

A new symmetrodont mammal from China and its implications for mammalian evolution

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A new symmetrodont mammal has been discovered in the Mesozoic era (Late Jurassic or Early Cretaceous period) of Liaoning Province, China. Archaic therian mammals, including symmetrodonts, are extinct relatives of the living marsupial and placental therians. However, these archaic therians have been mostly documented by fragmentary fossils. This new fossil taxon, represented by a nearly complete postcranial skeleton and a partial skull with dentition, is the best-preserved symmetrodont mammal yet discovered. It provides a new insight into the relationships of the major lineages of mammals and the evolution of the mammalian skeleton. Our analysis suggests that this new taxon represents a part of the early therian radiation before the divergence of living marsupials and placentals; that therians and multituberculates are more closely related to each other than either group is to other mammalian lineages; that archaic therians lacked the more parasagittal posture of the forelimb of most living therian mammals; and that archaic therians, such as symmetrodonts, retained the primitive feature of a finger-like promontorium (possibly with a straight cochlea) of the non-therian mammals. The fully coiled cochlea evolved later in more derived therian mammals, and is therefore convergent to the partially coiled cochlea of monotremes.

Systematic palaeontology

Class Mammalia
Subclass Theria
Order Symmetrodonta
Family Spalacotheriidae

Zhangheotherium quinquecuspidens gen. et sp. nov.

Holotype. IVPP V7466 (Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China), a well-preserved skeleton (Fig. 1) consisting of a partial skull, and most of the postcranial skeleton, including all cervical and thoracic vertebrae, forelimbs and pectoral girdle, as well as the excellent impressions of the hindlimbs and pelvic girdle, and ribs. Lumbar and sacral vertebrae are represented by poor impressions. Some tarsals and most caudal vertebrae are missing (for measurements, see Tables 1 and 2).

Etymology. Zhanghe, in honour of Zhang He, who collected and donated the holotype specimen to the Institute of Vertebrate Paleontology and Paleoanthropology; therium, beast (Greek); quin-

que, five (Latin); cuspis, point (Latin); dens, tooth (Latin), for the three main cusps plus two large accessory cuspules on the lower molars.

Locality. Jianshangou Valley (approximately 41° 41' 01" N, 120° 59' 30" E), about 32 km east of Chaoyang City, Liaoning Province, northeastern China¹.

Horizon. The Jianshangou Beds, consisting primarily of shales, are the lowest lacustrine intercalation in the neutro-basic volcanic beds of the Yixian Formation^{1–3}.

Associated fauna. The Jianshangou Beds have yielded diverse fossil fish⁴, the birds *Confuciusornis*, *Liaoningornis*^{5,6} and *Protarchaeopteryx*⁷, the theropod *Sinosauropteryx*⁸, and diverse gastropods, bivalves, ostracods, conchostracans and insects².

Age. The age of the Yixian Formation is equivocal. Vertebrate faunal correlation^{3,4,5} and previous radiometric dates⁴ suggest that the Jianshangou Beds are either of the latest Jurassic age, or near the Jurassic–Cretaceous transition⁶. An Early Cretaceous age was also suggested by invertebrate faunal correlation³, and supported by a

Table 1 Skeletal measurements of *Zhangheotherium quinquecuspidens*

Bone	Length (mm)
Dentary	30.2
Axis (C2)	5.0
Cervical vertebrae 3–7	10.0 (total length)
Thoracic vertebra 8	2.9
Caudal vertebra 2	3.5
Clavicle	11.6
Scapula (posterior border to glenoid)	17.2
Humerus	22.1
Ulna	21.5
Radius	17.1
Metacarpal III	6.5
Ilium	20.1
Ischium	8.5
Epipubis	9.1
Femur	22.0
Tibia	23.5
Fibula	23.5
Calcaneum	6.6
Matatarsal III	8.6

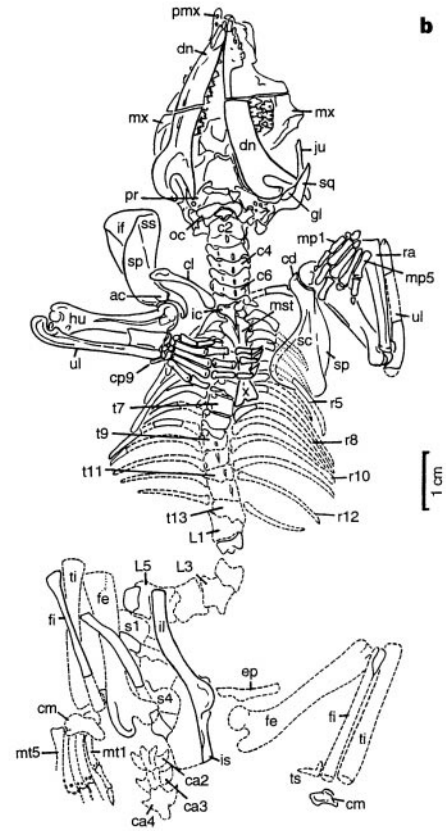
Table 2 Dental measurements of *Zhangheotherium quinquecuspidens*

Tooth	Length (mm)	Height (mm)
Lower dentition		
I1	1.2	
I2	0.5	
I3	0.5	
C	0.8	
P1	1.2	
P2	1.3	
M1	1.5	
M2	1.6	1.0
M3	1.8	1.7
M4	1.7	1.8
M5	1.5	1.8
M6	1.1	1.0
Upper dentition		
M2		1.5
M3	(1.6)	1.5
M4	(1.6)	1.6
M5	1.8	1.5

Parentheses indicate approximate estimates.



Figure 1 *Zhangheotherium quinquecupidens* (IVPP V7466, holotype). Stereophotographs **(a)** and outline **(b)** of the skeleton in ventral view of the dorsoventrally compressed specimen (broken lines indicate the morphology preserved in impressions). Vertical scale bar in **b** represents 1 cm. Abbreviations: ac, acromion of scapula; c1–c7, cervical vertebrae 1 to 7; ca1, canine; ca2–ca4, caudal vertebrae 2 to 4 (caudal vertebrae are incomplete); cd, coracoid process of scapula; cl, clavicle; cm, calcaneum; co? coronoid fossa?; cp 1–9, carpals 1 to 9; csp, crista parotica of petrosal; ctp, caudal tympanic recess of petrosal; dn, dentary; ep, epipubis; er, epitympanic recess; fc, fenestra cochlearis (round window); fe, femur; ff?, facial nerve foramen?; fi, fibula; frs, foramen for ramus superior; fst, fossa for stapedial muscle; fv, fenestra vestibuli (oval window); g, glenoid of the scapula; gj, groove for jugal (on the squamosal); gl, glenoid fossa of squamosal; hu, humerus; ic, interclavicle; if, infraspinous fossa; il, ilium; is, ischium; i1–i3, incisors 1 to 3; ju, jugal; L1–L6, lumbar vertebrae 1 to 6 (impressions only); lm, lambdoidal crest; mas, mastoid exposure of petrosal; mc, metacarpoid; mf,



mandibular foramen; mg, meckelian groove; mp1–mp5, metacarpals I–V; mt1–mt5, metacarpals I–V; mst, manubrium of sternum; mx, maxillary; oc, occipital condyle; of, obturator foramen of pectoral girdle; on, odontoid notch for dens of atlas; pc, procoracoid; pcd, condylar process of dentary; pcl, preclavicle (a homologue of procoracoid, *sensu* ref. 50); pr, coronoid process of dentary; pf, pterygoid fossa; pgc, postglenoid crest; pgd, postglenoid depression; pmx, premaxillary; pp, paroccipital process of petrosal; ppe, paroccipital process of exoccipital (incomplete); pr, promontorium of petrosal; prs, prootic sinus canal; ptc, post-temporal canal; pts, post-tympanic sinus; p1 and p2, premolars 1 and 2; ra, radius; r1–r13, thoracic ribs 1 to 13 (posterior thoracic ribs preserved only in impressions); sc, scapula; sl?, fossa for splenial? on the dentary; sm, stylomastoid notch; sp, spine of scapula; sq, squamosal; ss, supraspinous fossa of scapula; stb1–stb6, sternebra 1 to sternebra 6; stl, embryonic sternal bands; sym, mandibular symphysis; s1–s4, sacral vertebrae 1 to 4 (represented mostly by impression); th, attachment site for tympanohyal; ti, tibia; ts, lateral tarsal spur of ankle; t1–t13, thoracic vertebrae 1 to 13; ul, ulna; x, xiphoid process of sternum.

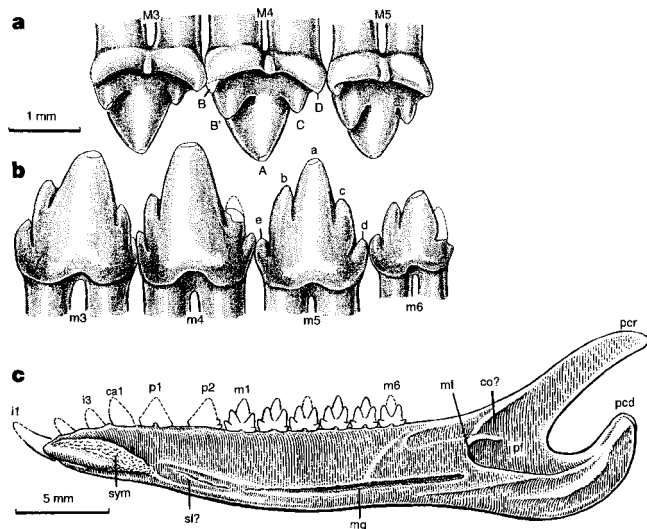


Figure 2 Dentition and mandible of *Zhangheotherium quinquecupidens*. **a**, Upper molars M^{3–5}; **b**, lower molars M_{3–6} (left, labial views); **c**, mandible (right side, reconstruction in medial view). *Zhangheotherium* closely resembles *Spalacotherium* in lower molars, and *Peralestes* in upper molars. *Spalacotherium* and *Peralestes* were established on some dissociated lower and upper teeth, respectively, from the same fauna in the Late Jurassic of England^{10–12}. The associated upper and lower dentitions of *Zhangheotherium* suggest that *Spalacotherium* and *Peralestes* are the lower and upper teeth of the same species, and that *Peralestes* should be synonymized with *Spalacotherium*^{10–12}. Cusp B' is too large and positioned too far lingually to be the stylocone (cusp B). It could be either a homologue to the much smaller intermediate cusp in the comparable position in other symmetrodonts, or a neomorphic cusp. We follow ref. 45 for the designation of cusps A, B, C, D and E on the upper molars, and cusps a, b, c, d and e on the lower molars. For abbreviations, see Fig. 1 legend.

recent radiometric date⁹. According to our most recent field investigation, this date⁹ should be regarded as an upper age limit for the Jianshangou Beds.

Diagnosis. A spalacotheriid symmetrodont (Fig. 2) with the dental formula 3·1·2·5/3·1·2·6; differing from all other known symmetrodonts in having a hypertrophied cusp B' between the main cusp A and the stylocone (cusp B) (Fig. 2); distinguishable from other spalacotheriids^{10–12} in the conical shape of the main cusps and the lack of lingual and labial cingulids on the lower molars¹¹; distinctive from *Spalacotherium*¹¹ in having more robust and rounded main cusps that lack connecting cristae; unique among early mammals^{13–18} in having fused sternebrae, and a posteriorly expanded xiphoid process.

Description and comparison

Zhangheotherium resembles other known spalacotheriid symmetrodonts^{10–12,19,20} in that the central cusp (a) and the two accessory cusps (b, d) of the lower molar form an acute triangle. The associated upper and lower teeth of *Zhangheotherium* could occlude into the embrasures of the opposing tooth row, a pattern unique to spalacotheriids among archaic therians¹⁰. This suggests that the teeth were used more for crushing and puncturing than shearing²⁰.

Zhangheotherium is unique among spalacotheriids in having short and weak cingula in the upper molars, and a relatively low trigonid and two large accessory cusps (cusps d and e) on the lower molars^{10–12,19,20}. Upper molars have a wide labial shelf and their cusp pattern resembles that of *Perallestes*, a Late Jurassic symmetrodont from England^{10–12}. Lower incisors are procumbent, with the first incisor I₁ being enlarged. C₁ is small and single-rooted, similar to I_{2–3}.

The dentary has a dorsally curved condylar process and a posteriorly tilted coronoid process. Like other symmetrodonts, it lacks an angular process (Fig. 2). The mandibular symphysis is oval, unfused and was probably mobile in life. The meckelian groove is narrow, and becomes shallow and faint anteriorly. The posterior part of the groove is separated from the mandibular foramen in the pterygoid fossa. The topographic relationships of these mandibular features (Fig. 2) are very similar to those of more derived therian mammals ('eupantotheres')^{10,16}, but differs from that of the earliest known therian *Kuehneotherium* (Late Triassic), and from those of the non-therian mammals *Morganucodon*²¹ and *Sinoconodon*²². A slightly rugose area along the anterior meckelian groove suggests the presence of the splenial, and a rough area near the base of the coronoid process is probably for a poorly developed coronoid, as occurs in the more derived therian *Henkelotherium* from the Upper Jurassic of Portugal¹⁶. No other postdentary bones are preserved.

The squamosal has an anteroposteriorly elongate glenoid fossa flanked by a low postglenoid crest (Fig. 3). The postglenoid region has a constricted neck between the glenoid and the broad cranial moiety that forms a wall lateral to the epitympanic recess. *Zhangheotherium* is similar in the latter two features to derived therians^{17,23,24}, but is different from non-therian mammals which have a narrow cranial moiety of the squamosal but no squamosal wall for the epitympanic recess^{25,26}. The postglenoid area of the squamosal has a posterolateral depression that resembles the broad external auditory meatus of *Vincelestes*¹⁷, the marsupial *Pucadelphys*²⁴ and placentals, in contrast to non-therian mammals in which the squamosal has no postglenoid region or the external auditory meatus^{21,22,27–29}.

The petrosal bones that contained the inner ear are complete but fractured and distorted in preservation. The promontorium that houses the cochlea has a cylindrical and finger-like shape (Fig. 3). Its structure is very similar to those of *Sinoconodon*²⁰, *morganucodontids*^{21,22,31}, *triconodonts*^{22,26} and *multituberculates*^{32–34}. As documented for a wide range of early mammals^{30,31,33–35}, a cylindrical and finger-like promontorium is closely correlated

with either a straight or slightly curved (but uncoiled) cochlea. We therefore infer from the slender promontorium of *Zhangheotherium* (Fig. 3) that it has a more or less straight (definitely uncoiled) cochlea. *Zhangheotherium* is very different from derived therian mammals, which have oval-shaped and more bulbous promontoria with cochleae coiled for at least 270 degrees^{17,23,33,36}.

The petrosal has a prominent paroccipital process that is similar to those of *morganucodontids*^{21,22}, *triconodonts*^{22,26}, *multituberculates* and *ornithorhynchids*³⁷. The post-temporal canal is positioned between the paroccipital region of the petrosal and lambdoidal crest of the squamosal, also a primitive character of mammals. *Zhangheotherium* has a large post-tympanic recess, and a broad and shallow epitympanic recess bound medially by a low crista parotica, and laterally by the squamosal. Both these features are characteristic of more derived therians.

Zhangheotherium has 7 cervical and 13 thoracic vertebrae. The postaxial cervical ribs remain unfused in adults, as in *morganucodontids*¹³ and *multituberculates*³⁸. All thoracic ribs are

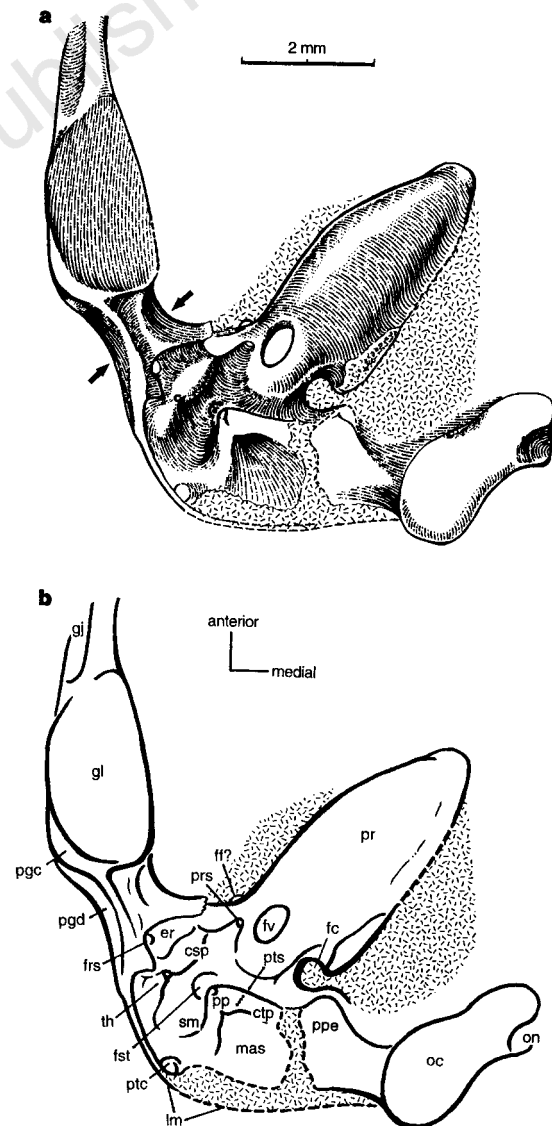


Figure 3 Reconstruction of the partial basicranium of *Zhangheotherium quiquecuspidens* (IVPP V7466). Right side, ventral view. Composite reconstruction (a) and outline with labels (b). Hatched pattern indicates the areas of damage or matrix. Arrows in a indicate the constricted neck of the squamosal. For abbreviations, see Fig. 1 legend.

robust and compressed anteroposteriorly. Six lumbar vertebrae and three or four sacral vertebrae are represented by impressions. The sacral vertebrae and three preserved caudal vertebrae have wide transverse processes (Fig. 1).

The interclavicle is V-shaped. It is clearly articulated with, and overlaps the ventral side of the anterior part of, the sternal manubrium. Its sharp posterior process is continuous with the sternal keel (Fig. 4). The manubrium, although fused to other sternbrae, is still discernible by its facet for the first thoracic rib. The short and broad lateral process of the interclavicle has a loose and mobile articulation with the clavicle. *Zhangheotherium* and multituberculates share strong similarities in the articulations of the interclavicle to the clavicle and to the sternum¹⁸. The lateral end of the clavicle has a spiral articular surface for the acromion of the scapula, allowing some mobility in the clavicle–scapular joint. The triangular scapular blade is demarcated from the glenoid by a scapular notch. The supraspinous fossa is developed along the entire length of the blade, but is much narrower than the infraspinous fossa. The spine is very high, with a prominent acromion. The coracoid process is hook-like. The glenoid faces ventrally, and is much narrower than the spherical humeral head. *Zhangheotherium* has mobile articulations of the interclavicle, clavicle and scapula that allow the clavicle to move and act as a pivotal strut³⁹ for a wider rotation of the scapula, as observed during the locomotion of the opossum⁴⁰.

The robust humerus of *Zhangheotherium* has a long deltopectoral crest. The intertubercular groove is narrow and deep, and separates the greater and lesser tubercles, the former being slightly wider than the latter. Torsion of the proximal end of humerus relative

to the distal end is about 30 degrees, about the same as in *Henkelotherium*¹⁶, and close to the 40 degree torsion in *Vincelestes*¹⁷. Distally, the humerus has an incipient trochlea for the ulna, a therian apomorphy^{16,17,41} that is absent in multituberculates^{14,18,42}. The humerus also has a weakly developed ulnar condyle, resembling those of non-therian mammals^{13,14,38,41}. The radial condyle is prominent and spherical, a primitive feature of non-therian mammals. Nine carpals are present. The pisiform is very large.

The pelvic bones are slender. The ilium is long and rod-like, and three times as long as the ischium. The acetabulum is partially preserved, showing a dorsal rim. Although the ischiopubic plate is not well preserved in IVPP V7466, its impressions indicate a shallow pelvis, differing from the deep pelvis of multituberculates³⁸. The epipubis is as long as the ischiopubic plate. As in multituberculates^{14,38}, the spherical femoral head is set off from the shaft by a well-defined neck, and the greater trochanter is directed dorsally. The calcaneum has an elongate tubercle and a well-defined peroneal tubercle. Its astragal process contacted the fibula, a plesiomorphy for therians²⁷. As in living monotremes and *Gobiconodon*¹⁵, *Zhangheotherium* has an external pedal spur. This spur is associated with a poisonous gland in the modern male platypus.

Phylogenetic implications for early mammals

The relationships of therians to extinct non-therian mammalian lineages have received much attention, as hypotheses of therian relationships are central to the understanding of early mammalian evolution^{27,43}. Therians have been hypothesized to be the sister taxon of either multituberculates^{18,26,27} or monotremes on the basis of some derived molar characters⁴⁴. Basicranial studies^{34,37} have suggested that monotremes and multituberculates were sister taxa to the exclusion of therians. There are few relatively complete fossils of archaic therians^{16,17}. The discovery of the skeleton of *Zhangheotherium* offers the first opportunity to assess the phylogenetic relationships of early therians using nearly all dental, basicranial and postcranial characters.

Symmetrodont mammals were previously known only from teeth and jaws. Owing to the lack of better evidence, the affinities of this lineage to the more derived therians have been based solely on dental evidence^{12,43–46}. It has been argued that dental characters are as homoplastic as non-dental characters^{27,43,47,48}, and the reliability of dental characters for inferring the relationships of major lineages of mammals has been questioned. *Zhangheotherium* has provided more extensive basicranial and postcranial evidence to corroborate the traditional hypothesis^{12,43–46} that symmetrodonts represent a part of the basal therian radiation. Our analysis (Fig. 5) suggests that *Zhangheotherium*, as the best-preserved taxon of all symmetrodonts, is a basal clade in therian phylogeny. It is more primitive than *Henkelotherium*¹⁶ and *Vincelestes*¹⁷ in retaining the interclavicle in its pectoral girdle. It also has a primitive dentition in which the lower molars have no distinct talonid, and the upper and lower molars occlude in the embrasures of the opposing tooth rows (Fig. 2), in contrast to more derived therians in which the lingual part of the upper molar occludes with the talonid of the lower molar^{16,45}.

The sister-taxon relationship between therians and multituberculates^{18,26,27} is strongly supported by the evidence from *Zhangheotherium*. Additional derived characters from *Zhangheotherium*, such as the clavicle–interclavicle joint and some features of the femur, corroborate the therian affinities of multituberculates (Fig. 5).

Implications for anatomical evolution

A large and reptile-like interclavicle is present in adult monotremes⁴⁹. In living marsupials (Fig. 4), it first appears embryonically as a separate ossification(s), but later becomes incorporated, at least in part, within the sternal manubrium in the adult⁵⁰. *Zhangheotherium* shows that the interclavicle was still present in at

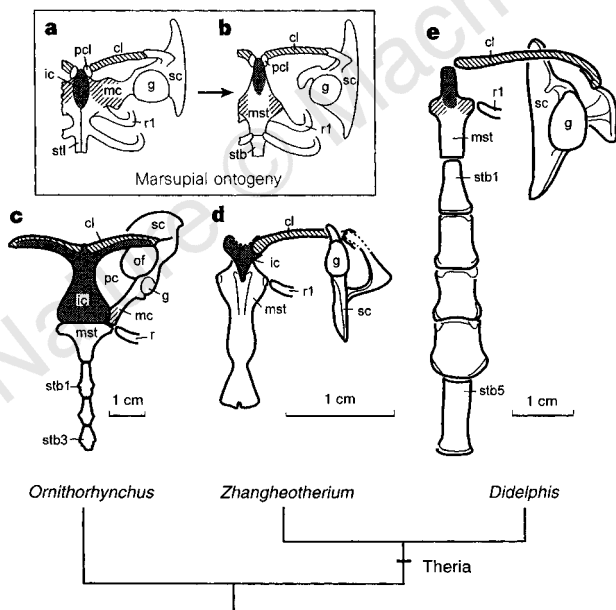


Figure 4 Comparison of the sternal apparatus and pectoral girdle of *Zhangheotherium* and living mammals. **a, b**, Embryonic (**a**) and adult (**b**) stages of the sternum and pectoral girdle in marsupials (modified from ref. 50). **c–e**, The adult sternal and girdle structures of *Ornithorhynchus* (modified from ref. 49) (**c**), *Zhangheotherium* (**d**) and *Didelphis* (CMNH c45, and several uncatalogued specimens at Carnegie Museum) (**e**). The chondral element of the interclavicle and the medial part(s) of the embryonic coraco–scapular plate are considered to be incorporated into the sternal manubrium in adult marsupials^{49,50}. *Zhangheotherium* has retained a separate interclavicle, a primitive character of non-therian mammals, but a more derived character of a mobile clavicle–interclavicle joint which is present in multituberculates and in a modified form in living therians. For abbreviations, see Fig. 1 legend.

least some archaic therians. The loss of the interclavicle, or its incorporation into the sternal manubrium, occurred only in more derived therians. The reduced interclavicle and the mobile clavicle–interclavicle articulation in *Zhangheotherium* are far more derived than the large interclavicle and the rigid clavicle–interclavicle articulation in living monotremes (Fig. 4).

In contrast to the sprawling posture of living monotremes, most living therian mammals have a more parasagittal posture (*sensu ref. 42*), with the elbows positioned close to the thorax^{39–41}. Such a forelimb posture has been hypothesized to have evolved only once in the common ancestry of multituberculates, living therians and their extinct relatives¹⁸, although this view has been contested⁴². Several osteological characters are considered to be crucial to the parasagittal posture of the forelimb of therians^{18,38,39,41}: a mobile joint between the clavicle and sternal apparatus (including the interclavicle); a greater tubercle much wider than the lesser tubercle; a narrow intertubercular groove⁴²; a humeral trochlea that constrains the movement of the ulna⁴¹; and possibly the lack of torsion of the humerus¹⁸ (but see ref. 42). The skeleton of *Zhangheotherium* provides additional information on the phylogenetic distribution of these characters.

Zhangheotherium, *Vincelestes*, modern therians, and multituberculates all have a mobile joint between the clavicle and the sternal apparatus. This allows the clavicle to function as a pivot for the shoulder joint, and allows a greater range of rotation of the scapula during locomotion^{39,40} than is possible in monotremes. However, torsion of the humerus and the large lesser tubercle relative to the greater tubercle in *Zhangheotherium*, *Henkelotherium* and *Vincelestes*¹⁷ suggest that the humeri of these archaic therians were more abducted than those of most living therians. The humerus of *Zhangheotherium* has an incipient trochlea but also retains a vestigial ulnar condyle. The trochlea is also incipient in the Late Jurassic *Henkelotherium*¹⁶, but more developed in the Early Cretaceous *Vincelestes*¹⁷. This differs from the fully functioning (but more primitive) ulnar condyle of multituberculates^{14,18,38,42}. The incipient trochlea in such archaic therians as *Zhangheotherium* and *Henkelotherium* represents an intermediate condition towards the less abducted posture of the forelimb in living therians.

These new data suggest that the mobility of the clavicle and scapula has a more ancient origin than the more parasagittal posture of the forelimbs (Fig. 5). The mobile and pivotal clavicle evolved before the divergence of multituberculates and therians. The parasagittal forelimb posture of living therians was not present in such

archaic therians as *Zhangheotherium*, *Henkelotherium*¹⁶ and *Vincelestes*¹⁷, and it is best considered to have arisen later in therian evolution.

Although the cochleae of living monotremes and therian mammals all have some degree of coiling, it remains unclear whether a coiled cochlea evolved only once or in parallel among monotremes and therians. In early marsupials and placentals^{33,36}, the promontorium that houses the cochlea is inflated and bulbous as a result of the cochlear coiling. Within the cochlear canal, the osseous spiral laminae of the bony labyrinth are well developed to support the membranous labyrinth³⁶. In contrast, the cochleae of monotremes lack such internal bony structures^{28,33}.

Because the finger-like promontorium is closely correlated to an uncoiled cochlea in diverse early mammals^{30,31,33–35}, its presence in *Zhangheotherium* suggests that the coiled cochlea and the inflated promontorium of more derived therians^{17,33,36} are not present in symmetrodonts. Within the framework of mammalian phylogeny supported by many independent characters (Fig. 5), the coiled cochlea of therians would best be considered to have evolved later in such derived mammals as *Vincelestes*¹⁷, marsupials and placentals, independently of the partially coiled cochlea of monotremes (Fig. 5).

Conclusions

The nearly complete skeleton of *Zhangheotherium quinquecuspidens* has yielded new and more comprehensive anatomical information about the early therian mammals. New evidence on basicranial and postcranial anatomy from *Zhangheotherium* corroborates the hypothesis that symmetrodonts are a part of the basal therian radiation. Postcranial features of this new therian mammal support a sister-group relationship between multituberculates and therian mammals. A mobile clavicle–interclavicle joint that allows a wide range of movement of the forelimb has an ancient origin in the mammalian phylogeny. The abducted forelimb inferred for *Zhangheotherium* and other archaic therians suggests that early therian mammals lacked the more parasagittal forelimb posture of most living therians. The presence of a finger-like promontorium in *Zhangheotherium* indicates, albeit indirectly, that an uncoiled cochlea was present in symmetrodonts and that the coiled cochlea was a development later in therian evolution. □

Methods

Phylogeny of mammals. Based on a most parsimonious tree from PAUP (3.1.1. Exhaustive search) from 66 dental, cranial and postcranial characters that can be examined in *Zhangheotherium* (see Supplementary information for the character list and matrix). The most parsimonious tree has: tree length = 108, consistency index = 0.759, retention index = 0.840. Numbers on the branches represent the bootstrap value of 100 bootstrap replicas (the 50% majority bootstrap consensus tree and the most parsimonious tree have identical topology).

Abbreviated apomorphy list. **Node A** (Mammalia of ref. 43 or Mammalia-formes of ref. 27): prezygapophysis absent on axis; shallow patellar groove present on femur; notches for quadrate and quadratojugal absent in squamosal; promontorium present, unilateral occlusion of lower jaw; rotation of lower jaw during occlusion; differentiation of postcanine crowns into premolars and molars. Equivocal apomorphies: proatlans neural arch absent in adults; number of divided postcanine roots is not more than three. **Node B** (*Gobiconodon* plus the crown group of mammals): atlas ribs fused in adults; postaxial ribs fused in adults; sesamoid bone present in the pedal flexor tendon; a distinctive mandibular foramen fully formed; meckelian groove is vestigial or absent in adult; glenoid of scapula concave (instead of saddle shaped) and facing posteroventrally. Equivocal apomorphies: acetabular dorsal emargination closed; presence of external pedal (tarsal) spur; foramen for superior ramus of stapedia artery enclosed. **Node C** (the crown group of mammals, or the Mammalia of ref. 27): presence of well-developed patellar groove on femur; greater rotation of the mandible during occlusion; main cusps of the molars arranged in reversed triangle; more transverse orientation of protocristid. Equivocal apomorphies: absence of meckelian groove on the mandible

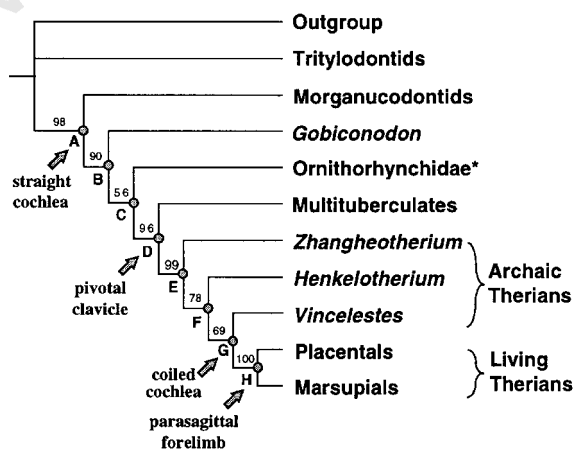


Figure 5 Phylogenetic relationships of *Zhangheotherium quinquecuspidens*. Asterisk: given this phylogeny, the coiled membranous labyrinth without corresponding coiling of the bony labyrinth in monotremes^{28,33} is considered to be a convergence to the coiled cochlea of derived therians. See Methods for details of nodes A–G.

(reversed in *Zhangheotherium* and *Henkelotherium*); main cusps of molar arranged in reverse triangle (lost in multituberculates). **Node D** (Theriiformes of ref. 27): mobile joint between clavicle and sterno-interclavicular apparatus; supraspinous fossa present on scapula; strong acromion extending below the level of glenoid of scapula; coracoid reduced to a process and fused to scapula; glenoid of scapula narrower than humeral head and facing posteroventrally; humeral and femoral heads spherical and strongly inflected; entepicondyle and ectepicondyle of humerus more reduced; styloid process of radius better developed; greater trochanter of femur directed dorsally; calcaneal tubercle elongate; presence of a separate peroneal tubercle; incipient superposition of astragalus over calcaneum; sesamoid bones in pedal flexor tendon paired; epitympanic recess in petrosal fully developed. Equivocal apomorphies: anterior sternal element (procoracoid) either fused with the manubrium sterni or lost; lesser trochanter of femur oriented ventromedially or ventrally; distinct tibial malleolus and fibular styloid process. **Node E** ('holotheres' of ref. 43): supraspinous fossa developed to the full length of scapula; flat medial surface of scapula; greater tubercle of humerus larger than the lesser; intertubercular groove very deep and narrow; squamosal with a postglenoid depression; cranial moiety of squamosal broad; post-tympanic recess present; craniomandibular joint anterior to fenestra vestibuli; crista interfenestralis limited to promontorium; squamosal wall flanking the epitympanic recess. Equivocal apomorphies: distal humerus forming a trochlea for ulnar articulation. **Node F**: talonid present on lower molar; wear facet present on talonid; protocristid of lower molar very transverse. Equivocal apomorphies: interclavicle absent in adults. **Node G** (Tribosphenida of ref. 43): upper molar with protocone; coronoid absent in adult; meckelian groove absent in adults. **Node H** (crown group of marsupials and placentals, or the Theria of ref. 27): manubria sterni small; the torsion of humerus weak; ulnar condyle on the humerus lost; fibula lost contact to calcaneum; cochlea elongate and coiled at least 360 degrees; lower molar talonid fully developed with a basin. Equivocal apomorphies: fusion of atlas neural arch. **Gobiconodon**: equivocal apomorphy: ulnar articulation on distal humerus forming a trochlea (convergent to therians). **Ornithorhynchidae**: equivocal apomorphies: postcanines with multiple roots (convergent to tritylodontids). Autapomorphy: lower molars with anteroposteriorly compressed talonid. **Multituberculates**: equivocal apomorphy: meckelian groove absent in adults. Autapomorphy: deep peroneal groove.

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