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A new mammal skull from the Lower Cretaceous of China with implications for the evolution of obtuse-angled molars and ‘amphilestid’ eutriconodonts

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We report the discovery of *Fuchilestes liaoningensis*, a new genus and species of eutriconodont mammal from the Lujiatun Site of the Lower Cretaceous Yixian Formation (123.2 ± 1.0 Ma; Lower Aptian). The holotype preserves a partial skull and full dentition. Among eutriconodonts, its lower dentition is similar to taxa formerly assigned to the paraphyletic group of ‘amphilestids’. Some have considered ‘amphilestid’ molars to represent the structural intermediate between the lower molars of the ‘triconodont’ pattern of cusps in alignment and the fully triangulate and more derived therian molars. However, ‘amphilestid’ taxa were previously represented only by the lower dentition. Our study reveals, for the first time, the upper dentition and skull structure of an ‘amphilestid’, and shows that at least some eutriconodonts have an obtuse-angled cusp pattern on molars in middle positions of the long molar series. Its petrosal is similar to those of other eutriconodonts and spalacotheroid ‘symmetrodonts’. Our phylogenetic analyses suggest that (i) *Fuchilestes* is most closely related to the Early Cretaceous *Hakusanodon* from Japan, in the same Eastern Asiatic geographic region; (ii) ‘amphilestids’ are not monophyletic; and (iii) eutriconodonts might not be a monophyletic group, although this hypothesis must be further tested.

Keywords: Mammalia; ‘amphilestid’ eutriconodonts; *Fuchilestes liaoningensis*; obtuse-angled molar pattern; Lower Cretaceous; China

1. INTRODUCTION

In the last twenty years, the study of early mammalian evolution has undergone a renaissance thanks to discoveries of remarkably complete fossils and the use of high-resolution imaging technology to interpret these fossils (e.g. Jenkins & Schaff 1988; Ji *et al.* 1999; Meng *et al.* 2006; Luo *et al.* 2007a,b). The new cranial and postcranial data have broadened our anatomic, taxonomic and palaeoecological views of Mesozoic mammals and led to major revisions of traditional hypotheses on phylogenetic relationships and morphological transformations, which previously hinged on fragmentary jaws and isolated teeth (e.g. Kielan-Jaworowska *et al.* 2004; Luo 2007).

A persisting problem concerns ‘amphilestid’-like eutriconodont mammals, a group that was previously regarded by some to be crucial to Mesozoic mammal dental

evolution. ‘Triconodont’ mammals possess a molar pattern of three main cusps in a mesiodistal line on a laterally compressed crown, a primitive arrangement also found in some non-mammalian cynodonts (Hopson 1994; Kemp 2005). Before the 1940s, ‘triconodont’ mammals were known from only the Middle to Late Jurassic (e.g. Simpson 1928, 1929). Since then, mammaliaforms with ‘triconodont’-like teeth have been discovered in the Late Triassic, Early Jurassic and Cretaceous (e.g. Parrington 1941; Jenkins & Crompton 1979). With these discoveries, it has become clear that mammaliaforms with ‘triconodont’-like teeth do not belong within a monophyletic unit (Kermack *et al.* 1973). The Late Triassic–Early Jurassic taxa were thus grouped in a new suborder of basal mammals (or mammaliaforms), the Morganucodonta, and the more advanced ‘triconodonts’ from the Middle Jurassic–Late Cretaceous, most of which are members of the classic group of Triconodonta (e.g. Simpson 1928, 1929), were resurrected as the Eutriconodonta and nested within crown Mammalia.

Among eutriconodonts, the amphilestids and triconodontids are the two main groups represented in the historical literature (Simpson 1928; Jenkins & Crompton 1979). They have mainly been distinguished by

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postcanine characteristics. The Amphilestidae have molars with one dominant central cusp, and two smaller subequal cusps on either side; molars that occlude at the embrasure of opposing molars; lower molars that lack a tongue-in-groove interlock; and premolars that tend to be symmetrical (Simpson 1928; Ji *et al.* 1999). They are known from the Middle Jurassic of Europe, the Late Jurassic of Asia, Africa and North America, the Early Cretaceous of Asia, and possibly the Early–Middle Jurassic of India and Middle Jurassic of South America (Kielan-Jaworowska *et al.* 2004; Averianov *et al.* 2005; Rougier *et al.* 2007*a,b*). In contrast, the Triconodontidae, from the Early Cretaceous of Europe and the Late Jurassic–Late Cretaceous of North America, have molars with three main cusps of subequal height. Two other families, the Gobiconodontidae and Jeholodontidae, have molars that are generally similar to amphilestids but are more robust in overall form. Gobiconodontids are known from the Early Cretaceous of Europe, Asia and North America (Kielan-Jaworowska *et al.* 2004), and jeholodontids are only known from the Early Cretaceous of Asia (Ji *et al.* 1999; Luo *et al.* 2007*a*).

Phylogenetic analyses that include eutriconodonts tend to show only weak support for the group and a labile position among Mesozoic mammals (Ji *et al.* 1999; Luo *et al.* 2002; Meng *et al.* 2003). As a result, the composition and arrangement of the Eutriconodonta have largely been considered provisional. In particular, the monophyly of the triconodontid and gobiconodontid families has been strongly supported, but taxa formerly assigned to the Amphilestidae have been scattered in different and even conflicting phylogenetic positions in recent analyses (Ji *et al.* 1999; Luo *et al.* 2002; Meng *et al.* 2006; Rougier *et al.* 2007*b*). Thus, the Amphilestidae, hereafter placed in quotation marks, is not considered a natural grouping and is probably a major source of the phylogenetic confusion. On the one hand ‘amphilestids’ have been proposed as a paraphyletic structural grade of basal eutriconodonts, and on the other hand as a composite group consisting of basal eutriconodonts and other taxa that are more closely related to more advanced mammals (e.g. spalacotheroid ‘symmetrodonts’) than to other eutriconodonts (Mills 1971; Rougier *et al.* 2007*b*).

A major gap in our knowledge of ‘amphilestids’ is that taxa formerly assigned to the group were known only by lower teeth, although *Paikasigudodon*, based on upper molariforms from the Early–Middle Jurassic of India, may be an ‘amphilestid’ (Prasad & Manhas 2002; Kielan-Jaworowska *et al.* 2004); the upper dentition and skull of ‘amphilestids’ are otherwise unknown. Here, we (i) describe, from the Lower Cretaceous Yixian Formation of northeastern China, a new eutriconodont skull that possesses ‘amphilestid’-like lower postcanines and, importantly, offers information on the upper dentition and parts of the skull; (ii) present two phylogenetic analyses, one emphasizing a more thorough sampling of nearly all eutriconodonts by their mandibular and dental characters, and the other placing a few eutriconodonts among the broader mammaliaform phylogeny with a broader sampling of anatomical data outside jaws and teeth; and (iii) discuss the morphological and palaeobiogeographical implications of this new ‘amphilestid’-like mammal.

2. MATERIAL AND METHODS

The holotype specimen, D2607, was scanned on the OMNI-X Universal HD600 Scanner at the Center of Quantitative Imaging (CQI), Energy Institute, Pennsylvania State University, in State College, Pennsylvania, USA. Images have a 1024-pixel resolution of $0.04 \times 0.04 \times 0.046 \text{ mm}^3$. Stacks of digital images were used to produce virtual renderings of the skull and dental morphology (figures 1 and 2), by the manual segmentation function of the AMIRA 4.1 software. Linear measurements were taken directly with IMAGEJ 1.41o[®] software. Phylogenetic analyses were performed with PAUP* 4.0b10 software.

3. SYSTEMATIC PALAEOLOGY

Mammalia Linnaeus 1758

Order indeterminate

Family indeterminate

Fuchilestes liaoningensis gen. et sp. nov.

(a) Etymology

Fu chi from the Chinese for sawtooth, in reference to the ‘triconodont’ postcanine pattern; *lestes* from the Greek word for robber, a common suffix for mammalian fossil taxa; *liaoning* in reference to the province in China where the specimen was discovered.

(b) Holotype

D2607 (Dalian Museum of Natural History, Dalian, Liaoning Province, China) is a crushed and somewhat distorted, three-dimensionally preserved skull with mandibles and cranium in articulation and associated hyoid elements affixed to a siltstone slab, ventral side up (figures 1 and 2). A few teeth, particularly from the left side of the skull, are missing or heavily damaged, as are aspects of the cranial roof and rostrum. The computed tomography (CT) scans detected no trace of unerupted teeth or replacement dental lamina in either the upper or lower jaws. By a number of morphological features indicative of ontogenetic growth, we interpret that D2607 represents a fully grown adult.

(c) Locality and horizon

The specimen was recovered in 2004 from the Lujiatun Site of the Yixian Formation Beipiao, western Liaoning Province, China. The Lujiatun Site is considered lower Aptian in age (Gradstein *et al.* 2004) and contains a tuff with a weighted-mean $^{40}\text{Ar}/^{39}\text{Ar}$ age of $123.2 \pm 1.0 \text{ Ma}$ (He *et al.* 2006).

(d) Diagnosis

Dentition I4, C1, P3, M5; i4, c1, p3, m6. Among all known eutriconodonts, *Fuchilestes liaoningensis* is most similar to *Hakusanodon archaeus* from the Early Cretaceous of Japan (Rougier *et al.* 2007*b*) in having only three premolariforms, a conspicuous gradient of size decrease in the more posterior molars and almost identical profiles of molar cusps in lingual and buccal views. *Fuchilestes* and *Hakusanodon* differ in that the ultimate premolar cusp b is taller than cusp c in the former, but c is taller than b in the latter; the main cusp a of the ultimate premolar is vertical in the former, but reclined posteriorly in the latter. The m2–4 of *Fuchilestes* has a more pronounced (albeit still low and obtuse)

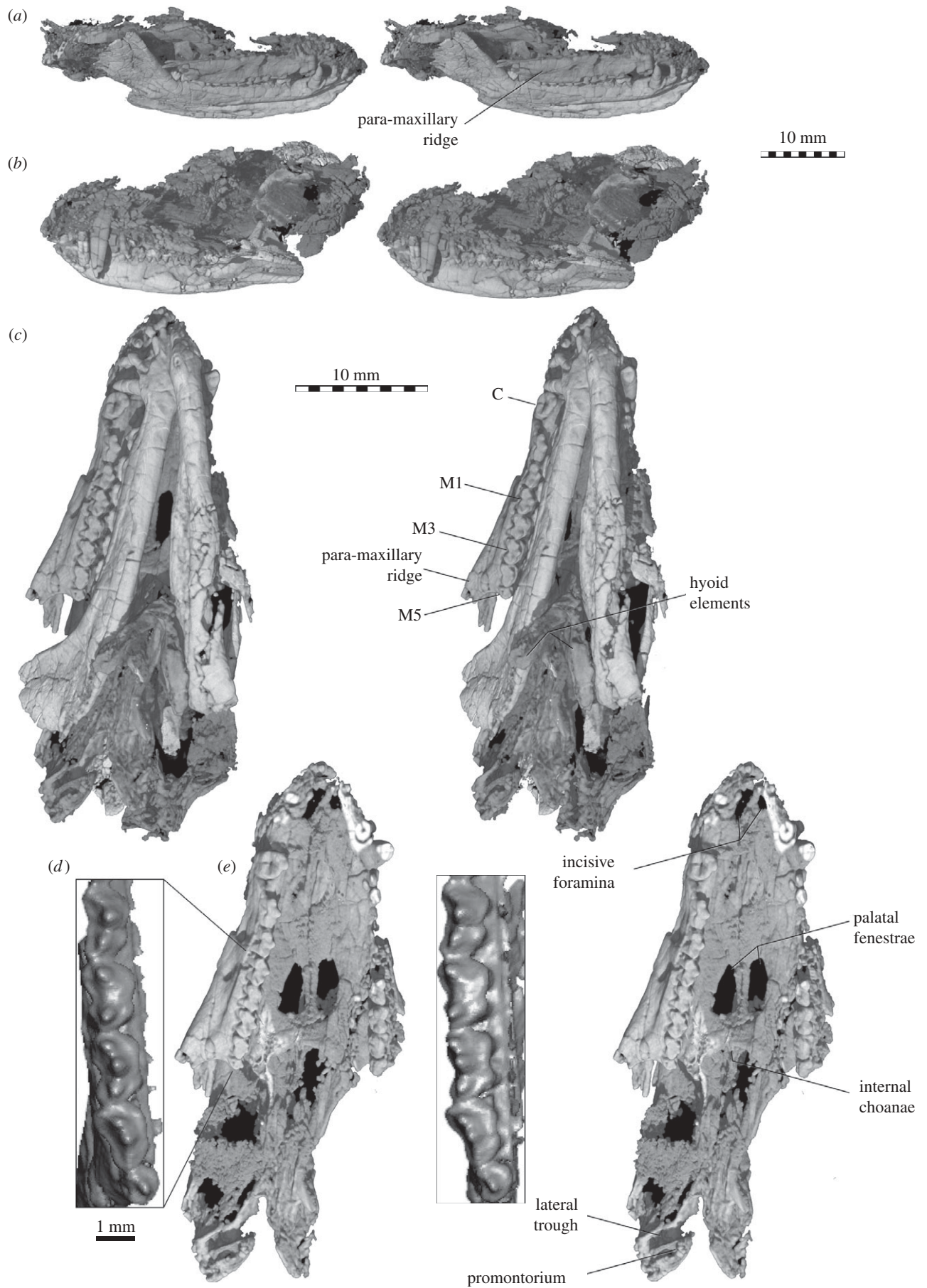


Figure 1. *Juchilestes liaoningensis* gen. et sp. nov. computed tomography (CT) stereo-images of the holotype (D2607) skull in (a) right lateral, (b) left lateral, (c) ventral and (e) ventral (without dentaries and hyoids) views; (d) right M1–5 of the same in high-magnification occlusal view. Scale bar for (a,b), 10 mm. Scale bar for (c,e), 10 mm. Scale bar for (d), 1 mm.

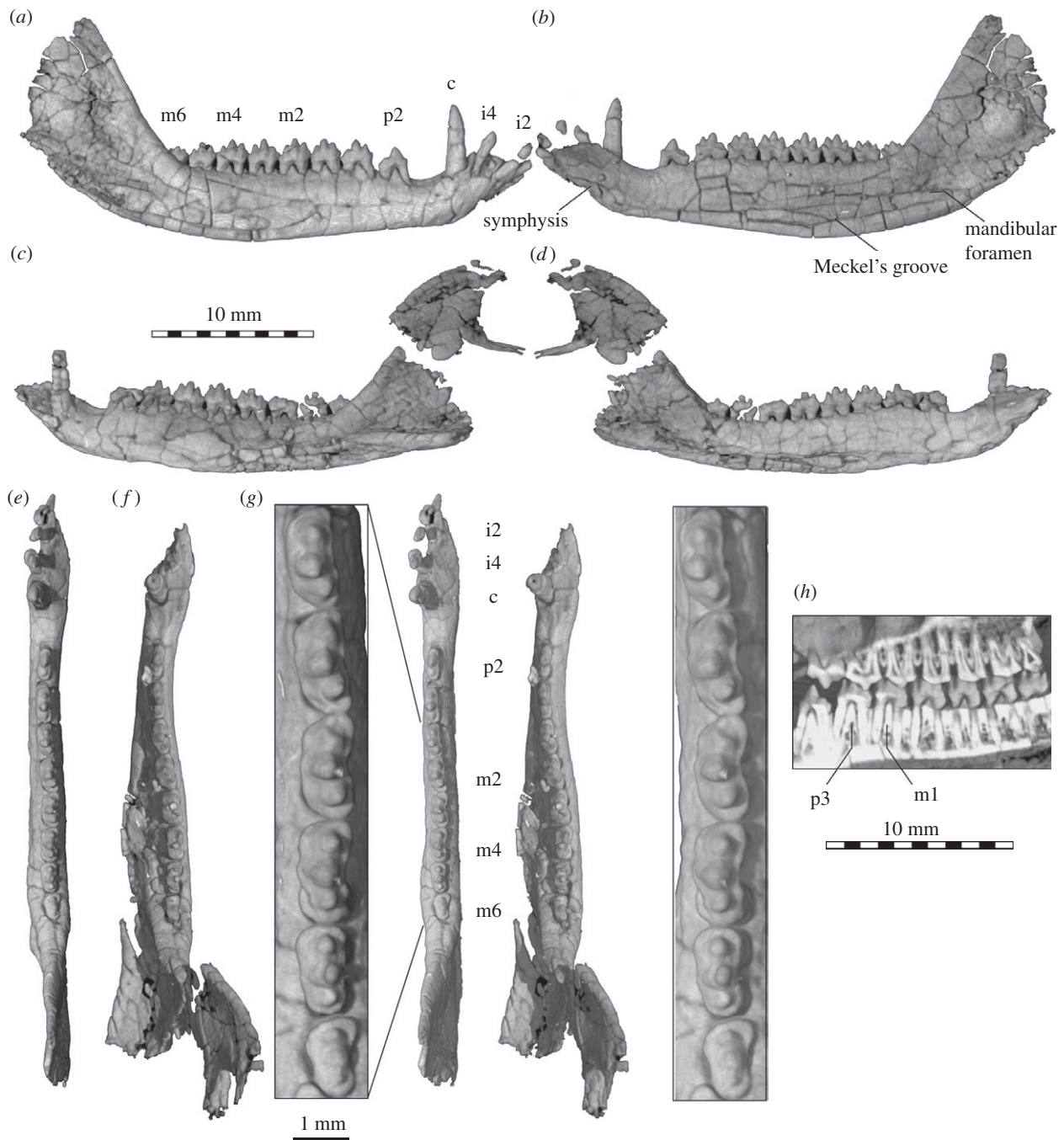


Figure 2. *Fuchilestes liaoningensis* gen et sp. nov. CT images of the right lower jaw of the holotype (D2607) in (a) lateral, (b) medial and (e) dorsal (stereopairs) views; left lower jaw of the same in (c) lateral, (d) medial and (f) dorsal (stereopairs) views; right m1–6 of the same in (g) high-magnification occlusal view. Sagittal slice through the right upper and lower jaws (h) reveals the postcanine root structure. Scale bars for (a–d) and (e, f, h), 10 mm. Scale bar for (g), 1 mm.

triangulation of cusps than in *Hakusanodon*. Each of the postcanines is 16 to 20 per cent smaller in *Hakusanodon* than in *Fuchilestes*. Autapomorphies of *Fuchilestes* include columnar and high crowned canines, a raised and arcuate alveolar margin of the lower incisors, lanceolate posterior incisors and a distinctive para-maxillary crest (for *M. buccinator*) on the facial part of the maxilla parallel to the alveolar margin of the upper postcanines. *Fuchilestes* differs from triconodontids and jeholodentids in that the upper posterior molars are not implanted on the zygomatic root of the maxilla, and in the embrasure occlusion of the upper and lower molars. *Fuchilestes* differs from tinodontids with obtuse-angled molars in having a

single-rooted, columnar and erect lower canine, instead of a two-rooted canine with a lower and conical profile of the latter.

4. DESCRIPTIONS AND COMPARISONS

The mandibles, basicranium and right maxilla, exposed on the surface of the specimen slab, are in good condition; the remainder of the cranium is largely crushed, but some anatomical details are discernible. Here, we provide a detailed description of the mandibles, maxillae and dentition, and a preliminary description of other

cranial elements. A more complete description of the latter will be published separately.

(a) *Cranium*

The cranium suffered *post-mortem* compression laterally and minor sideways distortion (figure 1*a,b*). The rostrum is short, about 25 per cent of the 41 mm total skull length. The premaxillae, nasals and septomaxillae on the dorsal and lateral surfaces of the anterior rostrum are indistinguishable as a multitude of tiny fragments. The fractured right maxilla preserves the entire alveolar margin, much of the facial portion and the orbital floor. Two large anterior infraorbital foramina are present at the level of the P3 and M2, respectively (figure 1*a*). The posterior infraorbital foramen appears to be positioned between the maxilla and the palatine in the orbit. Just above the alveolar margin of the maxilla, a prominent para-maxillary crest is present. This autapomorphic feature is interpreted as the site of attachment for the buccinator muscle and extends from the level of the M1 posterior to the anterior root of the zygoma. A slight longitudinal concavity is seen above this crest along the length of the maxilla. The anterior margin of the orbit is level with the M2. The zygomatic root of the maxilla contacts the anterior end of the jugal. The ventral border of this contact includes a prominent boss, which is also seen in the skulls of large gobiconodontids (e.g. *Repenomamus*; Meng *et al.* 2003). The right jugal is associated, probably *in situ*, with the zygomatic root of the maxilla, and continues posterodorsally as a thin, plate-like bone. In its intact position, the posterior part of the left jugal would have been dorsally overlapped by the squamosal zygoma. On the left side of the cranium, the zygomatic part of the squamosal shows the ventrally directed glenoid fossa with a constricted neck between the glenoid and the cranial moiety of the squamosal. The glenoid fossa is in articulation with a mediolaterally compressed dentary condyle. The two oval palatal fenestrae extend the length from P3 to M2 (figure 1*e*); this contrasts with the single merged vacuity of the triconodontid *Priacodon* (Simpson 1929). The posterior section of the maxilla–palatine suture is parallel to M2–M5, and then curves medially to end in the large palatal fenestra. The ventral margin of the internal choana recedes anteriorly so that the secondary bony palate margin is concave; its anterior-most point is level with M4, and its lateral parts extend laterally to the level of the M5. The palatal subtemporal margin between the internal choana and M5 is straight and obliquely oriented, and different from the much broader and deeper invaginations of the palatal margins lateral to the internal choanae of *Priacodon*. The condition of the subtemporal margin in *Juchilestes* is plesiomorphic, as it is also present in many mammaliaforms (Kermack *et al.* 1981; Crompton & Luo 1993). *Priacodon* is more derived, as are other ‘non-amphilestid’ triconodontids by extrapolation. The maxillary part of the bony palate lacks the occlusal pits for the tips of the lower molars that are seen in gobiconodontids.

(b) *Petrosal*

By both the virtual three-dimensional rendering of the petrosal (figure 1*e*) and the CT scan slices (not shown), the pars cochlearis can be seen to contain a straight and

tubular cochlear canal that extends 80 per cent of the length of the promontorium. The interior space of the cochlear canal has no primary or secondary bony laminae. The internal acoustic foramen has a simple opening for the cochlear nerve, without a bony cribriform floor. Although the right promontorium has a breached surface, there is no doubt that it has a cylindrical and finger-like form. The broad lateral trough has a vertical medial wall formed by the promontorium, and a vertical lateral ridge. The floor of the lateral trough is completed anteriorly, to the pole of the promontorium. This suggests that the ventral floor for the cavum epiptericum (for the trigeminal nerve ganglion) would be very small or non-existent, as in triconodontids (e.g. Crompton & Luo 1993; Rougier *et al.* 1996). Within the floor of the lateral trough, the prootic canal opening is present, but the opening for the hiatus fallopi is not clearly discernible and is probably obscured by the minor fractures. We interpret that the channel for the superior ramus of the stapedia artery is incompletely preserved and represented by a notch. On the medial side, the foramen cochleare is present, but its relationship to the perilymphatic channel (or foramen) is not clear. The anterior lamina of the petrosal is partially preserved and forms a part of the lateral wall of the braincase. There are two foraminae for the mandibular branch of the trigeminal nerve. At least one of these is completely encircled by the anterior lamina.

(c) *Mandible*

The dentary is robust. In lateral view (figure 2*a,c*), the ventral margin of the body is gently and uniformly convex, and has its maximum depth below m3–4. Anterior to the canine, the incisor alveolar margin of the symphyseal region of the dentary rises precipitously from the postcanine diastema (approx. 30° from horizontal). On the medial side (figure 2*b,d*), the symphyseal part of the mandible has a roughened surface that extends posteriorly to the level of the lower canine. More posteriorly, on the medial surface, a broad groove that housed Meckel’s cartilage is evident just above the ventral margin of the body. It extends, in parallel to the ventral margin of the mandible, from the level of the mesial root of p3 to the pterygoid fossa. The posterior foramen of the mandibular canal is at the anterior margin of the poorly defined pterygoid fossa just dorsal to the Meckelian groove. Laterally, the body of the dentary preserves at least four mental foraminae: two small foraminae below the canine, one below the p2 and one below the p3 (figure 2*a,c*). The masseteric fossa is well excavated. Its anteroventral margin gently grades into the body of the dentary, without a distinctive boundary. The masseteric fossa does not extend anteriorly and below the tooth row. More dorsally, the anterior margin of the masseteric fossa is a thin, distinctive and vertical ridge along the anterior margin of the coronoid process. The ventral margin of the masseteric fossa also has a distinct ridge that flares laterally. On the left dentary, it appears that the posteroventral margin gently curves dorsally towards a mediolaterally compressed condyle, which lies in articulation with the glenoid fossa of the squamosal. Despite the fracture of the mandible, it appears that the dentary condyle is raised above the imaginary line of the alveoli. The coronoid process is tall with a pointed and

recumbent dorsal angle. The anterior margin of the coronoid process forms an angle of approximately 123° with the tooth row at its junction with the body of mandible. Its posterior margin is concave, continuing ventrally as the supracondylar notch.

(d) *Dentition*

The dental formula of *Juchilestes* is 4.1.3.5/4.1.3.6. Dental measurements are presented in table S1 in the electronic supplementary material. Because D2607 is probably a fully grown adult (or nearly so), the CT scans detected no trace of unerupted teeth or replacement dental lamina in either the upper or lower jaws on both sides of the skull. Without ontogenetic replacement under the premolar(s) (Butler & Clemens 2001), a boundary between premolars and molars is determined by the contact between upper and lower postcanines, related wear patterns and root structure (see the electronic supplementary material).

Both right and left lower dentitions show four incisor loci, all incisor alveoli elevated above that of the canine (figure 2*a,b*). Three of four right lower incisors are preserved. All are slightly procumbent; the first two are small and pliculate; the third, represented by an alveolus, was probably similar in size; and the fourth is tall and lanceolate. The single-rooted canine has a tall, robust, vertically projecting and columnar crown. This morphology of the anterior dentition is seen in the 'amphilestid' *Phascolotherium*, but differs from the enlarged incisors and the reduced and procumbent canines of gobiconodontids (Kielan-Jaworowska *et al.* 2004). The lower canine is large but conical in the Triconodontidae (Simpson 1929; Kielan-Jaworowska *et al.* 2004) and conical, procumbent and small in the Jeholodontidae (Ji *et al.* 1999; Luo *et al.* 2007*a*).

The canine is separated from the postcanine dentition by a shallow, concave diastema (figure 2). CT data reveal that the diastema was produced by 'plugging' of alveoli of two roots of a single premolar (or two single-rooted premolars) via bone ingrowth. This condition has also been found in the 'amphilestids' *Hakusanodon* and *Phascolotherium* (Rougier *et al.* 2007*b*), as well as basal mammaliaforms (e.g. *Sinoconodon*; Crompton & Luo 1993).

Simpson (1928, 1929) recognized that the Triconodontinae (*sensu stricto*) have a more asymmetrical primary cusp a on premolars, in contrast to his Amphilestinae (*sensu stricto*), which have a more symmetrical primary cusp a on premolars. In addition, molars of 'amphilestids' are more symmetrical, with a taller primary cusp a than cusps b and c, in contrast to those of triconodontids with all three main cusps nearly equal in height. Molars of the 'amphilestid' pattern have embrasure occlusion in which the upper primary cusp A occludes between the two adjacent lower molars (Ji *et al.* 1999), whereas in the triconodontid pattern, the upper primary cusp A occludes between lower cusps b and a (Crompton 1974).

These 'amphilestid'-like features are plesiomorphic because they are also shared by the mammaliaform *Kuehneotherium* and the tinodontid 'symmetrodonts'. Nonetheless, the postcanines of *Juchilestes* exhibit many 'amphilestid'-like characters. The p2, supported by two

cylindrical and slightly splayed roots (figure 2*h*), is situated on a gentle incline posterior to the diastema and lower than p3 and the molariforms. Its crown is laterally compressed and dominated by a main cusp (cusp a) that is slightly mesial to the midpoint of the crown (figure 2*e,f*). Cusps b and c are small and indistinct. Buccal and lingual cingulids are absent. The p3 is emplaced above p2 (on the same alveolar level as the molariforms) and separated from p2 by a small gap (figure 2*a*). The p3 is taller, longer and wider than p2; cusp b is distinctive from cusp a; cusp c is small and little more than an undulation on the distal ridge of cusp a; p3 possesses a faint, discontinuous lingual cingulid with incipient mesial and distal cusps e and d. *Juchilestes* is similar to *Hakusanodon* in having only three premolariforms, but *Hakusanodon* differs in that its ultimate premolariform cusp a is taller and posteriorly recumbent, and its cusp c is larger than cusp b.

The m1 differs from the preceding premolariform (p3) in its larger size (see table S1 in the electronic supplementary material), in that both roots are vertical (not splayed; figure 2*h*), and cusps b and c have distinct distal and mesial ridges, respectively (figure 2*a,g*). Of the main cusps of m1, cusp a is the tallest, followed by cusp b and then a slightly shorter cusp c. Cusps b and c are almost equally distant (therefore symmetrical) to cusp a, an arrangement previously considered a key 'amphilestid'-like feature (e.g. Simpson 1929; Jenkins & Crompton 1979). The height ratio of cusps b and c is otherwise only found in molariforms of *Hakusanodon* (Rougier *et al.* 2007*b*), the Late Jurassic *Comodon* from North America, and an unnamed 'amphilestid' from the Early Cretaceous of western Siberia (Averianov *et al.* 2005). In most eutriconodonts, cusps b and c are subequal in height. These cusps are also in a slightly lingual position relative to cusp a. This arrangement is accentuated by the buccally bulging base of cusp a. The buccal face of the crown thus appears convex, whereas the lingual face is vertical or slightly concave (figure 2*e-g*). An undulating cingulid extends along the lingual base of the crown terminating mesially with a small cusp e and distally with a small cusp d. There is no mesiobuccal cusp f. This distinguishes *Juchilestes* from the mammaliaform *Kuehneotherium* with cusp f. Contact between successive lower molars thus does not occur via a tongue-in-groove joint common among some triconodontids, jeholodontids and gobiconodontids, but seems to occur in an 'echelon' fashion that is also found in *Hakusanodon* (Rougier *et al.* 2007*b*), *Phascolotherium* and *Amphilestes*. The lingual face of cusp d on m1 overlaps the buccal face of the mesiolingual cusp e on m2. Cusp b on m1 shows heavier wear than those on the preceding p3 and the succeeding m2. Also, m1 shows more overall crown wear than m2. This indicates that m1 has had a longer functional life than either the adjacent premolariform (p3) or molariform (m2). By inference, m1 erupted earlier than p3 and m2. This is a typical pattern of mammalian diphyodont replacements, and perhaps the most reliable evidence for inferring the position of the first lower molariform, short of a direct detection of replacing dental lamina at the locus of the ultimate premolar in the nearly adult growth stage.

The m2–5 is largely similar to m1, though some cusps have been blunted by breakage (figure 2*e-g*). The m1 and m2 are the two largest (longest) teeth, and the size of

molariforms decreases slightly from m2 to m4 and more sharply from m4 to m6 (see table S1 in the electronic supplementary material). The m6 has a simplified morphology with three low main cusps, barely discernible accessory cusps d and e, and a faint and discontinuous lingual cingulid. The m6 is aligned with the mid-line of the coronoid process and is partially wedged into the front of the coronoid process, similar to *Phascolotherium*, *Amphilestes* and gobiconodontids in which the ultimate lower molar is in alignment with the coronoid process. However, in triconodontids and jeholodontids, the ultimate lower molar erupts medial to the anterior margin of the coronoid process.

The four upper incisor loci can be identified by their partial crowns or alveoli on the right premaxilla (figure 1c,e). The fragmentary first and second incisors are small and pencilate, and the intact third and fourth are taller and lanceolate. Posterior to the fourth incisor and on the lateral wall of the premaxilla is a vertical surface groove to accommodate the lower canine during occlusion. The upper canine is single-rooted and has a robust, laterally compressed crown that is slightly recurved along the length of its anterior margin. Its apex projects to near the ventral margin of the dentary. The canine root length is more than three-quarters of the crown height.

The upper postcanine row has three premolariforms and five molariforms (figure 1c,e). Among the few other eutriconodonts known from complete upper dentitions, the triconodontid *Triconodon* shares the same high number of postcanines, whereas other taxa, including *Jeholodens*, *Yanoconodon*, and the triconodontids *Trioracodon* and *Priacodon*, have fewer upper postcanines (Kielan-Jaworowska *et al.* 2004). In gobiconodontids, the postcanine row has more loci over the lifetime, but at any given stage of life there are fewer upper molariforms because of their highly unique mode of molariform replacement (Jenkins & Schaff 1988). A small, double-rooted P1 lies immediately posterior to the upper canine. The laterally compressed P1 crown has a blunted main cusp A just mesial to the midpoint; cusps B and C are not evident. The right P2 is about twice the length of P1. Its crown is laterally compressed with the low and centrally placed cusp A. The mesial ridge of cusp A is sloping dorsally to the cingular level where there is an undulation of the ridge at the cusp B position but without a distinctive cusp. The distal ridge of cusp A is raised halfway between cusp A and distal cingulum, and this bears some resemblance to cusp C. On P3, cusps B and C remain indistinct as little more than risings on the mesial and distal ridges from cusp A, but they are in a buccal position relative to cusp A. P3 and M1 show a trend toward an increasing lingual expansion at the base of cusp A and an obtuse triangulation of the mesial and distal ridges of cusp A.

On M1, the ridge between cusp A and cusp B and the ridge between cusp A and cusp C are slightly triangulate (figure 1d); this arrangement is also found to a lesser degree in the upper molariforms of the possible 'amphilestid' *Paikasigudodon* (Prasad & Manhas 2002). Cusp B is heavily worn down to a slight swelling, but cusp C remains distinctive: it is separated from cusp A by a valley and has a lingually expanded base. M1 has a continuous buccal cingulum that rises ventrally at its mesial

and distal ends to slight swellings that represent cusps E and D, respectively. Owing to the development of the labial and lingual cingula, M1 is significantly wider than P2–3. The lingual cingulum has a pronounced point of convexity medio-anterior to cusp A, and a less pronounced point of convexity medial to cusp C. The two points of convexity correspond to the wide anterior and posterior roots below the crown. The buccal outline of M1 crown is slightly concave.

M2–3 have a much taller and more pronounced cusp B than M1, as well as a more distinctive and conical cusp C (figure 1d). At the two wide points corresponding to the anterior and the posterior roots, the cingular outline is progressively more convex on the lingual margin and concave on the buccal margin. This makes the ectoflexus opposite cusp A more prominent in the middle positions of the upper molar series. The buccal cingulum carries cusp E. M4 and M5 are in a slightly more internal position and rotated clockwise relative to the preceding molariforms. The crown of M4 has a simplified morphology relative to M2–3; cusp A is low, cusp B is closely approximated to cusp A, cusp C is barely discernible and the buccal margin is less concave. The M5 is further reduced; it is only half the length of the previous molars, and has an oval occlusal outline; cusp A is low, and cusps B and C are indistinct.

For the postcanine series as a whole, *Juchilestes* has embrasure occlusion in which the main cusp A of each upper molariform occludes between cusp c of the opposing lower molariform and cusp b of the succeeding lower molariform (figure 2h). Each molariform has two main shearing surfaces: the anterior facet (Crompton facet 1) supported by cusps A–B on the upper (cusps a–c on the lower), and the posterior facet (Crompton facet 2) supported by cusps A–C on the upper (cusps a–b on the lower; Crompton 1974). This two-to-one pattern of postcanine occlusion in *Juchilestes* is present in 'amphilestids', gobiconodontids and obtuse-angled 'symmetrodonts' (Crompton 1974; Kielan-Jaworowska *et al.* 2004; Luo *et al.* 2007a), but is very different from the one-to-one relationship seen in triconodontids, jeholodontids and morganucodonts (Crompton 1974; Luo *et al.* 2007a).

5. PHYLOGENETIC ANALYSIS

We performed two phylogenetic analyses of *Juchilestes*. Analysis 1 emphasized taxonomic sampling among eutriconodonts and sampling of mandibular and dental characters; this analysis used a data matrix modified from Rougier *et al.* (2007b) and Montellano *et al.* (2008) and three new characters of our own. The matrix consists of 67 characters scored for 30 taxa. Analysis 2 sampled a broader range of Mesozoic mammaliaforms and a broader range of cranial and skeletal characters; this analysis used the data matrix of Luo *et al.* (2007a) consisting of 436 characters scored for 103 taxa (see the electronic supplementary material).

The first analysis generated 18 most parsimonious trees with a tree length of 186 steps, a consistency index of 0.4839, and a retention index of 0.7506. Figure 3 shows the strict consensus of the shortest trees with decay indices for each node. The arrangement of basal mammaliaforms and crown mammals on our strict

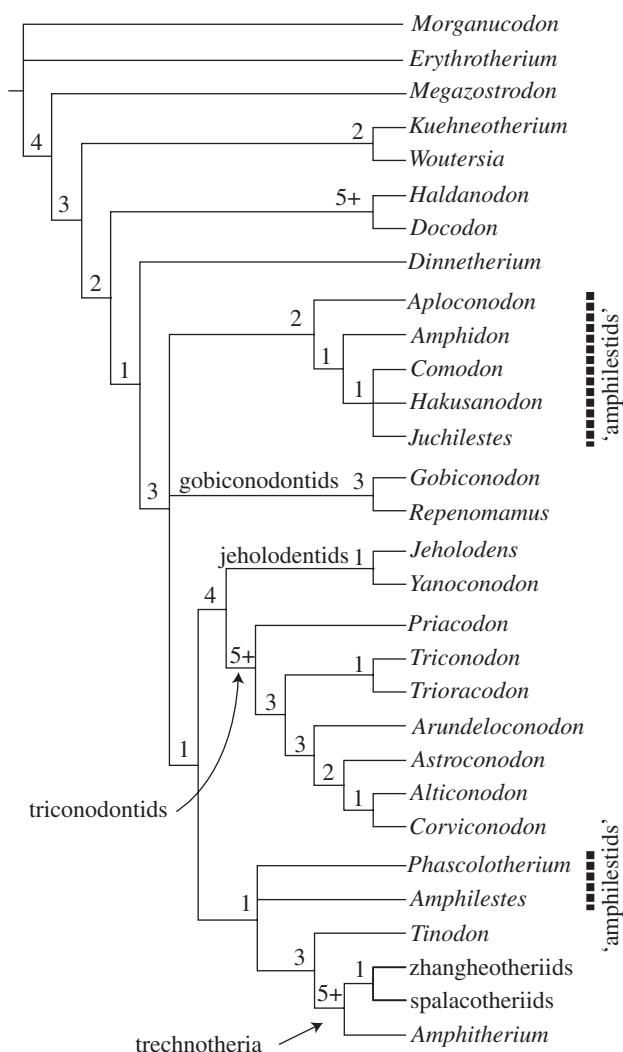


Figure 3. Strict consensus tree of the 18 most parsimonious trees generated from the phylogenetic analysis of mainly dental and mandibular characters (see appendix A in the electronic supplementary material). Decay indices are shown above each node.

consensus tree is identical to the most parsimonious tree of Rougier *et al.* (2007b) in that eutriconodonts are paraphyletic and the ‘amphilestid’ taxa are split between two groups: (i) a clade of ‘amphilestids’ (*Aploconodon* (*Amphidon* (*Comodon*, *Hakusanodon*, *Juchilestes*))); (ii) a clade composed of ‘amphilestids’ (*Phascolotherium*, *Amphilestes*) as outgroups to *Tinodon* and trechnotherians (see fig. S1a in the electronic supplementary material). However, in our consensus tree, the entirely ‘amphilestid’ clade is placed in a basal trichotomy among crown mammals whereas *Phascolotherium* and *Amphilestes* are deeply nested, resulting in a polyphyletic ‘Amphilestidae’. In contrast, Rougier *et al.* (2007b) recovered a paraphyletic ‘Amphilestidae’, whereas triconodontids occupy the basal position among crown mammals. Our analysis also found strong support for jeholodentids as a sister group to triconodontids rather than as a sister group to a clade composed of ‘amphilestids’, *Tinodon* and trechnotherians, as in Rougier *et al.* (2007b).

The second analysis generated 10 160 most parsimonious trees with a tree length of 2134 steps, a consistency index of 0.3482, and a retention index of 0.8011. The strict consensus of the shortest trees is

available in the electronic supplementary material (appendix B and fig. S1b). The parts of the tree relevant to this study are largely consistent with those produced from the dental and mandibular matrix of the first analysis. The main difference is that in the second analysis the Eutriconodonta is monophyletic, not paraphyletic. This is probably due to differences in taxonomic sampling of the two analyses. Most other recent analyses that have sampled multituberculates have also yielded trees that place them as sister group to trechnotherians and place eutriconodonts in a more basal position on the strength of postcranial and cranial characters (e.g. Luo *et al.* 2002; Meng *et al.* 2006). Thus, the issue of monophyly or paraphyly of the ‘Eutriconodonta’ is in part dependent on sampling in a broader taxonomic context. Another consideration is that in those analyses that have recovered a monophyletic Eutriconodonta (Luo *et al.* 2002, 2007a,b), jeholodentids and gobiconodontids are the only eutriconodonts represented by postcrania. Accordingly, it remains to be tested whether the monophyly of eutriconodonts is a by-product of long-branch attraction of jeholodentids and gobiconodontids.

6. DISCUSSION

(a) Morphology

The ‘amphilestid’-like molar pattern has long been considered plesiomorphic for eutriconodonts. These slightly triangulate molariforms with embrasure occlusion are supposed to be structurally intermediate between the fully triangulate therian molariforms and the triconodont-like molariforms with straight alignment of three main cusps. With its complete upper and lower dentition, *Juchilestes* shows systematic distribution of several dental morphological features with functional implications.

In the entire upper postcanine series, the only two fully developed and flat wear surfaces can be seen on the distolingual side of P3 and on the mesiolingual side of M1, presumably because the lower m1 and upper M1 are the first molariforms to erupt and function (figure 1d,e). The succeeding molariforms have yet to develop the complete wear facets, presumably because they had erupted later than M1. This is consistent with a common pattern of many mammaliaforms, in which the complete flat wear surfaces are developed by bevelling the contact surfaces, that is, wear facets are not present at eruption and only developed later (Crompton 1974; Mills 1984; Crompton & Luo 1993). This suggests that at least some ‘amphilestid’-like eutriconodonts retained the primitive mammaliaform mode of molariform wear facet development.

In *Juchilestes*, molariforms in the upper series have slightly more pronounced triangulation of the main cusps than their respective lower molariforms (figures 1d and 2g). This has been observed in some mammaliaforms (Crompton & Luo 1993) and has recently been documented for the tinodontids *Yermackia* and *Gobiotheriodon* (Averianov 2002; Lopatin *et al.* 2005; Averianov & Lopatin 2008). It was hypothesized that this difference in the orientation of wear facets in upper and lower molariforms can be accommodated by rotation of the lower jaw and its teeth during occlusion (Crompton & Luo 1993), especially in those taxa with embrasure occlusion. We posit that this is also the case for *Juchilestes*. This

is consistent with the loosely attached, and presumably mobile, mandibular symphysis in our specimen.

Perhaps the most important morphological implication of the new data from *Fuchilestes* is that the obtuse-angled molar cusp pattern is homoplastic in basal mammalian evolution. The issue of homoplasy of molar cusp triangulation first arose with the placement of kuehneotheriids in the mammaliaform phylogeny (reviewed in Luo *et al.* 2002). Kuehneotheriids have obtuse-angled molariforms and represent the first appearance of such molar structure in mammaliaform evolution. Because kuehneotheriids were placed outside crown Mammalia and not related to other 'symmetrodonts' with triangular cusp pattern in crown Mammalia (e.g. tinodontids, spalacotheroids), the obtuse-angled molar pattern has a homoplastic distribution within this phylogeny (Rowe 1993; Rougier *et al.* 1996; Luo *et al.* 2002). *Fuchilestes* also has an obtuse-angled molar cusp pattern. On our phylogenies by two different taxonomic and character samplings, it is placed among other eutriconodonts, but separate from tinodontids and spalacotheroids (figure 3; see fig. S1b in the electronic supplementary material). Thus, the similar molar cusp patterns of *Fuchilestes* and tinodontids should be regarded as convergent. Alternatively, if the obtuse-angled molar patterns of *Fuchilestes* and tinodontids were *a priori* considered homologous, then it would follow that the ancestral molar pattern of eutriconodonts would be obtuse-angled and the straight-aligned molar pattern of triconodontids (*sensu stricto*) would be a secondary evolutionary reversal to the morganucodont condition. The latter scenario is unlikely, given the upper molars of some tinodontids are now known (Rougier *et al.* 2003; Kielan-Jaworowska *et al.* 2004; Averianov & Lopatin 2008) and they are very different from the upper molars of *Fuchilestes* (figure 1d). On the consensus of recent comprehensive phylogenies and on the strength of all characters, we conclude that the obtuse-angled molar pattern of 'amphilestids', as seen in *Fuchilestes*, is homoplastic with regard to those in kuehneotheriids and tinodontids.

(b) Palaeobiogeography

The geographical distribution of Early Cretaceous mammals from East Asia has expanded in the last 20 years with new findings from Russia (Averianov *et al.* 2005; Lopatin *et al.* 2005), Japan (e.g. Tsubamoto *et al.* 2004; Kushahashi 2008), Korea and China (e.g. Ji *et al.* 1999; Luo *et al.* 2007a). These new data have led to suggestions that the Eastern Asiatic region during the Early Cretaceous was (i) the centre of origin for major groups, including eutherian and spalacotheriid 'symmetrodonts' (Manabe *et al.* 2000; Zhou *et al.* 2003; Tsubamoto *et al.* 2004); (ii) a refugium for Jurassic relicts, such as 'symmetrodonts', eutriconodonts and tritylodontids (Luo 1999; Tatarinov & Maschenko 1999; Manabe *et al.* 2000); and/or (iii) an area that was developing a cosmopolitan biotic character as geographic barriers to exchange were waning (Zhou *et al.* 2003).

Fuchilestes is one of many new fossils from Liaoning Province of northeastern China that offer new data for reflection on these palaeobiogeographic hypotheses. Our phylogeny (analysis 1 of §5; figure 3) shows a clade consisting of *Fuchilestes* from the early Aptian of China,

Hakusanodon from the Early Cretaceous of Japan and *Comodon* from the Late Jurassic of North America, to the exclusion of two other 'amphilestids' (*Aploconodon*, *Amphidon*) from the Late Jurassic of North America. This close relationship between *Hakusanodon* and *Fuchilestes* implies a cohesive East Asian biogeographic region during the Early Cretaceous, a pattern supported by a number of other taxa (e.g. gobiconodontids, psittacosaurid ceratopsians) that either have a high diversity in the region or are endemic to the region. That *Hakusanodon* and *Fuchilestes* are nested together to the exclusion of more ancient 'amphilestid' taxa is also consistent with the hypothesis that East Asia was a refugium for late surviving taxa. 'Amphilestids' that persisted into the Early Cretaceous are otherwise only known by an indeterminate 'amphilestid' taxon from western Siberia (Averianov *et al.* 2005). Intriguingly, its lower molar cusp pattern is similar to that of *Fuchilestes* and *Hakusanodon* in having cusp b higher than c (Averianov *et al.* 2005). Clearly, however, East Asia had a complex palaeogeographic history that included prolonged isolation and intermittent connections, of which the exact timing and pattern is still uncertain (Enkin *et al.* 1992; Haggart *et al.* 2006).

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