

Dentition and relationships of the Jurassic mammal *Shuotherium*

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Kielan-Jaworowska, Z., Cifelli, R.L., and Luo, Z.-X. 2002. Dentition and relationships of the Jurassic mammal *Shuotherium*. *Acta Palaeontologica Polonica* 47 (3): 479–486.

The Middle Jurassic mammal *Shuotherium* has lower molars that possess a trigonid and talonid, but are unique in having the talonid situated in front of the trigonid, rather than behind it, as in molars of usual tribosphenic pattern. *Shuotherium dongi* Chow and Rich, 1982 was based on a dentary bearing seven teeth, originally interpreted as three premolars and four molars. Based on comparison with other groups of early mammals, we reinterpret the premolar–molar boundary in the holotype of *S. dongi*, and propose a dental formula of four (or more) premolars and three molars. The ultimate lower premolar (previously identified as the first molar) has a completely developed trigonid and no talonid or pseudo-talonid. We hypothesize that the mesial cingulid on molars of Australosphenida is a highly plausible structural antecedent to the pseudo-talonid of *Shuotherium*. This and other shared, derived features support a relationship of *Shuotherium* and Australosphenida as sister-taxa. We hypothesize that the common ancestor of *Shuotherium* + Australosphenida had a global distribution no younger than early Middle Jurassic, and that the respective clades diverged prior to full separation of Gondwanan and Laurasian landmasses.

Key words: Australosphenida, *Shuotherium*, tribosphenic molars, Jurassic, China.

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Introduction

The Jurassic mammal *Shuotherium* has attracted broad attention among students of early mammals, owing to its peculiar, reversed-tribosphenic molar design. Chow and Rich (1982) described *Shuotherium dongi* from the Middle or Late Jurassic of China, based on a dentary bearing seven teeth (some represented only by roots) and one alveolus. The molars are characterized by a unique design, wherein the crushing heel (termed a pseudo-talonid) lies anterior to the shearing trigonid—a mirror-image to the analogous pattern of tribosphenic molars, in which the talonid is posterior to the trigonid. These authors offered a hypothetical reconstruction of upper molar structure in *Shuotherium*, including reconstruction of corresponding shearing surfaces (based on the study of Crompton 1971) between lower and upper molars. Paradoxically, the precociously-specialized molars of *Shuotherium* occur in a dentary that is notable for its plesiomorphies, such as the presence of a scar, trough, and ridge indicating attachment of the postdentary elements to the dentary, rather than incorporation into the middle ear.

Uniqueness of molar design led Chow and Rich (1982) to erect the legion Yinotheria, order Shuotheridia, and family Shuotheriidae to contain *Shuotherium*. Yinotheria, in turn, were regarded by them as a stem clade of Theria *sensu lato*.

Rowe (1988) advocated a restricted, taxon-based concept of Theria, to include only the crown group (i.e., the last common ancestor of Marsupialia and Placentalia, plus all of its descendants). On this basis, the more inclusive, traditional grouping was termed Holotheria by Hopson (1994), following the traditional view that included taxa comprise one of two clades thought to represent an early, fundamental dichotomy in mammalian history (e.g., Hopson 1969). Hopson's "holotherians" include monotremes but exclude eutriconodonts. The term Holotheria was formalized by Wible et al. (1995) as a taxon-based substitute for Theria *sensu lato*, defined as the last common ancestor of *Kuehneotherium* and living therians, plus all of its descendants to the exclusion of both eutriconodonts and monotremes, and this systematic scheme was endorsed by McKenna and Bell (1997). However, results of most later studies (e.g., Rougier et al. 1996; Luo et al. 2002) place monotremes within "Holotheria" (as defined by Wible et al. 1995, and as used by McKenna and Bell 1997). These results conflict with the primary intent of for formalizing Holotheria; that is, definition of a monophyletic group of mammals that excludes monotremes. For this reason, as well as several others detailed by Luo et al. (2002: 4), we do not use the term "Holotheria" herein.

Chow and Rich (1982) interpreted the postcanine tooth formula of *S. dongi* as p3, m4; however, they called attention

to the fact that the tooth identified as $m1$ differs significantly from the succeeding teeth, noting (p. 132): "It is possible that the tooth here regarded as M_1 should be more probably designated P_4 . It does differ from the undoubted molars behind it in lacking a pseudo-talonid and having a more antero-posteriorly expanded trigonid. However, the sharpest change in the form of adjacent postcanine teeth occurs between the simple, somewhat blade-like P_3 and the highly molariform M_1 ".

A rather different phylogenetic interpretation was subsequently proposed by K.A. Kermack et al. (1987): that *Shuotherium* may be related to Docodonta. The basis for this suggestion is the presence of an anteriorly-placed basin on lower molars of the Middle Jurassic docodont *Simpsonodon*, suggestive of a crushing function analogous to that of the pseudo-talonid in *Shuotherium*. This view contradicts prevailing opinion on cusp homologies of docodonts, and has received no support (e.g., Hopson 1995; Sigogneau-Russell 1998).

Some sixteen years after the initial report of Chow and Rich (1982), Sigogneau-Russell (1998) described several isolated lower and upper molars from the Bathonian of England, assigning two of the lower teeth to *Shuotherium dongi* and the remainder to *Shuotherium kermacki* Sigogneau-Russell, 1998, or to *Shuotherium* sp. She tentatively assigned three upper molars to ?*Shuotherium*. In the same year, Wang et al. (1998) described an upper molar fitting the design predicted for *Shuotherium dongi* by Chow and Rich (1982). This upper molar is from the same locality as the holotype of *Shuotherium dongi*, but is too large to belong to this species, and was therefore described as *S. shilongi* by Wang et al. (1998). This specimen brought welcome confirmation to Chow and Rich's (1982) hypothetical reconstruction of the coronal pattern and occlusal features of upper molars of *Shuotherium*. Wang et al. (1998) regarded Yinotheria as the sister-taxon to Cladotheria McKenna, 1975. This hypothesis is congruent with the classification of McKenna and Bell (1997), wherein Shuotheriidae are placed within a restricted Symmetrodonta that is, in turn, implicitly recognized as the sister-taxon to Cladotheria. The upper molars described by Sigogneau-Russell 1998 (especially her fig. 1F), differ from that described by Wang et al. (1998) in being transversely wider. Sigogneau-Russell (1998) suggested origin of Shuotheriidae from early symmetrodonts, thus implying a more remote position for the group than advocated by McKenna and Bell (1997) or Wang et al. (1998).

Previous studies addressing the affinities of *Shuotherium*, cited above, were framed within the context of a fossil record limited to Laurasia. Recent discoveries from parts of former Gondwana broaden the scope for comparison and provide new context for understanding the perplexing anatomical features of *Shuotherium*. Our recent analyses (Luo, Cifelli, and Kielan-Jaworowska 2001; Luo et al. 2002) suggest that *Shuotherium* is the sister-taxon to a southern calde, Australosphenida, defined as those tribosphenic mammals more closely related to monotremes than to *Shuotherium*. This clade includes the newly-discovered taxa *Ausktribosphenos*,

Bishops (Australia), *Ambondro* (Madagascar), and *Asfaltomylos* (Argentina), together with Monotremata. Our reinterpretation, herein, of the premolar-molar boundary in *Shuotherium* provides the basis for identifying additional synapomorphies related to the unusual molarization of the (newly designated) ultimate premolar in *Shuotherium* and in australosphenidans.

The holotype of *Ausktribosphenos nyktos* from the Early Cretaceous of Australia (Rich et al. 1997) is represented by a dentary with the last four cheek teeth: three molars of tribosphenic design, preceded by a molariform last premolar. Rich et al. (1997) suggested eutherian affinities for *Ausktribosphenos*, largely on the basis of molar count and structure of the ultimate premolar. This view was challenged by Kielan-Jaworowska et al. (1998), who pointed out that the genus retains numerous plesiomorphies in structure of the dentary. Rich et al. (1999) described another specimen of *Ausktribosphenos nyktos* and compared its dentition with those of erinaceids, some representatives of which have an ultimate premolar bearing a fully developed, acutely-angled, three-cusped trigonid. However, the ultimate premolar of erinaceids is conspicuously different from the premolar of *Ausktribosphenos* in having a distinctive talonid, totally absent in *Ausktribosphenos* (see below). Furthermore, this condition among erinaceids is restricted to rather advanced, Oligocene and later genera (e.g., Rich 1981) and is not characteristic of the family as a whole (e.g., Krishtalka 1976; Butler 1988). A second ausktribosphenid, *Bishops whitmorei*, from the same locality as *Ausktribosphenos* (Rich et al. 2001), is represented by a nearly complete dentary with six premolars and three molars, together with three other dentary fragments.

Another important recent discovery from southern realms is that of *Ambondro mahabo*, from the Middle Jurassic (Bathonian) of Madagascar (Flynn et al. 1999). *Ambondro* is known by a dentary fragment with three teeth: the ultimate premolar and the first two molars. Like *Ausktribosphenos*, the premolar has a molariform trigonid and the molars are fully tribosphenic. *Ambondro* is some 25 million years older than any other known mammal with tribosphenic molars, and its discovery thus represents a substantial extension of the geologic range for this molar pattern. The great antiquity of *Ambondro*, together with the surprising occurrence of tribosphenic mammals in the Early Cretaceous of Australia, challenges the long-held view that higher mammals (living therians and presumed close relatives, all of which have tribosphenic molars) arose on northern continents. In turn, this has provided a basis for renewed arguments promoting eutherian affinities for *Ausktribosphenos* and *Ambondro* (Rich and Vickers-Rich 1999).

In view of this controversy, we (Luo, Cifelli, and Kielan-Jaworowska 2001) made a preliminary attempt to place these new fossils in the context of mammalian phylogeny, through analyses including representatives of all three living mammalian groups and relevant Mesozoic taxa. The results suggested an alternative hypothesis for the affinities of

Ausktribosphenos and *Ambondro*: that they are related to monotremes, with which they collectively form an endemic, Gondwanan clade that appears to have diverged from Laurasian groups well back in the Jurassic. Implicit in this hypothesis is a dual origin for the complex, multifunctional tribosphenic molar pattern. Based on this hypothesis, Luo, Cifelli, and Kielan-Jaworowska (2001) erected two new mammalian infraclasses: Boreosphenida, or “typical” tribosphenic mammals (“tribotheres”, Metatheria, and Eutheria), which are unknown outside of Laurasia prior to the latest Cretaceous; and Australosphenida, whose known distribution is restricted entirely to landmasses of the former Gondwanan supercontinent.

In a follow up study (Luo et al. 2002), we proposed a phylogeny of all major groups of Mesozoic mammals based on analyses of an expanded data matrix, including 46 taxa and 275 osteological and dental characters. The study strongly supported the australosphenidan clade and its separation from Boreosphenida. Subsequently, Rauhut et al. (2002) described *Asfaltomylos patagonicus*, the first Jurassic mammal from Argentina. This new taxon is represented by a dentary with three preserved premolars and three molars. Phylogenetic analysis by Rauhut et al. (2002: fig. 3), based on a data matrix modified from that of Luo, Cifelli, and Kielan-Jaworowska (2001), supports the monophyly of Australosphenida, including *Asfaltomylos*. Taking into account the broad geographic distribution of known fossils, the authors concluded that australosphenidans had diversified and spread throughout Gondwana before the end of the Jurassic, and that the mammalian faunas of the southern and northern hemispheres were already distinct by the Middle–Late Jurassic.

One of the most surprising results of our phylogenetic analyses was the placement of *Shuotherium* as the sister-taxon to Australosphenida (Luo, Cifelli, and Kielan-Jaworowska 2001: fig. 1; Luo et al. 2002: figs. 1, 2). Though our previous character coding for *Shuotherium* followed the tooth homologies proposed by Chow and Rich (1982), we noted that an alternative interpretation of the premolar–molar boundary was viable (Luo et al. 2002: footnote to p. 23; see also Clemens and Lillegraven 1986: 73). Herein we reinterpret the postcanine tooth formula in *Shuotherium*, with particular reference to the premolar–molar boundary.

Abbreviations and terminology.—Institutional abbreviations: BMNH, The Natural History Museum, formerly British Museum (Natural History), London; IVPP, Institute of Vertebrate Palaeontology and Palaeoanthropology, Academia Sinica, Beijing; NMV P, Paleontology Collection, Queen Victoria Museum, Melbourne, Australia. We use lower case characters (e.g., p, premolars; m, molars) for lower teeth. We use two terms to summarize morphology of the ultimate lower premolars. The descriptor “premolariform” refers to simple teeth that are characterized by a dominant main cusp, with accessory cusps small or lacking, no triangulation of trigonid cusps (if more than one are present), and a small talonid consisting of a single cusp. The term “semimolari-

form” is applied to teeth with a triangulated trigonid (albeit with very low paraconid and metaconid) and expanded, with or without a flat talonid.

Results

We compared casts of the holotypes (dentaries) together with published illustrations of *Shuotherium dongi* and *Ausktribosphenos nyktos*, and illustrations of other non-monotreme australosphenidan taxa: *Bishops whitmorei*, *Ambondro mahabo*, and *Asfaltomylos patagonicus*. We also surveyed premolar–molar structure among all major, relevant groups of Mammalia, with particular reference to Mesozoic taxa. For reasons explained elsewhere (Luo et al. 2002), we employ a stem-group definition of Mammalia, conceived as the last common ancestor of *Sinoconodon* and living mammals, plus all of its descendants. The term “prototribosphenidan” follows the definition of Rougier, Wible, and Hopson (1996). The taxon *Peramura* McKenna, 1975 is currently believed to be paraphyletic, and we alternately use the term in quotes, or refer to *Peramus* and dentally similar taxa as “stem zatherians” (see Sigogneau-Russell 1999; Martin in press).

The fundamental distinction between premolars and molars is developmental: premolars developed from a secondary dental lamina and replace deciduous precursors (which may or may not erupt), whereas molars originate from the primary dental lamina and, by definition, neither replace precursors nor are replaced by successor teeth (e.g., Lockett 1993). Unfortunately, Mesozoic fossils for which these developmental patterns can be reasonably inferred are extremely rare (see Cifelli et al. 1996; Rougier et al. 1998; and especially Martin 1997 for a notable exception). In the absence of ontogenetic data for fossil taxa, morphologic criteria (which are not uniformly reliable; see Lockett 1993) stand as the only means to distinguish molars from premolars. A scholarly review, together with a summary account of premolar–molar structure in Mesozoic mammals, is provided by Clemens and Lillegraven (1986). We have drawn from this work, as well as from our own comparisons, in evaluating homologies of the cheek tooth series in *Shuotherium dongi*.

The premolar–molar boundary among early mammals is commonly drawn at an abrupt morphological change, often reflected in differing levels of complexity, in the cheek tooth series. The premolars are generally simple, dominated by the primary cusp (A/a), whereas molars commonly have enlarged (by comparison) subsidiary cusps, a complex coronal pattern relative to the premolars (different position of subsidiary cusps, presence of neomorphic cusps, elaboration of crests connecting cusps), and some form of interlocking pattern between teeth. Differences among the molars are common, but (except for specialized taxa) they are generally gradational in nature, varying in predictable ways through the series (e.g., Fox 1975; Cifelli 1990; Cifelli and Madsen 1999). The last premolar commonly has a primary cusp (A/a)

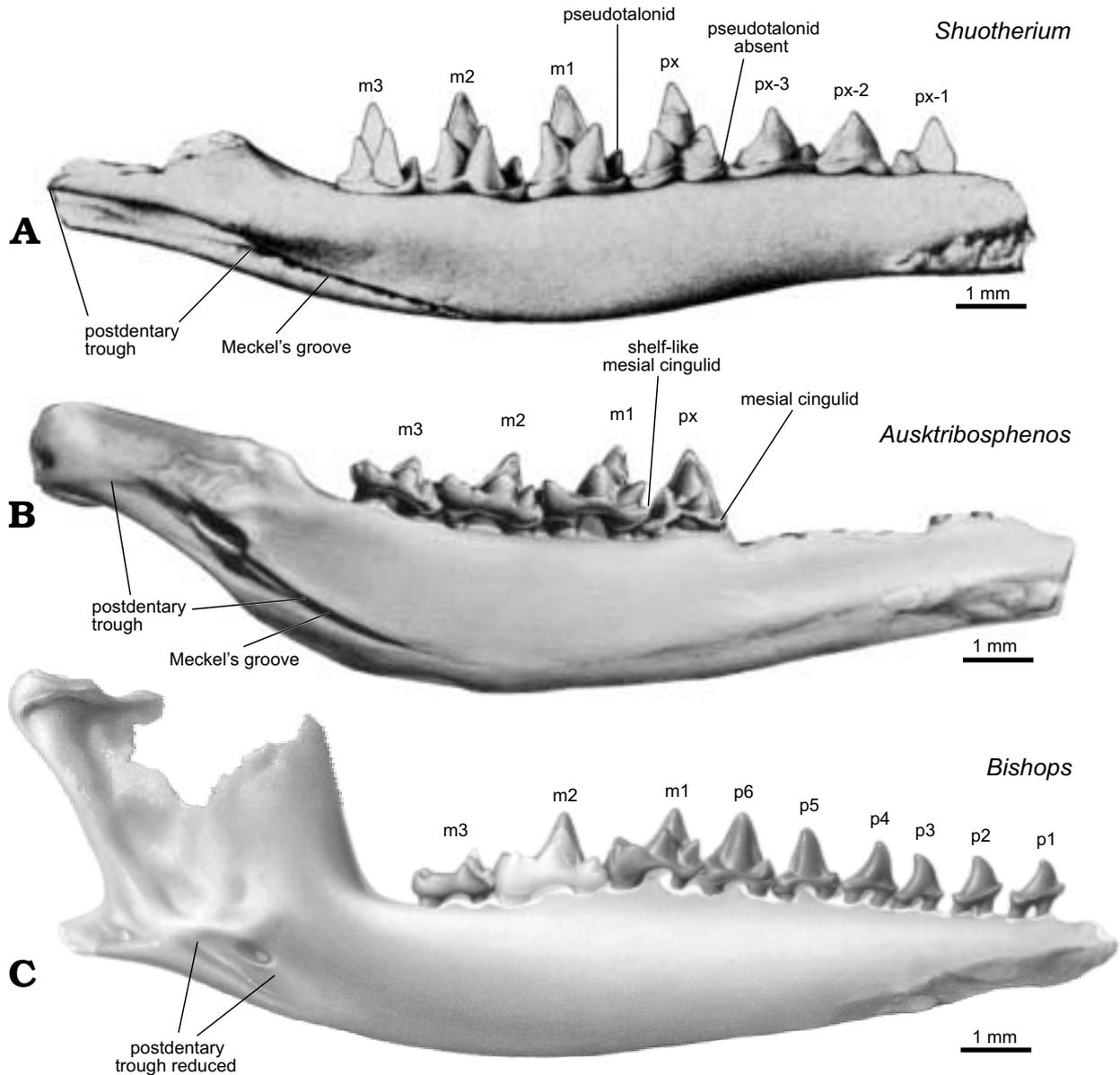


Fig. 1. Comparison of the dentaries and dentitions in *Shuotherium* and the australosphenidans *Bishops* and *Auskribosphenos*, in lingual view. **A.** *Shuotherium dongi*, left dentary (IVPP V6448, holotype). **B.** *Bishops whitmorei*, left dentary (NMV P210075, holotype). **C.** *Auskribosphenos nyktos*, right dentary, reversed (NMV P2080901, holotype). Modified after: A, Chow and Rich (1982); B, Rich, Vickers-Rich et al. (1999); C, Rich, Flannery et al. (2001).

that is noticeably taller than the crowns of the molars, though a number of exceptions are known (note McKenna 1975; Clemens and Lillegraven 1986). Cheek teeth of *Shuotherium* were identified by Chow and Rich (1982) on the basis of these general criteria.

We contend that the foregoing criteria are not appropriate in the case of the type specimen of *Shuotherium dongi*, because they do not account for some significant features in the cheek tooth series. *Shuotherium* is not unique in this respect. Several groups of mammals lack a clear and abrupt morphological change at the premolar–molar boundary. In such groups, there is a less discrete, more gradational transition from the premolar to the molar series. Most familiar among

these are Eutheria, early fossils of which are recognized, in large part, on the basis of molarization of the posterior pre-molar(s) (e.g., Kielan-Jaworowska and Dashzeveg 1989; Cifelli 1999). A celebrated example among extinct, non-eutherian taxa is *Peramus*, widely believed to be a proximal relative of living therians (e.g., Butler 1990; Rougier et al. 1998). The fifth of eight postcanine teeth in *Peramus* is semimolariform. Originally interpreted as the first molar (e.g., Simpson 1928; Mills 1964; Clemens and Mills 1971), this tooth is now generally accepted as representing a semimolariform last premolar, or P/p 5 (e.g., Butler and Clemens 2001 and literature cited therein). Among morphologically similar (if not closely related) “peramurans” (see

Sigogneau-Russell 1999; Martin in press), the tooth identified as the ultimate premolar is semimolariform in *Arguitherium* and *Arguimus* (Dashzeveg 1994), but premolariform in *Nanolestes* (Martin in press).

As mentioned above, difficulty in recognizing the premolar–molar boundary in *Shuotherium dongi* was noted in the initial description of the species (Chow and Rich 1982). Clemens and Lillegraven (1986) observed that the tooth in question (the fourth of seven preserved teeth) is not fully molariform in *Shuotherium*. These authors did not explicitly offer an opinion as to whether the tooth represents a premolar or a molar. However, they noted that: 1) *Shuotherium*, like *Peramus* and Eutheria, is characterized by a gradational transition between the premolar and molar series; and 2) the condition is apomorphic within the context of early mammals. Clemens and Lillegraven (1986: 75) suggested that the most reasonable explanation for the distribution of this condition is that “the eutherian-like patterns of morphological variation seen in the dentitions of *Peramus* and *Shuotherium*, which lack tribosphenic molars, must be interpreted as products of parallel evolution.”

Though damaged and incomplete, the fourth of seven preserved teeth in the holotype of *Shuotherium dongi* clearly differs in several respects from the three molars that succeed it: a pseudo-talonid is lacking, the trigonid angle is significantly greater, and the talonid is slightly better developed (Chow and Rich 1982). The trigonid angle is not necessarily informative as to the tooth family (the trigonid angle often becomes progressively more acute in the molar or molars succeeding m1, Crompton and Jenkins 1967; Cifelli 1990; Cifelli and Madsen 1999). It is worth pointing out that the trigonid angles in cheek teeth of *Shuotherium* do not vary gradationally: there is a single, abrupt difference between the fourth and fifth teeth in the jaw (referred to as “tooth 4” and “tooth 5” hereafter, and px and m1, respectively, in Fig. 1A). Most noteworthy, in our opinion, is the fact that the tooth 4 (px) completely lacks the pseudo-talonid. This structure is the most obvious and distinctive feature of lower molars in *Shuotherium*. Occlusal relations (inferred from wear facets and the referred upper molar) indicate that the pseudo-talonid and pseudo-protocone provided a crushing component to molar function, complementing the primitive shearing function of the trigonid (Wang et al. 1998). Hence, the disparity in function as well as structure is perplexing if this tooth is interpreted as the first of a molar series. Furthermore, tooth 4 (px in Fig. 1A) and the preceding teeth (which are undoubtedly premolars) form a gradational series, whereas tooth 5 (m1 in Fig. 1A) bears the morphological pattern of the succeeding molars: the two series are discrete. We follow current convention with regard to morphologically analogous mammals (e.g., “peramurans”, early eutherians, and australospheni-

ans; see below) in interpreting tooth 4 in the holotype of *Shuotherium dongi* as a semimolariform premolar (px). The premolar count in *Shuotherium* cannot be established with certainty, owing to incompleteness of the holotype (the only specimen that consists of more than an isolated tooth). Anteriorly, a short diastema separates the first preserved premolar from an alveolus thought by Chow and Rich (1982) to represent the ?canine locus. Depending on the original length of the mandibular symphysis, which is incomplete, it is possible that this socket represents an additional premolar locus. Regardless, by our interpretation the specimen preserves four premolars and three molars, yielding a postcanine dental formula of p4+, m3.

This alternate view of tooth homologies has significant implications for the affinities of *Shuotherium* (Fig. 1). Our previous analyses (Luo, Cifelli, and Kielan-Jaworowska 2001; Luo et al. 2002) provided some limited support for placement of *Shuotherium* as the sister-taxon to Australosphenida. We relegated *Shuotherium* to a relatively basal position in the mammalian tree, largely because of optimization of its plesiomorphies in the dentary (i.e., features associated with the attachment of postdentary elements to the dentary). In global parsimony analyses (Luo et al. 2002), these features outweigh apomorphic similarities of molar structure to Trechnotheria McKenna, 1975, such as complete prevallid shearing surface and acute angulation of trigonid cusps. *Shuotherium* also lacks numerous apomorphies characterizing successively more exclusive clades containing Boreosphenida and proximal relatives (e.g., Cladotheria McKenna, 1975; Zatheria McKenna, 1975).

Mammalian lower molars primitively bear individualized mesial cuspules that serve to help interlock adjacent molars (e.g., Crompton and Kielan-Jaworowska 1978; Luo 1994). These cuspules are lacking in both *Shuotherium*¹ and Australosphenida. We hypothesize that the elevated margin surrounding the pseudotalonid on lower molars of *Shuotherium* is homologous to the shelf-like mesial cingulid that wraps around the anterolingual corner of the teeth in most of Australosphenida (although secondarily reduced in some ornithorhynchids). Molar patterns of *Shuotherium* and Australosphenida are obviously divergent: after all, they are virtual mirror images of each other. Nonetheless, the hypertrophied, wrapping mesial cingulid of australosphenidans is a highly plausible structural antecedent to the bizarre pseudotalonid of *Shuotherium*.

The reinterpreted dental formula for *Shuotherium* yields an apomorphic molar count (presumed reduction to three, by comparison to the stem mammal *Kuehneotherium*, which had five to six molars, see D.M. Kermack et al. 1968; Gill 1974). A count of three or fewer molars is also known for *Ausktribosphenos*, *Bishops* (Rich et al. 2001), *Asfalatomylos*

¹ Dr. Sigogneau-Russell (personal communication, also see Sigogneau-Russell et al. 2001) mentioned that the published figures of *Ambondro* (Flynn et al. 1999: fig. 3) give impression that the interlocking cuspules might be present. However, one of us (Z-X L) examined the original specimen: the interlocking cuspules are absent, and their apparent presence in the published illustration is due to a shading of SEM photography.

(Rauhut et al. 2002), and monotremes (Archer et al. 1985, 1993). This condition is far from unique, however, as a similarly reduced molar count is seen in a variety of other early mammals, such as multituberculates, *Hadrocodium*, certain Triconodontidae, stem zatherians, and Eutheria (e.g., Simpson 1928, 1929; McKenna 1975; Clemens and Kielan-Jaworowska 1979; Kielan-Jaworowska and Dashzeveg 1989; Rougier 1993; Cifelli 1999; Luo, Crompton, and Sun 2001; Martin in press).

In our view, the most compelling evidence as to the affinities of *Shuotherium* lies in the structure of the last premolar, which shares striking similarities to that of Australosphenida. Indeed, this tooth differs from its respective molars in an equivalent manner in both. In *Shuotherium* the ultimate premolar lacks the pseudo-talonid (characteristic of the molars), whereas in Australosphenida it lacks the talonid (characteristic of the molars). As a result, the ultimate premolar in both groups consists only of a fully triangulated trigonid, a structure that is unique and highly distinctive among Mesozoic mammals. Given universal acceptance of tooth homologies in Australosphenida, this reason alone would be sufficient basis for the proposed re-interpretation of the teeth in *S. dongi*. We did not invoke the analogy herein, to avoid potentially circular reasoning, and instead interpreted the dental formula of *Shuotherium* on the basis of broader comparisons and considerations.

The apomorphies of the last premolar in *Shuotherium* and Australosphenida are based on a highly unusual form of molarization: despite the absence of a talonid (or pseudo-talonid), the trigonid is transversely broad and semi-molariform, with well-developed paraconid and metaconid arranged in a distinctly triangulated fashion with the protoconid.

Comparison with the last premolar of Trechnotheria, in terms of structure and pattern of molarization, is instructive. The ultimate lower premolar is simple (premolariform) in stem Trechnotheria, the Spalacotheriidae (Simpson 1928; Hu et al. 1997), as it is in basal Cladotheria (dryolestoids, see Krebs 1991; Martin 1999) and *Vincelestes* (Rougier 1993). In all these taxa, anterior cusp b is either minute or lacking, and there is no hint of cusp triangulation. In these respects, the conditions are similar in the stem zatherian *Peramus* (e.g., BMNH 47739, Clemens and Mills 1971). Here, as in certain other stem zatherians, but in contrast to *Shuotherium* + Australosphenida, the last lower premolar owes its molariform appearance to the strong development of a talonid: trigonid cusps b and c are miniscule, and arrangement of cusps a, b, and c is linear, not triangulated. Here we differ from the assessment by Sigogneau-Russell et al. (2001) on the ultimate premolar of *Peramus*.

Turning to crown Theria, the last premolar of early metatherians is uniformly simple (presumably a plesiomorphy, though serial homology of cheek teeth among the two groups of living therians remains problematic, e.g., Clemens and Lillegraven 1986; Luckett 1993). Molarization of the last premolar is a pervasive theme in the early evolution of

Eutheria, where progressive specialization apparently took place independently in various lineages, and possibly involved different mechanisms (e.g., Butler 1952, 1995). Overall, however, molarization of the last lower premolar follows a consistent pattern in early eutherians: the talonid develops first, prior to significant development of trigonid cusps b and c, and prior to triangulation of trigonid cusps. The direction of transformation is similar to that seen in stem zatherians, but contrasts with that of *Shuotherium* + Australosphenida. The precociously derived nature of premolar structure in *Shuotherium* and Australosphenida is emphasized by the stratigraphic record. The ultimate premolar of Australosphenida already has a fully molarized trigonid by the late Early Cretaceous. Ultimate premolars of contemporaneous Eutheria, which make their first appearance at about that time, either have faint cusps b and c (Cifelli 1999), or lack any molarization of the trigonid (Kielan-Jaworowska and Dashzeveg 1989; Sigogneau-Russell et al. 1992; Ji et al. 2002). Remarkably, eutherians with an ultimate premolar of fully tribosphenic pattern do not appear until the early Tertiary, some 50 million years later.

To summarize, molarization of the ultimate premolar likely occurred multiple times among Trechnotheria: at least once in stem Zatheria (see Clemens and Lillegraven 1986; and supplementary information of Rougier, Wible, and Novacek 1998), and perhaps iteratively among Eutheria. In each case within both of these two evolutionary lineages, full triangulation of the trigonid cusps occurred long after the development of the “molarized” talonid within each of these two evolutionary lineages: this pattern is opposite the molarization pattern seen in *Shuotherium* + Australosphenida.

Lower molar structure of *Shuotherium* and Australosphenida is obviously quite different, and for this reason we do not place *Shuotherium* within this Gondwanan clade. Based on the limited evidence available, however, we suggest that *Shuotherium* is a viable sister-taxon to Australosphenida. Their last common ancestor presumably had molars of “symmetrodon” construction, characterized by reverse triangulation of principal cusps of upper and lower molars, and limited in function to embrasure shear and puncture-crushing (note Crompton and Hiiemae 1970; Osborn and Sita-Lumdsen 1978; Mills 1984). Subsequent, divergent specializations for molar crushing function would then have taken place independently, and quite differently, among Australosphenida and the clade including *Shuotherium* (Yinothoria).

Pascual and Goin (2001) and Pascual et al. (2002) suggested separate origins of molar cusp triangulation in docodonts, toothed monotremes and “therians”. They raised the possibility that primary molar cusp triangulation, or the trigonid, is homoplastic among these groups. Luo et al. (2002) agreed that triangulation of molar cusps could be a convergent feature, both for the trigonid, and for the talonid. This hypothesis should be evaluated by parsimony analysis, in the context of other, non-molar characters.

Paleogeography

All known australosphenidans are from southern landmasses; hence, present data suggest that Australosphenida diverged from a common ancestor with *Shuotherium* and originated on the former Gondwanan supercontinent. Given that the known distribution (Madagascar, Australia, South America) of Australosphenida is considerable relative to the meager handful of fossils collected to date, not to mention the generally abysmal record of Mesozoic mammals from southern continents, it is plausible that australosphenidans were widespread in Gondwanaland by the Middle Jurassic.

The age of *Shuotherium* from the Shaximiao Formation, China, is imprecisely known, with estimates ranging from Bathonian–Callovian (Lucas 1996, 2001) to Oxfordian–Kimmeridgian (Wang et al. 1998). Age of the British occurrence of *Shuotherium* is far better understood. The specimens of the Kirtlington site are from the Forest Marble, which is late Bathonian (Evans and Milner 1994). The earliest australosphenidan, *Ambondro*, is also of Bathonian age (Flynn et al. 1999). Divergence of Australosphenida from the clade containing *Shuotherium* is thus temporally constrained as being no younger than Bathonian. Continental reconstructions (e.g., Smith et al. 1994; Scotese 1997) show persisting areas of contiguous terrestrial habitat between Laurasian and Gondwanan landmasses through the Middle Bathonian, which is consistent with our proposed hypothesis of relationships between Australosphenida and Yinotheria.

Acknowledgments

We thank William A. Clemens and Denise Sigogneau-Russell, who reviewed the paper and provided very useful comments. This research was supported by the Institute of Paleobiology, Polish Academy of Sciences, Warsaw (Z. Kielan-Jaworowska), a collaborative program between National Science Foundation and Polish Academy of Sciences (R. L. Cifelli and Z. Kielan-Jaworowska), the National Geographic Society (R. L. Cifelli and Z.-X. Luo), the National Science Foundation, USA (grant DEB-9870173 to R. L. Cifelli; grant DEB-9527892 to Z.-X. Luo), and the Carnegie Museum (Z.-X. Luo).

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