

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

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Abstract Development of the tribosphenic molar was a fundamental event that likely influenced the rise of modern mammals. This multi-functional complex combined shearing and grinding in a single chewing stroke, and provided the base morphology for the later evolution of the myriad dental morphologies employed by mammals today. Here a series of morphotypes are presented that represent stepwise acquisition of characters of the molar crown, in an effort to clarify homologies and functional analogies among molars of tribosphenic and tribosphenic-like mammals, as well as their putative sister groups. This is accomplished by evaluation of wear features, which 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 to a position more directly distal to the paracone (as 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 restricted to Laurasian taxa, with an origin at or just prior to the Jurassic-Cretaceous boundary.

Keywords 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; “eupantotheres” would later be placed variably under the Placentalia (Osborn 1907a) and Metatheria (Gregory 1910). It is clear from historical debate about the affinities of this group 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

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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; Wible et al. 2009), 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)—the possession of a lingual upper molar cusp (the protocone), which occludes into a distal basin on the lower molar (talonid basin). 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), and other early mammal lineages developed functionally similar molar patterns (docodonts and shuotheriids; see below). 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 possess molar morphologies that are not homologous with therian 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; 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. The primitive tribosphenic dentition is defined as one that possesses upper molars bearing a lingual cusp that occludes within a distal basin on the lower molars, as evidenced by the presence of wear facets (i.e., equiva-

lent to facets 5 and 6 of Crompton 1971). In the absence of known upper molars, a tribosphenic lower dentition must possess evidence of occlusion with a lingual upper molar cusp in the form of wear within a distal basin, separate from wear along shearing crests or apical wear from contact with food.

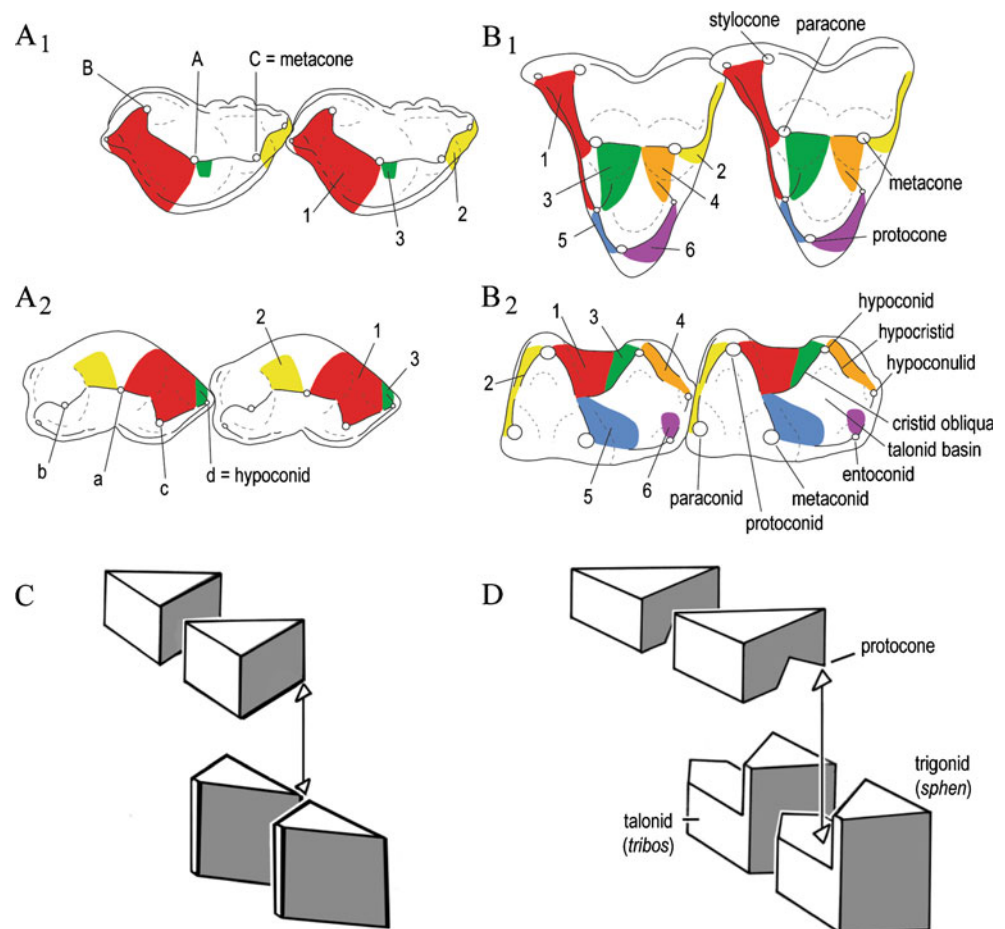
Molar terminology follows traditional designations, as illustrated in Kielan-Jaworowska et al. (2004: fig. 11.1). Where cusp homologies are uncertain or debated, the sequential lettering system proposed by Crompton and Jenkins (1968) is used. Wear facets developed by molar occlusion are numbered following 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 (2011).

Institutional Abbreviations BMNH, Natural History Museum, London, UK; NMV P, Palaeontology Collection, Museum Victoria, Melbourne, Australia.

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 that 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 mesial and distal 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

Fig. 1 Molar terminology and wear facet designation (in occlusal view). **A** Upper (**A₁**) and lower (**A₂**) molars of the archaic “symmetrodont” *Kuehneotherium* (Late Triassic-Early Jurassic of Britain); **B** upper (**B₁**) and lower (**B₂**) 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. Mesial is towards the left and buccal is towards the top of the page. Not to scale



central upper molar cusp (cusp A of Crompton and Jenkins 1968) to prevent over-occlusion, 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 distal cusp (traditionally referred to as cusp d; Crompton and Jenkins 1968) that 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. 1A₂, B₂). 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 that 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 distal 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 distolingual 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 distal 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. First, cusp d is homologous with the hypoconid. The primitive talonid cusp is initially situated centrally on the distal crown, and migrated buccally to its modern position as the talonid elongated in derived taxa. A neomorphic hypoconulid was later added distal and somewhat lingual to the hypoconid, in step with the lingual migration of the metacone and to support extension of shearing surface 4. This hypothesis focuses on retaining the occlusal relationship between the cristid obliqua/hypoconid and the paracone/postparacrista throughout this transformation, though the interlocking mechanism between adjacent lower molars must have been transferred from the hypoconid to the hypoconulid.

Alternately, cusp d is homologous with the hypoconulid. This hypothesis centers on maintaining contact between cusp d and the mesial basal cusps of the succeeding molar as the talonid lengthened, while the distal anchor for the cristid obliqua must have been transferred to a neomorphic hypoconid. To achieve a modern configuration, either the hypoconid migrated buccally as its upper molar embrasure deepened, or the hypoconulid migrated lingually along with the metacone. These competing hypotheses of homology are equivalent from the perspective of the single-cusped talonid found in plesiomorphic taxa: in each, cusp d anchors the distal end of the cristid obliqua (equivalent to the distal shearing crest of stem mammaliaforms such as *Kuehneotherium*; see Fig. 1A₂, B₂) and participates in the interlocking mechanism between adjacent molars (by fitting in a groove on the mesial face of the succeeding molar, typically formed by cusps e and f). Interpreting the transformations of both upper and lower molar morphology in more derived lineages illustrates where the hypotheses differ.

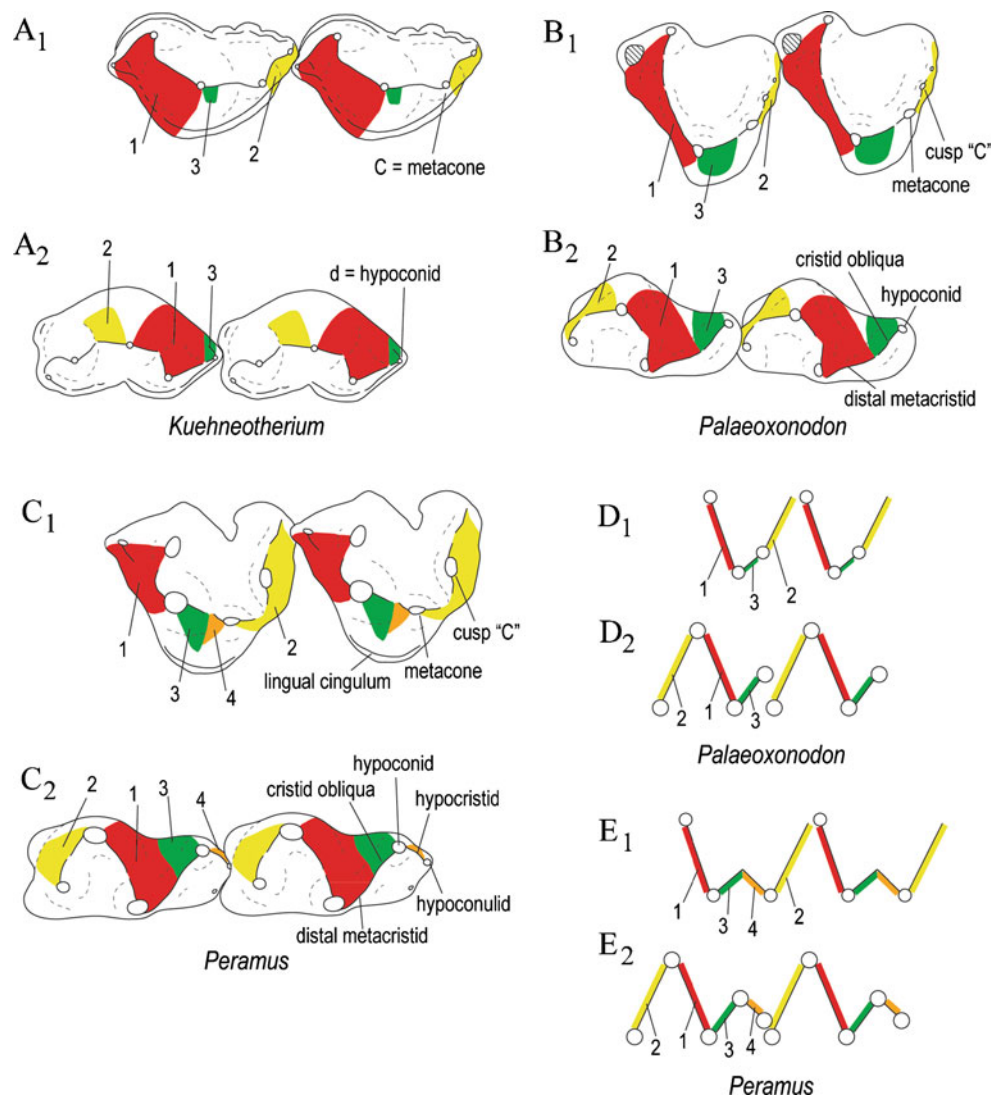
Upper molar morphology changed to match elaboration of the talonid through a general rearrangement of the internal cusps and shearing surfaces. As compared with a stem mammaliaform morphotype such as that represented by *Kuehneotherium*, the elongated cristid obliqua in lower molars of amphitheriids is coupled with an increase in the

functional area on the distal face of the paracone (facet 3; Fig. 2A, 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 distal to the paracone and the two cusps are more or less subequal (Fig. 1B₁). 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 an appropriate 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 mesiodistal midline of the crown (Fig. 1A₂). Other obtuse-angled “symmetrodonts,” such as *Tinodon* from the Late Jurassic of the USA and Early Cretaceous of Britain (including *Eurylambda*, Prothero 1981), are possibly derived in the reduction of cusp d and the morphology of

Fig. 2 Molars and wear facets of the archaic “symmetrodont” *Kuehneotherium*, the amphitheriid *Palaeoxonodon*, and the “peramuran” *Peramus* (in occlusal view). **A** Upper (**A₁**) and lower (**A₂**) molars of *Kuehneotherium* (Late Triassic–Early Jurassic of Britain); **B** upper (**B₁**) and lower (**B₂**) molars of *Palaeoxonodon* (Middle Jurassic of Britain); **C** upper (**C₁**) and lower (**C₂**) molars of *Peramus* (Early Cretaceous of Britain); **D** and **E** stylized illustration of the major shearing surfaces in upper (**D₁–E₁**) and lower (**D₂–E₂**) 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. Mesial is towards the left and buccal is towards the top of the page. Not to scale



the mesial portion of the upper molar (but see Rougier et al. 2003b 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 that are weakly triangulated. A broad wear facet occupies the entire mesial surface of the upper molar (facet 1 of Crompton 1971; Fig. 1A₁). Facet 2 extends from the metastylar corner to the distal face of cusp C (= metacone, as originally proposed by Kermack et al. 1968; see discussion in next section on homology of this cusp). Two additional facets were recognized and illustrated by Crompton (1971: fig. 7), but in derived taxa these either merge with adjacent facets (facet B merges with facet 3) or they disappear due to substantial structural rearrangements of the crown (facet A is lost as the trigon and trigonid become more acutely triangulated). They have therefore

been omitted from consideration in this paper for the sake of clarity.

Lower molars of *Kuehneotherium* have a similar occlusal outline to the upper molars, but with a distinct but low cusp d situated distally 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 that is topologically and functionally equivalent to the crisid 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 on 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 primitive relative to *Peramus* in that the metacone is buccally positioned relative to the paracone (no embrasure for the hypoconid; Fig. 2). In terms of lower molar morphology, at least, it is of the same structural grade as *Amphitherium*. Sigogneau-Russell (2003) is tentatively followed 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 buccally to a single cusp. This cusp is positioned distal to the protoconid, and it denotes the distal margin of wear facet 3, which occupies the mesiobuccal face of the cristid obliqua (Fig. 2B₂). In topology and function, the single talonid cusp in amphitheriids lends support to the hypothesis that cusp d is homologous with the hypoconid of tribosphenic taxa (though later evolution of a neomorphic cusp in the position of the hypoconid, or splitting of cusp d cannot be excluded). The upper molar paracone shears mesially against the distal metacristid and the protocristid, and distally against the elongate cristid obliqua; consequently, facet 3 on the upper molar is broad relative to that in *Kuehneotherium* (apomorphy)(Fig. 2A₁, B₁). There is no upper molar embrasure for the hypoconid (see next section), and no additional wear features are

typically 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). However, one specimen of *Palaeoxonodon* (BMNH 36504) shows evidence of a tiny wear facet on the mesiolingual tip of the metacone, presumably from contact with the distal face of the single talonid cusp (the metacone on this particular upper molar is positioned somewhat closer to the paracone than in other specimens, so much so that it has been illustrated with these cusps nearly in a mesiodistal line; Sigogneau-Russell 1999: fig. 21B). Occlusal contact between the metacone and the principal talonid cusp provides additional support for homology between cusp d and the hypoconid, and demonstrates that the plesiomorphic single talonid cusp can participate in occlusion while maintaining a role in the interlocking mechanism. The range of degrees of interlock, from imbrication in *Amphitherium* to the deep embrasure formed by cusps e and f in *Peramus*, suggest the possibility that there may have been some plasticity in this character. Modifications of the occlusal relationship of cusp d therefore need not necessarily be constrained by its structural role in this mechanism.

As noted above, a cusp occurs variably in specimens of *Palaeoxonodon*, at the base of the trigonid where the distal metacristid meets the cristid obliqua. This cusp is also variably present in other zatherians, such as *Peramus* and *Arguimus*. While Dashzeveg (1979) identified this cusp as the hypoconid in *Arguimus*, it actually serves to demarcate two major shearing surfaces—the distal metacristid (facet 1) and the cristid obliqua (facet 3). As pointed out by Butler (1990), this cusp is not referable to any primitive tribosphenic feature and instead likely improves shearing efficiency of the lower molar crests. 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 distal 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 distal cusp (traditionally labeled cusp C, but called the metacone by Kermack et al. 1968; Fig. 2A₁). In more derived taxa (e.g., dryolestids, stem zatherians, some tribosphenidans), there is

at least one additional cusp present along the distal margin of the tooth, buccal to the cusp typically labeled the metacone (Fig. 2B₁, C₁). 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 distal face of the metacone, lingual to cusp “C” (Fig. 2B₁). In fact, in all relevant taxa (*Kuehneotherium* and all trechnotheres), facet 2 always extends to the lingual-most cusp on the distal upper molar crest (the cusp closest to the paracone; 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 buccal 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 linguallly-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. 2). 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 mesial and distal 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 homologized with cusps of tribosphenic taxa—a hypoconid placed directly distal to the protoconid, and a hypoconulid set distolingually 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 distobuccally between the two talonid cusps along the hypocristid (facet 4). Thus, the shearing surfaces of the lower molar run in alternating directions (Fig. 2D). 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 linguallly-placed metacone (Fig. 2C₁). The shift in position of this cusp (from a distobuccal 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 mesial face of the metacone developed a special role in occlusion by shearing against the new surface on the distal face of the hypoconid, creating facet 4. Migration of the metacone to a functional position directly distal 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. 2C₁). It does not appear to have been involved in occlusion, and it is incomplete mesially and distally. A similar and often stronger structure is present in tinodontid and zhangheotheriid “symmetrodonts” (Rougier et al. 2003a, b; Lopatin et al. 2005), and it provides a possible example of a structural 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 linguallly expanded and basined, as the mesial surface of the protocone wears against the talonid distal 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 distal 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. 2C₁). 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). While there remain some significant differences between amphitheriid and “peramuran” morphotypes, the two illustrate step-wise acquisition of characters for improved shearing, especially in light of a possible example of a transitional morphology between the two (in *Palaeoxonodon*, see above).

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. 3B). This facet is produced by the mesial slope of the protocone as it occludes on the lingual side of the distal metacristid and finally in the mesial portion of the talonid basin at the end of the chewing stroke.

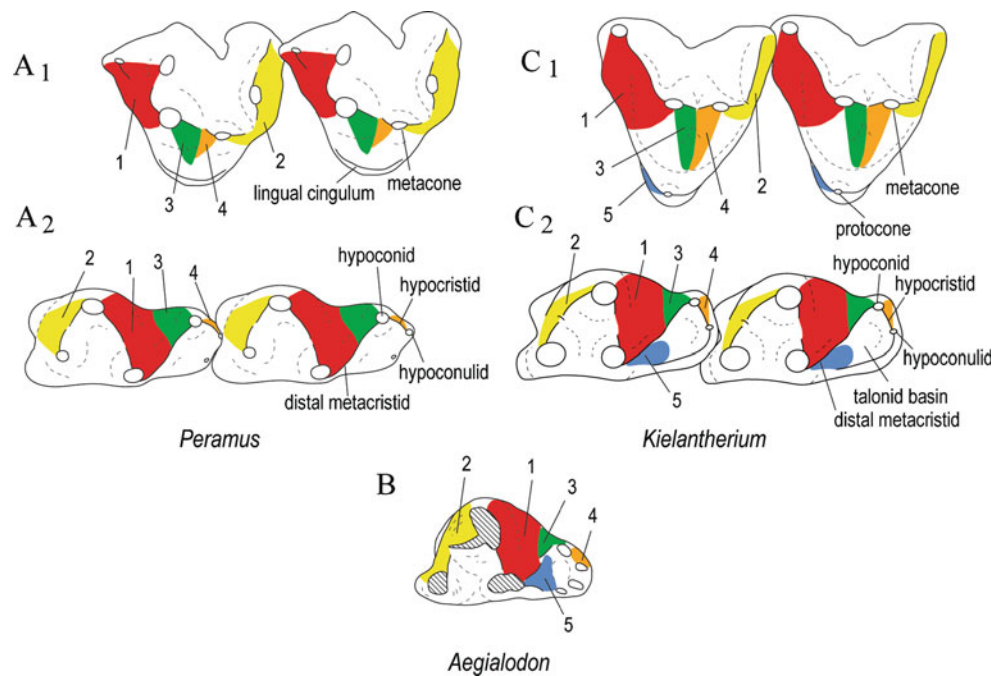
A number of dentally advanced mammals appeared across Laurasia by the end of the Early Cretaceous: from the Barremian Jehol biota of China, the eutherians *Eomaia*

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; Davis and Cifelli in press). 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* based on lower molar morphology (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 (also supported by plesiomorphies of the dentary; Dashzeveg and Kielan-Jaworowska 1984). The hypoconid and hypoconulid are situated close to one another, matching the narrow upper molar embrasure between the closely appressed paracone and metacone (Fig. 3C). 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. 3C). The distolingual 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 distal 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. 3A₁, C₁). The first

Fig. 3 Molars and wear facets of the “peramuran” *Peramus* and the aegialodontids (basal Tribosphenida) *Aegialodon* and *Kielantherium* (in occlusal view). **A** Upper (**A₁**) and lower (**A₂**) molars of *Peramus* (Early Cretaceous of Britain); **B** lower molar of *Aegialodon* (Early Cretaceous of Britain); **C** upper (**C₁**) and lower (**C₂**) molars of *Kielantherium* (Early Cretaceous of Mongolia). Molars are duplicated to show adjacent wear facets, and are not intended to indicate serial loci. **C₁**, modified from Lopatin and Averianov (2006b). Mesial is towards the left and buccal is towards the top of the page. Not to scale



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 mesiolingual portion of the upper molar and the distolingual slope of the lower molar trigonid (facet 5). While no fossils with transitional morphologies of this character 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 distal root and, in tandem, the area of the crown above it (compare Fig. 2B₂ and C₂). A lingual talonid shelf, cusps, or crests, as previously discussed, could have functioned like a styler shelf. Until the expansion of the opposing lingual 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 styler region on the buccal 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 distal 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 is vital to the multi-functional nature of the tribosphenic dentition.

While no pre-tribosphenic taxon possesses an entoconid (a small cusplule is present but without occlusal function 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 Deltatheroidea, 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 that 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 Deltatheroidea). 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 that 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 employed by Luo et al. (2001). However, it is first important to note some other lineages that 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

Docodonta are known from the Middle Jurassic through Early Cretaceous, with a Laurasian distribution (for good reviews, see Ch. 5 of Kielan-Jaworowska et al. 2004; Luo and Martin 2007; Averianov et al. 2010). They are skeletally primitive mammaliaforms (Krusat 1991; Martin 2005), 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 a mesial expansion of the lower molars (Fig. 4A). This cusp-on-basin occlusion provides a grinding function, giving docodonta dual-purpose molars. However, their phylogenetic placement is generally near the base of mammals (e.g., Luo et al. 2007).

The molars of docodonta 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;

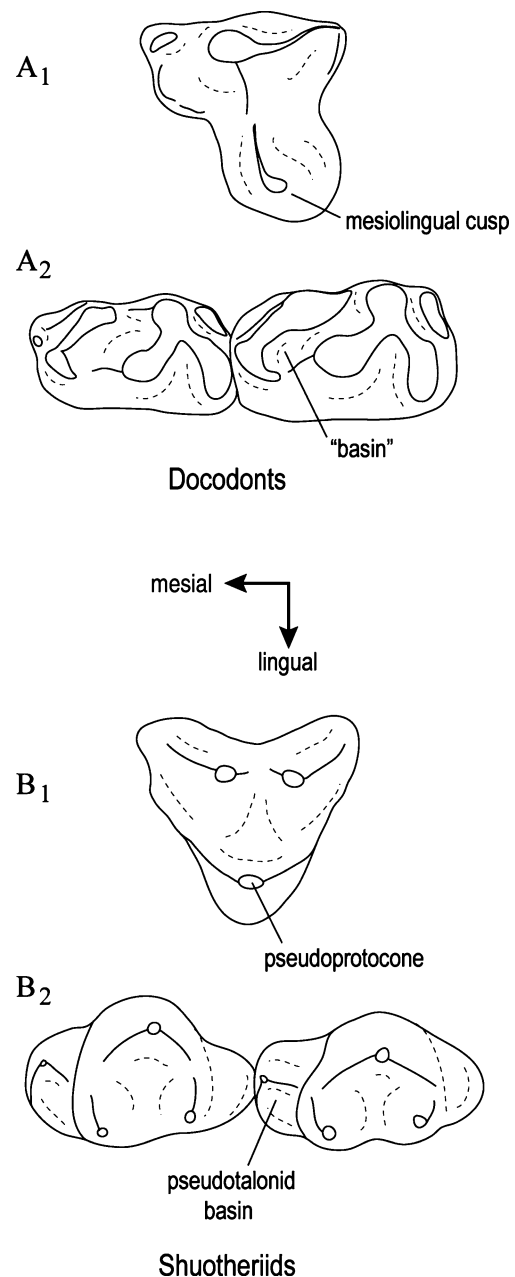


Fig. 4 Molars of the docodont *Haldanodon* and the shuotheriid *Shuotherium* (in occlusal view). **A** Upper (**A**₁) and lower (**A**₂) molars of *Haldanodon* (Late Jurassic of Portugal); **B** upper (**B**₁) and lower (**B**₂) molars of *Shuotherium* (Middle–Late Jurassic of Britain and China). **A** Modified from Krusat (1980); **B**₁, modified from Chow and Rich (1982); **B**₂ modified from Wang et al. (1998). Mesial is towards the left and buccal is towards the top of the page. Not to scale

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 distal to a lower, basined structure—the reverse of the condition in otherwise topologically similar tribosphenic molars (Fig. 4B₂). 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. 4B₁). The lingual upper molar cusp and mesial lower molar basin were termed the “pseudoprotocone” and “pseudotalonid basin” to highlight their functional but non-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 close 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, 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. 5). They exhibit well-developed, basined, and multicuspated 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, 1998, 2001). The

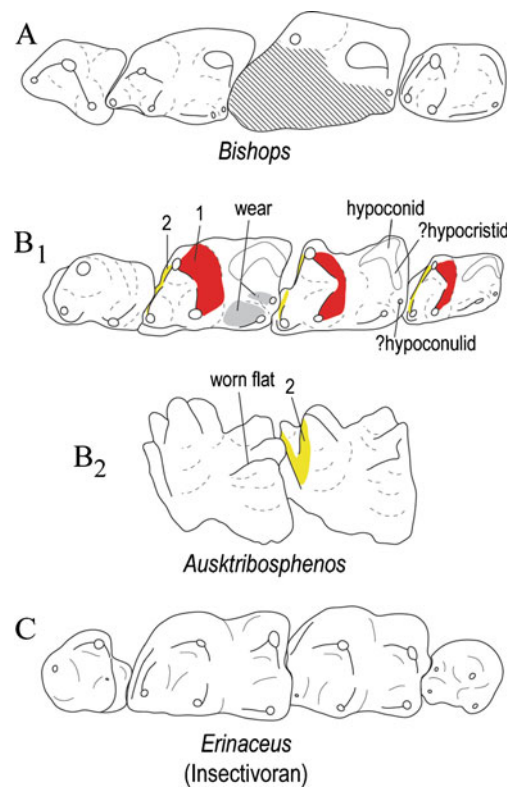


Fig. 5 Lower dentition and wear facets of the ausktribosphenids (Australosphenida) *Bishops* and *Ausktribosphenos*, and the insectivoran (Eutheria) *Erinaceus*. **A** Lower ultimate premolar and m1–3 of *Bishops* (NMV P210075, Early Cretaceous of Australia); **B** lower ultimate premolar and m1–3 (**B**₁) and m1–2 (**B**₂, buccal view, reversed) of *Ausktribosphenos* (NMV P208089, Early Cretaceous of Australia); **C** lower ultimate premolar and m1–3 of *Erinaceus* (Recent of Britain), for comparison of general morphology: note the molari-form 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 (buccal view, reversed relative to **B**₁). Mesial is towards the left and buccal is towards the top of the page. Not to scale

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. 6A). 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 with 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

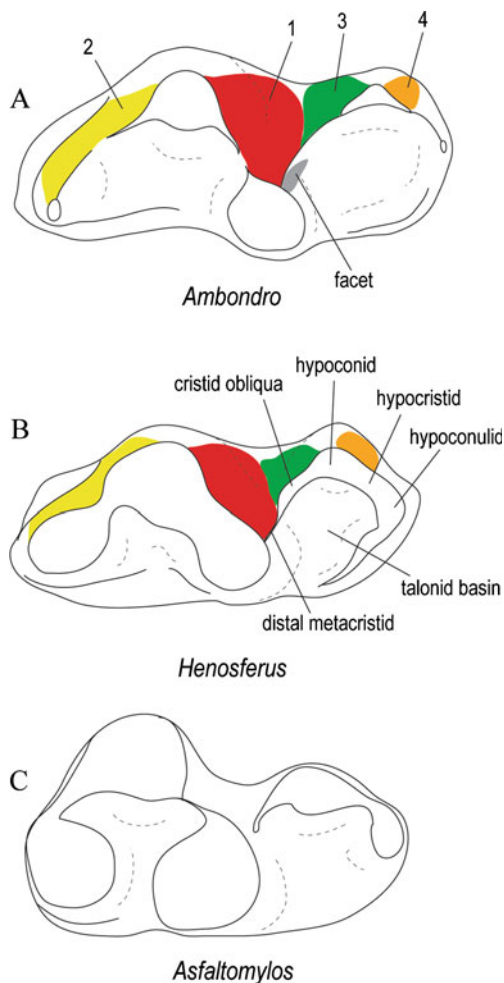


Fig. 6 Lower molars and wear facets of the henosferids (Australosphenida) *Ambondro*, *Henosferus*, and *Asfaltomylos* (in occlusal view). **A** Lower molar of *Ambondro* (Middle Jurassic of Madagascar); **B** lower molar of *Henosferus* (Middle Jurassic of Argentina); **C** lower molar of *Asfaltomylos* (Middle Jurassic of Argentina). **C** Modified from Martin and Rauhut (2005). Mesial is towards the left and buccal is towards the top of the page. Not to scale

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 australosphenid 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. 6), 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, australosphenidans generally 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 buccal 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 agreed that australosphenidans did not possess 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 mesial 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 felt 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.

Personal observations of original material and casts of all non-monotreme australosphenidan taxa except for *Asfaltomylos* reveal some evidence to support limited occlusal contact by a lingual upper molar structure in some members of this group. Below, the wear features of each taxon are described; it should be noted in advance that the identification of wear on a particular specimen is highly dependent on both the age of the individual (development of wear) and preservation.

Ausktribosphenos (Fig. 5B)—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 mesiobuccal 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 distal 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 distal surface of the hypoconid. A distal metacristid is absent from the distal 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 (buccal) 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. 5A)—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. 6A)—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 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 distal portion of the m2), and the hypoconid on m1 is still conical, maintaining the shallow but distinct talonid basin. While Flynn et al. (1999) identified wear facets 5 and 6, this interpretation is not followed here. 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 sheared against the distal metacristid and had no occlusal contact with the talonid, perhaps paralleling the trajectory of the paracone as it sheared along the buccal edge of the distal metacrista. Based on the available evidence, it appears that upper molars of *Ambondro* possessed a lingual upper molar structure that should not be considered a protocone, as the molars of this specimen were functionally tribosphenic (as defined earlier in this paper).

Henosferus (Fig. 6B)—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. 6C)—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 here it is suspected that both features would be revealed in better preserved specimens of *Asfaltomylos*.

The distal 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. 7). *Ambondro* and *Henosferus* have a more typical, obliquely-oriented hypocristid that bears a wear facet on its distobuccal face (facet 4 of Crompton 1971; Fig. 7F–H), presumably caused by action against the mesial slope of the upper molar metacone as in tribosphenidans and *Peramus* (Fig. 3). 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 distal face of the upper molar) is well developed (Fig. 5B₂), 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, as well). 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) is the most appropriate hypothesis for upper molar structure in these taxa (Fig. 7E). The upper molar lophs would abrade directly against the hypoconid and other talonid structures, while the mesial and distal 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, it is argued here that the differences between the taxa are very slight and the morphological and functional similarities are very strong (Fig. 6). They clearly cluster among australosphenidans to the exclusion of ausktribos-

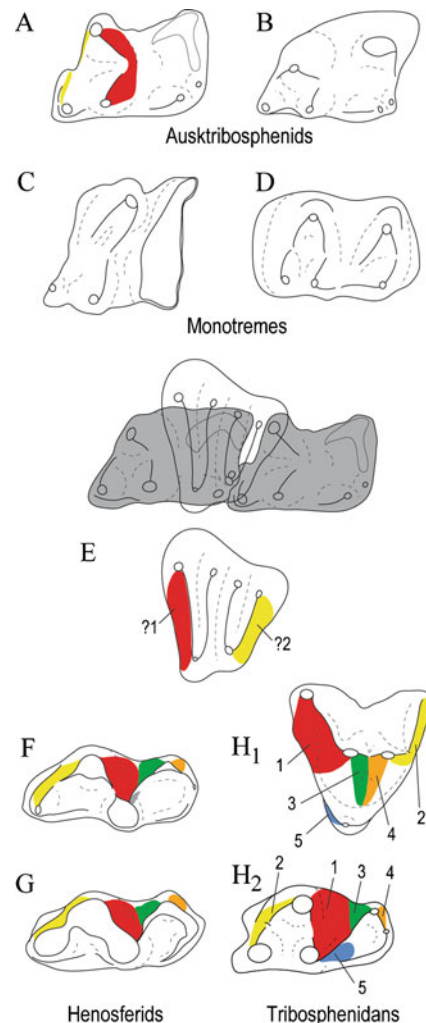


Fig. 7 Functional comparisons of lower molar morphology and wear facets of australosphenidans as discussed in the text (in occlusal view). The ausktribosphenids *Ausktribosphenos* and *Bishops* (A, B, respectively, Early Cretaceous of Australia) resemble toothed monotremes such as *Teinolophos* and *Steropodon* (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. 5B₂. The henosferids *Ambondro* (F, Middle Jurassic of Madagascar) and *Henosferus* (G, Middle Jurassic of Argentina) more closely resemble basal tribosphenidans such as *Kielantherium* (H₂, Early Cretaceous of Mongolia); upper molars of henosferids are most likely to resemble basal tribosphenidans (H₁) or shuotheriids (Fig. 4B₁). D Modified from Rich et al. (2001); E modified from Martin and Rauhut (2005); H₁, modified from Lopatin and Averianov (2006b). Mesial is towards the left and buccal is towards the top of the page. Not to scale

phenids—they share premolariform or non-triangular ultimate premolars (though likely a plesiomorphy) and, presumably, a functional upper molar embrasure for the hypoconid, as indicated by the presence of facets 3 and 4 (Fig. 6). In light of this, it is proposed 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* (Fig. 7; Pascual et al. 1992). 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.

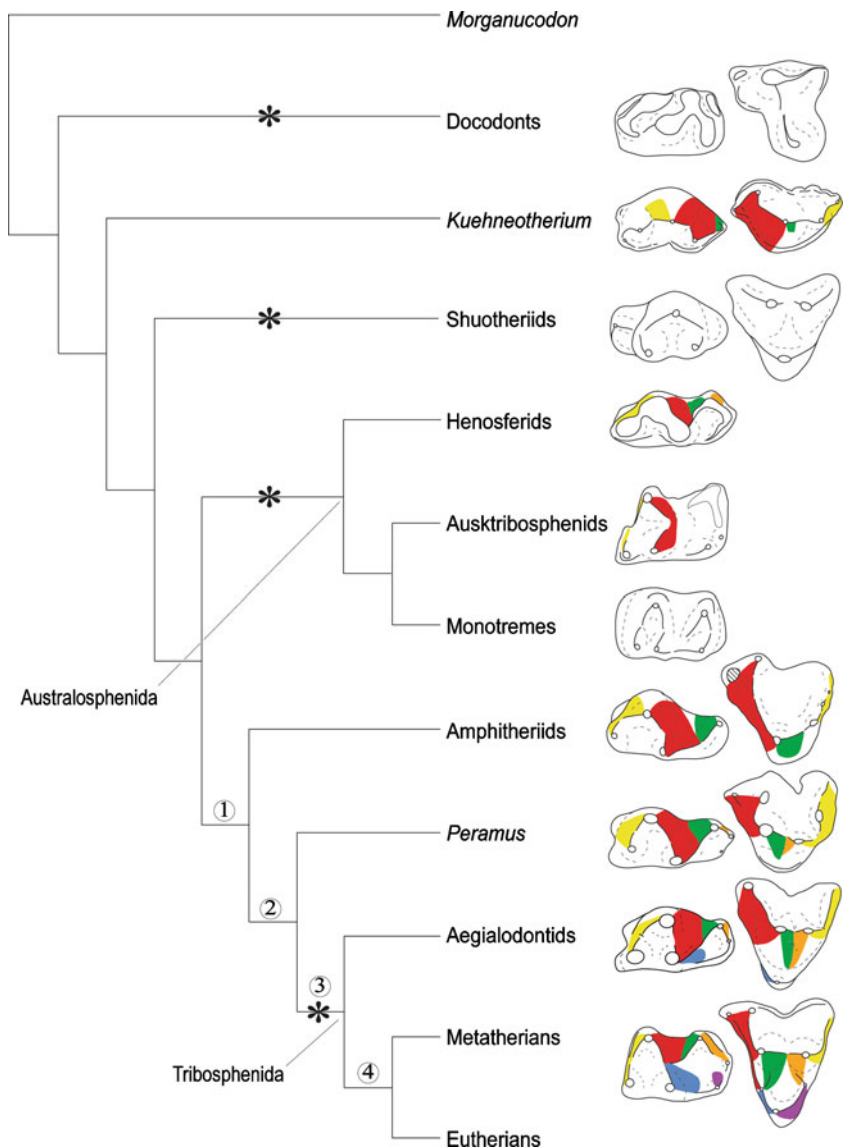
Ultimately, more complete fossils with upper dentitions are necessary to fully evaluate the role of the australosphen-

nidan talonid during mastication, and their relationships to each other and to northern tribosphenic mammals. However, recent analyses (one of which is simplified in Fig. 8) 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 modifi-

Fig. 8 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, mesial is towards the left and buccal is towards the top of the page. Not to scale



cation 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) that supported a very short crest (cristid obliqua), functioning to prevent overclosure of the jaws and producing limited shear against the distal 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, buccally-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 distal to the paracone, in *Peramus*; this creates an embrasure for the hypoconid and produces a new wear surface (facet 4) between the mesial surface of the metacone and the lower molar hypocristid (as noted earlier, there is at least one example in *Palaeoxonodon* of minor shear occurring between the mesial surface of the tip of the metacone and the distal surface of cusp d, suggesting an intermediate stage in the development of a two-cusped talonid). A second talonid cusp (hypoconulid) occupies the distal margin of the expanded talonid, securing it between the e and f cusps of the succeeding molar, and anchoring the distal 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 distolingual 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 mesial 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 (though the wear patterns are most similar in *Ambondro*, facets are still limited to shearing surfaces and do not appear to be present within the talonid basin). This clade appears to be highly variable in structure and presumably function, which reflects either separate evolutionary origins of taxa within the group or a substantial morphological divergence (perhaps in congruence with the wide stratigraphic and geographic range of the Australosphenida). 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, as defined earlier in this paper as a lingual upper molar cusp that produces wear within a distal lower molar basin (necessarily separate from wear along shearing crests or apical wear from contact with food) evolved only once, though there were several convergences on functionally or morphologically similar dentitions (Fig. 8). 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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