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NEW MULTITUBERCULATE MAMMALS FROM THE LOWER CRETACEOUS (SHAHAI AND FUXIN FORMATIONS), NORTHEASTERN CHINA

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ABSTRACT—Two eobaatarid multituberculates, *Heishanobaatar triangulus* gen. et sp. nov. and Eobaataridae gen. et sp. indet., and an ?albionbaatarid multituberculate, *Kielanobaatar badaohaoensis* gen. et sp. nov., from the Lower Cretaceous (Aptian to Albian) Shahai and Fuxin formations in Liaoning Province, northeastern China, are described. *Heishanobaatar triangulus* is a moderate-sized multituberculate characterized by lower jaw dental formula 1.0.3.2, slender lower incisor, single-rooted p2, triangular p3 in lateral view, p4 with eight serrations, m1 with cusp formula 2:2, and m2 with cusp formula 1 (coalesced):2. *Kielanobaatar badaohaoensis* is characterized by upper anterior premolars with relatively flat occlusal surfaces, roughly pentangular P1 in occlusal view, P1 and P2 with three cusp rows (cusp formulae 1:3:2), and P3 with four cusps (cusp formula 2:2). Together with already described three species of eobaatarids from the same localities, they demonstrate that there were quite diverse multituberculates in Asia in the late Early Cretaceous, and suggest that the mammalian fauna known from the Shahai and Fuxin formations probably show a transitional state from the mammalian fauna of the Yixian Formation to Late Cretaceous Asian faunas.

INTRODUCTION

Multituberculates are an order of mammals that appeared in the Middle Jurassic, and continuously evolved and diversified through the rest of the Mesozoic and Paleogene until their extinction in the Eocene to Oligocene. Since their appearance, they occupied a relatively major part of Mesozoic mammalian faunas in the Northern Hemisphere (Kielan-Jaworowska et al., 2004). Their early diversification took place in the Late Jurassic of Europe and North America, though Early Cretaceous fossil records of them are mainly from Asia and Europe. Most of these primitive multituberculates belong to a paraphyletic group of 'plagiaulacidans' (Kielan-Jaworowska and Hurum, 2001; Kielan-Jaworowska et al., 2004). More advanced multituberculates referred to the monophyletic suborder Cimolodonta McKenna, 1975, appeared in the mid-Cretaceous, and then flourished during the Late Cretaceous in the Northern Hemisphere, especially in Asia and North America (e.g., Kielan-Jaworowska et al., 2004). Putative cimolodontans are also known from the Southern Hemisphere (Kielan-Jaworowska et al., 2007; Rich et al., 2009).

The oldest fossil records of Asian multituberculates to date are *Hakusanobaatar* Kusuhashi, 2008, and *Tedoribaatar* Kusuhashi, 2008, from the Lower Cretaceous (tentatively thought to be Barremian to ?Aptian) Kuwajima Formation, central Japan, and *Sinobaatar* Hu and Wang, 2002, from the Yixian Formation (Barremian to Aptian), northeastern China. Jurassic multituberculates have not been discovered from Asia up to now,

and this implies that Asian multituberculates originally migrated from outside of Asia, most likely from Europe. Multituberculates were without doubt one of the most successful group of mammals in the Late Cretaceous of Asia. Therefore, they are an interesting group for understanding the Cretaceous mammalian faunal evolution in Asia. In the present paper, we describe two eobaatarid multituberculates and one taxon possibly related to the family Albionbaataridae Kielan-Jaworowska and Ensom, 1994, and briefly discuss their implications for the mammalian faunal transition in the Early Cretaceous of Asia.

Specimens reported here were discovered in the Lower Cretaceous (Aptian to Albian) Shahai and Fuxin formations in western Liaoning Province, northeastern China (Fig. 1). These two formations are slightly younger than the Yixian Formation, which yields unusually well preserved vertebrate fossils (including mammals), and the Fuxin Formation conformably overlies the Shahai Formation (Wang et al., 1989; Yang and Li, 1997). The present materials were discovered from coaly rocks of the Shahai and Fuxin formations at small coal mines in Badaohao (Heishan County) and Fuxin City areas, respectively. See Kusuhashi et al. (2009a, 2009b) for a more detailed geologic setting.

Institutional Abbreviations—**BMNH**, Natural History Museum, London, United Kingdom; **DORCM**, Dorset County Museum, Dorchester, Dorset, United Kingdom; **IVPP**, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China; **PIN**, Paleontological Institute of the Russian Academy of Sciences, Moscow, Russia; **SBEI**, Shiramine Institute of Paleontology, Hakusan City Board of Education, Ishikawa Prefecture, Japan (formerly Shiramine Village Board of Education, Ishikawa Prefecture).

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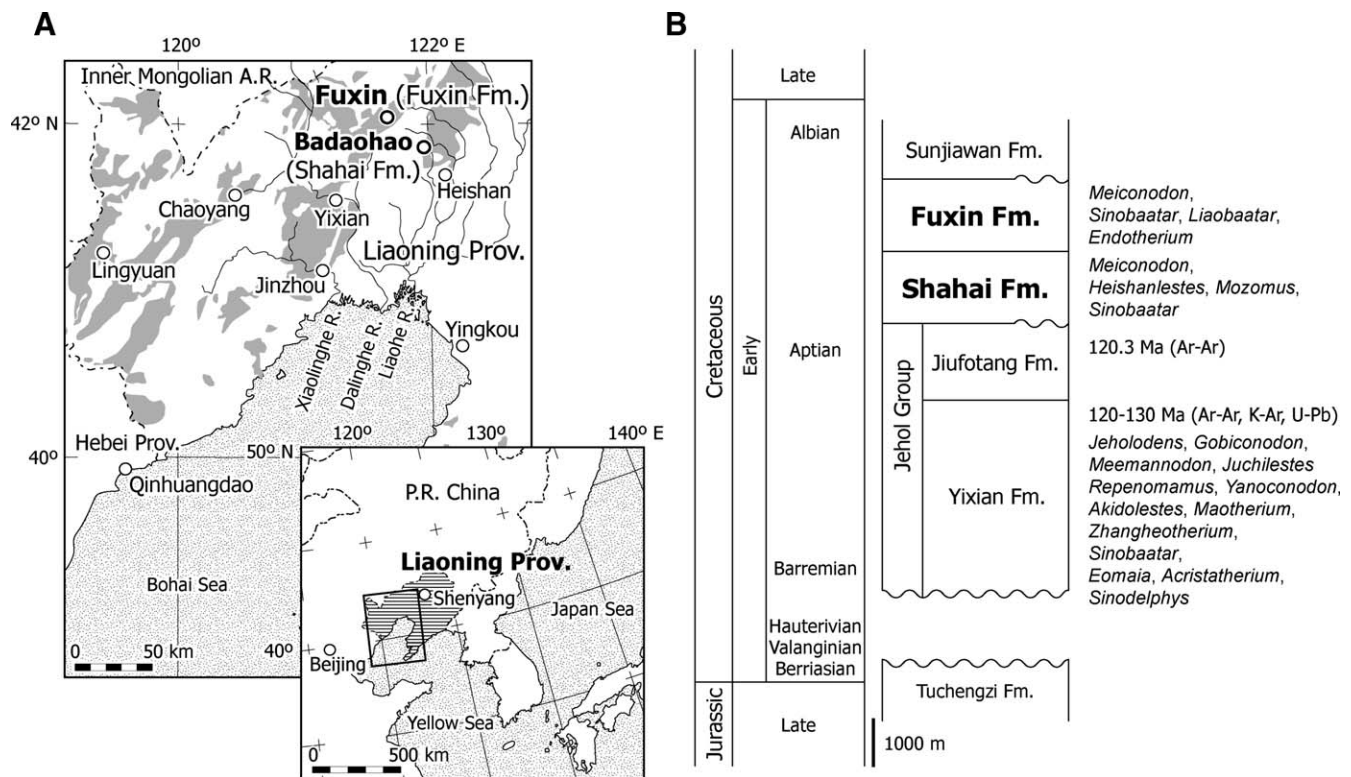


FIGURE 1. **A**, Distribution of the late Mesozoic strata in Liaoning Province (gray areas of enlarged map; modified after the Editorial Board of Chinese Geologic Maps, 2002) and the locations of Fuxin and Badaohao, Liaoning Province, northeastern China. **B**, Schematic stratigraphic table of the major late Mesozoic strata distributed in western Liaoning Province, northeastern China. Mammalian fossil records are based on Meng et al. (2006), Luo et al. (2007), Gao et al. (2009), Hu et al. (2009), and Kusuhashi et al. (2009a, 2009b) and references therein. Radiometric ages are based on previous studies (see Kusuhashi et al., 2009b, and references therein).

SYSTEMATIC PALEONTOLOGY

Order MULTITUBERCULATA Cope, 1884

Family EOBAATARIDAE Kielan-Jaworowska, Dashzeveg,
and Trofimov, 1987

HEISHANOBAATAR gen. nov.

Type and Only Species—*Heishanobaatar triangulus* gen. et sp. nov.

Etymology—‘Heishan,’ after Heishan County where the type specimen of the type and only species was collected; ‘baatar,’ Mongolian, means hero, which has been used as a suffix for generic names of many Asian Cretaceous multituberculates.

Diagnosis—As for the type and only species.

HEISHANOBAATAR TRIANGULUS sp. nov.
(Figs. 2–6; Table 1)

Holotype—Left dentary with incisor, p2–p4, and m1 (IVPP V14493; Figs. 2 and 4).

Paratypes—Fragment of right dentary with broken incisor, p2–p4, and m1–m2 (V14484; Figs. 3 and 5); and fragment of right dentary with broken incisor, and p2–p4 (V14492; Figs. 3 and 6).

Type Locality and Horizon—Badaohao, Heishan, Liaoning, northeastern China; Early Cretaceous (Aptian to Albian); Shahai Formation.

Other Locality and Horizon (V14484 and V14492)—Fuxin, Liaoning, northeastern China; Early Cretaceous (Aptian to Albian); Fuxin Formation.

Etymology—The word ‘triangulus,’ Latin, means triangular, referring to the triangular crown of p3 in lateral view, which is one of the diagnostic characters of this species.

Diagnosis—Moderate-sized eobaatarid multituberculata with lower jaw dental formula 1.0.3.2; lower incisor slender, completely covered with enamel; p2 single-rooted, peg-like; p3 double-rooted, crown shape triangular in lateral view; p4 having eight serrations; m1 cusp formula 2:2; m2 cusp formula 1 (coalesced):2. Differing from other ‘plagiaulacids’ except for eobaatarids in having three lower premolars rather than four, a peg-like p2, an anteroposteriorly elongated p4 relative to p3, and eight serrations on p4. Differing from *Hakusanobaatar*, *Liaobaatar*, and *Sinobaatar* in having a triangular p3 rather than oval in lateral view. Differing from *Eobaatar*, *Janumys*, *Liaobaatar*, *Loxaulax*, and *Sinobaatar* in cusp formula of m1. Differing from *Eobaatar* in having a lower incisor completely covered with enamel. Differing from *Tedoribaatar* in having three lower premolars and a double-rooted p3.

Description—Dentaries, lower incisors, premolars, m1s, and right m2 are preserved in specimens of *Heishanobaatar triangulus*. Upper teeth have yet to be discovered. The type specimen of this species was mentioned by Wang et al. (1995) as a plagiaulacid similar to *Plagiaulax* Falconer, 1857. The specimens of this species were mentioned by Kusuhashi et al. (2007, 2008) as plagiaulacids, but the later investigation revealed that this species should be attributed to the Eobaataridae.

A dentary of the type specimen (V14493) is damaged but relatively complete. Posterior parts including condyle and coronoid process are not preserved in the right dentaries of V14484 and V14492, and the anterior-most part of the dentary of V14484 is

TABLE 1. Measurements of lower teeth in *Heishanobaatar triangulus* gen. et sp. nov., Eobaataridae gen. et sp. indet., *Eobaatar magnus* Kielan-Jaworowska, Dashzeveg, and Trofimov, 1987, *E. clemensi* Sweetman, 2009, *Hakusanobaatar matsuo*i Kusuhashi, 2008, *Liaobaatar changi* Kusuhashi, Hu, Wang, Setoguchi, and Matsuoka, 2009b, *Sinobaatar lingyuanensis* Hu and Wang, 2002, *S. fuxinensis* Kusuhashi, Hu, Wang, Setoguchi, and Matsuoka, 2009b, *S. xiei* Kusuhashi, Hu, Wang, Setoguchi, and Matsuoka, 2009b, and *Tedoribaatar reini* Kusuhashi, 2008.

	D	p3		p4		m1		m2	
		L	H	L	H	L	W	L	W
<i>Heishanobaatar triangulus</i>									
IVPP V14493	3.3	1.3	1.5	3.2	1.7	1.5	1.1		
IVPP V14484	4.8	1.2	1.5	3.6	2.3	1.6	1.3	1.8	1.4
IVPP V14492	3.9	1.2	1.4	3.3	1.8				
<i>Eobaataridae, gen. et sp. indet.</i>									
IVPP V14498	—	1.1	1.3	3.0	1.5				
<i>Eobaatar magnus</i>									
PIN 3101-57	—	3.5	2.0						
<i>Eobaatar clemensi</i>									
BMNH M 45482	—	1.4	0.9						
<i>Hakusanobaatar matsuo</i> i									
SBEI 1736	—	1.0	1.4	3.5	2.1				
<i>Liaobaatar changi</i>									
IVPP V14489	—	2.2	2.7	6.8	4.6	2.5	2.0	2.7	1.9
<i>Sinobaatar lingyuanensis</i>									
IVPP V12517	—	1.2	1.9	4.1	2.5				
<i>Sinobaatar fuxinensis</i>									
IVPP V14479	—	1.4	2.4	4.0	2.6	1.7	1.4	1.9	1.7
<i>Sinobaatar xiei</i>									
IVPP V14491	—	1.2	1.7	3.1	2.3	1.7	—	1.8	—
<i>Tedoribaatar reini</i>									
SBEI 1570	—	3.7	2.4						

Personal data of N. K. for *E. magnus* and *S. lingyuanensis*, and the others are after Kusuhashi (2008), Kusuhashi et al. (2009b), and Sweetman (2009). **Abbreviations:** **D**, dentary depth below p4; **H**, height; **L**, longitudinal length; **W**, transverse width.

broken. The anterior part of the dentary bends anterodorsally. The horizontal ramus is deepest dorsoventrally below p4 and the molars. It is shallow in V14493, but much deeper in V14484 (Table 1). The coronoid process extends posterodorsally from lateral to the position of m2. There is a condyle placed slightly below the occlusal level of molars and facing posterovertrally in V14493. A mental foramen is situated approximately 1 mm below p2 in V14484, approximately 1 mm anterior to p2 and 2 mm above the ventral margin of the dentary in V14492, and approximately 0.5 mm anterior to p2 and 1 mm above the ventral margin of the dentary in V14493. The masseteric fossa extends anteriorly below the posterior root of p4 on the labial surface of the horizontal ramus in V14484 and V14493, and weakly reaches below the anterior root of the p4 in V14484. This part is damaged and the masseteric fossa is not clearly preserved in V14492. Distal to p4, deformed alveoli for m1 and m2 are preserved in V14492.

The left lower incisor is well preserved in V14493, and the right lower incisor preserved in V14492 is broken. Only the base of the right lower incisor is barely observable in labial view in V14484. The outline of the incisor is similar to that of *Sinobaatar*. It is slender with rounded labial surface and more flattened lingual, and thinner toward the tip of the tooth. The ventral margin of the lingual surface is slightly swollen. Enamel completely covers the lower incisor.

Lower second premolars are preserved in all specimens. It is a tiny, single-rooted, peg-like, and non-functional tooth with somewhat swollen crown. The crown of p2 is not positioned below the crown of p3 as seen in species of *Sinobaatar* from the same locality (Kusuhashi et al., 2009b), but anterior to it.

Lower third premolars are also preserved in all specimens. The crown shape of p3 is triangular rather than rectangular or oval in lateral view, with a relatively long dorsal margin. Lower p3 is double-rooted. The posterior root is thinner than the anterior one. Anteroventral parts of the crown in both labial and lingual sides project ventrally like the anterior triangular lobe of p4 (called exodaenodont lobe in many references, such as Kielan-Jaworowska et al. 1987) in V14492. This lobe-like projection is present only on the lingual side of the crown in V14493, and

there is no kind of projection on both labial and lingual sides in V14484. The ventral margins of the p3s are somewhat damaged in all specimens. There probably are three serrations accompanied by ridges extending anteroventrally, but these ridges are weak or indistinct. The posterior margin of p3 is almost equal in height to the anterior margin of p4, and p3 and p4 together form a slightly curved shearing edge.

The crown shape of the p4s preserved in V14484, V14492, and V14493 is parallel-sided and rectangular in lateral view. Its dorsal margin is slightly arcuate. The crown is anteroposteriorly elongated relative to p3. In the plagiaulacids, the crown of p4 is almost twice as long as that of p3 (Simpson, 1928; Kielan-Jaworowska et al., 2004), but the length ratios of p4/p3 in V14484, V14492, and V14493 are 3.0, 2.8, and 2.5, respectively (Table 1). The crown is low relative to its longitudinal length especially in V14493. Lower p4 of V14484 is slightly larger than those of V14492 and V14493 (Table 1). The anterior triangular lobe points ventrally to posterovertrally and it is moderate in size relative to the crown size. There are eight serrations, and six of them except for the first and last ones are accompanied by ridges on the labial and lingual sides of the crown. There is another ridge for the first serration on each labial and lingual side in V14484, but they are not connected with the serration. The last serration is accompanied by a short and weak ridge only on the lingual side in V14484. The last ridge is weak on the labial side in V14492. It is weak and short on the lingual side, and is worn out on the labial side in V14493. The second serration is missing in V14492. Posterior labial cusps in V14484 and V14492 are strongly worn, and posterior wear shelves (Kielan-Jaworowska et al., 1987) are present at a lower position, near the crown-root junction. It is at a slightly higher position in V14493. Because of the wear, it is not obvious whether there were multiple posterior labial cusps or only one in all specimens. The posterior wear shelf extends anteriorly nearly half the length of the crown in V14492, and more than one-third of the length of the crowns in V14484 and V14493. The shelf is somewhat anteroposteriorly longer than those of other eobaatarids. This might imply the presence of multiple posterior labial cusps, but the number of cusps should be fewer than those

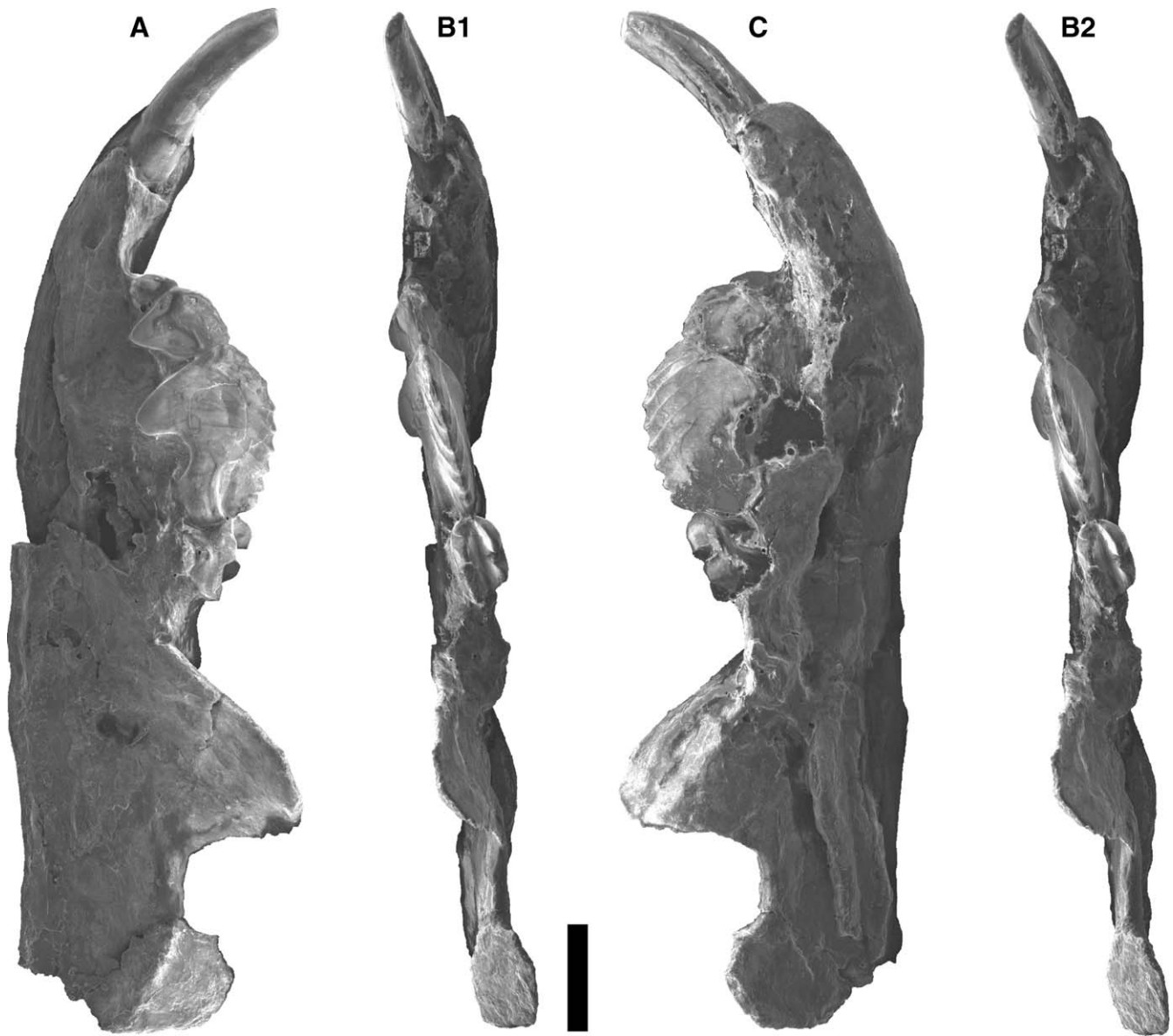


FIGURE 2. Eobaatarid multituberculate mammal *Heishanobaatar triangulus* gen. et sp. nov., holotype (IVPP V14493), left dentary with incisor, p2–p4, and m1; Lower Cretaceous Shai Formation, Badaohao, Heishan, Liaoning, China. SEM micrographs. **A**, labial view; **B**, occlusal view, stereopairs; **C**, Lingual view. Scale bar equals 2 mm.

of plagiulacids. Dorsal to the posterior wear shelf, a wear facet is present.

Right and left m1s preserved in V14484 and V14493, respectively, are asymmetrical in occlusal view with an oblique posterior margin. Cusp formula of m1 is 2:2. In the labial cusp row, the second cusp is strongly worn in V14484, and both first and second cusps are strongly worn in V14493; thus it is hard to estimate their original heights. The second labial cusp is probably somewhat longer anteroposteriorly than the first one in V14484. Lingual cusps are subequal in size. They are crescentic and face towards the middle of the tooth. Labial cusps are positioned slightly posterior to the corresponding lingual cusps.

Right m2 in V14484 is also asymmetrical with a strongly oblique posterior margin in occlusal view. Cusp formula is 1 (coalesced):2, and it is similar to those of *Bolodon* Owen, 1871, and eobaatarids. The labial cusp is coalesced and is shaped like a protruded labium. The posterior part of the cusp is taller than the

anterior. The lingual wall of it is ornamented by grooves. The dorso-lingual part of the lingual anterior cusp is broken. Two lingual cusps have subequal height and the anterior one is slightly larger than the posterior one. They are crescentic and face towards the middle of the tooth.

Measurements—See Table 1.

Remarks—*Heishanobaatar triangulus* is different from cimolodontans in having three lower premolars (see Kielan-Jaworowska et al., 2004), and should be classified as a ‘plagiulacidan.’ It shares the number of premolars and elongated p4 with *Arginbaatar* Trofimov, 1980, and eobaatarids, but it is obviously distinguished from *Arginbaatar* in its rectangular p4 in lateral view. *Heishanobaatar triangulus* is assigned to the Eobaataridae based on following set of characters: slender lower incisor, a single-rooted and peg-like p2, a more anteroposteriorly elongated p4 relative to p3 than that of plagiulacids, eight serrations on p4, and single or fewer posterior labial cusp(s) than

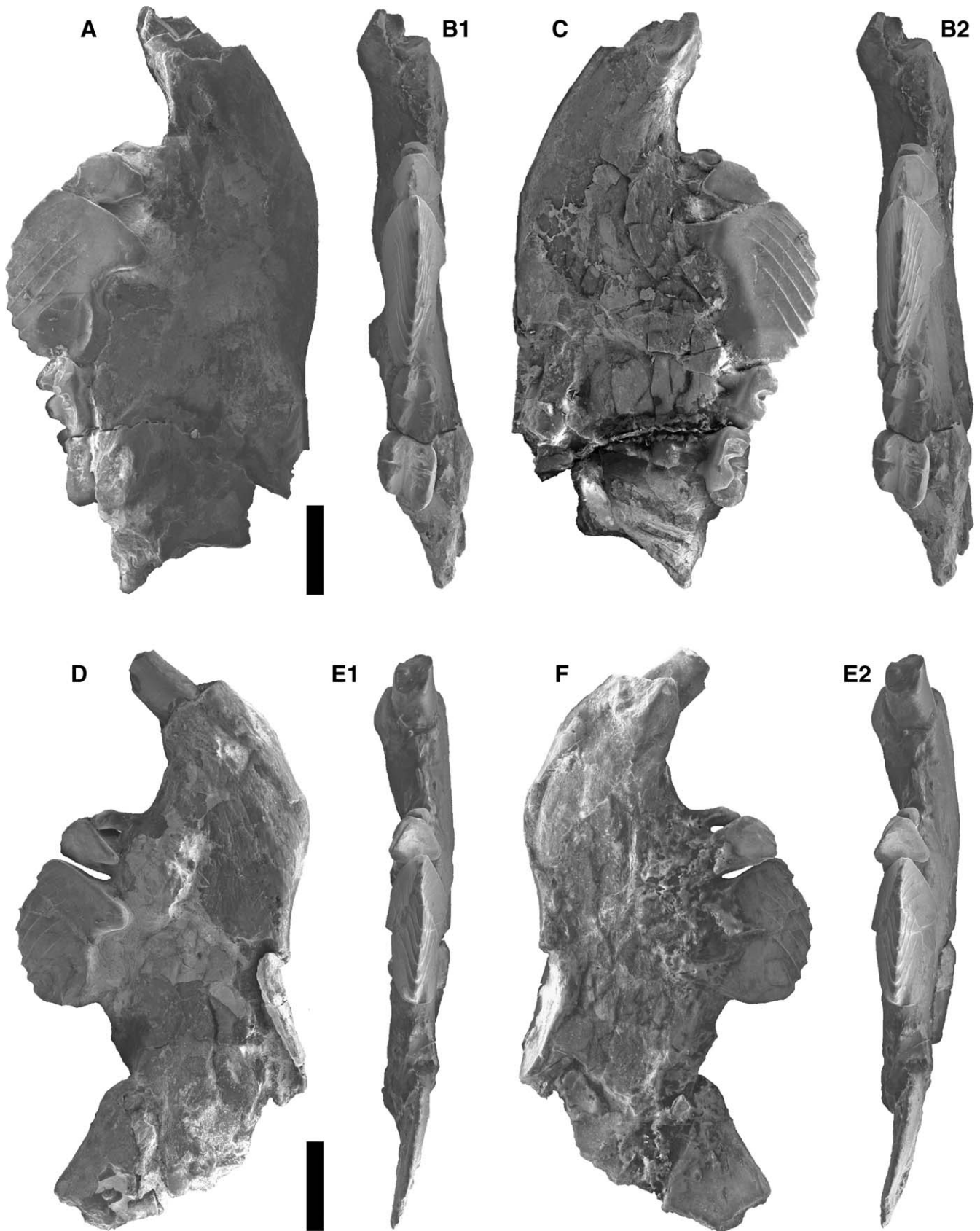


FIGURE 3. Eobaatarid multituberculate mammal *Heishanobaatar triangulus* gen. et sp. nov.; Lower Cretaceous Fuxin Formation, Fuxin, Liaoning, China. SEM micrographs. **A–C**, paratype (IVPP V14484), fragment of right dentary with broken incisor, p2–p4, and m1–m2; **A**, labial view; **B**, occlusal view, stereopairs; **C**, lingual view. **D–F**, V14492, fragment of right dentary with broken incisor, and p2–p4; **D**, labial view; **E**, occlusal view, stereopairs; **F**, lingual view. Scale bars equal 2 mm.

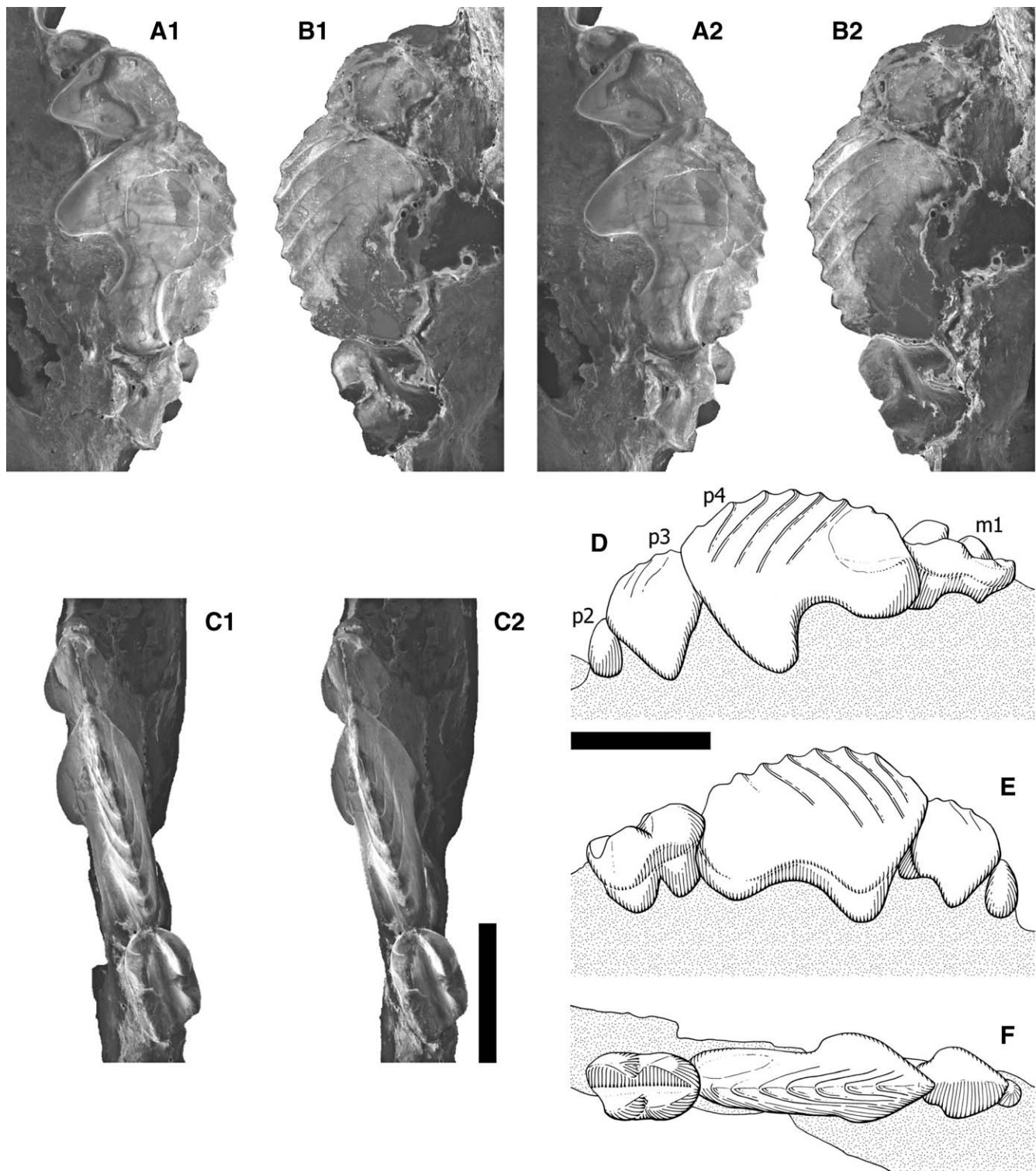


FIGURE 4. Cheek teeth of eobaatarid multituberculate mammal *Heishanobaatar triangulus* gen. et sp. nov., holotype (IVPP V14493); Lower Cretaceous Shaihai Formation, Badaohao, Heishan, Liaoning, China. SEM micrographs (A–C, stereopairs) and line drawings (D–F) of left cheek teeth. A, D, labial view; B, E, lingual view; C, F, occlusal view. Scale bars equal 2 mm.

in plagiulacids. However, at the same time, *H. triangulus* is distinguished from other eobaatarids by its triangular p3 in lateral view, which is a diagnostic feature of the Plagiulacidae Gill, 1872 (Kielan-Jaworowska and Hurum, 2001; Kielan-Jaworowska

et al., 2004). Eobaatarids where known have an oval p3 in lateral view (Hu and Wang, 2002; Kusuhashi, 2008; Kusuhashi et al., 2009b). Therefore, dental morphology of *H. triangulus* is intermediate between plagiulacids and eobaatarids.

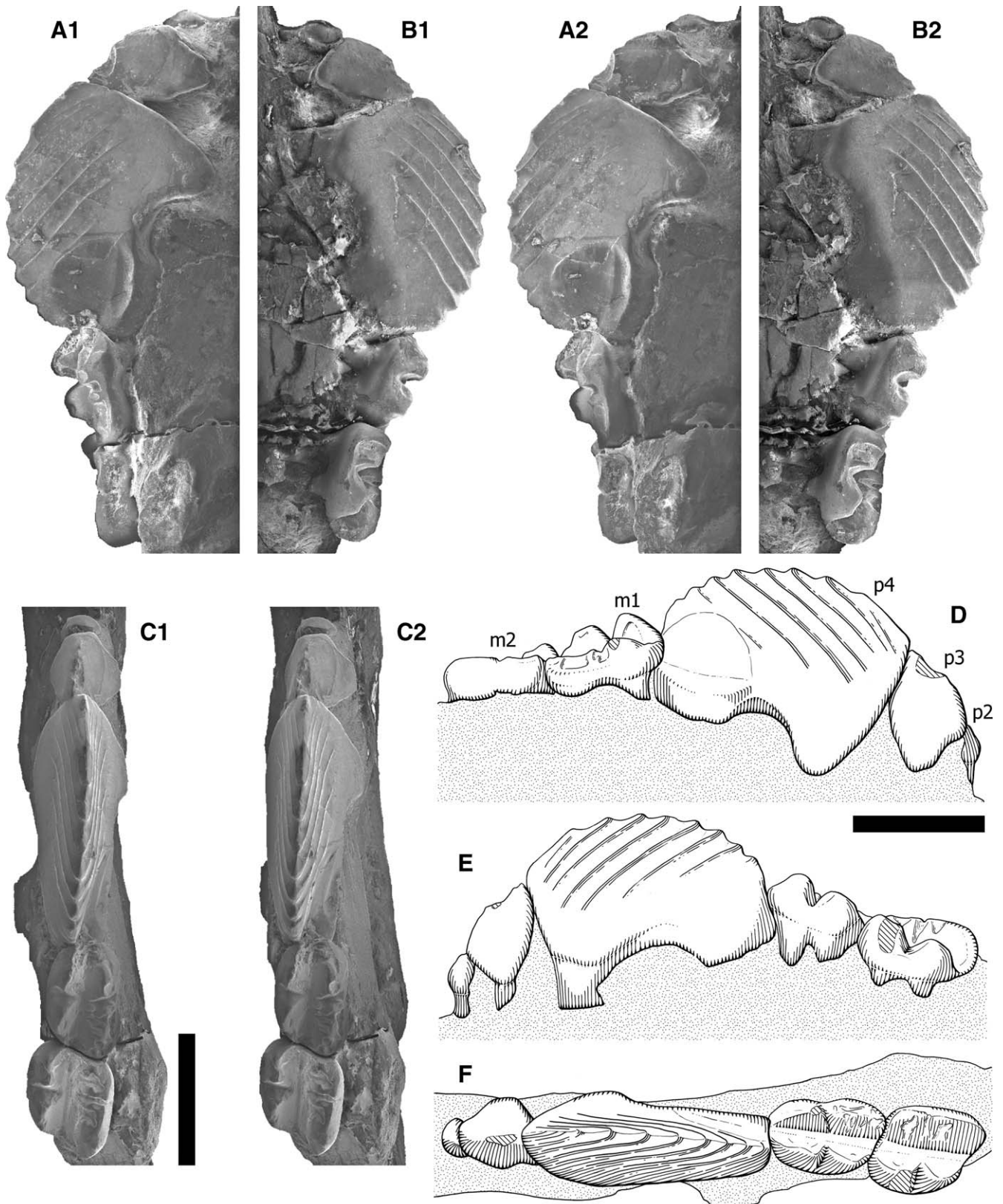


FIGURE 5. Cheek teeth of eobaatarid multituberculate mammal *Heishanobaatar triangulus* gen. et sp. nov., IVPP V14484; Lower Cretaceous Fuxin Formation, Fuxin, Liaoning, China. SEM micrographs (A–C, stereopairs) and line drawings (D–F) of right cheek teeth. A, D, labial view; B, E, lingual view; C, F, occlusal view. Scale bars equal 2 mm.

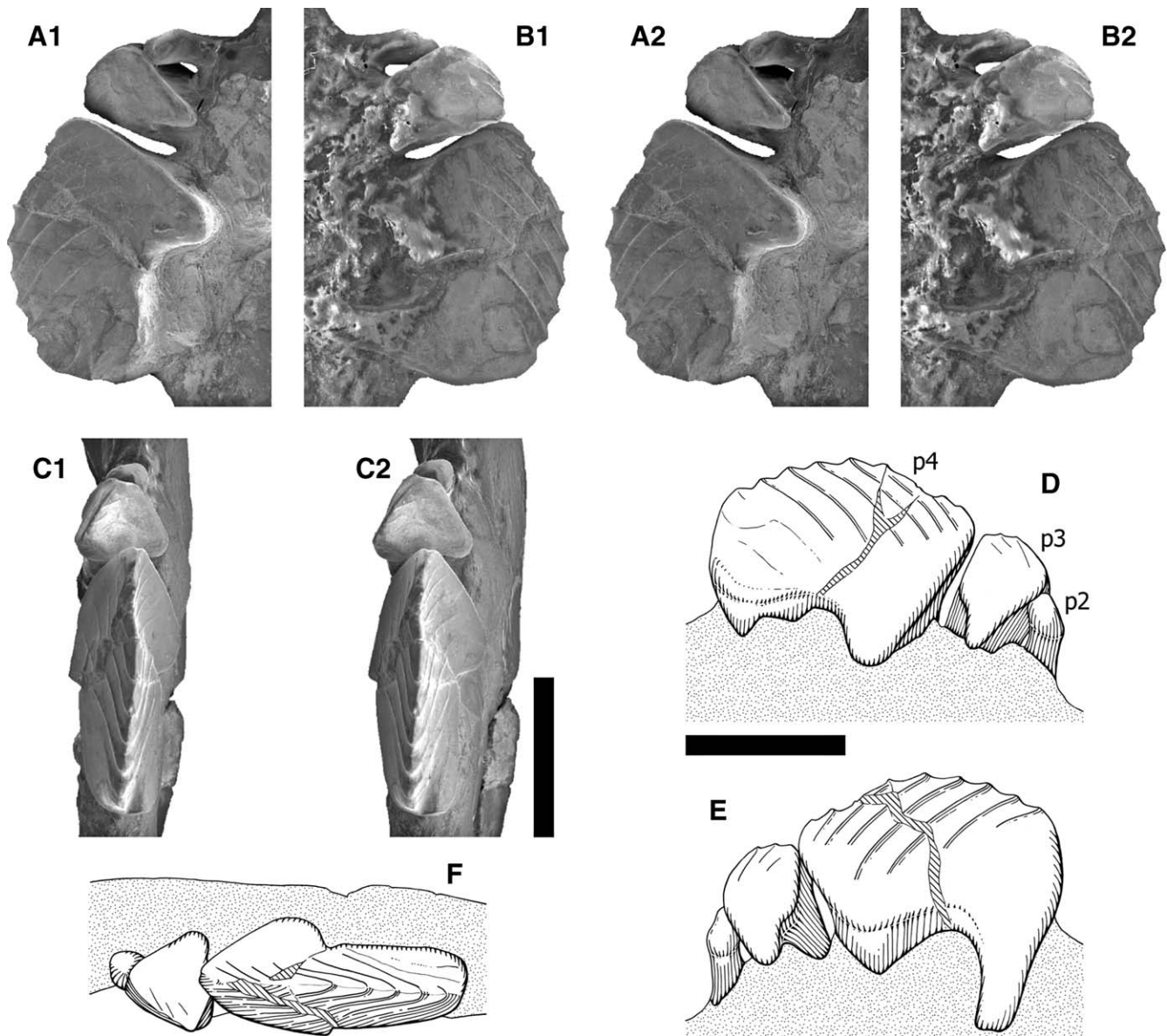


FIGURE 6. Cheek teeth of eobaatarid multituberculate mammal *Heishanobaatar triangulus* gen. et sp. nov., IVPP V14492; Lower Cretaceous Fuxin Formation, Fuxin, Liaoning, China. SEM micrographs (A–C, stereopairs) and line drawings (D–F) of right cheek teeth. A, D, labial view; B, E, lingual view; C, F, occlusal view. Scale bars equal 2 mm.

Compared with eobaatarids, the p4 of *Heishanobaatar triangulus* is almost the same size as those of *Eobaatar magnus* Kielan-Jaworowska, Dashzeveg, and Trofimov, 1987, *Hakusanobaatar*, *Sinobaatar xiei* Kusuhashi, Hu, Wang, Setoguchi, and Matsuoka, 2009b, and *Tedoribaatar*, and smaller than those of *Sinobaatar fuxinensis* Kusuhashi, Hu, Wang, Setoguchi, and Matsuoka, 2009b, *S. lingyuanensis* Hu and Wang, 2002, and *Liaobaatar* Kusuhashi, Hu, Wang, Setoguchi, and Matsuoka, 2009b (Table 1). This implies that *H. triangulus* probably larger than *Monobaatar* Kielan-Jaworowska, Dashzeveg, and Trofimov, 1987. The m1 of *H. triangulus* is almost same the size as or slightly larger than *Eobaatar clemensi* Sweetman, 2009. As mentioned above, *H. triangulus* is clearly different from *Hakusanobaatar*, *Liaobaatar*, *Sinobaatar*, and *Tedoribaatar* in having a double-rooted triangular p3 in lateral view. It is also distinguished from *Eobaatar* Kielan-Jaworowska, Dashzeveg, and Trofimov, 1987,

?*Janumys* Eaton and Cifelli, 2001, *Liaobaatar*, *Loxaulax* Simpson, 1928, and *Sinobaatar* in cusp formula of m1. *Heishanobaatar triangulus* shares a lower incisor completely covered by enamel with *Hakusanobaatar*, *Liaobaatar*, and *Sinobaatar*, and different from *Eobaatar* in this point. Lower p4 of *H. triangulus* is different from the p4 described as Plagiaulacidae or Eobaataridae gen. et sp. indet., by Badiola et al. (2008) from Spain in having an anteroposteriorly longer posterior wear shelf. *Heishanobaatar triangulus* is, therefore, recognized as a new genus and species of the Eobaataridae, though it cannot be sufficiently compared with *Parendothierium* Crusafont-Pairó and Adrover, 1966, and *Monobaatar*.

Specimens of *Heishanobaatar triangulus* (V14484, V14492, and V14493) show variability of size and some characters. The p4 of V14484 is somewhat larger and taller relative to length than those of the other two specimens (Table 1). The horizontal ramus of the

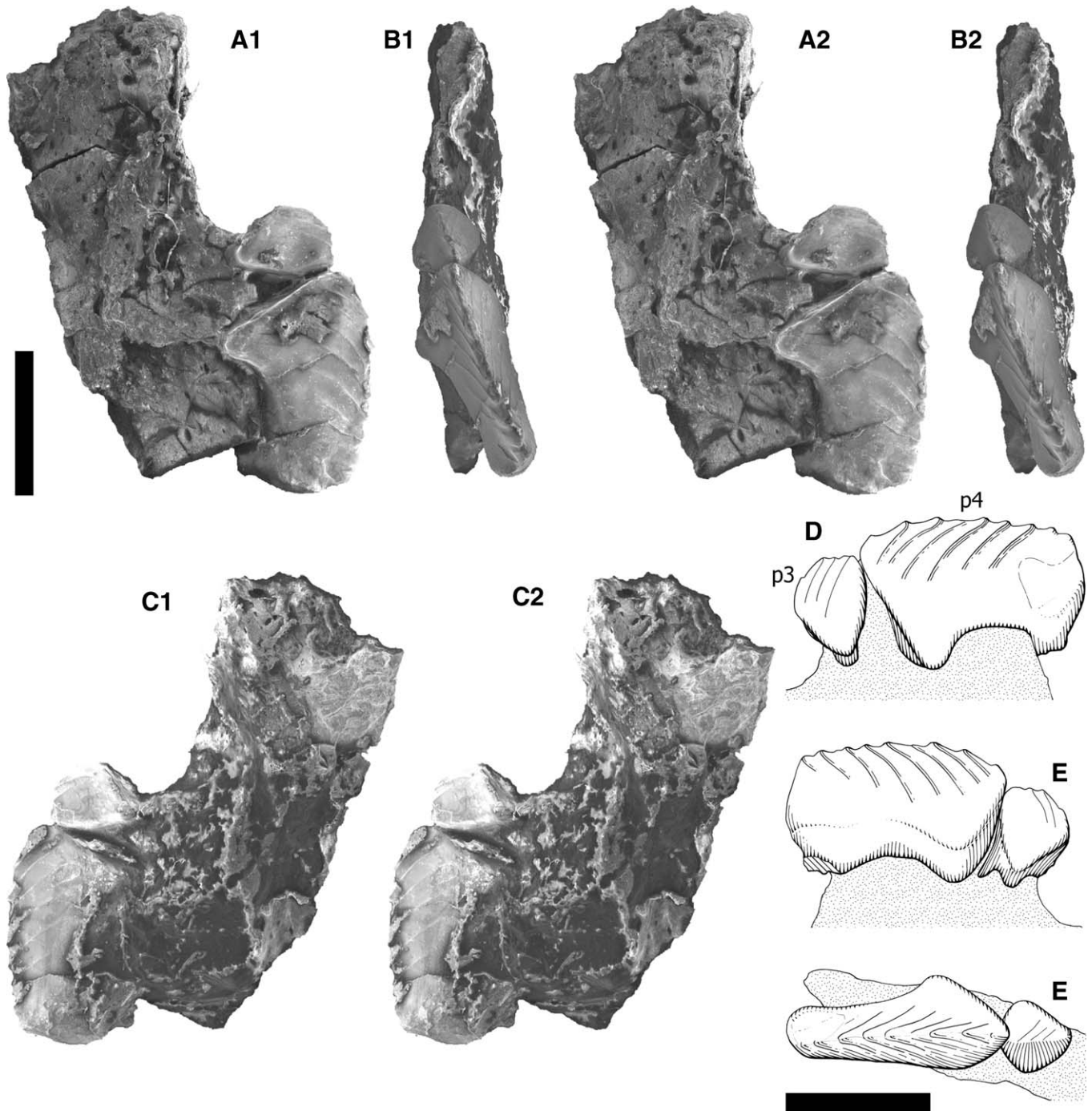


FIGURE 7. Eobaataridae gen. et sp. indet., V14498, fragment of left dentary with p3–p4; Lower Cretaceous Fuxin Formation, Fuxin, Liaoning, China. SEM micrographs (A–C, stereopairs) and line drawings of the cheek teeth region (D–F). A, D, labial view; B, F, occlusal view; C, E, lingual view. Scale bars equal 2 mm.

dentary of V14484 is over 1.4 times deeper than that of V14493 (Table 1). The depth of the horizontal ramus of V14492 is intermediate between them, although the dentary of V14492 is damaged. The anteroventral parts of the crown of p3 project like a lobe in both labial and lingual sides in V14492, whereas the projection is only seen in the lingual side in V14493 and is not seen in both labial and lingual sides in V14484. It is, however, difficult to judge whether these differences are intraspecific or interspecific, because of the poorness of the specimens. Here, in spite of these

differences, we tentatively assign all of them to one species, *H. triangulus*.

Family EOBAATARIDAE Kielan-Jaworowska, Dashzeveg, and Trofimov, 1987

Gen. et sp. indet.

(Fig. 7; Table 1)

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

Locality and Horizon—Fuxin, Liaoning, northeastern China; Early Cretaceous (Aptian to Albian); Fuxin Formation.

Description—V14498 is a fragment of left lower jaw with p3 and p4. The dentary is badly damaged and most of it is missing. A mental foramen is situated approximately 1 mm anterior to p3 and 0.5 mm below the dorsal margin of the preserved part of the dentary. Masseteric fossa is not preserved.

Crowns of p3 and p4 preserved in V14498 are also damaged. The crown shape of the double-rooted left p3 is triangular rather than rectangular or oval in lateral view. As seen in *Heishanobaatar*, the posterior root is thinner than the anterior one, but it is thicker than those in other eobaatarids such as *Hakusanobaatar*. There are four tiny serrations. Three of them except for the anterior-most one are accompanied by weak ridges extending anteroventrally on the labial side, and the third ridge is quite indistinct on the lingual side. On the anterior surface of the crown, there is a trace of compression, indicating the presence of p2. The posterior margin of p3 is the same height as the anterior margin of p4.

The crown shape of the left p4 is parallel-sided and rectangular. The dorsal margin of p4 is damaged but it is assumed to be rather straight, not as arcuate as those in *Heishanobaatar*. The crown is low relative to its longitudinal length, and is antero-posteriorly elongated relative to p3 (Table 1). The anterior triangular lobe is small relative to the crown size, and points ventrally. There are nine serrations and eight of them except for the first one are accompanied by ridge. The last ridge is weak and short on the lingual side, and it is worn out on the labial side. The posterior root of the p4 is broken in V14498. It is antero-posteriorly thin, much thinner than those of eobaatarids. On the posterolabial part of the tooth, there is a posterior wear shelf at approximately half the height of distal margin of p4. It is antero-posteriorly shorter than those of *Heishanobaatar*, and the number of posterior labial cusps is estimated to be probably only one.

Measurements—See Table 1.

Remarks—V14498 is also thought to be a dentary of an eobaatarid based on anteroposteriorly elongated p4 relative to p3, nine serrations on p4, and probably single posterior labial cusp, though its triangular p3 and rectangular p4 in lateral view are more similar with those of plagiulacids than with those of eobaatarids. Compared with eobaatarids, the p4 of V14498 is slightly smaller than those of *Eobaatar*, *Hakusanobaatar*, *Heishanobaatar*, *Liaobaatar*, *Sinobaatar*, and *Tedoribaatar* (Table 1). V14498 is clearly distinguished from *Hakusanobaatar*, *Liaobaatar*, *Sinobaatar*, and *Tedoribaatar* by having a double-rooted triangular p3 in lateral view. It shares this feature with *Heishanobaatar*, but is different from *Heishanobaatar* in having a p4 with a small anterior triangular lobe and straight dorsal margin. Latter feature also distinguishes V14498 from other eobaatarids with slightly arcuate dorsal margin of p4. V14498 is probably smaller than ?*Eobaataridae* gen. et sp. indet., reported by Kusuhashi et al. (2009b) on the basis of an upper premolar. Lower p4 of V14498 is also different from the p4 described as *Plagiulacidae* or *Eobaataridae* gen. et sp. indet., by Badiola et al. (2008) in having a straight dorsal margin. Therefore, V14498 probably belongs to a new genus and species of the *Eobaataridae*, although here it is conservatively assigned to *Eobaataridae* gen. et sp. indet., because the specimen is damaged and not sufficiently preserved to be certain of its affiliations.

Family ?*ALBIONBAATARIDAE* Kielan-Jaworowska and
Ensom, 1994
KIELANOBAATAR gen. nov.

Type and Only Species—*Kielanobaatar badaohaoensis* gen. et sp. nov.

Etymology—In honor of Dr. Zofia Kielan-Jaworowska, who is one of the leading specialists of Mesozoic mammals and has greatly contributed to our understanding of Asian Mesozoic mammals, including multituberculates.

Diagnosis—As for type and only species.

KIELANOBAATAR BADAOHAOENSIS sp. nov.
(Figs. 8 and 9; Table 2)

Holotype and Only Known Specimen—Fragment of left maxilla with two premolars (probably P1 and P3; IVPP V14504; Fig. 8).

Type Locality and Horizon—Badaohao, Heishan, Liaoning, northeastern China; Early Cretaceous (Aptian to Albian); Sha-hai Formation.

Etymology—After the type locality.

Diagnosis—P1 to P3 with relatively flat occlusal surfaces; P1 and P2 having three cusp rows, cusp formula 1:3:2 (labial:medial:lingual); P3 having four cusps, cusp formula 2:2 (labial:lingual). Differs from *Albionobaatar* in numbers of cusps on P1 to P3, pentangular P1 in occlusal view rather than rectangular, and ridges of premolars not extending onto lingual slopes.

Description—Fragment of left maxilla and two upper premolars (probably P1 and P3) are preserved in the only known specimen of *Kielanobaatar badaohaoensis* (V14504). There was another tooth (probably P2) between them, but it has been lost during preparation. Lower teeth and most of the upper teeth are yet to be discovered. V14504 was briefly mentioned by Wang et al. (1995) as a specimen with upper premolars similar to those of *Albionobaatar* Kielan-Jaworowska and Ensom, 1994, and was assigned to *Plagiulacoidea*, fam. gen. et sp. indet.,. Our tooth designation of the specimen (discussed below) is, however, not coincident with that of Wang et al. (1995). P1 and P3 of the specimen here are called P3 and P1, respectively, by Wang et al. (1995). The preserved part of maxilla of V14504 is a small, very fragmentary piece, and no characteristics were observed in it.

Double-rooted left P1 is roughly pentangular in occlusal view, and has a relatively flat occlusal surface. It is larger than P3 in occlusal view, and is almost the same size as the lost P2. The height of the crown of P1 is taller than that of P3, and was lower than that of the lost P2 (Fig. 9). Cusp formula is 1:3:2 (labial:medial:lingual). The medial and lingual cusps are arranged longitudinally. The labial cusp is the largest. Medial first and second cusps are almost the same size and are slightly smaller than the labial and lingual cusps. The third medial cusp is smaller than the other two. The first lingual cusp is taller than the second. The lingual cusps are slightly smaller than the labial cusp. There is a cuspule anterior to the labial cusp. Labial to the labial cusp, three cuspules are arranged along the labial margin of the crown. All cusps are ornamented with radiating ridges, and ridges do not extend onto the lingual surface of the tooth. On the posterior part of the tooth, a posterior cingulum is moderately developed.

Left P2 (Fig. 9) was also double-rooted, and its crown was roughly rectangular in occlusal view. The lingual side of the crown was broken. Cusp formula was 1:3:2. The labial cusp was slightly larger than the others. Cuspules were present both anterior and posterior to the labial cusp. In the medial cusp row, the second cusp was the largest and tallest of the three. The first medial cusp was situated slightly lingually, and was as small as the third one. Anterior to the first medial cusp, there was a tiny cuspule. Two lingual cusps were subequal-sized, and almost as large as the second medial cusp. A cuspule was present posterolabial to the second lingual cusp. A cingulum was not obviously developed.

The crown of double-rooted left P3 is roughly rectangular in occlusal view. There are three subequal cusps arranged triangularly (one labial and two lingual) and a smaller cusp anterior to the labial cusp. Cusp formula is 2:2 (labial:lingual). The occlusal surface of the crown is relatively flat, and three cusps are

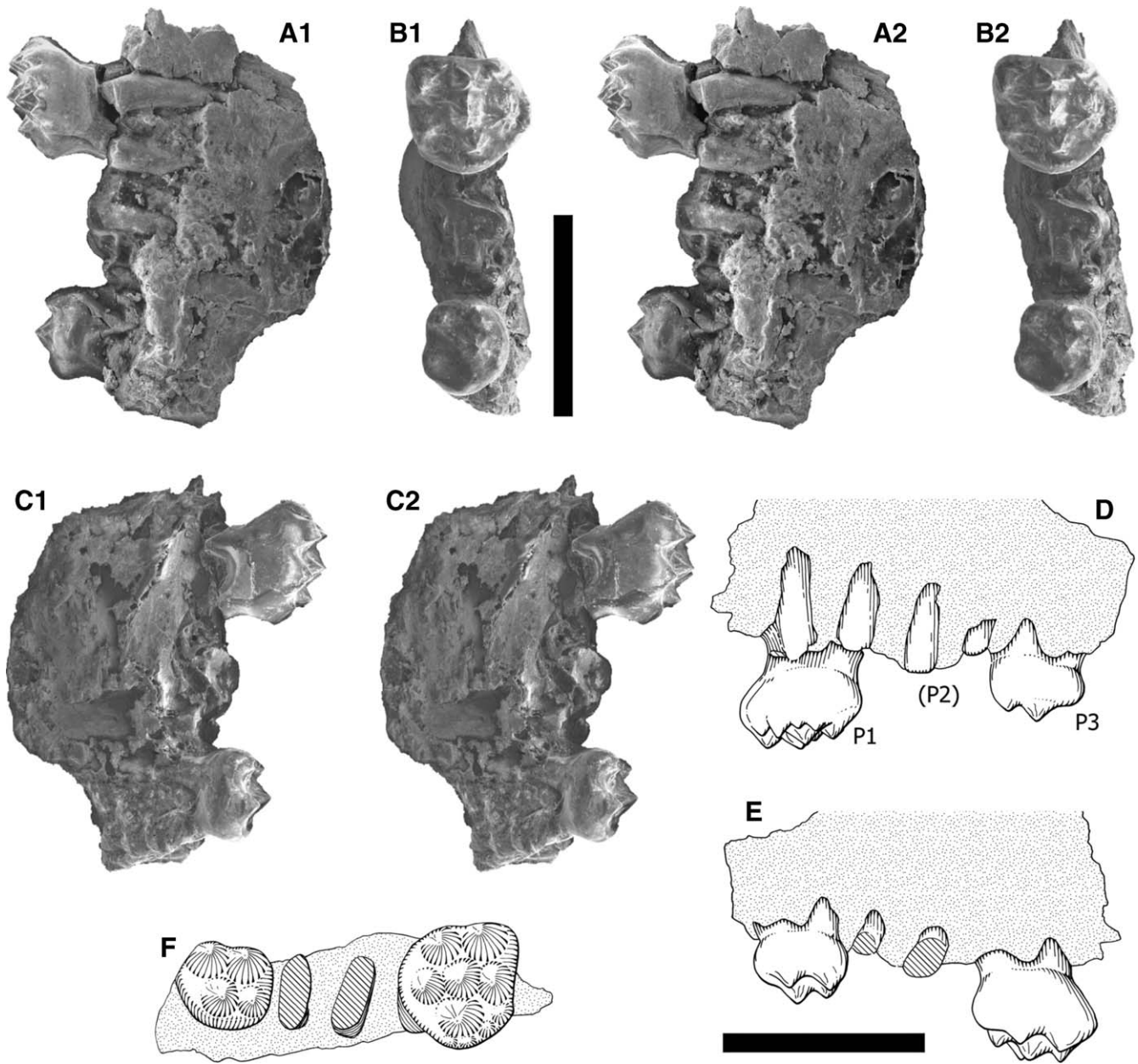


FIGURE 8. ?Albionbaatarid multituberculata mammal *Kielanobaatar badaohaoensis* gen. et sp. nov., holotype (IVPP V14504), fragment of left maxilla with P1 and P3; Lower Cretaceous Shihai Formation, Badaohao, Heishan, Liaoning, China. SEM micrographs (A–C, stereopairs) and line drawings (D–F). A, D, labial view; B, F, occlusal view; C, E, lingual view. Scale bars equal 2 mm.

relatively shorter than those of the tri-cusped anterior premolars of eobaatarids. This tooth is much smaller than P1 and the lost P2. There is a developed posterior cingulum.

Measurements—See Table 2.

Remarks—Two preserved teeth in V14504 are identified as upper premolars because the shapes of their crowns are neither blade-like nor mesiodistally long, and because their conical cusps are ornamented with radiating ridges (Krause et al., 1992; Kielan-Jaworowska and Ensom, 1994). Their longitudinal lengths are almost equal with their transverse widths (Table 2). This suggests that they are probably anterior upper premolars, P1 to P3. P4 and P5 are usually much longer than wide in multituberculata. A distally prominent posterior cingulum is frequently seen on

anterior upper premolars of multituberculata (see Marsh, 1887; Lillegraven, 1969; Hahn, 1977, 2001; Hahn et al., 1987; Kielan-Jaworowska et al., 1987; Storer, 1991; Hahn and Hahn, 1992; Kielan-Jaworowska and Ensom, 1992; Kusuhashi et al., 2009b). Cingula seen on two upper premolars in V14505 are, therefore, identified as posterior cingula. Based on these cingula, the smallest tooth preserved in V14505 is interpreted as P3, with the other preserved tooth as P1, and P2 having been lost. In many ‘plagiaulacidan’ multituberculata, such as *Arginbaatar*, *Bolodon osborni* Simpson, 1928, *Ctenacodon laticeps* (Marsh, 1881), *Hakusanobaatar*, *Renatodon* Hahn, 2001, *Sinobaatar fuxinensis*, and *S. xiei*, P3 is the smallest in their upper premolar series (see Marsh, 1887; Simpson, 1928; Trofimov, 1980; Kielan-Jaworowska et al.,

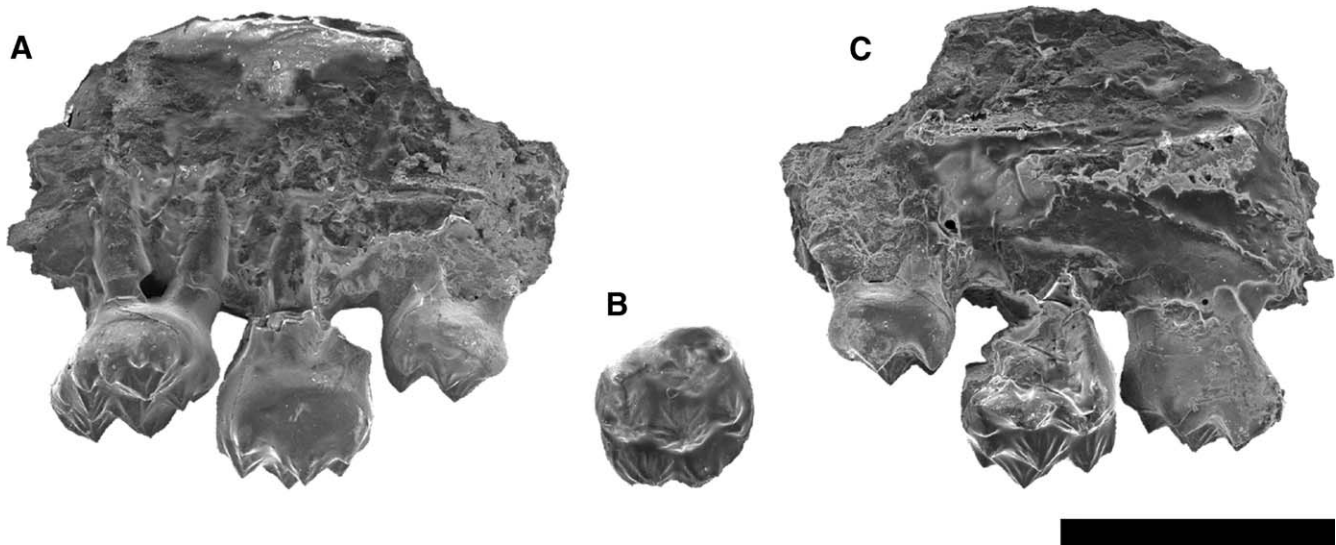


FIGURE 9. ?Albionbaatarid multituberculate mammal *Kielanobaatar badaohaoensis* gen. et sp. nov., holotype (IVPP V14504 before the P2 was lost), fragment of left maxilla with P1–P3; Lower Cretaceous Shai Formation, Badaohao, Heishan, Liaoning, China. SEM micrographs. **A**, labial view; **B**, the P2, occlusal view; **C**, lingual view. Anterior towards left for **B**. Scale bar equals 2 mm.

1987; Hahn, 2001; Kusuhashi, 2008; Kusuhashi et al., 2009b). This fact supports our tooth designation of V14505, although there are some anomalies. P3 of V14505 has three subequal cusps arranged triangularly on its crown. On upper premolars with three cusps, two of them are ordinarily arranged in a lingual row and one is labial. The side possessing two subequal cusps in P3 is, therefore, interpreted to be lingual. The rather straight lateral margin of the crown of P1 also implies that this side is lingual. Two teeth preserved in V14505 are, therefore, assigned to left P1 and P3, and the lost one to left P2.

The sizes of three teeth of V14505 are probably within the size range of anterior upper premolars of *Heishanobaatar* from the same locality, whose upper teeth have yet to be discovered. However, V14505 is not thought to be anterior upper premolars of *Heishanobaatar*, because eobaatarids where known have only three or four cusps on P1 to P3, whereas the P1 and the lost P2 of V14505 have three cusp rows. Moreover, most of multituberculates had simple upper premolars usually with three or four cusps in two rows, and V14505 is clearly distinguished from them by this feature. Upper teeth of *Liaobaatar* from the Fuxin formation have also yet to be discovered, but V14505 is too small to be attributed to *Liaobaatar*. There still is a possibility that they are deciduous and successors have simpler crowns. But a decid-

uous P1 preserved in a specimen of *Sinobaatar fuxinensis* has only three cusps and almost the same morphology as the permanent P1 (Kusuhashi et al., 2009b). This implies that P1 and P2 of V14505 are probably not deciduous teeth preceding simpler permanent ones. Here we consider these teeth to be permanent. However, the possibility that P3 is simpler and smaller than P1 and P2 because it is deciduous can also not be easily rejected.

Kielanobaatar badaohaoensis shares three cusp rows on upper anterior premolars and relatively flat occlusal surfaces containing somewhat small cusps only with *Albionbaatar*. Based on these dental similarities, *K. badaohaoensis* is possibly attributed to the Albionbaataridae, though we still cannot assert it because both *Kielanobaatar* and albionbaatarids have yet to be known well. *Kielanobaatar badaohaoensis* is slightly larger than *Albionbaatar* (Table 2), and is distinguished from *Albionbaatar* by the numbers of cusps on P1 to P3. P1 to P3 of *Albionbaatar* have many more cusps (Kielan-Jaworowska and Ensom, 1994). The pentangular P1 in occlusal view also distinguishes *K. badaohaoensis* from *Albionbaatar*, which has rectangular P1 (Kielan-Jaworowska and Ensom, 1994). *Albionbaatar* has ridges that extend onto the lingual slopes of the premolars (Kielan-Jaworowska and Ensom, 1994), but ridges of *K. badaohaoensis* do not extend onto the lingual faces. *Kielanobaatar badaohaoensis* is, therefore, attributed to a new genus and species probably related to the Albionbaataridae, though it cannot be compared with another albionbaatarid genus, *Proalbionbaatar* Hahn and Hahn, 1998.

TABLE 2. Measurements of upper anterior premolars in *Kielanobaatar badaohaoensis* gen. et sp. nov., and *Albionbaatar denisae* Kielan-Jaworowska and Ensom, 1994.

	P1		P2		P3	
	L	W	L	W	L	W
<i>Kielanobaatar badaohaoensis</i>						
IVPP V14504	1.2	1.3	1.2	1.2	0.9	1.0
<i>Albionbaatar denisae</i>						
DORCM GS 23*	0.9	0.73				
DORCM GS 24*		0.7	0.6			
DORCM GS 282*		0.8	0.56			

Data of *Albionbaatar* are after Kielan-Jaworowska and Ensom (1994).

Abbreviations: L, longitudinal length; W, transverse width.

*Tooth designation is uncertain.

DISCUSSION AND CONCLUSION

Multituberculates from the Shai and Fuxin formations reported here, together with eobaatarids from the same localities and horizons (Kusuhashi et al., 2009b), demonstrate that there were quite diverse multituberculates in Asia in the late Early Cretaceous. More than four genera including five species have been known from the formations: *Heishanobaatar*, *Liaobaatar*, *Kielanobaatar*, and two species of *Sinobaatar*. There also are unnamed taxa such as Eobaataridae gen. et sp. indet, and ?Eobaataridae gen. et sp. indet. Most of them belong to the Eobaataridae, and *Sinobaatar* occupies a great part of this multituberculate fossil assemblage. One of the interesting aspects of this fauna is the occurrence of ?albionbaatarid genus

Kielanobaatar. Only two families of Early Cretaceous multituberculates have previously been described from Asia: Eobaataridae from Mongolia, China, and Japan, and Arginbaataridae Hahn and Hahn, 1983, from Mongolia (Trofimov, 1980; Kielan-Jaworowska et al., 1987; Hu and Wang, 2002; Kusuhashi, 2008; Kusuhashi et al., 2009b). *Kielanobaatar* is the first record of possible albionbaatarid multituberculate from Asia. The Albionbaataridae currently includes two genera only from Europe (e.g., Kielan-Jaworowska et al., 2004; Hahn and Hahn, 2006): *Albionbaatar* from the lower Lower Cretaceous of England *Proalbionbaatar* from the Upper Jurassic of Portugal. Together with fossil records of eobaatarid multituberculates reported previously (Woodward, 1911; Simpson, 1928; Trofimov, 1980; Kielan-Jaworowska et al., 1987; Hahn and Hahn, 1992, 2001, 2002, 2006; Kielan-Jaworowska and Hurum, 2001; Hu and Wang, 2002; Kielan-Jaworowska et al., 2004; Badiola et al., 2008; Kusuhashi, 2008; Kusuhashi et al., 2009b; Sweetman, 2009), the occurrence of ?albionbaatarid *Kielanobaatar* in the Early Cretaceous of Asia supports faunal exchanges of terrestrial vertebrates between Asia and Europe in the Early Cretaceous.

The number of multituberculate specimens occupy about one-third of the mammalian fossil assemblage composed of more than one hundred specimens from the Shahai and Fuxin formations. These facts suggest that multituberculates were fairly flourishing in the mammalian fauna known from the Shahai and Fuxin formations (designated as the Fuxin mammalian fauna below). This apparently contrasts with mammalian fauna known from the Yixian Formation (designated as the Yixian mammalian fauna below), which is distributed in the same region with but slightly older than the Shahai and Fuxin formations. Thirteen genera of mammals have been reported from the Yixian Formation up to now (e.g., Meng et al., 2006; Luo et al., 2007; Gao et al., 2009; Hu et al., 2009; Fig. 1). The half of these genera belongs to 'triconodonts,' and this fauna currently contains only one genus and species of multituberculate, *Sinobaatar lingyuanensis*. 'Triconodonts' seems to have been still diverse in the Fuxin mammalian fauna, and there are two species of alticonodontine triconodontids (*Meiconodon lii* Kusuhashi, Hu, Wang, Hirasawa, and Matsuoka, 2009a, and *M. setoguchii* Kusuhashi, Hu, Wang, Hirasawa, and Matsuoka, 2009a) and gobiconodontids (Kusuhashi et al., 2008, 2009a), but multituberculates were apparently far more diverse and dominant than in the Yixian mammalian fauna. Eutherians are another dominant group in the Fuxin mammalian fauna, whereas they seem to have been a minor element in the Yixian mammalian fauna. Although fossil records only show a small part of the actual fauna, it is probably permissible to consider that such rich fossil assemblages somewhat reflect their faunal compositions. There also is a possibility that this apparent faunal difference is partly biased by the difference of sedimentary environment. Lacustrine deposits are dominant in the Yixian Formation (e.g., Wang et al., 1999), whereas the Shahai and Fuxin formations are interpreted to be mainly composed of alluvial fan deposits (e.g., Wu et al., 1992). However, this environmental difference is not drastic enough to ascribe the faunal difference only to it.

The Fuxin mammalian fauna shows an intermediate state between the Yixian mammalian fauna and Late Cretaceous Asian mammalian fauna. Multituberculates and eutherians are major two groups in the Late Cretaceous mammalian faunas in Asia (Kielan-Jaworowska et al., 2004). As mentioned above, these groups are also dominant in the Fuxin mammalian fauna. However, some Early Cretaceous taxa such as eobaatarid multituberculates and 'triconodonts,' which also occur in the Yixian mammalian fauna, still persists in the Fuxin mammalian fauna. Especially, there is a common multituberculate genus *Sinobaatar* among the Yixian and Fuxin mammalian faunas. 'Triconodonts' are not dominant but still diverse in the Fuxin fauna, whereas no Late Cretaceous 'triconodonts' have been discovered in Asia up

to now (Kielan-Jaworowska et al., 2004). Therefore, the Fuxin mammalian fauna probably show a transitional state from the Yixian mammalian fauna to Late Cretaceous Asian mammalian faunas, and the dominance of multituberculates and eutherians in the Fuxin mammalian fauna indicates that such kind of faunal composition, which is typical in the Late Cretaceous Asian fauna, already appeared in the late Early Cretaceous in Asia.

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