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Early Cretaceous multituberculate mammals from the Kuwajima Formation (Tetori Group), central Japan

NAO KUSUHASHI



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Hakusanobaatar matsui gen. et sp. nov. and *Tedoribaatar reini* gen. et sp. nov. are multituberculate mammals recovered from the Lower Cretaceous (Barremian to lower Aptian) Kuwajima Formation of the Tetori Group in the Shiramine district, Hakusan City, Ishikawa Prefecture, central Japan. *Hakusanobaatar matsui* is an eobaatarid multituberculate characterized by a P4 with cusp formula 3:5, and a P5 with cusp formula 2:6:2. One of the specimens of *H. matsui* has the best preserved upper premolar series among known eobaatarid specimens. Based on the dentition of *H. matsui*, it is highly probable that the cimolodontan P4 is homologous with the “plagiaulacidan” P5. *Tedoribaatar reini* is also tentatively attributed to Eobaataridae, and shows a single-rooted p3 and loss of at least the permanent p2. On the basis of these apomorphic features, *T. reini* is considered to be the “plagiaulacidan” multituberculate that is most closely related to cimolodontans.

Key words: Mammalia, Multituberculata, Eobaataridae, *Hakusanobaatar*, *Tedoribaatar*, Early Cretaceous, Kuwajima Formation, Tetori Group, Japan.

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Introduction

Multituberculata comprise the most diverse mammalian group of the Mesozoic, characterized by unique dental features adapted for an omnivorous to herbivorous diet. Multituberculates appeared in the Late or Middle Jurassic, and were common in the Cretaceous, especially in the Late Cretaceous; they were major elements of Mesozoic mammalian faunas in the Northern Hemisphere (e.g., Kielan-Jaworowska et al. 2004). They survived into the Cenozoic with three extant mammalian groups, monotremes, marsupials, and placentals, but became extinct in the Eocene to Oligocene. Multituberculates are an important and interesting group in the context of early mammalian history.

The order Multituberculata currently consists of two suborders: the primitive and paraphyletic “Plagiaulacida”, and the derived and apparently monophyletic Cimolodonta (Kielan-Jaworowska and Hurum 2001; Kielan-Jaworowska et al. 2004). “Plagiaulacidans” occurred in the Late Jurassic and the Early Cretaceous, whereas cimolodontans ranged mainly from the Late Cretaceous to the Eocene. Cimolodontans became a major component of Cretaceous and Paleogene mammalian faunas in Asia and North America (Kielan-Jaworowska et al. 2000, 2004). Phylogenetic transition from plagiaulacidans to cimolodontans is, therefore, significant to the understanding of the evolutionary history of multituberculates as a successful group in the Mesozoic Era. However, this important process is still poorly known because the fossil record of multituberculates in the Early Cre-

taceous, which is thought to be the transitional period for multituberculate evolution, is scant worldwide.

Among multituberculates the “plagiaulacidan” family Eobaataridae is considered to be closely related to cimolodontans (Kielan-Jaworowska and Hurum 2001; Kielan-Jaworowska et al. 2004) and provides important information about the “plagiaulacidan”-cimolodontan transition. Five genera (*Eobaatar* Kielan-Jaworowska, Dashzeveg, and Trofimov, 1987; *Loxaulax* Simpson, 1928; *Monobaatar* Kielan-Jaworowska, Dashzeveg, and Trofimov, 1987; *Parendotherium* Crusafont-Pairó and Adrover, 1966; and *Sinobaatar* Hu and Wang, 2002) are attributed to the Eobaataridae (Kielan-Jaworowska and Hurum 2001; Kielan-Jaworowska et al. 2004), though *Parendotherium* is assigned to another family, Paulchoffatiidae, and *?Janumys* Eaton and Cifelli, 2001, was attributed to the Eobaataridae by Hahn and Hahn (2006). Most of them are based on fragmentary materials.

Many Early Cretaceous multituberculates have been recently reported from several localities of East Asia and cast new light on the evolutionary history of the group (Wang et al. 1995; Takada and Matsuoka 2001; Takada et al. 2001; Hu and Wang 2002a, b; Kusuhashi 2005, 2006; Kusuhashi et al. 2007). One of the localities is the “Kuwajima Kaseki-kabe” site, an outcrop of the Kuwajima Formation (Tetori Group) in the Shiramine district, Hakusan City (former Shiramine Village), Ishikawa Prefecture, central Japan (Manabe et al. 2000; Takada and Matsuoka 2001; Takada et al. 2001). The Kuwajima Formation has yielded a number of vertebrate remains as well as fossil plants and mollusks; vertebrate fauna of the Kuwajima Formation includes fishes, a frog, dino-

sauers, turtles, lizards, non-mammalian cynodonts and mammals (e.g., Matsuoka 2000; see also Matsuoka et al. 2002).

Two new genera and species of multituberculate mammals from the Kuwajima Formation are described in the present paper. Based on upper premolars of the newly described multituberculates, the possible homologies of the premolars of “plagiaulacidans” and cimolodontans are discussed.

Institutional abbreviations.—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, Hakusan, Japan (formerly Shiramine Village Board of Education, Shiramine, Japan).

Other abbreviations.—dp, deciduous premolar; I, incisor; M, molar; P/p, premolar; teeth belonging to the upper and lower dentition are indicated with upper and lower case letters, respectively; SE, standard error.

Geological setting

The Tetori Group, which consists of marine and continental deposits, ranges from the Middle Jurassic to Early Cretaceous in age and is distributed in the Inner Zone of central Japan (Fig. 1). This Group is subdivided into three units. From bottom to top, these include the Kuzuryu Subgroup, which is dominated with marine deposits, the Itoshiro Subgroup, which is characterized by a set of mixed marine and terrestrial sediments, and the Akaiwa Subgroup, which consists of mainly terrestrial sediments (Maeda 1961b; see also Kusuhashi et al. 2002). The Tetori group overlies the Hida Gneiss and granites in the northern area and rests on the Paleozoic sedimentary rocks and the Sangun Schists in the southern area (Maeda 1961b). It has yielded a variety of fossil vertebrates including dinosaurs, non-mammalian cynodonts, and mammals, as well as invertebrates and plant fossils.

The Tetori Group in the Shiramine district, Hakusan City (former Shiramine Village), Ishikawa Prefecture, central Japan, represents the northwestern distribution of the Group around Mount Hakusan (Fig. 1). In the Shiramine district, the Gomijima (Ishikawa Prefecture Board of Education 1978) and Kuwajima (Nagao in Oishi 1933) formations of the Itoshiro Subgroup and the Akaiwa and Myodani formations (Kawai 1961) of the Akaiwa Subgroup are exposed (e.g., Ishikawa Prefecture Board of Education 1978; see also Kusuhashi et al. 2002; Fig. 1). The Tetori Group in this district unconformably overlies, or is in faulted contact with, the Hida Gneiss, and is unconformably overlain by the Upper Cretaceous Omichidani Formation (Maeda 1958, 1961a; Ishikawa Prefecture Board of Education 1978). The Kuwajima Formation is mainly composed of non-marine sandstones and mudstones that are interpreted as deposits of a fluvial-dominated prograding delta system (Ishikawa Prefecture Board of Education 1978; Okazaki and Isaji 1999).

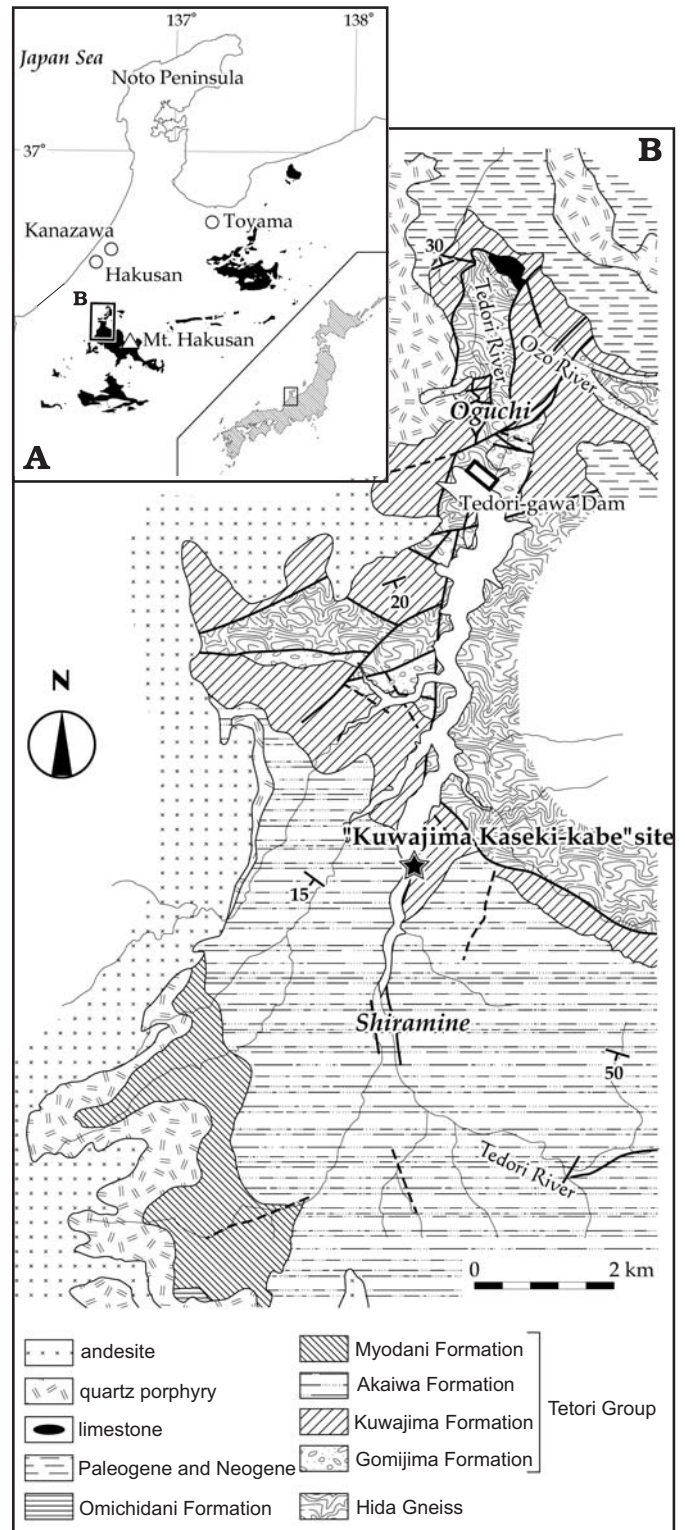


Fig. 1. A. Location of the Shiramine area and distribution of the Tetori Group (dark areas); modified after Maeda (1961b). B. Geologic map of the Tetori Group in the Shiramine area, central Japan; modified after Maeda (1961a).

The fossils described here are from the upper part of the Kuwajima Formation at the “Kuwajima Kaseki-kabe” site (Fig. 1). The “Kuwajima Kaseki-kabe” outcrop consists of alternating fine- to coarse-grained arkoses, fine-grained sand-

stones and mudstones (e.g., Kaseno 1993), and is interpreted to represent the channel and inter-channel deposits of a braided river (Okazaki and Isaji 1999; Isaji et al. 2005). This site has yielded numerous fossil vertebrates, including fishes, a frog, dinosaurs, turtles, lizards, non-mammalian cynodonts, and mammals, as well as fossil plants and mollusks (e.g., Matsuoka 2000; see also Matsuoka et al. 2002). Fossil mammals from the “Ku wajima Kaseki-kabe” are eutriconodontans, including *Hakusanodon archaeus* Rougier, Isaji, and Manabe, 2007, and multituberculates (Rougier et al. 1999, 2007; Manabe et al. 2000; Takada and Matsuoka 2001; Takada et al. 2001).

The age of the Tetori Group has not been precisely determined, and the age of the Ku wajima Formation is also uncertain (Isaji 2000). The group mainly consists of non-marine deposits, thus only a few formations are correlated to the geologic time scale by marine index fossils. Reliable radiometric ages, moreover, have seldom been reported. Few index fossils have been reported from the Ku wajima Formation, and thus it is impossible to estimate the age of the Ku wajima Formation through biostratigraphic correlations with other formations of the Tetori Group that have already been correlated to the geologic time scale. The Ku wajima Formation has been thought to be correlated to the lower Neocomian (e.g., Isaji 2000), but radiometric dating recently reported from the Tetori Group suggested that the age of the Ku wajima Formation is younger than the early Neocomian, probably somewhere between the Barremian to early Aptian (Matsumoto et al. 2006). The zircon U-Pb age of 130.7 ± 0.8 (2 SE) Ma from a tuff intercalated in the lower part of the Ku wajima Formation reported by Matsumoto et al. (2006) indicates that the Ku wajima Formation is younger than the latest Hauterivian in age (Gradstein et al. 2004). The Ku wajima Formation is stratigraphically correlated with the Okurodani Formation (Maeda 1952) distributed in the Shokawa district, Takayama City (former Shokawa Village), Gifu Prefecture, central Japan (Maeda 1961b). From the tuff beds of the Okurodani Formation, Kusuhashi et al. (2006) reported zircon U-Pb ages of 132.9 ± 0.9 (2 SE) Ma and 117.5 ± 0.7 (2 SE) Ma, and concluded that the formation is correlated to the Barremian to Aptian. These zircon U-Pb ages constrain the older limit of the age of the Ku wajima Formation to the Barremian.

Geomagnetic data obtained from the lower part of the Akaiwa Formation of the Akaiwa Subgroup in the Shiramine district suggest that the deposition of this part of the formation did not occur during the period of the Cretaceous Normal-Polarity Super-Chron C34n (Kunugiza et al. 2002) that ranges from the Late Aptian to Late Santonian (Gradstein et al. 2004). Because the Akaiwa Formation conformably overlies the Ku wajima Formation it should not be younger than the Late Santonian in age. The lower part of the Akaiwa Subgroup in the Shiramine district is older than M^{-1r}, of mid-Aptian age. The Myodani Formation of the Akaiwa Subgroup is correlated with the Kitadani Formation that yielded the spalacotheriid “symmetrodont” *Symmetrolestes parvus* Tsubamoto and Rougier, 2004 (Tsubamoto et al. 2004). The Kitadani Formation yields fresh water trigonoidid bivalves, and is correlated

to the upper Hauterivian to upper Aptian (Isaji 1993, 2000; Tsubamoto et al. 2004). These age correlations of the Akaiwa and Myodani formations suggest that the Ku wajima Formation is not younger than mid-Aptian in age. The Ku wajima Formation is, therefore, thought to be correlative with the Barremian and/or early Aptian in age.

Systematic paleontology

Order Multituberculata Cope, 1884

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

Genus *Hakusanobaatar* nov.

Type species: Hakusanobaatar matsuo gen. et sp. nov., by monotypy.

Etymology: Hakusan, after Mt. Hakusan, around which the Tetori Group is distributed, and also after Hakusan City, the city in which the discovery locality of the present materials is situated; *baatar*, Mongolian, means hero, which is used as a suffix for generic names of many Asian Cretaceous multituberculates.

Diagnosis.—As for the type species.

Hakusanobaatar matsuo sp. nov.

Figs. 2–7.

Etymology: In honor of Dr. Hidekuni Matsuo, who contributed greatly to paleontological study of the “Ku wajima Kaseki-kabe” site and, as a leader of the research group, to management of the research on the fossils from the Ku wajima Formation.

Holotype: SBEI 1736, isolated right lower incisor, left I2, left and right M1, fragmentary left upper jaw with I3, and P1 to P5, and fragment of right lower jaw with p3 and p4 (all are thought to be of the same individual); Figs. 2–4.

Type locality: “Ku wajima Kaseki-kabe” site, Shiramine district, Hakusan City, Ishikawa Prefecture, central Japan.

Type horizon: Upper part of the Ku wajima Formation (Tetori Group), Barremian to early Aptian (Early Cretaceous).

Referred specimens.—SBEI 581, fragmentary left lower jaw with damaged p4 (Fig. 5A); SBEI 582, damaged right upper premolar (probably P2; Fig. 6B); SBEI 1519, ?left p3 (Fig. 6A); SBEI 1520, damaged left p4 (Fig. 5C); SBEI 1526, fragment of right lower dentary with incisor (Fig. 5B); and SBEI 1949, tentatively assigned poorly preserved upper premolar (two ?labial cusps of probably right P5; Fig. 6C).

Diagnosis.—Moderate-sized eobaatarid multituberculate with dental formula $?3.0.5.?2/1.0.3.?2$. Enamel is possibly not limited to the outer surface of the lower incisor; p3 is double-rooted and its crown is oval rather than triangular or rectangular in lateral view; p4 has ten serrations and one posterior labial cusp. Upper I2 has one main cusp and one accessory cusp; I3 is thin in lateral view and is leaf-shaped in anterior view; P1 to P3 have triangularly arranged three cusps (1:2); cusp formula of P4 is 3:5; cusp formula of P5 is 2:6:?2; M1 has postero-lingual wing and cusp formula is 3:4. Differs from other eobaatarids (*Eobaatar*, *Monobaatar*, and *Sinobaatar*) in cusp formulae of P4 and P5. Differs from ?*Janumys* in the cusp formula of P4 and in having postero-lingual wing on M1.

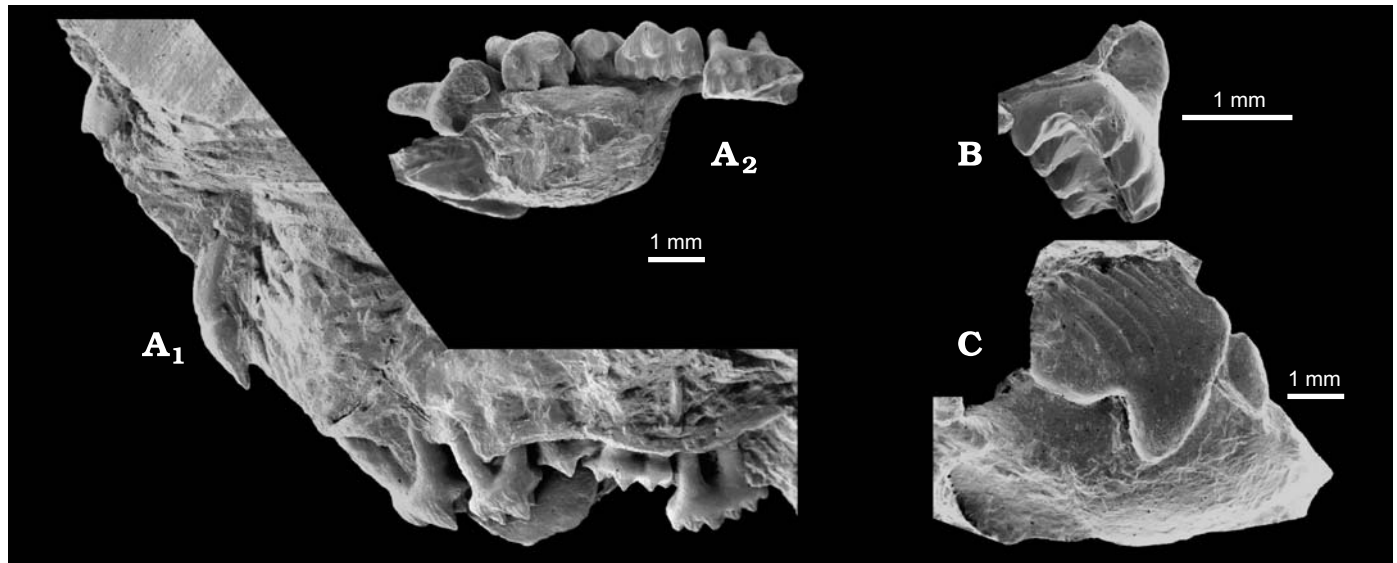


Fig. 2. Eobatarid multituberculate mammal *Hakusanobaatar matsuo* gen. et sp. nov., SBEI 1736, holotype; Lower Cretaceous Kuwajima Formation, Shiramine, Japan. SEM photograph of resin casts. **A**. Left upper dentition; **A**₁, labial view (I3, P1–P5 and the base of I2); **A**₂, occlusal view (only cheek teeth), left to anterior. **B**. Isolated right M1, postero-labial view. **C**. Right lower jaw fragment with p3 and p4, labial view.

Description.—Parts of dentaries, incisors, p3s and p4s of lower jaws, and I2, I3, P1 to P5, and M1s of upper jaw are preserved among the specimens of *Hakusanobaatar matsuo*. SBEI 1736 has the upper dentition but skull elements, including maxilla and premaxilla, are not preserved (Fig. 2A). The lower molars and upper M2 have yet to be discovered. Dental formula is considered to be $?3.0.5.?2/1.0.3.?2$ based on available materials.

Fragmentary dentaries are preserved in SBEI 581, 1526, and 1736 (Figs. 2C, 4A, 5A, B). There is no specimen in which the anterior and posterior parts of dentary including condyle and coronoid process are preserved. A mental foramen, at 1.1 mm posterior to incisor and 1.4 mm above ventral margin of the dentary, is situated closer to the incisor than to p2 in SBEI 1526 (Fig. 5B). On SBEI 2352 (a resin cast of SBEI 581 made before the anterior part of the dentary was lost), a mental foramen is situated at 1.5 mm anterior to the alveolus of p2 and 1.5 mm above the ventral margin of the dentary, though the dentary is slightly deformed (Fig. 7). This part is now missing in SBEI 581 (Fig. 5A). The masseteric fossa extends anteriorly below the posterior root of p4 (Figs. 5A, B, 7). Anterior to the p4, somewhat damaged alveoli for single-rooted p2 and double-rooted p3 are present in SBEI 2352 (Fig. 7). These were mentioned by Takada et al. (2001: fig 2), although this part is also now missing in SBEI 581.

Lower incisors are preserved in SBEI 1526 and 1736 (Figs. 4B, 5B). The lower incisor is slender with a rounded labial surface and more flattened lingual surface, and thinner anteriorly. The ventral margin of the lingual surface is slightly swollen and bends lingually. Enamel may have been present on the inner as well as outer surface.

Lower p3s are preserved in SBEI 1519 and 1736 (Figs. 2C, 4A, 6A). The crown shape of p3 is oval rather than triangular or rectangular and is slightly attenuated antero-ventrally. The

lower p3 is double-rooted; the anterior root is robust whereas the posterior one is thin and projects obliquely from a higher position than the anterior one. There are two small serrations on p3 (Fig. 6A). Each serration is accompanied by a short and indistinct ridge that extends antero-ventrally. In anterior view, there is no trace of a depression in the crown but the anterior margin is indented upward, indicating the presence of p2. The apex of p3 reaches the anterior margin of p4 (Figs. 2C, 4A).

Two damaged and one complete p4 are preserved in SBEI 581 and 1520, and 1736, respectively (Figs. 2C, 4A, 5A, C). The crown shape of p4 is parallel-sided in lateral view and is not fully rectangular, nor is it fully arcuate. Its antero-posterior length is not much greater than its height. The U-shaped anterior triangular lobe (exodaenodont lobe in many references, such as Kielan-Jaworowska et al. 1987) points ventrally and is large relative to crown size. The p4 of SBEI 1736 has ten serrations, of which at least eight of them, except for the first (most anterior) and the last (most posterior), are accompanied by ridges (Fig. 4A). Because of wear it is not obvious whether the last serration had originally been accompanied by a ridge that is now obliterated. The other specimens are damaged and it is impossible to count serrations and ridges. SBEI 581 has at least six ridges (Fig. 5A), and SBEI 1520 has at least seven (Fig. 5C). There is one posterior labial cusp on the distal margin of p4, positioned approximately midway between the base of the crown and the last serration (Figs. 2C, 4A, 5A, 7). Dorsal to this cusp, a wear facet, which reaches the last serration in height and extends to anterior end of the cusp, is observed on SBEI 1736 (Figs. 2C, 4A). The posterior root of the p4 is long antero-posteriorly relative to the crown length, and is more than twice as long as the anterior one (Figs. 5A, 7).

An isolated left I2 is preserved in SBEI 1736 and its base is preserved in the matrix that contains other upper teeth

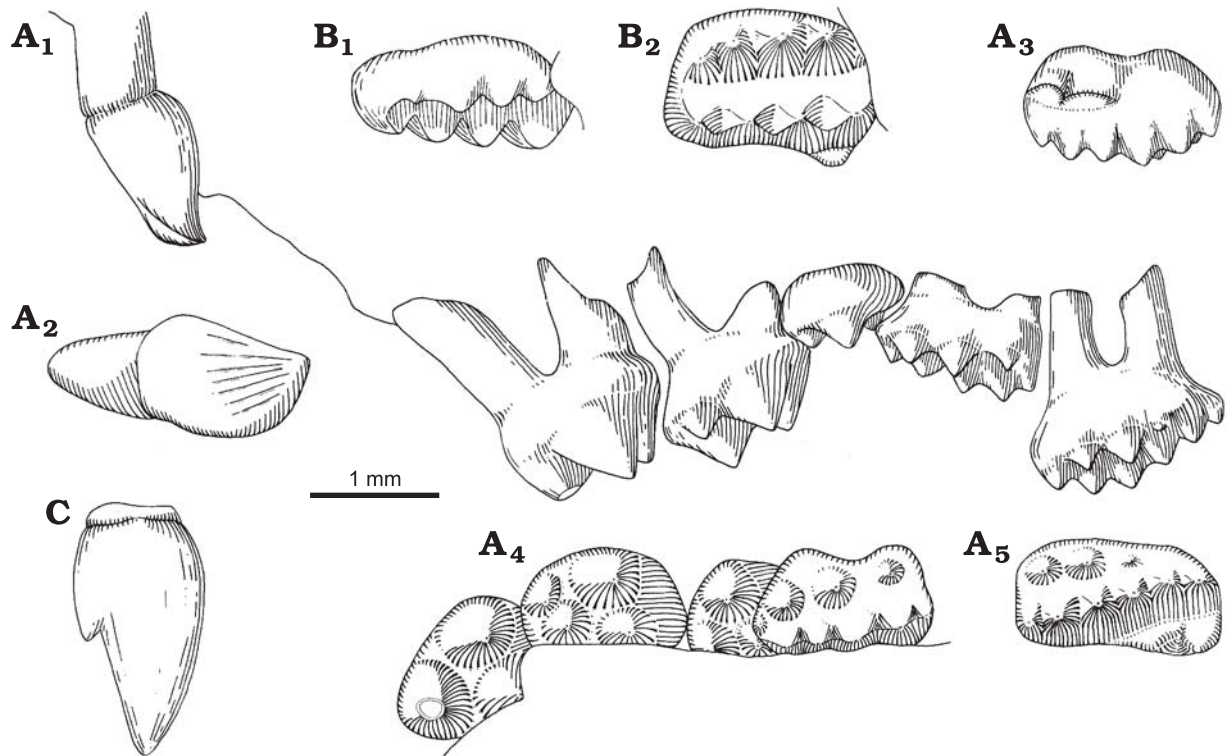


Fig. 3. Eobatarid multituberculate mammal *Hakusanobaatar matsui* gen. et sp. nov., SBEI 1736 holotype; Lower Cretaceous Kuwajima Formation, Shiramine, Japan. **A.** Left upper dentition; A₁, I3 and P1 to P5 in labial view; A₂, I3 in anterior view; A₃, P5 in lingual view, right to anterior; A₄, P1 to P4 in occlusal view, left to anterior; A₅, P5 in occlusal view, left to anterior. **B.** Isolated left M1; B₁, in labial view; B₂, in occlusal view, left to anterior. **C.** Isolated I2 in lateral view.

(Figs. 2A, 3C). I2 is a single-rooted, small and conical tooth with one main cusp and one tiny cusp projecting distally from about midway along the main cusp.

The left I3 is preserved in SBEI 1736 (Figs. 2A, 3A). I3 is probably situated at the lateral margin of the premaxilla, not medially. I3 is thin in lateral view, tapering toward the tip, and is leaf-shaped in anterior view. It is single-rooted and bears weak ridges on its crown.

Three anterior upper premolars, identified as P1–P3, are preserved in SBEI 582 and 1736 (Figs. 2A, 3A, 6B). The three teeth have similar shapes, with three cusps arranged triangularly: one on the labial side and two on the lingual. On each tooth the three cusps are subequal in size. P2 differs in having a tiny cusp anterior to the labial cusp. All cusps are ornamented with radiating (in occlusal view) ridges. The sizes of P1 and P2 are similar, and P3 is smaller than the other two. P3 has a distinct cingulum that extends posteriorly. On the premolar (probably right P2) of SBEI 582, there is an incipient antero-lingual cingulum (Fig. 6B). The anterior part of P2 overlaps the posterior part of P1, and the posterior part of P2 slightly overlaps P3 in SBEI 1736 (Figs. 2A, 3A). The posterior cingulum of P3 is overlapped by the anterior part of P4.

A left P4 is preserved in SBEI 1736 (Figs. 2A, 3A). There are two cusp rows on P4; cusp formula is 3:5 (labial:lingual). The tooth is morphologically similar to P4 of *Eobaatar*, though the cusp formula is different. The height of cusps of the

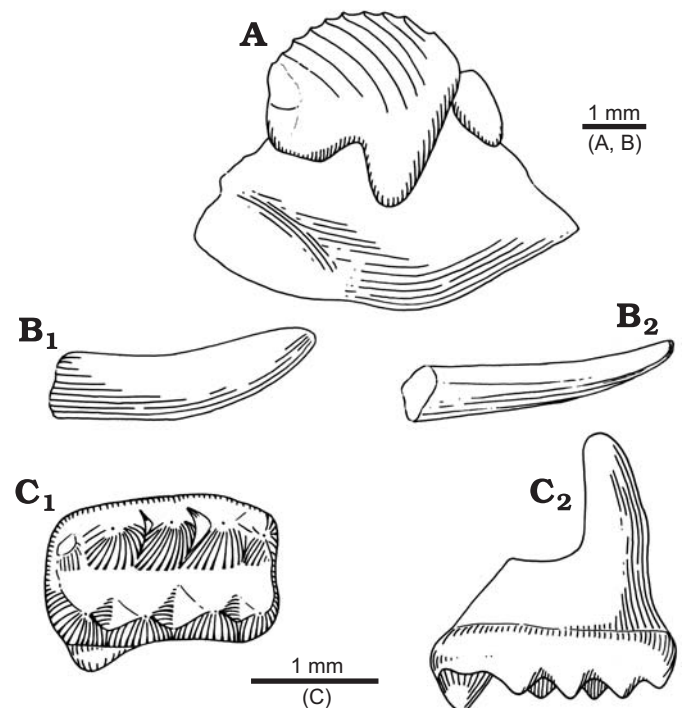


Fig. 4. Eobatarid multituberculate mammal *Hakusanobaatar matsui* gen. et sp. nov., SBEI 1736, holotype; Lower Cretaceous Kuwajima Formation, Shiramine, Japan. **A.** Right lower jaw fragment with p3 and p4, labial view. **B.** Isolated right lower incisor; B₁, labial view; B₂, somewhat occlusal view. **C.** Isolated right M1; C₁, occlusal view, right to anterior; C₂, labial view.

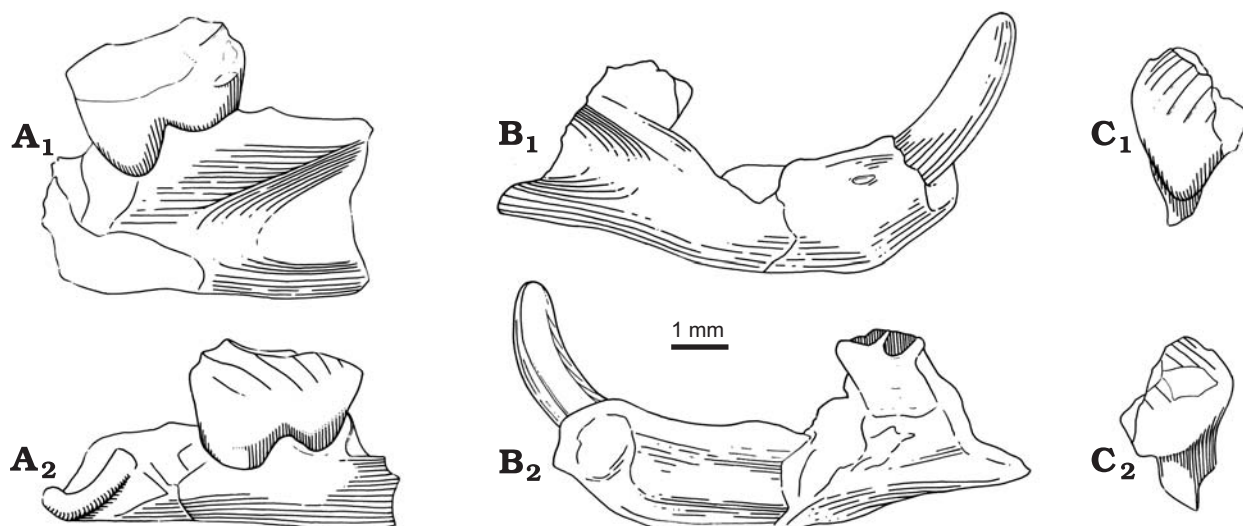


Fig. 5. Eobatarid multituberculate mammal *Hakusanobaatar matsuoii* gen. et sp. nov.; Lower Cretaceous Kuwajima Formation, Shiramine, Japan. **A.** SBEI 581, fragment of left lower jaw with damaged p4; A₁, labial view; A₂, lingual view. **B.** SBEI 1526, fragment of right lower dentary with incisor; B₁, labial view; B₂, lingual view. **C.** SBEI 1520, damaged left p4; C₁, labial view; C₂, lingual view.

labial row does not vary greatly, though the second cusp is larger than the other two. The third labial cusp is clearly separated from the second, whereas the first and second cusps are close to each other. The cusps of the lingual row increase in height posteriorly, with the fourth cusp being the highest; the fifth cusp is small. There is a tiny cuspule situated between the cusp rows at the anterior margin of the tooth. The three posterior cusps of the lingual row are higher than those of the labial row. All cusps are ornamented with fine ridges. The lingual wall of the tooth forms a shearing surface.

The left P5 is preserved in SBEI 1736 (Figs. 2A, 3A). The crown is almost rectangular in occlusal view. The cusp formula is 2:6:2 (labial:medial:lingual). The labial two cusps are situated lateral to the notch between the first and second cusps of the medial cusp row, and to the third cusp, respectively. A cuspule is present posterior to the second labial cusp. The medial cusp row is diagonally oriented postero-labially from the antero-lingual corner of the crown. The third medial cusp is the highest in the row, with the cusps decreasing in height both anteriorly and posteriorly. The cusps of the medial main cusp row are higher than the labial cusps. All cusps are ornamented with fine ridges. On the postero-lingual corner of the tooth, there is a terrace-like flattened region with a transverse groove. At least two cusps of the lingual cusp row were probably present in this region but have been lost by wear or by postmortem erosion.

Left and right M1s are preserved in SBEI 1736 (Figs. 2B, 3B, 4C). The cusp formula is 3:4. All cusps have approximately the same height, but the fourth lingual cusp is slightly larger than the others. There is a cuspule anterior and slightly medial to the first labial cusp. The cuspule is somewhat ridge-like and not fully separated from the first cusp. A crescentic wing without any cusp is present at the postero-lingual corner of the tooth. The anterior margin is slightly oblique to the longitudinal axis of the tooth. The labial cusps are posi-

tioned about opposite the embrasures between the cusps of the lingual row. Posterior to the third labial cusp there is a small flattened surface. The posterior ends of the cusp rows are connected by ridges.

Measurements.—See Tables 1, 2.

Remarks.—*Hakusanobaatar matsuoii* differs from cimolodontans in having five upper premolars (see Kielan-Jaworowska et al. 2004), and should be placed in the “Plagiaulacida”. It is clearly distinguishable from “plagiaulacidans”, except for eobaatarids and *Arginbaatar* Trofimov, 1980, in having a much

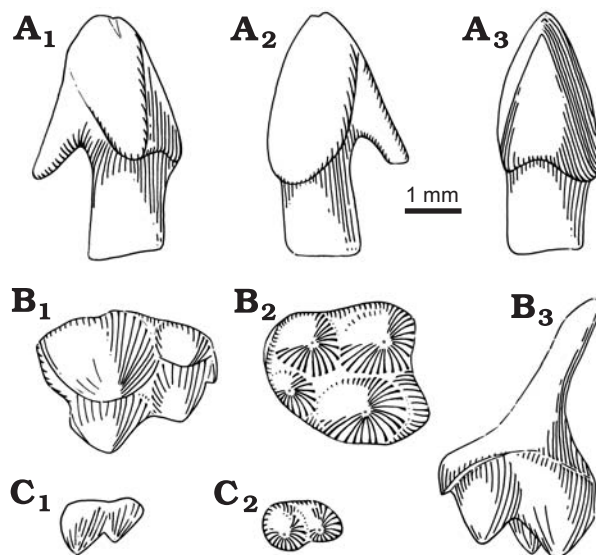


Fig. 6. Eobatarid multituberculate mammal *Hakusanobaatar matsuoii* gen. et sp. nov.; Lower Cretaceous Kuwajima Formation, Shiramine, Japan. **A.** SBEI 1519, ?left p3; A₁, ?lingual view; A₂, ?labial view; A₃, anterior view. **B.** SBEI 582, damaged right upper premolar (probably P2); B₁, labial view; B₂, occlusal view, left to anterior; B₃, lingual view. **C.** SBEI 1949, poorly preserved upper premolar fragment (two ?labial cusps of probably right P5); C₁, ?labial view; C₂, occlusal view, ?right to anterior.

reduced p3 (Kielan-Jaworowska et al. 2004). The lower p4 of *Hakusanobaatar matsuo*i is not fully arcuate in lateral view, which distinguishes *H. matsuo*i from cimolodontans and *Arginbaatar* (see Trofimov 1980; Kielan-Jaworowska et al. 1987; Kielan-Jaworowska et al. 2004). *Hakusanobaatar* is distinguished from alibionbaatarids by P1 to P3 with only three cusps and by the morphology of P5 (Kielan-Jaworowska and Ensom 1994; Kielan-Jaworowska et al. 2004).

Compared with eobaatarids, *H. matsuo*i is almost the same size as *Eobaatar magnus* Kielan-Jaworowska, Dashzeveg, and Trofimov, 1987, and is slightly smaller than *Sinobaatar lingyuanensis* Hu and Wang, 2002 (Tables 1 and 2). *Hakusanobaatar matsuo*i shares a similar morphology of p4 with *Eobaatar* and *Sinobaatar*, being slightly more arcuate than those of plagiaulacids and other primitive “plagiaulacidans” in lateral view (see Kielan-Jaworowska et al. 1987; Hu and

Table 1. Measurements of lower premolars in *Hakusanobaatar matsuo*i gen. et sp. nov., *Tedoribaatar reini* gen. et sp. nov., Lower Cretaceous Kuwajima Formation, Shiramine, Japan; *Sinobaatar lingyuanensis* Hu and Wang, 2002, Lower Cretaceous Yixian Formation, Dawangzhangzi, China; and *Eobaatar magnus* Kielan-Jaworowska, Dashzeveg, and Trofimov, 1987, Lower Cretaceous Höövör Beds, Höövör, Mongolia. All data are original. L, longitudinal length; H, height.

| | p3 | | p4 | |
|---------------------------------|-----|-----|-----|-----|
| | L | H | L | H |
| <i>Hakusanobaatar matsuo</i> i | | | | |
| SBEI 581 | | | 3.2 | |
| SBEI 1519 | 0.9 | 1.1 | | |
| SBEI 1736 | 1.0 | 1.4 | 3.5 | 2.1 |
| <i>Tedoribaatar reini</i> | | | | |
| SBEI 1570 | | | 3.7 | 2.4 |
| <i>Sinobaatar lingyuanensis</i> | | | | |
| IVPP V 12517 | 1.2 | 1.9 | 4.1 | 2.5 |
| <i>Eobaatar magnus</i> | | | | |
| PIN 3101-57 | | | 3.5 | 2.0 |
| PIN 3101-60 | | | 3.0 | 2.1 |

Table 2. Measurements of upper teeth in *Hakusanobaatar matsuo*i gen. et sp. nov., Lower Cretaceous Kuwajima Formation, Shiramine, Japan; *Sinobaatar lingyuanensis* Hu and Wang, 2002, Lower Cretaceous Yixian Formation, Dawangzhangzi, China; and *Eobaatar magnus* Kielan-Jaworowska, Dashzeveg, and Trofimov, 1987, Lower Cretaceous Höövör Beds, Höövör, Mongolia. All data are original. L, longitudinal length; W, transverse width.

| | P1 | | P2 | | P3 | | P4 | | P5 | | M1 | |
|---------------------------------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|
| | L | W | L | W | L | W | L | W | L | W | L | W |
| <i>Hakusanobaatar matsuo</i> i | | | | | | | | | | | | |
| SBEI 582 | | | 1.4 | 1.2 | | | | | | | | |
| SBEI 1736 left | 1.4 | 1.0 | 1.4 | 0.8 | 0.9 | 0.9 | 1.6 | 1.0 | 1.7 | 1.1 | 1.7 | 1.2 |
| SBEI 1736 right | | | | | | | | | | | 1.5 | 1.1 |
| <i>Sinobaatar lingyuanensis</i> | | | | | | | | | | | | |
| IVPP V 12517 | | | | | | | 1.7 | 0.8 | 2.1 | 1.1 | 1.8 | 1.4 |
| <i>Eobaatar magnus</i> | | | | | | | | | | | | |
| PIN 3101-66 | | | | | | | | | | | 1.8 | 1.1 |

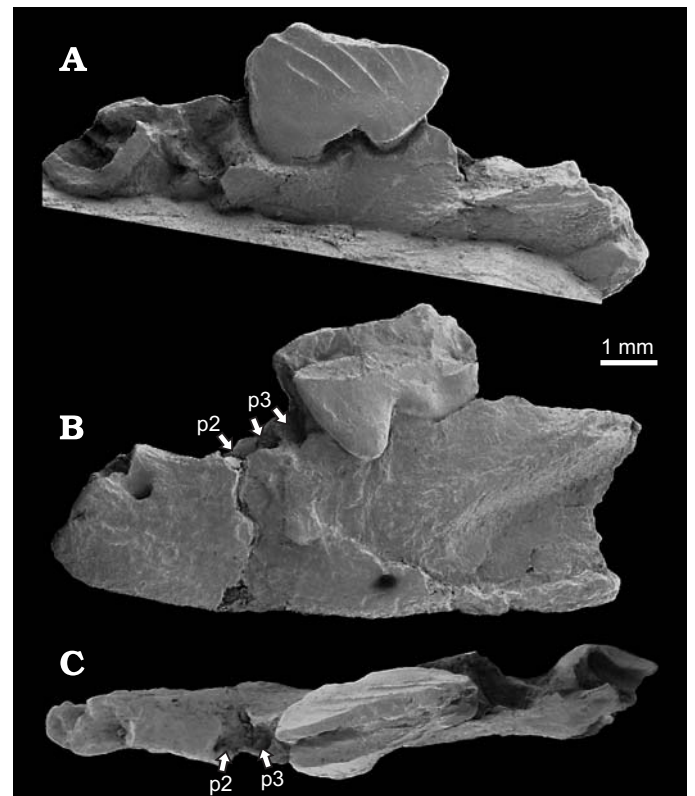


Fig. 7. Eobaatarid multituberculata mammal *Hakusanobaatar matsuo*i gen. et sp. nov.; Lower Cretaceous Kuwajima Formation, Shiramine, Japan; SEM photograph of SBEI 2352 (a resin cast of SBEI 581 before the anterior part of the dentary was lost), left lower jaw fragment with damaged p4. A. Lingual view. B. Labial view; arrows indicate alveoli of a single-rooted p2 and a double-rooted p3. C. Occlusal view; arrows indicate the alveolus of a p2 and the anterior alveolus of a p3.

Wang 2002a, b), and the much reduced p3 is similar to those of *Sinobaatar* and, possibly, *Eobaatar* (see Kielan-Jaworowska et al. 1987; Hu and Wang 2002a, b). It also shares similar P1 to P3 morphology with *Eobaatar* and *Monobaatar* in having three main cusps (see Kielan-Jaworowska et al. 1987), but this feature is present in “plagiaulacidans” of other families such as the Arginbaataridae (e.g., Trofimov 1980; Kielan-Jaworowska et al. 1987; Kielan-Jaworowska et al. 2004). These dental similarities suggest that *H. matsuo*i is phylogenetically related to the Eobaataridae.

*Hakusanobaatar matsuo*i is distinguished from *Eobaatar* by the following characters (see Kielan-Jaworowska et al. 1987): P4 with cusp formula 3:5 (those of *Eobaatar* have only four lingual cusps); P5 has three cusp rows (only two are present in *Eobaatar*; tooth designation of P5 of *Eobaatar* in Kielan-Jaworowska et al. 1987 is, however, somewhat questionable). The cusp formulae of P4 and P5 and morphology of P5 also distinguish *H. matsuo*i from *Sinobaatar* (see Hu and Wang 2002a, b). *Hakusanobaatar matsuo*i is also distinguished from *Monobaatar* by the cusp formula of P4 (see Kielan-Jaworowska et al. 1987). *Hakusanobaatar matsuo*i differs from ?*Janumys* in the cusp formula of P4 and in having a postero-lingual wing on M1 (Eaton and Cifelli 2001).

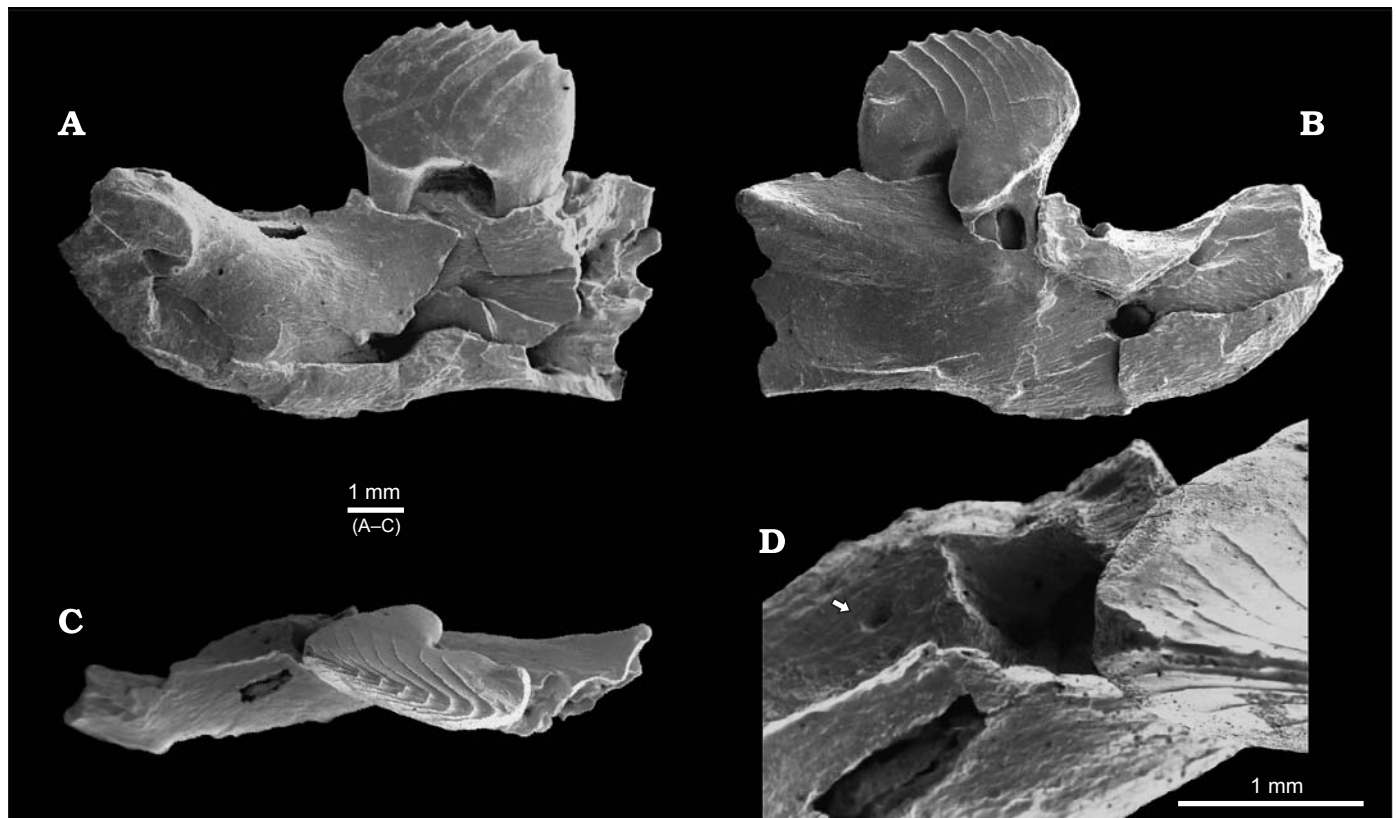


Fig. 8. Eobaatarid multituberculate mammal *Tedoribaatar reini* gen. et sp. nov., SBEI 1570, holotype, right lower jaw fragment with p4; Lower Cretaceous Kuwajima Formation, Shiramine, Japan. SEM photograph of the resin cast. A. Lingual view. B. Labial view. C. Occlusal view, left to anterior. D. Occlusal view of the alveoli of p2 (arrow) and p3, left to anterior.

Hakusanobaatar matsuo can not be sufficiently compared with the other two poorly known eobaatarid and ?eobaatarid genera, *Loxaulax* and *Parendotherium*; it is, however, reasonable to recognize *H. matsuo* as a new genus and species of the Eobaataridae.

The holotype of *H. matsuo* gen. et sp. nov. (SBEI 1736) has the best preserved upper dentition among known eobaatarids and provides a complete premolar series (Figs. 2A, 3A). It shows the precise dental characters of eobaatarid upper cheek teeth, especially those of the premolars, and provides the key to resolving homology of “plagiaulacidan” and cimolodontan premolars that has yet to be sufficiently understood.

Genus *Tedoribaatar* nov.

Type species: *Tedoribaatar reini* gen. et sp. nov., by monotypy.

Etymology: *Tedori*, after Tedori River, which runs through the locality where the present material was discovered; *baatar*, Mongolian, means hero, which is used as a suffix for generic names of many Asian Cretaceous multituberculates.

Diagnosis.—As for the type species.

Tedoribaatar reini sp. nov.

Figs. 8, 9.

Etymology: In honor of Dr. Johannes Justus Rein, a German geographer who first collected fossil plants from the Kuwajima Formation (reported by Geyler 1877).

Holotype: SBEI 1570, fragment of right lower jaw with p4 (Figs. 8, 9).

Type locality: “Kuwajima Kaseki-kabe” site, Shiramine district, Hakusan City, Ishikawa Prefecture, central Japan.

Type horizon: Upper part of the Kuwajima Formation (Tetori Group), Barremian to early Aptian (Early Cretaceous).

Diagnosis.—Lower dental formula 1.0.?.?.?; lower p3 single-rooted; p4 having ten serrations and one posterior labial cusp. Differs from other “plagiaulacidans,” including eobaatarids, in having a small number of lower permanent premolars and a single-rooted p3.

Description.—SBEI 1570, fragmentary right dentary preserves p4 in the holotype (Figs. 8, 9). The other teeth are not known. The dental formula of lower dentition is 1.0.?.?.?

SBEI 1570 (Figs. 8, 9) does not preserve a definitive mental foramen. At 1.5 mm anterior to p4 and 1.2 mm above ventral margin of the dentary, there is a relatively large hole that might be in the position of the mental foramen. The masseteric fossa extends anteriorly below the posterior root of p4, and becomes indistinct below the anterior root of p4. Broken alveoli for a p3 and a double-rooted m1 are preserved anterior and posterior to p4, respectively (Figs. 8, 9). There is no trace of two roots in the broken alveolus of a p3, though the possibility that the p3 was double-rooted cannot be definitely ruled out. Anterior to the alveolus of p3, there is a tiny pit that is possibly an alveolus for a shed dp2. There is no trace of permanent p2.

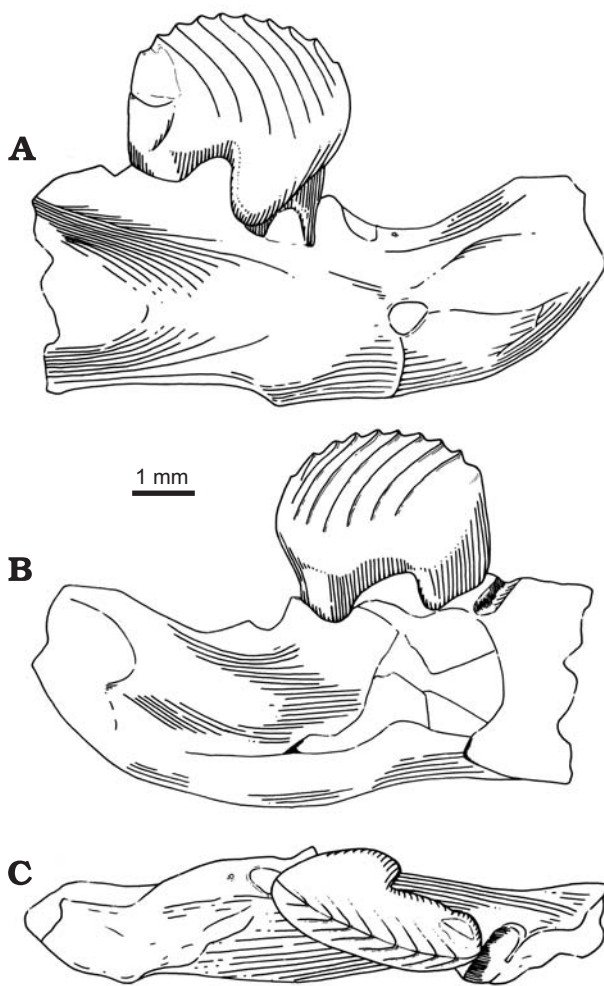


Fig. 9. Eobaatarid multituberculate mammal *Tedoribaatar reini* gen. et sp. nov., SBEI 1570, holotype; Lower Cretaceous Kuwajima Formation, Shiramine, Japan. Fragment of right lower jaw with p4. **A.** Labial view. **B.** Lingual view. **C.** Occlusal view, left to anterior.

The p4 is not fully parallel-sided and is neither fully arcuate nor rectangular in lateral view. The U-shaped anterior triangular lobe is large relative to crown size; it extends postero-ventrally. The anterior part of p4 probably slightly overhung p3. The fourth lower premolar has ten serrations, eight of which (except for the terminal ones) are accompanied by ridges. Only one posterior labial cusp is present. It is located high on the crown, somewhat above half the height of the distal margin of p4 (Figs. 8, 9). The position of this cusp is higher than that in *Hakusanobaatar matsuo*i. Dorsally, a wear facet extends from a position above the last serration to the anterior end of this cusp. The length of the posterior root of the p4 is modest, and is less than twice as long as the anterior one (Figs. 8, 9).

Measurements.—See Table 1.

Remarks.—The tiny pit positioned anterior to the alveolus of p3 in SBEI 1570 is interpreted as an alveolus for a shed dp2. The mental foramen is usually larger than this pit, and is situated in lower position on the labial side of the dentary, possi-

bly at the position of the large hole in SBEI 1570. There is a possibility that the tiny pit is a foramen for a blood vessel; however, this is unlikely because such a foramen does not normally open to the occlusal surface of the dentary. The lower cheek teeth of multituberculates are obliquely arranged to the dentary in occlusal view. Taking this into account, the position of the pit is thought to be just anterior to the p3 in tooth row, and it is the position of a p2, if present. Therefore, this tiny pit is more likely to be an alveolus for a dp2 or p2 than a blood vessel foramen. This alveolus is very tiny and it is hard to imagine that it contained a tooth. The alveolus is, thus, thought to be for a shed dp2. Lacking the eruption of a permanent p2, the alveolus is interpreted to have become reduced its size. *Tedoribaatar reini* is, therefore, thought to have had only two lower permanent premolars.

Tedoribaatar reini is thought to have had only two lower permanent premolars. The pit situated anterior to the alveolus for p3 on the holotype (SBEI 1570) is interpreted as the alveolus for a shed dp2, as mentioned above, and no trace of a permanent p2 is present. Although there is a possibility that this pit is a blood vessel foramen, it still is the case that *T. reini* does not have p2. Cimolodontans have at most only two lower premolars (Kielan-Jaworowska et al. 2004), but the morphology of the p4 seen in *T. reini* is intermediate between the typical “plagiaulacidan” and cimolodontan conditions. In lateral view p4 of *T. reini* is neither fully arcuate nor extended forward to overhang the crown of p3 as seen in cimolodontans. From the size of the alveolus, p3 of *Tedoribaatar reini* is estimated to have been larger than the peg-like p3 of cimolodontans. *Tedoribaatar reini* is, therefore, assigned to “Plagiaulacida”. *Tedoribaatar reini* has a single-rooted p3, which indicates that the p3 crown was reduced. *Tedoribaatar reini* differs from “plagiaulacidans” except for eobaatarids and *Arginbaatar* in this feature (see Trofimov 1980; Kielan-Jaworowska et al. 1987; Kielan-Jaworowska et al. 2004). The morphology of p4 of *T. reini* is clearly different from that of *Arginbaatar*, which has a highly arcuate, specialized p4, and is rather similar to those of eobaatarids (see Trofimov 1980; Kielan-Jaworowska et al. 1987). The number of serrations of p4 (ten) is in the range of Eobaataridae. *Tedoribaatar reini* is tentatively considered as a member of the Eobaataridae and the most derived “plagiaulacidan” multituberculate yet discovered.

Compared with eobaatarids, *T. reini* is almost the same size as *Eobaatar magnus* and *Hakusanobaatar matsuo*i, and slightly smaller than *Sinobaatar lingyuanensis* (Table 1). *Tedoribaatar reini* shares a reduced p3 with *Eobaatar*, *Sinobaatar* (see Kielan-Jaworowska et al. 1987; Hu and Wang 2002a, b) and *Hakusanobaatar*. *Tedoribaatar reini* is, however, distinguished from *Hakusanobaatar matsuo*i, discovered from the same locality, by the higher position of the posterior labial cusp of the p4 and the antero-posteriorly shorter posterior root of the p4. A single-rooted p3 is present only in *T. reini* among “plagiaulacidans”, and clearly distinguishes *T. reini* from *Eobaatar*, *Sinobaatar* (see Kielan-Jaworowska et al. 1987; Hu and Wang 2002a, b) and *Hakusanobaatar*.

Tedoribaatar reini also differs from *Eobaatar*, *Sinobaatar*, and *Hakusanobaatar* in having a lower number of lower premolars. The lack of p2 and a single-rooted p3 are clearly apomorphic characters among “plagiaulacidans”. *Tedoribaatar reini* is, therefore, recognized as a new genus and species of Eobaataridae, and as a species that is most closely related to cimolodontans among “plagiaulacidans”, although it can not be compared with the other three eobaatarid and ?eobaatarid genera (*Monobaatar*, *Loxaulax* and *Parendotherium*) whose p4s have not been discovered.

Discussion and conclusions

One of the diagnostic features of the suborder Cimolodonta is the presence of one to four upper premolars rather than five as in “plagiaulacidans”. At least one upper premolar was lost in the evolutionary transition from “Plagiaulacida” to Cimolodonta. Cimolodontan premolars are generally designated as P1 to P4, and those of “plagiaulacidans” as P1 to P5. There are several hypotheses concerning homology of “plagiaulacidan” and cimolodontans premolars that were briefly reviewed in Kielan-Jaworowska et al. (2004). With a few exceptions, the lost premolar has been considered to be an anterior premolar (e.g., Hahn 1978 cited in Kielan-Jaworowska et al. 2004), P4 (e.g., Clemens 1963; Kielan-Jaworowska et al. 2004), or P5 (Peláez-Campomanes et al. 2000). Eaton and Cifelli (2001) noted that the P4 of the “plagiaulacidan” *Janumys erebos* Eaton and Cifelli, 2001, is morphologically similar to those of cimolodontans but may represent P5. Well-preserved upper cheek tooth series have never been reported for eobaatarids, which are the “plagiaulacidans” most similar to cimolodontans, and this makes discussion of the homology of relevant teeth difficult. SBEI 1736 shows for the first time a complete premolar series of an eobaatarid multituberculate. The tooth count and morphology of SBEI 1736 support the view that the cimolodontan P4 is homologous to “plagiaulacidan” P5 and that it was the “plagiaulacidan” P4 that was lost.

Most cimolodontans have anterior upper premolars with simple crowns consisting of three to four cusps, and those of plagiaulacids and eobaatarids are of similar morphology (e.g., Kielan-Jaworowska et al. 2004). In eobaatarids, there are major morphological differences between the anterior three premolars and P4. P1 to P3 are simple tri-cusped teeth, whereas P4 has two cusp rows and more than four cusps are present in the lingual row. Cusps in the lingual row of P4 increase their height posteriorly. This morphology is quite different from P3 of cimolodontans. “Plagiaulacidan” P3 is, in contrast, rather similar to cimolodontan P3. No clear trend of P4 simplification is observed in “plagiaulacidans”. Three anterior premolars of cimolodontans, therefore, are thought to be homologous to “plagiaulacidan” P1 to P3. This fact suggests that the first tooth lost in evolution was the plagiaulacidan P4 or P5.

P5 is clearly distinguishable from P4 by its morphology in *Sinobaatar* and *Hakusanobaatar*. In *Eobaatar*, P4 and P5

are morphologically similar to each other but descriptions of P4 and P5 of *Eobaatar magnus*, the only *Eobaatar* species for which both premolars are known, are based on isolated teeth and questions about tooth homologies persist. P4 in eobaatarids has two cusp rows and the lingual cusps increase in height posteriorly. P5 has two to three cusp rows and there are at least three cusps in the main row. Cusps of the main row of P5 are obliquely arranged from antero-lingual to postero-labial, and increase in height posteriorly to about the middle of the tooth, before decreasing in height posteriorly. In *Sinobaatar*, the posterior half of the lingual main cusp row is rather ridge-like (see Hu and Wang 2002a, b; Kielan-Jaworowska et al. 2004). Crown morphology of P5 of “plagiaulacidans” similar to that of *Sinobaatar* and *Hakusanobaatar* is seen in paulchoffatiids and pinheirodontids, such as *Lavocatia* Canudo and Cuenca-Bescós, 1996, with three cusp rows (Kielan-Jaworowska et al. 2004), but shearing surfaces are much more developed on those of *Sinobaatar* and *Hakusanobaatar* than on those of paulchoffatiids and pinheirodontids. *Lavocatia* has a main medial cusp row that extends obliquely from antero-lingual to postero-labial (Canudo and Cuenca-Bescós 1996). There are antero-labial and postero-lingual cusp rows of small cusps (Canudo and Cuenca-Bescós 1996). The similarity of P5 between eobaatarids and paulchoffatiids or pinheirodontids indicates that eobaatarids might be derived from a lineage with a *Lavocatia*-like P5. In the evolution of *Hakusanobaatar*, anterior and posterior small cusps of lingual and labial cusp rows were reduced. The ridge-like posterior half of the main cusp row in *Sinobaatar* is interpreted to be derived from the posterior cusps. *Sinobaatar* has indistinct cuspules on the labial wall of P5, as depicted in Kielan-Jaworowska et al. (2004: fig. 8.34A), and these cusps are interpreted to be of reduced remnants of the labial cusp row.

In most of Cretaceous cimolodontans, at least in *Bryceomys* Eaton, 1995, *Cedaromys* Eaton and Cifelli, 2001, *Cimexomys* Sloan and Van Valen, 1965, *Cimolodon* Marsh, 1889, *Cimolomys* Marsh, 1889, *Dakotamys* Eaton, 1995, *Kryptobaatar* Kielan-Jaworowska, 1970, *Mesodma* Jepsen, 1940, *Paracimexomys* Archibald, 1982, and *Stygimys* Sloan and Van Valen, 1965, cusps in the main (or medial) cusp row of P4 increase in height posteriorly and there are two ridges that extend to the highest and posterior-most cusp from the postero-labial and -lingual corners of the crown, forming a posterior basin between them (see illustrations and plates in e.g., Lillegraven 1969; Fox 1971, 1989; Sahni 1972; Novacek and Clemens 1977; Clemens and Kielan-Jaworowska 1979; Archibald 1982; Johnston and Fox 1984; Lillegraven and McKenna 1986; Storer 1991; Montellano 1992; Eaton 1995; Kielan-Jaworowska and Hurum 1997; Montellano et al. 2000; Eaton and Cifelli 2001). This morphology of cimolodontan P4 is obviously closer to that of eobaatarid P5 (at least of *Sinobaatar* and *Hakusanobaatar*) than that of P4, and the morphology of the eobaatarid P5 is here interpreted to represent an intermediate stage between *Lavocatia*-like P5 and cimolodontan P4. Therefore, based on morphological evidence, it is

postulated that cimolodontan P4 is derived from “plagiaulacidan” P5, and that “plagiaulacidan” P4 was lost in the evolutionary process from “plagiaulacidans” to cimolodontans. Cimolodontan P1 to P4 are, therefore, interpreted to be homologous to plagiaulacidan P1 to P3 and P5, respectively. Under this interpretation, P4s with somewhat different shape from other cimolodontans, as seen in *Meniscoessus* Cope, 1882 (see figures in e.g., Sahni 1972; Archibald 1982), represent secondary transformations that occurred later in the evolutionary history of the group.

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