

Dual origin of tribosphenic mammals

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Marsupials, placentals and their close therian relatives possess complex (tribosphenic) molars that are capable of versatile occlusal functions. This functional complex is widely thought to be a key to the early diversification and evolutionary success of extant therians and their close relatives (tribosphenidans). Long thought to have arisen on northern continents, tribosphenic mammals have recently been reported from southern landmasses. The great age and advanced morphology of these new mammals has led to the alternative suggestion of a Gondwanan origin for the group. Implicit in both biogeographic hypotheses is the assumption that tribosphenic molars evolved only once in mammalian evolutionary history. Phylogenetic and morphometric analyses including these newly discovered taxa suggest a different interpretation: that mammals with tribosphenic molars are not monophyletic. Tribosphenic molars evolved independently in two ancient (holotherian) mammalian groups with different geographic distributions during the Jurassic/Early Cretaceous: an australosphenidan clade endemic to Gondwanan landmasses, survived by extant monotremes; and a boreosphenidan clade of Laurasian continents, including extant marsupials, placentals and their relatives.

Because most mammals are only represented in the fossil record by their teeth, dental evidence has prominently figured in interpreting the relationships of early mammals. The highly distinctive tribosphenic molars, capable of both shearing (*sphen*) and grinding (*tribein*) occlusal functions, are the most important dental feature of marsupials and placentals (extant therians) and their close fossil relatives, collectively known as tribosphenidans¹. The tribosphenic molar has been used to distinguish these therians from other Mesozoic mammals^{1–4}, including stem holotherians such as “symmetrodonts” and “eupantotheres”^{3,4}, and from living monotremes.

The traditional view that tribosphenic molars arose in the Early Cretaceous, and that the early diversification of therians took place on northern continents⁵, has been challenged by recent discoveries on Gondwanan landmasses. *Ambondro*, from Madagascar, has fully tribosphenic molars⁶ yet is of Middle Jurassic age, and is therefore some 25 Myr older than the earliest northern therians. *Ausktribosphenos*, a tribosphenic mammal from the Early Cretaceous of Australia, is thought to have been a placental, possibly even a member of the living hedgehog family^{7,8}. Thus, these new fossils have important implications for reconstructing the paleobiogeography and timing of divergence of the main extant mammalian groups. Here we re-evaluate the phylogenetic relationships of these newly discovered mammals, with respect to other Mesozoic and extant mammal groups.

Phylogenetic relationships

Parsimony analysis of the available evidence from the dentition and mandible (Fig. 1; also see Methods) places the tribosphenic mammals *Ambondro*⁶ and *Ausktribosphenos*^{7,8}, together with the earliest known monotreme *Steropodon*⁶ (Australia, Early Cretaceous), in a monophyletic group, which we term the Australosphenida (concept modified from Ausktribosphenida⁷; see ‘Systematic Palaeontology’). This group is characterized by a well-developed, continuous mesial cingulid that wraps around and extends to the lingual side of the trigonid (Fig. 2); a mesiodistally short, buccolingually broad talonid; and reduced height of the trigonid—at least when compared with other Jurassic/Early Cretaceous holotherians. Notably, *Ausktribosphenos* retains plesiomorphies of the jaw as seen in stem mammals⁹, and we provisionally recognize some of these primitive characters to be preserved also in *Steropodon*. By contrast, the Boreosphenida, a clade of northern mammals with tribosphenic molars^{10–12} (Fig. 1), have distinctive cingulid cuspules (cuspule e, cuspule f, or both) but lack a continuous mesial cingulid. The mesial

cingulid does not wrap around or extend to the lingual side of the molars. Furthermore, boreosphenidans and proximal relatives, such as *Henkelotherium*, are more derived in that they have a mandibular angle far more posteriorly positioned than australosphenidans, *Kuehneotherium*, *Morganucodontids* and *Sinoconodon*.

Further dental apomorphies are consistent with the monophyly of australosphenidans. For example, *Steropodon*¹³ and *Ausktribosphenos*⁷ both have the ‘twinned’ paraconid and metacoenid, and a well-developed lingual cusp on the talonid (Fig. 2). *Ambondro*⁶ and *Ausktribosphenos*^{7,8} share an unusual feature in which the premolars seem to be molariform, with a distinctive triangulation of the three main cusps and a prominent lingual cingulid. The posterior part of the premolar is buccolingually wide. This derived feature is shared by *Obdurodon dicksoni*¹⁴ (Australia, Miocene), an ornithorhynchid monotreme^{14,15} widely accepted to be a relative of *Steropodon* (in which the premolar is not preserved¹³). None of these derived premolar features of fossil ornithorhynchids, *Ambondro* and *Ausktribosphenos* is present in the earliest known eutherians^{10,11}, metatherians¹², nor stem taxa of the northern tribosphenidans^{16–18}. They are also absent in a wide variety of non-tribosphenic (eupantother) mammals including *Peramus*¹⁷ and *Henkelotherium*¹⁸.

Australosphenidans may have affinities with the northern holothere *Shuotherium*^{19–21} (Fig. 1), some unknown early “symmetrodonts”⁹, or the holotherian Dryolestidae¹⁴. However, by any previous interpretation they are independent from boreosphenidans and their proximal relatives, including *Henkelotherium*¹⁹ and pre-tribosphenic *Peramus*^{17,22}. The clade of *Ausktribosphenos*, *Ambondro* and the monotreme *Steropodon* (Fig. 1), as inferred from mandibular and postcanine tooth morphology, is consistent with the phylogenies established by independent studies of basicranial^{23,24} and postcranial^{25–27} features of the main Mesozoic mammal groups documented by well-preserved fossils. In our expanded analysis (Fig. 1b), we added the cranial and postcranial features for those better-preserved taxa (for example, *Morganucodon*, *Jeholodens* and *Henkelotherium*). The simultaneous analysis (Fig. 1b) of cranial and postcranial data, together with the dental and mandibular characters, corroborates the australosphenidan clade and the boreosphenidan clade. Hence, the hypothesis of a diphyletic origin for tribosphenic mammals is supported by morphological characteristics other than teeth and mandibles.

Independent multivariate analysis of the shape of the lower molar shows that *Ausktribosphenos* and *Steropodon* are grouped together

(Fig. 3; *Ambondro* is not sufficiently complete for inclusion). These australosphenidans occupy their own morphospace and are distinct from the stem taxa of boreosphenidans, metatherians and eutherians (Fig. 3). Both parsimony analysis of discrete characters (Fig. 1) and shape analysis (Fig. 3) suggest that *Ausktribosphenos* does not belong to the crown group of therians^{9,15}, and that it may have close affinities to the monotreme *Steropodon*^{15,28}.

Extant monotremes are considered to represent an archaic clade, although they are also highly specialized in their own ways^{29,30}. The Early Cretaceous monotreme *Steropodon*¹³ bears some dental similarities to *Peramus*²² and also to dryolestoids¹⁴, which leads to the hypothesis that monotremes may be related to some pre-tribosphenic therian mammals. All recent morphological parsimony analyses^{2,23–27} of the Mesozoic mammals with well-preserved fossils, however, have consistently placed ornithorhynchid monotremes (members of the australosphenidan clade) at a more basal position on the mammalian tree than the pretribosphenic, tribosphenic and extant therians. The australosphenidan clade that includes the monotreme *Steropodon* is consistent with these recent analyses of the combined dental, skull and skeletal characteristics^{23–27}. Our

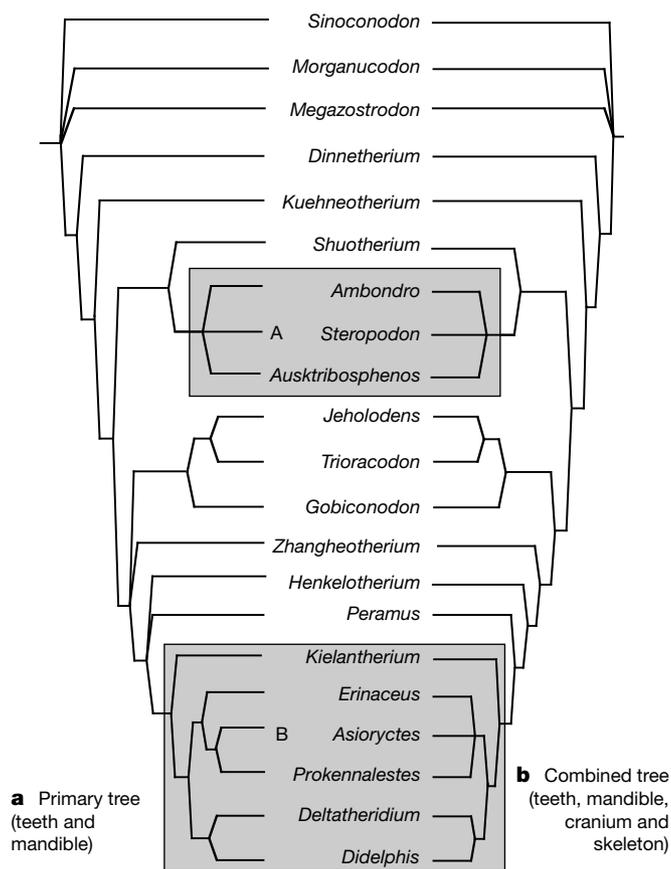


Figure 1 Phylogenetic relationships of main taxa of therian tribosphenic mammals. The Australosphenida (Box A) and Boreosphenida (Box B) are both monophyletic and separate from each other. **a**, Primary analysis: the strict consensus of 18 equally parsimonious and shortest trees from the 55 dental and mandibular characters that are known for the southern tribosphenic mammals (see Supplementary Information). **b**, Extended analysis: the strict consensus of eight equally parsimonious and shortest trees from an expanded analysis including cranial and postcranial data for the better preserved taxa (118 informative characters; see Supplementary Information). Placement of the australosphenidan clade on the mammalian tree is consistent, whether it is based on just the dental and mandibular features known for southern taxa (**a**), or on combined data of the dentition, mandible, plus cranium^{23,24} and postcranium^{25–27} (**b**). Apomorphies supporting the main cladogram nodes are presented in Supplementary Information (see Methods for details).

phylogeny is also consistent with the latest molecular evidence (on the basis of imprinted genes³¹) that would place monotremes outside the extant therians; but is contrary to the “Marsupionta” hypothesis³² that would link monotremes to extant marsupials, exclusive of placentals (on the basis of mitochondrial genes³³).

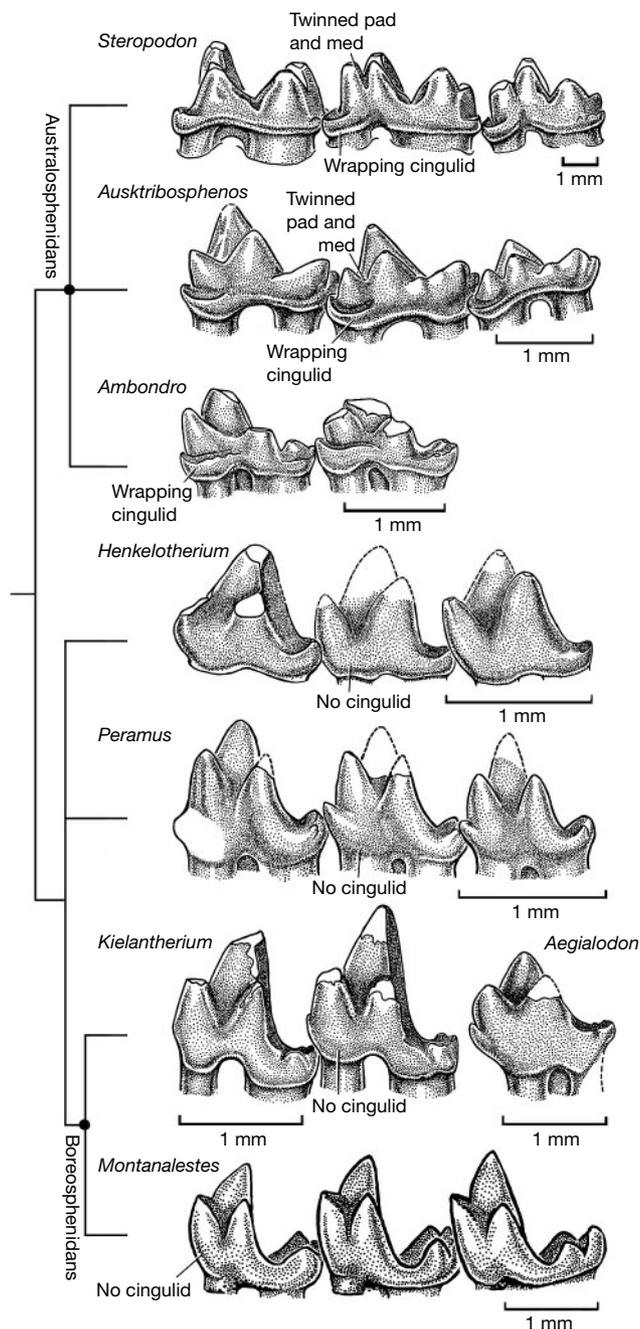


Figure 2 Comparison of molars of australosphenidans, pretribosphenidans (‘eupantotheres’: *Henkelotherium* and *Peramus*) and boreosphenidans, in lingual view. Tree topology pruned from Fig. 1a. Lower molars of australosphenidans are characterized by a mesial cingulid wrapping around to the lingual side of the paraconid (pad), and the reduced height of the trigonid relative to the talonid. *Steropodon* and *Ausktribosphenos* share the derived feature of the twinned paraconid and metaconid (med) and the hypertrophied lingual cusp of the talonid. *Ambondro* and *Ausktribosphenos* share the derived features of a lingual cingulid on molariform premolars (not illustrated). None of these derived dental characters is present in the northern eupantotheres (*Henkelotherium*, *Peramus*), primitive tribosphenidans (*Kielantherium*, *Aegialodon*) or therians (*Montanalestes*).

Molar evolution

The tribosphenic lower molar is defined by a basin-like heel (talonid), which grinds (*tribein*) with the large inner cusp (protocone) on the upper molar—functionally analogous to mortar-to-pestle grinding. This is in addition to a wedge-like trigonid (*sphen*) to shear with the crests of the corresponding upper tooth. Such molars are therefore capable of both shearing and grinding, and provide more versatile occlusal functions than the primitive (for example, “symmetrodont”) teeth that have simple, wedge-like trigonids limited to shearing. The increased versatility of this functional complex is considered to be the precursor condition to many mammalian dental specializations that are correlated with the adaptive radiations of marsupials and placentals³⁴.

Evolution of tribosphenic molars has been a focal point for interpreting early mammal history, owing to influential studies on cusp homologies^{3,35} and the evolution of wear facets⁴, postulating a transformation of the elaborated tribosphenic occlusion through a stepwise assembly of discrete dental characters with seemingly simple wear functions. On the basis of these fundamental under-

standings, the tribosphenic complex with mortar-to-pestle function has been considered to be a ‘hallmark’ apomorphy distinguishing marsupials, placentals and their Laurasian fossil therian relatives^{1,16}.

The trigonid wedge of the tribosphenic molar is primitive: its basic structure consists mainly of plesiomorphies shared by non-tribosphenic holotheres^{1,3,4,16–19,35}. Only the mortar-to-pestle grinding features on the talonid heel comprise the apomorphies that define the tribosphenic condition (where upper molars are not known, the presence of a protocone is inferred on the basis of talonid structure and wear surfaces^{6,7}). The traditional view that such a highly sophisticated functional complex could evolve only once has been contradicted by the discovery of the unique holotherian *Shuotherium*¹⁹, in which the pseudo-talonid basin (mortar) is developed anterior to the trigonid, opposite to the posterior talonid of tribosphenic mammals^{20,21}. The main lingual cusp (“pseudo-protocone”²⁰) of *Shuotherium* upper molars could nonetheless occlude with this mortar of the pseudo-talonid^{20,21}, and is functionally analogous to the tribosphenic condition. This homoplasy provides a plausible case that evolution of the mortar-to-pestle functional complex occurred more than once among holotherian mammals.

Our study corroborates the interpretation that *Ambondro* has a fully functional talonid basin typical of tribosphenic molars⁶. *Steropodon*, as with *Obdurodon*¹⁴, lacks mortar-to-pestle occlusion^{13,14,22} on its talonid. We concur with the observation that *Steropodon* and *Obdurodon* have an elevated talonid floor¹⁴, and thus differ from the earliest known, northern tribosphenic mammals in which the talonid floor is lower and more excavated, despite their convergent resemblance in other aspects of the talonid. Given the evidence for monophyletic grouping of *Steropodon*, *Ambondro* and *Ausktribosphenos*, it is equally plausible that the mortar-to-pestle occlusion on the talonid developed independently in *Ausktribosphenos*^{7,8} and *Ambondro*⁶ in australosphenidans (Fig. 1a), or that the hypertrophied transverse crests evolved secondarily in place of a functional basin on the talonid in *Steropodon*¹³ and the earliest ornithorhynchid *Obdurodon*^{13,14,28}. Correspondingly, the hypertrophied crests also developed secondarily in place of a functional protocone on the upper molars, as seen in *Obdurodon*^{13,14}. These autapomorphic molar features of *Steropodon* and ornithorhynchids represent a convergent pattern that has occurred in many unrelated lineages in marsupials, such as diprotodontoids, and in placentals, such as perissodactyls.

The classical theory on functional evolution of tribosphenic molars^{3,4} and the monophyly hypothesis of tribosphenic mammals¹ were developed on the basis of the available fossil record up to the early 1970s, when tribosphenic mammals were known exclusively from the Laurasian continents, and long before their relatively recent discoveries in Gondwana. The precociously derived talonid features^{13–15} and great antiquity⁶ of australosphenidan mammals are most parsimoniously explained, on the basis of present evidence, if the functional evolution of the mortar-to-pestle molar occlusion, as originally formulated⁴, occurred more than once. Our analysis not only supports the long-established clade of the northern tribosphenic mammals (“tribosphenidans”^{1,12,16}), but also suggests that the newly discovered southern tribosphenic mammals form a monophyletic clade in their own right.

Palaeobiogeography

The earliest tribosphenic mammals (earliest Cretaceous) were originally known only from Eurasia, or an adjacent—and biogeographically related—part of northwestern Africa^{36,37}. The earliest eutherians are from the late Early Cretaceous of Asia¹⁰ and, perhaps, North America¹¹; similarly, early metatherians are known from these landmasses^{12,38}. These distributions have been viewed as consistent with the hypothesis that tribosphenidans and subgroups thereof⁵ have a northern origin.

Recent discoveries have led to a different interpretation.

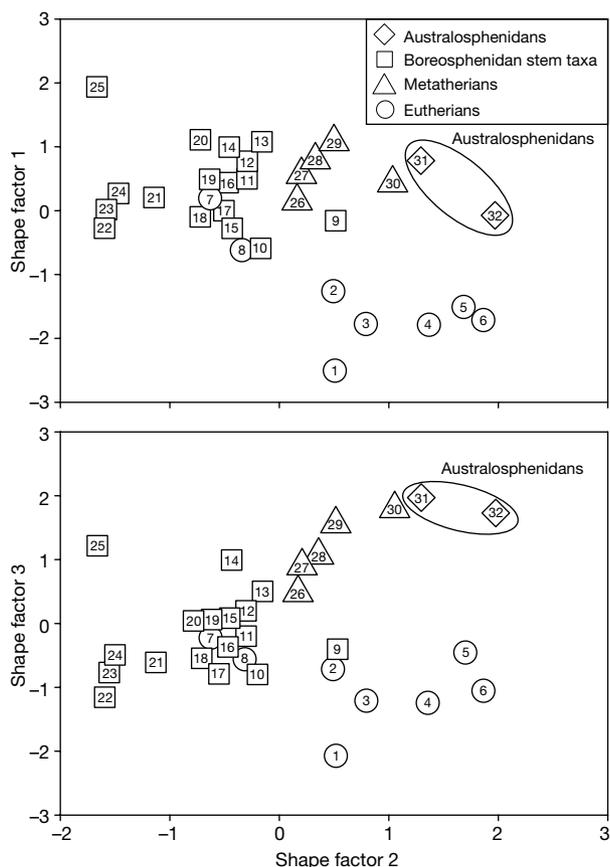


Figure 3 Lower molar shape in early mammals. Morphometric analysis (see Methods) shows australosphenidan taxa to be distinct from other Mesozoic tribosphenic mammals in the shape of their lower molars. Circles, stem taxa of boreosphenidans (eupantothere and ‘tribotheres’): 1, *Peramus*; 2, *Kermackia*; 3, *Hypomylos*; 4, *Kielantherium*; 5, *Potamotelses*; 6, *Deltatheridium*; 7, *Holoclemensia*; 8, *Pappotherium*. Squares, eutherians: 9, *Prokennalestes* spp.; 10, *Montanalestes*; 11, *Gypsonictops hypoconus*; 12, *Paranyctoides* spp.; 13, *Purgatorius unio*; 14, *Gallolestes pachymandibularis*; 15, *Procerberus*; 16, *Otlestes*; 17, *Batodon*; 18, *Kennalestes*; 19, *Asioryctes*; 20, *Protungulatum* spp.; 21, *Cimolestes cerberoides*; 22, *Cimolestes propalaeoryctes*; 23, *Cimolestes incisus*; 24, *Cimolestes magnus*; 25, *Zalambdalestes*. Triangles, metatherians: 26, *Kokopellia*; 27, *Pediomys elegans*; 28, *Glasbius intricatus*; 29, *Didelphodon vorax*; 30, *Alphadon marshi*. Diamonds, southern australosphenidan taxa: 31, *Ausktribosphenos*; 32, *Steropodon*. *Ambondro* is omitted because of incompleteness.

Ambondro, from the Middle Jurassic of Madagascar, is at least 25 Myr older than any previously reported tribosphenic mammals⁶; *Ausktribosphenos*, from the late Early Cretaceous of Australia^{7,8}, is nearly as old as the earliest northern therians. This early presence of tribosphenic mammals in Gondwana has led to the proposal that they originated on the southern continents^{6–8,37}. Each of the preceding biogeographical hypotheses assumed that the apomorphic, mortar-to-pestle structure of tribosphenic molars had a monophyletic origin.

We propose a new model: mammals with the mortar-to-pestle structure of the talonid (tribosphenic condition) underwent vicariant and diphyletic evolution on Gondwanan and Laurasian continents, respectively (Fig. 1). We suggest that the Australosphenida represent an endemic radiation of mammals on southern continents during the Jurassic/Early Cretaceous, surviving through the Tertiary^{22,28,39} as the extant monotremes.

A diphyletic origin and early vicariant evolution of mammals with tribosphenic dentitions is consistent with the well-documented provincialism of mammals in the Mesozoic of South America, which (before the latest Cretaceous) includes highly distinctive, endemic taxa related to Jurassic forms of northern continents^{39–41}. The known record suggests that boreosphenidans and their subgroups were largely or wholly confined to northern continents during much of their Mesozoic history, until a later dispersal of marsupials and placentals into South America^{6,42} and other southern continents occurred during the Late Cretaceous/Early Tertiary.

Systematic palaeontology

Class Mammalia Linnaeus 1758

Subclass Holotheria Wible *et al.* 1995 (ref. 24)

Infraclass Australosphenida nov.

(Include Monotremata; Ausktribosphenida^{7,8}; and *Ambondro*⁶).

Etymology. From *australis* (Latin, meaning southern) and *sphen* (Greek, meaning wedge), referring to their origin on the Gondwanan continents during the Jurassic and to the tribosphenic molars.

Diagnosis. Holotherians^{2,24} with tribosphenic molars; differ from boreosphenidans in having a continuous, shelf-like mesial cingulid that extends to the lingual side of the lower molar, rather than individualized cingulid cusps, and ultimate lower premolar with fully triangulated trigonid, a derived condition unseen in any other holotherians of the Jurassic/Early Cretaceous; differ from all non-tribosphenic holotherians in having a transversely wide talonid; differ from *Shuotherium* in having talonid placed posterior to the trigonid; and differ from boreosphenidans (including extant therians) by primitive retention, at least in *Ausktribosphenos*, of the postdentary trough on the dentary (also see Supplementary Information).

Distribution. Middle Jurassic of Madagascar; Early Cretaceous to recent of Australian region; Palaeocene of South America. The oldest australosphenidan is *Ambondro* from the Middle Jurassic of Madagascar.

Infraclass Boreosphenida, nov.

(include Tribosphenida McKenna, 1975 (ref. 1))

Etymology. From *boreas* (Latin, meaning northern wind) and *sphen* (Greek, meaning wedge), referring to their origin on the northern continents during the Mesozoic and to tribosphenic molars; meaning Tribosphenida¹ of the northern continents.

Revised diagnosis. Differ from all non-boreosphenidans in the posterior placement of the mandibular angle (to the level of dentary condyle); differ from kuehneotheriid holotherians^{16,43}, some eupantotheres and australosphenidans by absence of the primitive postdentary trough for the postdentary bones (except coronoid) in the dentary; differ from all mammals except Australosphenida by presence of tribosphenic molars; differ from *Shuotherium* in having talonid placed posterior to the trigonid in the lower molars, but convergent to the latter's pseudo-protocone of the upper molar; differ from Australosphenida by having distinctive

cingulid cusps but lacking the continuous mesial cingulid on the molars of the latter, and lacking the triangulated trigonid on the ultimate lower premolar in the Early Cretaceous taxa (also see Supplementary Information).

Distribution. Restricted to the Northern Hemisphere during the Early Cretaceous; present in latest Cretaceous of South America, India and northern continents; Tertiary to recent of the world. The oldest boreosphenidans are Berriasian in age^{36,37}.

Methods

Hypothesis of relationships among tribosphenic mammals is based on PAUP (3.1.1, Swofford, 1993) analyses of 21 selected taxa (see Supplementary Information). Our primary analysis (Fig. 1a) concentrated on 55 dental and mandibular characters that are preserved in many southern taxa (*Ambondro*, *Ausktribosphenos* and *Steropodon*). We grouped the southern and northern tribosphenic mammals into independent clades, by the strict consensus of 18 equally parsimonious and shortest trees. Our extended analysis (Fig. 1b) added 70 cranial and postcranial characters (from refs 23–27) that are preserved in the more complete taxa in our dataset to the 55 dental and mandibular characters known for the southern mammals, with requisite missing values coded for the taxa known only by teeth and jaws. The australosphenidan clade (including monotremes) and boreosphenidan clade (including extant therians) are supported by simultaneous analyses of 118 parsimony-informative characters of dentition, skull and skeleton for the well-preserved taxa of early mammals^{23–27} (Fig. 1b), and with 125 characters in additional tests of 26 taxa.

Diagnoses and relative strength of tree nodes

The australosphenidan clade is a more robust node (that takes more steps to collapse) than many widely accepted clades, such as the boreosphenidan clade (*Kielantherium* plus extant therians), the extant therian clade and the eutherian clade (Fig. 1). Apomorphies for each node of the cladograms are listed in Supplementary Information.

Additional tests

Both the australosphenidan and the boreosphenidan clades are maintained if five more taxa (tritylodontids, *Obdurodon*, *Ornithorhynchus*, multituberculates and *Vincelestes*) are added to the simultaneous analysis of 125 dental, mandibular, cranial and postcranial datasets (see Supplementary Information). The extant platypus (*Ornithorhynchus*) is nested in the australosphenidan clade. Bootstrap majority consensus trees from separate searches of the 55 dental and mandibular data partitions and the total 125 morphological characters have replicated both the australosphenidan clade and the boreosphenidan clade (Supplementary Information). These analyses (Fig. 1) and other independent morphological analyses^{23–27} have all shown that monotremes (herein considered to be a part of the australosphenidan clade) are more distant from the living therians than the non-tribosphenic symmetrodonts (*Zhangheotherium*) and eupantotheres (*Henkelotherium*).

Multivariate shape analysis

Plots in Fig. 3 show the first three principal components of principal components analysis, in which data have been standardized and variation owing to size has been removed. Positive scores for the first component reflect an anteroposteriorly compressed, narrow trigonid; for the second component, wide talonid and longer distance from hypoconid to hypoconulid; and for the third, a short metaconid and (of lesser importance) protoconid. Factor 1 distinguishes the southern australosphenidan taxa (*Ausktribosphenos*, *Steropodon*) from stem boreosphenidans, whereas factors 2 and 3 distinguish them from marsupials and eutherians. Methods for data collection and multivariate analysis are given in refs 11 and 44.

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