

A new eutriconodont mammal from the early Cretaceous Jehol Biota of Liaoning, China

Shilin Hou · Jin Meng

Received: 18 November 2013 / Accepted: 20 December 2013 / Published online: 15 January 2014
© Science China Press and Springer-Verlag Berlin Heidelberg 2014

Abstract A new genus and species of eutriconodont mammal, *Chaoyangodens lii* gen. et sp. nov., from the Dawangzhangzi bed of Yixian Formation, Lingyuan, Liaoning, is reported. The new species has a tooth formula I5-C1-P1-M3/i4-c1-p1-m4, unique among eutriconodonts in having only one premolar in lower and upper jaws, respectively, and a distinctive diastema between the canine and the premolar. Its simple incisors and reduced premolars show a mosaic combination of primitive and derived features. This new taxon adds to the diverse group of Jehol eutriconodonts. Among the known species from at least three horizons, there seems no evolutionary trend in morphology that is recognizable, except for that larger species are all from the Lujiatun bed of the Yixian Fm. A thorough and systematic analysis involving all the Jehol eutriconodonts is needed to understand their phylogenetic relationships.

Keywords Eutriconodonta · Mammalia · Jehol Biota · Early Cretaceous · Liaoning · China

1 Introduction

The early Cretaceous is a critical period of time in mammalian evolution, during which diverse groups of non-tribosphenic, such as Eutriconodonta, and basal tribosphenic mammals were common in several continents, including Asia, Europe, North America, Australia, and South America [1–5]. Eutriconodonts had once been considered as part of the paraphyletic group Triconodonta, which include some Late Triassic and Early Jurassic forms such as *Sinoconodon* and *Morganucodon*, but more recent works regarded eutriconodonts as a natural group nested within the crown Mammalia [5–11]. Eutriconodonts, an extinct group of mammals that had lived from the Jurassic to the Late Cretaceous, were carnivorous and/or insectivorous mammals, judging from their tooth pattern, and have attracted numerous studies concerning mammalian evolution [5, 12–26].

Since 1999, several eutriconodonts have been reported from the Jehol Biota and its related faunas in northeastern China, including *Jeholodens jenkinsi* [25], *Repenomamus robustus* [26], *R. giganticus* [27], *Gobiconodon zofiae* [28], *G. luodianus* [29], *Meemannodon lujiatunensis* [30], *Yanoconodon allini* [10], and *Liaconodon hui* [11]. Unlike most of the eutriconodonts that are represented by fragmentary material from other parts of the world, these species from China are commonly represented by well-preserved skeletal specimens, which provide a significant set of data on eutriconodont morphology and evolution of early mammals. Here we report yet another new eutriconodont, which adds to the diverse eutriconodonts from

S. Hou
Department of Geology, Northeastern University, Shenyang
110819, China

S. Hou
Paleontological Institute, Shenyang Normal University,
Shenyang 110034, China

J. Meng (✉)
Division of Paleontology, American Museum of Natural History,
New York 10024, NY, USA
e-mail: jmeng@amnh.org

J. Meng
Key Laboratory of Vertebrate Evolution and Human Origin of
Chinese Academy of Sciences, Institute of Vertebrate
Paleontology and Paleoanthropology, Chinese Academy of
Sciences, Beijing 100044, China

the Jehol Biota and casts new light on the distributions and phylogenetic relationships of eutriconodonts.

2 Systematic paleontology

Class Mammalia Linnaeus, 1758

Order Eutriconodonta Kermack, Mussett et Rigney, 1973

Family incertae sedis

Chaoyangodens gen. nov.

Type species *Chaoyangodens lii* gen. et sp. nov.

Diagnosis As for the type species

Etymology *Chaoyang*, the name of the prefecture where many Jehol mammal fossils from the Yixian Formation were discovered [31], including the holotype reported here; *odens* (Latin): tooth.

Chaoyangodens lii gen. et sp. nov.

Holotype A skeleton preserved in a laminated siltstone that is split into two slabs (JZT005-2010, Ji-Zan-Tang Paleontological Museum, Chaoyang, Liaoning) (Figs. 1–3).

Etymology The species name is after Hai-Jun Li, the collector of the holotype specimen.

Locality and horizon. The holotype is from the lacustrine Dawangzhangzi bed of the Yixian Formation at the Dawangzhangzi locality, Lingyuan, western Liaoning. The age has been generally considered as Early Cretaceous with the radiometric dates varying from 122.2 Ma [32] to 124.6 Ma [33, 34]. Other mammals from this locality include the multituberculate *Sinobaatar lingyuanensis* [35], the trechnotherian *Akidolestes cifellii* [36], the metatherian *Sinodelphys szalayi* [37], and the eutherian *Eomaia scansoria* [38].

Diagnosis A small eutriconodont with the body length 109 mm from the tip of rostrum to the end of the ischium; typical triconodont postcanine teeth with three main cusps aligned mesiodistally; differing from *Sinoconodon* and morganucodontids in lacking a post-dentary trough but retaining the ossified Meckel's cartilage; tooth formula I5-C1-P1-M3/i4-c1-p1-m4; unique among eutriconodonts in having only one premolar in lower and upper jaws, respectively, and a diastema between the canine and the premolar in both upper and lower jaws; further differing from gobiconodontids in lacking enlarged first lower incisors, from amphilestids in having asymmetrical cheek teeth in lateral view, and from triconodontids in having cusps a

and A significantly higher than other main cusps; further differing from *Yanoconodon* and *Liaoconodon* in having more and smaller incisors; further differing from *Liaoconodon* and *Repenomamus* in being smaller and having small incisors and less inflated cheek teeth that have distinctive cingula; further differing from *Jeholodens* in having larger and vertical lower and upper canines, cusp a of lower molar occluding between two upper molars and a triangular scapula.

3 Description

The specimen is a squashed skeleton, with the dorsal side of the skull exposed (Fig. 1). The bone surrounding the nasal cavity was peeled off so that the anterior dentition of the lower jaw is exposed. A slab fragment containing parts of the right mandible and maxilla was prepared from the ventral side to reveal the cheek teeth (Fig. 2).

The skull is 33.7-mm long from the rostrum tip to the posterior edge of the occipital condyles and 23.4-mm wide. The tooth eruption indicates that the new species is at the similar developmental stage of *Jeholodens* [25] and *Liaoconodon* [11]. The mandible is slender and has a flat ventral border; its depth at m1 on the buccal side is 2.8 mm. There are three mental foramina under the canine, the diastema, and m1, respectively, with their sizes increasing posteriorly. The ossified Meckel's cartilage (OMC) is preserved in each side of the mandibles. As in other triconodonts [10, 11, 28, 39, 40], the posterior end of the OMC is thick and bends medially away from the dentary; it gradually tapers anteriorly. Impression and part of the preserved left mandible shows that the coronoid process is broad in lateral view, with m4 being on the medial side of the process. The pterygoid fossa is shallow on the medial side of the mandible.

There are four lower incisors on each lower jaw (Fig. 2). All incisors are small, subequal in size, and simple, with a slightly concave lingual surface. The right i1 is turned 90° along its long axis in preservation so that its lateral profile is visible. It reveals that the incisors are dorsoventrally deeper than transversely wide. There is a small (tooth-wide) gap between adjacent incisors.

The right lower canine is partly preserved and is the tallest lower tooth (Fig. 3). It is double-rooted, and the jawbone containing the roots is slightly expanded to have a convex surface. There is a distinctive diastema between the canine and the premolar, subequal to the length of the premolar, which differs from all known Jehol eutriconodonts [10, 11, 25–30, 41]. In the buccal view, the jawbone at the diastema is concave, in contrasting the convex area at the canine. In dorsal view, the bone narrows to form a ridge at the diastema.

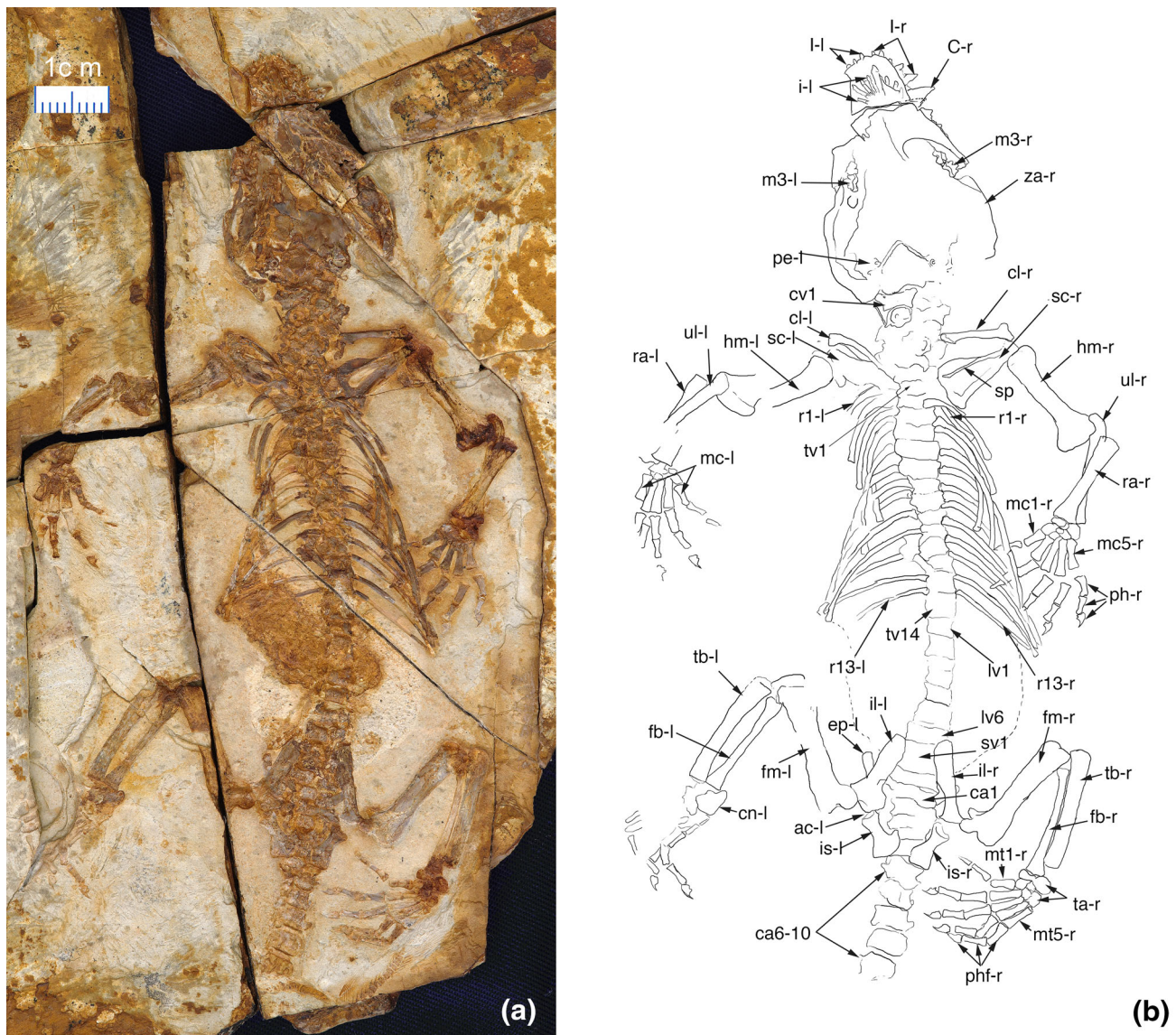


Fig. 1 The skeleton of *Chaoyangodens lii* (JZT005-2010, holotype). **a** The slab contains most of the skeletal elements in dorsal view. **b** Line drawing illustrates structures of the specimen. ac-l, acetabulum; C-r, upper canine; ca1, 1st caudal vertebra; ca6-10, 6th-10th vertebrae; cl-l, left clavicle; cl-r, right clavicle; cn-l, left calcaneum; cv-1, 1st cervical vertebra; ep-l, left epipubic; fb-l, left fibula; fb-r, right fibula; fm-l, left femur; fm-r, right femur; hm-l, left humerus; hm-r, right humerus; i-l, left lower incisors; I-l, left upper incisors; I-r, right upper incisors; il-l, left ilium; il-r, right ilium; is-l, left ischium; is-r, right ischium; lv1, 1st lumbar vertebra; lv6, 6th lumbar vertebra; m3-l, left m3; m3-r, right m3; mc-l, left metacarpal; mc1-r, 1st right metacarpal; mc5-r, 5th right metacarpal; mt-l, left metatarsal; mt1-r, 1st right metatarsal; mt5-r, 5th right metatarsal; pe-l, left petrosal; ph-r, right phalanges (hand); phf-r, right phalanges (foot); r1-l, 1st left rib; r1-r, 1st right rib; r13-l, 13th left rib; r13-r, 13th right rib; ra-l, left radius; ra-r, right radius; sc-l, left scapula; sc-r, right scapula; sp, scapular spine; sv1, 1st sacral vertebra ta-r, right tarsus; tb-l, left tibia; tb-r, right tibia; tv1, 1st thoracic vertebra; tv14, 14th thoracic vertebra; ul-l, left ulna; ul-r, right ulna; za-r, right, zygomatic arch

There is only one lower premolar, which we refer as p4 (Figs. 2, 3). By position, it is comparable with the ultimate premolar in other eutriconodonts, such as p2 in *Jeholodens* [25], *Meemannodon* [30], and *Liaconodon* [11] or p4 in *Gobiconodon* [8, 28]. Although the homology of the ultimate premolar remains unclear in eutriconodonts, it is best to treat it as p4 for convenience of description as well as for character coding in the phylogenetic analysis. We follow the common

terminology in describing cheek tooth structures [5, 42]. The p4 is double-rooted and the tallest postcanine tooth. It has a strong cusp a and a very small cusp c. In addition, there is a weak swelling at the anterior base of the tooth crown that may be considered as a rudimentary cusp b. Similar to the molars, there is no cingulid on the buccal side of the premolar.

There are four lower molars, with the ultimate one not yet erupted. The lower molar has the labial surface more

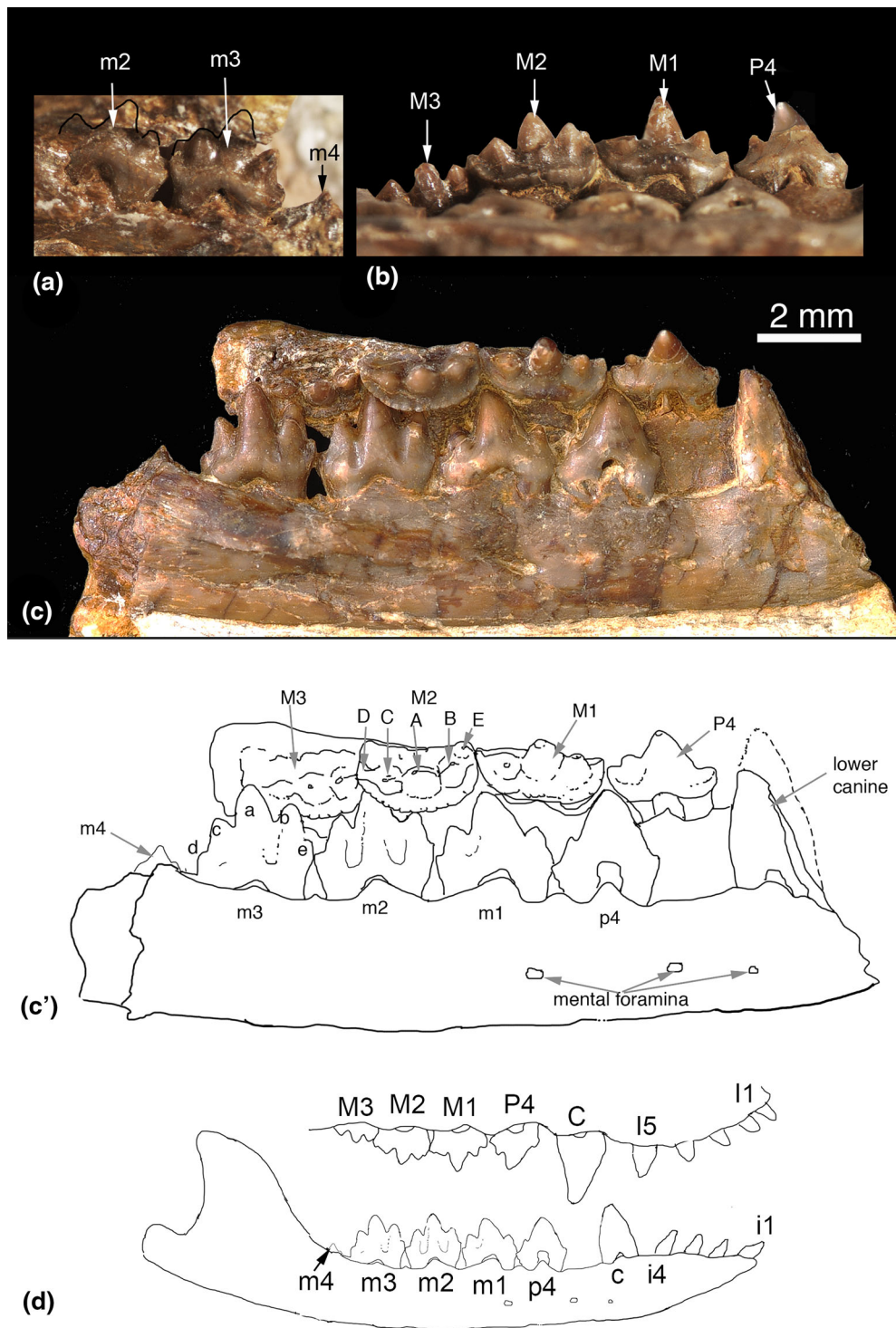


Fig. 2 Cheek teeth of *Chaoyangodens lii* (JZT005-2010, holotype). **a** Lingual view of the right m2 and m3. **b** Lingual view of P4-M3. **c** Occlusal view of right P4-M3 and labial view of lower canine and p4-m3. **c'** Outline of the teeth **c** illustrates tooth assignments and cusp structures. **d** Reconstructed upper and lower dentitions of *Chaoyangodens*. **a–c** are on the same scale. Measurements of teeth (length/width in mm): P4 2.2/0.7; M1 2.5/1.2; M2 2.5/1.4; M3 2.2/1.5; p4 2.1/?; m1 2.3/?; m2 2.4/?; m3 2.4/1.0

convex than the lingual side. There is no cingulid on the buccal side of the crown, and the lingual cingulid is smooth and undulant, extending from cusp e to d in m2-3. In lateral

view, the tooth cusps show a slightly posterior inclination so that the tooth is not symmetrical. Cusp a is distinctively larger and higher than cusps b and c in all molars. In the

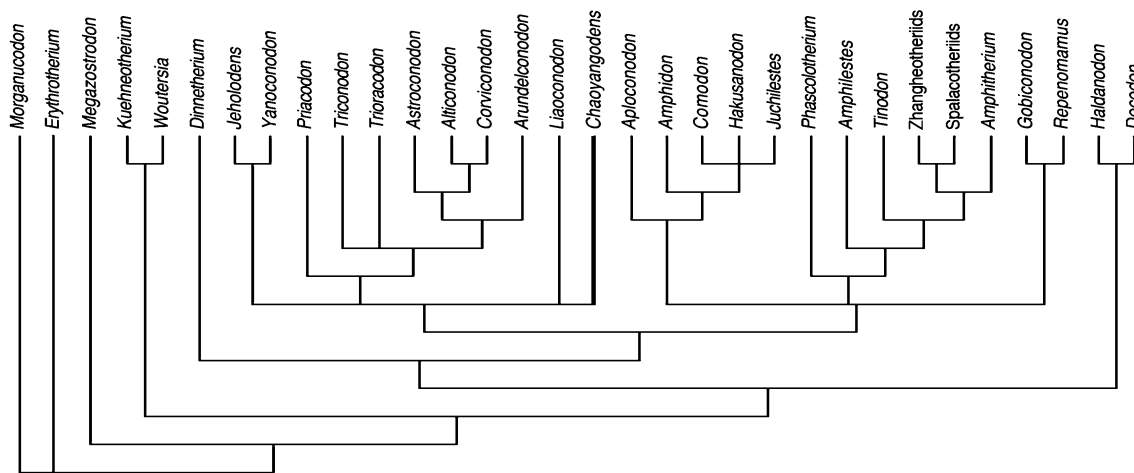


Fig. 3 The strict consensus result of the phylogenetic analyses. The cladistics analysis is based 32 taxa and 67 characters. Phylogenetic analyses were performed with PAUP* 4.0b10 software. A total of 36 equally most parsimonious trees are obtained; each has a tree length 209, consistency index 0.431, homoplasy index 0.57 and retention index 0.7

lateral view, although the lower molars are not quite symmetrical, but cusp a is centrally placed on the crown. Cusps b and c are slightly more lingual than cusp a; this trend is most distinct in m3.

Cusp a of m1 is longer than those of m2-3, and cusp b is smaller than cusp c. Both cusps b and c of m1 are smaller than those of m2-3. Cusps b and c are subequal in m2, whereas cusp b is taller than cusp c in m3. Cusp d is rudimentary in m1 and becomes slightly larger in m2-3. Cusp e is absent in m1 and m2 but is present in m3. Cusp e is absent in *Jeholodens* [25]. There is neither cusp f, nor is there the interlocking structure. The right m4 is still in jawbone, and the left m4 is visible due to breakage, which is subequal to m3 in size. The pattern of tooth eruption is similar to those of *Jeholodens* and *Liaconodon* [11], probably representing a young adult.

The preserved lower dentition is probably in a position that had shifted posteriorly one tooth position in relation to the upper dentition. For instance, M2 would bite between m2 and m3 in life. The occlusal pattern is probably two-to-one (embrasure) occlusion as in *Gobiconodon* [5] where cusp A or a occludes between molars of the opposing series. This differs from *Jeholodens* in which cusp a of the lower molar occludes into the valley-groove between cusps A and B of the opposite upper molar. In *Chaoyangodens*, cusp a of the lower molar appears too big to fit between the valley of cusp A and B of the upper molar.

There are five upper incisors, preserved in poor condition (Fig. 2). Similar to the lower incisors, all upper incisors are small and simple, and there is a tooth-wide space separating adjacent teeth. The I5 seems to be the largest incisor with its crown being wider than the root.

The right upper canine is preserved. It is doubt-rooted and the tallest upper tooth with a pointed tip. A diastema

smaller than the lower one exists between the canine and the upper premolar. There is only one upper premolar, which we refer to as P4. It is double-rooted and taller than molars. Similar to the lower premolar, cusp A of the upper premolar is stronger than those of upper molars (Fig. 2). The premolar does not have the cingulum, and the swelling at the anterior base of the tooth may be called cusp B. Cusp C is small but distinctive.

Three molars are preserved, with M3 being partly erupted. Compared to the lower molars, cusp A is slightly slimmer and sharper than cusp a. M1 and M2 are similar in length whereas M3 the shortest. The tooth width increases from M1 to M3. In all upper molars, cusp A is significantly taller than cusps B and C. In M1, the three main cusps are aligned mesiodistally in a straight line, whereas in M2-3, cusps B and C are slightly lingual to cusp A. The buccal and lingual cingula are weak and bear only a few small cuspules on M1. Cusp E of M1 is small and mesial, and slightly buccal, to cusp B. Cusp D of M1 is absent.

In occlusal view, M2 differs from M1 in having wider cingula. The lingual cingulum is arched and decorated with numerous small cuspules. The labial cingulum is relatively straight and bears fewer but larger cuspules, of which the mesial one is cusp E that is shifted more buccally to cusp B compared to that of M1. Cusp D is small and confluent to the base of cusp C. The M3 is not fully erupted, but its occlusal morphology is visible (Fig. 2). It is similar to M2 but differs from the latter in having even broader cingulum and more buccally positioned cusps D and E.

There are 14 thoracic, 6 lumbar, and 2 or 3 sacral vertebrae. The clavicle is a sizable, curved element. The scapular spine is well developed, and the scapula has a triangular outline. Detailed description of the postcranial skeleton will be treated in another work.

4 Comparison

Chaoyangodens differs from triconodontids [7, 13, 22, 43–45] in having the molar cusp A/a much higher than other cusps and from amphilestids and amphilestid-like eutriconodonts in having fewer molars that are not symmetrical in labial or lingual views. *Chaoyangodens* differs from gobiconodontids and *Repenomamus* in having fewer molars but more incisors, of which none is enlarged. In addition, the upper molars of gobiconodontids and *Repenomamus* are more transversely wide with cusp A being inflated.

Chaoyangodens is similar to *Jeholodens* [25] in having four lower incisors, three upper and four lower molars and in lacking lower cingular cuspules f and g (kuhneocone), and the interlocking mechanism. However, *Jeholodens* has two lower premolars and a single-rooted, small canine, contrasting to the double-rooted, and tall canine in *Chaoyangodens*. The upper molar of *Jeholodens* was considered linguobuccally compressed with three main cusps in a straight alignment [25], whereas in *Chaoyangodens*, cusp A is slightly lingual to cusps B and C on M2-3. In *Jeholodens*, cusp a of the lower molar occludes into the valley between cusps A and B of the opposite upper molar. This appears unlikely for *Chaoyangodens* because cusp a is too large to be received by the valley between cusps A and B of the upper molar. It is more probable that cusp a of the lower molar bites in the embrasure between two opposite upper molars during the occlusion in *Chaoyangodens*.

Jeholodens lacks cingular cuspules e and f in the lower molars, whereas *Chaoyangodens* has at least cusp e on m3. In *Jeholodens*, the lower molars are interlocked, with a crescent-shaped distal cusp d of the preceding molar fitted into the concave mesial margin of cusp b of the succeeding molar [25]. This feature was considered diagnostic of the Triconodontidae [7, 22, 43, 44] but is also present in gobiconodontids, such as *Gobiconodon* [8, 28] and *Mee-mannodon* [30]. In *Chaoyangodens*, there is no interlocking structure.

The detail morphology, particularly the dentition, of *Yanoconodon* is not available so that it is difficult to compare it with *Chaoyangodens*. It was considered that *Yanoconodon* is most similar to *Jeholodens*, and their molar characteristics are identical [10]. *Yanoconodon* differs from *Jeholodens* in having two (instead of four) lower incisors, in the enlargement of the first incisor, and in lacking the spoon-shaped lower incisors of the latter. The incisor condition also distinguishes *Yanoconodon* from *Chaoyangodens*.

Chaoyangodens differs from *Liaconodon* in several accounts. The latter is unique among eutriconodonts in having the lower incisors, canine and first premolar proportionally enlarged, closely packed, and possessing a

similar morphology (more or less incisiform) [11]. In addition, *Chaoyangodens* differs from *Liaconodon* in their dental formula, with that of *Liaconodon* being I3.C1.P2.M3/i2.c1.p2.m4.

Kemchugia magna [46] differs from *Chaoyangodens* in having molars with transversely inflated cusps and relatively higher and stronger cusps A/a.

5 Phylogeny

The cladistics analysis is based 32 taxa and 67 characters. The characters and data matrix are adopted from Meng et al. [11], which are based on two works [4, 41]. We performed a heuristic search using PAUP* 4.0b10 software with 1,000 random addition sequence replicates. Settings for the analysis are the same as others [11, 41]. Among the 67 characters, nine are ordered (1, 5, 6, 11, 13, 20, 24, 65), and the others are unordered. A total of 36 equally most parsimonious trees are obtained; each has a tree length 209, consistency index 0.431, homoplasy index 0.57 and retention index 0.72. The 67 characters coded for *Chaoyangodens lii* are as the following: 1(0), 2(0), 3(0), 4(1), 5(2), 6(2), 7(?), 8(0), 9(0), 10(0), 11(0), 12(1), 13(0), 14(1), 15(0), 16(1), 17(0), 18(0), 19(1), 20(1), 21(0), 22(1&2), 23(1), 24(0&1), 25(0&1), 26(0), 27(0), 28(0), 29(0), 30(0), 31(0), 32(2), 33(1), 34(0), 35(0), 36(?), 37(0), 38(0), 39(0), 40(1), 41(0), 42(1), 43(0), 44(1), 45(1), 46(1), 47(?), 48(?), 49(1), 50(1), 51(?), 52(1), 53(1), 54(1), 55(1), 56(?), 57(?), 58(0), 59(1), 60(0), 61(0), 62(0), 63(0), 64(0), 65(0), 66(0), and 67(0). The reader should refer to Meng et al. [11] for the list of the characters. The strict consensus tree is presented in Fig. 3.

6 Discussion and conclusion

In the phylogenetic analysis, *Chaoyangodens* falls into a polytomy with *Liaconodon* and other eutriconodonts. This topology justifies for the taxonomic placements of *Liaconodon* [11] and *Chaoyangodens* as family uncertain within Eutriconodonta and shows again that the Cretaceous eutriconodonts are quite diverse.

Chaoyangodens is the first eutriconodont from the Dawangzhangzi bed of the Yixian Formation from the Lingyuan County. *Liaconodon* from the Jiufotang Formation, Jianchang, is younger than *Chaoyangodens* and is the youngest eutriconodont of the Jehol Biota. Other Jehol eutriconodonts are older than *Chaoyangodens*, including *Yanoconodon allini* from the Yixian Formation at Daluozigou locality in Fengning County, Hebei Province; *Jeholodens jenkinsi* from the Jianshangou bed of the Yixian Formation at the Sihetun locality; *Gobiconodon zofiae*, G.

luoianus, *Meemannodon lujiatunensis*, *Repenomamus robustus*, *R. giganticus* from the Lujiatun bed of the Yixian Formation at Lujiatun locality. The ages of the beds containing mammals are not fully resolved [31], but it is likely that some age differences exist between these rock units. Among all the localities, the Lujiatun bed has yielded most eutriconodont species. This is probably owing to the unique taphonomic process that preserved the fossils in three dimensions, although the exact mechanism for the formation of Lujiatun deposits is still unclear.

Of all the eutriconodonts from this region, there seems no evolutionary trend in morphology that can be recognized from these well-preserved specimens. For instance, compared to the younger *Liaconodon* and other older eutriconodonts from the region, *Chaoyangodens* displays a mosaic pattern of dental features. Its incisors remain primitive with five upper and four lower incisors that are small and simple, whereas the reduction of the premolars is certainly a derived condition, unique among all Jehol eutriconodonts. However, there appears a pattern in body size distribution: all larger species are from the Lujiatun bed, contrasting the smaller species preserved two dimensionally in lacustrine beds of other localities. Whether this is attributable to different evolutionary stages of eutriconodonts or to taphonomic processes remains unknown. Interestingly, the pairing of *Gobiconodon* and *Repenomamus* is not clustered with other typical eutriconodonts in our phylogenetic analysis, which further complicated the various eutriconodont phylogenies proposed in several recent studies [4, 11, 41, 47]. These indicate that the diversity of eutriconodonts is higher than what we know previously and that a more thorough and systematic analysis on eutriconodonts and related mammalian groups is desperately needed.

Acknowledgments We thank En-Pu Gong (Northeastern University, Liaoning), Hai-Jun Li (Jizantang Paleontological Museum, Liaoning Province), and Lian-Hai Hou (Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing) for their field assistance, specimen collecting, and discussion during the course of the study; Shu-hua Xie (IVPP) for specimen preparation. The manuscript was improved by anonymous comments. The study has been supported by the National Basic Research Program of China (2012CB821906), Public Science and Technology Research Funds Projects of Land and Resources (2013111120), the National Natural Science Foundation of China (41202014) and the American Museum of Natural History, New York.

References

1. Fox RC (1978) Molar structure and function in the Early Cretaceous mammal Pappotherium: evolutionary implications for Mesozoic Theria. *Can J Earth Sci* 2:412–442
2. Butler PM (1978) A new interpretation of the mammalian teeth of tribosphenic pattern from the Albian of Texas. *Breviora* 446:1–27
3. Smith P, Tchernov E (1992) Structure, function and evolution of teeth. Tel Aviv Freund Publishing House Ltd
4. Rougier GW, Isaji S, Manabe M (2007) An Early Cretaceous mammal from the Kuwajima Formation (Tetori Group), Japan, and a reassessment of triconodont phylogeny. *Ann Carn Mus* 76:73–115
5. Kielan-Jaworowska Z, Cifelli RL, Luo ZX (2004) Mammals from the age of dinosaurs—origins, evolution, and structure. Columbia University Press, New York
6. Rougier GW, Wible JR, Hopson JA (1996) Basicranial anatomy of *Priacodon fruitaensis* (Triconodontidae, Mammalia) from the Late Jurassic of Colorado, and a reappraisal of mammaliaform interrelationships. *Am Mus Novit* 3183:1–38
7. Cifelli RL, Wible JR, Jenkins FA Jr (1998) Triconodont mammals from the Cloverly formation (Lower Cretaceous), Montana and Wyoming. *J Vert Paleontol* 18:237–241
8. Kielan-Jaworowska Z, Dashzeveg D (1998) Early Cretaceous amphilestid (“triconodont”) mammals from Mongolia. *Acta Palaeontol Pol* 43:413–438
9. Rougier GW, Novacek MJ, McKenna MC et al (2001) Gobiconodonts from the Early Cretaceous of Oshih (Ashile), Mongolia. *Am Mus Novit* 3348:1–30
10. Luo ZX, Chen PJ, Li G et al (2007) A new eutriconodont mammal and evolutionary development of early mammals. *Nature* 446:288–293
11. Meng J, Wang YQ, Li CK (2011) Transitional mammalian middle ear from a new Cretaceous Jehol eutriconodontan. *Nature* 472:181–185
12. Owen R (1871) Monograph of the fossil Mammalia of the Mesozoic formations. *Lond Paleont Soc* 24:115
13. Simpson GG (1928) A catalogue of the Mesozoic Mammalia in the Geological Department of the British Museum. Oxford University Press, London
14. Simpson GG (1929) American Mesozoic Mammals. *Memoirs of Peabody Museum of Yale University* 3:1–171
15. Kermack KA (1963) The cranial structure of the triconodonts. *Philos Trans R Soc Lond* 246:83–103
16. Patterson B (1956) Early Cretaceous mammals and the evolution of mammalian molar teeth. *Fieldiana Geol* 13:1–105
17. Slaughter RH (1969) Astroconodon, the Cretaceous triconodont. *J Mamm* 50:102–117
18. Fox RC (1969) Studies of Late Cretaceous vertebrates (III) a triconodont mammal from Alberta. *Can J Zool* 47:1253–1256
19. Rasmussen TE, Callison G (1981) A new species of triconodont mammal from the Upper Jurassic of Colorado. *J Paleontol* 55:628–634
20. Krusat G (1989) Isolated molars of a triconodont and a symmetrodont (Mammalia) from the uppermost Jurassic of Portugal. *Berliner Geowiss Abhand* 106:277–289
21. Zhou MZ, Cheng ZW, Wang YQ (1991) A mammalian lower jaw from the Jurassic of Lingyuan, Liaoning. *Vert PalAs* 29:165–175
22. Sigogneau-Russell D (1995) Two possibly aquatic triconodont mammals from the Early Cretaceous of Morocco. *Acta Palaeontol Pol* 40:149–162
23. Cifelli RL, Madsen SK (1998) Triconodont mammals from the medial Cretaceous of Utah. *J Vert Paleontol* 18:403–411
24. Godefroit P, Guo DY (1999) A new amphilestid from the Early Cretaceous of Inner Mongolia (P.R. China). *Bull l’Inst R Sci Nat Belgique* 69(Supplement B):7–16
25. Ji Q, Luo ZX, Ji SA (1999) A Chinese triconodont mammal and mosaic evolution of the mammalian skeleton. *Nature* 398:326–330
26. Li JL, Wang Y, Wang YQ et al (2000) A new family of primitive mammal from the Mesozoic of western Liaoning, China. *Chin Sci Bull* 45:2545–2549 (in Chinese)
27. Hu YM, Meng J, Li CK et al (2005) Large Mesozoic mammals fed on young dinosaurs. *Nature* 433:149–153

28. Li CK, Hu YM, Wang YQ et al (2003) A new species of Gobiconodon (Triconodonta, Mammalia) and its implication for the age of Jehol Biota. *Chin Sci Bull* 48:1129–1134
29. Yuan CX, Xu L, Zhang XL et al (2009) A new species of Gobiconodon (Mammalia) from western Liaoning, China and its implication for the dental formula of Gobiconodon. *Acta Geol Sin Engl* 83:207–211
30. Meng J, Hu YM, Wang YQ et al (2005) A new gobiconodont species (Mammalia) from the Early Cretaceous Yixian Formation of Liaoning, China. *Vert PalAs* 43:1–10
31. Meng J, Hu YM, Wang YQ et al (2006) The mammal fauna in the Early Cretaceous Jehol Biota: implications to diversity and biology of Mesozoic mammals. *Geol J* 41:439–463
32. Smith PE, Evensen NM, York D et al (1995) Dates and rates in ancient lakes: ^{40}Ar - ^{39}Ar evidence for an Early Cretaceous age for the Jehol Group, Northeast China. *Can J Earth Sci* 32:1426–1431
33. Swisher CC, Wang YQ, Wang XL et al (1999) Cretaceous age for the feathered dinosaurs of Liaoning, China. *Nature* 398:58–61
34. Swisher CCIII, Wang XL, Zhou ZH et al (2002) Further support for a Cretaceous age for the feathered-dinosaur beds of Liaoning, China: new ^{40}Ar - ^{39}Ar dating of the Yixian and Tuchengzi formations. *Chin Sci Bull* 47:135–138
35. Hu YM, Wang YQ (2002) Sinobaatar gen. nov.: first multituberculate from the Jehol Biota of Liaoning, Northeast China. *Chin Sci Bull* 47:933–938
36. Li G, Luo ZX (2006) A Cretaceous symmetrodont therian with some monotreme-like postcranial features. *Nature* 439:195–200
37. Luo ZX, Ji Q, Wible JR et al (2003) An early Cretaceous tribosphenic mammal and metatherian evolution. *Science* 302:1934–1940
38. Ji Q, Luo ZX, Yuan CX et al (2002) The earliest known eutherian mammal. *Nature* 416:816–822
39. Wang YQ, Hu YM, Meng J et al (2001) An ossified Meckel's cartilage in two Cretaceous mammals and origin of the mammalian middle ear. *Science* 294:357–361
40. Meng J, Hu YM, Wang YQ et al (2003) The ossified Meckel's cartilage and internal groove in Mesozoic mammaliaforms: implications to origin of the definitive mammalian middle ear. *Zool J Lin Soc* 138:431–448
41. Gao CL, Wilson GP, Luo ZX et al (2010) A new mammal skull from the Lower Cretaceous of China with implications for the evolution of obtuse-angled molars and 'amphilestid' eutriconodonts. *Proc R Soc B* 277:237–246
42. Crompton AW (1974) The dentitions and relationships of the southern African Triassic mammals, *Erythrotherium parringtoni* and *Megazostrodon rudnerae*. *Bull Brit Mus Nat Sci* 24(Supplement 3):399–437
43. Fox RC (1976) Additions to the mammalian local fauna from the upper Milk River Formation (Upper Cretaceous), Alberta. *Can J Earth Sci* 13:1105–1118
44. Lillegraven JA, Kielan-Jaworowska Z, Clemens WA (1979) Mesozoic mammals: the first two-thirds of mammalian history. California University Press, Berkeley
45. Kusuhashi N, Hu YM, Wang YQ et al (2009) New triconodontids (Mammalia) from the Lower Cretaceous Shahai and Fuxin formations, northeastern China. *Geobios* 44:1–17
46. Averianov AO, Skutschas PP, Lopatin AV et al (2005) Early Cretaceous mammals from Bol'shoi Kemchug 3 locality in West Siberia, Russia. *Russ J Theriol* 4:1–12
47. Averianov AO, Lopatin AV (2011) Phylogeny of triconodonts and symmetrodonts and the origin of extant mammals. *Doklady Biol Sci* 436:32–35