



A New Eobaatarid Multituberculate (Mammalia) from the Lower Cretaceous Fuxin Formation, Fuxin-Jinzhou Basin, Liaoning, Northeastern China

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Published online: 23 August 2019

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Abstract

Five multituberculate species have been reported to date from the upper Lower Cretaceous (Aptian–Albian) Shaihai and Fuxin formations in Liaoning Province, northeastern China. We herein describe an additional species of eobaatarid multituberculate from the Fuxin Formation, *Dolichoprion lii*, gen. et sp. nov., with a long (relative to height) crown of the fourth lower premolar, which is unique among eobaatarids. We also describe the upper dentition possibly referable to another eobaatarid genus previously known only from lower jaws, *Liaobaatar*, based on a newly discovered specimen. The new species is the sixth multituberculate (and the fourth eobaatarid) species described from the Shaihai and Fuxin formations. These species suggest that multituberculates, especially eobaatarids, were taxonomically quite diverse in the mammalian fauna of East Asia at that time.

Keywords China · Early Cretaceous · Eobaataridae · Fuxin Formation · Mammalia · Multituberculata

Introduction

The Multituberculata were one of the most successful mammalian groups during the late Mesozoic, and survived into the Cenozoic across the K–Pg boundary. In Asia, although they were diverse and abundant in the Late Cretaceous mammalian fauna, the fossil record suggests that they were relatively minor components of the Jurassic mammalian fauna (e.g., Meng 2014; Meng et al. 2015). Jurassic multituberculates have been found only from two formations in Asia (except for India, which was not a part of Asia at that time): the earliest Asian

multituberculate fossil records known to date were reported but have yet to be described from the Bathonian Itat Formation in West Siberia (Averianov et al. 2015); and a slightly younger paulchoffatiid *Rugosodon eurasiaticus* Yuan et al., 2013, was described from the Middle to Upper Jurassic Tiaojishan Formation, Liaoning, northeastern China. In contrast, ‘haramiyidans’ are much more diverse from the Jurassic of Asia (e.g., Maisch et al. 2005; Martin et al. 2010; Averianov et al. 2011; Zheng et al. 2013; Zhou et al. 2013; Bi et al. 2014; Han et al. 2017; Meng et al. 2017; Luo et al. 2017), at least some of which might have been closely related to multituberculates (e.g., Zheng et al. 2013; Bi et al. 2014). Early Cretaceous multituberculates are, therefore, crucial to investigate the mammalian faunal transition in Asia during the Late Jurassic to Late Cretaceous.

Of the 20 mammalian species known from the Barremian–lower Aptian Jehol Group (here considered to be comprised of the Yixian and Jiufotang formations) of northeastern China (Meng 2014 and references therein; Han and Meng 2016; Bi et al. 2018), only one multituberculate species, the eobaatarid *Sinobaatar lingyuanensis* Hu and Wang, 2002, has been reported to date. Two multituberculate species, *Hakusanobaatar matsuoii* Kusuhashi, 2008, and *Tedoribaatar reini* Kusuhashi, 2008, have been reported from the slightly older or almost contemporaneous Kuwajima Formation (Tetori Group), Japan (Matsumoto et al. 2006; Sakai et al. 2019; see also

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Kusuhashi et al. 2006; Kusuhashi 2008). Recently, another species of multituberculate, *Baidabatyx clivosus* Averianov et al., 2017, was reported from the Ileik Formation of Siberia, which is currently considered to be Barremian to Aptian (Kurochkin et al. 2011; O'Connor et al. 2014). These fossil records suggest that multituberculates became more diverse in Asia in the mid-Early Cretaceous than in the Jurassic, but their dominance in Asian mammalian fauna at that time is not apparent mainly because of the scanty mammalian fossil record.

Multituberculate dominance seems to have already increased at latest in the late Early Cretaceous. Diverse multituberculates have been reported from the Shahai and Fuxin formations (Aptian to Albian) of northeastern China including *Heishanobaatar triangulus* Kusuhashi et al., 2010, *Liaobaatar changi* Kusuhashi et al., 2009b, *Sinobaatar fuxinensis* Kusuhashi et al., 2009b, *S. xiei* Kusuhashi et al., 2009b, and *Kielanobaatar badaohaensis* Kusuhashi et al., 2010. They occupy about one-third of the mammalian fossil assemblage composed of more than 100 specimens from the formations, and multituberculates and eutherians were two major members among the mammalian fauna (Kusuhashi et al. 2010). Further contemporaneous species are known from Mongolia (Höövör; ?Aptian to Albian) including *Arginbaatar dmitrievae* Trofimov, 1980, *Eobaatar magnus* Kielan-Jaworowska et al. 1987, *E. minor* Kielan-Jaworowska et al., 1987, and *?Monobaatar mimicus* Kielan-Jaworowska et al., 1987. We here report a new multituberculate species from the Fuxin Formation. The new species, together with the already described species, demonstrates that multituberculates, especially eobaatarids, were already taxonomically diverse in the East Asian mammalian fauna at that time.

Institutional Abbreviations GI PST, Institute of Geological Sciences, Mongolian Academy of Sciences, Ulaanbaatar, Mongolia; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China; PIN, Borissiak Paleontological Institute of the Russian Academy of Sciences, Moscow, Russia; SBEL, Shiramine Institute of Paleontology, Hakusan City Board of Education, Ishikawa Prefecture, Japan.

Materials and Methods

The fossil specimens described here were discovered from the Fuxin Formation in small coal mines, Fuxin, Liaoning, northeastern China (Fig. 1). The Fuxin Formation and the underlying Shahai Formation have yielded various mammalian remains such as eutriconodontans, multituberculates including materials described herein, spalacotheriids, a stem zatherian, and eutherians (Shikama 1947; Wang et al. 1995, 2018; Hu et al. 2005a, 2005b; Li et al. 2005; Kusuhashi et al.

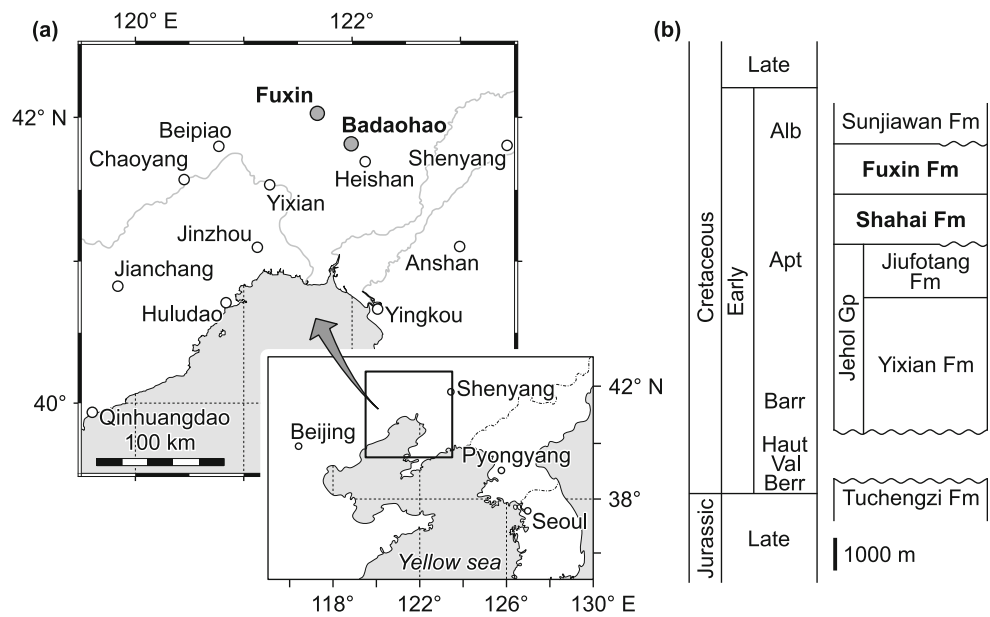
2009a, 2009b, 2010, 2016). Among more than 100 mammalian specimens recovered from these formations, multituberculate specimens represent nearly 40% of them, being one of the most abundant groups in the mammalian fossil assemblage. The depositional ages of the Shahai and Fuxin formations are still not well known, but we consider them to be somewhere between the Aptian to Albian mainly based on radiometric ages (ca. 130–120 Ma; Barremian–early Aptian) obtained from the Yixian and Jiufotang formations (Swisher et al. 1999, 2002; He et al. 2004, 2006; see also Pan et al. 2013), which are stratigraphically lower than Shahai and Fuxin formations (e.g., Wang et al. 1989; Yang and Li 1997; Li and Matsuoka 2015) (Fig. 1b). See Kusuhashi et al. (2009a, 2009b) for more details of the geological setting.

Specimens were scanned by X-ray micro-computed tomography (micro-CT) using the 225 kV micro-CT (developed by the Institute of High Energy Physics, Chinese Academy of Sciences) at the Key Laboratory of Vertebrate Evolution and Human Origins, Chinese Academy of Sciences, Beijing. The specimens were scanned with beam energy of 120 kV (IVPP V22641 except for an isolated m2) or 110 kV (the isolated m2 of V22641) and a flux of 100 μ A at a detector resolution of 7.84 μ m (the left lower jaw of V22641) or 4.70 μ m (the isolated m2) per pixel using a 360° rotation with a step size of 0.5° and an unfiltered aluminum reflection target. A total of 720 transmission images were reconstructed in a 2048 \times 2048 matrix of 1536 slices using a two-dimensional reconstruction software developed by the Institute of High Energy Physics, Chinese Academy of Sciences. Multiplanar reconstructions and surface rendering were performed using AMIRA 5.3.2 software at the Museum of Nature and Human Activities, Hyogo, Japan.

In the descriptions below, premolars and molars are abbreviated as p and m, respectively, and upper (P and M) and lower (p and m) cases designate the upper and lower dentitions, respectively. The prefix d denotes deciduous teeth (e.g., dp, lower deciduous premolar). Numbers following abbreviations indicate the order of teeth in each tooth class, i.e., tooth position, counting from the mesial to the distal end of each, and we here follow the widely accepted homology of the lower premolars where multituberculates sequentially lost their premolars from the mesial to the distal during their evolution. Cusp formulae of premolars and molars are given as labial:lingual.

The phylogenetic analyses of the Multituberculata were performed using the data matrices slightly modified from that of Kielan-Jaworowska and Hurum (2001) with additional taxa (see below). The matrices were analyzed using the traditional search algorithm (tree bisection reconnection branch swapping with 1000 replicates and ten trees held per replicate) in TNT 1.5 (Goloboff and Catalano 2016). The results were examined by analyzing the same matrices by the heuristic search algorithm of the PAUP* 4.0a (Swofford 2003).

Fig. 1 **a** Map showing the fossil localities (Fuxin and Badaohao, Liaoning Province, northeastern China). **b** Schematic stratigraphic table of the major late Mesozoic strata distributed in western Liaoning Province, northeastern China adopted from Wang et al. (1989), Yang and Li (1997), and Li and Matsuoka (2015) among others



The micro-CT data analyzed during the current study are available from the corresponding author on reasonable request. The character states for the added taxa for the phylogenetic analyses in this study are included in the Appendix of this published article.

Systematic Paleontology

Order Multituberculata Cope, 1884
 Family Eobaataridae Kielan-Jaworowska et al., 1987

Emended Diagnosis Dental formula $\text{?}3.0.5.2/1.0.3-2.2$; lower incisor slender, completely covered with enamel or with a limited enamel band; p2 reduced in size and peg-like, or absent; p3 small compared with p4, triangular to oval in lateral view; p4 with eight to 12 serrations and single distal labial cusp; lower molars asymmetrical in occlusal view with shorter lingual margin than labial one, with coalescing cusps; m1 cusp formula 2–4:2–3; m2 cusp formula 1(coalesced):2. P1 to P3 with three to four cusps; P4 cusp formula 2–4:4–5, lingual cusps increase in height distally; P5 having two to three cusp rows or blade-like with single cusp row, showing tendency to form a shearing edge; M1 cusp formula 3–4:4 with a distolingual wing; M2 cusp formula 3:2–4 with a mesiolabial wing.

Included Genera *Eobaatar* Kielan-Jaworowska et al., 1987 (type genus), *Liaobaatar* Kusuhashi et al., 2009b, and *Sinobaatar* Hu and Wang, 2002. *Dolichoprion*, gen. nov., *Loxaulax* Simpson, 1928, *?Monobaatar* Kielan-Jaworowska et al., 1987, and *Tedoribaatar* Kusuhashi, 2008, are here also assigned to the family. *Hakusanobaatar* Kusuhashi, 2008, is either a member of the family or a closely related taxon.

Iberica Badiola et al., 2011, was attributed to the Plagiaulacidae or Eobaataridae. The attribution of *Heishanobaatar* Kusuhashi et al., 2010, to the family is questionable. *Indobaatar* Parmar et al., 2013, is also not likely to belong to this family. *Parendotherium* Crusafont-Pairó and Adrover, 1966, was suggested to be *nomen dubium* by Badiola et al. (2012).

Genus *Dolichoprion*, gen. nov.

Type and Only Species *Dolichoprion lii*, gen. et sp. nov.

Etymology ‘dolichos’ and ‘prion,’ Greek, long and saw, respectively, referring to the diagnostic long crown of p4 of this species.

Diagnosis As for the type and only species.

***Dolichoprion lii*, sp. nov.**

(Figs. 2, 3, 4, 5, 6 and Table 1)

Holotype A partial right dentary with incisor, p3–p4, and m1, a partial left dentary with incisor, p3–p4, and the mesiolabial part of m1, and an isolated left m2 (IVPP V22641).

Type Locality and Horizon Zhenjiang (=Hanjiadian #6) coal mine, Fuxin, Liaoning, northeastern China; Early Cretaceous (Aptian to Albian); Fuxin Formation.

Etymology In honor of a vertebrate paleontologist Dr. Chuankui Li who has greatly contributed to the study on Mesozoic mammals from the Fuxin and neighboring areas of northeastern China.

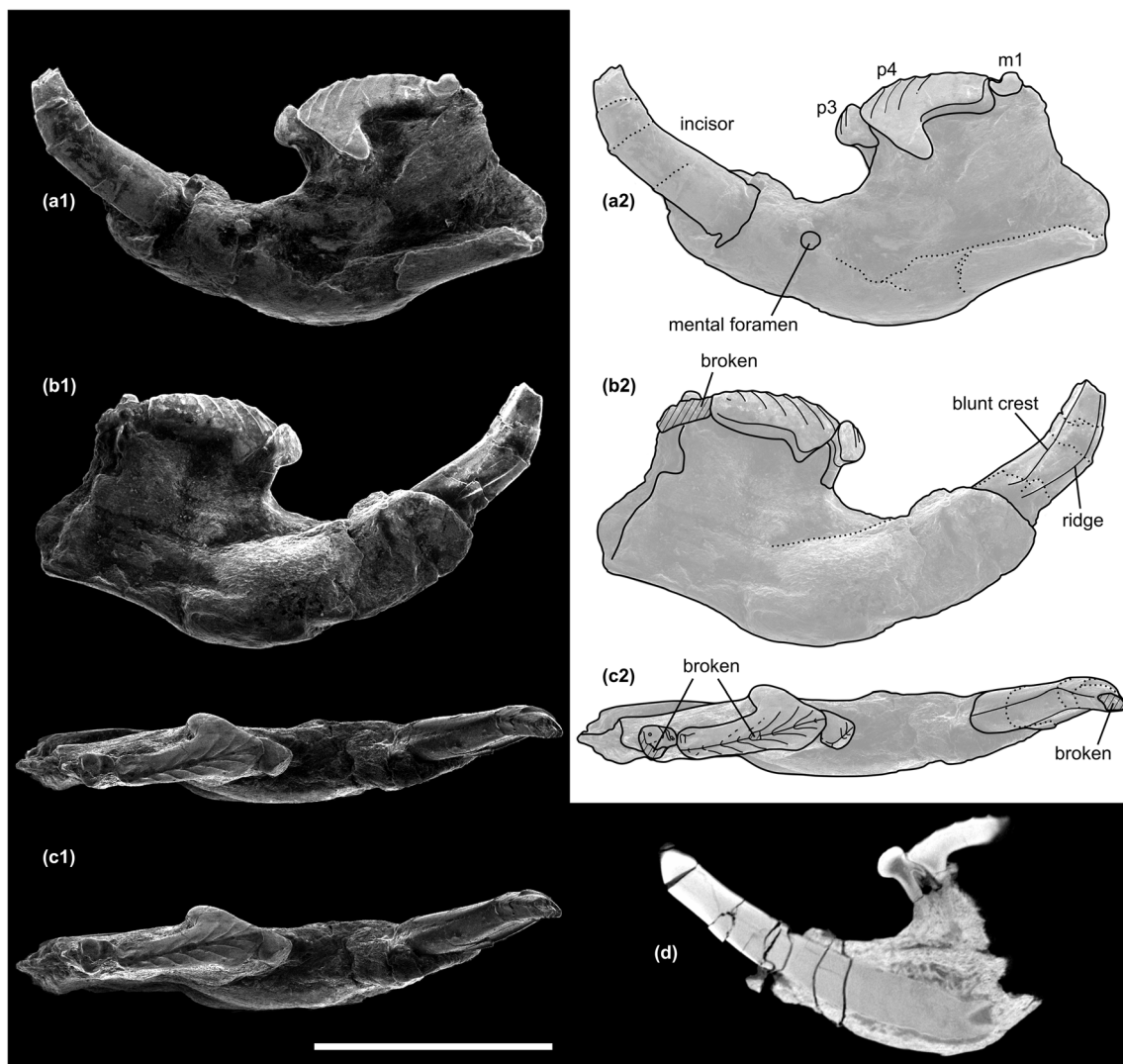


Fig. 2 The holotype (IVPP V22641) of *Dolichoprion lii*, gen. et sp. nov.; a partial left dentary with incisor, p3–p4, and the mesiolabial part of m1; Lower Cretaceous Fuxin Formation, Fuxin, Liaoning, northeastern China. **a–c** The specimen in **a** labial, **b** lingual, and **c** occlusal (anterior to right) views. Scanning electron micrographs (a1, b1, c1; c1 as

stereopair) and interpretive sketches (a2, b2, c2). **d** A nearly sagittal section of the left lower jaw showing roots of incisor and p3 reconstructed from microcomputed tomography images using AMIRA 5.3.2 software. Scale bar equals 5 mm

Diagnosis Relatively small eobaatarid multituberculate with lower jaw dental formula 1.0.? 2 . 2 ; lower incisor slender, completely covered with enamel; p3 double-rooted, triangular in lateral view; p4 mesiodistally long and dorsoventrally low, having eight serrations; m1 cusp formula 3:2, the first labial cusp being much smaller than the second and third ones; m2 cusp formula ?:2.

Differential Diagnosis Differs from the other eobaatarids in having a mesiodistally long and dorsoventrally low crown of p4 (mesiodistal length/height is about 2.55), and in having a triangular p3 rather than oval in lateral view. Differs from most other eobaatarids but resembles *Tedoribaatar* in possible loss of p2. Differs from *E. magnus* (but not *E. clemensi* Sweetman, 2009), *Liaobaatar*, and *Loxaulax* in having m1 with cusp

formula 3:2. Differs from *Eobaatar* in having a lower incisor completely covered with enamel. Differs from *Tedoribaatar* in having a double-rooted p3.

Description Only right and left lower jaw fragments and an isolated lower molar of an individual are preserved, and upper jaw elements including teeth have yet to be discovered. Both right and left dentaries are damaged and the posterior part of each dentary including the condyle and the coronoid process is not preserved (Figs. 2 and 3). The anterior part of the mandibular body bends anterodorsally. A mental foramen is situated at approximately 1 mm anterior to p3 and 2.5 mm above the ventral margin of the left dentary (Fig. 2). The foramen on the right dentary is estimated to be situated in an almost comparable position with the left one, although the exact position

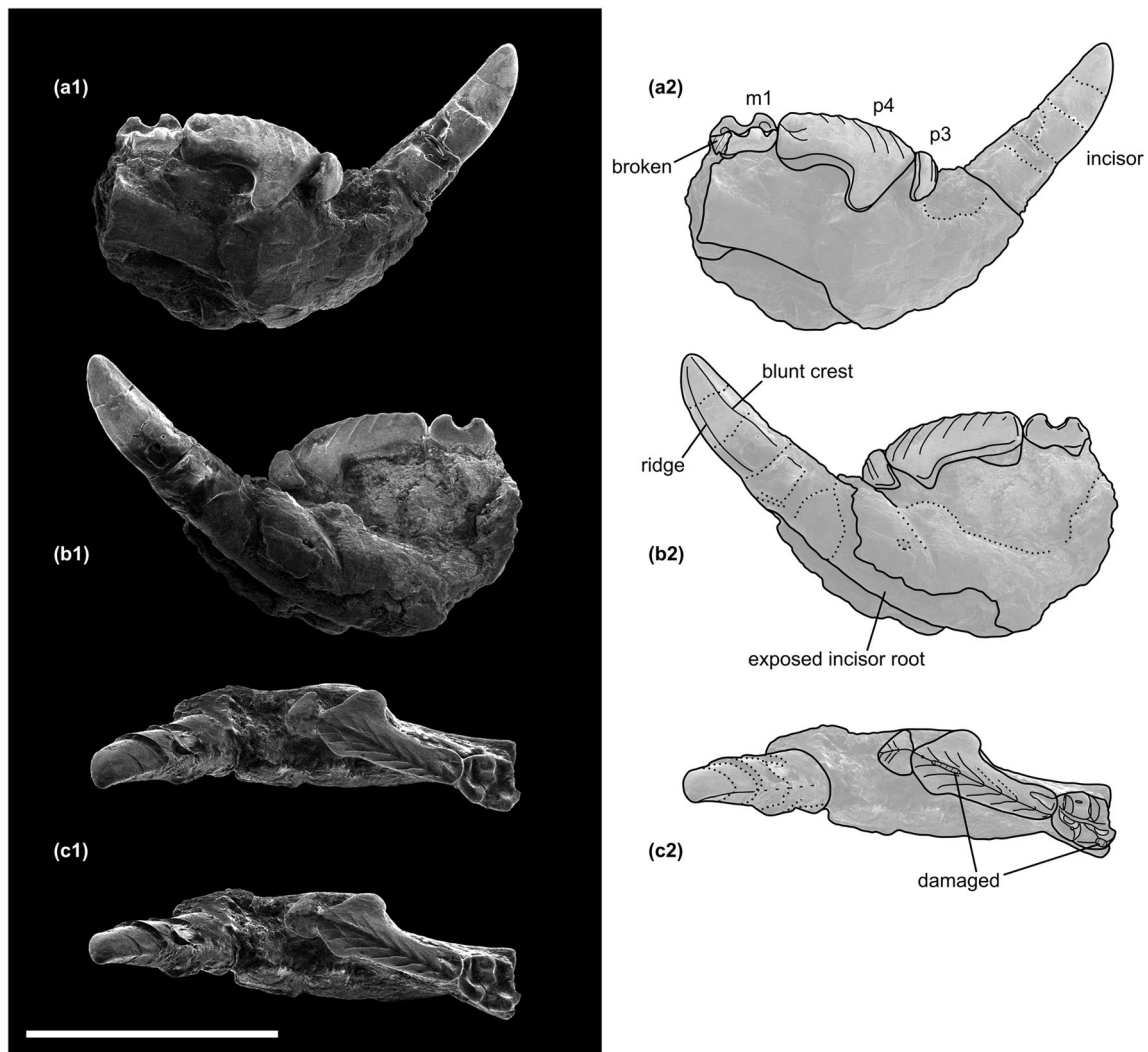


Fig. 3 The holotype (IVPP V22641) of *Dolichoprion lii*, gen. et sp. nov.; a partial left dentary with an incisor and p3–m1; Lower Cretaceous Fuxin Formation, Fuxin, Liaoning, northeastern China. **a–c** The specimen in **a**

labial, **b** lingual, and **c** occlusal (anterior to left) views. Scanning electron micrographs (a1, b1, c1; c1 as stereopair) and interpretive sketches (a2, b2, c2). Scale bar equals 5 mm

of the foramen is difficult to determine due to the damage. The masseteric fossa is not preserved on the dentaries, but on the right dentary the anteriormost part of the fossa is likely to weakly reach below the posterior root of the p4.

Both the right and left lower incisors are preserved but damaged (Figs. 2 and 3). The general outline of the lower incisor is morphologically similar to that of eobaatarids such as *Sinobaatar* from the same formation and *Hakusanobaatar* (Kusuhashi 2008; Kusuhashi et al. 2009b). It is a relatively slender but proportionally large tooth relative to the size of the dentary with rounded labial surface and more flattened lingual surface, and is thinner toward the tip of the tooth. The lingual surface is divided into a dorsal one-third and ventral two-thirds by a blunt crest, which is not related with wear, extending from the tip of the tooth toward the base, and the dorsal part faces more dorsally (Figs. 2 and 3). Along the ventral margin of

the lingual surface of the tooth, a ridge extends from the tip of the tooth to the base, and it extends slightly dorsally at the base of the tooth (Figs. 2 and 3). The root of the tooth extends far distally, reaching ventral to the mesial root of the p4 (Fig. 2d). Enamel completely covers the lower incisor.

Mesial to the p3, the alveolus of p2 is not present on the occlusal surface of the left lower jaw (Fig. 6a), indicating the absence of p2 at least on this jaw. This part of the right dentary has been damaged and deformed, and it cannot be determined whether the alveolus is present or absent. In reconstructed sections based on micro-CT data of the left lower jaw, there is a lower density space immediately mesial to the mesial root of p3 (Fig. 6b). It is not clear whether or not this space represents an alveolus for a tooth (p2, dp2, or dp3). If it is related with an alveolus, the tooth probably was a tiny non-functional tooth like p2 of other eobaatarid species from the same formation (Kusuhashi et al. 2009b).

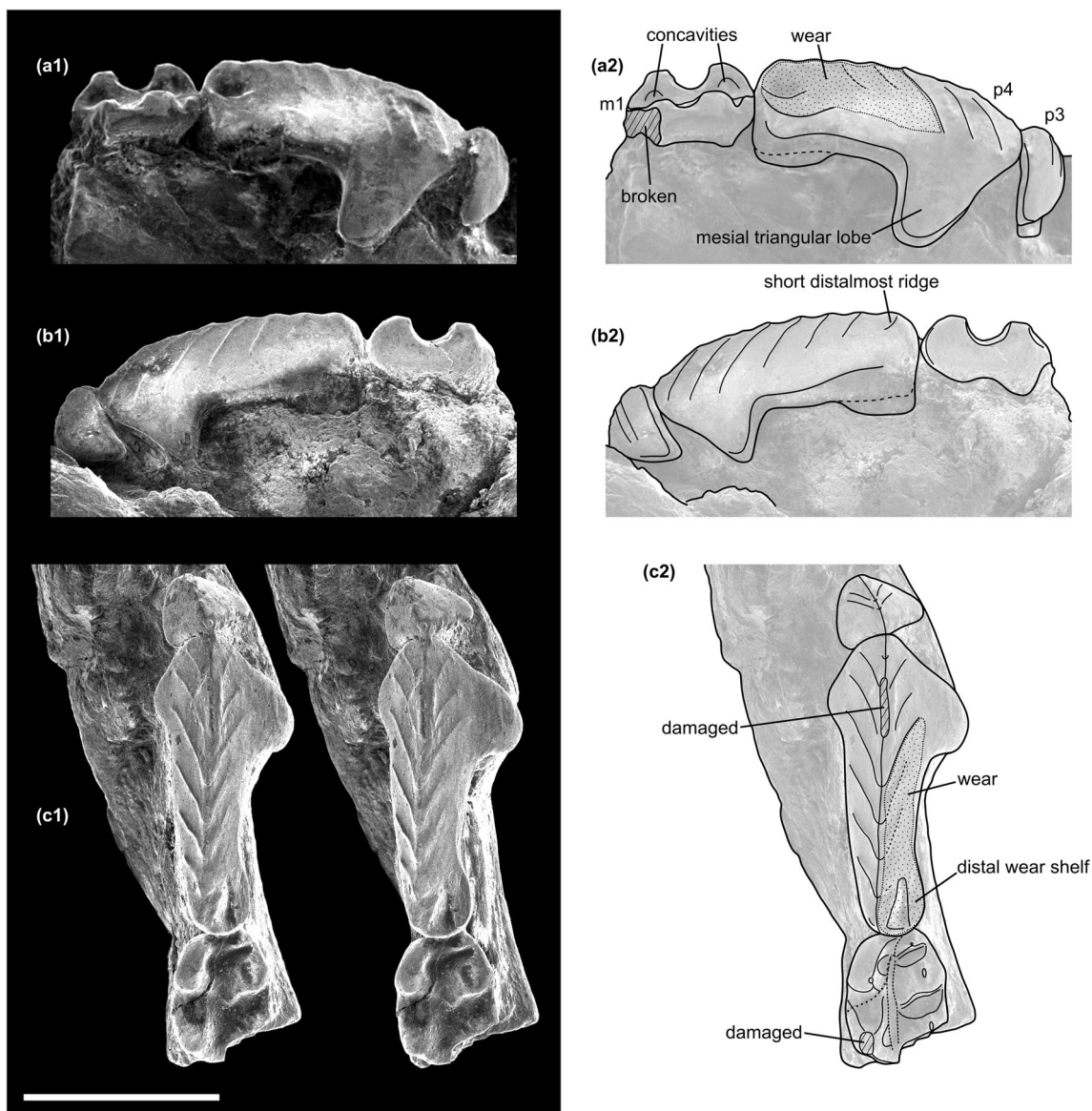


Fig. 4 The dentition of the holotype (IVPP V22641) of *Dolichoprion lii*, gen. et sp. nov.; Lower Cretaceous Fuxin Formation, Fuxin, Liaoning, northeastern China. **a–c** The right cheek teeth in **a** labial, **b** lingual, and **c**

occlusal (mesial to top) views. Scanning electron micrographs (a1, b1, c1; c1 as stereopair) and interpretive sketches (a2, b2, c2). Scale bar equals 2 mm

The lateral crown profile of p3 is triangular rather than rectangular or oval, being similar to that of *Heishanobaatar* from the same formation (Kusuhashi et al. 2010). It is a double-rooted tooth with a robust mesial root and a much thinner and distoventrally projecting distal root (Fig. 2d). On both the labial and lingual sides of the tooth, the ventralmost part of the crown forms a ventral to distoventral projecting lobe (Fig. 4). On the dorsal margin of the crown, there are two small serrations accompanied by ridges extending mesioventrally. The distal margin of p3 is almost equal in height to the mesial margin of p4, and p3 and p4 together form a shearing edge.

In lateral view, the crown of p4 is mesiodistally long and dorsoventrally low (Figs. 2, 3 and 4, Table 1). The ratio

between its mesiodistal length (L) and height (H, without mesial triangular lobe) is about 2.55 (L/H). It is not parallel-sided with an almost erect distal margin and a more procumbent mesial margin. The long dorsal margin of the crown is slightly arcuate, comparable to that observed in other eobaatarids such as *Eobaatar* and *Sinobaatar*. Although the dorsal margin is slightly eroded on the both right and left p4s, the serrations are distinct. There are eight serrations, and seven of them are accompanied by ridges on the lingual side of the crown (absent on the first serration), although the distalmost ridge is very short and bulged. The labial ridges were probably in the same condition as the lingual, but the distal four ridges are almost worn out on both right and left p4 (Fig. 4a). The first serration is tiny and weaker than the proceeding seven.

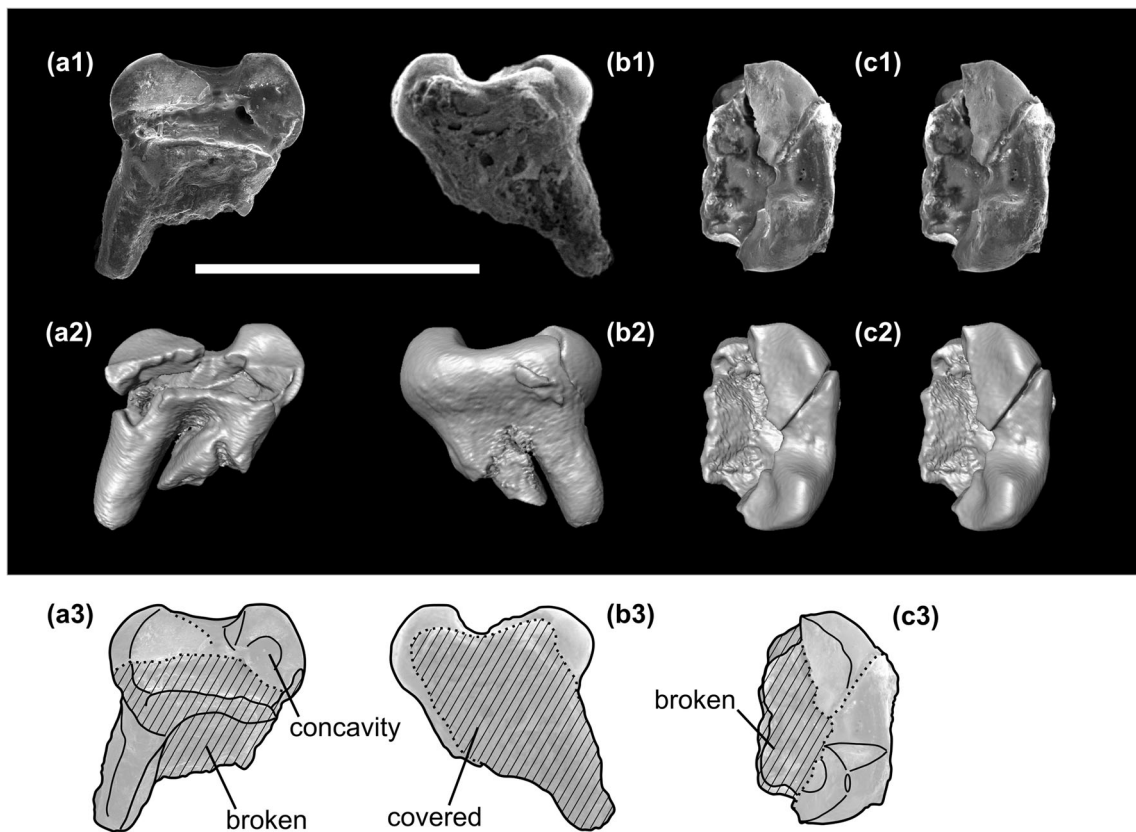


Fig. 5 The isolated left m2 of the holotype (IVPP V22641) of *Dolichoprion lii*, gen. et sp. nov.; Lower Cretaceous Fuxin Formation, Fuxin, Liaoning, northeastern China. **a–c** The specimen in **a** labial, **b** lingual, and **c** occlusal (mesial to top) views. Scanning electron

micrographs (a1, b1, c1), images reconstructed from micro-computed tomography images using AMIRA 5.3.2 software (a2, b2, c2), and interpretive sketches (a3, b3, c3). (c1) and (c2) Stereopairs. Scale bar equals 2 mm

The crown has a distinct and U-shaped mesial triangular lobe (= anterior triangular lobe of Kielan-Jaworowska et al. 2004) on its labial side projecting distoventrally (Fig. 4). The distal labial cusp on both right and left p4 is strongly worn, and a distal wear shelf is present at a relatively low position (Fig.

4a). The mesiodistally short distal wear shelf, which is comparable in relative size to those of *Sinobaatar* from the same formation, suggests that there was only one distal labial cusp, though the exact number of the cusps is unknown because of the wear. A large wear facet is present at the distolabial face of the crown dorsal to the level of the distal wear shelf; it reaches near the dorsal margin of the crown and extends mesially to the third ridge (Fig. 4a).

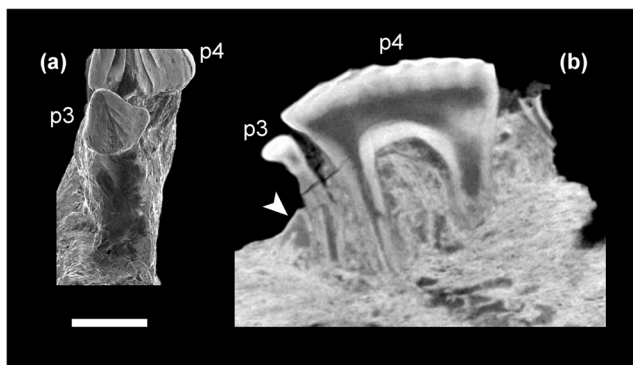


Fig. 6 The left lower jaw of the holotype (IVPP V22641) of *Dolichoprion lii*, gen. et sp. nov.; Lower Cretaceous Fuxin Formation, Fuxin, Liaoning, northeastern China. **a** A scanning electron micrograph of the p3 and dentary mesial to it in mesial view; **b** a nearly sagittal section of the dentary around p3 and p4. An arrow indicates the low density space in the dentary immediately mesial to the p3. Scale bar equals 1 mm

The distolabial part of the right m1 is preserved but broken, and the tooth is slightly eroded probably during a postmortem taphonomic process (Figs. 3 and 4). On the left lower jaw, only the mesiolabial part of m1 is preserved (Fig. 2). Because of the damage to the third labial cusp on the right m1, the exact cusp count of the labial cusp row is unknown. Judging from the size and morphology of the preserved part of the third labial cusp, the cusp formula of m1 is most likely to be 3:2. In the labial row, the second and third cusps are well separated from each other, whereas the first cusp is less separated but still distinct from the second (Fig. 4). The first cusp is much smaller than the second and third ones (Fig. 4). Because of damage, it is impossible to compare sizes of the second and third labial cusps. Original shapes of labial cusps are unknown because they are more or less worn and eroded. The labial

Table 1 Measurements (mm) of lower dentition in *Dolichoprion lii* gen. et sp. nov., *Dolichoprion* sp., other eobaatarid species, and *Heishanobaatar*. Measurement values of *Eobaatar magnus* are from Kielan-Jaworowska et al. (1987); those of *E. clemensi* are from Sweetman (2009); those of *Liaobaatar changi*, *S. fuxinensis*, and *S. xiei* are from Kusuhashi et al. (2009b); those of *Hakusanobaatar matsuo*,

Sinobaatar lingyuanensis, and *Tedoribaatar reini* are from Kusuhashi (2008); and those of *Heishanobaatar badaohaoensis* are from Kusuhashi et al. (2010). Abbreviations: H, height; L, mesiodistal length; W, labiolingual width. Note that the Table 1 of Kusuhashi et al. (2010) was not correctly arranged

	p3		p4		m1			m2	
	L	H	L	H ^a	L	W	L	W	
<i>Dolichoprion lii</i>									
IVPP V22641									
right	0.74	1.10	2.88	1.13	1.40	0.99	–	–	
left	0.70	1.10	2.90	1.14	–	–	1.44	–	
<i>Dolichoprion</i> sp.									
IVPP V14498 ^b	1.00	1.30	3.04	1.58					
<i>Eobaatar magnus</i>									
PIN 3101/57 ^c			3.6	2.1					
PIN 3101/53					1.8	1.1	1.8	1.4	
<i>E. clemensi</i>									
BMNH M 45482 ^c					1.4	0.9			
<i>Liaobaatar changi</i>									
IVPP V14489 ^c	2.2	2.7	6.8	4.6	2.5	2.0	2.7	1.9	
<i>Hakusanobaatar matsuo</i>									
SBEI 1736 ^c	1.0	1.4	3.5	2.1					
<i>Sinobaatar lingyuanensis</i>									
IVPP V12517 ^c	1.2	1.9	4.1	2.5					
<i>S. fuxinensis</i>									
IVPP V14160 ^c									
right	1.3	2.4							
left							2.1	–	
IVPP V14479	1.4	2.4	4.0	2.6	1.7	1.4	1.9	1.7	
<i>S. xiei</i>									
IVPP V14491 ^c	1.2	1.7	3.1	2.3	1.7	–	1.8	–	
<i>Tedoribaatar reini</i>									
SBEI 1570 ^c			3.7	2.4					
<i>Heishanobaatar triangulus</i>									
IVPP V14493 ^c	1.3	1.5	3.2	1.7	1.5	1.1			
IVPP V14484	1.2	1.5	3.6	2.3	1.6	1.3	1.8	1.4	

^a Height without the mesial triangular lobe

^b Newly measured

^c Holotype of the species

cuspid row is situated just distal to, and now almost as high as (because of the wear), the distal wear shelf of p4. The lingual cusps are now taller than the labial. They are crescentic with a round lingual and flat labial face, and are labiolingually thinner than the labial ones (Fig. 4). The two lingual cusps are subequal in size. The labial wall of the mesial cusp in the lingual row is ornamented by a faint concavity (Fig. 4). The distal cusp also has such a concavity, but it is less obvious than that of the mesial one probably due to erosion. The second

labial cusp is positioned slightly distal to the mesial lingual cusp, and the third labial cusp is estimated to be almost opposite to or positioned slightly distal to the distal lingual cusp.

An isolated left m2 is preserved, but the labial part of the crown and the distal root are broken and missing (Fig. 5). It has two lingual cusps of subequal height, and the mesial one is mesiodistally longer than the distal one. They are crescentic and face towards the middle of the tooth. The labial surface of the distal lingual cusp is ornamented by a shallow concavity (Fig. 5);

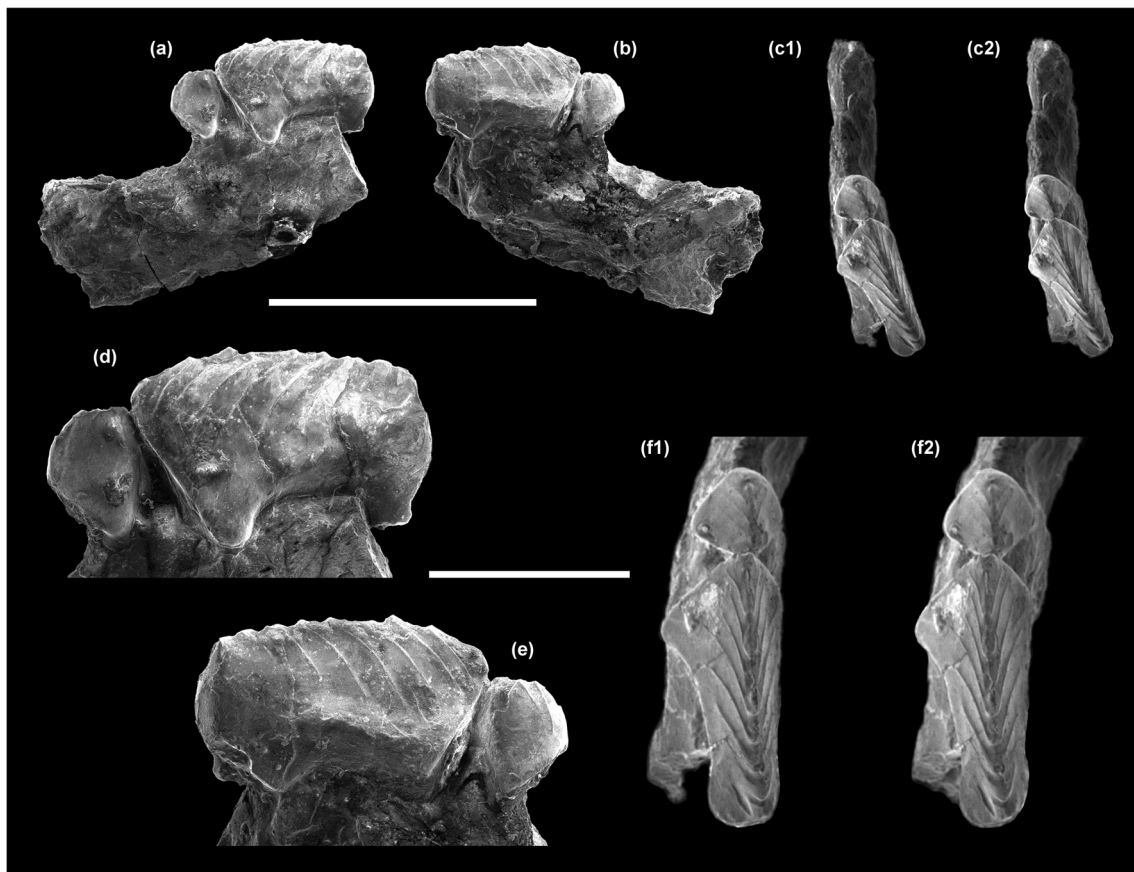


Fig. 7 Scanning electron micrographs of the specimen of *Dolichoprion* sp. (IVPP V14498); a fragment of left dentary with p3–p4; Lower Cretaceous Fuxin Formation, Fuxin, Liaoning, northeastern China. **a–c** The specimen in **a** labial, **b** lingual, and **c** occlusal (stereopair, anterior to

top) views; **d–f** premolars in **d** labial, **e** lingual, and **f** occlusal (stereopair, mesial to top) views. Scale bars for **(a)–(c)** and **(d)–(f)** equal 5 mm and 2 mm, respectively

such ornamentation of the mesial lingual cusp is unclear, probably due to postmortem erosion. The distolabial margin of the distal lingual cusp is slightly turned labially at its base.

Measurements See Table 1.

Remarks We are confident that left and right jaws and an isolated m2 of IVPP V22641 are of the same individual, because they were preserved overlapping each other. The isolated tooth is here identified as m2. The preserved cusps on the tooth are crescentic and face towards the middle of the tooth, being morphologically similar only to lingual cusps of lower molars in multituberculates from the same formation and *Eobaatar* (Kielan-Jaworowska et al. 1987; Kusuhashi et al. 2009b, 2010). The tooth is thus considered to be m1 or m2. The base of the mesiolabial part is preserved in each m1 of both the left and right jaws, and this part is also preserved in the isolated tooth, suggesting the tooth is m2. In *Eobaatar*, *Sinobaatar*, and *Heishanobaatar*, the lingual cusps of m1 are generally subequal in size, but the mesial cusp is mesiodistally longer than the distal one in m2 (Kielan-Jaworowska et al. 1987; Kusuhashi et al. 2009b, 2010). The tooth is, therefore, identified as left m2. This identification is also supported by the fact that the basal part of the distolabial margin

of the distal lingual cusp is slightly turned labially, suggesting that the medial valley between the labial and lingual cusp rows was not completely open distally. In eobaatarids, the medial valley of m1 is usually open both mesially and distally, and that of m2 is open mesially at least (Kielan-Jaworowska et al. 1987; Eaton and Cifelli 2001; Kusuhashi et al. 2009b).

Dolichoprion sp.

(Fig. 7 and Table 1)

Eobaataridae, gen. et sp. indet.; Kusuhashi et al. 2010: 1509, fig. 7.

Referred Specimen Fragment of left dentary with p3 and p4 (IVPP V14498; Fig. 7).

Locality and Horizon Xindi #3 coal mine, Fuxin, Liaoning, northeastern China; Early Cretaceous (Aptian to Albian); Fuxin Formation.

Description A description of the only known specimen (IVPP V14498) can be found in Kusuhashi et al. (2010).

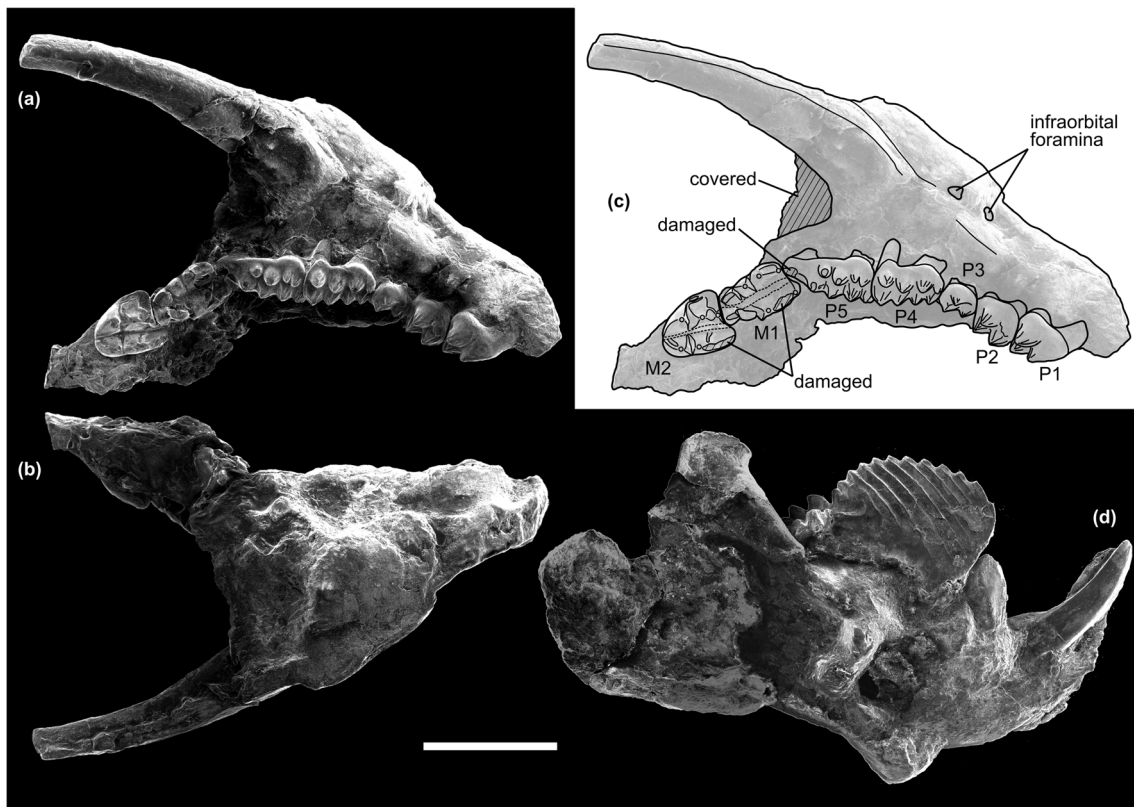


Fig. 8 a–c The specimen of *?Liaobaatar* sp. (IVPP V22642); a right upper jaw fragment with P1–P5 and M1–M2; Lower Cretaceous Fuxin Formation, Fuxin, Liaoning, northeastern China. a–b Scanning electron micrographs of the specimen in a ventral and b dorsal views; c an

interpretive sketch of a. d A scanning electron micrograph of the holotype (IVPP V14489) of *L. changi* for reference; a damaged right dentary with incisor and p2–m2; Lower Cretaceous Fuxin Formation, Fuxin, Liaoning, northeastern China. Scale bar equals 5 mm

Remarks The specimen is here attributed to *Dolichoprion* based on its dorsoventrally low crown of the p4, which is unique among eobaatarids. It also resembles *D. lii* in a triangular p3 in lateral view. It is, however, different from the type and only known specimen of *D. lii* (V22641) in various features (Fig. 7): it has four serrations on p3 rather than two; the p4 is parallel sided in lateral view with more erected mesial margin than in *D. lii*; the mesial triangular lobe is much less developed than *D. lii*; and the dorsal margin of the p4 is not as arcuate as that in *D. lii*. Because V14498 is not well preserved, and because currently there are not sufficient specimens to discuss intraspecific variations, we here tentatively assign V14498 to *Dolichoprion* sp.

Genus *Liaobaatar* Kusuhashi et al., 2009b

?Liaobaatar sp.

Specimen Examined A fragment of right upper jaw with P1–P5 and M1–M2 (IVPP V22642; Figs. 8 and 9, Table 2).

Locality and Horizon Zhenjiang (=Hanjiadian #6) coal mine, Fuxin, Liaoning, northeastern China; Early Cretaceous (Aptian to Albian); Fuxin Formation.

Description The specimen (IVPP V22642) is a right upper jaw fragment with premolars and molars. The right maxilla is preserved but damaged. The right nasal might be partly preserved on the dorsal part of the specimen, but it is hard to identify because the bones are badly crushed and no suture between the maxilla and nasal can be recognized. The zygomatic arch of the maxilla is preserved but damaged at its dorsal part (Fig. 8). The anterior zygomatic ridge is preserved. Anterior to the zygomatic arch, there are two damaged infraorbital foramina (Fig. 8). The anterior one is larger than the posterior one and situated above the distal root of P3. The posterior one is situated above the mesial root of P4.

P1 to P3 are similar in shape with three triangularly arranged cusps: one on the labial side and two on the lingual (Fig. 9). The mesiolingual face of the mesiolingual cusp of the P1 is slightly damaged. The crown of P1 is labiolingually compressed, but the other two teeth are less compressed than the P1. The distal cingulum, which is present on mesial upper premolars of *Sinobaatar* from the same formation (Kusuhashi et al. 2009b), is modestly present at the distolingual part of P1 and P2. It is least developed in P3. The mesial part of P2 and P3 hang over the distal cingulum of P1 and P2, respectively (Fig. 9). P1 is slightly larger than P2, and P3 is obviously smaller than the other two (Table 2). Three cusps on each tooth are ornamented with radiating ridges extended from the tips of

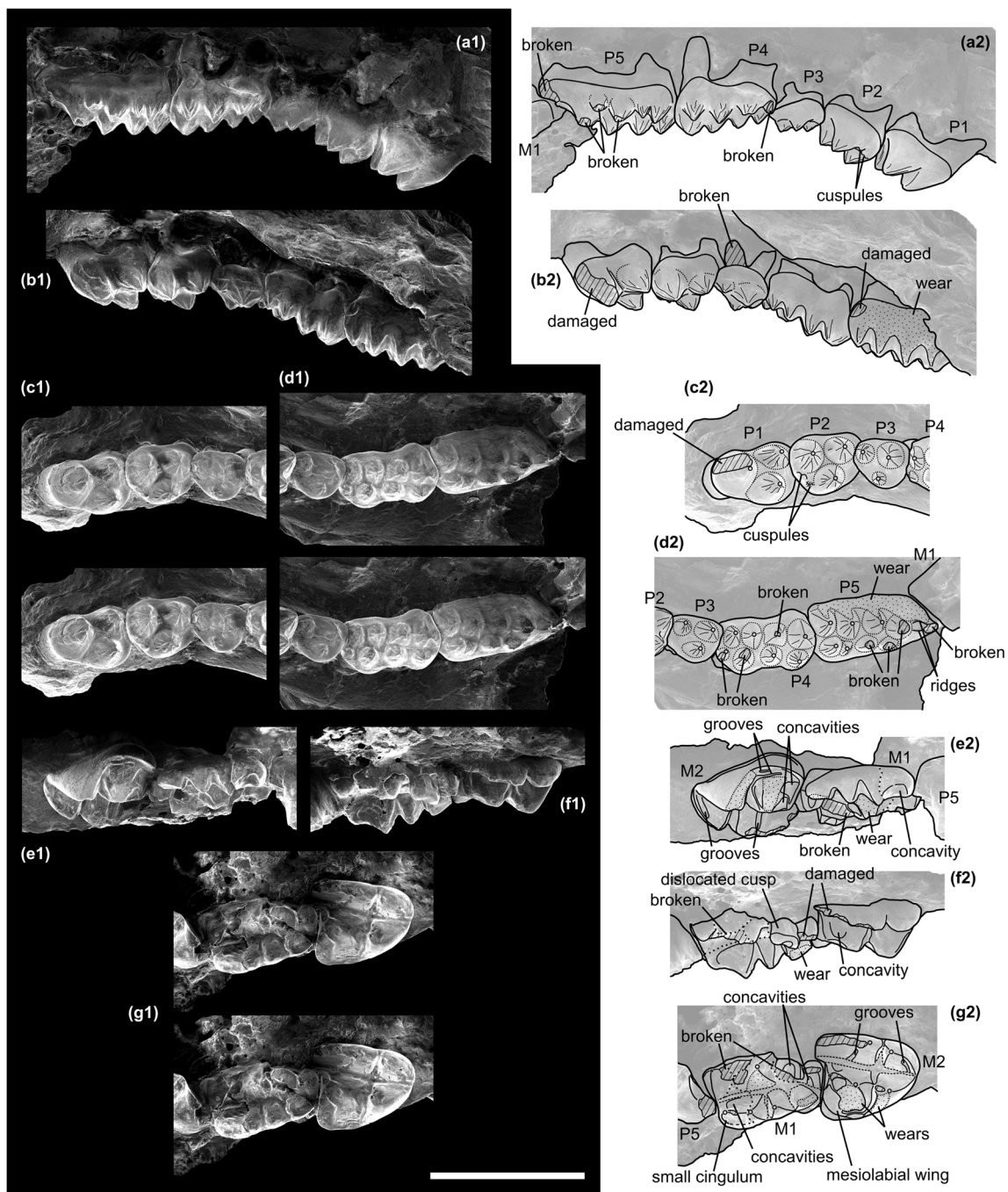


Fig. 9 Cheek teeth of the specimen of *?Liaobaatar* sp. (IVPP V22642); Lower Cretaceous Fuxin Formation, Fuxin, Liaoning, northeastern China. **a–b** P1–P5 in **a** labial and **b** lingual views; **c–d** occlusal views of **c** P1–P3, **d** P3–P5; **e–g** M1–M2 in **e** labial, **f** lingual, and **g** occlusal

views. Scanning electron micrographs (1; occlusal views as stereopairs) and interpretive sketches (2). Mesial to left in occlusal views. Scale bar equals 5 mm

the cusps; on surfaces facing the tooth margin, especially on the labial surface, these ridges are short and restricted to surfaces of the apical part of the cusps, and do not reach to the bases of the cusps. In P1 and P2, the three cusps are nearly subequal in size (Fig. 9). In both teeth, the labial one is slightly smaller than the other two, and the distolingual one is slightly larger than the mesiolingual one in P1, whereas the

mesiolingual cusp is slightly larger than but almost as tall as the distolingual one in P2. The distolingual cusp is obviously larger than the other two in P3, and the labial one is slightly smaller than the mesiolingual one (Fig. 9). Cuspules are not present on P1 and P3. There are at least three tiny cuspules at the mesiolabial part of the mesiolingual cusp on P2 (Fig. 9).

Table 2 Measurements (mm) of upper dentition in ?*Liaobaatar* sp. and other eobaatarid species. Measurement values of *Eobaatar magnus* are from Kielan-Jaworowska et al. (1987); those of *Hakusanobaatar matsuoii*, and *Sinobaatar lingyuanensis* are from Kusuhashi (2008); those

of *S. fuxinensis*, *S. xiei*, and ?Eobaataridae gen. et sp. indet. are from Kusuhashi et al. (2009b). Abbreviations: H, height; L, mesiodistal length; W, labiolingual width. M2 width was measured at the mesial widest part

	P1			P2			P3			P4			P5			M1			M2					
	L	W	H	L	W	H	L	W	H	L	W	H	L	W	H	L	W	H	L	W	H			
? <i>Liaobaatar</i> sp.																								
IVPP V22642	1.92	1.62	1.59	1.84	1.56	1.57	1.37	1.20	1.13	2.69	1.59	1.69	3.26	1.59	1.72	2.98	1.93	1.20	2.64	2.25	1.57			
<i>Eobaatar magnus</i>																								
GI PST 10–33																1.9	1.3	–						
PIN 3101/63										1.88												1.7	1.5	–
<i>Sinobaatar lingyuanensis</i>																								
IVPP V12517 ^a										1.7	0.8	–	2.1	1.1	–	1.8	1.4	–						
<i>S. fuxinensis</i>																								
IVPP V14160 ^a	2.1	–	1.2	1.7	–	1.1	1.4	–	0.9	1.8	–	0.9	2.5	–	1.6									
IVPP V14482	1.8	1.2	1.2	1.6	1.2	1.0	1.5	1.1	0.9	1.8	1.1	1.0	2.2	1.2	1.4	2.2	1.5	0.8	2.1	1.8	1.0			
<i>S. xiei</i>																								
IVPP V14491 ^a	1.4	1.1	0.9	1.3	1.0	0.9	1.0	0.9	0.8	1.3	1.0	0.9	2.0	1.1	1.3	1.7	1.5	0.7	1.9	1.8	0.9			
<i>Hakusanobaatar matsuoii</i>																								
SBEI 582 ^a	1.4	1.0	–	1.4	0.8	–	0.9	0.9	–	1.6	1.0	–	1.7	1.1	–	1.7	1.2	–						
?Eobaataridae gen. et sp. indet.																								
IVPP V14509 ^b	1.9	1.4	1.7																					

^a Holotype of the species

^b Tooth designation is not clear

The cusp formula of P4 is 4:4, but the first labial cusp is much smaller than the others (Fig. 9). The lingual cusps are positioned higher (ventrally) than the labial ones. The lingual cusps are arranged slightly obliquely (distolabial to the mesiodistal axis of the crown), and the fourth lingual cusp is situated at nearly the transverse midpoint of the crown. The tip of the second labial cusp is broken, and thus its size is difficult to compare with the other cusps. Judging from its base, it probably was almost the same size as the third labial cusp but slightly lower than the latter. The fourth labial cusp is slightly larger than but almost as tall as the third one. The cusps of the lingual row increase in size and height from mesial to distal, the fourth cusp being the largest and tallest. The height of the base of these cusps is also elevated distally. No additional cuspule is observed on the tooth. All cusps are ornamented with radiating fine ridges. The crown has bulging labial bases below the second and fourth labial cusps. Being different from *Sinobaatar* from the same formation, the crown is roughly rectangular in occlusal view with a posterior margin that is not oblique (Fig. 9).

The crown of P5 has two mesiodistally oriented cusp rows in occlusal view, with a cusp formula of 4:4, and it is not blade-like as *Sinobaatar* (Hu and Wang 2002; Kusuhashi et al. 2009b) (Fig. 9). All cusps are conical, and are ornamented with radiating fine ridges. The tips of the third and fourth labial cusps are broken and missing. Judging from their bases, the third one was probably the largest and tallest within the row (Fig. 9). The second labial cusp is much

smaller than the others in the row. It is positioned just distal and very slightly labial to the base of the first cusp, being not well separated from the latter. The fourth one probably was smaller than the first one. It is slightly more labially positioned than the others, and projects from a lower position than the others (Fig. 9). The first labial cusp is positioned slightly distal to the corresponding lingual cusp, and the third and fourth labial cusps are positioned slightly mesial to their corresponding lingual cusps; the second labial cusp is situated at just labial to the second lingual cusp. As the lingual cusps of P4, the lingual cusps of P5 are arranged slightly obliquely, and the fourth lingual cusp is situated at nearly the transverse midpoint of the crown (Fig. 9). The mesial three cusps increase in size and height distally. The tip of the fourth cusp is broken. Judging from its base, it was probably slightly smaller and lower than the third cusp. Distal to the cusps, the basal part of the crown is elongated distally, the distalmost part of which is slightly damaged. Here, the crown decreases in labiolingual width distally; this is mainly due to the distolingual margin of the tooth curving to face distolabially (Fig. 9). Two subparallel ridges extend distally and slightly labially from the base of the fourth lingual cusp, and the crown is somewhat concave between them (Fig. 9).

M1 is preserved but broken (Fig. 9). The cusp formula is most likely 4:4. The first labial cusp is situated at the mesiolabial corner of the crown. It is small and not well separated from the second cusp, instead they are connected by a ridge, being in a similar condition to *Sinobaatar* from the same formation (Kusuhashi et al. 2009b). The other labial

cusps are well separated from each other. The second labial cusp is the largest and tallest in the labial cusp row, and is mesiodistally longer than the others. The fourth labial cusp is substantially worn (Fig. 9), and it is difficult to compare its size with the others. There is a small cingulum near the mesiolabial base of the crown; its crested margin extends apically at its mesialmost part and joins with the first labial cusp (Fig. 9). The valley between the two cusp rows is oblique in distolabial orientation to the mesiodistal axis of the crown. Although the first lingual cusp is slightly damaged, it is the smallest cusp in the lingual cusp row. It is situated at the mesiolingual corner of the crown. The second and third cusps are estimated to be similar in size, and they are larger than the fourth one. The second labial cusp is positioned slightly mesial to the second lingual cusp, and the third labial cusp, which is now broken and dislocated, is estimated to be positioned about opposite to the embrasures between the second and third cusps of the lingual row. The positions of the fourth cusps of both rows are difficult to compare because of damage to the tooth. The distolingual wing (= posterolingual wing of Kielan-Jaworowska et al. 2004) is not preserved (Fig. 9); it is unknown whether the wing was absent in life or is broken on the specimen.

M2 is better preserved than M1, but the mesiolabial part of the crown and the first lingual cusp are slightly damaged. It is roughly trapezoidal in occlusal view (Fig. 9). The mesial margin of the tooth is slightly sigmoid in occlusal view, the lingual part protruding mesially with a longer lingual cusp row than that of the labial, but this is not as distinct as in *Loxaulax* (e.g., Clemens 1963; Clemens and Lees 1971). The cusp formula likely is 3:2. In the labial cusp row, the first cusp is much smaller and lower than the others, and the third one is slightly taller than the second (Fig. 9). As on M1, the first labial cusp is not well separated from the second and is connected with the latter by a ridge. The second labial cusp is mesiodistally longer than the third one. The labial face of the labial cusps are worn (Fig. 9). The lingual cusps are as high as or slightly lower than the second labial cusp. The first lingual cusp is much longer and also estimated to be higher than the second one. Its tip is positioned almost opposite the second labial cusp, and it has a long mesial tail extending mesially from the tip to the mesiolingual base of the crown. The labial face of this cusp is ornamented by vertically extending grooves (Fig. 9), which might suggest that this mesiodistally long cusp is a coalesced one. A mesiolabial wing (= antero-lateral wing of Kielan-Jaworowska et al. 1987) is present, and its mesiolabial corner curves apically. The ornamentation of the wing is not obvious because of wear; at the labial base of the second cusp, thin and nearly horizontal grooves are barely visible. There are concavities at the labial surface just below the ridge between the first and second labial cusps and the mesio-basal part of the labial surface of the crown (Fig. 9), but it is not clear whether these were present in life or not.

Measurements See Table 2.

Remarks The upper dentition for *Liaobaatar* is not known. Although we consider that the specimen is most likely an upper jaw of *Liaobaatar* based on its morphology and size of dentition as follows, we here conservatively attribute it to ?*Liaobaatar* sp. The number of premolars (five) and general morphology of the upper dentition of the specimen, such as three main cusps on P1–P3 and oblique cusp arrangement in the lingual cusp row of P5, compares best with those of eobaatarid multituberculates (Kielan-Jaworowska et al. 1987, 2004; Hu and Wang 2002; Kusuhashi 2008; Kusuhashi et al. 2009b). Molar morphology also resembles eobaatarids. V22642 is, therefore, considered to be the upper jaw of an eobaatarid multituberculate. A distinct difference of V22642 from the other eobaatarids is the large size of the posterior dentition (P4–M2): for example, its P4 and P5 are about 1.5–2 and 1.3–1.9 times as long as those in other eobaatarids, respectively (at least *Hakusanobaatar* and three species of *Sinobaatar*) (Table 2). *Liaobaatar* is the largest eobaatarid multituberculate known to date. Its p4 is approximately 1.5–2 times as large as those in other eobaatarids (Kusuhashi et al. 2009b), being comparable with the size differences of P4 and P5 between V22642 and other eobaatarids. Moreover, at least among eobaatarids, the combined lengths of P4–P5 and M1–M2 are comparable with the lengths of p4 and m1–m2, respectively (and thus the combined length of P4–M2 is nearly equal with that of p4–m2; Table 3). This is also the case in P4–M2 of V22642 and p4–m2 of *Liaobaatar changi* (Table 3). Mesial upper premolars are, conversely, proportionally smaller compared to P4–M2 in V22642; they are about as large as those of *S. fuxinensis* (Table 2). Although mesial portions of the dentaries in specimens of *L. changi* are deformed (right dentary of the type specimen, IVPP V14489; Kusuhashi et al. 2009b; fig. 18) (Fig. 8d) or broken (another referred specimen, V14483; Kusuhashi et al. 2009b; fig. 20), they are estimated to be proportionally short compared with *S. fuxinensis*, being compatible with relatively small mesial premolars of V22642. As V22642 was recovered from the same formation as *L. changi* and that there are no other multituberculates of comparable size to V22642 known from the Shahaai and Fuxin formations, we consider it probable that V22642 can be attributed to *Liaobaatar*.

There is an isolated upper premolar (V14506) recovered from the Shahaai Formation, which is described as a right mesial premolar (probably P1 or P2) of ?Eobaataridae, gen. et sp. indet. by Kusuhashi et al. (2009b; fig. 22) (Fig. 10). The labiolingually compressed crown of V14506 is similar to the P1 of V22642. V14506 has lingual cusps slightly larger than the labial one, as is the case in P1 (and P2) of V22642. A cusplule seen in V14506 is absent on

Table 3 Length relationships between upper and lower distal premolar(s) and molars in eobaatarids (including *Hakusanobaatar*). Measurement values (mm) of *Eobaatar magnus* are from Kielan-Jaworowska et al. (1987); those of *Hakusanobaatar matsuo*i and

Sinobaatar lingyuanensis are from Kusuhashi (2008); and those of *S. fuxinensis*, *S. xiei*, and *Liaobaatar changi* (lower) are from Kusuhashi et al. (2009b)

	Upper				Lower			Ratio		
	P4	P5	M1	M2	p4	m1	m2	P4–5/p4	M1–2/m1–2	P4–M2/p4–m2
<i>Eobaatar magnus</i>								0.92	1.00	0.96
PIN 3101/57 ^a					3.6					
PIN 3101/53						1.8	1.8			
GI PST 10-27 ^b	1.6									
GI PST 10–31, 24, 45 ^b		1.7								
GI PST 10–33			1.9							
PIN 3101/63				1.7						
<i>Sinobaatar lingyuanensis</i>								0.93	–	–
IVPP V12517 ^a	1.7	2.1		1.8	4.1					
<i>S. fuxinensis</i>								0.95	1.10	1.02
IVPP V14160 ^a	1.8	2.5						(1.02)		(1.06)
IVPP V14482	1.8	2.2	2.2	2.1						
IVPP V14499					4.2	1.8	2.1			
<i>S. xiei</i>								1.07	1.03	1.05
IVPP V14491 ^a	1.3	2.0	1.7	1.9	3.1	1.7	1.8			
<i>Liaobaatar changi</i>								0.88	1.08	0.96
IVPP V14489 ^a					6.8	2.5	2.7			
IVPP V14483					6.4	2.2		(0.93)		
IVPP V22642 ^c	2.69	3.26	2.98	2.64						
<i>Hakusanobaatar matsuo</i> i								0.94	–	–
SBEI 1736 ^a	1.6	1.7	1.7		3.5					

^a Holotype of the species

^b Tooth designation is not fully reliable

^c ?*Liaobaatar* sp.

P1 of V22642, but tiny cuspules are present on the P2 of the latter (the number and positions are different from V14506), suggesting a potential that cuspule(s) might be variably present on P1. There is, therefore, a possibility that V14506 is referable to the P1 of the same species with V22642. The crown size of V14506 is close to those of P1 and P2 of V22642 (Table 2), but it also matches that of P1 of contemporaneous *S. fuxinensis*. V14506 is, however, different from P1 (and P2) of V22642 with regard to its radiating ridges and the distal cingulum. The radiating ridges of the cusps of V14506 are finer and longer than those of P1 and P2 of V22642; they extend to the base of the cusps in V14506 on the surfaces facing the tooth margin (Kusuhashi et al. 2009b: fig. 22) (Fig. 10). The distal cingulum of V14506 is only very slightly developed, being less developed than P1 and P2 of V22642. Although these differences may be intraspecific or intrageneric variations, we still prefer to retain V14506 as ?Eobaataridae, gen. et sp. indet., and to wait for additional materials for further

investigation; ultimately, upper mesial premolars (P1–P3) with three cusps are not very diagnostic among eobaatarids.

Phylogenetic Analyses

The phylogeny of multituberculates is poorly established (e.g., Rougier et al. 1997; Kielan-Jaworowska and Hurum 2001). Our analyses were not intended to solve this problem but to roughly examine our attribution of the new genus, *Dolichoprion*, to the family Eobaataridae. We adopted the data matrix of Kielan-Jaworowska and Hurum (2001). In their matrix, characters regarding p3 (24, 25, and 26) of *Eobaatar* were coded as 0, 2, and 1, but we revised all of these into unknown because, as far as published, the crown of p3 is not known for *Eobaatar*. We added some genera to the matrix of Kielan-Jaworowska and Hurum (2001). The specimen described above as ?*Liaobaatar* sp. (V22642) is here treated as a member of the genus. Although all the considered taxa should be

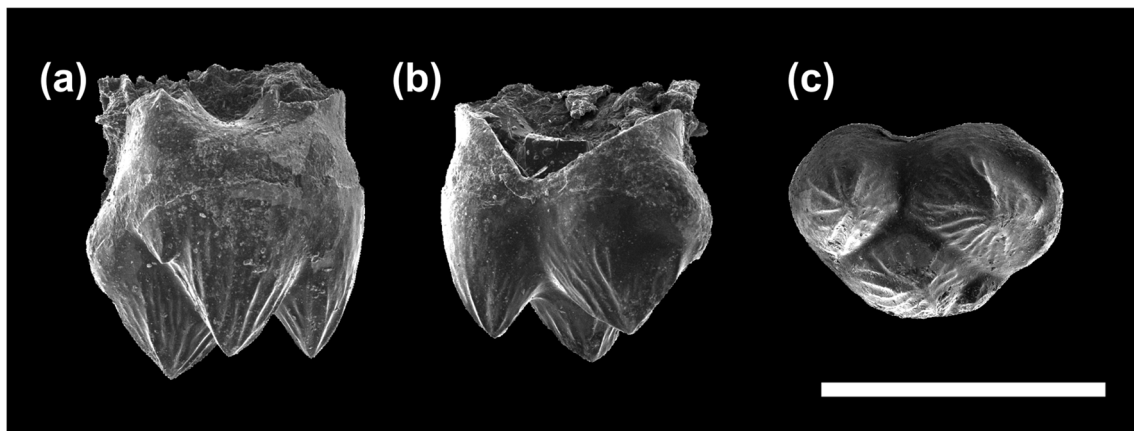


Fig. 10 Scanning electron micrographs of the specimen of ?Eobaataridae, gen. et sp. indet. (IVPP V14506, previously reported by Kusuhashi et al. 2009b); an isolated right upper premolar; Lower

Cretaceous Shai Formation, Badaohao, Heishan, Liaoning, northeastern China. **a** Labial, **b** lingual, and **c** occlusal (mesial to left) views. Scale bar equals 2 mm

included in one analysis, to avoid the result being strongly affected by unknown character states of added genera, we analyzed five different matrices: (1) the matrix of Kielan-Jaworowska and Hurum (2001) with character states of *Sinobaatar* and *Liaobaatar*, which are better known than the other multituberculates from the Lower Cretaceous of East Asia; (2) the matrix (1) + *Hakusanobaatar*; (3) the matrix (1) + *Dolichoprion*; (4) the matrix (2) + *Dolichoprion*, and (5) the matrix (1) + *Heishanobaatar*.

All analyses show the monophyly of the Cimolodonta (Fig. 11), and this is the same result as Kielan-Jaworowska and Hurum (2001). The TNT analysis of the matrix (1) obtained 557 trees of 216 steps. The strict consensus (SC) tree of these trees shows a polytomy of all ‘plagiaulacidan’ genera with the Cimolodonta, but the 50% majority rule (MR) tree shows a clade of *Eobaatar*, *Liaobaatar*, and *Sinobaatar* (Fig. 11a). This clade is also supported by the SC tree from 2,100 trees (216 steps) of PAUP* analysis of the same matrix. The clade is also present in the SC tree from 102 trees (216 steps) obtained by TNT analysis of the matrix (2) as the sister taxon of the clade *Hakusanobaatar* and Cimolodonta (Fig. 11b), and the similar SC tree was obtained by the PAUP* analysis (840 trees of 216 steps). The SC tree (725 trees of 217 steps) obtained by TNT analysis of the matrix (3) shows, again, polytomy of all ‘plagiaulacidan’ genera with Cimolodonta, whereas the MR tree shows a clade of *Dolichoprion*, *Eobaatar*, *Liaobaatar*, and *Sinobaatar*, which is also supported by the PAUP* analysis (MR tree, 10,460 trees, 217 steps) (Fig. 11c). *Dolichoprion*, *Eobaatar*, *Hakusanobaatar*, *Liaobaatar*, and *Sinobaatar* compose a polytomy with Cimolodonta in the SC tree (240 trees of 217 steps) by the TNT analysis of the matrix (4), and the latter four genera compose a polytomy with a clade of *Dolichoprion* and Cimolodonta in the MR tree (Fig. 11d). The same results were obtained by the PAUP* (9,520 trees, 217 steps). In the MR trees obtained by the TNT (120 trees of 216 steps) and the PAUP* (480 trees of 216 steps) analyses of the matrix (5), *Heishanobaatar* is placed as

one of the sister taxa of a clade including *Arginbaatar*, *Eobaatar*, *Liaobaatar*, *Sinobaatar*, and Cimolodonta (Fig. 11e).

Discussion and Concluding Remarks

Dolichoprion lii shows various affinities to the Eobaataridae. The lower p4 forms a shearing edge with (and only with) the p3 in *D. lii*. This condition is seen in plagiaulacids, eobaatarids (except for *Liaobaatar*), and *Arginbaatar*, but not in early ‘plagiaulacidans’ and cimolodontans (e.g., Trofimov 1980; Kielan-Jaworowska et al. 1987, 2004; Hu and Wang 2002; Kusuhashi 2008; Kusuhashi et al. 2009b, 2010). The p4 of *Arginbaatar* has a fully arcuate dorsal margin and more than 15 serrations (Trofimov 1980; Kielan-Jaworowska et al. 1987), being obviously different from that of *D. lii*. The double-rooted p3 of *D. lii* is triangular in lateral view, a condition previously known only in plagiaulacids (Kielan-Jaworowska and Hurum 2001; Kielan-Jaworowska et al. 2004) and *Heishanobaatar* (Kusuhashi et al. 2010), but the p3 of *D. lii* is much more reduced in size than those of plagiaulacids and shows an intermediate state between plagiaulacids and other eobaatarids. The slender lower incisor, the mesiodistally elongated p4 with eight serrations and probably single distal labial cusp also suggest that *D. lii* belongs to the Eobaataridae. The general morphology of the molars is consistent with those of eobaatarids.

The attribution of *Dolichoprion* to the Eobaataridae is modestly supported by the result of phylogenetic analyses. We consider the clade composed of *Eobaatar*, *Liaobaatar*, and *Sinobaatar*, which was obtained by the analyses of the matrices (1) and (2), as the family Eobaataridae (Figs. 11a, b). The results of the analyses (3) shows a clade of *Dolichoprion*, *Eobaatar*, *Liaobaatar*, and *Sinobaatar* (Fig. 11c), suggesting that *Dolichoprion* is a member of the family. These results are not supported by analyses (4) (Fig. 11d), but the synapomorphy of

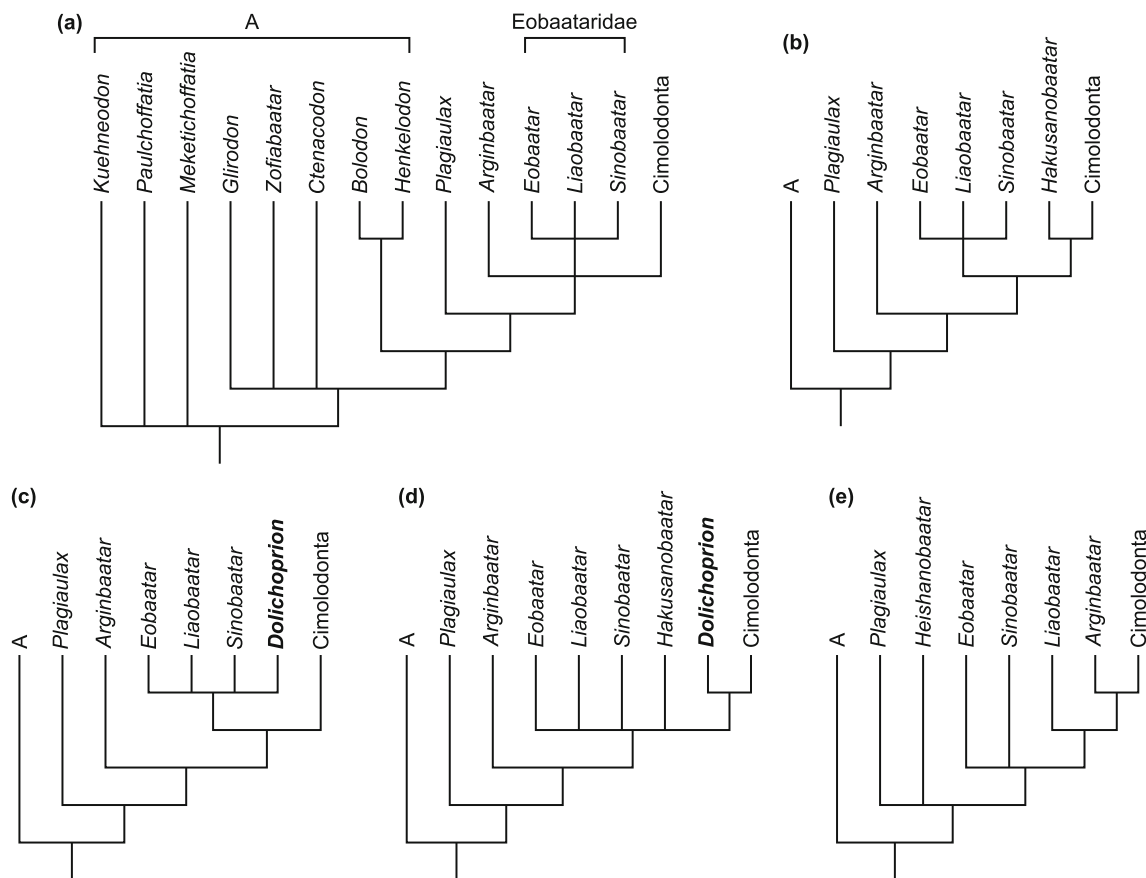


Fig. 11 Phylogenetic (50% majority rule) trees obtained by analyses using data matrices slightly modified from Kielan-Jaworowska and Hurum (2001) with **a** *Liaobaatar* and *Sinobaatar* (matrix/analysis 1 in the text), **b** *Liaobaatar*, *Sinobaatar*, and *Hakusanobaatar* (matrix/analysis 2), **c** *Liaobaatar*, *Sinobaatar*, and *Dolichoprion*, gen. nov. (matrix/

analysis 3), **d** *Liaobaatar*, *Sinobaatar*, *Hakusanobaatar*, and *Dolichoprion* (matrix/analysis 4), and **e** *Liaobaatar*, *Sinobaatar*, and *Heishanobaatar* (matrix/analysis 5). The interrelationship among the Cimolodonta is not shown. Estimated phylogeny among group A (including eight genera) is not necessarily the same between each tree

the clade of *Dolichoprion* and Cimolodonta is only the absence of p2. Among eobaatarids, p2 is reduced in size and morphology (Kielan-Jaworowska et al. 1987; Hu and Wang 2002; Kusuhashi 2008; Kusuhashi et al. 2009b), and thus the absence of p2 is not sufficient to completely deny the attribution of *Dolichoprion* to the Eobaataridae. It is impossible to discuss further based on the present specimens, and we here conclude that *Dolichoprion* is most likely an eobaatarid genus.

Hakusanobaatar is placed outside of this clade in the analysis (2), and it forms a clade with the Cimolodonta (Fig. 11b). The synapomorphy of the clade of *Hakusanobaatar* and the Cimolodonta is, however, only the cusp formula of P4 (character 18 of the matrix). In fact, *Hakusanobaatar* has six cusps on the middle cusp row of its P5 (the ‘plagiaulacidan’ P5 is probably homologous with the cimolodontan P4 as discussed by Kusuhashi 2008), but the morphology of its P5 is rather plesiomorphic, being intermediate between pinheirodontids, such as *Lavocatia* Canudo and Cuenca-Bescós 1996, and *Sinobaatar* (Kusuhashi 2008). Taking the results of the analyses (4), in which *Hakusanobaatar* composes a polytomy with

Eobaatar, *Liaobaatar*, and *Sinobaatar* (Fig. 11d), into account, we here tentatively consider that *Hakusanobaatar* is either a member of the Eobaataridae or a closely related taxon. The results of the analyses (5) suggest that the attribution of *Heishanobaatar* to the Eobaataridae is questionable (Fig. 11e). More complete specimens are, again, necessary for further discussion.

The lower incisor of *D. lii* is completely covered by enamel, and it shares this character with *Liaobaatar*, *Hakusanobaatar*, and *Sinobaatar* (Kusuhashi 2008; Kusuhashi et al. 2009b, 2010), but is different from *Eobaatar*, which has a limited enamel band on the lower incisor (Kielan-Jaworowska et al. 1987). Eobaatarids usually have three lower premolars (p2–p4). *Dolichoprion lii* probably has only two (at least permanent) premolars, further distinguishing *D. lii* from other eobaatarids except for *Tedoribaatar*, also reported as having only two lower premolars (Kusuhashi 2008). *Dolichoprion lii* is, however, different from *Tedoribaatar* in having a double-rooted p3.

Dolichoprion lii can be clearly distinguished from the other eobaatarids by its mesiodistally long and dorsoventrally low

crown of p4 (e.g., Kielan-Jaworowska et al. 1987, 2004; Hu and Wang 2002; Kusuhashi 2008; Kusuhashi et al. 2009b, 2010; Miyata et al. 2016). The ratio 2.55 (L/H) of the tooth is much larger than those of other eobaatarids (which range about 1.3–1.9). The posterior part of the p4 tentatively assigned to *Iberica hahni* Badiola et al., 2011, seems to have a taller crown than *D. lii*.

The m1 cusp formula of *D. lii* is most likely to be 3:2. *Dolichoprion lii* resembles *E. clemensi* and *S. xiei* (Kusuhashi et al. 2009b; Sweetman 2009), and differs from *E. magnus* (4:2; Kielan-Jaworowska et al. 1987), *Janumys* (4:3; Eaton and Cifelli 2001), *Liaobaatar* (2–3:3; Kusuhashi et al. 2009b), *Loxaulax* (4:3; Woodward 1911; Simpson 1928), and *S. fuxinensis* (4:2; Kusuhashi et al. 2009b) in the cusp formula of m1. A broken m1 attributed to Eobaataridae, gen. et sp. indet., from northern Germany was reported to have three lingual cusps, the mesialmost one of which is much smaller than the others (Martin et al. 2016). If this is correct, *D. lii* is different from this specimen in having only two lingual cusps. The description of the specimen is, however, problematic; they designate the tooth as a right m1 (Martin et al. 2016: 175), and described the smallest cusp as the mesialmost cusp in the lingual cusp row. However, if it is a right m1 and the smallest cusp is the mesialmost one, the preserved portion of the tooth should be the labial part rather than lingual; they actually indicated the external side of the preserved cusp row as labial in the caption of their Fig. 4k. The preserved cusp row of the specimen is likely to be the labial part of the tooth rather than lingual, because in eobaatarids the mesialmost labial cusp on m1 is often much smaller than the others (at least in *E. clemensi*, *Janumys*, *Liaobaatar*, *S. xiei*, *S. fuxinensis*, and *D. lii*; Eaton and Cifelli 2001; Kusuhashi et al. 2009b; Sweetman 2009) and not well separated from the second one as seen in the German specimen (at least in *S. xiei* and *S. fuxinensis*; Kusuhashi et al. 2009b). Additionally, the lingual cusps of m1 are usually more crescentic than cusps seen in the German specimen (Kielan-Jaworowska et al. 1987; Sweetman 2009; Kusuhashi et al. 2009b, 2010). If this is true and the specimen has three labial cusps, *D. lii* shares the number with that specimen. The m2 of *D. lii* has two lingual cusps, and all other eobaatarids whose m2s are known, including m2 tentatively assigned to *Janumys* and that tentatively assigned to *E. clemensi*, have the same number of lingual cusps (Butler and Ford 1977; Kielan-Jaworowska et al. 1987; Eaton and Cifelli 2001; Kusuhashi et al. 2009b, 2010). These differences and similarities between *D. lii* and the other eobaatarid species validate that *D. lii* is a new genus and species of the Eobaataridae, although it cannot be compared with *Monobaatar*, which is only known from the upper dentition.

Dolichoprion lii is the sixth multituberculate species described from the Shihai and Fuxin formations. Within these six species, four of them belong to the Eobaataridae. *Dolichoprion lii*, together with the other multituberculates

described from the formations, suggests that multituberculates, especially eobaatarids, were already taxonomically diverse in the mammalian fauna of East Asia at that time. As mentioned earlier, among the mammalian fauna from the underlying Jehol Group in the same geographic area, only one eobaatarid species, *S. lingyuanensis*, has been reported to date. Mammals described from the Jehol Group are, however, very biased toward well-preserved (and high-impact) specimens, and thus it is difficult to say whether or not the faunal composition estimated from the described materials represents actual one. The timing when they started diversification within the Asian mammalian fauna is, therefore, still unclear, but multituberculates from the Shihai and Fuxin formations demonstrate that it was before the late Early Cretaceous.

Acknowledgments We would like to express our sincere gratitude to late Z.-L. Chang (Investigation Team No. 107, Northeast Coalfield Geological Bureau, Fuxin, China) for his assistance, advice, and support to this study, and we dedicate this paper to the memory of him. We also thank S.-H. Xie, C.-K. Li, Y.-M. Hou, as well as many other colleagues and technicians of IVPP, for their various and substantial supports to this study. H. Saegusa and T. Ikeda (Museum of Nature and Human Activities, Hyogo, Japan) kindly allowed us to use AMIRA 5.3.2 software at their museum. B. M. Davis (University of Louisville) kindly helped us with improving English of the manuscript. This paper is greatly improved by comments and advice of anonymous reviewers and J. R. Wible (Carnegie Museum of Natural History), editor-in-chief.

Funding This study was supported by the Strategic Priority Research Program (B) of Chinese Academy of Sciences (no. XDB18000000), the National Natural Science Foundation of China (no. 41688103, 41541015), and the Grant-in-Aid for Young Scientists (B) (no. 24740349, 16K17830) of Japan Society for the Promotion of Science.

Compliance with Ethical Standards

Conflict of Interest The authors declare that they have no conflict of interest.

Appendix

Character states of *Dolichoprion*, gen. nov., *Hakusanobaatar*, *Heishanobaatar*, *Liaobaatar*, and *Sinobaatar* for the data matrix of Kielan-Jaworowska and Hurum (2001).

Dolichoprion: 1[?]; 2[?]; 3[?]; 4[?]; 5[?]; 6[?]; 7[?]; 8[?]; 9[?]; 10[?]; 11[?]; 12[?]; 13[?]; 14[?]; 15[?]; 16[?]; 17[?]; 18[?]; 19[?]; 20[0]; 21[0]; 22[1]; 23[1]; 24[1]; 25[2]; 26[1]; 27[0]; 28[1]; 29[1]; 30[1]; 31[2]; 32[2]; 33[?]; 34[1]; 35[?]; 36[0]; 37[0]; 38[0]; 39[1]; 40[?]; 41[?]; 42[?]; 43[?]; 44[?]; 45[?]; 46[?]; 47[?]; 48[?]; 49[?]; 50[?]; 51[?]; 52[?]; 53[?]; 54[?]; 55[?]; 56[?]; 57[?]; 58[?]; 59[?]; 60[?]; 61[?]; 62[?]

Hakusanobaatar: 1[?]; 2[?]; 3[?]; 4[0]; 5[1]; 6[0]; 7[0]; 8[0]; 9[2]; 10[0]; 11[2]; 12[0]; 13[0]; 14[0]; 15[?]; 16[?]; 17[?]; 18[1]; 19[1]; 20[0]; 21[0]; 22[1]; 23[0]; 24[1]; 25[2]; 26[1]; 27[0]; 28[1]; 29[1]; 30[1]; 31[?]; 32[?]; 33[?]; 34[1];

35[?]; 36[?]; 37[?]; 38[?]; 39[?]; 40[?]; 41[?]; 42[?]; 43[?]; 44[?]; 45[?]; 46[?]; 47[?]; 48[?]; 49[?]; 50[?]; 51[?]; 52[?]; 53[?]; 54[?]; 55[?]; 56[?]; 57[?]; 58[?]; 59[?]; 60[?]; 61[?]; 62[?]

Heishanobaatar: 1[?]; 2[?]; 3[?]; 4[?]; 5[?]; 6[?]; 7[?]; 8[?]; 9[?]; 10[?]; 11[?]; 12[?]; 13[?]; 14[?]; 15[?]; 16[?]; 17[?]; 18[?]; 19[?]; 20[0]; 21[0]; 22[1]; 23[0]; 24[0]; 25[2]; 26[1]; 27[0]; 28[1]; 29[1]; 30[?]; 31[2]; 32[2]; 33[2]; 34[1]; 35[0]; 36[0]; 37[0]; 38[0]; 39[1]; 40[?]; 41[?]; 42[?]; 43[?]; 44[?]; 45[?]; 46[?]; 47[?]; 48[?]; 49[?]; 50[?]; 51[?]; 52[?]; 53[?]; 54[?]; 55[?]; 56[?]; 57[0]; 58[0]; 59[?]; 60[0]; 61[?]; 62[?]

Liaobaatar: 1[?]; 2[?]; 3[?]; 4[?]; 5[?]; 6[0]; 7[0]; 8[0]; 9[2]; 10[0]; 11[?]; 12[?]; 13[?]; 14[0]; 15[?]; 16[0]; 17[?]; 18[0]; 19[1]; 20[0]; 21[0]; 22[1]; 23[0]; 24[1]; 25[2]; 26[1]; 27[0]; 28[2]; 29[1]; 30[1]; 31[2]; 32[2]; 33[2]; 34[1]; 35[0]; 36[0]; 37[0]; 38[0]; 39[1]; 40[?]; 41[?]; 42[?]; 43[2]; 44[0]; 45[?]; 46[?]; 47[?]; 48[?]; 49[?]; 50[?]; 51[?]; 52[?]; 53[?]; 54[?]; 55[?]; 56[?]; 57[0]; 58[0]; 59[?]; 60[0]; 61[?]; 62[?]

Sinobaatar: 1[?]; 2[0]; 3[1]; 4[0]; 5[1]; 6[0]; 7[0]; 8[0]; 9[2,3]; 10[0]; 11[2]; 12[0]; 13[0]; 14[0]; 15[2]; 16[0]; 17[0]; 18[0]; 19[0,1]; 20[0]; 21[0]; 22[1]; 23[0]; 24[1]; 25[2]; 26[1]; 27[0]; 28[1,2]; 29[1]; 30[1]; 31[2]; 32[2]; 33[2]; 34[1]; 35[0]; 36[0]; 37[0]; 38[0]; 39[1]; 40[0]; 41[1]; 42[?]; 43[2]; 44[0]; 45[?]; 46[0]; 47[1]; 48[?]; 49[0]; 50[?]; 51[?]; 52[?]; 53[?]; 54[?]; 55[?]; 56[?]; 57[0]; 58[0]; 59[?]; 60[0]; 61[?]; 62[?]

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