

New basal eutherian mammal from the Early Cretaceous Jehol biota, Liaoning, China

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A new genus and species of eutherian mammal, *Acristatherium yanensis* gen. et sp. nov., is described from the Early Cretaceous Jehol biota, China. The new taxon is based on a partial skull that is preserved in three dimensions from the Lujiatun bed of the Yixian Formation and dated 123.2 ± 1.0 Ma. Its right upper and lower dentitions are nearly complete and it has a dental formula 4.1.5.3/3.1.5.3. The new mammal reveals several craniodental characteristics of Early Cretaceous eutherians previously unknown in fossil records of therians, such as a possible vestige of the septomaxilla. The craniodental features of the new taxon are compared with those of relevant Early Cretaceous eutherians and therians. Phylogenetic analyses based on a data matrix containing 70 taxa and 408 characters place *A. yanensis* as the most basal eutherian in the selected group. The morphological differences between *Acristatherium* and *Eomaia* indicate that eutherians already had a significant degree of generic diversification *ca* 125 Ma.

Keywords: Early Cretaceous; mammal; eutherian; Jehol biota; septomaxilla; therian dentition

1. INTRODUCTION

Eutherians include extant placentals and all mammals that are phylogenetically closer to placentals than to marsupials (Rougier *et al.* 1998; Kielan-Jaworowska *et al.* 2004). The earliest eutherians date to the Barremian–Aptian, Early Cretaceous (112–125 Ma; Kielan-Jaworowska *et al.* 2004), younger than the age estimate from a recent molecular study of the earliest placental ordinal diversification *ca* 148–130 Ma (Bininda-Emonds *et al.* 2007). Characteristics of the ancestral eutherian morphotype are still poorly known because of fragmentary fossils. A handful of eutherian species from the Early Cretaceous are known from isolated teeth, jaws and cranial fragments, such as *Prokennalestes* (Kielan-Jaworowska & Dashzeveg 1989; Sigogneau-Russell *et al.* 1992; Wible *et al.* 2001), *Murtoilestes* (Averianov & Skutschas 2001) and *Montanalestes* (Cifelli 1999). *Eomaia* (Ji *et al.* 2002) is by far the best preserved specimen, represented by a crushed skeleton. The age assignment of the *Eomaia scansoria* type specimen depends on the stratigraphic correlation of the type locality, which is now putatively considered to be 124–126 Ma. Owing to the preservation, in which its skull and teeth are known from flattened bones and impressions, detailed craniodental morphologies are not clear. Several eutherians from the earliest Late Cretaceous (Early Cenomanian), such as *Bobolestes*, *Sheikhdzheilia*, *Eozhelestes*, and unnamed zalambdalestid and zhelestid taxa, are also known from fragmentary specimens (Nessov 1993; Nessov *et al.* 1994; Averianov & Archibald 2005).

Here we report a new eutherian from the basal beds of Yixian Formation. It is represented by a partial skull with

the dentition preserved in three dimensions. As one of the earliest eutherians, the new taxon reveals many craniodental characteristics of Early Cretaceous eutherians previously unknown from the fossil record.

2. MATERIAL AND METHODS

All photographs were taken using a Nikon DS-Fi1 mounted to a Nikon SMZ-U microscope and were edited using Adobe PHOTOSHOP v. 8.0. The data matrix was constructed in MESQUITE v. 2.0 for Mac (Maddison & Maddison 2005a) and converted to PAUP-readable data file using MACCLADE v. 4.08 for Mac OS X (Maddison & Maddison 2005b). The phylogenetic analysis was performed using PAUP v. 4.0.b10 for Mac (Swofford 2002).

Eutheria is defined as a monophyletic clade containing placentals and all taxa more closely related to placentals than to marsupials, whereas Metatheria is the monophyletic group containing marsupials plus all taxa closer to marsupials than to placentals (Kielan-Jaworowska *et al.* 2004). Theria is the last common ancestor of placentals and marsupials plus all of its descendants (McKenna & Bell 1997; Rougier *et al.* 1998). Anatomical terminology follows Kielan-Jaworowska *et al.* (2004) and Wible *et al.* (2004).

3. SYSTEMATIC PALAEOLOGY

Mammalia Linnaeus 1758.

Eutheria Gill 1872.

Acristatherium yanensis gen. et sp. nov.

(a) *Etymology*

‘Acrista’, crestless, in reference to the absence of a sagittal crest on the skull; ‘therion’, beast; ‘yan’ representing Yanzigou, the name of type locality.

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Figure 1. Stereo photographs of the partial skull of *A. yanensis* (holotype, IVPP V15004). de, dentary; fr, frontal; nfs, nasofrontal suture; fps, frontoparietal suture; ju, jugal; la, lacrimal; mx, maxilla; iof, infraorbital foramen; na, nasal; pa, parietal; pm, premaxilla; sm, septomaxilla; sq, squamosal. Scale bar, 5 mm.

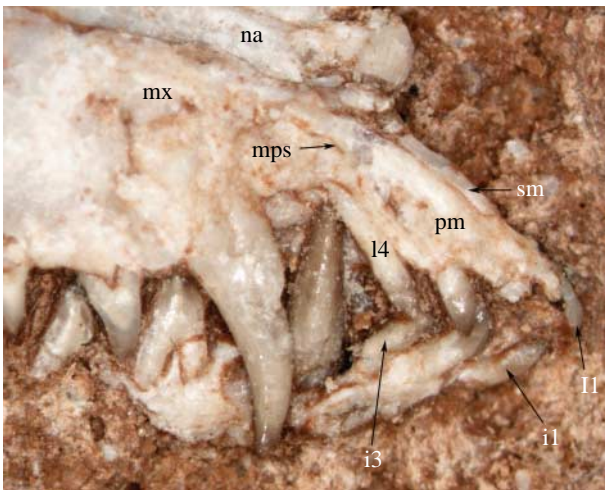


Figure 2. Snout of *A. yanensis* (holotype, IVPP V15004) with the septomaxilla marked with an arrow. mps, maxillopremaxillar suture; mx, maxilla; na, nasal; pm, premaxilla; sm, septomaxilla.

(b) *Holotype*

Partial skull with associated partial right lower jaw that bears nearly complete right upper and lower dentitions (IVPP V15004, Institute of Vertebrate Paleontology and Paleoanthropology; figures 1–3). The right half of the skull is largely preserved and most of the orbit and basicranium are missing. The left half of the skull has only a partial nasal, frontal, part of the parietal and occipital complex preserved. The upper and lower dentitions are tightly occluded and further preparation to separate them would damage the specimen. The crown views of the upper and lower teeth are mostly observable through narrow spaces when the specimens are held in various angles under the microscope, but these views are difficult to image.

(c) *Horizon and locality*

Yanzigou, Shangyuan, Beipiao, Liaoning, China; Lujiatun bed of the Yixian Formation, Early Aptian, Cretaceous, 123.2 ± 1.0 Ma (He *et al.* 2006).

(d) *Diagnosis*

Dental formula 4.1.5.3/3.1.5.3; canines large and single-rooted; P3/p2 smallest upper and lower premolars, respectively; p1 larger than p2; P5/p5 bearing a single principal cusp; styler shelves of upper molars broad; ectoflexus deep; parastylar lobe much larger than metastylar one; paracone and metacone connate; protocone small; conules weak or absent; pre- and postcingula weak or absent; distolabial region of M3 reduced; paraconid of lower molar smaller and more labially positioned than metaconid; cusp e prominent; precingulid absent; talonid three-cusped, considerably shorter and narrower than trigonid; hypoconulid not shifted towards the entoconid; vestigial septomaxilla present; zygomatic arch slender; sagittal crest absent.

4. DESCRIPTION

(a) *Cranium and dentary*

The skull length (from the tip of the premaxilla to the occipital condyle) is 25 mm. The preorbital portion is narrow and long, subequal to the postorbital portion in length. The cranial roof is somewhat bulbous. The mesocranial region is long, with a weak interorbital constriction. The premaxilla has a posterodorsal (facial) process and houses I1–3. A unique feature in the rostrum is that on the dorsal side of the premaxilla that contains I2–3, there is a slim bone that sutures with the premaxilla. Its posterior portion is obscured by breakage, but it was probably posterodorsally inserted between the premaxilla and nasal and contacted the maxilla posteriorly. The bone is probably not an anterior branch of the nasal, nor an anterior projection of the maxilla. By its position and size, we interpret this bone a vestigial septomaxilla. The nasal bones are narrow anteriorly, with parallel lateral edges for most of their anterior length, and expand posteriorly. The nasal is half of the total length of the skull roof. Each nasal contacts the maxilla laterally, the lacrimal posterolaterally and the frontal posteriorly. The facial component of the maxilla is long, but posteriorly the maxilla does not contribute to the zygomatic arch. A sizeable infraorbital foramen is situated within the maxilla, dorsal to the embrasure between the last two premolars. The alveolar margin of the maxilla accommodates the last upper incisor, canine and cheek teeth. The lacrimal has a large facial exposure that is roughly triangular and wedges between the nasal and frontal dorsally, and the maxilla and jugal ventrally. There are two lacrimal foramina located within a recess that is at the emargination of the lacrimal bone. The orbital component of the lacrimal is small, contacting the maxilla ventrally, the frontal posterodorsally and possibly the palatine posteriorly. A recess between the lacrimal and the maxilla leads to the maxillary foramen of the infraorbital canal. The frontal is large and is slightly shorter than the parietal; both are nearly equal in width. The roof of the frontal is bulbous, indicating a pair of sizeable olfactory lobes. The interparietal suture is hardly visible, where two parietals together form a shallow longitudinal depression. The sagittal crest is absent. The lambdoidal

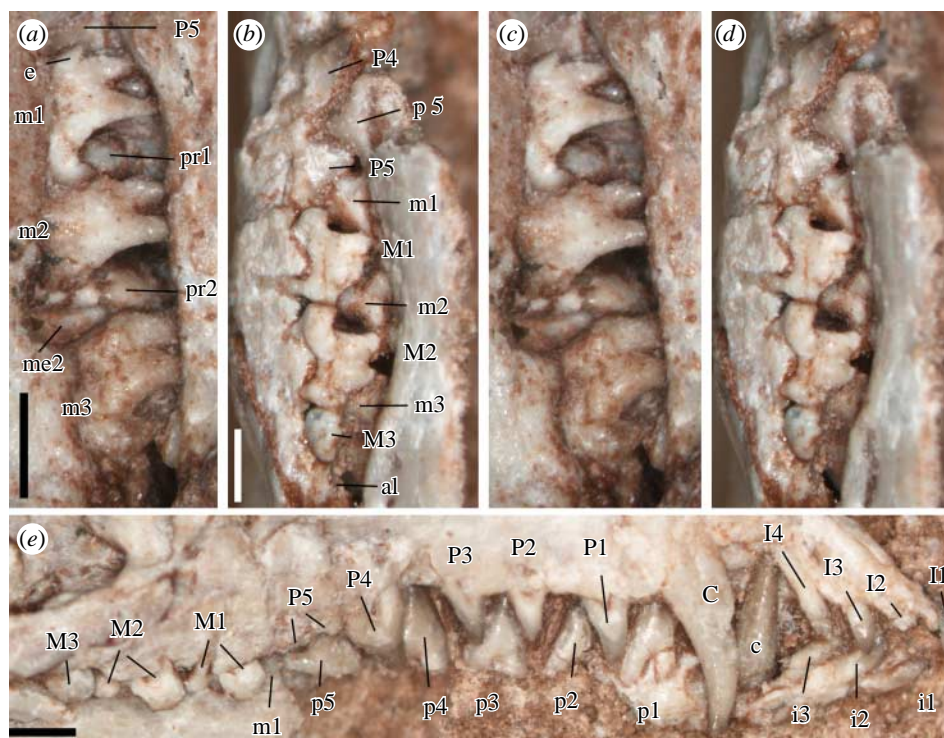


Figure 3. Dentitions of *A. yanensis* (holotype, IVPP V15004). (a,c) Stereo photographs of lingual views of mainly lower molars; (b,d) Stereo photographs of labial views of mainly upper molars. (e) Lateral view of upper and lower dentitions. al, alveolus for posterolabial root of M3; e, cusp e of m1; me2, metacone of M2; pr1, protocone of M1; pr2, protocone of M2. Measurements in mm: upper tooth length: I1, 0.25; I2, 0.4*; I3, 0.4; I4, 0.4; C, 1.0; P1, 0.7; P2, 0.6; P3, 0.5; P4, 1.0; P5, 1.3; M1, 1.3; M2, 1.4 (width, 1.5; M3, 0.7; lower tooth length, i1, 0.4; i2, 0.5; i3, 0.4; c, 0.8*; p1, 0.8; p2, ?; p3, 0.9; p4, 0.9; p5, 1.0; m1, 1.3; m2, 1.3*; m3, 1.4 (asterisks indicate estimated measurements). Scale bar, 1 mm.

crest is low and transversely short. The occipital condyles are broken. The squamosal has a sizeable squama, pierced by a large subsquamosal foramen (Wible *et al.* 2004) in the centre of the element. The glenoid fossa faces anteriorly. The postglenoid process is present, but broken at the base. The jugal is the principal element of the zygoma; it is interposed anteriorly between the maxilla and lacrimal, and posteriorly butts ventrally with the zygomatic process of the squamosal, but does not contribute to the anterior wall of the glenoid fossa.

Much of the dentary is damaged. Its remaining portion shows a low coronoid process with a tip pointed posteriorly and a gently sloped anterior edge. The coronoid notch is shallow and wide. The condyle is situated slightly above the level of the tooth row and is expanded transversely and supported by a short peduncle. The masseteric fossa is deep and delimited anterodorsally by a distinct coronoid crest. The anterior extremity of the fossa is posteroventral to m3. The preserved portion of the mandible posterior to the anterior edge of m1 does not bear a mental foramen.

(b) Dentition

The dental formula is I4.C1.P5.M3/i3.c1.p5.m3. All antemolar teeth have deep grey colour, showing no wear; whereas the molars are light grey in colour with some wear. These suggest that antemolar teeth probably erupted later than molars and represented the permanent replacement teeth. They also indicate that the specimen is of a relatively young adult.

All incisors are small, single-rooted and with simple crown. The lower incisors are procumbent. The middle teeth (I2–3 among uppers and i2 among lowers) are

slightly larger than neighbouring teeth. I1 is peg-like. I2 has the crown missing. I3 and I4 are somewhat mediolaterally compressed and do not have a constriction at the root–crown junction. I4 is behind the premaxilla–maxilla suture and implanted mainly within the maxilla; its anterior side may be in contact with the premaxilla. Lower incisors are slightly larger than uppers. They are essentially conical in shape, but have small anteromesial and distolateral ridges extending from the principal cusp.

The canines are single-rooted and much larger than neighbouring teeth. The upper canine is dagger-like, slightly bending distoventrally. The lateral side of the root has a shallow longitudinal sulcus, indicating the root might be bifurcate. The cross section of the tooth crown is oval. The lower canine is short (in height) but slightly more robust than the upper. It is straight and roughly taper-shaped with a triangular cross section.

Upper and lower premolars are spaciouly positioned with a gap between adjacent teeth to accommodate the opposite tooth. Each premolar is double-rooted. The P3 and p2 are the smallest of the upper and lower series, respectively. For the upper premolars, the tooth length increases of the order of P3 < P2 < P1 < P4 < P5. P1–3 are similar in having a single trenchant cusp with sharp anterior and posterior crests. P4 possesses anterobasal and posterobasal cusps in addition to the principal cusp. The basal cusps on P5 are larger than those of P4 and are shifted to more labial positions, and are connected by a labial cingulum to form a very narrow styler shelf. Although broken, the preserved portion shows that the principal cusp of P5 is similar to those of other premolars; there is no trace of any lingual cusp. The tooth length order of lower premolars is p2 < p1 < p3 ≈ p4 < p5. p1–3

are similar to their counterparts in having a principal cusp and no basal cuspules. p4 has a posterobasal cuspule whereas p5 has both antero- and posterobasal cuspules in addition to the principal cusps. There is no sign of a trigonid.

Among upper molars, M1–2 are well preserved except for damaged tips of the paracone and metacone. M1–2 are similar in structure, with M1 being slightly smaller, and both are slightly wider than long. The stylar shelf is wide, with the ectoflexus being moderately deep on M1 and deeper on M2. The parastylar lobe is larger than the metastylar lobe, but the latter does not lingually retract compared with the parastylar lobe. The stylocone is low due to the wear. The parastyle is large and projects anterolabially. The preparastyle is a minute cuspule and the metastyle is small. There is no other cuspule along the ectoflexus. The paracone and metacone are connate and connected by the centracrista; the paracone is larger than the metacone. The preparacrista is steeper than the postmetacrista. The latter bears a sizeable cusp ‘C’ in the middle. The lingual flanks of the paracone and metacone are nearly vertical. The protocone is small. M2 occlusal view is visible through the space between m2 and m3 and shows weak or no conule. The pre- and postcingula are weak or absent. The pre- and postproto-crista do not extend labially beyond the base of paracone or metacone, respectively. M3 only preserves the anterolabial portion. The lingual shift of the alveolus for the posterolabial root of M3 indicates that the tooth probably has three roots, as in M1–2, and that the posterolabial lobe of the tooth is reduced.

m1 is best preserved among lower molars. The m2 talonid is damaged and the m3 hypoconulid is not preserved. m1 is the smallest lower tooth, but is only slightly smaller than m2. The trigonid of lower molars are notably higher, longer and wider than the talonid. The angle of the trigonid is estimated to be 30–45°, that of m1 being the greatest. Three trigonid cusps are trenchant, of which the protoconid is the highest and the paraconid the lowest. The paraconid is more labially placed than the metaconid, and the two cusps are connate at the base. The metaconid is slightly more posteriorly positioned than the protoconid. m1–2 possess a sizeable cusp e anterolingual to the base of the paraconid, but the m2 cusp e was broken. On m3 there is only a swelling at the same position. The paracristid is deeply notched, while the protocristid has only a shallow notch in the middle. Both are oblique to the direction of tooth row. The posterior wall of the trigonid is steep except that the posterior flank of the metaconid slopes towards, not reaching to, the entoconid. The hypoflexid is wide. The hypoconid and entoconid are distinct, with the former being slightly larger. The hypoconulid is obscured on m1, and broken on m2 and m3. The preserved base indicates that the cusp is small and positioned nearly in the mid-position between the hypoconid and the entoconid.

5. DISCUSSION

(a) Comparison

The skull roof configuration of *Acristatherium*, such as a long, narrow and posteriorly expanded nasal, a large frontal and a bulbous parietal, is in general similar to those in other Cretaceous eutherians (*Daulestes*, *Asioryctes*, *Kennalestes*, *Maelestes* and *zalambdalestids*;

Kielan-Jaworowska 1981, 1984; McKenna *et al.* 2000; Wible *et al.* 2004, 2007). A similar condition also occurs in some basal marsupials (Marshall & Muizon 1995; Szalay & Trofimov 1996; Muizon 1998) as well as in many Mesozoic mammals (sinoconodontids, morganucodontids, eutriconodonts, symmetrodonts and *Vincelestes*). This suggests that the mammalian condition in architecture of the skull roof is retained in the earliest eutherians.

The most notable cranial feature of *Acristatherium* is the vestigial septomaxilla. If correctly identified, it is the first record for an unequivocal therian mammal. A large septomaxilla with a posterodorsal process (facial exposure) and a medial transverse shelf is commonly present in non-mammalian therapsids (Wible *et al.* 1990; Hillenius 2000). Among mammals, the septomaxilla has been reported occur in *Sinoconodon* (Patterson & Olson 1961; Wible *et al.* 1990), *Gobiconodon* (Jenkins & Schaff 1988), *Repenomamus* (J. Meng 2009, personal observation), *Vincelestes* (Rougier 1993) and recent monotremes (Wible *et al.* 1990). A purported ‘septomaxilla’ in dasypoids has been considered to be a neomorph (Wible *et al.* 1990). In these taxa, the septomaxilla lacks the medial transverse shelf and is overall reduced compared with that of non-mammalian therapsids. In *Morganucodon* (Kermack *et al.* 1981) and *Haldanodon* (Lillegraven & Krusat 1991), a facet on the premaxilla has been interpreted as for the septomaxilla, which was probably similar to that of *Sinoconodon* in morphology. Compared with those in other Mesozoic mammals, the septomaxilla of *Acristatherium* appears further reduced in size. It is perhaps equivalent to only the posterodorsal process of the septomaxilla in other Mesozoic mammals. The vast majority of Mesozoic therian mammals do not have the rostrum preserved, so whether the septomaxilla is present in these taxa is unknown. The presence of a vestigial septomaxilla in *Acristatherium* is indicative of a broader distribution of the element among Mesozoic mammals. If our identification is correct, the same element should also be found in the other earliest therian mammals. In addition, because the premaxilla has a distinctive facial process, the presence of the vestigial septomaxilla in *Acristatherium* supports the view that the septomaxilla does not fuse with the premaxilla to become its facial process (Wible *et al.* 1990).

The dentition of *Acristatherium* furnishes by far the most informative morphology for Jehol therian mammals. The incisor count for *Acristatherium* (I4/i3) is the same as *Kennalestes*, while several primitive eutherians (such as *Asioryctes*, *Ukhaatherium* and *Eomaia*) and marsupials (such as *Pucadelphys*, *Mayulestes*, *Didelphis*) have an incisor count of I5/i4. Some other eutherians, such as *Prokennalestes*, *Bobolestes* and *Eozhelestes*, have four lower incisors but the number of upper incisors is unknown. *Vincelestes* and *Deltatheridium* have an incisor count of I4/i3. The I5/i4 condition has been regarded as primitive for both metatherians and eutherians (Clemens & Lillegraven 1986), although a primitive metatherian, *Sinodelphys*, has an incisor count of I4/i4 (Luo *et al.* 2003). The incisor count of *Acristatherium* is more similar to that of *Sinodelphys* than *Eomaia*.

The upper posterior incisors of *Acristatherium* somewhat resemble those of several metatherians, such as *Sinodelphys* (Luo *et al.* 2003). The reconstructed incisor shapes of *Eomaia* (Ji *et al.* 2002) do not make

much meaningful sense and cannot be compared. The single-rooted and enlarged canines of *Acristatherium* are widely distributed among Cretaceous eutherians (*Eomaia*, *Zhelestes*, *Cimolestes*, *Maelestes* and *Ukhaatherium*) and primitive metatherians (*Deltatheridium*, *Pucadelphys* and *Mayulestes*). Small canines (either lower or both upper and lower) were found in *Bobolestes*, *Zalambdalestes*, *Barunlestes*, *Zhangolestes*, *Paranyctoides* and *Eozhelestes*. The canine morphology and size of *Acristatherium* are more similar to those of *Sinodelphys* (Luo *et al.* 2003) than *Eomaia* (Ji *et al.* 2002).

The majority of eutherians, including most Late Cretaceous groups, have four or fewer premolars, but the oldest ones such as *Acristatherium*, *Prokennalestes*, *Bobolestes* (*Otlestes*) and *Eomaia* have five in both upper and lower dentitions. Among proximate outgroups of eutherians, metatherians have only three premolars. The early Cretaceous tribosphenic *Kielantherium* has at least four lower premolars, whereas pretribosphenic *Peramus*, *Arguimus*, *Arguitherium* and *Amphitherium* have been alternatively interpreted as having either four or five premolars (Dashzavag & Kielan-Jaworowska 1984; Butler & Clemens 2001; Kielan-Jaworowska *et al.* 2004). A recent study suggested that *Arguimus* (including *Arguitherium* as its junior subjective synonym) had five premolars (Lopatin & Averianov 2006). Having five premolars has been interpreted as the primitive condition of eutherians (McKenna 1975; Clemens & Lillegraven 1986; Novacek 1986). Alternatively, some workers (Clemens 1973; Luckett 1993) proposed that the so-called P3/p3 are actually retained deciduous teeth of the second premolar loci, rather than replacement teeth as for others of the series, and that eutherians primitively have four premolars. If so, they would be somewhat more complex and erupt earlier than at least P2/p2 in primitive eutherians. The premolars of *Acristatherium* clearly show that they are well integrated into the morphological and functional gradient of the premolar series and that there is no clue to indicate any one as a deciduous tooth.

The premolars of *Acristatherium* are simple with a trenchant main cusp (plus basal cuspules in posterior premolars) and slightly increase in morphological complexity posteriorly. The ultimate premolars of eutherians are usually somewhat molariform. Among the earliest eutherians, *Prokennalestes* has P5 (with three roots) semimolariform and p5 nonmolariform, whereas both *Montanalestes* (Cifelli 1999, 2000) and *Bobolestes* (Kielan-Jaworowska *et al.* 2004) have p5 semimolariform (P5 unknown in either). Compared with these eutherians, *Acristatherium* is more primitive in having nonmolariform P5 and p5. This condition resembles that of metatherians, where a sharp morphological break exists between premolar and molar series. Nevertheless, with antero- and posterolabial cuspules connected by labial cingulum, P5 of *Acristatherium* exhibits a tendency towards a molariform. *Eomaia* was reported having nonmolariform premolars, but the premolars of *Eomaia* display a peculiar size variation in that the upper premolars decrease in size from P1 to P4, with P4 being the smallest, but P5 is significantly large (Ji *et al.* 2002). By contrast, lower premolars increase in size from p1 to p5, with p1 being the smallest. In *Eomaia*, p3 has a posterobasal cusp and both p4 and 5 have antero- and posterobasal cuspules. *Eomaia* differs from *Acristatherium* in these premolar features, but

they are similar in having the premolars evenly spaced. *Sinodelphys* (Luo *et al.* 2003) has a premolar count of P4/p4. The detailed morphology of these premolars is not clear given the preservation of the specimen. Nonetheless, the distinctive diastema between p1 and p2 in *Sinodelphys* differs from the *Acristatherium* condition.

Acristatherium differs from all known Cretaceous eutherians in some molar morphologies. For example, the width of the upper molar of *Acristatherium* is only slightly greater than its length, in contrast to the more transverse upper molars in most Cretaceous eutherians for which the upper molars are known. Upper molars of *Acristatherium* have weak or no conules while all other taxa have distinct para- and metaconules. In both features, *Acristatherium* is plesiomorphic, but these features are unknown in both *Sinodelphys* and *Eomaia*. The m1, probably m2 as well, of *Acristatherium* has a distinctive cusp e. The cusp e is either small or absent in other Cretaceous eutherians, such as *Eomaia*. *Acristatherium* further differs from several early eutherians in lacking features that are present in the following genera. *Prokennalestes* has tiny styler cuspules decorating the edge of the styler shelf in upper molars and has m1–2 talonid longer than the trigonid. *Murtoilestes* and *Bobolestes* have upper molars with paracone and metacone separated by a deep furrow and lower molars with the talonid subequal to trigonid in width. *Eozhelestes* has a prominent precingulid but lacks cusp e, and the height difference between the trigonid and the talonid is smaller than in *Acristatherium*. *Montanalestes* has lower molars with the paraconid larger than metaconid. M3 is the only preserved upper molar of *Eomaia* and differs from that of *Acristatherium* in having the paracone and metacone distinctively separated. In general shape of lower teeth, *Acristatherium* seems again more similar to *Sinodelphys* (fig. 1c in Luo *et al.* 2003) than to *Eomaia* (fig. 2 in Ji *et al.* 2002) in several aspects. The trigonid of *Eomaia* is proportionally much higher than the talonid, with the posterior wall of the trigonid being vertical in both lateral and medial views, and its talonid is longer than the trigonid.

(b) Phylogenetic placement

Morphological comparisons reveal many derived features shared by *Acristatherium* and other eutherians, implying a close relationship. On the other hand, *Acristatherium* resembles other groups of Mesozoic mammals and several Palaeocene marsupials in having some plesiomorphic craniodental features. To identify the phylogenetic relationship of *Acristatherium* with other relevant mammals, we conducted analyses using PAUP v. 4.0.b10 by plotting the new species in a recently published morphological data matrix (electronic supplementary material in Wible *et al.* 2007). This dataset includes most well-known Cretaceous eutherians and a sizeable sample of placental species. The dataset consists of a total of 70 taxa, including *Acristatherium*, and 408 characters. A total of 178 craniodental characters are applicable to *Acristatherium*, accounting for 44 per cent of the complete dataset. The 178 scored characters for *Acristatherium* are listed in the legend to figure 4.

Heuristic search settings include: parsimony as optimality criterion; all characters unordered and with equal weight; 387 characters being parsimony-informative characters; gaps treated as 'missing'; multistate taxa

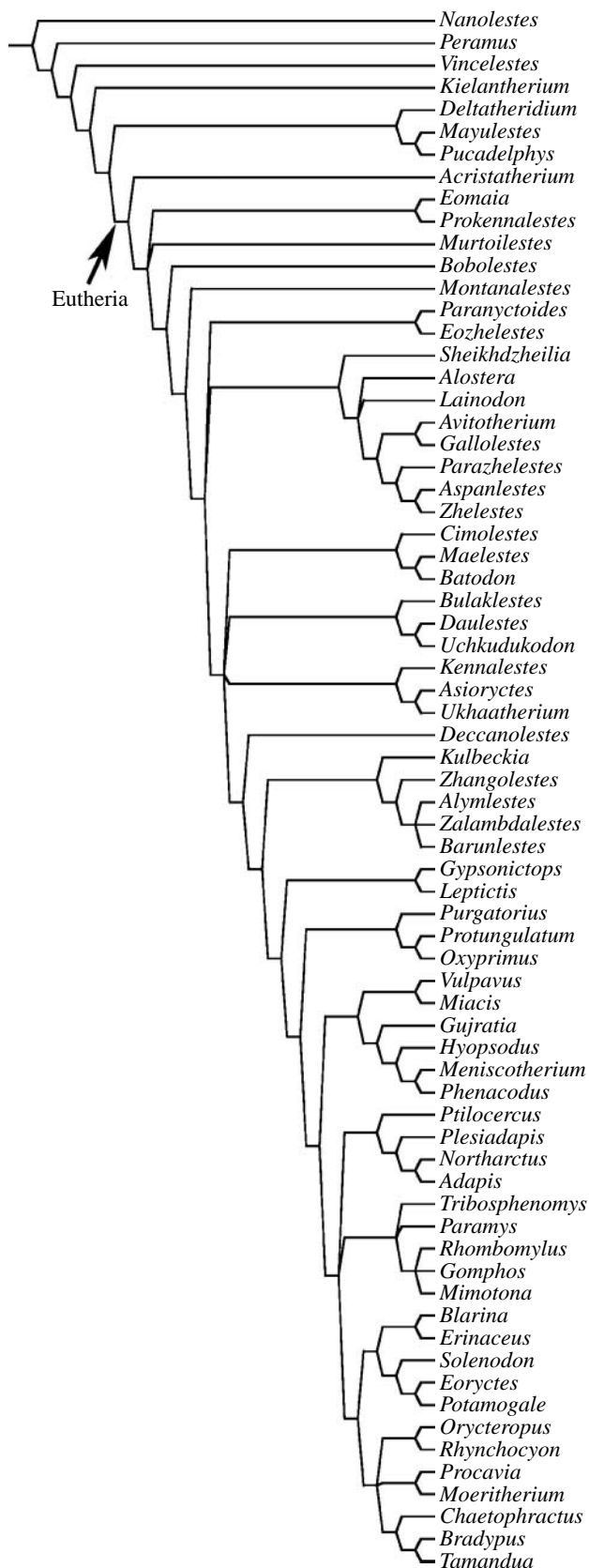


Figure 4. Phylogenetic position of *A. yanensis*. See text for discussion of the tree. All characters and states are adopted from Wible *et al.* (2007). Only those applicable to *Acristatherium*, based on the sole specimen of *A. yanensis* (IVPP V15004), are listed below. The numbers correspond to those of characters in the list of Wible *et al.* (2007) and the state scored for each character is in parentheses. Character scoring for *Acristatherium*: 1(0); 2(0); 3(0); 4(0/1); 5(0); 6(0); 7(1); 8(1); 9(0); 10(0); 11(0); 12(0); 13(0); 14(2); 15(0);

interpreted as uncertainty; random addition sequence searches in 1000 replicates; branch-swapping algorithm in tree-bisection–reconnection; topological constraints not enforced; trees are unrooted; 239 trees retained. The consensus of the retained trees is shown in figure 4. Statistics derived from consensus tree are: component information (consensus fork) = 57 (normalized = 0.851); Mickevich's consensus information = 0.298; Colless weighted consensus fork (proportion max. information) = 0.374; Rohlf's CI (1) = 0.783.

The cladogram retains the basic topology of the tree presented in the electronic supplementary material of Wible *et al.* (2007). Craniodental data place *Acristatherium* at the position between the nodes 'Theria' and 'Eutheria' as defined in Wible *et al.* (2007). Given the definition of Eutheria we accept here, *Acristatherium* is the most basal member of Eutheria represented by the selected taxa in the study.

(c) Age constraints

The Lujiatun bed yielding the specimen of *Acristatherium* was previously considered to be basal of the Yixian Formation (Wang & Zhou 2003; Zhou *et al.* 2003), but a recent study dated the bed as 123.2 ± 1.0 Ma and regarded it as being chronologically correlative to that of Jianshangou beds of the formation (He *et al.* 2006). *Eomaia* from the Dawangzhangzi beds of the Yixian Formation in Liaoning was regarded as the earliest known eutherian with an age of 125 Ma (Ji *et al.* 2002). This age, however, is based on stratigraphic correlations with Jianshangou beds of the Yixian Formation in Shihetun–Jianshangou–Huangbanjigou area, which were dated as 124.6 ± 0.1 Ma (Swisher *et al.* 1999). New dating data for the volcanic rock underlying the lacustrine silty shales containing *Eomaia* at the Dawangzhangzi locality gave an average of 126.3 ± 2.7 Ma (Ji *et al.* 2004). Although this does not help with the age of *Eomaia*, it

16(4); 17(1); 18(0); 19(0); 20(0); 21(1); 22(0); 23(0); 24(1); 25(0); 26(1); 27(0); 29(0); 31(1); 32(0); 33(0); 34(1); 35(0); 36(0); 37(0); 38(0); 39(0); 40(0); 41(0); 42(0); 43(0); 44(0); 45(0); 46(0); 47(0); 48(0); 49(1); 50(0); 51(0); 52(0); 53(0); 54(0); 55(0); 56(0); 57(0); 58(0); 59(0); 60(0); 61(1); 62(1); 63(1); 64(1); 65(1); 66(1); 67(0); 68(1); 69(1); 70(0); 71(0); 72(0); 73(0); 74(0); 75(0); 76(0); 77(1); 78(1); 79(0); 80(0); 81(0); 82(0); 83(0); 84(0); 85(0); 86(0); 87(1); 88(0); 89(0); 91(1); 92(2); 93(0); 94(0); 95(0); 96(0); 97(0); 98(0); 101(0); 103(1); 106(0); 107(0); 108(0); 109(0); 110(0); 111(1); 112(0); 113(0); 115(1); 117(0); 118(1); 119(1); 120(1); 122(1); 123(0); 124(0); 125(0); 126(0); 127(0); 131(0); 132(1); 133(0); 134(0); 135(0); 136(1); 138(0); 139(1); 148(0); 149(0); 150(1); 153(0); 159(0); 160(0); 161(0); 162(0); 163(0); 164(1); 165(1); 166(0); 167(1); 168(0); 170(0); 171(0); 173(0); 174(0); 175(1); 176(0); 177(0); 178(1); 179(1); 180(0); 181(0); 196(0); 197(1); 198(0); 199(0); 200(0); 201(0); 202(1); 203(0); 205(0); 213(1); 215(0); 216(2); 218(0); 219(0); 226(0); 227(1); 228(1); 229(0); 230(0); 232(1); 233(0/1); 251(0); 252(0); 253(0); 254(1); 256(1); 337(0); 338(1). Diagnoses for the node of Eutheria (only characters scored for *Acristatherium*): diastema posterior to first upper premolar present; three molars; preorbital length relative to postorbital more than one-third; zygomatic process of maxilla vestigial; zygomatic arch delicate; postorbital process absent; fronto-parietal suture with anterior process of parietal off the midline; glenoid process of jugal present without facet.

was considered to set the oldest limit for the age of Dawangzhangzi beds that produced the specimen of *Eomaia* (Ji *et al.* 2004). Here we regard the age of *Acristatherium* as to be equivalent to that of *Eomaia*. The ages of these two eutherians and the metatherian *Sinodelphys* probably fall in the time range from 123 to 125 Ma.

(d) Conclusion

Acristatherium yanensis from the Early Cretaceous Jehol biota is one of the earliest, if not the earliest, eutherians known to date and the most basal eutherian among the known Cretaceous eutherian mammals. Its locality and age constraint are more reliable than those of *Eomaia*. It displays a suite of unambiguous craniodental morphologies for eutherians from the Early Cretaceous Jehol biota. The dental morphology of *Acristatherium* is primitively more similar to that of *Sinodelphys* than to *Eomaia*, but the latter retains a primitive incisor count of I5/i4. The morphology of *Acristatherium* shows that the earliest eutherians share many primitive features with their metatherian sisters and that the significant differences between *Acristatherium* and *Eomaia* indicate a significant degree of generic diversification of eutherians *ca* 125 Ma.

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REFERENCES

- Averianov, A. & Archibald, J. D. 2005 Mammals from the mid-Cretaceous Khokzhakul Formation, Kyzylkum Desert, Uzbekistan. *Cretaceous Res.* **26**, 593–608. (doi:10.1016/j.cretres.2005.03.007)
- Averianov, A. O. & Skutschas, P. P. 2001 A new genus of eutherian mammal from the Early Cretaceous of Transbaikalia, Russia. *Acta Palaeontol. Pol.* **46**, 431–436.
- Bininda-Emonds, O. R. P. *et al.* 2007 The delayed rise of present-day mammals. *Nature* **449**, 507–512. (doi:10.1038/nature05634)
- Butler, P. M. & Clemens, W. A. 2001 Dental morphology of the Jurassic holotherian mammal *Amphitherium*, with a discussion of the evolution of mammalian post-canine dental formulae. *Palaeontology* **44**, 1–20. (doi:10.1111/1475-4983.00166)
- Cifelli, R. L. 1999 Tribosphenic mammal from the North American Early Cretaceous. *Nature* **401**, 363–366. (doi:10.1038/43860)
- Cifelli, R. L. 2000 Counting premolars in early eutherian mammals. *Acta Palaeontol. Pol.* **45**, 195–198.
- Clemens Jr, W. A. 1973 Fossil mammals of the type Lance Formation Wyoming—Part III. Eutheria and summary. *Univ. Calif. Publ. Geol. Sci.* **94**, 1–102.
- Clemens, W. A. & Lillegraven, J. A. 1986 New Late Cretaceous, North American advanced therian mammals that fit neither the marsupial nor eutherian molds. *Contrib. Geol. Univ. Wyo. Special Paper* **3**, 55–85.
- Dashzeveg, D. & Kielan-Jaworowska, Z. 1984 The lower jaw of an aegialodontid mammal from the Early Cretaceous of Mongolia. *Zool. J. Linn. Soc.* **82**, 217–227. (doi:10.1111/j.1096-3642.1984.tb00544.x)
- He, H.-Y., Wang, Z.-H., Zhou, Z.-H., Jin, F., Wang, F., Yang, L.-K., Ding, X., Boven, A. & Zhu, R.-X. 2006 $^{40}\text{Ar}/^{39}\text{Ar}$ dating of Lujiatun bed (Jehol Group) in Liaoning, northeastern China. *Geophys. Res. Lett.* **33**, L04303. (doi:10.1029/2005GL025274)
- Hillenius, W. J. 2000 The septomaxilla of nonmammalian synapsids: soft-tissue correlates and a new functional interpretation. *J. Morphol.* **245**, 29–50. (doi:10.1002/1097-4687(200007)245:1<29::AID-JMOR3>3.0.CO;2-B)
- Jenkins Jr, F. A. & Schaff, C. R. 1988 The Early Cretaceous mammal *Gobiconodon* (Mammalian, Triconodonta) from the Cloverly Formation in Montana. *J. Vertebrate Paleontol.* **6**, 1–24.
- Ji, Q., Luo, Z.-X., Yuan, C.-X., Wible, J. R., Zhang, J.-P. & Georgi, J. A. 2002 The earliest eutherian mammal. *Nature* **416**, 816–822. (doi:10.1038/416816a)
- Ji, Q. *et al.* 2004 *A synthetic study on the Mesozoic Jehol biota and related stratigraphy in western Liaoning*. Beijing, China: Geological Press. [In Chinese]
- Kermack, K. A., Mussett, F. & Rigney, H. W. 1981 The skull of *Morganucodon*. *Zool. J. Linn. Soc.* **71**, 1–158. (doi:10.1111/j.1096-3642.1981.tb01127.x)
- Kielan-Jaworowska, Z. 1981 Evolution of the therian mammals in the Late Cretaceous of Asia. Part IV. Skull structure in Kennalestes and Asioryctes. *Palaeontol. Pol.* **42**, 25–78.
- Kielan-Jaworowska, Z. 1984 Evolution of the therian mammals in the Late Cretaceous of Asia. Part V. Skull structure in Zalambdalestidae. *Palaeontol. Pol.* **46**, 107–117.
- Kielan-Jaworowska, Z. & Dashzeveg, D. 1989 Eutherian mammals from the Early Cretaceous of Mongolia. *Zool. Scr.* **18**, 347–355. (doi:10.1111/j.1463-6409.1989.tb00460.x)
- Kielan-Jaworowska, Z., Cifelli, R. L. & Luo, Z.-X. 2004 *Mammals from the age of dinosaurs: origins, evolution, and structure*. New York, NY: Columbia University Press.
- Lillegraven, J. A. & Krusat, G. 1991 Cranio-mandibular anatomy of *Haldanodon exspectatus* (Docodontia; Mammalia) from the Late Jurassic of Portugal and its implications to the evolution of mammalian characters. *Contrib. Geol. Univ. Wyo.* **28**, 39–138.
- Lopatin, A. V. & Averianov, A. O. 2006 An aegialodontid upper molar and the evolution of mammal dentition. *Science* **313**, 1092. (doi:10.1126/science.1128530)
- Lockett, W. P. 1993 An ontogenetic assessment of dental homologies in therian mammals. In *Mammal phylogeny: Mesozoic differentiation, multituberculates, monotremes, early Therians, and marsupials* (eds F. S. Szalay, M. J. Novacek & M. C. McKenna), pp. 182–205. New York, NY: Springer.
- Luo, Z.-X., Ji, Q., Wible, J. R. & Yuan, C.-X. 2003 A new tribosphenic mammal with implications for early metatherian evolution. *Science* **302**, 1934–1940. (doi:10.1126/science.1090718)
- Maddison, W. P. & Maddison, D. R. 2005a *MESQUITE: a modular system for evolutionary analysis*, v. 1.06. See <http://mesquiteproject.org>.
- Maddison, W. P. & Maddison, D. R. 2005b *MACCLADE: analysis of phylogeny and character evolution*, v. 4.08. Sunderland, MA: Sinauer Associates.
- Marshall, L. G. & Muizon, C. de 1995 Part II: the skull. In *Pucadelphs andinus (Marsupialia, Mammalia) from the Early Paleocene of Bolivia* (ed C. Muizon). *Mémoires du Muséum national d'Histoire naturelle* **165**, 1–164.

- McKenna, M. C. 1975 Toward a phylogenetic classification of the Mammalia. In *Phylogeny of the primates* (eds W. P. Luckett & F. S. Szalay), pp. 21–46. New York, NY: Plenum Publishing Corporation.
- McKenna, M. C. & Bell, S. K. 1997 *Classification of mammals above the species level*. New York, NY: Columbia University Press.
- McKenna, M. C., Kielan-Jaworowska, Z. & Meng, J. 2000 Earliest eutherian mammal skull, from the late Cretaceous (Coniacian) of Uzbekistan. *Acta Palaeontol. Pol.* **45**, 1–54.
- Muizon, C. de 1998 *Mayulestes ferox*, a borhyaenoid (Metatheria, Mammalia) from the early Paleocene of Bolivia. Phylogenetic and palaeobiologic implications. *Geodiversitas* **20**, 19–142.
- Nessov, L. A. 1993 New Mesozoic mammals of middle Asia and Kazakhstan, and comments about evolution of theriofaunas of Cretaceous coastal plains of ancient Asia. *Trudy Zoologicheskogo Instituta RAN* **249**, 105–133. [In Russian]
- Nessov, L. A., Sigogneau-Russell, D. & Russell, D. E. 1994 A survey of Cretaceous tribosphenic mammals from middle Asia (Uzbekistan, Kazakhstan and Tajikistan), of their geological settings, age and faunal environment. *Palaeovertebrata* **23**, 51–92.
- Novacek, M. J. 1986 The skull of leptictid insectivorans and the higher-level classification of eutherian mammals. *Bull. Am. Mus. Nat. Hist.* **183**, 1–112.
- Patterson, B. & Olson, E. C. 1961 A triconodontid mammal from the Triassic of Yunnan. In *International colloquium in the evolution of lower and non-specialized mammals* (ed. G. Vandebroek), pp. 129–191. Brussels, Belgium: Koninklijke Vlaamse Academie voor Wetenschappen, Letteren en Schone Kunsten van België.
- Rougier, G. W. 1993 *Vincelestes neuquenianus* Bonaparte (Mammalia, Theria) un primitivo mamífero del Cretácico Inferior de la Cuenca Neuquina. Dissertation, University of Buenos Aires, p. 720.
- Rougier, G. W., Wible, J. R. & Novacek, M. J. 1998 Implications of *Deltatheridium* specimens for early marsupial history. *Nature* **396**, 459–463. (doi:10.1038/24856)
- Sigogneau-Russell, D., Dashzeveg, D. & Russell, D. E. 1992 Further data on *Prokennalestes* (Mammalia, Eutheria *inc. sed.*) from the Early Cretaceous of Mongolia. *Zool. Scr.* **21**, 205–209. (doi:10.1111/j.1463-6409.1992.tb00322.x)
- Swisher, C. C., Wang, Y.-Q., Xu, X. & Wang, Y. 1999 Cretaceous age for the feathered dinosaurs of Liaoning, China. *Nature* **400**, 58–61.
- Swofford, D. L. 2002 *Phylogenetic analysis using parsimony (* and other methods)*, v. 4.0.b10. Sunderland, MA: Sinauer.
- Szalay, F. S. & Trofimov, B. A. 1996 The Mongolian Late Cretaceous *Asiatherium*, and the early phylogeny and paleobiogeography of Metatheria. *J. Vertebrate Paleontol.* **16**, 474–509.
- Wang, X.-L. & Zhou, Z.-H. 2003 A new pterosaur (Pterodactyloidea, Tapejaridae) from the Early Cretaceous Jiufotang Formation of western Liaoning, China and its implications for biostratigraphy. *Chinese Sci. Bull.* **48**, 16–23. (doi:10.1360/03tb9003)
- Wible, J. R., Miao, D. & Hopson, J. A. 1990 The septomaxilla of fossil and recent synapsids and the problem of the septomaxilla of monotremes and armadillos. *Zool. J. Linn. Soc.* **98**, 203–228. (doi:10.1111/j.1096-3642.1990.tb01207.x)
- Wible, J. R., Rougier, G. W., Novacek, M. J. & McKenna, M. C. 2001 Earliest eutherian ear region: a petrosal of *Prokennalestes* from the Early Cretaceous of Mongolia. *Am. Mus. Novit.* **3322**, 1–44. (doi:10.1206/0003-0082(2001)322<0001:EEERAP>2.0.CO;2)
- Wible, J. R., Novacek, M. J. & Rougier, G. W. 2004 New data on the skull and dentition in the Mongolian Late Cretaceous eutherian mammal *Zalambdalestes*. *Bull. Am. Mus. Nat. Hist.* **281**, 1–144. (doi:10.1206/0003-0090(2004)281<0001:NDOTSA>2.0.CO;2)
- Wible, J. R., Rougier, G. W., Novacek, M. J. & Asher, R. J. 2007 Cretaceous eutherians and Laurasian origin for placental mammals M.J. near the K/T boundary. *Nature* **447**, 1003–1006. (doi:10.1038/nature05854)
- Zhou, Z. H., Barrett, P. M. & Hilton, J. 2003 An exceptionally preserved Lower Cretaceous ecosystem. *Nature* **421**, 807–814. (doi:10.1038/nature01420)