots are deep and the bone between the alveoli is solid, all suggesting that this tooth is not undergoing replacement. Whether it is a retained deciduous tooth or if replacement was extremely delayed cannot be assessed. A pit was identified between the P3 and P4 by Clemens and Mills (1971), but the CT data are equivocal as to whether or not this represents a plugged alveolus or a textural abnormality. The P4 is very large (by far the largest in the preserved series), with an uninflated and nearly symmetrical main cusp. At least one small anterior basal cuspule is present, but a crack passes through this portion of the crown. A weak but sharp crest descends down the main cusp, but ends in a notch at the base. The heel is short but broad with two large cusps. The larger of the two is centrally positioned and bears a weak crest which curls around the posterolingual corner of the crown, while the smaller cusp is positioned at the posterolabial edge of the crown. The P5 is slightly transversely wider than the P4 but it is lower and anteroposteriorly shorter. As in the other premolars, it has two roots. A small but distinct, posterolabially-oriented metacone is present directly posterior to the main cusp. A large cusp is present at the posterolabial corner of the crown (possibly cusp “C” or the metastyle), separated from the metacone by a trough. A few additional cuspules are present on the labial cingulum, which is briefly discontinuous anterolabial to the main cusp before widening to form an anterior shelf bearing one or two small cuspules. A weak but continuous lingual cingulum is present.

The molars have three roots and are distinctly transversely wider than the P5. On the M1, the paracone is large and inflated, while the metacone is small, closely appressed, and directly posterior to the paracone. The parastylar lobe is wide and broad; though broken, the stylocone was probably large (contrary to previous interpretations; see Clemens and Mills 1971; Sigogneau-Russell 1999). The preparacrista is worn and arcs to the broken area occupied by the stylocone. The parastyle forms a prominent anterior projection and is set labial to the stylocone. The metastylar lobe is distorted by pressure from the M2, but it appears to have a large cusp “C” separated from the metacone by a distinct notch. No stylar cusps are present, though there is a tiny cuspule situated just anterior to the deepest point of the ectoflexus. The lingual cingulum is stronger than in the P5, but it is largely limited to the lingual base of the paracone; it was either incomplete or has been elsewhere obliterated by wear. A worn groove is visible in the centrocrista, and both facets 3 and 4 are present.

The M2 is generally similar to the M1. The metacone is relatively larger and the lingual cingulum is somewhat wider (though its labial extent is obscured on both ends). There is some breakage on the metastylar lobe, but it appears that it may have been relatively narrower than on the M1. The parastylar lobe is pressed against the M1; though the stylocone is still broken, its lingual portion is preserved. The preparacrista arcs posteriorly and ends lingual to the stylocone instead of meeting it. A large swelling is present midway between the paracone and the stylocone, similar to the B` cusp seen in some symmetrodontans (see Rougier *et al.* 2003). Most of the M3 is missing, and the preserved portion is pressed against the M2. A wing-shaped fragment bearing a series of cusps and cuspules is visible, but it is unclear which part of the crown it represents; in general morphology it resembles a metastylar lobe, but this means that this portion of the crown was not reduced, contrary to the condition in ultimate upper molars of most morphologically comparable taxa.

BMNH M47739. M47739 (holotype; Text-fig. 6) is the best preserved specimen in the peramuran sample from the Purbeck Group. The postcanine dentition is complete, and alveoli for the posterior three incisors are present (bone is missing anterior to this). The body of the dentary is remarkably straight both dorsally and ventrally, and tapers abruptly below the canine. The symphysis is low and long, extending anteriorly from below the p1. Mental foramina are preserved below the ultimate incisor, the anterior root of p2, and between the p4 and p5. A substantial portion of the posterior dentary is also preserved, including the anterior and ventral margins of the masseteric fossa. This fossa is very deep, and a large masseteric foramen is present and becomes confluent with the mandibular canal below the m3. This feature was described by Simpson (1928) and Clemens and Mills (1971) as a pocket, but from CT data it is clearly a foramen (Text-fig. 3C). The posteriormost portion of the dentary appears to begin to flare medially before the break, suggesting the beginning of the angular process. A deep Meckel’s groove is present but ends abruptly well before reaching the level of the m3. The groove is bounded dorsally by a distinct medial ridge which weakens posteriorly before ending well prior to the break in the dentary. The presence of a continuous medial ridge extending to the condyle has been linked with retained contact with the postdentary bones and a primitive middle ear morphology (see Allin 1975; Luo *et al.* 2007). It is unlikely such contact persisted in peramurans (since in no specimen does the groove or medial ridge extend posterior to the mandibular foramen), but the preserved morphology does suggest that a substantial portion of Meckel's cartilage was present and likely anchored the middle ear elements to the posterior dentary (a transitional mammalian middle ear morphology; see Luo *et al*. 2007); whether or not this connecting structure was ossified (as preserved in some eutriconodontans; Meng *et al.* 2003; Luo *et al.* 2007) is unknown. The medial ridge forms the ventral boundary of a shallow but distinct pterygoid fossa. The opening of the mandibular foramen is not preserved, but it was positioned very far posteriorly as in other peramuran specimens.

The root of the penultimate incisor is present; the other incisors and the large, single-rooted canine are not preserved. The anterior four premolars essentially share the same morphology and differ only in relative size. All are trenchant with no anterior basal cuspule and a single, small heel cusp. The p1 is the smallest and there is a very gradual increase in size through p3, but the p4 is substantially larger though it maintains the same general outline. The p5 is lower than the p4 and differs in having a heavy, roughly symmetrical main cusp. A metaconid is present as a small swelling, and the main cusp is broken so it is impossible to judge if a paraconid was also present. A pair of small cusps is present on a broad anterolingual basal shelf, and the heel bears a single cusp positioned on the midline of the crown.

Despite the presence of a metaconid on the p5, there is a distinct morphological break between it and the m1. The first molar has a well-triangulated trigonid (approximately 90 degrees); the paraconid is a smaller cusp than the metaconid but it is positioned much higher on the protoconid and more labially. Cusp e contacts the heel of the p5, and cusp f appears to be absent. The distal metacristid is separated from the cristid obliqua by a distinct notch. The talonid is small but complex; though not basined, it does possess a large hypoconid and a smaller but clearly separate hypoconulid in a median position. A small, isolated cuspule is present in the position of the entoconid, but it lacks any crests. Wear facet 4 cannot be discerned, but this is likely due to preservation or preparation.

There is no appreciable difference in anteroposterior length through the molar series, and in morphology the m2 and m3 are largely similar to the m1 but differ in some important ways. There is a trend towards greater acuteness of the triangulation of the trigonid cusps (m3 = 65 degrees). Cusp e is extremely prominent on the m2 and to a lesser extent on the m3, and on both these molars cusp f is well developed to create an embrasure for the hypoconulid of the preceeding molar. The talonid on the m2 is larger than on the m1, and the hypoconulid projects farther posteriorly. The talonid on the m3 is somewhat abraded, but it appears to have been approximately the same size as on the m1 though the presence of a hypoconulid cannot be established with confidence. The m3 trigonid is somewhat lower crowned than the anterior molars, and there is barely any height difference between the paraconid and metaconid (though the former is still slightly higher, largely as a function of its placement on and approximation to the protoconid). A small, isolated entoconid is present on all three molars. There is a relatively wider gap between the m3 and the ascending ramus in M47739 than in other peramuran specimens, but there is no evidence of any additional molars in the jaw (despite original interpretations by Owen 1871; Osborn 1888).

BMNH M47754. M47754 (Text-fig. 7) is a left dentary fragment missing the condylar and angular processes, and crushed into uninformative fragments anterior to the p1. Only two crowns are preserved, the p5 and m1. Mental foramina are present between the c and p1 and under the p5. The posteriormost margin of the symphysis is visible under the p1just prior to the breakage. The masseteric fossa is deep as in other peramuran specimens; this jaw is mineralized such that it is difficult to assess the size of the masseteric foramen, but it is clearly present and merges with the mandibular canal posterior to the m3 (Text-fig. 3D). Meckel’s groove is present and appears to extend all the way to the p4 before fading. The pterygoid fossa is floored by a substantial shelf; this shelf forms the medial ridge which bounds Meckel’s groove. The ridge is still present but fading as it approaches the broken end of the dentary, a point just anterior to the mandibular foramen.

A single large canine alveolus is probably present, but the crushing of the anterior portion of the dentary makes it difficult to be certain. Only roots of the p1–p4 are present. There is a gradual increase in anteroposterior length from the p1 through the p3, and a more substantial increase between the p3 and p4. Based on the preserved roots, it is unclear if the p4 was any larger than the p5. The p5 is heavily abraded and shows no obvious trace of additional trigonid cusps. The main cusp is otherwise oddly asymmetrical and pointed, probably due to abrasion. There is a faint bulge in the position of an anterolingual cusp, and the heel is small with a single cusp. The m1 is also heavily abraded, with a trigonid angle of about 90 degrees. Though broken, the paraconid was situated high on and very close to the protoconid, while the metaconid was much lower (also broken). There is some evidence of cusp e. The talonid is too damaged to make out any morphology.

BMNH M48404. M48404 (Text-fig. 8) is a right dentary fragment preserving the roots of the p3 and the crowns of the p4, p5, and m1–m3. This specimen was broken in roughly equal halves (below the m1) and glued together backwards sometime prior to its first mention in Simpson (1928: pl. 8, fig. 5), though not corrected during preparation in the 1960s (see Mills 1964: pl. 1); it has been digitally repaired for this paper. The dentary is broken cleanly anterior and posterior to these teeth. The ventral margin of the bone is straight and parallel to the preserved portion of the tooth row. The beginning of the ascending ramus is preserved directly labial to the m3. The posterior mental foramen is preserved underneath the posterior root of the p4. On the lingual side, a deep Meckel's groove is present and terminates below the posterior root of the m2. Though no portion of the posterior dentary is preserved, it is evident in sagittal section that a large masseteric foramen was present, separated from the mandibular canal by a distinct bony septum (Text-fig. 3E). The two become confluent below the m2.

The main cusp of the p4 is broken, but it looks to have been taller than the p5 (but not likely as tall as the m1). A faint bulge on the anterior base is present, and the heel is very small and bears a single, centrally-positioned cusp. The main cusp of the p5 is anteroposteriorly shorter than that of the p4 and also broken, but a distinct metaconid is present. This cusp is low and small, and positioned more posteriorly than lingually relative to the main cusp. A narrow anterior shelf bearing one or two small cuspules is present, and the heel is similar to that of the p4 except more linugally developed, with a small posterolingual cuspule present.

The m1has a trigonid angle of about 90 degrees, with the paraconid set high on and close to the protoconid. The metaconid is slightly shorter and heavier (bordering on blunt). Both cusps e and f are equally developed, and cusp f bears a distinct wear facet. A weak cingulid extends from cusp e nearly to the lingual base of the paraconid. The distal metacristid terminates at a small cusp situated at the base of the trigonid (the “mesoconid” of Butler 1990). The cristid obliqua is separated from this cusp by a notch. The hypoconid is slightly smaller than the “mesoconid” and very closely approximated to the hypoconulid. An entocristid is present, but it is short and ends posterior to the “mesoconid”.

The trigonid of the m2 is more acute (70 degrees), but the paraconid and metaconid are almost equal in height by means of the relatively more lingual position of the paraconid (the metaconid is very slightly lower, but much heavier). Cusps e and f are larger than on the m1 (but not nearly as pronounced as in M47739), and the weak lingual cingulid bears a faint cuspule positioned directly lingual to the paraconid. The hypoconulid is better separated from the hypoconid, which is somewhat more labially positioned than on the m1. The m3 is distinctly smaller and lower crowned than the other two molars, and is the only known instance in *Peramus* where the paraconid is lower than the metaconid. The paraconid is strongly inclined and much smaller than the metaconid. The talonid is generally similar to that of the m2.

Genus *Kouriogenys* nov.

Derivation of the name. From the Greek *kourios*, youthful, and *genys*, jaw, in reference to the retention of plugged alveoli for deciduous premolars in the only known specimen.

Included species. *Kouriogenys minor* (Owen, 1871), type and only species.

Diagnosis. As for the type species.

Distribution. As for the type species.

Kouriogenys minor (Owen, 1871)

Table 4, Text-figures 3F, 9

*1871 *Spalacotherium minus* Owen, p. 28, pl. 1, fig. 39.

1928 *Peramus tenuirostris* Owen; Simpson, p. 122, pl. 7, fig. 6.

Holotype. BMNH M47751, a left dentary fragment preserving a portion of the posterior dentary, alveoli for the p1–p3 and m3, roots of the p4, and crowns of the p5 and m1–m2.

Revised diagnosis. Differs from other peramurids in having a p4 shorter in anteroposterior length than p5, and a single-rooted p1; differs from *Peramus* in less development of cusps e and f on molars; differs from *Peramuroides* in larger size, trigonid angle on m1 of 90 degrees, and m2 and m3 subequal in anteroposterior length; differs from *Tendagurutherium* in absence of evidence for a coronoid bone and shorter distance between m3 and the ascending ramus.

Remarks. The species name is emended to reflect the gender (feminine) of the genus.

Distribution. Purbeck Group, Lower Cretaceous (Berriasian) of England.

Description

BMNH M47751. M47751 (holotype; Text-fig. 9) is a left dentary fragment broken anterior to the p1 and missing the angular and condylar processes. It preserves roots of the p2–p4 and broken crowns of the p5 and m1–m2. The ventral and dorsal margins of the dentary are generally parallel, except for the anteriormost preserved portion which flares gently ventrally, indicating the symphysis (the bone on the lingual surface is abraded, so other evidence of this structure is lost). The body is slender when taken as a ratio relative to the length of the molar series, similar to M47799 (*Peramuroides*). Mental foramina are present under the anterior roots of the p2 and p5. The masseteric fossa is very deep and opens anteriorly into a short but large foramen which joins the mandibular canal posterior to the roots of the m3 (Text-fig. 3F). Meckel's groove is prominent posteriorly but extends anteriorly as a faint trace to a level below the m2; as in *Peramus* and *Peramuroides*, a transitional mammalian middle ear was possibly present. The groove is separated from the pterygoid fossa by a medial ridge, which ends at the posteriorly-placed mandibular foramen.

The p1 is apparently represented by a single alveolus with a labial ridge, indicating that it was either a single-rooted tooth or had two fused roots. There is no evidence on the surface of a smaller anterior alveolus, and the specimen is broken prior to the canine. In horizontal section (Text-fig. 9F), there is a slightly smaller subsurface structure situated anterolingual to the presumed p1 alveolus. Similar but smaller chambers are present anterolingual to the alveoli for the p2 and p3. These likely represent plugged alveoli for deciduous premolars. There is no replacement at the p1 locus in living mammals (with few exceptions; Simpson 1945; Ziegler 1971), but it is known to occur in dryolestids (Martin 1997). Replacement patterns are unknown in more proximal outgroups, such as stem zatherians. However, in sagittal section this anteriormost chamber is slightly inclined (Text-fig. 3F), leaving the possibility that it could represent a posterior alveolus for a two-rooted deciduous canine (if this was the juvenile condition). Where discernable in other peramuran specimens, there is very limited evidence of plugged alveoli for anterior deciduous premolars, but evidence of a dp1 cannot be detected.

The p2 and p3 are represented only by roots, while the p4 preserves a very small heel. The p4 is larger than the p3 but smaller than the p5 (differing from all other peramurids). The p5 is heavily abraded but appears to have had a large, triangular but asymmetrical main cusp (though this could be due to wear or breakage). There is no trace of a metaconid or paraconid, but there is a large anterolingual cusp. The heel is poorly preserved but appears small. There is faint evidence of an entocristid.

The m1 is also heavily abraded, lacking the anteriormost portion of the crown. The trigonid angle was probably 90 degrees. The talonid has a well-developed notch between the cristid obliqua and distal metacristid. The hypoconulid is well-separated from the hypoconid, and there is evidence of an entoconid. The m2 is better preserved, and has a trigonid angle of 70 degrees. The paraconid is smaller than the metaconid but set higher on the slope of the protoconid, in a more labial position. Cusp f is either very small or damaged, while cusp e is fairly prominent (though not as large as in *Peramus*). The talonid is abraded but shows evidence of at least two cusps (hypoconid and hypoconulid); an entoconid was likely also present.

Genus *Peramuroides* nov.

Derivation of the name. From the Latin *-oides*, like, in reference to the similarities between this genus and *Peramus*.

Included species. *Peramuroides tenuiscus* sp. nov., type and only species.

Diagnosis. As for the type and only species.

Distribution. As for the type and only species.

Peramuroides tenuiscus sp. nov.

Table 5, Text-figures 3G, 10–11

1871 *Peramus* cf. *tenuirostris* Owen, p. 43, pl. 2, fig. 12.

1928 *Peramus tenuirostris* Owen; Simpson, p 121.

Derivation of the name. Diminutive of the Latin *tenuis*, thin, in reference to the very slender dentary of this species.

Holotype. BMNH M47744, a left dentary fragment preserving alveoli for i1–i5, the canine, and the m2, and crowns of the i3, p1–p5, and m1.

Referred material. BMNH M47799, a right dentary fragment preserving the angular process, an alveolus for the p5, and broken crowns of the m1–m3.

Diagnosis. Differs from other peramurids in smaller size, having a relatively very small increase in size between p3 and p4, and an obtuse trigonid angle on m1 (approximately 110 degrees); differs from *Peramus* in somewhat weaker development of cusps e and f;

differs from *Kouriogenys* in having a two-rooted p1, p4 equal to p5 in anteroposterior length, and m3 anteroposteriorly much shorter than m2; differs from *Tendagurutherium* in absence of subcondylar fossa and absence of evidence for the coronoid bone.

Distribution. Purbeck Group, Lower Cretaceous (Berriasian) of England.

Description

BMNH M47744. M47744 (holotype; Text-fig. 10) is a left dentary preserving evidence of the entire anterior dentition through the m1. A portion of the symphysis is visible below the p1, and two small mental foramina are present below the i3 and i4. Additional mental foramina are present under the p1 and the p5. The dentary is broken below the m2 (the anterior half of a single alveolus is present), and Meckel's groove was either not present or did not extend this far anteriorly. Alveoli for five incisors are present, with the broken crown of the procumbent i3 preserved (Text-fig. 10D). The specimen is crushed in the region of the canine alveolus, but the tooth appears to have been large judging from the distance between the i5 and p1 (the posterior margin of the alveolus is visible just anterior to the p1, showing no diastema was present), and comparisons with M47739 (*Peramus dubius*; Text-fig. 6B).

The anterior three premolars are simple, trenchant teeth with a slight size increase posteriorly. The anterior margin is more convex than the posterior margin. No anterior basal cuspule is present, and the heel is small and low. The p4 is taller than the p3 and equal in height to the m1. The main cusp is slender and symmetrical; there is a faint bulge on the anterior base, and the heel is larger than on the anterior premolars but still bears a single cusp. The posterior root is larger than the anterior root. The p5 is anteroposteriorly shorter than the p4, and though the main cusp is broken, it was likely symmetrical but lower than either the p4 or the m1. A low but wide anterior basal cuspule is present, as is a single small posterior heel cusp. This tooth is entirely premolariform; there is no evidence of a paraconid or metaconid.

The trigonid of the m1 is dominated by a very large protoconid. The paraconid is substantially smaller, procumbent, and only very slightly taller than the metaconid. The metaconid is positioned lingual to and slightly lower than the paraconid, and is conical but somewhat blunt. The three trigonid cusps form an obtuse angle (approximately 110 degrees). Cusps e and f are present but barely discernable on the anterior base of the trigonid. A distinct distal metacristid runs down the posterior face of the metaconid from its apex. The talonid is small and low, and though the occlusal surface is broken it seems likely that at least two cusps were present. The hypoconulid would have been positioned centrally at the back of the talonid, not far from the hypoconid. From the shape of the lingual edge of the broken surface, it looks as if an entoconid or entocristid may have also been present. Wear features are not observable on the original specimen due to a coat of preservative, but it appears from the 3-D rendering that the talonid bears facet 4 on its posterolabial face. This strongly suggests that the upper molars of *Peramuroides* had a lingually positioned metacone, as in *Peramus*.

BMNH M47799. M47799 (Text-fig. 11) is a right dentary fragment preserving much of the posterior part of the element and portions of three molars. The bone is broken anterior to the posterior alveolus for the p5, and no mental foramen is preserved. The body appears somewhat stout in ventral view, but it is relatively shallow; combined with the relatively short molar series, this makes M47799 one of the smallest specimens in the peramuran sample from the Purbeck Group (seemingly as small as M47744, but there is little overlap in preserved morphology). The masseteric fossa is very deep and bounded by strong ridges ventrally and anterodorsally; it appears that a thin layer of bone floors the pocket at the anterior extent of the fossa, separating it from the mandibular canal (Text-fig. 3G); it is possible this instead represents postburial infill. The canal is otherwise very expansive at the base of the ascending ramus anterior to the pocket, and has the same extent as in other peramuran specimens with a complete masseteric foramen. Though the condylar and coronoid processes are broken, this is the only specimen preserving a complete angular process. It has a stout tip, projects primarily straight ventrally with a vertical posterior face, and curls slightly medially (though not nearly to the extent as in marsupials). There is a small (perhaps nutrient) foramen on the posterolateral side of the angular process (a similar feature is present in the stem zatherian *Nanolestes*; see Martin 2002). A prominent shelf forms the ventral floor of the pterygoid fossa. The shelf becomes a weak medial ridge which separates the pterygoid fossa from Meckel’s groove, and ends at the mandibular foramen (though there is a suggestion of a weak ridge climbing towards the broken condylar process). Meckel’s groove is pronounced and deep but with a limited anterior extent; it ends beneath the start of the ascending ramus. The overall morphology of the groove is similar to *Peramus dubius* (M47739; Text-fig. 6A), suggesting a similar transitional mammalian middle ear was present in *Peramuroides*. The groove widens and becomes indistinct posterior to the mandibular foramen. This foramen is positioned very far posteriorly, at the point at which the angular process begins to extend ventrally. Between the mandibular foramen and the tip of the angular process is a small depression containing a foramen. There is a small irregularity at the anterior extent of the pterygoid fossa which could possibly be evidence of a scar for a small coronoid bone (an element which is described as present in *Tendagurutherium*; Heinrich 1998).

The badly damaged crowns of the m1–m3 are preserved; only the anterior root and the heavily abraded talonid remain for the m1. It looks as if a cusp similar to the "mesoconid" of M48404 (*Peramus dubius*; Text-fig. 8E) is present, but other aspects of the morphology cannot be determined. The trigonid of the m2 is broken; it is likely that the paraconid was a much smaller cusp than the metaconid, but their heights cannot be determined. There is a shallow embayment on the anterior face of the trigonid for the talonid of the m1, but cusps e and f cannot be identified due to preservation. The talonid is smaller, and probably had at least two cusps judging from the position and orientation of the cristid obliqua. There is evidence of either an entocristid or entoconid. A "mesoconid" similar to that on the m1 was probably present. The m3 is much smaller than the other molars, with a more acute trigonid (approximately 70 degrees, versus 80 degrees for the m2). The embrasure for the preceding hypoconulid is preserved, and cusp f is large (cusp e is abraded). The protoconid and paraconid are broken near their bases, and the metaconid is missing most of its apex. The distal metacristid is preserved, and terminates at a small "mesoconid". The talonid is small and seemingly less lingually developed than on the m2, and only one cusp was probably present.

DISCUSSION

Variation within the Peramura, and their relationship to the Tribosphenida

The original hypodigm of *Peramus tenuirostris* (see Clemens and Mills 1971) included a tremendous amount of variation, in terms of both size and tooth morphology (see, for example, Text-fig. 3). This has been noted by previous authors; both Simpson (1928) and Mills (1964) suggested the possibility that the sample could be split into two taxa based on size, and both included BMNH M47742 in the larger species. However, Clemens and Mills (1971) did not feel size alone demonstrated sufficient heterogeneity, and instead proposed that the only consistent morphological variation was the presence/absence of a posterior accessory cusp ("mesoconid" of Butler 1990; Martin 2002). Ultimately, the variation in the sample has been historically interpreted as within appropriate intraspecific limits.

In the present revision of the peramurans from the Purbeck Group, size is in fact an important feature accounting for some of the taxonomic variation in the sample, and varies consistently with other characters. The two largest specimens (BMNH M47742 and M21888, *Peramus tenuirostris sensu stricto*) also share other morphological features to the exclusion of the other specimens, namely a deep, robust dentary and very large posterior premolars (Text-figs 2, 4). M47799 is substantially smaller and more gracile than the rest of the sample and it, along with M47744, constitute another taxon (*Peramuroides tenuiscus* gen. et sp. nov.) also separated by premolar proportions and obtuse triangulation of the m1 trigonid (Text-figs 10–11). The medium-sized specimens all, with one exception, belong to a third taxon (*Peramus dubius*), united by little to no decrease in molar size posteriorly (Text-figs 5–8). A fourth taxon is represented by a single specimen (M47751, *Kouriogenys minor* gen. nov.) which differs in having a single-rooted p1 and a relatively small p4 (Text-fig. 9). These features are here considered to represent significant variation, enough to warrant taxonomic separation within the material. It is important to note that additional variation is present within and between the new taxa, though seemingly without patterns. Some specimens have a metaconid on the p5, though none have any molarization of the talonid at this locus (see Text-figs 2F, 4E, 6F, 7F, 8E, 10F). An entoconid or entocristid is variably present across specimens and even loci of the same specimen. The same is true for a differentiated hypoconulid, even though this is a hallmark peramuran character. Every specimen has a separate hypoconulid on at least one molar, but some m3s (and in one case an m1) demonstrate a more plesiomorphic single-cusped talonid (see Text-figs 2F, 4E, 11F). Other variable features include the anterior extent of Meckel's groove and the length of the masseteric canal (see below for a discussion of the latter).

Despite the variation present in the sample (and that added by the African taxa), peramurans are united by the development of an important functional complex, reflected in both upper and lower molars (Text-fig. 12). The upper molar metacone is in a lingual position directly posterior to the paracone in peramurans, instead of posterolabially along the postcrista as in dryolestoids and stem zatherians (Text-fig. 13). This position causes an inflection of the postvallum shearing surface through the development of the centrocrista (postparacrista plus premetacrista), which serves as an embrasure for the lower molar hypoconid. The resulting new contact surface (wear facet 4 of Crompton 1971) is elongated on the lower molar through differentiation of the hypoconulid (Text-fig. 13C,F). The elaboration of these structures allows for an increase in functional shearing area without increasing the dimensions of the crown or adding additional molars (as employed by spalacotheriid symmetrodontans and dryolestids, which can have up to nine molars). Lingual expansion of the talonid through the addition of the hypoconulid, and the incorporation of the center of the upper molar crown into occlusion, paved the way for the evolution of tribospheny through enlargement and eventual overlap of these regions of the crown. The Peramura are therefore structurally and functionally intermediate between stem zatherians and tribosphenidans, and serve as the most appropriate sister group to the living Eutheria and Metatheria (see Davis in review for a recent detailed discussion of the origin of the tribosphenic molar).

It follows that the contents of the Peramura are restricted to those taxa with unequivocal evidence of wear facet 4, or possession of the requisite morphology to produce it (i.e. a lingually-positioned metacone or a differentiated hypoconulid). As such, most of the taxa placed as "peramurans *incertae sedis*" by Kielan-Jaworowska *et al.* (2004: table 10.2) are instead stem zatherians, and are no closer to peramurans than is *Amphitherium* or *Arguimus* (at least based on current knowledge). Though preservation is problematic in some taxa, the important peramuran character complex appears to be missing. In taxa with known upper molars (e.g. *Palaeoxonodon*), the metacone is posterolabial to the paracone and the shearing embrasure for the hypoconid is absent. In those known by lower molars (e.g. *Minimus*), only a single talonid cusp is present. It is conceivable that an upper molar embrasure for the hypoconid can be functional (i.e. produce both wear facets 3 and 4) without the addition of a separate hypoconulid; in fact, it is almost a certainty that peramurans are derived from such a morphological stage. However, the evidence for a posterolabially-directed wear facet in a taxon with a single-cusped talonid is scant. Mills (1964) identified a minute facet in this location on the talonids of *Amphitherium*, but the subsequent review of this taxon by Clemens and Mills

(1971) and personal observations have failed to corroborate it. Dashzeveg (1979) described the presence of facet 4 on the holotype of the stem zatherian *Arguimus* (which he placed in the Peramuridae). In their review of this taxon, Lopatin and Averianov (2006*a*: 345) described this facet on the ultimate molar of a single specimen, but this feature is absent from the rest of the referred material despite substantial wear on other portions of the molars. For the posterior surface of the hypoconid to function in an upper molar embrasure, it must be expanded posteriorly to sufficiently separate it from its embrasure with cusps e and f of the succeeding lower molar. The interlocking mechanism between adjacent lower molars simply does not provide any room for the development of facet 4 in known taxa with one talonid cusp (Text-fig. 13B,E). The only non-tribosphenidans to show facet 4 also have a differentiated hypoconulid—peramurans *sensu stricto* (i.e. as defined in this study).

Two characters which have previously been used to define the Peramura, a stylocone groove on the upper molar and an incipiently-basined talonid, are here given lesser importance. The parastylar region of taxa such as *Palaeoxonodon*, *Abelodon*, and *Magnimus* are somewhat flange- or hook-shaped and bear a lingually-developed groove, presumably for the protoconid. This feature has been linked to the development of advanced prevallum/postvallid shear, as in more derived tribosphenic mammals (Crompton and Kielan-Jaworowska 1978; Cifelli 1993). A stylocone groove is cited as probably missing in *Peramus*, placing this taxon farther from tribosphenic ancestry than those with the feature (Sigogneau-Russell 1999). The upper molar morphology in *Peramus* was instead suggested to have been independently derived from a tinodontid ancestor. I would argue that the stylocone is damaged in *Peramus* and was likely much larger than previously determined (e.g. Clemens and Mills 1971), and most certainly would have participated in shear against the protoconid. Upper molars are known from only one crushed specimen, but the similarities in molar topology and function (as inferred from wear facets) between *Peramus* and basal tribosphenidans (especially aegialodontids; Kermack *et al.* 1965; Lopatin and Averianov 2006*b*; Text-fig. 13C–D) are far more likely to have arisen via common ancestry than convergence. A far more important character complex is the hypoconid embrasure formed by the centrocrista (as discussed above), which is present only in peramurans *sensu stricto* and tribosphenidans.

The variable presence of an entoconid or entocristid, which lingually encloses a basin or "incipient" basin, is also of questionable utility. This feature is seen as a precursor to the expanded talonid basin which receives the crushing action of the protocone, a hallmark of tribosphenic dentitions. However, there is no upper molar structure which can render any function from this region of the talonid (despite the presence of a weak lingual cingulum on upper molars of *Peramus*; Text-fig. 5G). The important improvement towards tribospheny is, at this stage, not the development of a rim which encloses the talonid lingually, but lingual expansion of the entire talonid such that it is in a position to occlude with the matching lingual expansion of the upper molar in tribosphenidans (facet 5, produced by the protocone and talonid basin; Text-fig. 13D). The necessary groundwork for tribospheny is accomplished in *Peramus* and allies through the differentiation and posterolingual placement of the hypoconulid.

The development and elaboration of the hypoconid embrasure, through a neomorphic hypoconulid and accompanying lingual expansion of the talonid, thereby lays the necessary groundwork for the evolution of tribospheny. The principal upper molar cusps (paracone and metacone) are positioned in an anteroposterior line and bear wear facets 3 and 4, while the talonid has a matching set of alternating shearing surfaces on the cristid obliqua and the hypocristid (Text-fig. 13C,F). The talonid is lingually expanded relative to stem zatherians by mechanical necessity, due to the posterolingual placement of the hypoconulid and irrespective of the presence/absence of an entoconid or entocristid. The final transformation involves development of a lingual cingular cusp on the upper molars to occlude against the widened talonid; see Davis (in review) for an expanded discussion of this transition.

Masseteric foramen in peramurans

The masseteric fossa is very deep in peramurans, and ends anteroventrally in either a large pocket with a thin wall of bone or a substantial foramen (Text-fig. 3). The foramen becomes a large canal in some specimens, and does not taper appreciably prior to merging with the main mandibular canal. In specimens seeming to lack a large masseteric foramen, the mandibular canal appears as a large chamber anterior to the masseteric fossa and only a thin wall of bone separates the two. Part of the variation in the sample may be due to crushing of the dentary, which could result in collapse of internal structures, or postburial infill/mineralization.

A masseteric foramen or foramina (= labial mandibular foramen) is present in a number of taxa across diverse lineages: the triconodontids *Corviconodon* and *Trioracodon* (Cifelli *et al.* 1998; pers. obs.), the enigmatic “eupantotherian” *Vincelestes* (Rougier 1993), the stem zatherian *Arguimus* (Lopatin and Averianov 2006*a*), the aegialodontid tribosphenidan *Kielantherium* (Dashzeveg and Kielan-Jaworowska 1984), the metatherians *Alphadon* and *Kokopellia* (Cifelli and Muizon 1997, 1998), the Recent marsupial *Petaurus* (pers. obs.), the basal eutherian *Prokennalestes* (Kielan-Jaworowska and Dashzeveg 1989) as well as a number of Late Cretaceous eutherians (see Archibald and Averianov 2006; Wible *et al.* 2009), and the Recent seal *Phoca* (pers. obs.). In most instances these structures are very small and probably represent nutrient foramina. However, there are a few taxa which possess a large foramen similar to that in peramurans. CT data from the triconodontid *Arundelconodon* (Cifelli *et al.* 1999: fig. 2B; Text-fig. 3H) shows evidence of a narrow, isolated canal below the roots of the m3. This structure appears to taper and does not join the mandibular canal. The basal eutherian *Montanalestes* shows a deep masseteric fossa with a large anteroventral pocket (Cifelli 1999; pers. obs., R. Cifelli unpub. data), but further evaluation requires CT data. Interestingly, *Montanalestes* also has a very posteriorly-positioned mandibular foramen as in peramurans, but it is unclear if there is any correlation between these two characters. The ornithorhynchids *Obdurodon* and *Ornithorhynchus* have a very large anterior extension of the masseteric fossa, which terminates abruptly at a small foramen joining the mandibular canal (Musser 1998; Text-fig. 3I). BMNH M47742 (*Peramus tenuirostris*; Text-fig. 3A) does bear some superficial resemblance to this condition, but as noted, this could be a preservational artefact. Lastly, the masseteric fossa in macropodids (kangaroos and allies) is expanded anteriorly and ventrally, with a very small foramen extending anteriorly into the mandibular canal and a large opening through the lingual side of the dentary into the pterygoid fossa (pers. obs.). However, this opening meets the posterior extent of the mandibular foramen and is not adjacent to and eventually confluent with the mandibular canal in the same manner as in peramurans.

The expansion of the masseteric fossa in macropodids allows for insertion of a portion of the masseter musculature (Abbie 1939) and is structurally very different from that of peramurans. The same is likely true for the large extension of the fossa in *Ornithorhynchus* (pers. obs. of a dried specimen), but the small foramen continuing into the mandibular canal in this taxon (and in macropodids) could not have functioned for muscle attachment. In peramurans, the masseteric canal is large and maintains most of its diameter until joining the mandibular canal (in one specimen, as far anteriorly as below the m1; Text-fig. 3B). It is highly unlikely that this structure accommodated expanded muscle attachment, but it seems inordinately large for a neurovascular passage. For now, the function of this unusual feature in peramurans remains unknown.

CONCLUSIONS

This study demonstrates the enormous utility of CT data for applications ranging from specimen curation and collections management (preparation of fragile material can be done digitally without risk to the original material) to taxonomic revision. The employment of CT technology allowed the digital preparation of a sample of peramurans from the Lower Cretaceous Purbeck Group of England, for the first time allowing study of the material unencumbered by preservative coats or matrix. The data helped identify morphological diversity within the sample, justifying allocation of the specimens into four taxa, and provided a glimpse of an autapomorphy of the Peramura—the presence of a very large masseteric canal. The contents of the Peramura are restricted to only those taxa possessing an upper molar embrasure for the hypoconid (formed by the centrocrista and requiring a lingually-positioned metacone) or, when known by only lower molars, those with a differentiated hypoconulid or evidence of wear facet 4.

The Peramura are functionally intermediate between groups with a single talonid cusp and a posterolabially-positioned metacone, such as dryolestoids and stem zatherians, and tribosphenidans. While the group is taxonomically diverse in the Early Cretaceous of England, the oldest probable peramuran is from the Late Jurassic of Tanzania, hinting at a possible Gondwanan origin and earliest Cretaceous dispersal to Laurasia. It is perhaps not a coincidence that the earliest tribosphenidans occur temporally and geographically alongside peramurans: *Tribactonodon* from the Purbeck Group of England (Sigogneau-Russell *et al.* 2001), and *Hypomylos* from the Synclinal d'Anoual of Morocco (Sigogneau-Russell 1992). More material from Gondwana, which has traditionally been poorly sampled, will perhaps help further elucidate the role peramurans played in the evolution of tribospheny.

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Table Titles

Table 1: Classification followed in this paper, modified from Kielan-Jaworowska *et al.* (2004).

Table 2: Measurements (in mm) of *Peramus tenuirostris* Owen, 1871. Numbers in brackets indicate estimates, and include measurements for loci represented only by alveoli. Abbreviations: ANW, anterior width; AP, anteroposterior length; DD, depth of dentary (as measured below the m2); POW, posterior width.

Table 3: Measurements (in mm) of *Peramus dubius* (Owen, 1871) comb. nov. Numbers in brackets indicate estimates, and include measurements for loci represented only by alveoli. Abbreviations: ANW, anterior width; AP, anteroposterior length; DD, depth of dentary (as measured below the m2); POW, posterior width.

Table 4: Measurements (in mm) of *Kouriogenys minor* (Owen, 1871) gen. nov. Numbers in brackets indicate estimates, and include measurements for loci represented only by alveoli. Abbreviations: ANW, anterior width; AP, anteroposterior length; DD, depth of dentary (as measured below the m2); POW, posterior width.

Table 5: Measurements (in mm) of *Peramuroides tenuiscus* gen. et sp. nov. Numbers in brackets indicate estimates, and include measurements for loci represented only by alveoli. Abbreviations: ANW, anterior width; AP, anteroposterior length; DD, depth of dentary (as measured below the m2); POW, posterior width.

Figure Captions

Text-figure 1: Illustration of peramuran upper (A) and lower (B) molar terminology, in occlusal view. Abbreviations: cc, centrocrista; co, cristid obliqua; dm, distal metacristid; ef, ectoflexus; ent, entoconid; hycd, hypocristid; hyd, hypoconid; hyld, hypoconulid; lc, lingual cingulum; me, metacone; med, metaconid; pa, paracone; pad, paraconid; ppc, preparacrista; pst, parastyle; prd, protoconid; st, stylocone.

Text-figure 2: 3-D renderings of the peramuran *Peramus tenuirostris* from the Berriasian Purbeck Group, England. BMNH M47742 (holotype), left dentary fragment in lingual (A, E), posterolabial (B), occlusal (C, F, steroeopairs), and labial (D, G) views. Only the p4–5 and m1–3 shown in E–G.

Text-figure 3: 3-D renderings showing the masseteric foramen in peramurans and comparative taxa (all parasagittal section except I, which shows both coronal and parasagittal sections). *Peramus tenuirostris sensu stricto*: BMNH M47742 (A, reversed), M21888 (B); *Peramus dubius* comb. nov.: M47739 (C, reversed), M47754 (D), M48404 (E); *Kouriogenys minor* gen. nov.: M47751 (F, reversed); *Peramuroides tenuiscus* gen. et sp. nov.: M47799 (G); the triconodontid *Arundelconodon hottoni*: USNM 497729 (H); the ornithorhynchid *Ornithorhynchus anatinus*: AMNH 200255 (I). Abbreviation: mfm, masseteric foramen. H, I courtesy of DigiMorph.org. H, I not to scale.

Text-figure 4: 3-D renderings of the peramuran *Peramus tenuirostris* from the Berriasian Purbeck Group, England. BMNH M21888, right dentary fragment in labial (A, D), occlusal (B, E, steroeopairs), and lingual (C, F) views. Only the p4–5 and m1–3 shown in D–F.

Text-figure 5: 3-D renderings of the peramuran *Peramus dubius* comb. nov. from the Berriasian Purbeck Group, England. BMNH M21887, left maxilla fragment in labial (A, D), occlusal (B, E, steroeopairs), lingual (C, F), and oblique occlusal (G) views. Only the P4–5 and M1–3 shown in D–G.

Text-figure 6: 3-D renderings of the peramuran *Peramus dubius* comb. nov. from the Berriasian Purbeck Group, England. BMNH M47739 (holotype), left dentary fragment in lingual (A, E), occlusal (B, F, steroeopairs), labial (C, G), and posterolabial (D) views. Only the p4–5 and m1–3 shown in E–G.

Text-figure 7: 3-D renderings of the peramuran *Peramus dubius* comb. nov. from the Berriasian Purbeck Group, England. BMNH M47754, left dentary fragment in lingual (A, E), occlusal (B, F, steroeopairs), labial (C, G), and posterolabial (D) views. Only the p4–5 and m1–3 shown in E–G.

Text-figure 8: 3-D renderings of the peramuran *Peramus dubius* comb. nov. from the Berriasian Purbeck Group, England. BMNH M48404, right dentary fragment in labial (A, D), occlusal (B, E, steroeopairs), and lingual (C, F) views. Only the p4–5 and m1–3 shown in D–F.

Text-figure 9: 3-D renderings of the peramuran *Kouriogenys minor* gen. nov. from the Berriasian Purbeck Group, England. BMNH M47751 (holotype), left dentary fragment in lingual (A, G), occlusal (B, H, steroeopairs), labial (C, I), and posterolabial (D) views. E, F, progressive horizontal sections through the anterior portion of the dentary, showing the p1–p3 loci and possible plugged alveoli for deciduous teeth. Only the p4–5 and m1–3 shown in G–I.

Text-figure 10: 3-D renderings of the peramuran *Peramuroides tenuiscus* gen. et sp. nov. from the Berriasian Purbeck Group, England. BMNH M47744 (holotype), left dentary fragment in lingual (A, E), occlusal (B, F, steroeopairs), labial (C, G) views. D, oblique occlusial view of the anterior portion of the dentary, showing alveoli for five incisors. Only the p4–5 and m1 shown in E–G.

Text-figure 11: 3-D renderings of the peramuran *Peramuroides tenuiscus* gen. et sp. nov. from the Berriasian Purbeck Group, England. BMNH M47799, right dentary fragment in labial (A, E), occlusal (B, F, steroeopairs), lingual (C, G), and posterolabial (D) views. Only the m1–3 shown in E–G.

Text-figure 12: Illustrations of peramuran taxa. *Peramus*: dentary (A_1, lingual view), upper molar (A_2, occlusal view), lower molar (A_3, occlusal view); *Peramuroides*: dentary (B, lingual view); *Tendagurutherium*: dentary (C_1, lingual view), lower molar (C_2, occlusal view); *Afriquiamus*: upper molar (D, occlusal view). C_1, from Heinrich (1998); C_2, modified from Heinrich (1998). Abbreviations: hyd, hypoconid; hyld, hypoconulid; me, metacone; mf, mandibular foramen; pa, paracone; st, stylocone.

Text-figure 13: Illustrations of mammalian upper (A_1–F_1) and lower (A_2–F_2) molar morphotypes. A, dryolestids; B, stem zatherians (represented by amphitheriids); C, peramurans; D, tribosphenidans. E, F, representation of major cusps and shearing surfaces in amphitheriids (E) and peramurans (F). Note increasing complexity of the talonid and lingual translation of the metacone in peramurans (relative to amphitheriids), creating an embrasure for the hypoconid. Molars are duplicated to show occlusal relationships and are not intended to represent adjacent loci. Progression of morphotypes is not necessarily intended to suggest direct phylogenetic descent of the groups illustrated. Numbering of wear facets follows Crompton (1971). D_1, modified from Lopatin and Averianov (2006). Abbreviations: hyd, hypoconid; hyld, hypoconulid; me, metacone; pr, protocone; tb, talonid basin. Not to scale.

Table 1

- Superorder Zatheria McKenna, 1975
  - Order Peramura McKenna, 1975 (new rank)
    - Family Peramuridae Kretzoi, 1946
      - *Peramus tenuirostris* Owen, 1871
        - *P. dubius* (Owen, 1871)
      - *Kouriogenys minor* (Owen, 1871), gen. nov.
      - *Peramuroides tenuiscus* gen. et sp. nov.
      - *Tendagurutherium* Heinrich, 1998
    - Family ?Peramuridae Kretzoi, 1946
      - *Afriquiamus* Sigoneau-Russell, 1999
  - Order *incertae sedis* (stem Zatheria after Martin 2002)
    - Family Amphitheriidae Owen, 1846
      - *Amphitherium* de Blainville, 1838
      - *Amphibetulimus* (Lopatin and Averianov 2007)
      - *Palaeoxonodon* Freeman, 1979
    - Family *incertae sedis*
      - *Abelodon* Brunet *et al.*, 1990
      - *Arguimus* Dashzeveg, 1979
      - *Magnimus* Sigogneau-Russell, 1999
      - *Minimus* Sigogneau-Russell, 1999
      - *Nanolestes* Martin, 2002

Table 2

Specimen Number	Locus	AP	ANW	POW	DD
BMNH M47742	p1	[0.75]	[0.36]		
	p2	[1.12]	[0.44]		
	p3	[1.13]	[0.56]		
	p4	[1.60]	[0.61]		
	p5	1.28	0.50		
	m1	1.30	0.60	0.39	
	m2	1.17	[0.60]	0.36	2.22
	m3	0.90	0.47	0.24	
	m1–m3	3.24			
BMNH M21888	p3	[1.14]	[0.46]		
	p4	[1.45]	[0.52]		
	p5	1.30	0.47		
	m1	1.14	0.43	0.32	
	m2	1.17	0.56	0.32	2.23
	m3	[1.04]	0.47	-	
	m1–m3	[3.20]			

Table 3

Specimen Number	Locus	AP	ANW	POW	DD
BMNH M21887	P1	0.60	0.27		
	P2	0.63	0.33		
	P3	0.67	0.29		
	P4	1.02	0.42		
	P5	0.95	0.45		
	M1	[0.92]	0.66	0.76	
	M2	0.87	0.75	0.76	
	M3	-	-	-	
BMNH M47739	?i3	-	-		
	?i4	[0.40]	[0.34]		
	?i5	[0.39]	[0.31]		
	c	[0.91]	[0.42]		
	p1	0.51	0.22		
	p2	0.63	0.29		
	p3	0.72	0.27		
	p4	0.96	0.37		
	p5	0.90	0.39		
	m1	1.01	0.53	0.33	
	m2	0.98	0.48	0.33	1.63
	m3	0.91	0.47	0.32	

	m1–m3	2.73			
BMNH M47754	p1	[0.71]	[0.31]		
	p2	[0.87]	[0.38]		
	p3	[1.05]	[0.47]		
	p4	[1.18]	[0.46]		
	p5	1.17	0.39		
	m1	1.03	0.43	0.29	
	m2	[1.01]	[0.54]	[0.38]	1.90
	m3	[0.95]	[0.55]	[0.29]	
	m1–m3	[3.00]			
BMNH M48404	p3	-	-		
	p4	1.02	0.40		
	p5	1.00	0.41		
	m1	1.17	0.55	0.31	
	m2	1.15	0.58	0.30	1.90
	m3	1.05	0.49	0.29	
	m1–m3	3.16			

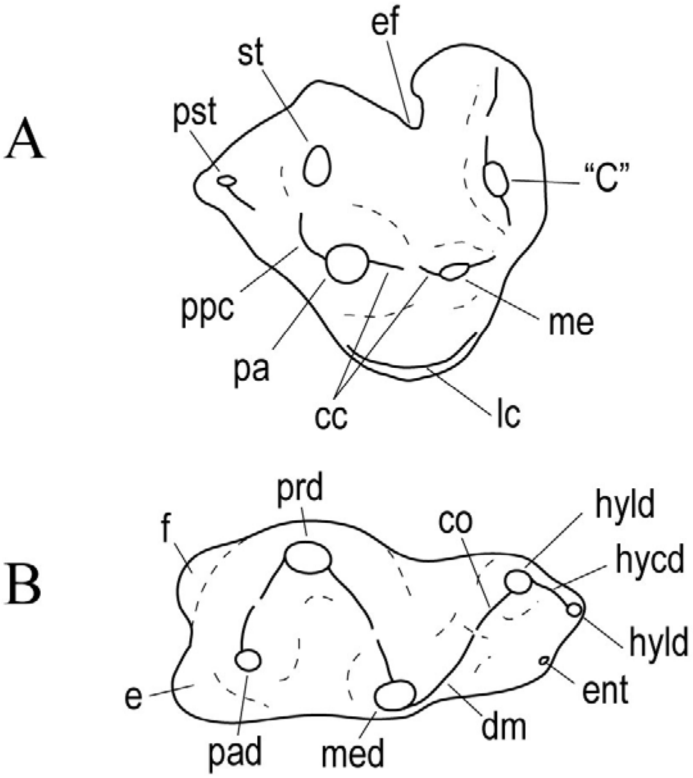
Table 4

Specimen Number	Locus	AP	ANW	POW	DD
BMNH M47751	p1	[0.54]	[0.33]		
	p2	[0.76]	[0.39]		
	p3	[0.91]	[0.42]		
	p4	[1.04]	[0.44]		
	p5	1.10	0.51		
	m1	1.15	0.54	0.36	
	m2	1.07	0.66	0.34	1.99
	m3	[1.16]	[.53]	[0.38]	
	m1–m3	3.24			

Table 5

Specimen Number	Locus	AP	ANW	POW	DD
BMNH M47744	i1	[0.27]	[0.27]		
	i2	[0.27]	[0.25]		
	i3	0.37	0.33		
	i4	-	-		
	i5	-	-		
	c	-	-		
	p1	0.59	0.26		
	p2	0.67	0.22		
	p3	0.76	0.36		
	p4	0.95	0.43		
	p5	0.87	0.34		
	m1	0.90	0.43	0.27	
	m2	-	-	-	1.44
BMNH M47799	m1	[1.09]	[0.44]	0.25	
	m2	0.87	0.41	0.23	
	m3	0.78	0.42	0.22	1.53
	m1–m3	2.59			

Figure 1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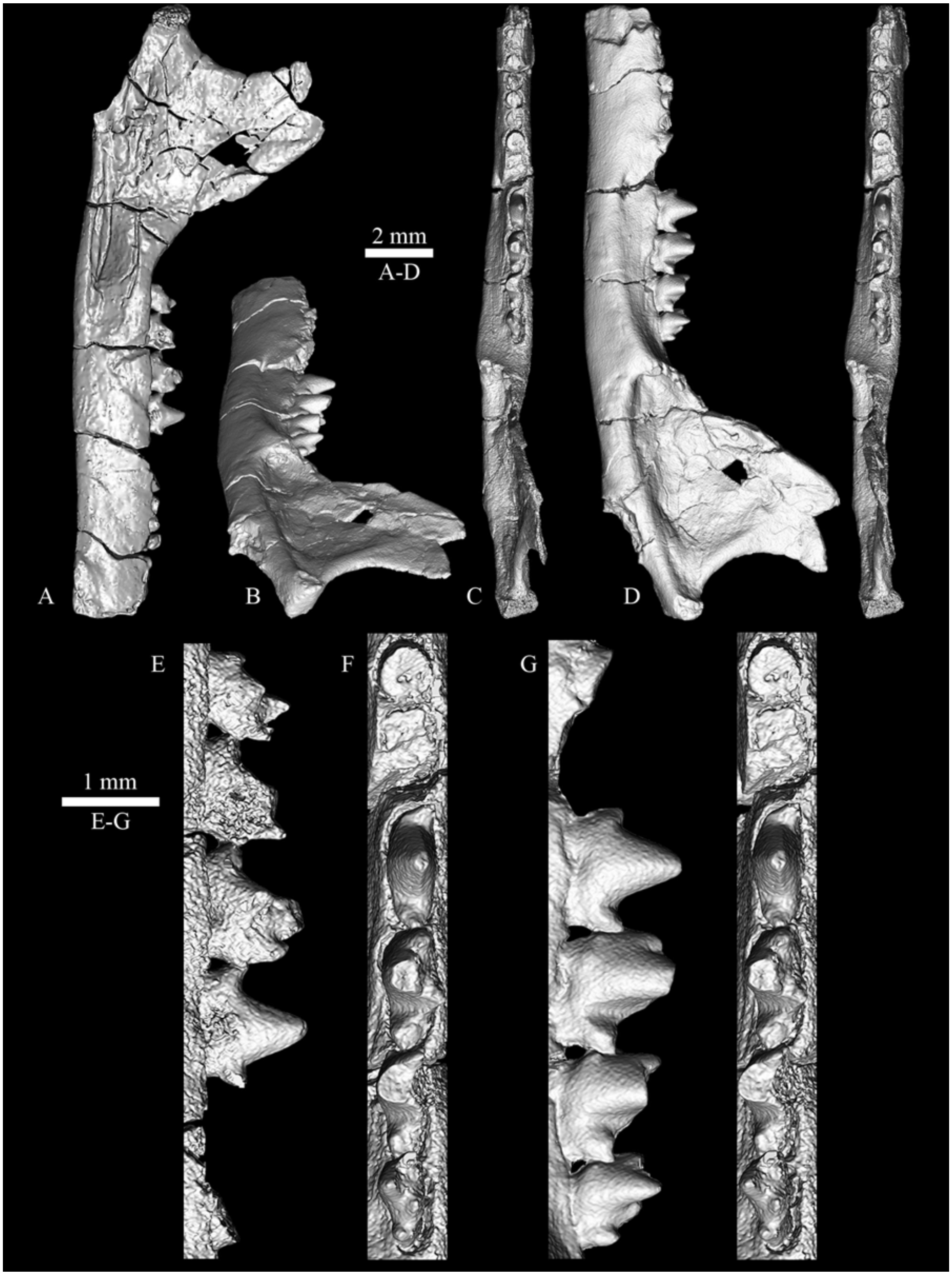

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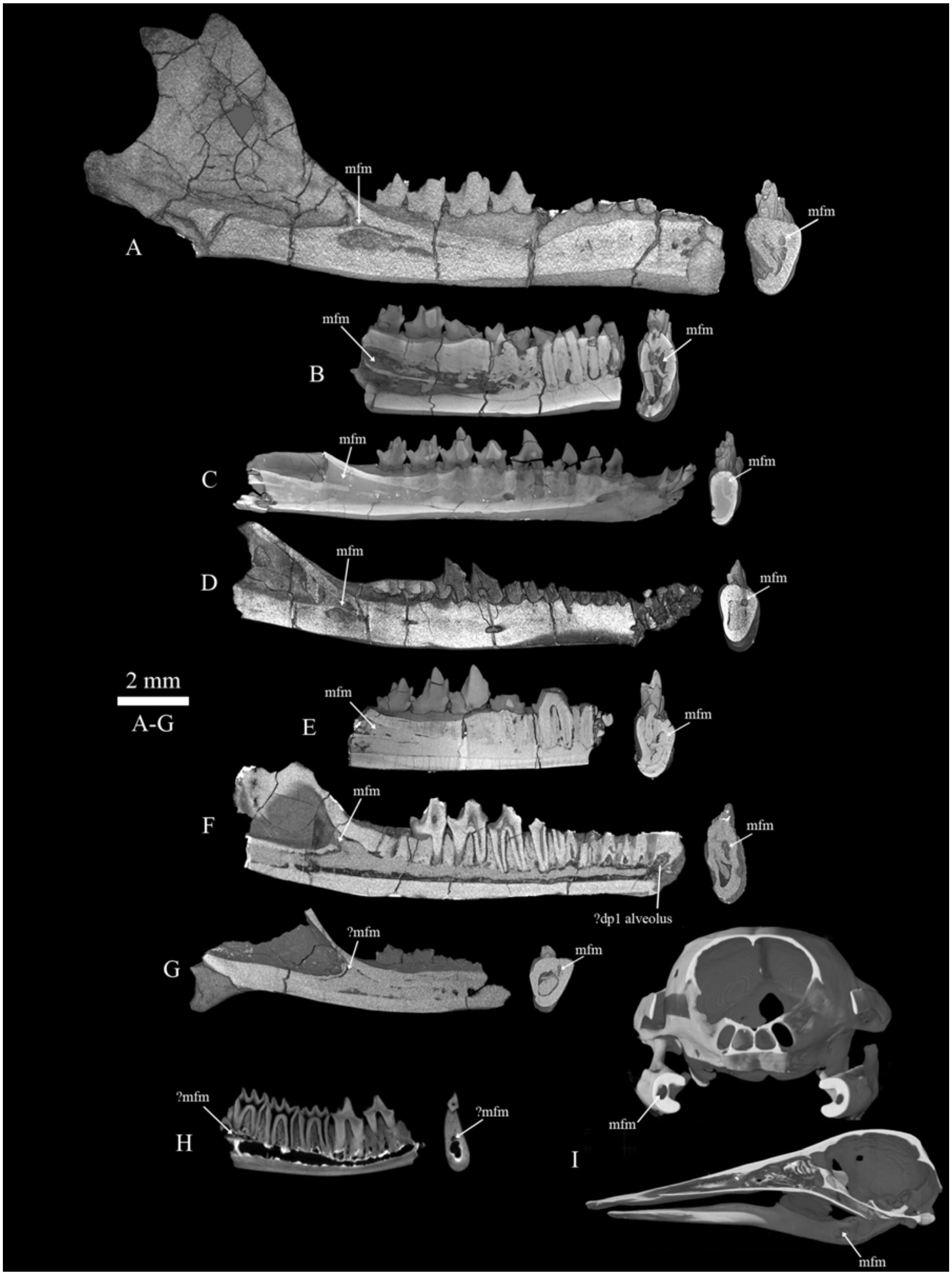
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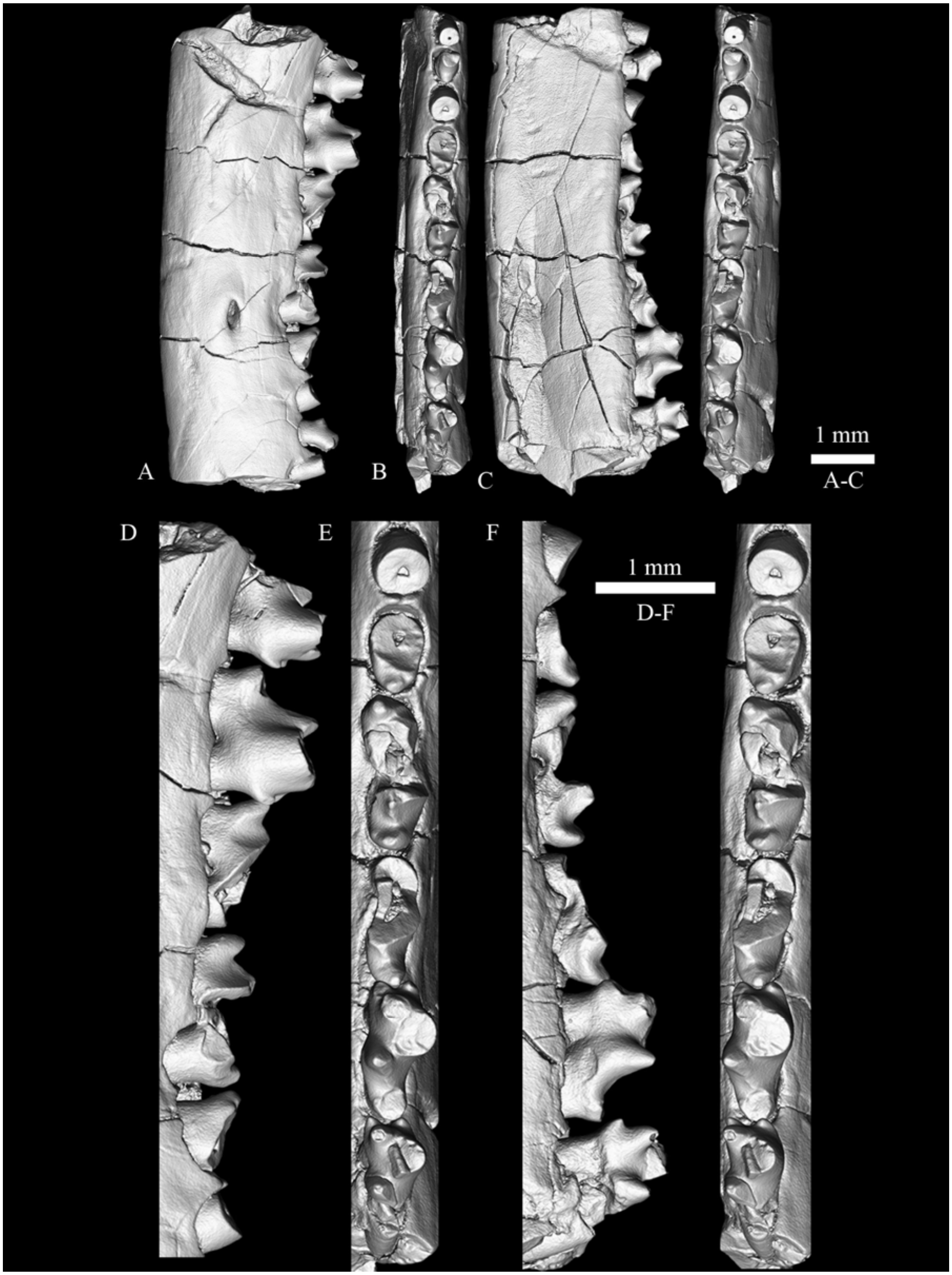

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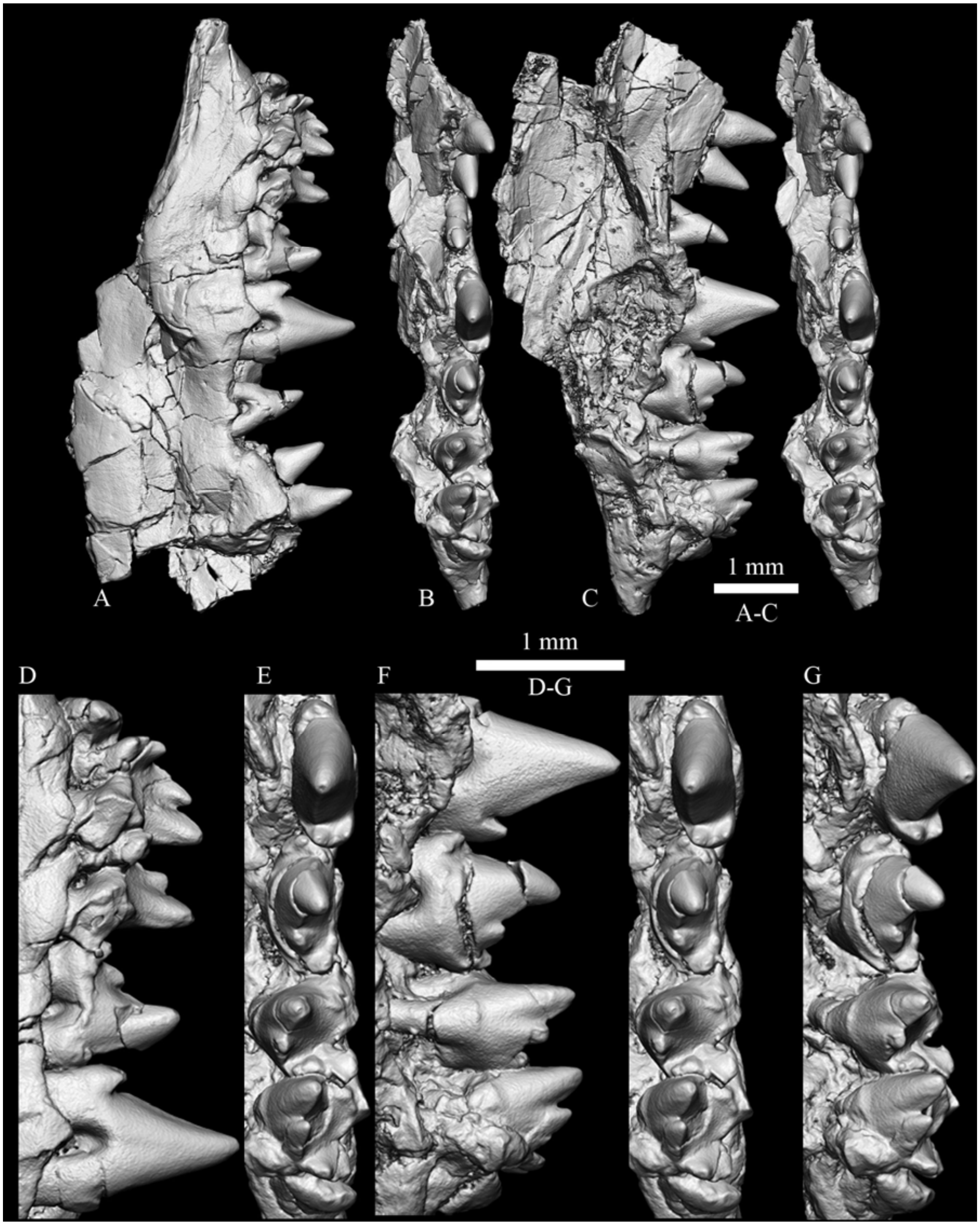

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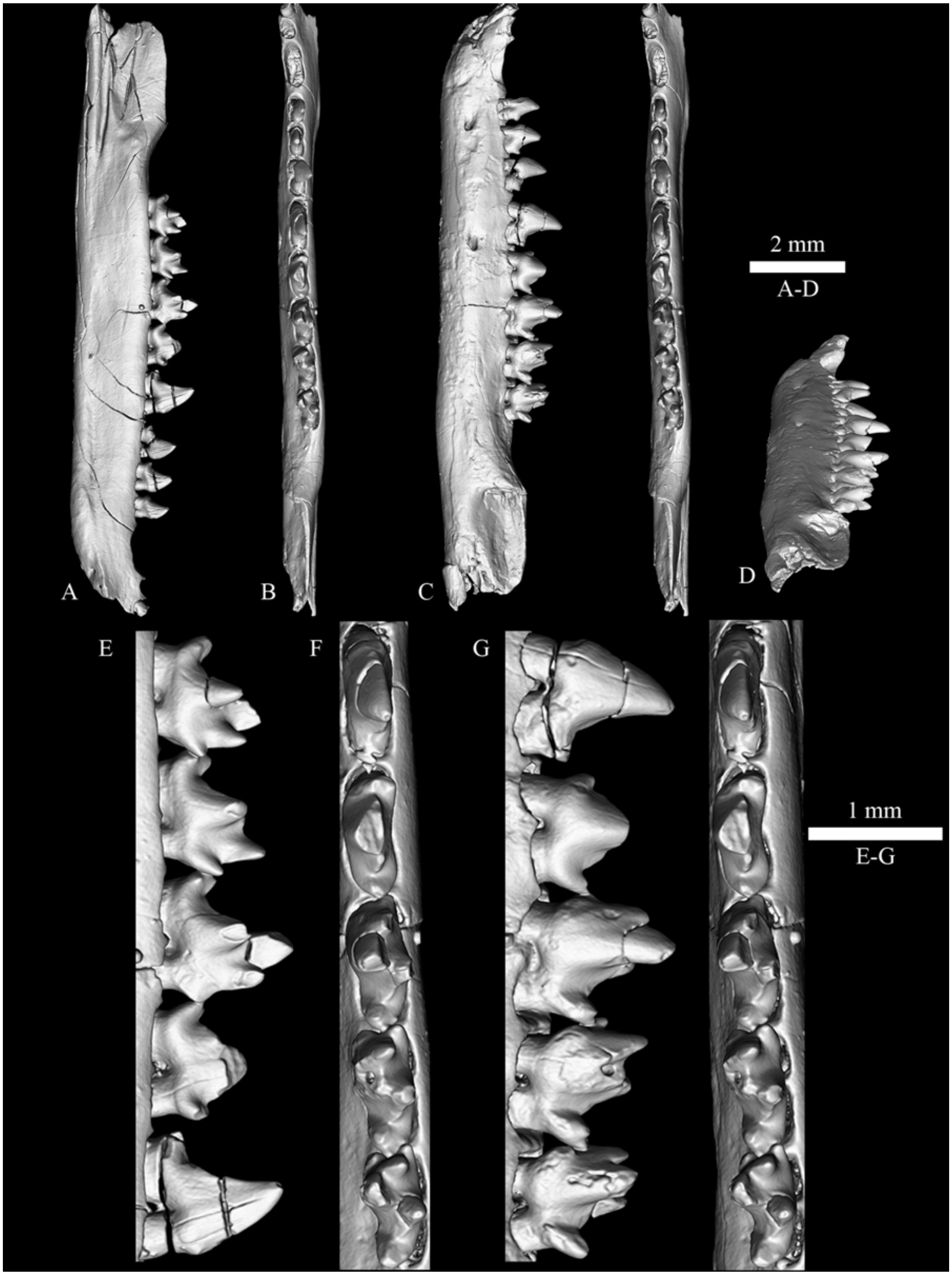

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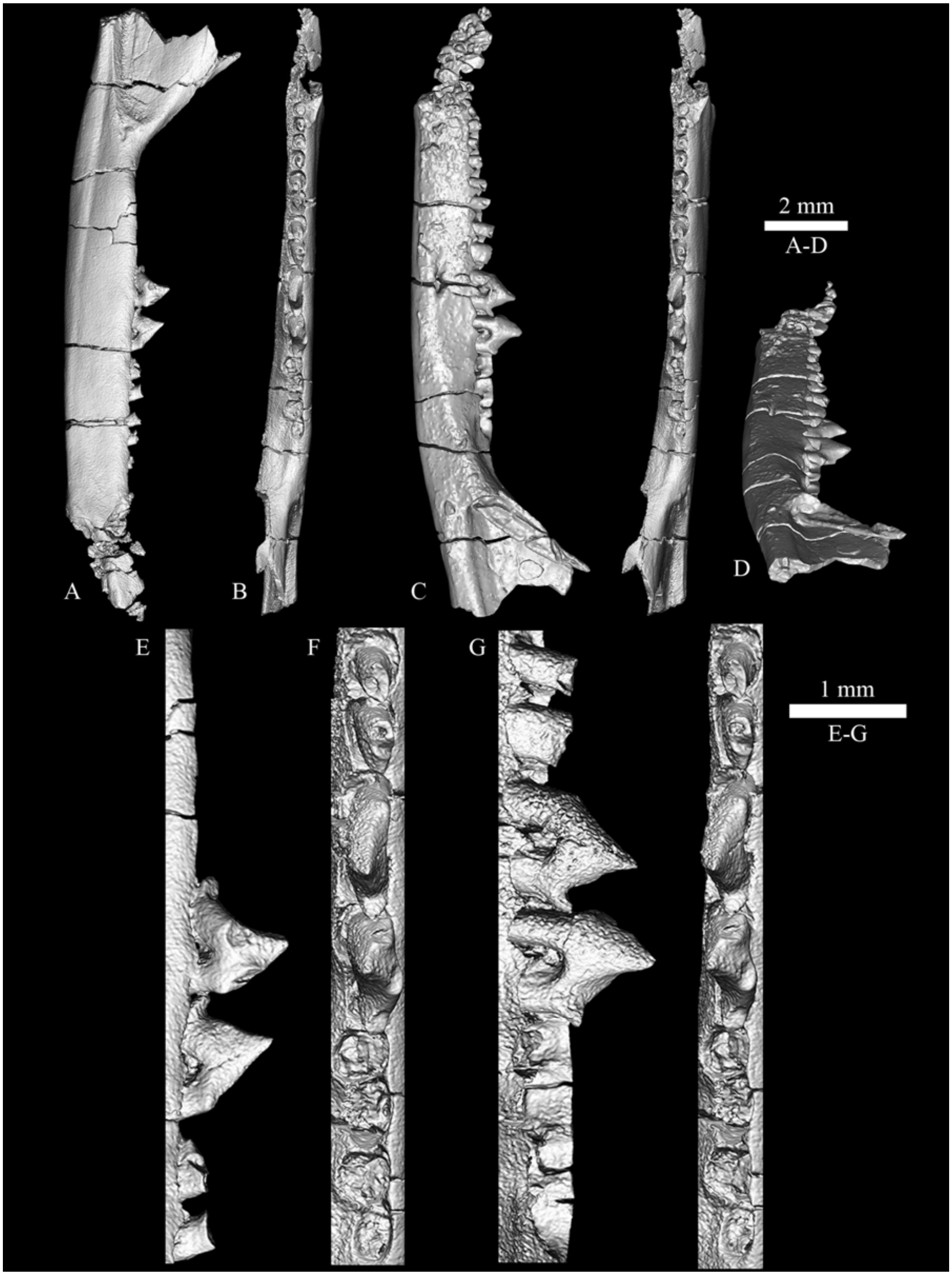

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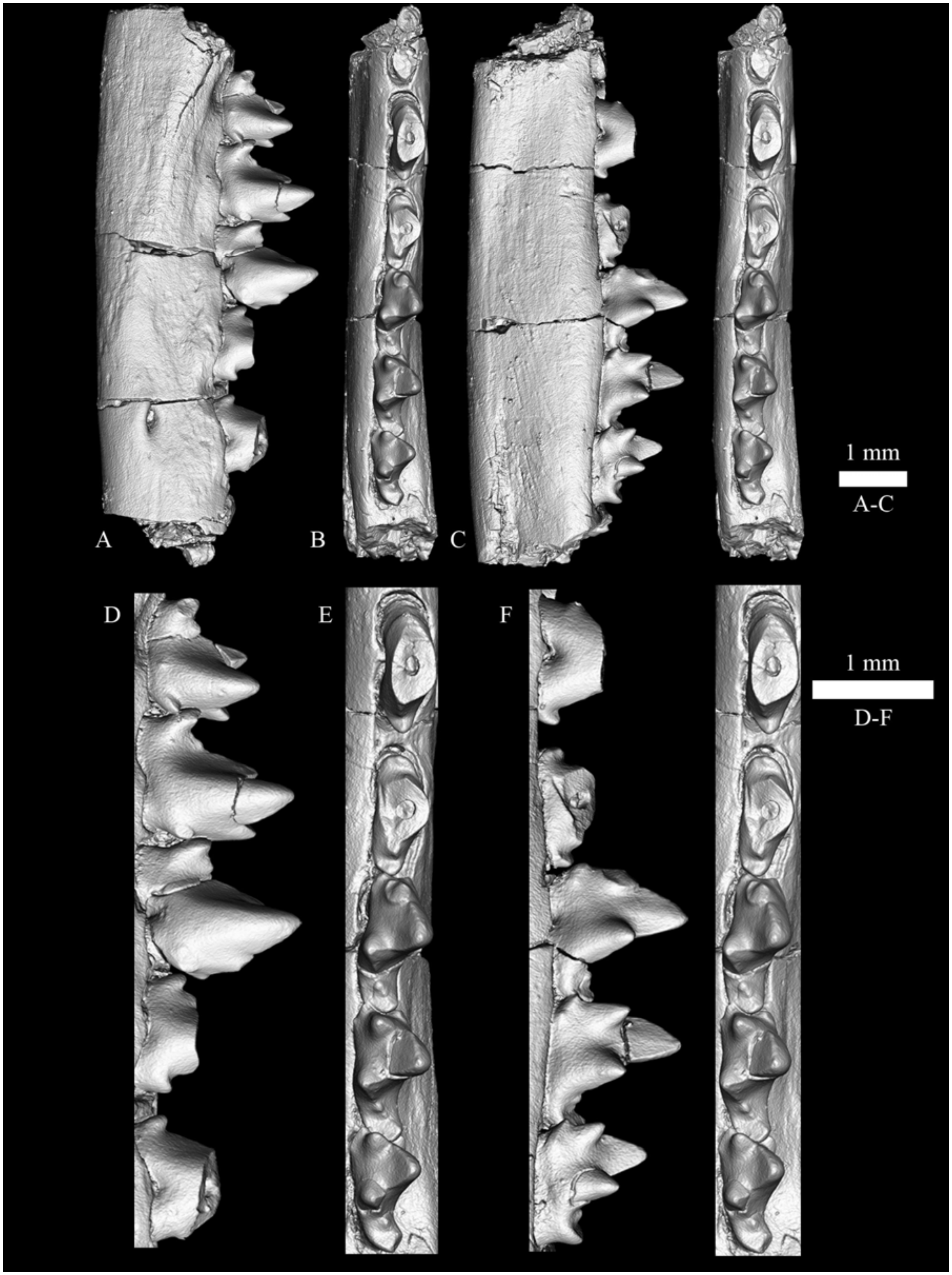

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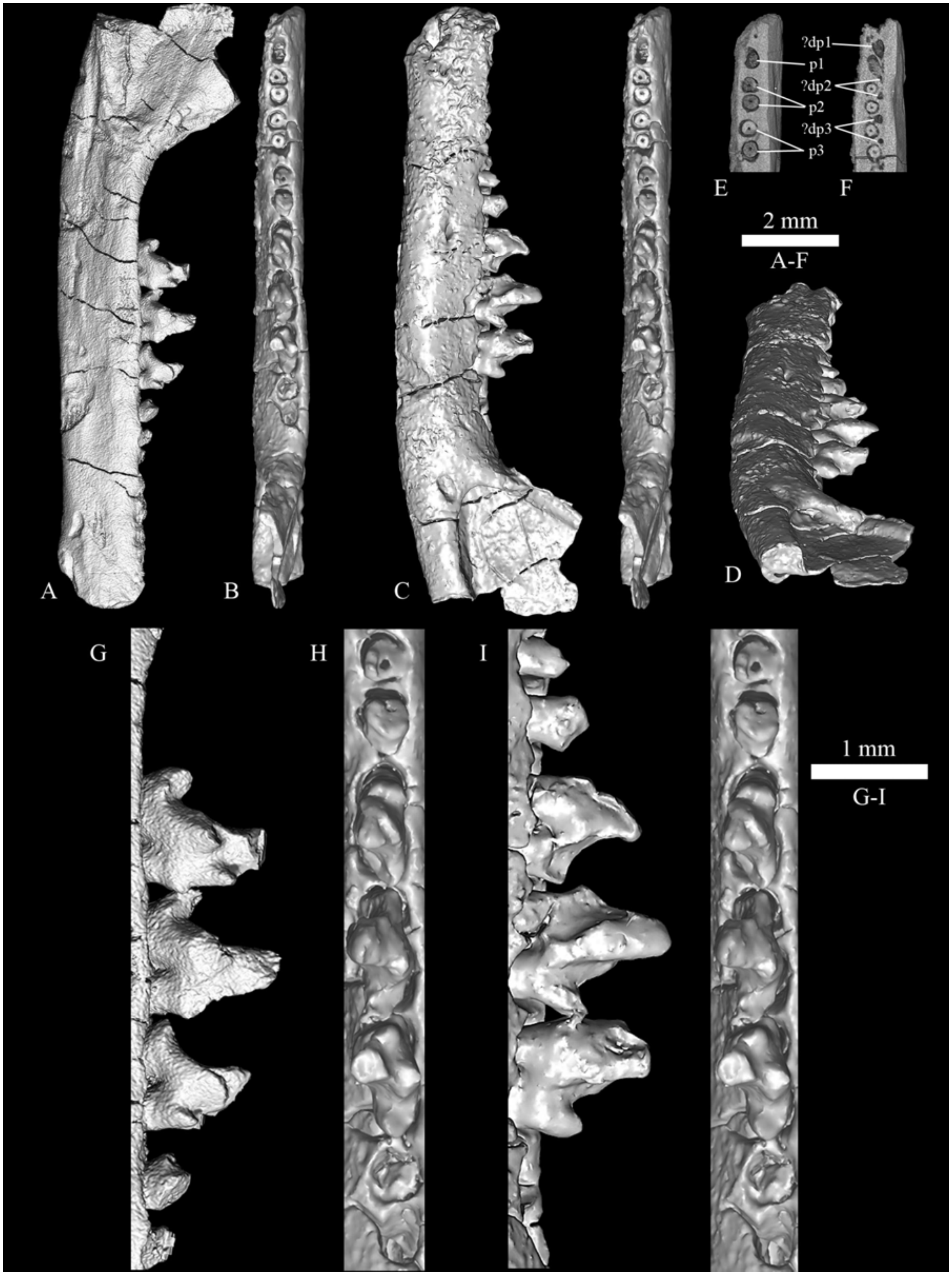

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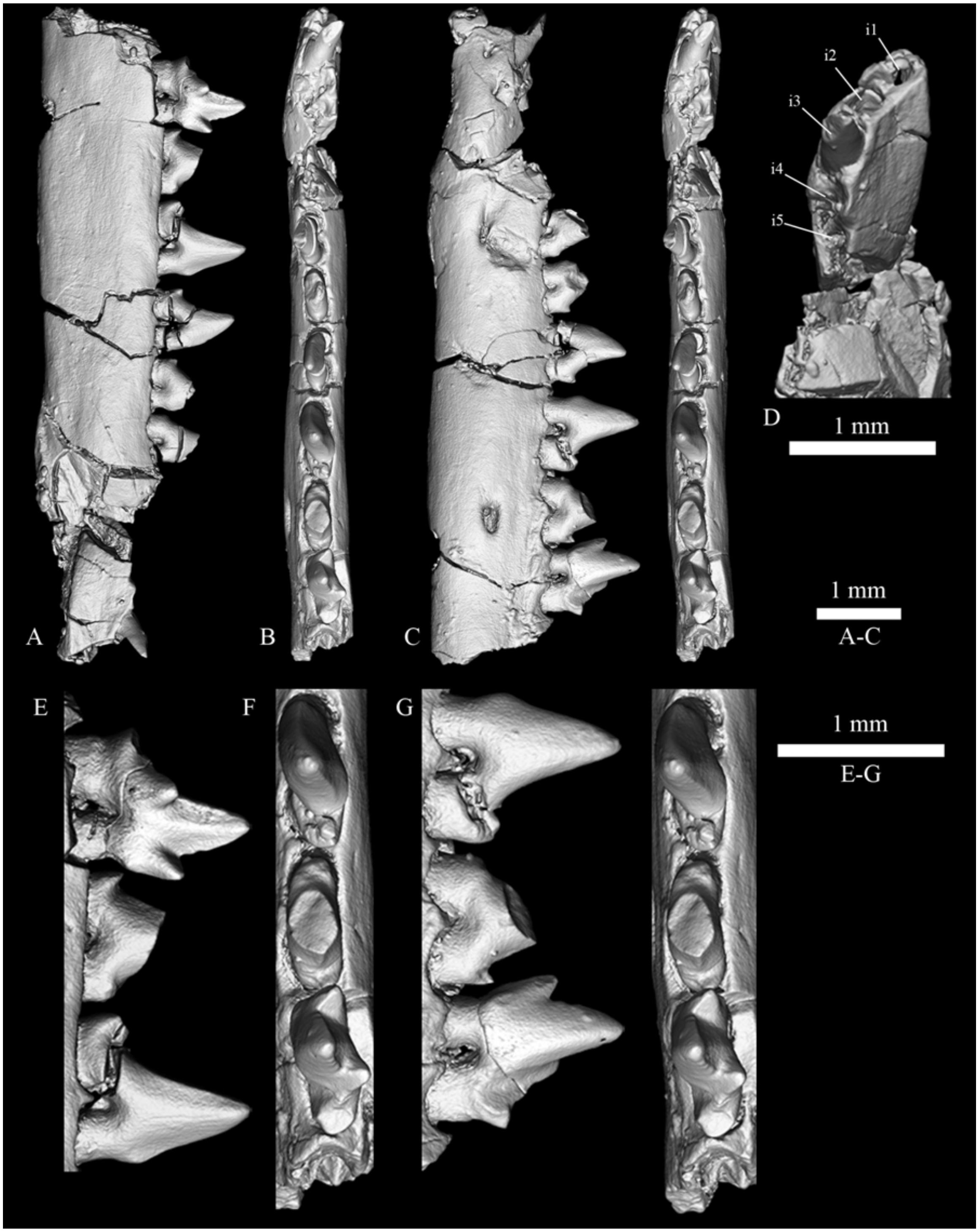

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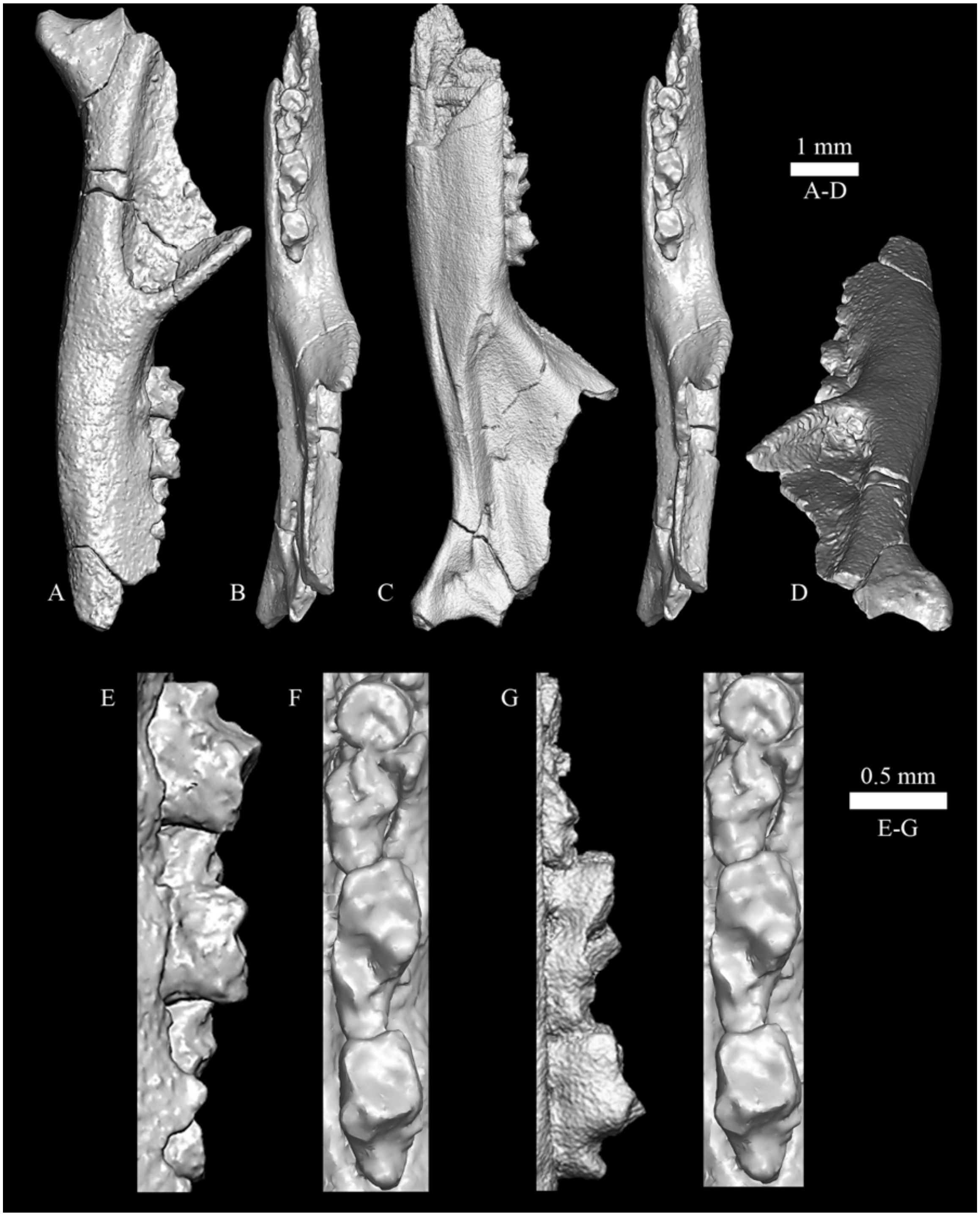

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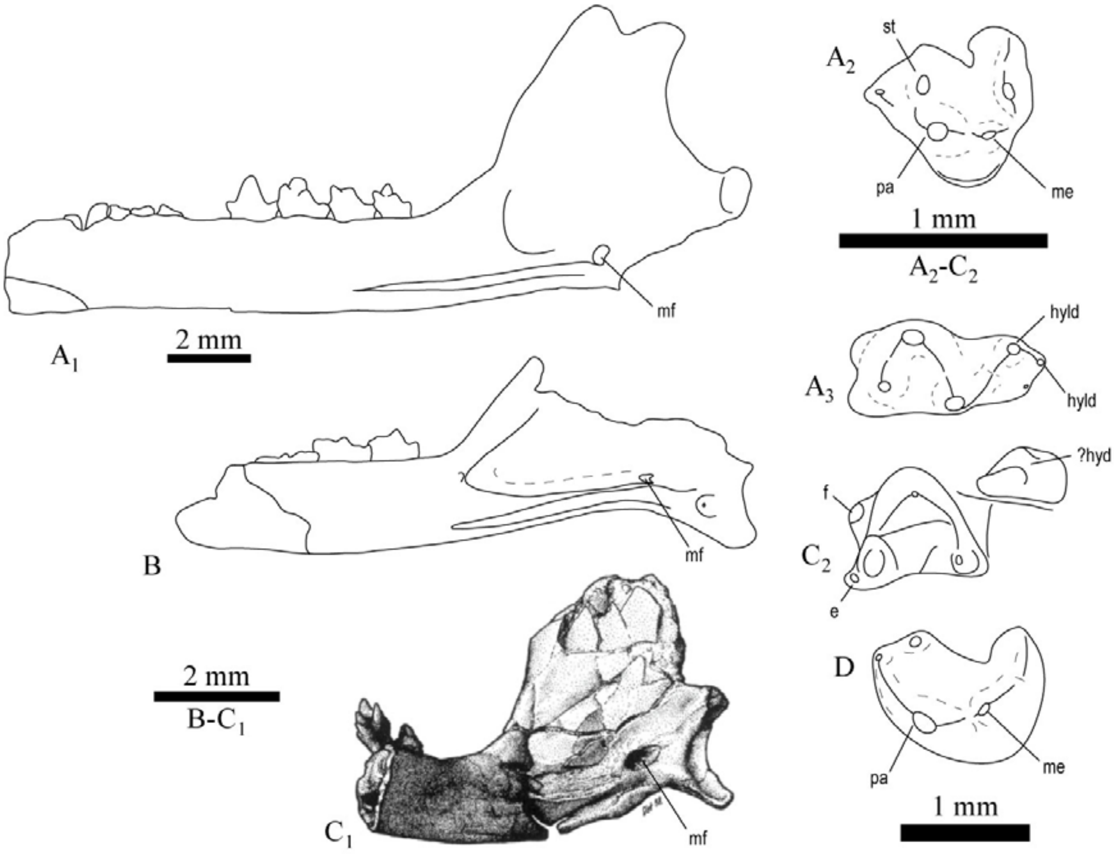
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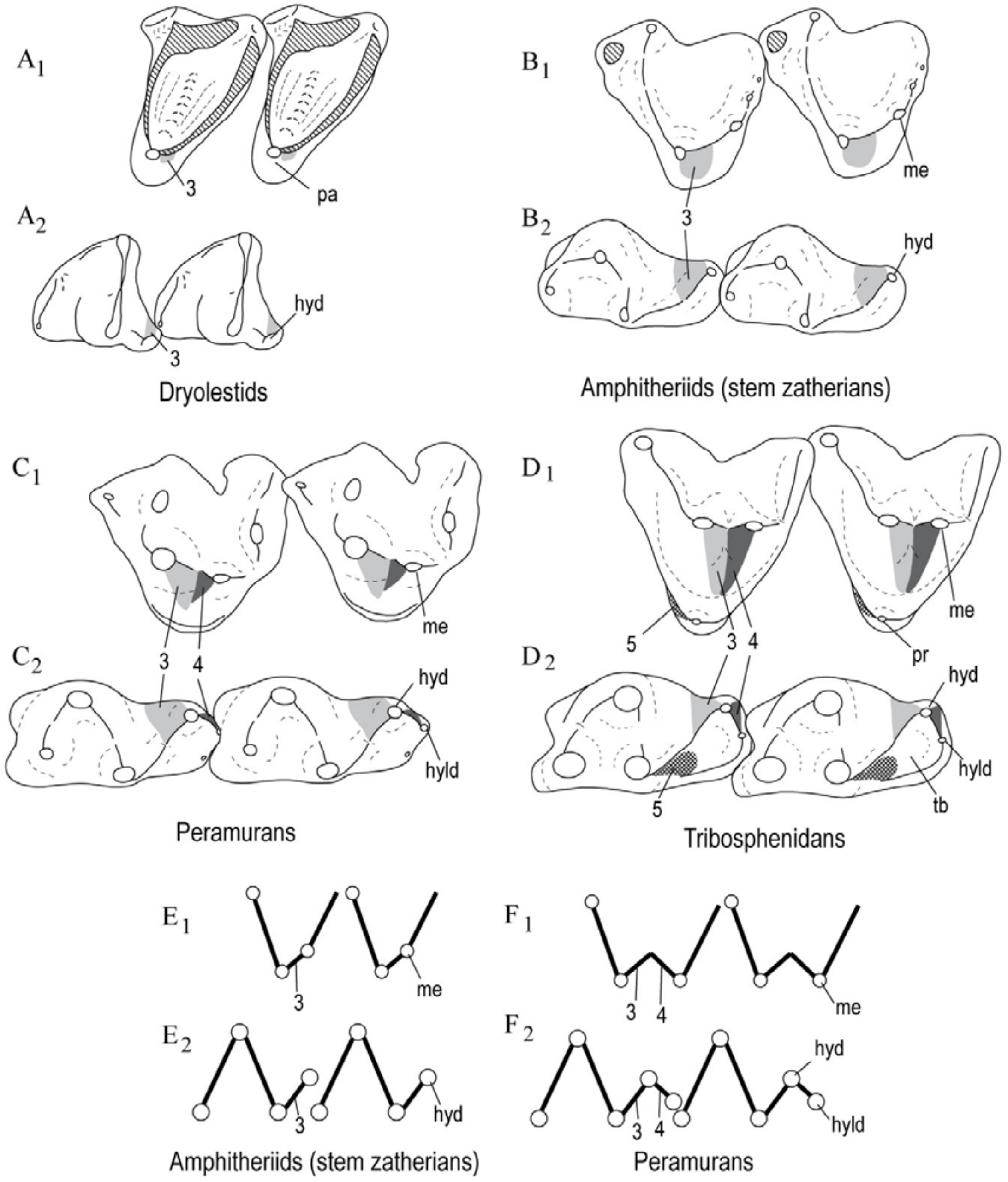
Figure 13



Dryolestids

Amphitheriids (stem zatherians)

Peramurans

Tribosphenidans

Amphitheriids (stem zatherians)

Peramurans