

# Multituberculata from the Early Cretaceous of Mongolia

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**Abstract**—The multituberculata assemblage from the Early Cretaceous Khovoor locality in Mongolia, based on the study of 112 specimens in PIN collection, includes three taxa: arginbaatarid *Arginbaatar dmitrievae* Trofimov, 1980 (= *Monobaatar mimicus* Kielan-Jaworowska et al., 1987, new synonym) and two eobaatarids, *Eobaatar magnus* Kielan-Jaworowska et al., 1987 and *Nokerbaatar minor* (Kielan-Jaworowska et al., 1987), comb. nov. Both eobaatarid taxa from Khovoor differ from other known eobaatarids by lower incisors with enamel restricted to ventrolateral side. Contrary to the previous claims, in both *Eobaatar magnus* and *Nokerbaatar minor* P5 is sectorial tooth, as in other eobaatarids, different in morphology from P4. In *Eobaatar* and *Nokerbaatar* gen. nov., there is pronounced sculpture of radiating ridges on the upper premolars, which is partially also present on the upper molars. In *Nokerbaatar*, there is a ventrolingual groove on the lower incisor and p3 is relatively small, lacking serrations. In *Eobaatar*, there is a pronounced ventrolingual ridge on the lower incisor and p3 is relatively larger, with serrations. The number of infraorbital foramina is variable in *Arginbaatar*, with most specimens having two foramina. In *Arginbaatar*, the cusp ornamentation is poorly developed or absent on upper premolars and absent on upper molars. The sectorial dP5 was likely not replacing by P5. The molars (M2, m1–2) have conical cusps. The p4 is very large and highly variable in size and number of denticles (11–18). It lacks labial cusps and has restricted enamel. The p4 rotates mesioventrally during the ontogeny, which is unique for the Multituberculata. The p2 and dp3 are shed early during the ontogeny. The p3 is fully formed but cannot erupt because it is overhang by p4. In upper dentition, there is a replacement of dP3 by P3. Arginbaataridae are currently known only from Khovoor valley in Mongolia, while Eobaataridae were widely distributed in the Early Cretaceous in Asia and Europe.

**Keywords:** Mammalia, Multituberculata, Early Cretaceous, Mongolia, Khovoor

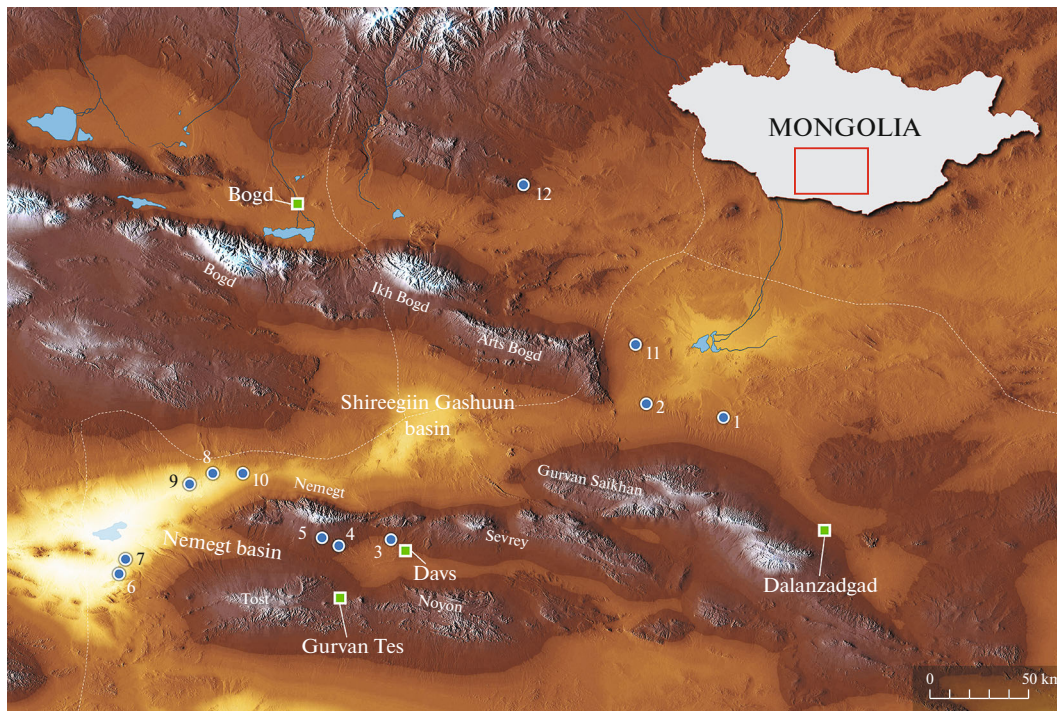
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## INTRODUCTION

The multituberculata from the Early Cretaceous Khovoor locality in Mongolia were first reported by Trofimov (1972) and Trofimov in Belyaeva et al. (1974), referred to as a new undescribed genus and species of Plagiaulacidae. Subsequently Trofimov (1980) in a short note established *Arginbaatar dmitrievae* from Khovoor, provisionally attributed to the Taeniolabididae. This was the first multituberculata mammal described from the Early Cretaceous of Asia. That time the Early Cretaceous multituberculata were virtually unknown, being represented by *Loxaulax valdensis* from the Valanginian of England and undescribed specimens from the Albian of Texas, USA (Woodward, 1911; Simpson, 1928; Patterson, 1956; Clemens, 1963; Butler and Ford, 1977; Clemens and Kielan-Jaworowska, 1979) (the Berriasian multituberculata from the Purbeck Limestone Group of England were considered Late Jurassic in age). *Arginbaatar* was referred to the monotypic family Arginbaataridae of Plagiaulacoidea by Hahn and Hahn (1983).

Kielan-Jaworowska et al. (1987) described in detail all available multituberculata specimens from Khovoor housed in the Moscow (PIN) and Ulanbaatar (GI) collections. Two new taxa, *Eobaatar magnus* and *Eobaatar minor*, were attributed to the new family Eobaataridae (Taeniolabidoidea). Arginbaataridae were provisionally retained within the Plagiaulacoidea. Fosse et al. (1985) identified gigantoprismatic enamel in *A. dmitrievae* and then undescribed *Eobaatar minor* (based on GI PST 10-23). These were the oldest occurrences of the gigantoprismatic enamel in Multituberculata. Eobaataridae and Arginbaataridae are now placed in the Plagiaulacida and Multituberculata suborder incertae sedis, respectively (Kielan-Jaworowska and Hurum, 2001; Kielan-Jaworowska et al., 2004).

The collection of multituberculata from Khovoor described by Kielan-Jaworowska et al. (1987) consist of 68 specimens (39 from PIN collection and 29 from GI collection). Subsequent sorting of the fossils and concentrate from Khovoor produced additional



**Fig. 1.** The main localities of Cretaceous mammals in Mongolia: (1) Bayan Zag, (2) Toogrik Shire, (3) Ukhaa Tolgod, (4) Khu-lsan, (5) Nemegt, (6) Hermin Tsav II, (7) Hermin Tsav I, (8) Bugin Tsav, (9) Khaichin Ula, (10) Guriliin Tsav, (11) Udan Sayr, (12) Khovoor.

73 specimens of multituberculates. Thus the total number of the multituberculates currently housed in the PIN collection is 112 specimens (26 of *Eobaatar magnus*, 17 of *Nokerbaatar minor*, and 69 of *Arginbaatar dmitrievae*).

Besides Khovoor, in Mongolia the Early Cretaceous multituberculates were found in a nearby locality Zuun-Khovoor, where they are represented by two taxa, *Arginbaatar dmitrievae* and *Eobaatar magnus* (Lopatin, 2013).

The present paper continues our study of mammalian assemblage from the Khovoor locality in Mongolia (Fig. 1). Previously we published on eutriconodontans, symmetrodontans, stem therians, and stem placentals (Averianov, 2002; Lopatin and Averianov, 2006b, a, 2007, 2015, 2017, 2018).

For measurements, we used drawings taken from the binocular microscope and ImageJ image analysis software (version 1.53a). For all teeth, we measured greatest crown mesiodistal length (L) and greatest crown labiolingual width (W). We measured the length of the lower premolars from the labial side. All other measurements were taken in the occlusal view. We did not measure heavily worn teeth. For statistical analysis we used also measurements of the specimens held in Ulanbaatar Institute of Geology provided by Kielan-Jaworowska et al. (1987). In few cases, when measurements were taken differently, we retake them from the

published illustrations using other measurements as references and ImageJ program for calculations.

**Institutional abbreviations.** (GI PST) Institute of Geology, Mongolian Academy of Sciences, Ulanbaatar, Mongolia; (PIN) Borissiak Paleontological Institute, Russian Academy of Sciences, Moscow, Russia.

## SYSTEMATIC PALEONTOLOGY

CLASS MAMMALIA LINNAEUS, 1758

Order Multituberculata Cope, 1884

Suborder Plagiaulacida Ameghino, 1889

**Family Eobaataridae Kielan-Jaworowska, Dashzeveg et Trofimov, 1987**

Eobaataridae: Kielan-Jaworowska et al., 1987: p. 7; Kielan-Jaworowska et al., 2000: p. 586; Kielan-Jaworowska and Hurum, 2001: p. 415; Kielan-Jaworowska et al., 2004: p. 316; Hahn and Hahn, 2006: p. 236; Kusuhashi et al., 2019: p. 3.

Type genus. *Eobaatar* Kielan-Jaworowska, Dashzeveg et Trofimov, 1987.

Included genera. Type genus, *Loxaulax* Simpson, 1928, *Sinobaatar* Hu et Wang, 2002, *Hakusanobaatar* Kusuhashi, 2008, *Liaobaatar* Kusuhashi et al., 2009, *Heishanobaatar* Kusuhashi et al., 2010, *Dolichoprion* Kusuhashi et al., 2019, *Jeholbaatar* Wang, Meng et Wang, 2019, *Cheruscodon* Martin et al., 2021, and *Nokerbaatar* gen. nov.

**Remarks.** Several multituberculate genera represented by fragmentary materials have been included in the Eobaataridae by various authors. These taxa are not included here in the Eobaataridae and briefly discussed below.

*Parendotherium herreroi* Crusafont-Pairó et Adrover, 1966 was based on an isolated upper incisor (I2) from the Barremian Camarillas Formation of Spain (Crusafont Pairó and Adrover, 1966). Hahn and Hahn (1992) referred to this taxon some isolated upper premolars described by Crusafont and Gibert (1976). *Parendotherium* was referred to the Paulchoffatiidae (Hahn and Hahn, 1983, 2006), Plagiaulacidae (Hahn and Hahn, 1992), Eobaataridae (Kielan-Jaworowska et al., 2004), or considered a nomen dubium (Badiola et al., 2012). The holotype of *P. herreroi* has a well developed basal cusp, which is characteristic for I2 in Paulchoffatiidae (Hahn, 1977), but not in Eobaataridae (Kusuhashi et al., 2009). Based on this, *Parendotherium* is likely a paulchoffatiid rather than eobaatarid.

*Janumys erebos* Eaton et Cifelli, 2001 is known from isolated teeth, including P4, M1, m1, and m2, from the Albian-Cenomanian Cedar Mountain Formation in Utah, United States (Eaton and Cifelli, 2001). Originally this taxon was provisionally placed in the Plagiaulacida because of possible presence of five upper premolars (Eaton and Cifelli, 2001). Subsequently *Janumys* was referred provisionally (Hahn and Hahn, 2006), or unconditionally (Badiola et al., 2008) to the Eobaataridae. Currently *Janumys* is placed to the family incertae sedis within the Plagiaulacida (Kielan-Jaworowska et al., 2004). According to Kielan-Jaworowska et al. (2004), *Janumys* shares with *Eobaatar* the structure of cusps in lingual row on m1, which are crescentic, facing medially, with first two partially coalesced. Actually, cusps in the lingual row of m1 in *Janumys* are quite different from those in *Eobaatar*. These cusps are not crescentic but conical and similarly convex from both labial and lingual sides (Eaton and Cifelli, 2001: text-figs. 4a, 4b). In *E. magnus* the labial side of lingual cusps is flat or slightly convex even on unworn teeth. There are no reasons to consider close relationships between *Janumys* and *Eobaatar* or other eobaatarids.

*Iberica hahni* Badiola, Canudo et Cuenca-Bescós, 2011 is represented by isolated upper and lower premolars from the Barremian Camarillas Formation of Spain (Crusafont and Gibert, 1976; Badiola et al., 2008, 2011, 2012). In original description this taxon was referred to either Plagiaulacidae or Eobaataridae (Badiola et al., 2011). The holotype of *I. hahni* (Badiola et al., 2011: text-fig. 2-1) is an elongated four-cusped anterior upper premolar with two small mesial additional cusps and a distal talon. This morphology is not found in any uncontested eobaatarid and thus attribution of *Iberica* to the Eobaataridae is unlikely.

An isolated upper premolar (P4), the holotype of *Indobaatar zofiae* Parmar, Prasad et Kumar, 2013, comes from the Kota Formation in Andhra Pradesh, India (Parmar et al., 2013). The age of the Kota Formation is uncertain but likely not Early-Middle Jurassic as was claimed but the authors. *Indobaatar*, known solely from this tooth, was referred to the Eobaataridae in original description (Parmar et al., 2013). The tooth has two labial and three lingual cusps (cusp formula 2:3), which is different from the cusp formula 2:4 in P4 of *E. minor*. The P4 of *I. zofiae* further differs from that tooth in *E. minor* by having labial cusps higher than lingual cusps (opposite in *E. minor*), lingual cusps of similar height (height increases distally in *E. minor*), lingual cingulum, and obliquely set roots. These characters are not found also in any other eobaatarid. We exclude here *Indobaatar* from the Eobaataridae.

The holotype and only known specimen of *Tedoribaatar reini* Kusuhashi, 2008 is the dentary fragment with p4 from the Kuwajima Formation (Barremian-Aptian) of Japan. The p4 in this specimen is identical in size and morphology to p4 of *Hakusanobaatar matsuoii* Kusuhashi, 2008 from the same locality. *T. reini* was differentiated from *H. matsuoii* by a single-rooted p3 and lack of p2, although a possible dp2 alveolus was found in the holotype (Kusuhashi, 2008). In all eobaatarids p2 is likely a non-replaced dp2 and its absence in some specimens is expectable. It is absent in a dentary fragment PIN 3101/635 of *Nokerbaatar minor*. Similarly, absence of p2 on the holotype dentary of *Dolichoprion lii* Kusuhashi et al., 2019 from the Aptian-Albian Fuxin Formation of Liaoning, China (Kusuhashi et al., 2019), is an individual variation or ontogenetic trait rather than diagnostic character. The number of roots of p3 may vary in the population because the distal root of this tooth is greatly reduced compared with the mesial root. We consider here *Tedoribaatar reini* Kusuhashi, 2008 a junior subjective synonym of *Hakusanobaatar matsuoii* Kusuhashi, 2008.

#### **Genus *Eobaatar* Kielan-Jaworowska, Dashzeveg et Trofimov, 1987**

*Eobaatar*: Kielan-Jaworowska et al., 1987: p. 7; Kielan-Jaworowska et al., 2004: p. 317; Hahn and Hahn, 2006: p. 238.

**Type species.** *Eobaatar magnus* Kielan-Jaworowska, Dashzeveg et Trofimov, 1987.

**Diagnosis.** Differs from *Loxaulax* by presence of 3 labial cusps on M2 (2 in *Loxaulax*) and 4 labial cusps on m1 (3 in *Loxaulax*). Differs from *Sinobaatar lingyuanensis* Hu et Wang, 2002 in having 1 labial cusp on P5 (3 in *S. lingyuanensis*), 6 middle cusps on P5 (5 in *S. lingyuanensis*), lower incisor with restricted enamel, and 10 serrations on p4 (11 in *S. lingyuanensis*). Differs from *Sinobaatar xiei* Kusuhashi et al., 2009 by presence of 1 labial cusp on P5 (no cusps in *S. xiei*), 6 middle cusps on P5 (3 in *S. xiei*), 3 labial cusps on M1 (4 in *S. xiei*), lower incisor with restricted

enamel, 10 serrations on p4 (8–9 in *S. xiei*), 4 labial cusps on m1 (3 in *S. xiei*), and 3 lingual cusps on m1 (2 in *S. xiei*). Differs from *Sinobaatar fuxinensis* Kusuhashi et al., 2009 in having 1 labial cusp on P5 (no cusps in *S. fuxinensis*), 6 middle cusps on P5 (3 in *S. fuxinensis*), 10 serrations on p4 (9 in *S. fuxinensis*), and 3 lingual cusps on m1 (2 in *S. fuxinensis*). Differs from *Sinobaatar pani* Mao et al., 2020 by presence of 6 middle cusps on P5 (4 in *S. pani*), 4 labial cusps on M1 (3 in *S. pani*), 3 labial cusps on M2 (2 in *S. pani*), 4 labial cusps on m1 (3 in *S. pani*), and 3 lingual cusps on m1 (2 in *S. pani*). Differs from *Hakusanobaatar* by presence of 1 labial cusp on P5 (2 in *Hakusanobaatar*) and serrated p3. Differs from *Liaobaatar* by presence of 4 labial cusps on m1 (2–3 in *Liaobaatar*). Differs from *Heishanobaatar* by presence of 10 serrations on p4 (8 in *Heishanobaatar*), 4 labial cusps on m1 (3 in *Heishanobaatar*), and 3 lingual cusps on m1 (2 in *Heishanobaatar*). Differs from *Dolichoprion* in having lower incisor with restricted enamel, 10 serrations on p4 (8 in *Dolichoprion*), 4 labial cusps on m1 (3 in *Dolichoprion*), and 3 lingual cusps on m1 (2 in *Dolichoprion*). Differs from *Jeholbaatar* by presence of 1 labial cusp on P5 (2 in *Jeholbaatar*), 6 middle cusps on P5 (3 in *Jeholbaatar*), 4 labial cusps on M1 (5 in *Jeholbaatar*), 10 serrations on p4 (8 in *Jeholbaatar*), 4 labial cusps on m1 (3 in *Jeholbaatar*), and 3 lingual cusps on m1 (2 in *Jeholbaatar*). Differs from *Cheruscodon* by presence of 10 serrations on p4 (11 in *Cheruscodon*), 1 mesial serration on p4 not associated with the ridge (2 in *Cheruscodon*), and by smaller distolabial cusp on p4. Differs from *Nokerbaatar* gen. nov. by presence of 6 middle cusps on P5 (5 in *Nokerbaatar*), 4 labial cusps on M1 (3 in *Nokerbaatar*), ventrolingual ridge on lower incisor (groove in *Nokerbaatar*), and serrated p3.

**Included species.** Type species only.

**Remarks.** In the diagnosis above, *Eobaatar* is compared separately with the each species of *Sinobaatar* because some of them may belong to distinct genera.

Kielan-Jaworowska et al. (1987) diagnosed *Eobaatar* as having P4 and P5 similar to each other. The specimens identified in that paper as P5 of *E. magnus* are reinterpreted here as P4 of *Nokerbaatar minor*. Currently P4 is unknown for *E. magnus*. In *N. minor* P4 and P5 considerably differ in morphology, as in other eobaatarids.

“*Eobaatar*” *clemensi* Sweetman, 2009 is represented by isolated upper incisor (I3) and lower molars (m1 and m2) from the Barremian Wessex Formation of Isle of Wight, England (Butler and Ford, 1977; Sweetman, 2009). This taxon is similar with eobaatarids in the structure of I3 and lower molars, which have lingual side shorter than labial side, lingual cusps with flat labial sides, and coalesced labial cusps on m2. However, the cusp formula for m1 (3–4:2) in “*Eobaatar*” *clemensi* is different from that in *E. magnus*

(4:3; m1 is unknown for *Nokerbaatar minor*). Thus, “*Eobaatar*” *clemensi* is likely an eobaatarid but not attributable to the genus *Eobaatar*.

The holotype of “*Eobaatar*” *hispanicus* Hahn et Hahn, 1992, a supposed P5 from the Barremian Camarillas Formation of Spain (Hahn and Hahn, 1992, text-fig. 5) is similar with P4 of *Nokerbaatar minor* and should be considered a P4. The P4 is unknown for *E. magnus* and this tooth is not variable between other eobaatarid taxa. Several other upper premolars and upper molars have been attributed to “*Eobaatar*” *hispanicus* (Crusafont and Gibert, 1976; Hahn and Hahn, 1992, 2002b, 2006). Among these teeth, one M2 (Hahn and Hahn, 1992, text-fig. 10) is similar with M2 of *E. magnus* by having sculpture of radiating ridges on the mesiolabial lobe and labial side of the labial cusps, but differs in having three small and one large cusps in the lingual row (three to four lingual cusps of similar size in M2 of *E. magnus*). “*Eobaatar*” *hispanicus* is likely an eobaatarid but certainly not *Eobaatar*.

“*Eobaatar*?” *pajaronensis* Hahn et Hahn, 2001 is based on isolated upper anterior premolars from the Barremian Pie Pajarón site and Barremian-Aptian Artoles Formation in Spain (Hahn and Hahn, 2001; Badiola et al., 2012). These premolars are not diagnostic at the generic level and attribution of this taxon to *Eobaatar* cannot be confirmed.

***Eobaatar magnus* Kielan-Jaworowska, Dashzeveg et Trofimov, 1987**

Figures 2–9, 10a–10h, 10j

*Eobaatar magnus*: Kielan-Jaworowska et al., 1987: p. 8, text-figs. 1A–1D, 2A–2C, 3B; pl. 1, figs. 1–4; pl. 2; pl. 3, figs. 1, 2; pl. 7, fig. 4; pl. 16, fig. 1; Barsbold and Sigogneau-Russell, 1992: text-fig. B on p. 109; Kielan-Jaworowska and Ensom, 1992: text-fig. 4C; Kielan-Jaworowska and Nesov, 1992: text-fig. 3B; Bakker, 1998: text-fig. 3; Kielan-Jaworowska et al., 2000: p. 586, text-fig. 29.9A; Kielan-Jaworowska and Hurum, 2001: pl. 2, figs. 3, 4; pl. 3, fig. 2; Kielan-Jaworowska et al., 2004: text-figs. 8.34C, 8.35D, 8.36B; Hahn and Hahn, 2004: text-figs. 13j, 14b, 15c; Hahn and Hahn, 2006: p. 243, text-figs. 241–248.

**Holotype.** PIN 3101/57, left p4.

**Type locality and horizon.** Khovoor, Mongolia; Early Cretaceous (Aptian-Albian).

**Referred specimens. Maxilla fragment.** PIN 3101/630, left maxillary fragment with P5 and M1.

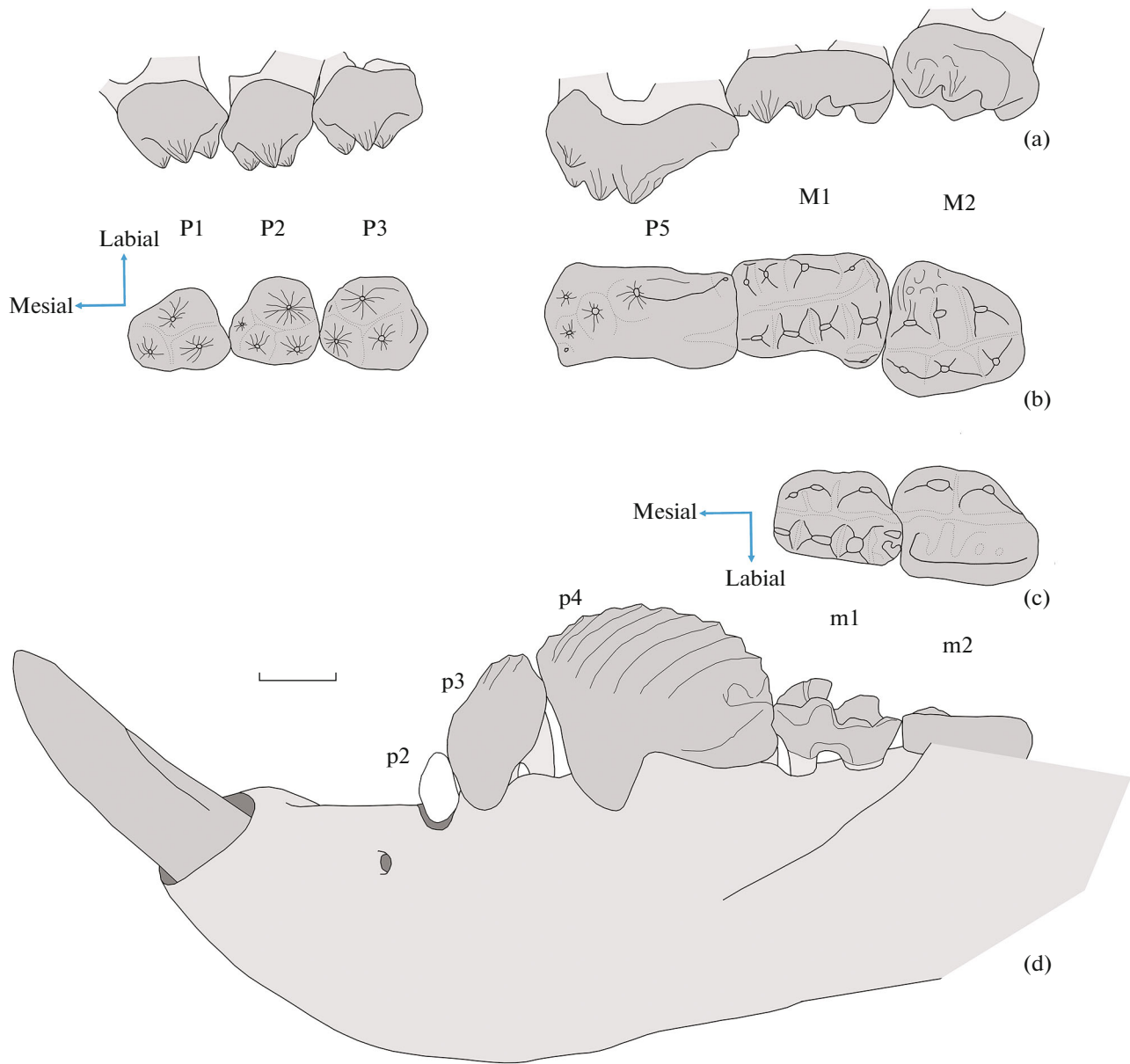
**P1.** PIN 3101/683, left P1; PIN 3101/684, right P1.

**P2.** PIN 3101/685, right P2; PIN 3101/686, right P2.

**dP3 or P3.** PIN 3101/676, right dP3 or P3; GI PST 10-34, right dP3 or P3; GI PST 10-35, left dP3 or P3.

**M2.** PIN 3101/62, right M2; PIN 3101/629, right M2; PIN 3101/631, left M2.

**Dentary fragments.** PIN 3101/53, left dentary fragment with m1–2; PIN 3101/634, right dentary fragment with alveoli for lower incisor and p2–4; GI PST 10-43, right dentary fragment with m2.



**Fig. 2.** *Eobaatar magnus* Kielan-Jaworowska et al., 1987, reconstruction of the left upper cheek teeth in labial (a) and occlusal (b) views, left lower molars in occlusal view (c), and left dentary in labial view (d). Khovoor locality, Mongolia; Lower Cretaceous. The reconstruction is based on the following specimens: PIN 3101/684, right P1, reversed; PIN 3101/685, right P2, reversed; PIN 3101/676, right P3, reversed; PIN 3101/630, left maxillary fragment with P5 and M1; PIN 3101/629, right M2, reversed; PIN 3101/662, right lower incisor, reversed; PIN 3101/634, right dentary fragment with alveoli for lower incisor and p2–4, reversed; PIN 3101/661, right p3, reversed; PIN 3101/60, right p4, reversed; PIN 3101/53, left dentary fragment with m1–2. Scale bar, 1 mm.

**Lower incisor.** PIN 3101/662, right lower incisor; PIN 3101/663, right lower incisor; PIN 3101/687, right lower incisor.

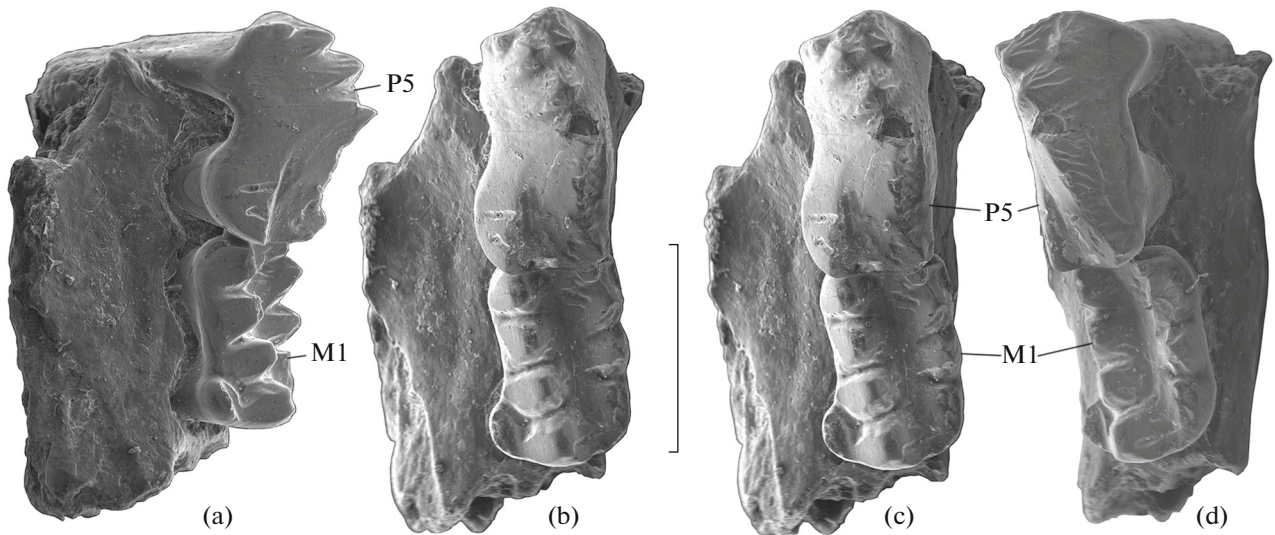
**p3.** PIN 3101/658, right p3; PIN 3101/659, right p3; PIN 3101/660, left p3; PIN 3101/661, right p3.

**p4.** PIN 3101/60, right p4; PIN 3101/59a, left p4 mesial fragment; PIN 3101/59b, left p4 distal fragment; PIN 3101/59c, left p4 mesial fragment; PIN 3101/632, left p4 mesial fragment; PIN

3101/650, left p4 mesial fragment; PIN 3101/651, left p4 mesial fragment; PIN 3101/652, right p4 mesial fragment.

**m1.** PIN 3101/50e, left m1; PIN 3101/628, left m1.

**Description.** *E. magnus* is known from most of the dentition (except upper incisors, P4, and p2) and dentary fragments (Fig. 2). The only maxilla fragment referred to *E. magnus* is PIN 3101/630 with P5 and M1



**Fig. 3.** *Eobaatar magnus* Kielan-Jaworowska et al., 1987. Khovoor locality, Mongolia; Lower Cretaceous. Specimen PIN, no. 3101/630, left maxillary fragment with P5 and M1, in lingual (a), occlusal (b, c, stereopair), and occlusolabial (d) views. Scale bar, 2 mm.

in place (Fig. 3). The posterior end of the zygomatic root is at the level between roots of P5.

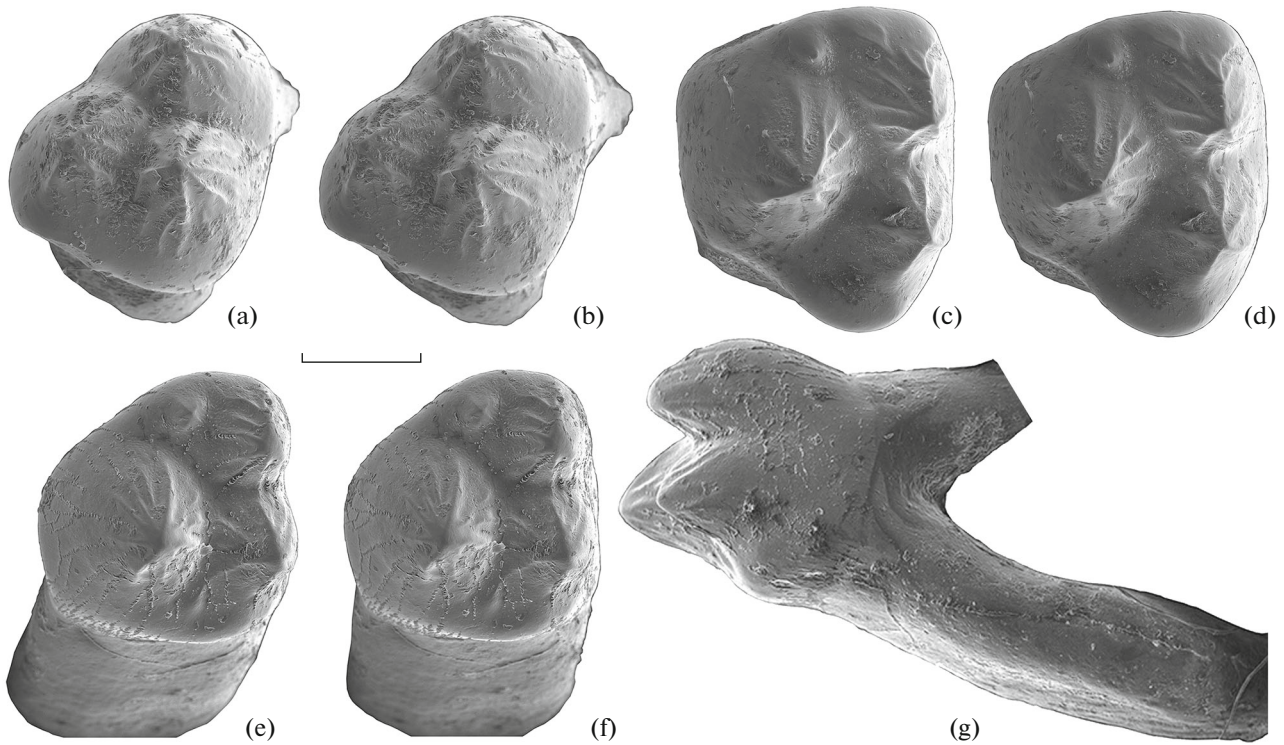
The crown of P1 is oval or triangular in occlusal view, longer than wide (Figs. 4a, 4b). There are three cusps, one labial and two lingual. The labial cusp is placed at the level between the lingual cusps. The mesial lingual cusp is somewhat smaller than the distal lingual cusp. The cusps are ornamented by radiating ridges. The P2 is similar with P1 but more oval in occlusal view, with crown length similar to crown width. In PIN 3101/685 the lingual cusps are of similar size and there a small additional mesial cusp between the labial and mesial lingual cusps (Figs. 4e–4g). On this specimen and on PIN 3101/686 there is a distinct distal cingulum posterior to the distal lingual cusp. On the latter specimen, the mesial lingual cusp is much smaller than the mesial distal cusp (Fig. 5). The roots of P2 are robust, widely separated and curved (Fig. 5).

The third upper premolar (dP3 or P3) is represented by three isolated specimens, two of which were previously described (Kielan-Jaworowska et al., 1987: pl. 3, figs. 1, 2). The crown is triangular in occlusal view, longer than wide. There are four cusps, with additional mesiolabial cusp minute (PIN 3101/676; Figs. 4c, 4d) or large (GI PST 10-35). The distal labial cusp is distinctly higher than the lingual cusps and placed at the level between the lingual cusps. The mesial lingual cusp is slightly higher than the distal lingual cusp. The labial and lingual cusps are separated by relatively wide valley. The distal cingulum is more pronounced than in P2. The cusps are ornamented by strong ridges radiating from the apices. The ornamentation covers about half of the crown height. The mesial margin of the mesial root is placed some distance distal to the mesial margin of the crown.

The P4 is unknown for *E. magnus*. The isolated P4 GI PST 10-27 referred to *E. magnus* by Kielan-Jaworowska et al. (1987: pl. 4, fig. 1), is attributed here to *A. dmitrievae*.

A single P5 attributed here to *E. magnus* is preserved in a maxilla fragment PIN 3101/630 together with M1 (Fig. 3). The tooth is longer than M1. The crown of P5 is subrectangular in occlusal view, with the mesial end expanding labially and the distal end expanding lingually. The three cusps of the middle cusp row dominate the crown. The single labial cusp is small and placed lower on the crown compared with the first middle cusps. Also were at least three cusps in the lingual cusp row, which are eliminated by wear. Only two short grooves separating these cusps indicate their presence. In the middle cusp row were six cusps. The cusp M1 is very small. The cusps M2–4 gradually increase in size distally. The cusp M4 is the highest cusp, occupying the center of the crown. The cusp M5 is the longest; it is eliminated by wear. The short furrows on the lingual side delimit its mesial and distal margins. The M6 cusp is placed at the distal end of the crown. It is small and little worn. Thus, the cusp formula for the P5 is 1:6:3. All the labial crown side is covered by heavy sculpture of vertical ridges. On lingual side, this sculpturing is present only in unworn areas. The mesial root is mesiodistally compressed. The distal root is oval in cross-section.

The tooth M1 is known only from the maxilla fragment PIN 3101/630 (Fig. 3). PIN 3101/66 and GIN PST 10-33, referred to *E. magnus* by Kielan-Jaworowska et al. (1987: pl. 6, figs. 3, 4), are distinctly smaller and attributed here to *Nokerbaatar minor*. The crown is subrectangular in occlusal view, with the distal end slightly wider than the mesial end. There are

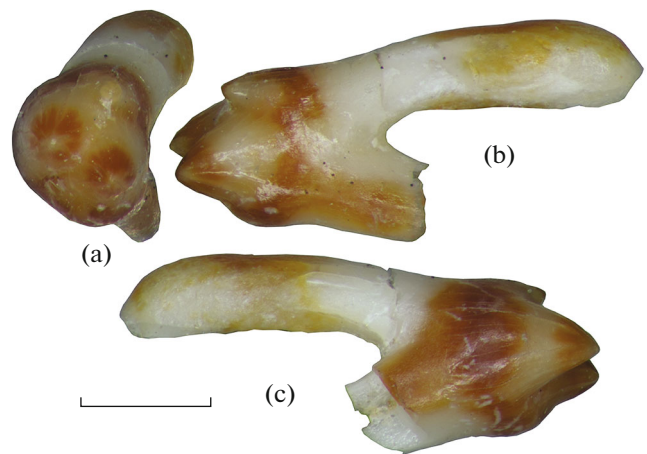


**Fig. 4.** *Eobaatar magnus* Kielan-Jaworowska et al., 1987. Khovoor locality, Mongolia; Lower Cretaceous. SEM images of isolated anterior upper premolars: (a, b) specimen PIN, no. 3101/684, right P1 in occlusal view (stereopair); (c, d) specimen PIN, no. 3101/676, right dP3 or P3 in occlusal view (stereopair); (e–g) specimen PIN, no. 3101/685, right P2, in occlusal (e, f, stereopair) and lingual (g) views. Scale bar, 0.5 mm.

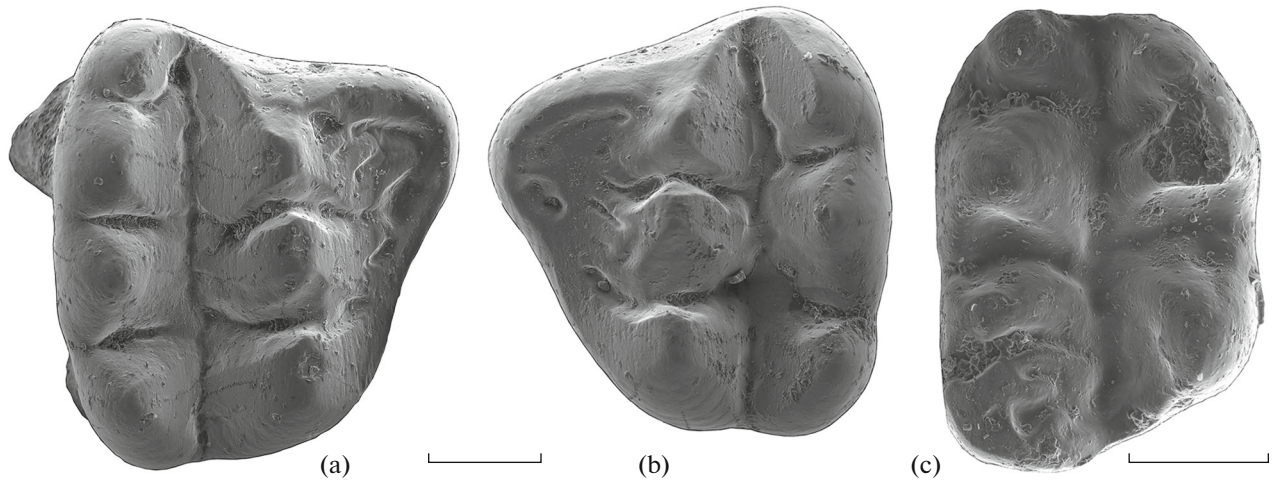
four labial and four lingual cusps and a small distolingual wing (the cusp formula is 4:4:Ri). The labial cusps are conical and labiolingually compressed. The cusp B2 is the largest. The cusp B3 is similar in shape but distinctly lower. The cusp B1 is smaller than the cusp B3 and closely appressed to the cusp B2. The cusp B4 is low and ridge-like. It is separated from the cusp B3 by a deep notch. There are fine ridges radiating from the apices of the labial cusps. These ridges are mostly eliminated by wear on the lingual side. The lingual cusps are pyramidal. The cusps L1 and L2 are similar in size. The cusp L3 is slightly higher but shorter mesiodistally. The cusp L4 is slightly larger and higher than the other lingual cusps. The lingual cusps are separated by wide transverse valleys, which are staggered to the shallower transverse grooves of the labial cusp row. The distolingual wing is semicircular in outline, with low but distinct marginal ridge. The longitudinal valley between the cusp rows is obliquely set, between the middle of the mesial crown margin and distolingual corner of the crown. This valley is wide mesially and especially in the middle, but becomes shallow and narrow between the cusps B4 and L4. The longitudinal valley is closed mesially and distally by shallow semicircular ridges.

Three isolated M2 are attributed here to *E. magnus*, one of which was known previously (Kielan-Jawor-

owska et al., 1987: pl. 7, fig. 4). PIN 3101/629 and PIN 3101/631 are similar in size but PIN 3101/62 is about 10% smaller (Figs. 6a, 6b). However, the latter tooth is still too large to be attributed to *Nokerbaatar minor* when compared with M1 of that taxon. The M2 has three roots, two mesial and one distal. The mesiolin-



**Fig. 5.** *Eobaatar magnus* Kielan-Jaworowska et al., 1987. Khovoor locality, Mongolia; Lower Cretaceous. Specimen PIN, no. 3101/686, right P2, in occlusal (a), lingual (b), and labial (c) views. Scale bar, 1 mm.



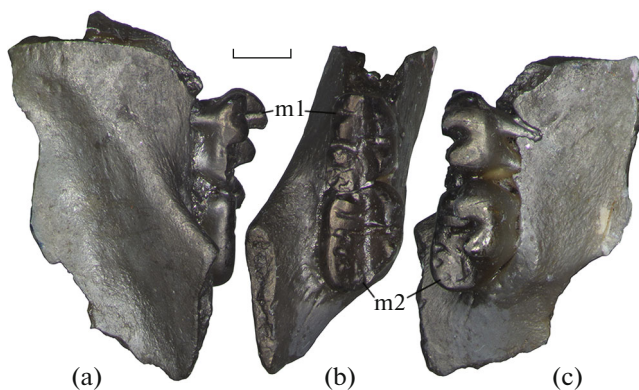
**Fig. 6.** *Eobaatar magnus* Kielan-Jaworowska et al., 1987. Khovoor locality, Mongolia; Lower Cretaceous. SEM images of isolated molars: (a) specimen PIN, no. 3101/631, left M2 in occlusal view; (b) specimen PIN, no. 3101/629, right M2 in occlusal view; (c) specimen PIN, no. 3101/628, left m1 in occlusal view. Scale bars, 0.5 mm.

gual root is deflecting dorsolingually. The size of mesial roots of PIN 3101/629 and PIN 3101/631 matches closely the M2 alveoli in a maxillary fragment PIN 3101/630 of *E. magnus*, which also shows dorso-lingual deflection of the mesiolingual root of M2. The crown of M2 is oval-shaped in occlusal view with labially extending rounded triangular labial wing and sinusoidal mesial margin. The concavity of the mesial margin is variable developed, being largest in PIN 3101/631 (Fig. 6a) and smallest in PIN 3101/62. The lingual crown side is convex. There are three labial and three to four lingual cusps (the cusp formula is Ri:3:3–4). The labial cusps are large and pyramidal, slightly increasing in size posteriorly. The labial side of the cusps B1 and B2 is sculptured by radiating ridges that extend to the labial wing (Figs. 6a, 6b). The transverse grooves between the labial cusps separate them only

superficially and extend along the cusp bases labially and lingually. The lingual cusps are conical and labio-lingually compressed, with flat labial and slightly convex lingual sides. There are four lingual cusps in PIN 3101/631 (Fig. 6a) and three cusps in PIN 3101/62 and PIN 3101/629 (Fig. 6b). In two last specimens, the cusp L2 is slightly larger than other lingual cusps. In PIN 3101/631, the cusps L2 and L3 are similar in size (Fig. 6a). The distalmost lingual cusp is separated by the deepest notch. The transverse valleys separated the distal cusp in each cusp row is on one line. The longitudinal valley separating the cusp rows is sinusoidal and open mesially and distally.

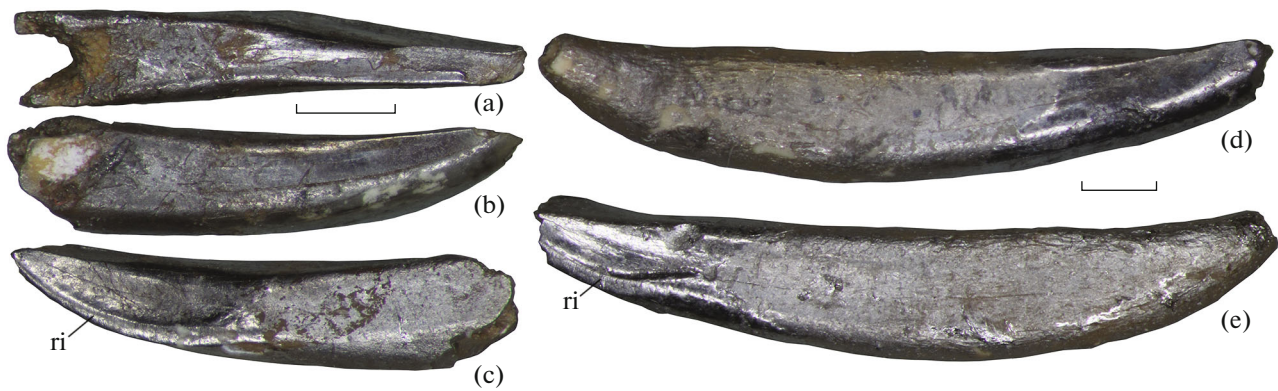
The dentary is represented by three specimens, anterior edentulous fragment PIN 3101/634 and posterior fragments PIN 3101/53 with m1–2 (Fig. 7) and GI PST 10-43 with m2. The anterior end of the mandibular body is upturned. There is a strong longitudinal ridge between the alveoli for the lower incisor and p3, which separates the labial and lingual sides of dentary. The alveolus of p2 is set lingual to this ridge and not visible from labial side. A relatively large mental foramen is placed at the level of the middle of diastema. The alveolus of p2 is smaller than the alveolus of the mesial root of p3. The symphysis is a narrow flat strap-like area around the anterior end of dentary. The coronoid process is placed relatively close to m2. Its anterior end is at the distal root of m1 (Figs. 7a, 7b).

There are two isolated lower incisor that fit the size of *E. magnus* and referred to that taxon. PIN 3101/662 is a juvenile, freshly erupted lower incisor with pointed mesial end (Figs. 8a–8c). It is little curved in the preserved length. The tooth is trihedral mesially, with flat dorsal and lingual margins, separated by a ridge, and convex labioventral margin. Posteriorly the cross-section of the tooth becomes U-shaped. All mesial part of the tooth is covered by enamel. On the lingual side,



**Fig. 7.** *Eobaatar magnus* Kielan-Jaworowska et al., 1987. Khovoor locality, Mongolia; Lower Cretaceous. Specimen PIN, no. 3101/53, left dentary fragment with m1–2, in labial (a), occlusal (b), and lingual (c) views. Scale bar, 1 mm.





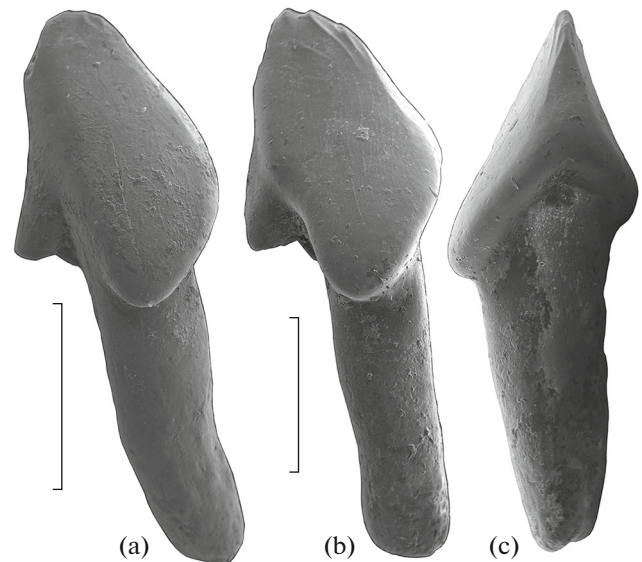
**Fig. 8.** *Eobaatar magnus* Kielan-Jaworowska et al., 1987. Khovoor locality, Mongolia; Lower Cretaceous. Isolated lower incisors: (a–c) specimen PIN, no. 3101/662, right lower incisor, in dorsal (a), labial (b), and lingual (c) views; (d, e) specimen PIN, no. 3101/663, right lower incisor, in labial (d) and lingual (e) views. Abbreviation: ri, ridge. Scale bars, 1 mm.

there is a prominent ridge along the enameled part of the tooth (Fig. 8c). Mesially this ridge follows closely the ventral margin of the lingual side. Farther distally, it shifts more dorsally, but still parallel to the ventral margin. There is a distinct strap-like facet on the dorsal side of the tooth, close to the mesial end (Fig. 8a). PIN 3101/663 represents a more adult lower incisor, with worn mesial end and open root distally (Figs. 8d, 8e). The enamel covers about one-third of the tooth length and restricted to the ventrolabial side. The mesial part is U-shaped in cross section, with flat dorsal and lingual sides and convex labial and ventral sides. More distally, the tooth becomes oval in cross-section. On the lingual side, there is a prominent semi-lunar ridge along the ventral margin, similar to that in PIN 3101/662, but relatively shorter (Fig. 8e). The enamel on the lingual side covers this ridge and a space distoventral to it. On the labial side, there is an enamel band of consistent height. Because of increasing diameter of the lower incisor in the middle part, the enamel covers most of the labial side at the mesial end but only half of the tooth height at the distal end of enamel distribution. There is a distinct triangular wear facet on dorsal side near the mesial end.

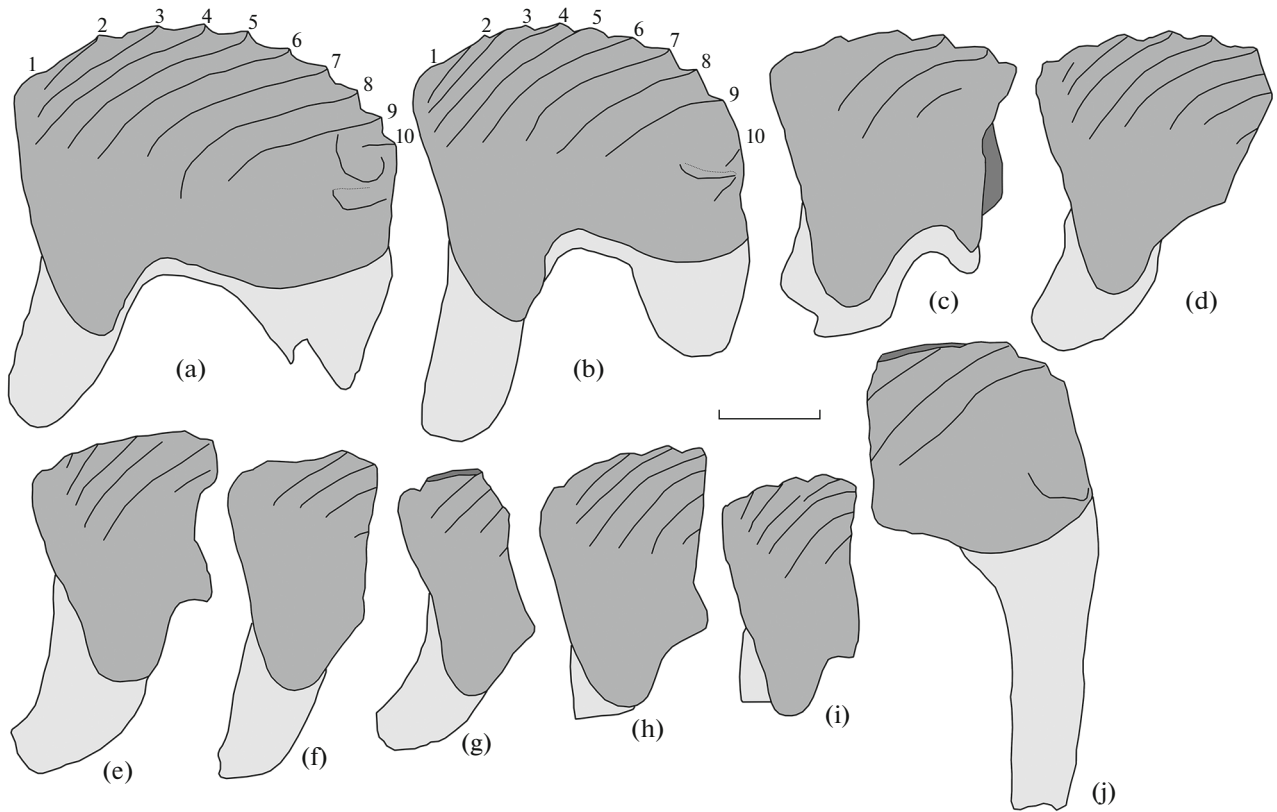
The p2 was a small single-rooted tooth as it is evident from the alveolus in PIN 3101/634. The p3 is represented by four isolated specimens, which slightly differ in size and morphology. The p3 is double rooted, with a large straight mesial root and smaller and shorter distal root (Fig. 9). The crown is teardrop-shaped in labial and lingual views. It extends along the mesial root further more downwards on the labial side compared with the lingual side. This labial extension of the crown is analogous with the mesial triangular lobe of p4. The crown is labiolingually wide at the base and tapers towards the blade-like occlusal and mesial margins (Fig. 9c). In PIN 3101/661 there are four serrations, three closely spaced on the dorsal side and one more distant posteriorly (Fig. 9b). Two of these serrations are associated with very short ridges on both labial

and lingual sides. On heavily worn PIN 3101/659 and PIN 3101/658 (Fig. 9a), there are two short ridges on the labial side but no serrations. The serrations and ridges are absent on PIN 3101/660, possibly because of wear.

There are two complete p4, PIN 3101/57 (holotype; Kielan-Jaworowska et al., 1987: text-fig. 1A; pl. 1, fig. 1; pl. 16, fig. 1) and PIN 3101/60 (Kielan-Jaworowska et al., 1987: text-figs. 1B, 3B; pl. 1, fig. 3) (Figs. 10a, 10b), which differ considerable in size and proportions, as was already noted by Kielan-Jaworowska et al. (1987). Several p4 fragments are more similar in size with PIN 3101/60 than with the holo-



**Fig. 9.** *Eobaatar magnus* Kielan-Jaworowska et al., 1987. Khovoor locality, Mongolia; Lower Cretaceous. SEM images of isolated p3: (a) specimen PIN, no. 3101/658, right p3 in labial view; (b, c) specimen PIN, no. 3101/661, right p3 in labial (b) and mesial (c) views. Scale bars, 1 mm.



**Fig. 10.** *Eobaatar magnus* Kielan-Jaworowska et al., 1987 (a–h, j) and *Nokerbaatar minor* (Kielan-Jaworowska et al., 1987) (i). Khovoor locality, Mongolia; Lower Cretaceous. Drawing of p4 in labial view: (a) holotype PIN, no. 3101/57, left p4; (b) specimen PIN, no. 3101/60, right p4, reversed; (c) specimen PIN, no. 3101/632, left p4 mesial fragment; (d) specimen PIN, no. 3101/59c, left p4 mesial fragment; (e) specimen PIN, no. 3101/652, right p4 mesial fragment, reversed; (f) specimen PIN, no. 3101/651, left p4 mesial fragment; (g) specimen PIN, no. 3101/650, left p4 mesial fragment; (h) specimen PIN, no. 3101/59a, left p4 mesial fragment; (i) holotype PIN, no. 3101/70, right p4 mesial fragment, reversed; (j) specimen PIN, no. 3101/59b, left p4 distal fragment. Scale bar, 1 mm.

type (Fig. 10). We follow Kielan-Jaworowska et al. (1987) in referring of PIN 3101/57 and PIN 3101/60 to a single species. The holotype likely represents the marginal size variant of p4 of *E. magnus*. The crown is subrectangular in labial and lingual view, with the arcuate dorsal margin, oblique mesial margin, and straight vertical distal margin. There are prominent mesial triangular lobe on labial side and distinctly smaller mesial triangular lobe on lingual side. Specimens PIN 3101/57 and PIN 3101/60 were reconstructed previously (Kielan-Jaworowska et al., 1987: text-figs. 1A, 1B) as having enamel on labial side extending down the root more on distal root compared with the mesial root. This reconstruction is not correct; the enamel does not extend much downward along the distal root (Figs. 10a, 10b, 10j). On the lingual side, the enamel extends far more downwards along the distal root compared with the labial side. There are ten serrations on the holotype and PIN 3101/60, although on the latter specimen the tenth serration is poorly developed (Figs. 10a, 10b). The first serration is not associated with a ridge on both sides. The ridge of the second serration is distinctly shorter than that of the third ser-

ration on both sides. On the labial side, the ridges of sixth and seventh serrations are shorter than that of adjacent serrations. The ridges cover about half of the crown height on both sides. On the holotype and PIN 3101/60, the tenth serration has a short ridge on labial side and no ridge on lingual side. There are a short distolabial cusp and a small depression above it. In labial view, the mesial crown margin could be slightly convex (holotype), straight (PIN 3101/59a, PIN 3101/59c, PIN 3101/60, PIN 3101/632, PIN 3101/651), or slightly concave (PIN 3101/650, PIN 3101/652). The roots are widely separated. The mesial root is curved mesially to a various extent and has a concave mesial side (Fig. 10). The distal root is also curved mesially, but to a lesser extent. The distal root is best preserved in PIN 3101/59b (Kielan-Jaworowska et al., 1987: pl. 1, fig. 4), where it is very long, much higher than the crown (Fig. 10j). The mesial root is subtriangular in cross section, with flat labial, concave mesial, and pointed lingual sides. The distal root is round in cross section. The mesial root is widely open in most specimens, with the pulp opening completely occupying the apical end. In PIN 3101/650, the

pulp opening is smaller, occupying less than half of the apical end.

The m1 is known from a dentary fragment PIN 3101/53 (Kielan-Jaworowska et al., 1987: text-fig. 2A; pl. 2, fig. 2) (Fig. 7) and two isolated specimens, including the previously described PIN 3101/50e (Kielan-Jaworowska et al., 1987: text-fig. 2C; pl. 2, fig. 3). The crown is oval in occlusal view, with the lingual margin distinctly shorter than the labial margin (Fig. 6c). The labial cusp row extends slightly more mesially compared with the lingual cusp row. There are four labial and three lingual cusps (the cusp formula is 4:3). In the labial cusp row the cusps b1–3 are pyramidal. The cusp b2 is the largest and the cusp b1 is the smallest. The cusps b2 and b3 are separated by a wider and deeper transverse groove than the cusps b1 and b2. The fourth labial cusp (b4) is low and ornamented by short grooves and ridges on the sloping lingual side. This cusp is separated by a narrow and shallow transverse groove from the cusp b3. The lingual cusps are conical and labiolingually compressed, with flat labial and convex lingual sides. They are distinctly higher than the labial cusps. The lingual cusps are hook-like in labial or lingual view, with strongly convex mesial side and concave distal side. The lingual cusps increase in size from l1 to l3. The cusps l1 and l2 are closely appressed and separated mostly by a vertical groove on the labial side. The cusps l2 and b3 are separated by a wide and deep transverse groove. This groove is placed somewhat anterior to the transverse groove separating the cusps b2 and b3. The longitudinal groove separating the cusps rows is open mesially and distally. Two roots are closely spaced and compressed mesiodistally. The mesial root is placed some distance distal to the mesial margin of the crown.

The m2 is represented by two specimens in dentary fragments, PIN 3101/53 (Fig. 7) and GI PST 10-43 (Kielan-Jaworowska et al., 1987: text-figs. 2A, 2B; pl. 2, figs. 1, 2). The crown is oval in occlusal view, with the length differential between the lingual and labial crown sides greater than in m1. In contrast with m1, the lingual cusp row extends more mesially compared with the labial cusp row. The cusps in the labial cusp row are low and coalesced. In mesial part of the labial cusp row, there are two distinct transverse grooves, separating the first three labial cusps. The distal part of the labial cusp row is ornamented by irregular grooves and ridges. Two lingual cusps are high, labiolingually compressed, flat labially and convex lingually. They are hook-like in labial or lingual view, with the strongly convex mesial side and concave distal side. The cusp l1 is distinctly larger than the cusp l2. On the labial side of the cusp l1 there is a groove, which may indicate formation of this cusp from two coalesced cusps. The groove separating the cusps l1 and l2 extends shortly on lingual side and longer on the labial side, towards the longitudinal groove separating the cusp rows. The latter groove is open mesially and distally.

**Table 1.** Measurements (in mm) of anterior upper premolars in *Eobaatar magnus* (L, crown length; W, crown width)

Specimen	LP1	WP1	LP2	WP2	LP3*	WP3*
PIN 3101/683	1.13	0.80				
PIN 3101/684	1.52	1.16				
PIN 3101/685			1.29	1.16		
PIN 3101/686			1.29	1.11		
PIN 3101/676					1.48	1.24
GI PST 10-34**					1.10	1.10
GI PST 10-35**					1.20	1.20
Mean	1.33	0.98	1.29	1.14	1.26	1.18
Standard error	0.20	0.18	0	0.03	0.11	0.04

\* Or dP3.

\*\* Measurements from Kielan-Jaworowska et al. (1987).

**Table 2.** Measurements (in mm) of posterior upper premolars and upper molars in *Eobaatar magnus* (L, crown length; W, crown width)

Specimen	LP5	WP5	LM1	WM1	LM2	WM2
PIN 3101/630	2.62	1.62	2.21	1.72		
PIN 3101/62					1.74	1.52
PIN 3101/629					1.90	1.73
PIN 3101/631					2.08	1.92
Mean	2.62	1.62	2.21	1.72	1.91	1.72
Standard error	0	0	0	0	0.10	0.12

Measurements. See Tables 1–3.

Remarks. Kielan-Jaworowska et al. (1987) considered the cusp formula 3:4 and 2:4 for P4 and P5, respectively, of *E. magnus* based on provisionally

**Table 3.** Measurements (in mm) of lower premolars and molars in *Eobaatar magnus* (L, crown length; W, crown width)

Specimen	Lp3	Wp3	Lp4	Wp4	Lm1	Wm1	Lm2	Wm2
PIN 3101/620	1.15	1.25						
PIN 3101/658	1.21	1.20						
PIN 3101/659	1.19	1.07						
PIN 3101/661	1.31	1.37						
PIN 3101/60			3.55	1.42				
PIN 3101/57*			3.84	1.30				
PIN 3101/50e					1.74	1.19		
PIN 3101/628					1.71	1.24		
PIN 3101/53					1.76	1.25	1.97	1.54
GI PST 10-43**							1.96	1.50
Mean	1.22	1.22	3.70	1.36	1.74	1.23	1.97	1.52
Standard error	0.03	0.06	0.15	0.06	0.02	0.02	0.01	0.02

\* Holotype.

\*\* Measurements from Kielan-Jaworowska et al. (1987).

assigned isolated teeth. Those teeth are referred here to *Arginbaatar*. The P4 is unknown for *E. magnus*. The P5 of *E. magnus*, known from a single specimen, has the cusp formula 1:6:3.

Kielan-Jaworowska et al. (1987) diagnosed *E. magnus* as having p4 with 9–10 serrations with ridges. Actually, the number of ridges is less by one than the number of serrations because the first serration is not associated with a ridge.

Kielan-Jaworowska et al. (1987) consider m1 of *E. magnus* having two lingual cusps (the cusp formula 4:2), with the mesial lingual cusp subdivided “medially” (=labially) by a vertical groove. However, the less worn specimen PIN 3101/628 clearly shows two closely appressed mesial cusps in the lingual row, subdivided not only labially, but also lingually (Fig. 6c). Thus, the cusp formula for m1 in *E. magnus* is 4:3.

#### Genus *Nokerbaatar* gen. nov.

**E t y m o l o g y.** From *nöker*, Mongolian, military comrade in the medieval Mongolian army, and *baatar*, Mongolian, hero, a common suffix for generic names of Asian Cretaceous multituberculates.

**T y p e s p e c i e s.** *Eobaatar minor* Kielan-Jaworowska, Dashzeveg et Trofimov, 1987.

**D i a g n o s i s.** Differs from *Eobaatar* by presence of 5 middle cusps on P5 (6 in *Eobaatar*), 3 labial cusps on M1 (4 in *Eobaatar*), smaller distolingual wing of M1, ventrolingual groove on lower incisor (ridge in *Eobaatar*), and p3 lacking serrations. Differs from *Sinobaatar lingyuanensis* in having 2 labial cusps on P4 (3 in *S. lingyuanensis*), 1 labial cusp on P5 (3 in *S. lingyuanensis*), and lower incisor with restricted enamel. Differs from *Sinobaatar xiei* by presence of 1 labial cusp on P5 (no cusps in *S. xiei*), 5 middle cusps on P5 (3 in *S. xiei*), 3 labial cusps on M1 (4 in *S. xiei*), and lower incisor with restricted enamel. Differs from *Sinobaatar fuxinensis* by presence of 1 labial cusp on P5 (no cusps in *S. fuxinensis*), 5 middle cusps on P5 (3 in *S. fuxinensis*), 3 labial cusps on M1 (4 in *S. fuxinensis*), and p3 lacking serrations. Differs from *Sinobaatar pani* by presence of 2 labial cusps on P4 (1 in *S. pani*) and 5 middle cusps on P5 (4 in *S. pani*). Differs from *Hakusanobaatar* by presence of 2 labial cusps on P4 (3 in *Hakusanobaatar*), 4 lingual cusps on P4 (5 in *Hakusanobaatar*), 1 labial cusp on P5 (2 in *Hakusanobaatar*), and 5 middle cusps on P5 (6 in *Hakusanobaatar*). Differs from *Liobaatar* and *Heishanobaatar* in having relatively smaller p3 lacking serrations. Differs from *Dolichoprion* by lower incisor with restricted enamel, ventrolingual groove on lower incisor (ridge in *Dolichoprion*), and p3 lacking serrations. Differs from *Jeholbaatar* by presence of 1 labial cusp on P5 (2 in *Jeholbaatar*), 5 middle cusps on P5 (3 in *Jeholbaatar*), and 3 labial cusps on M1 (5 in *Jeholbaatar*). Differs from *Cheruscodon* by presence of

1 mesial serration on p4 not associated with ridge (2 in *Cheruscodon*).

**I n c l u d e d s p e c i e s.** Type species only.

#### *Nokerbaatar minor* (Kielan-Jaworowska, Dashzeveg et Trofimov, 1987) comb. nov.

Figures 10i, 11–16

*Eobaatar minor*: Kielan-Jaworowska et al., 1987: p. 13, text-figs. 1E, 1F; pl. 1, fig. 5; pl. 8, fig. 3; Barsbold and Sigogneau-Russell, 1992: text-fig. A on p. 109; Kielan-Jaworowska et al., 2000: p. 587, text-fig. 29.9B; Hahn and Hahn, 2006: p. 247, text-fig. 249.

*Eobaatar magnus*: Kielan-Jaworowska et al., 1987: pl. 4, figs. 2, 3; pl. 5; pl. 6, fig. 3; Hahn and Hahn, 2004: text-fig. 8d.

*Eobaatar magnus* (?): Kielan-Jaworowska et al., 1987: pl. 6, fig. 4.

*Eobaatar* sp. a: Kielan-Jaworowska et al., 1987: p. 14; pl. 8, fig. 5; Hahn and Hahn, 2006: p. 250, text-fig. 251.

*Eobaatar* sp. b: Kielan-Jaworowska et al., 1987: p. 14; pl. 8, fig. 4; Hahn and Hahn, 2006: p. 250, text-fig. 252.

*Arginbaatar dimitrievae* [sic]: Kielan-Jaworowska et al., 1987: pl. 22, fig. 2.

**H o l o t y p e.** PIN 3101/70, right dentary fragment with p2, roots of p3, mesial part of p4, and alveolus of lower incisor.

**T y p e l o c a l i t y a n d h o r i z o n.** Khovoor, Mongolia; Early Cretaceous (Aptian-Albian).

**R e f e r r e d s p e c i m e n s:** **P1.** PIN 3101/50b, left P1.

**P3.** PIN 3101/669, right dP3 or P3.

**P4.** PIN 3101/614, right P4; PIN 3101/664, left P4; GI PST 10-16, right P4; GI PST 10-24, left P4; GI PST 10-31, left P4; GI PST 10-45, left P4.

**P5.** PIN 3101/636, left P5; PIN 3101/637, right P5; PIN 3101/627, left P5 mesial fragment.

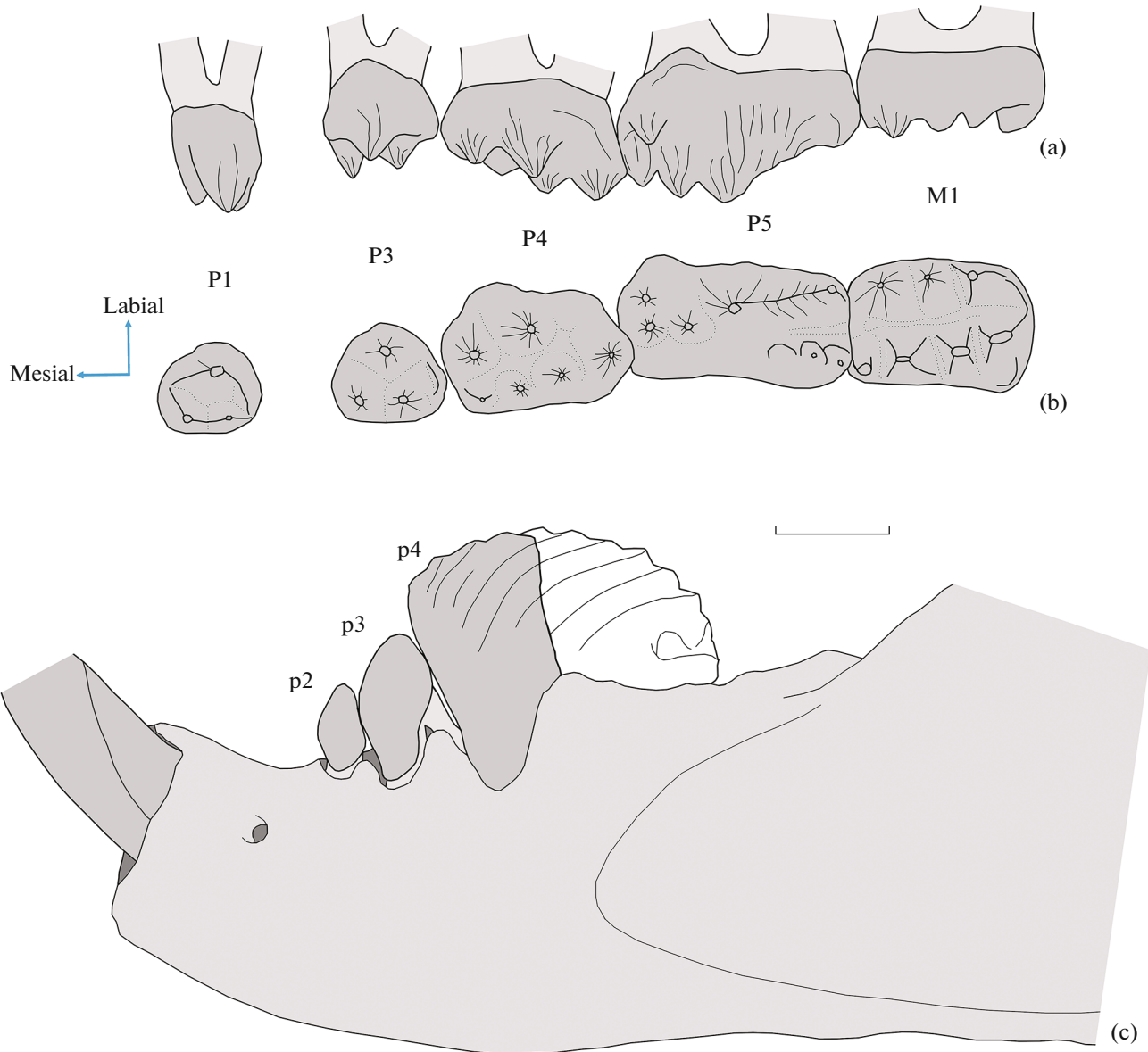
**M1.** PIN 3101/66, right M1; GI PST 10-33, left M1.

**D e n t a r y f r a g m e n t s.** PIN 3101/653, left dentary fragment with lower incisor and alveoli for p2–4 and m1–2; PIN 3101/635, left dentary fragment with p3 and alveoli for lower incisor and p4.

**L o w e r i n c i s o r.** PIN 3101/67, left lower incisor; PIN 3101/654, right lower incisor; PIN 3101/655, left lower incisor; PIN 3101/656, left lower incisor; PIN 3101/657, right lower incisor; GI PST 10-25, right lower incisor.

**p4.** GI PST 10-23, left p4 mesial fragment.

**D e s c r i p t i o n.** *N. minor* is known from isolated lower incisors, upper and lower premolars (except P2), and dentary fragments (Fig. 11). The anterior upper premolars (P1–3) are similar in size with those of *A. dimitrievae* but differ in having ornamentation of ridges radiating from the cusps apices. The P1 PIN 3101/50b was attributed previously to *A. dimitrievae* (Kielan-Jaworowska et al., 1987: pl. 22, fig. 2). The crown of P1 is relatively high, with one large labial cusp and two smaller lingual cusps. The crown is oval in occlusal view, wider than long. The labial cusp is placed closer to the distal margin of the crown. The lingual cusps are closely appressed. The mesial lingual cusp is about

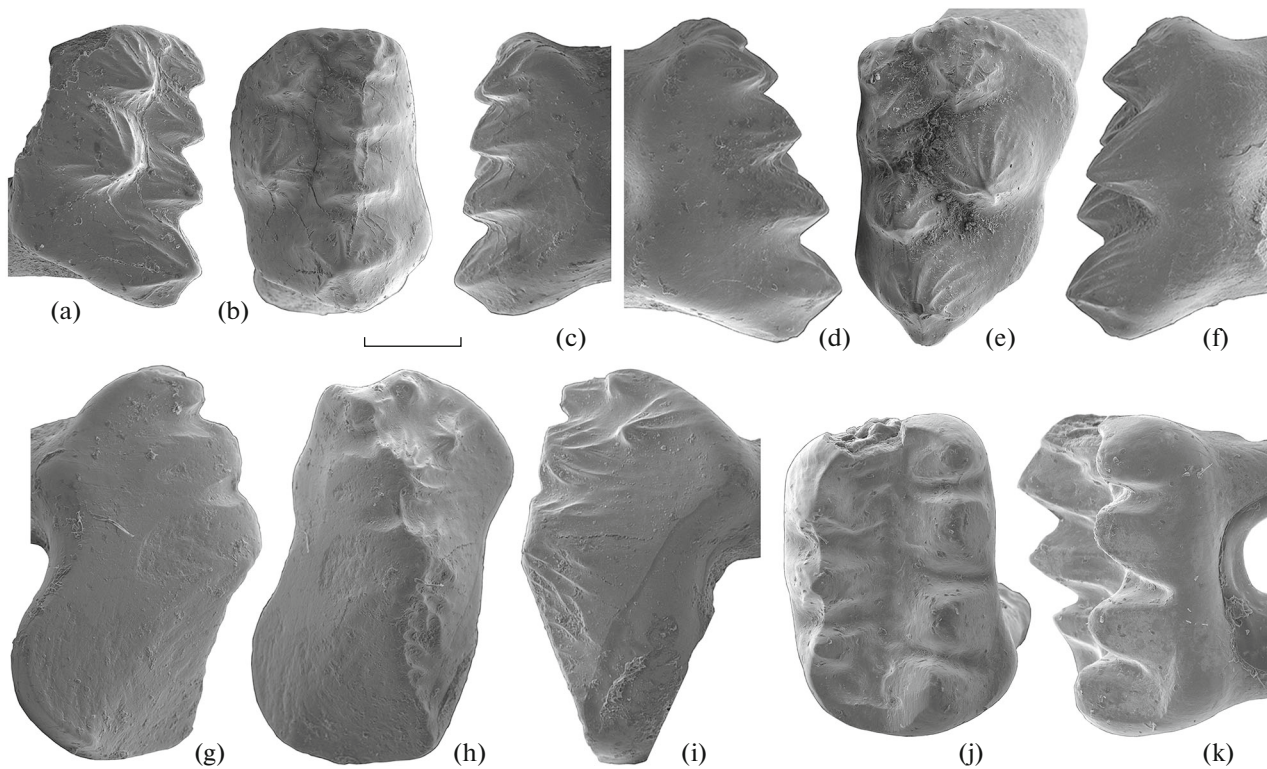


**Fig. 11.** *Nokerbaatar minor* (Kielan-Jaworowska et al., 1987), reconstruction of the left upper cheek teeth in labial (a) and occlusal (b) views and left dentary in labial view (c). Khovoor locality, Mongolia; Lower Cretaceous. The reconstruction is based on the following specimens: PIN 3101/50b, left P1; PIN 3101/669, right P3, reversed; PIN 3101/664, left P4; PIN 3101/637, right P5, reversed; PIN 3101/66, right M1, reversed; PIN 3101/653, left dentary fragment with lower incisor and alveoli for p2–3 and m1–2; PIN 3101/656, left lower incisor; PIN 3101/70, holotype, right dentary fragment with p2, roots of p3, mesial part of p4, and alveolus of lower incisor, reversed; PIN 3101/635, left dentary fragment with p3 and alveoli for lower incisor and p4. Scale bar, 1 mm.

twice smaller than the distal lingual cusp. The valley between the labial cusp and mesial lingual cusp is open mesially and extends down the crown for about half of the crown height. The ornamentation covers the apical half of the cusps height. The mesial root is curved distally and lingually. The distal root is wide labiolingually and short mesiodistally. The dP3 or P3 (PIN 3101/669) is similar in construction and proportions with PIN 3101/676, identified as dP3 or P3 of *E. magnus*, but smaller. The crown is lower than in P1. The crown is triangular in occlusal view, longer than

wide. The labial cusp is placed at the level between the lingual cusps. The lingual cusps are similar in size. There is a distinct distal cingulum posterior to the distal lingual cusp. The ornamentation covers only apical part of the crown, as in P1.

In a new PIN material, there are two isolated P4 which are attributed here to *N. minor* (Figs. 12a–12f). Also we identified as P4 of *N. minor* four isolated teeth which were identified as P5 and referred to *E. magnus* by Kielan-Jaworowska et al. (1987: pl. 4, figs. 2, 3; pl. 5). The crown of P4 is subrectangular in occlusal



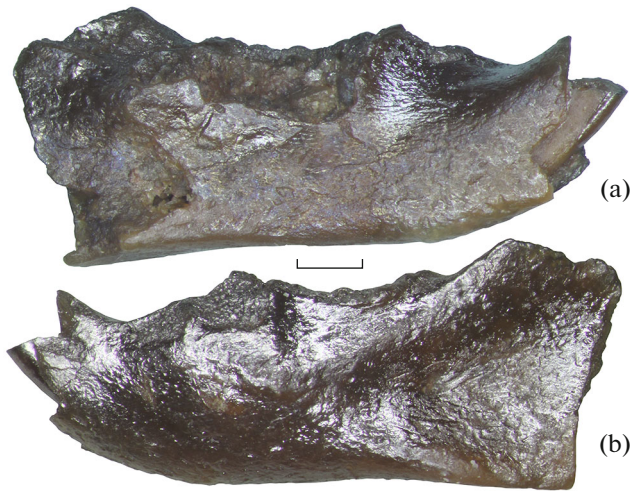
**Fig. 12.** *Nokerbaatar minor* (Kielan-Jaworowska et al., 1987). Khovoor locality, Mongolia; Lower Cretaceous. SEM images of isolated P4, P5, and M1: (a–c) specimen PIN, no. 3101/614, right P4, in occlusolabial (a), occlusal (b), and lingual (c) views; (d–f) specimen PIN, no. 3101/664, left P4, in lingual (d), occlusal (e), and labial (f) views; (g–i) specimen PIN, no. 3101/636, left P5, in lingual (g), occlusal (h), and labial (i) views; (j, k) specimen PIN, no. 3101/66, right M1, in occlusal (j) and lingual (k) views. Scale bar, 0.5 mm.

view, with slightly convex mesial margin and more convex distal margin. There are two labial and four lingual cusps (the cusp formula is 2:4). The labial and lingual cusp rows are not parallel but converging mesially. The labial and lingual cusps are conical, gradually increasing in size distally, and ornamented by strong vertical ridges from all sides. The cusp B1 is distinctly larger than the cusp L1. The cusp B2 is about twice larger than the cusp B1. The cusp L4 is largest on the tooth. Distal to the cusp B2 there is a sloping area. There is a minute cuspule on the mesial crown margin between the cusps B1 and L1. The roots are long and widely separated. The distal root is convex distally.

There are two complete and one fragmented P5 referable to *N. minor*. PIN 3101/637 is less worn than PIN 3101/636 (Figs. 12g–12i). The crown is asymmetrical in occlusal view. The mesial end is expanded labially, while the distal end is expanded lingually. There are three cusp rows, with one labial, five medial, and three lingual cusps (the cusp formula is 1:5:3). The cusps in the labial and middle cusp rows are heavily ornamented by radiating ridges. The middle cusps are high. The cusps in the lingual row are low, lack ornamentation, and easily removed by wear (completely absent in a worn specimen PIN 3101/636; Figs. 12g, 12h). The single labial cusp is placed on the labially

expanded mesial part of the crown. The middle cusps M1–4 are gradually increasing in size distally. The cusp M4 is the highest and largest cusp, placed in the center of the crown. A long shearing ridge ornamented by vertical ridges separates the cusps M4 and M5. The cusp M5 is similar in size with the cusp M2. The two roots are widely spaced. The distal root is convex distally. The fragmented P5 PIN 3101/627 is slightly larger than PIN 3101/627.

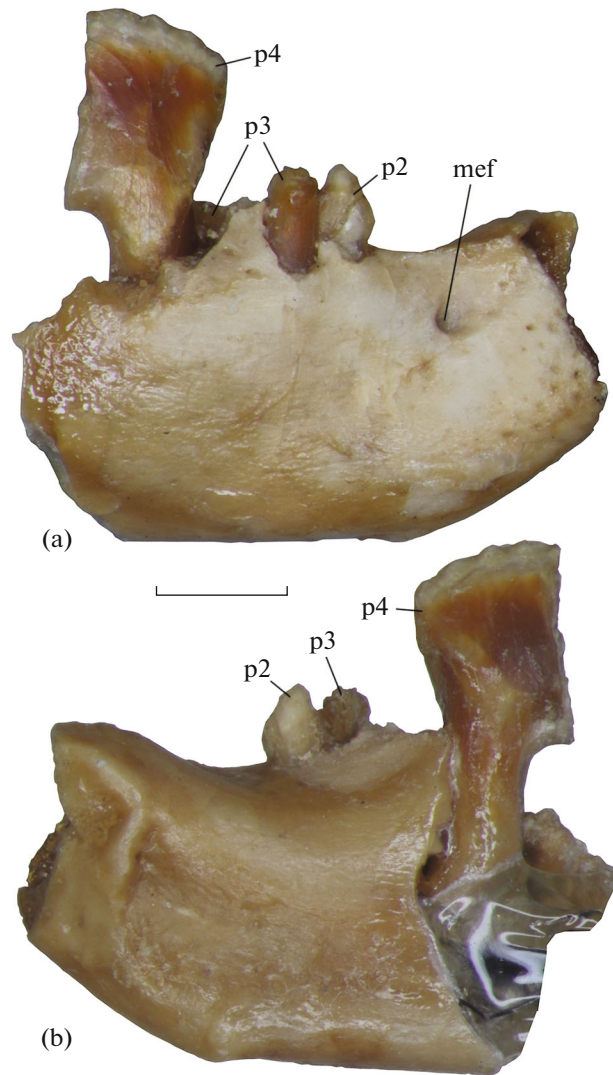
Two isolated M1 (PIN 3101/66 and GI PST 10-33) were attributed to *E. magnus* by Kielan-Jaworowska et al. (1987: pl. 6, figs. 3, 4). These teeth are about 20% smaller than a M1 in maxilla fragment PIN 3101/630 of *E. magnus* and referred here to *N. minor*. PIN 3101/66 is little worn (Figs. 12j, 12k). The crown is subrectangular in occlusal view, about twice longer than wide. There are three labial and four lingual cusps and a minute distolingual wing (the cusp formula is 3:4:Ri). The labial cusps are conical, with convex labial and flat lingual sides. They rapidly decrease in size from B1 to B3. The cusps B1 and B2 are ornamented by radiating ridges, with two strong ridges on the lingual side and more numerous fine ridges on the labial side. The lingual cusps are pyramidal and lack ornamentation. They are more uniform in size, with L2 being the largest and L1 the smallest cusps. The cusps L3 and L4



**Fig. 13.** *Nokerbaatar minor* (Kielan-Jaworowska et al., 1987). Khovoor locality, Mongolia; Lower Cretaceous. Specimen PIN, no. 3101/653, left dentary fragment with lower incisor and alveoli of p2–4 and m1–2, in labial (a) and lingual (b) views. Scale bar, 1 mm.

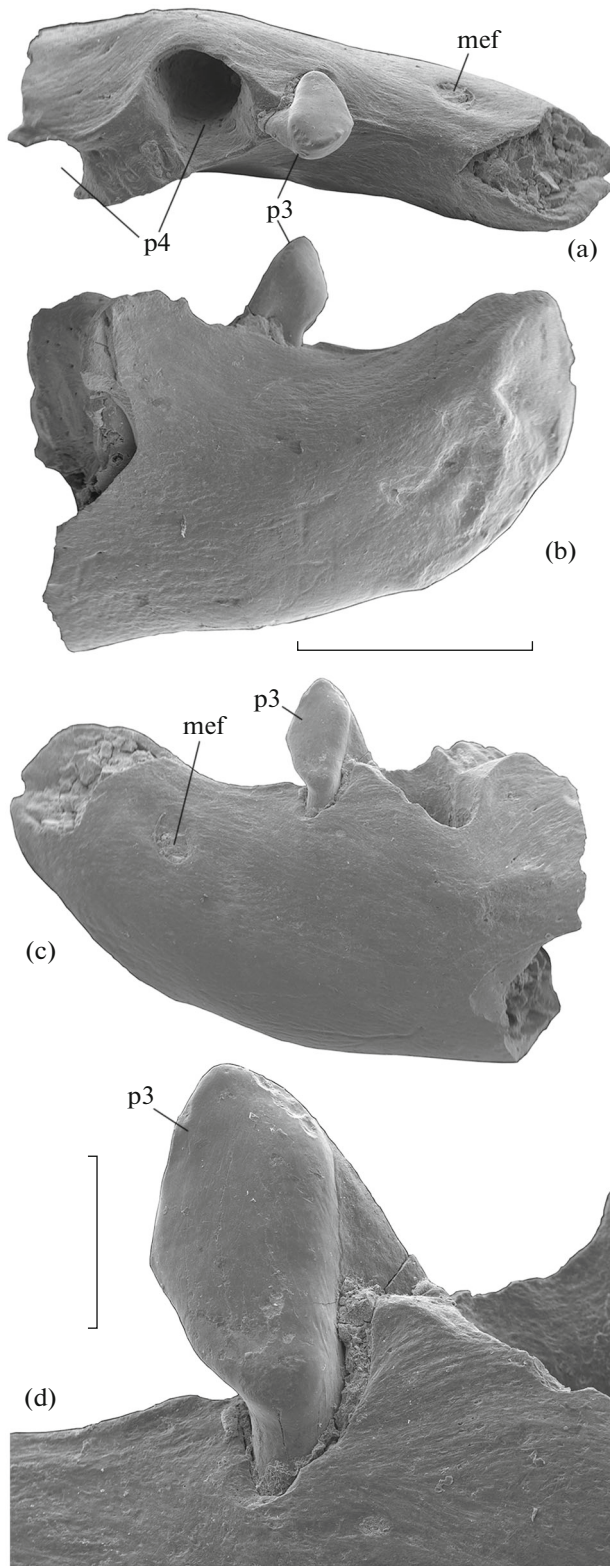
are similar in size. The distolingual wing is very small, cingulum-like. The transverse valleys separating the lingual cusps are much deeper than the valleys separating the labial cusps. The longitudinal groove, separating the labial and lingual cusp rows, is obliquely oriented, extending between the middle of mesial margin and distolabial corner. The longitudinal valley is closed mesially by a high semicircular ridge between the apices of the cusps B1 and L2. A similarly circular, but much lower ridge between the cusps B3 and L4 closes the longitudinal valley distally. At the bottom of the longitudinal valley, there is a narrow straight groove, which terminates some distance prior to the mesial and distal crown margins. A large space separates the roots.

The dentary is known from three specimens including the holotype (Figs. 13–15). PIN 3101/653 is an almost complete dentary missing only the posterior margin of the mandibular ramus including the condyloid process and tip of the coronoid process (Fig. 13). This specimen is somewhat larger than the holotype but significantly smaller than dentary fragments referred to *E. magnus*. The anterior end of dentary is upturned. The alveolus for the lower incisor is narrow, with the dorsoventral diameter exceeding more than twice the labiolingual diameter. The diastema is short, with a distinct ridge separating labial and lingual sides. A relatively large mental foramen is placed at the middle of the diastema, close to the dorsal border of dentary. The mandibular ramus gradually increases in height posteriorly. The ventral margin of the mandibular border is sinusoidal, with a convexity at the p2–3 and a concavity at the distal root of p4. The labial side of the crown is bulbous at the region of anterior premolars and mesial root of p4. The masseteric fossa is



**Fig. 14.** *Nokerbaatar minor* (Kielan-Jaworowska et al., 1987). Khovoor locality, Mongolia; Lower Cretaceous. Holotype PIN, no. 3101/70, right dentary fragment with p2, roots of p3, mesial part of p4, and alveolus of lower incisor, in labial (a) and lingual (b) views. Abbreviation: mef, mental foramen. Scale bar, 1 mm.

shallow, poorly delimited anteriorly and anterodorsally. Its deepest part is in the middle. The anterior end of the masseteric fossa is at the distal root of p4. In PIN 3101/653, there are alveoli for single-rooted p2 and double-rooted p3. In PIN 3101/635, there is a double-rooted p3 but p2 is lacking (Fig. 15). The coronoid process is lateral to m2 with the anterior end placed between m1 and m2. There is a large space between the coronoid process and alveoli of m2. The distal alveolus of m2 is distinctly longer than the mesial alveolus. The symphysis is a flat strap-like area around the mesial margin of dentary. The pterygoid fossa is not delimited dorsally. The mandibular foramen is large, facing mostly posteriorly.



**Fig. 15.** *Nokerbaatar minor* (Kielan-Jaworowska et al., 1987). Khovoor locality, Mongolia; Lower Cretaceous. Specimen PIN, no. 3101/635, left dentary fragment with p3 and alveoli of lower incisor and p4, in occlusal (a), lingual (b), and labial (c) views, and p3 in labial view (d). Abbreviation: mef, mental foramen. Scale bars, 2 mm (a–c) and 0.5 mm (d).

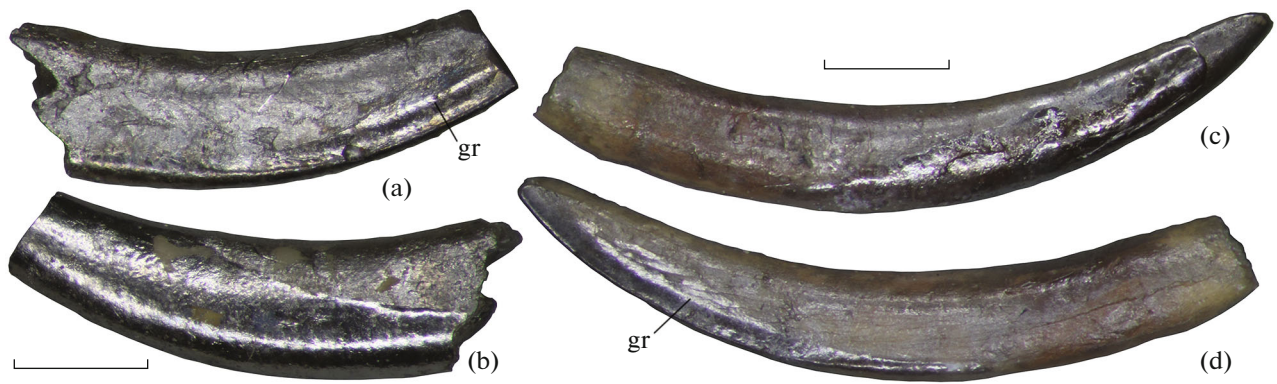
The lower incisor is known from a tooth in situ in dentary PIN 3101/653 (Fig. 13) and several isolated specimens (Fig. 16). Two of these specimens were referred previously to *Eobaatar* sp. a and b (Kielan-Jaworowska et al., 1987: pl. 8, figs. 4, 5). The lower incisor is ever-growing tooth and it varies significantly in size and curvature depending on the ontogenetic age of the individual. The dorsoventral diameter of the lower incisor is about twice greater than its labiolingual diameter. The labial side is convex. The lingual side is flat or slightly concave. The enamel is restricted to the ventral and ventrolabial sides. The amount of enamel coverage of the labial side is variable. The posterior part of the lower incisor lacks enamel. PIN 3101/657 is a complete juvenile unworn lower incisor (Figs. 16c, 16d). The mesial end is pointed. The distal end represents the open root. The enamel covers about two-thirds of the tooth. The labial side is almost completely covered by enamel in mesial part, but in the distal part, the enamel-dentine boundary is gradually shifting ventrally. On the lingual side, there is a narrow enamel band along the ventral tooth margin of consistent thickness. In PIN 3101/657 and PIN 3101/656, there is a distinct groove on the lingual side along the mesial half of the dorsal border of the enamel band (Figs. 16a, 16d).

The lower premolars are known from the holotype, PIN 3101/635 (Fig. 15), and a fragmentary p4 GI PST 10-23 (Kielan-Jaworowska et al., 1987: text-figs. 1E, 1F; pl. 1, fig. 5; pl. 8, fig. 3). On the holotype, the p2 is a single-rooted small tooth with rhomboid crown in labial or lingual view and smooth enamel (Fig. 14). There is no p2 or its alveolus in PIN 3101/635 (Fig. 15). The p3 is completely preserved in PIN 3101/635 (Fig. 15) and there are roots of p3 on the holotype (Fig. 14). The tooth is double-rooted, with the distal root much smaller and placed at the distolingual corner of the mesial root. The crown of p3 is more than twice larger than that of p2. The crown of p3 is smooth, without serrations. The p3 is rhomboid in labial or lingual view, with smooth enamel. In occlusal view, the crown is teardrop-shaped, with wide lingual side and narrow labial side. The crown is higher on the labial side compared with the lingual side.

The p4 is known only from anterior fragments (Figs. 10i, 14). There is a prominent mesial triangular lobe on labial side. On the lingual side, this lobe is absent. The mesial margin of the crown is slightly concave in labial view. There are five serrations preserved on the holotype. The first serration is not associated with ridges. On the labial side, the ridge of the missing sixth serration is the longest. The ridges cover about one half of the crown height on labial side. On the holotype, the ridges are poorly preserved on lingual side of p4. The serrations are eliminated by wear in GI PST 10-23. The mesial root is slightly curved mesially and bulbous at the end.

**M e a s u r e m e n t s.** See Tables 4 and 5.





**Fig. 16.** *Nokerbaatar minor* (Kielan-Jaworowska et al., 1987). Khovoor locality, Mongolia; Lower Cretaceous. Isolated lower incisors: (a, b) specimen PIN, no. 3101/656, left lower incisor, in lingual (a) and labial (b) views; (c, d) specimen PIN, no. 3101/657, right lower incisor, in labial (c) and lingual (d) views. Abbreviation: gr, groove. Scale bars, 1 mm.

**Remarks.** According to the original diagnosis (Kielan-Jaworowska et al., 1987), *N. minor* differs from *E. magnus* mostly by smaller size and size-related characters, as more closely spaced ridges on p4. The only qualitative character cited in that diagnosis, is a rounded ventral margin of mesial triangular lobe of p4 (V-shaped in *E. magnus*). However, this character is variable in *E. magnus*. Some specimens have pointed mesial triangular lobe of p4 (PIN 3101/59c), while in others this lobe has a rounded ventral margin (PIN 3101/60, PIN 3101/650).

#### Family Arginbaataridae Hahn et Hahn, 1983

Arginbaataridae: Hahn and Hahn, 1983: p. 127; Kielan-Jaworowska et al., 2000: p. 588; Kielan-Jaworowska and Hurum, 2001: p. 415; Kielan-Jaworowska et al., 2004: p. 319; Hahn and Hahn, 2006: p. 64.

**Type genus.** *Arginbaatar* Trofimov, 1980.

**Diagnosis.** Differs from all other multituberculates in having a very large p4 with limited enamel, ontogenetically rotating mesioventrally. Differs from all plagiaulacidans and some cimolodontans by lack of labial cusps on p4. Differs from all cimolodontans by having three lower premolars, including single rooted small p2 and double rooted dp3 (and p3). Ornamentation on upper premolars (P1–4) absent or poorly developed. Ornamentation on upper and lower molars absent. The lower incisor completely covered with enamel. The anterior lower premolars (p2 and dp3) shed on early ontogenetic stage. The p3 is impacted tooth, which cannot erupt because of overhanging p4. Upper molars (M2) and lower molars (m1, m2) with conical cusps. Enamel gigantoprismatic.

**Included genera.** Type genus only.

**Table 4.** Measurements (in mm) of upper premolars and molars in *Nokerbaatar minor* (L, crown length; W, crown width)

Specimen	LP1	WP1	LP3*	WP3*	LP4	WP4	LP5	WP5	LM1	WM1
PIN 3101/50b	0.88	0.86								
PIN 3101/669			1.11	0.93						
PIN 3101/636							2.12	1.42		
PIN 3101/637							2.25	1.23		
PIN 3101/66									1.79	1.29
GI PST 10-33**									1.90	1.30
PIN 3101/614					1.60	1.13				
PIN 3101/664					1.67	1.16				
GI PST 10-24**					1.70	1.20				
GI PST 10-31**					1.70	1.20				
GI PST 10-42**					1.70	1.20				
Mean	0.88	0.86	1.11	0.93	1.67	1.18	2.19	1.33	1.85	1.30
Standard error	0	0	0	0	0.02	0.01	0.07	0.10	0.06	0.01

\* Or dp3.

\*\* Measurements from Kielan-Jaworowska et al. (1987).

**Table 5.** Measurements (in mm) of lower premolars in *Nokerbaatar minor* (L, crown length; W, crown width)

Specimen	Lp2	Wp2	Lp3	Wp3
PIN 3101/70*	0.52	0.42		
PIN 3101/635			0.72	0.63
Mean	0.52	0.42	0.72	0.63
Standard error	0	0	0	0

\* Holotype.

**Remarks.** *Ameribaatar zofiae* Eaton et Cifelli, 2001 from the mid-Cretaceous (Albian-Cenomanian) Cedar Mountain Formation of Utah, USA, shows some similarity with *Arginbaatar dmitrievae* in the structure of m1, specifically in having U-shaped valleys between the widely spaced cusps in side view (Eaton and Cifelli, 2001). *Ameribaatar* was provisionally placed in the Arginbaataridae by Hahn and Hahn (2006) and unequivocally cited as an arginbaatarid by Badiola et al. (2011). A newly discovered m2 of *Arginbaatar dmitrievae* is similar with that tooth in *Ameribaatar zofiae* in lack of ornamentation, cusp formula (3:2), and a hook-like mesial lingual cusp. However, *Arginbaatar* lacks the unique type of molar wear that leaves wide transverse valleys between the cusps characteristic for *Ameribaatar* (Eaton and Cifelli, 2001; Kielan-Jaworowska et al., 2004). Thus, the placement of *Ameribaatar* in the Arginbaataridae is not justified. Currently *Ameribaatar* is placed provisionally in the cimolodontan *Paracimexomys* group (Kielan-Jaworowska et al., 2004). However, *Ameribaatar* shows no cimolodontan synapomorphies and should be considered *Multituberculata incertae sedis*.

#### Genus *Arginbaatar* Trofimov, 1980

*Arginbaatar*: Trofimov, 1980: p. 209; Hahn and Hahn, 1983: p. 127; Kielan-Jaworowska et al., 1987: p. 21; Kielan-Jaworowska et al., 2004: p. 320; Hahn and Hahn, 2006: p. 68.

*Monobaatar*: Kielan-Jaworowska et al., 1987: p. 18.

**Type species.** *Arginbaatar dmitrievae* Trofimov, 1980.

**Included species.** Type species only.

#### *Arginbaatar dmitrievae* Trofimov, 1980

Figures 17–34

*Arginbaatar dmitrievae*: Trofimov, 1980: p. 210, text-fig. 1; Barsbold and Sigogneau-Russell, 1992: text-fig. on p. 107; Kielan-Jaworowska et al., 2004: p. 320, text-figs. 8.34I, 8.35F; Hahn and Hahn, 2004: text-figs. 8f, 10e, 12f; Hahn and Hahn, 2006: p. 70, text-figs. 38–41.

*Eobaatar magnus*: Kielan-Jaworowska et al., 1987: pl. 4, fig. 1.

*Arginbaatar dimitrievae* [sic]: Kielan-Jaworowska et al., 1987: p. 21, text-figs. 2E–2G, 3G, 4, 5, 6A; pl. 7, figs. 1, 2; pl. 9, fig. 1; pls. 13–15; pl. 16, figs. 2, 3; pl. 17, figs. 1, 2; pls. 18–21; pl. 22, figs. 1, 3, 4; Kielan-Jaworowska et al., 2000: p. 588, text-figs. 29.9C, 29.9D.

*Monobaatar mimicus*: Kielan-Jaworowska et al., 1987: pl. 3, fig. 3; pl. 7, fig. 3; pl. 9, figs. 2, 3; Barsbold and Sigogneau-Russell, 1992: text-fig. on p. 109; Kielan-Jaworowska et al., 2000: p. 587.

[*Multituberculata* indet.]: Kielan-Jaworowska et al., 1987: pl. 6, figs. 1, 2; pl. 9, fig. 4.

**Holotype.** PIN 3101/49, right dentary fragment with lower incisor, p2, dp3, p4, m1, and alveoli for lower incisor and m2.

**Type locality and horizon.** Khovoor, Mongolia; Early Cretaceous (Aptian-Albian).

**Referred specimens. Maxilla fragments.** PIN 3101/54, left maxillary fragment with P1–2 and dP3; PIN 3101/74, left maxillary fragment with P1–2 and alveoli for P3; PIN 3101/65, holotype of *Monobaatar mimicus* Kielan-Jaworowska et al., 1987, left maxillary fragment with P2–4 and alveoli of P5; PIN 3101/68, right maxillary fragment with P1–4; PIN 3101/69, right maxillary fragment with P2–3 and alveoli for P4; PIN 3101/72, right maxillary fragment with P2–3 and alveoli for P4; PIN 3101/603, left maxillary fragment with dP3 and P4; PIN 3101/604, left maxillary fragment with P2–3 and alveoli for P4; GI PST 10-15, right maxillary fragment with P4 and alveoli for P3 and P5.

**I2.** PIN 3101/677, left I2; PIN 3101/678, right I2; PIN 3101/679, left I2; PIN 3101/680, right I2; PIN 3101/681, left I2; PIN 3101/682, left I2; GI PST 10-29, left I2.

**P1.** PIN 3101/622, left P1; PIN 3101/624, right P1; PIN 3101/670, left P1; PIN 3101/673, left P1; PIN 3101/674, right P1.

**P2.** PIN 3101/625, right P2; PIN 3101/672, right P2.

**dp3.** PIN 3101/626, right dP3; PIN 3101/671, right dP3.

**P3.** PIN 3101/50a, associated right P3 and right M2; PIN 3101/620, left P3; PIN 3101/621, left P3; PIN 3101/623, left P3; PIN 3101/675, left P3.

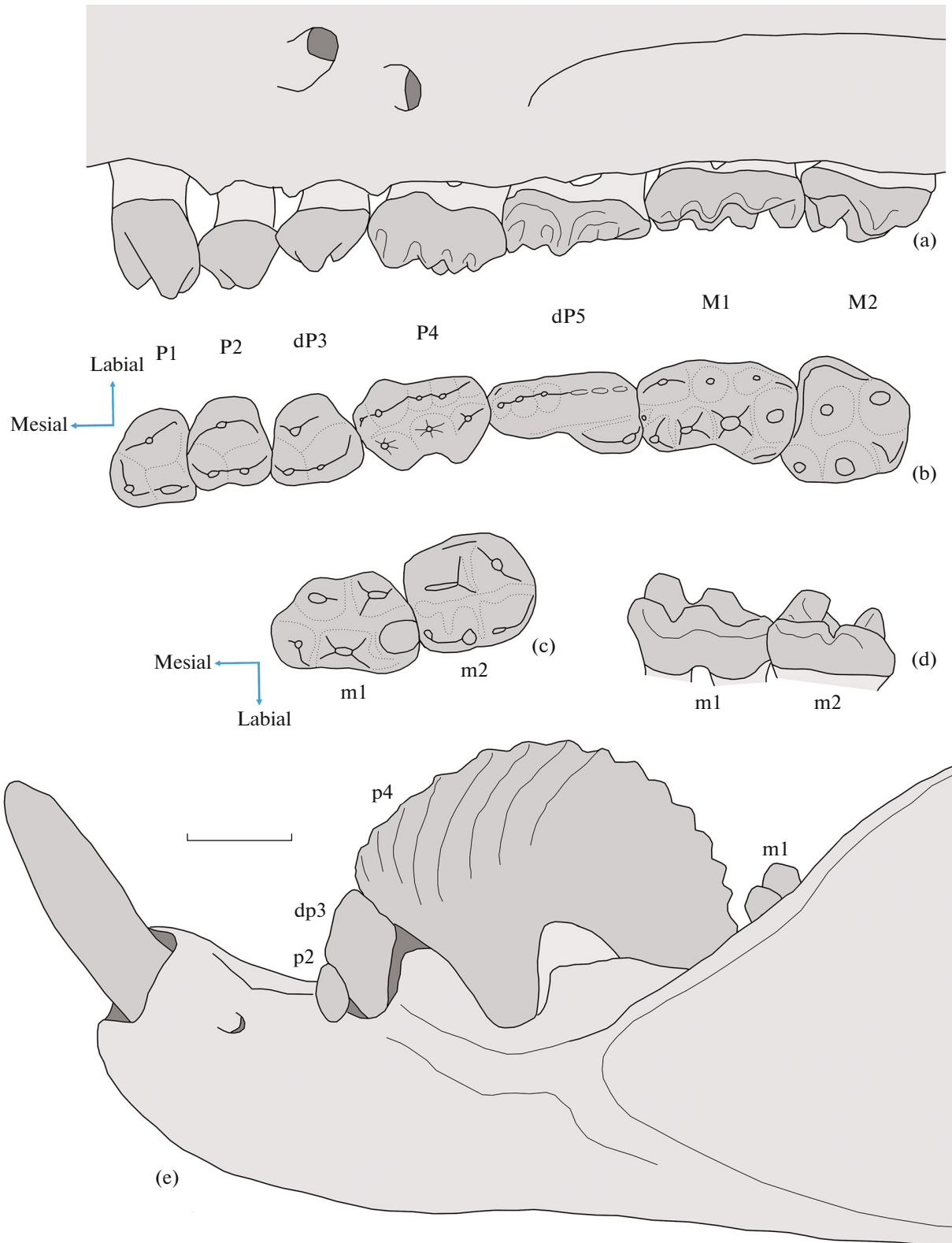
**P4.** PIN 3101/612, left P4; PIN 3101/613, right P4; PIN 3101/615, right P4; PIN 3101/616, left P4; PIN 3101/617, left P4; PIN 3101/618, left P4; PIN 3101/619, left P4; GI PST 10-26, left P4; GI PST 10-27, right P4; GI PST 10-36, right P4; GI PST 10-44a, left P4.

**dp5.** PIN 3101/665, left dP5; PIN 3101/666, left dP5; PIN 3101/667, right dP5; PIN 3101/668, right dP5.

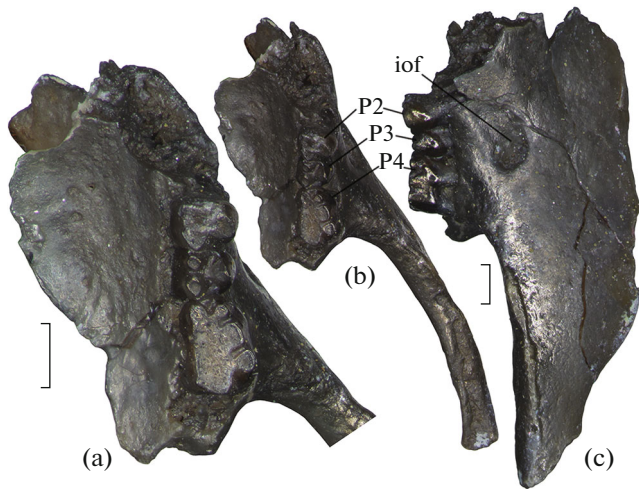
**M1.** PIN 3101/55, left M1; PIN 3101/649, right M1; PIN 3101/611, incomplete left M1; GI PST 10-63, left M1.

**M2.** PIN 3101/61, left M2; PIN 3101/610, incomplete left M2; GI PST 10-20, left M2.

**Dentary fragments.** PIN 3101/644, left dentary fragment with lower incisor and erupting p3; PIN 3101/52, left dentary fragment with lower incisor and incomplete p4; PIN 3101/51, right dentary fragment with p2, dp3, and p4; PIN 3101/56, left dentary fragment with p4, erupting p3, and alveolus for lower incisor; PIN 3101/58, right dentary fragment with p4 and erupting p3; PIN 3101/638, right dentary frag-



**Fig. 17.** *Arginbaatar dmitrievae* Trofimov, 1980, reconstruction of the left maxilla and upper cheek teeth in labial view (a), left upper cheek teeth in occlusal view (b), left lower molars in occlusal (c) and labial (d) views, and left dentary in labial view (e). Khovoor locality, Mongolia; Lower Cretaceous. The reconstruction is based on the following specimens: PIN 3101/54, left maxillary fragment with P1–2 and dP3; PIN 3101/65, holotype of *Monobaatar mimicus*, left maxillary fragment with P2–4 and alveoli of P5; PIN 3101/613, right P4, reversed; PIN 3101/665, left dP5; PIN 3101/649, right M1, reversed; PIN 3101/61, left M2; PIN 3101/49, holotype, right dentary fragment with p2, dp3, p4, and m1, reversed; PIN 3101/633, left m2; PIN 3101/643, left lower incisors; PIN 3101/642, right dentary fragment with alveoli for lower incisor, p2–4, and m1–2, reversed. Scale bar, 1 mm.



**Fig. 18.** *Arginbaatar dmitrievae* Trofimov, 1980. Khovoor locality, Mongolia; Lower Cretaceous. Specimen PIN, no. 3101/65, holotype of *Monobaatar mimicus* Kielan-Jaworowska et al., 1987, left maxillary fragment with P2–4 and alveoli of P5, in occlusal (a, b) and labial (c) views. Abbreviation: iof, infraorbital foramen. Scale bars, 1 mm.

ment with erupting p3 and incomplete p4; PIN 3101/640, left dentary fragment with erupting p3 and alveolus for lower incisor; PIN 3101/642, right

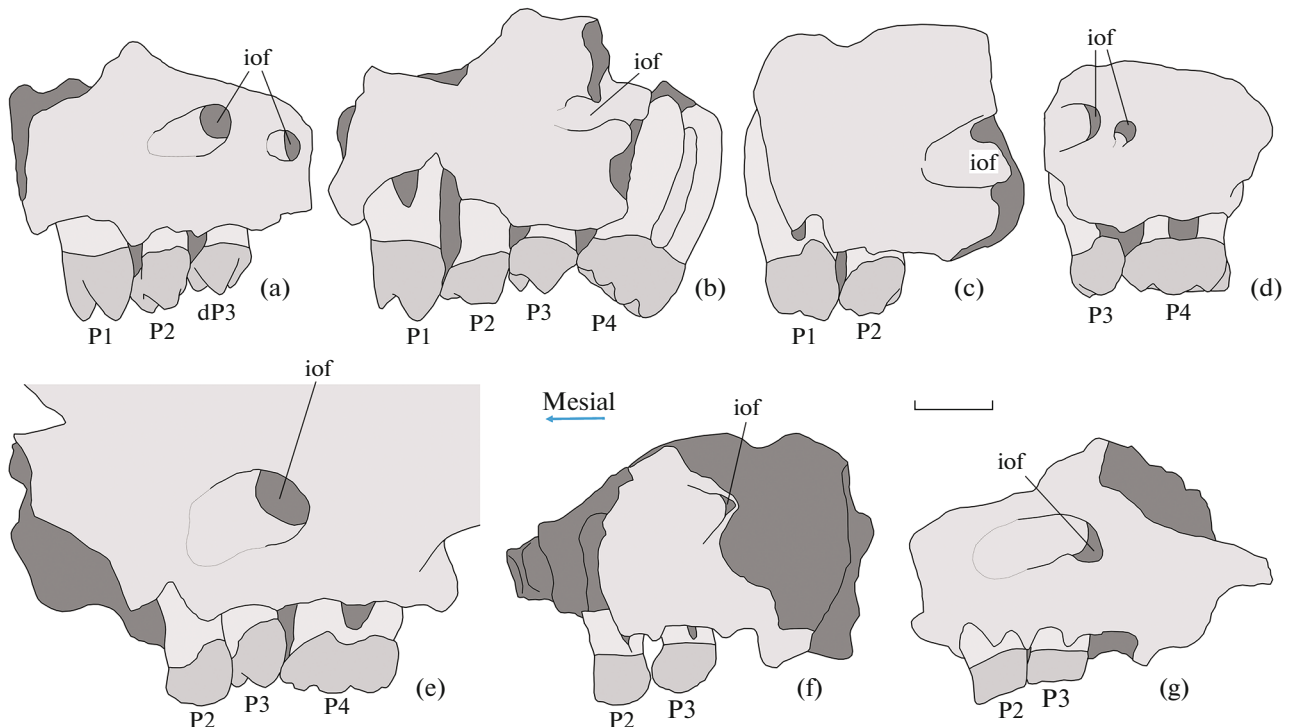
dentary fragment with alveoli for lower incisor, p2–4, and m1–2; PIN 3101/639, left dentary fragment with alveoli for m1–2; GI PST 10-11, right dentary fragment with p2, dp3, and p4; GI PST 10-40, right dentary fragment with dp3, p4, and alveolus for p2; GI PST 10-12, left dentary fragment with p3–4; GI PST 10-60, left dentary fragment with p4.

**Lower incisor.** PIN 3101/643, left lower incisor.

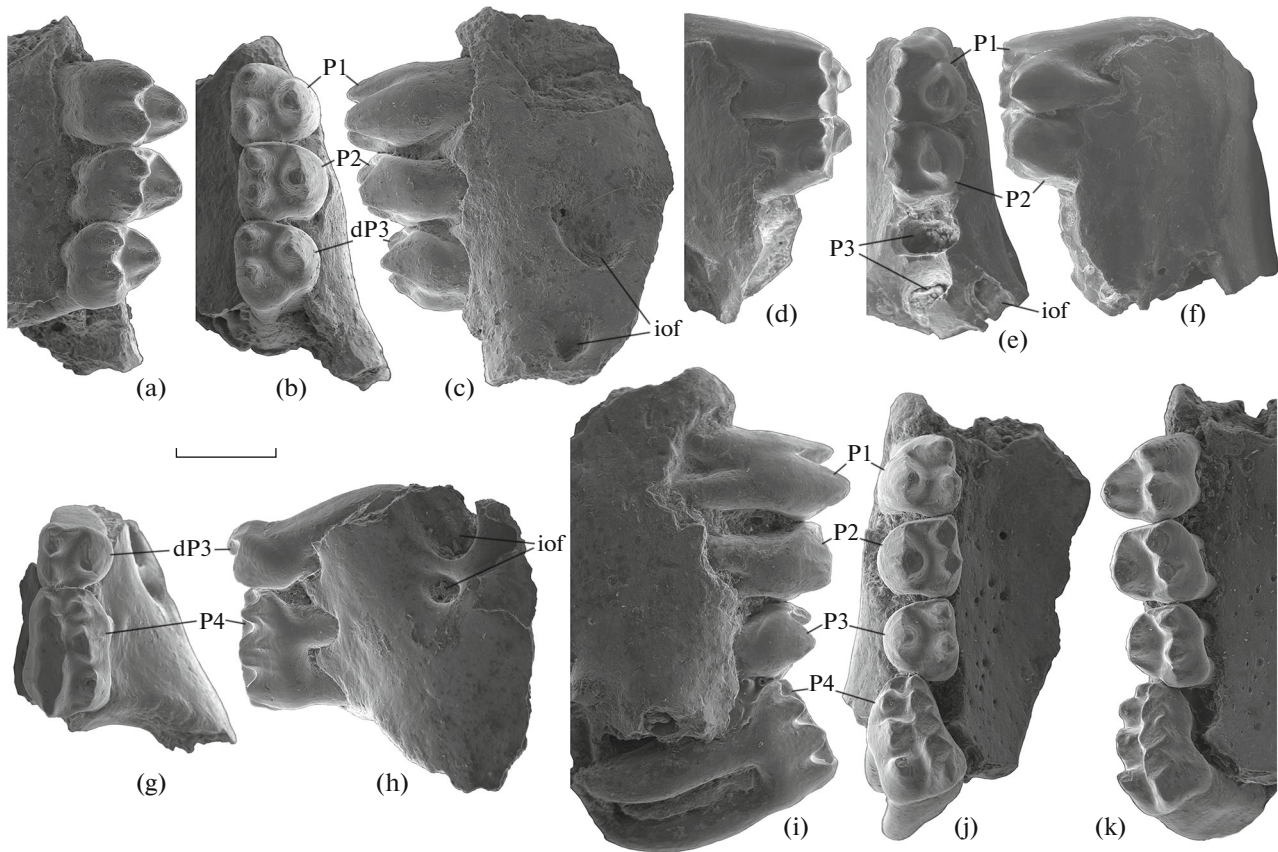
**p4.** PIN 3101/64, left p4; PIN 3101/71a, right p4; PIN 3101/71b, right p4; PIN 3101/71c, left p4; PIN 3101/73b, left p4; PIN 3101/73h, right p4; PIN 3101/73a, p4 distal fragment; PIN 3101/73c, p4 fragment; PIN 3101/73d, p4 fragment; PIN 3101/73e, p4 fragment; PIN 3101/73f, p4 fragment; PIN 3101/73g, p4 fragment; PIN 3101/641, p4 distal fragment; PIN 3101/645, p4 fragment; PIN 3101/646, p4 distal fragment; PIN 3101/647, p4 fragment; PIN 3101/648, p4 fragment; GI PST 10-13, right p4; GI PST 10-41, right p4; GI PST 10-4, right p4 distal fragment.

**m1.** PIN 3101/50c, right m1; PIN 3101/50d, left m1; PIN 3101/605, right m1; PIN 3101/606, left m1; PIN 3101/607, right m1; PIN 3101/608, right m1; GI PST 10-42, right m1; GI PST 10-44b, right m1.

**m2.** PIN 3101/609, left m2; PIN 3101/633, left m2.



**Fig. 19.** *Arginbaatar dmitrievae* Trofimov, 1980. Khovoor locality, Mongolia; Lower Cretaceous. Maxillary fragments showing variation of the infraorbital foramen (iof), in labial view: (a) specimen PIN, no. 3101/54, left maxillary fragment with P1–2 and dP3; (b) specimen PIN, no. 3101/68, right maxillary fragment with P1–4, reversed; (c) specimen PIN, no. 3101/74, left maxillary fragment with P1–2; (d) specimen PIN, no. 3101/603, left maxillary fragment with P3–4; (e) specimen PIN, no. 3101/65, holotype of *Monobaatar mimicus* Kielan-Jaworowska et al., 1987, left maxillary fragment with P2–4; (f) specimen PIN, no. 3101/69, right maxillary fragment with P2–3, reversed; (g) specimen PIN, no. 3101/604, left maxillary fragment with P2–3. Scale bar, 1 mm.



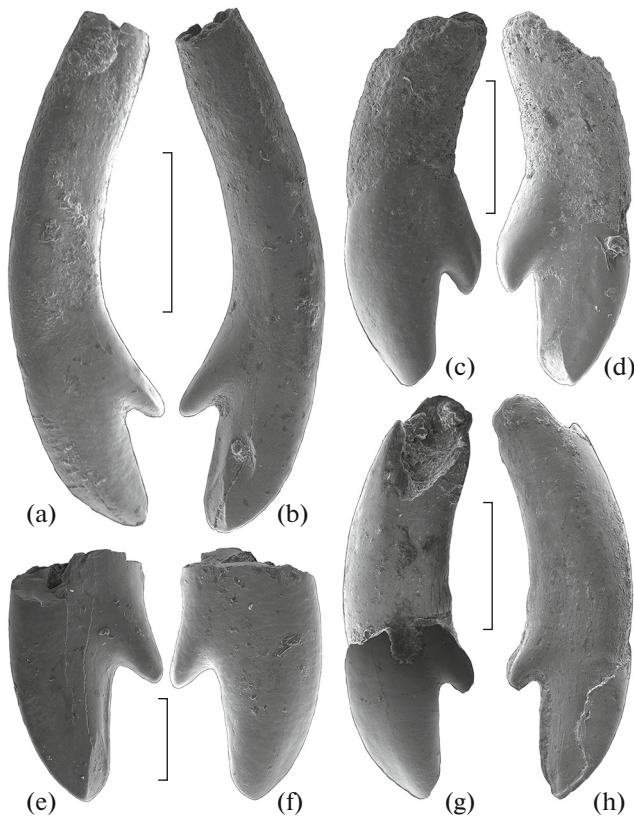
**Fig. 20.** *Arginbaatar dmitrievae* Trofimov, 1980. Khovoor locality, Mongolia; Lower Cretaceous. SEM images of maxillary fragments: (a–c) specimen PIN, no. 3101/54, left maxillary fragment with P1–2 and dP3, in lingual (a), occlusal (b), and labial (c) views; (d–f) specimen PIN, no. 3101/74, left maxillary fragment with P1–2 and alveoli of P3, in lingual (d), occlusal (e), and labial (f) views; (g, h) specimen PIN, no. 3101/603, left maxillary fragment with dP3 and P4, in occlusal (g) and labial (h) views; (i–k) specimen PIN, no. 3101/68, right maxillary fragment with P1–4, in labial (i), occlusal (j), and occlusolingual (k) views. Abbreviation: iof, infraorbital foramen. Scale bar, 1 mm.

**Description.** *A. dmitrievae* is known from jaw fragments and isolated teeth representing all the dentition except I1 and I3 (Fig. 17). Several maxillary fragments are attributed here to *A. dmitrievae*, including two fragments previously referred to *Monobaatar mimicus* (PIN 3101/65) (Kielan-Jaworowska et al., 1987: pl. 3, fig. 3; pl. 9, fig. 3). The zygomatic process of maxilla is most complete in PIN 3101/65 where there is no facet for the jugal (Fig. 18). Most specimens have two anterior openings of the infraorbital canal (Figs. 19, 20). The single opening is present in PIN 3101/65 and PIN 3101/604 (Figs. 18c, 19e, 19g). In the latter specimen, it is subdivided in two parts. There is prominent depression associated with the anterior opening of the infraorbital canal, which is variable in shape and size and placed above P2–4. The zygomatic root is nested between P2–3 and P4–5.

Seven isolated upper incisors of similar construction are identified as I2 and attributed here to *A. dmitrievae* (Fig. 21). One of these specimens was described as unidentified upper incisor (Kielan-Jaworowska et al., 1987: pl. 9, fig. 4). The crown and root are gently

curved. The enamel is smooth and covers about one third of tooth length. There are prominent main cusp and much smaller additional distal cusp, which greatly varies in size. The main cusp follows the curvature of the root. The distal cusp is straight and directed ventrally or distoventrally. The labial crown side is slightly convex. The lingual side is flat and bears variable developed wear facets (Figs. 21b, 21d, 21e). PIN 3101/682 is a complete tooth with open root (Figs. 21a, 21b).

The anterior upper premolars are known from maxillary fragments and isolated specimens. The replacement is documented in the third upper premolar locus by differential wear (Fig. 22). It is not clear if the first two upper premolars are deciduous or permanent teeth. By tradition, they are described here as P1–2. There is some variation within the sample of P1: some teeth are wider than long while others are longer than wide. Perhaps both dP1 and P1 are present in the sample but they cannot be clearly differentiated. The three upper anterior premolars are three-cusped (the cusp formula is 1:2, but see description of dP3), with a large



**Fig. 21.** *Arginbaatar dmitrievae* Trofimov, 1980. Khovoor locality, Mongolia; Lower Cretaceous. SEM images of isolated I2: (a, b) specimen PIN, no. 3101/682, left I2, in labial (a) and lingual (b) views; (c, d) specimen PIN, no. 3101/679, left I2, in labial (c) and lingual (d) views; (e, f) specimen PIN, no. 3101/678, right I2, in lingual (e) and labial (f) views; (g, h) specimen PIN, no. 3101/677, left I2, in labial (g) and lingual (h) views. Scale bars, 1 mm (a–d, g, h), 0.5 mm (e, f).

labial cusp and two smaller lingual cusps, and double-rooted. The anterior premolars (P1–3, dP3) differ from those in *Eobaatar* by lack or poor development of ornamentation. The crowns of P1–3 are wider than long in most specimens. There are three specimens of P1, which has crown longer than wide. The dP3 has crown width similar to the length. The crown of P1 is of triangular shape in occlusal view, with convex mesiolabial side (Fig. 23). It is most asymmetrical of all three upper premolars, with the labial cusp placed closer to the distal margin. In P2 the crown is symmetrical, with the labial cusp is placed at the level between the lingual cusps. The labial cusp in P1–2 is conical, with the lingual side more convex than the labial side. The distolingual cusp (L2) of P1 is only little lower than the labial cusp and labiolingually compressed. The mesiolingual (L1) cusp of P1 is conical. It is distinctly shorter mesiodistally than the cusp L2. The lingual cusps are deeper separated on the lingual side in P1 compared with P2 and dP3. The longitudinal valley separating the labial and lingual cusps is open mesially

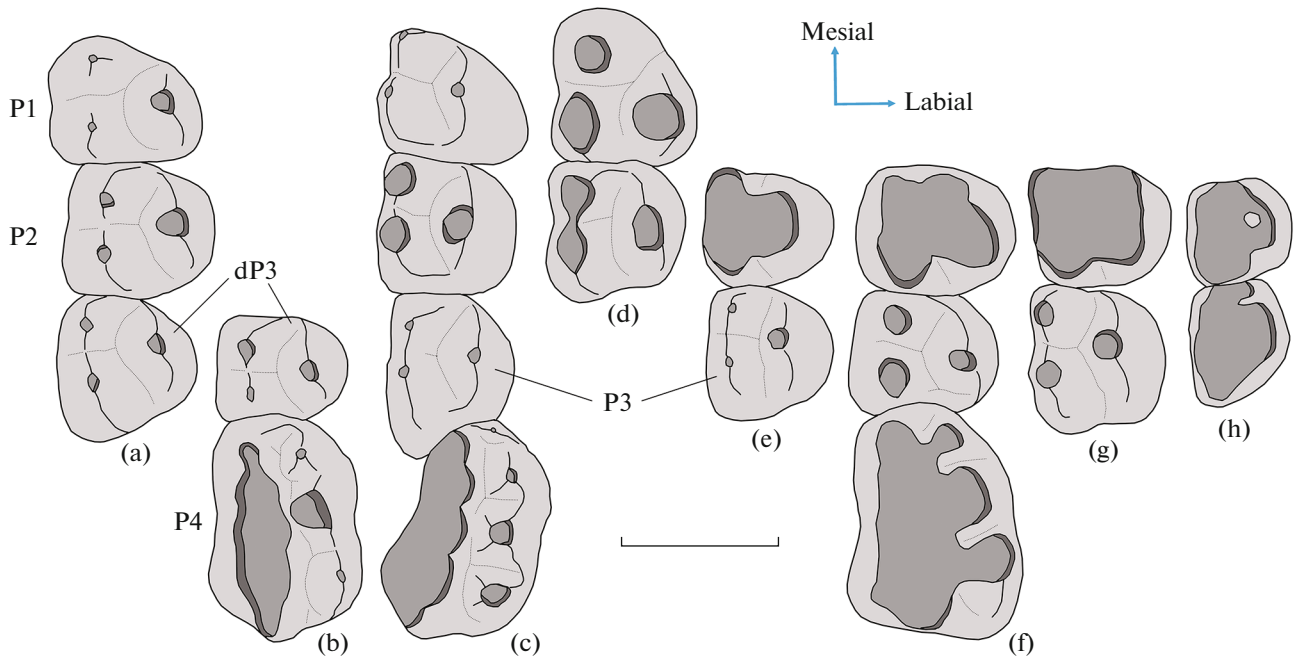
and continues mesially as a notch down the root-enamel junction. The enamel of P1 is higher mesially than distally. The roots of P1 are well separated and curved.

The P2 is somewhat smaller and has a lower crown compared with P1 (Figs. 24a–24c). The lingual cusps are similar in size and labiolingually compressed, relatively smaller than on P1. These cusps are closely appressed, with only a short notch separating them on the lingual side. The P2 differs from P1 in having a ridge extending mesiolingually from the apex of the labial cusp and forming the mesial cingulum. In PIN 3101/54, the mesial cingulum ends lingually in a minute mesial cuspule at the base of the cusp L1. This ridge closes mesially the transverse valley separating the labial and lingual cusps.

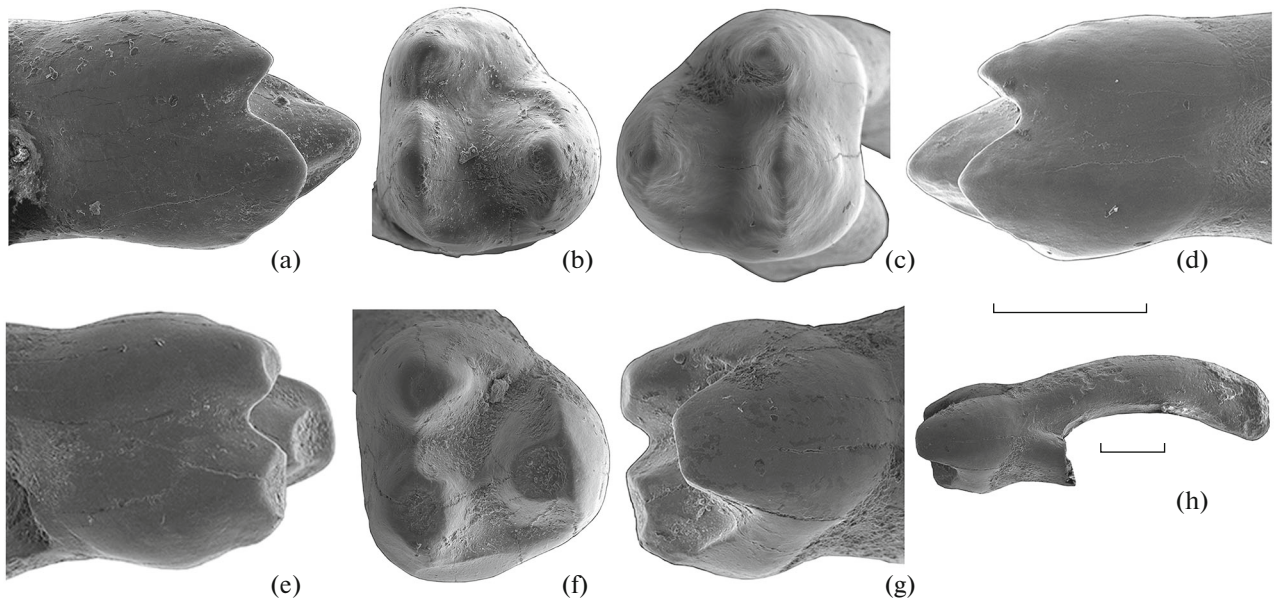
The dP3 is similar in size but has lower crown compared with P2 (Figs. 20a–20c, 20g, 20h, 24d–24f). The crown shape of dP3 mirrors that of P1, with the labial cusp placed closer to the mesial side and convex distolabial margin. As in P2, there is a mesial cingulum, closing the longitudinal valley mesially, and a short mesial ridge, extending to the apex of the labial cusp. The lingual cusps are slightly wider spaced compared with P2, but the lingual notch separating them is similarly shallow. The distolingual corner of the crown is formed by a distinct shelf, extending distolabially from the apex of the cusp L2.

The P3 is preserved in situ in three specimens (Figs. 20i–20k, 22). In PIN 3101/69 and PIN 3101/72 a little worn P3 is preserved with heavily worn P2. In PIN 3101/65 a little worn P3 is between the heavily worn P2 and moderately worn P4. The P3 is smaller and distinctly shorter mesiodistally than dP3 (Figs. 24g–24i). The crown is symmetrical in occlusal view, with the labial cusp placed at the level between the lingual cusps. The labial cusp is conical, with the labial side more convex than the lingual side. The lingual cusp L2 is only slightly larger and more labiolingually compressed compared with the cusp L1. On the lingual side, the crown is distinctly higher at the cusp L2. The notch separating the lingual cusps is very shallow. As in P2, there is a prominent mesial cingulum connected by a ridge with apex of the labial cusp. Distal to the cusp L2 there is a transverse shelf overhang by P4, but there no distal cingulum (elevated ridge). In one specimen (PIN 3101/675), there is a small but distinct fourth cusp mesial to the labial cusp. The roots are well separated and curved, similar to those in P1.

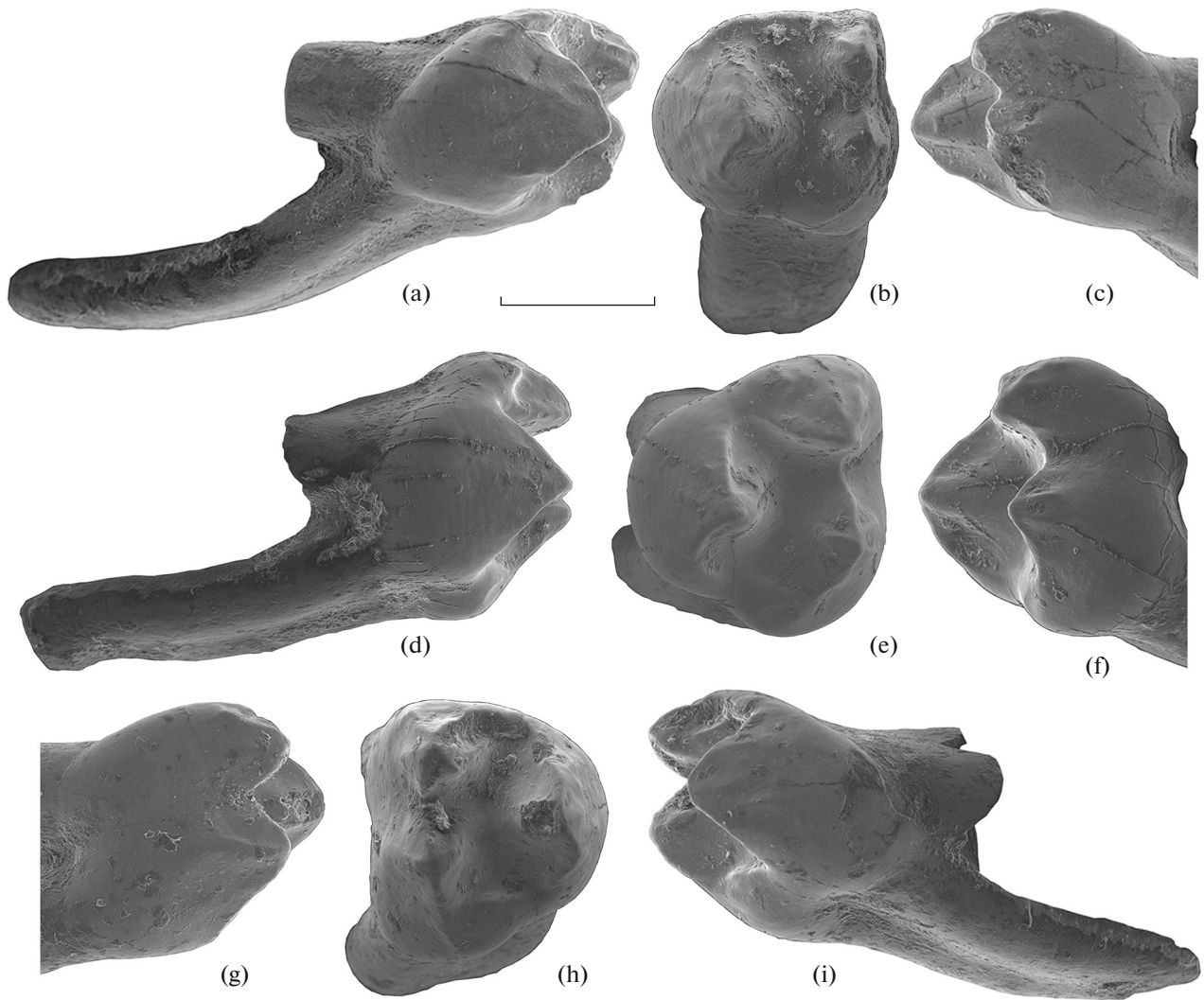
The P4 is preserved in three maxillary fragments (Figs. 18, 20g–20k) and also known from several isolated specimens (Figs. 25a–25f). One of these maxillary fragments (PIN 3101/65) and one isolated tooth (GI PST 10-26) were referred previously to *Mono-baatar mimicus* (Kielan-Jaworowska et al., 1987: pl. 3, fig. 3; pl. 9, fig. 2). Also one isolated P4 (GI PST 10-27) was attributed to *E. magnus* (Kielan-Jaworowska et al., 1987: pl. 4, fig. 1). PIN 3101/613, PIN 3101/618, and



**Fig. 22.** *Arginbaatar dmitrievae* Trofimov, 1980. Khovoor locality, Mongolia; Lower Cretaceous. Tooth rows from maxillary fragments arranged according to the wear state of the upper premolars, in occlusal view: (a) specimen PIN, no. 3101/54, left maxillary fragment with P1–2 and dP3; (b) specimen PIN, no. 3101/603, left maxillary fragment with dP3 and P4; (c) specimen PIN, no. 3101/68, right maxillary fragment with P1–4, reversed; (d) specimen PIN, no. 3101/74, left maxillary fragment with P1–2; (e) specimen PIN, no. 3101/69, right maxillary fragment with P2–3, reversed; (f) specimen PIN, no. 3101/65, holotype of *Mono-baatar mimicus*, left maxillary fragment with P2–4, reversed; (g) specimen PIN, no. 3101/72, right maxillary fragment with P2–3, reversed; (h) specimen PIN, no. 3101/604, left maxillary fragment with P2–3. Scale bar, 1 mm.



**Fig. 23.** *Arginbaatar dmitrievae* Trofimov, 1980. Khovoor locality, Mongolia; Lower Cretaceous. SEM images of isolated P1: (a, b) specimen PIN, no. 3101/622, left P1, in lingual (a) and occlusal (b) views; (c, d) specimen PIN, no. 3101/624, right P1, in occlusal (c) and lingual (d) views; (e–h) specimen PIN, no. 3101/673, left P1 in lingual (e), occlusal (f), occlusolabial (g), and labial (h) views. Scale bars, 0.5 mm.

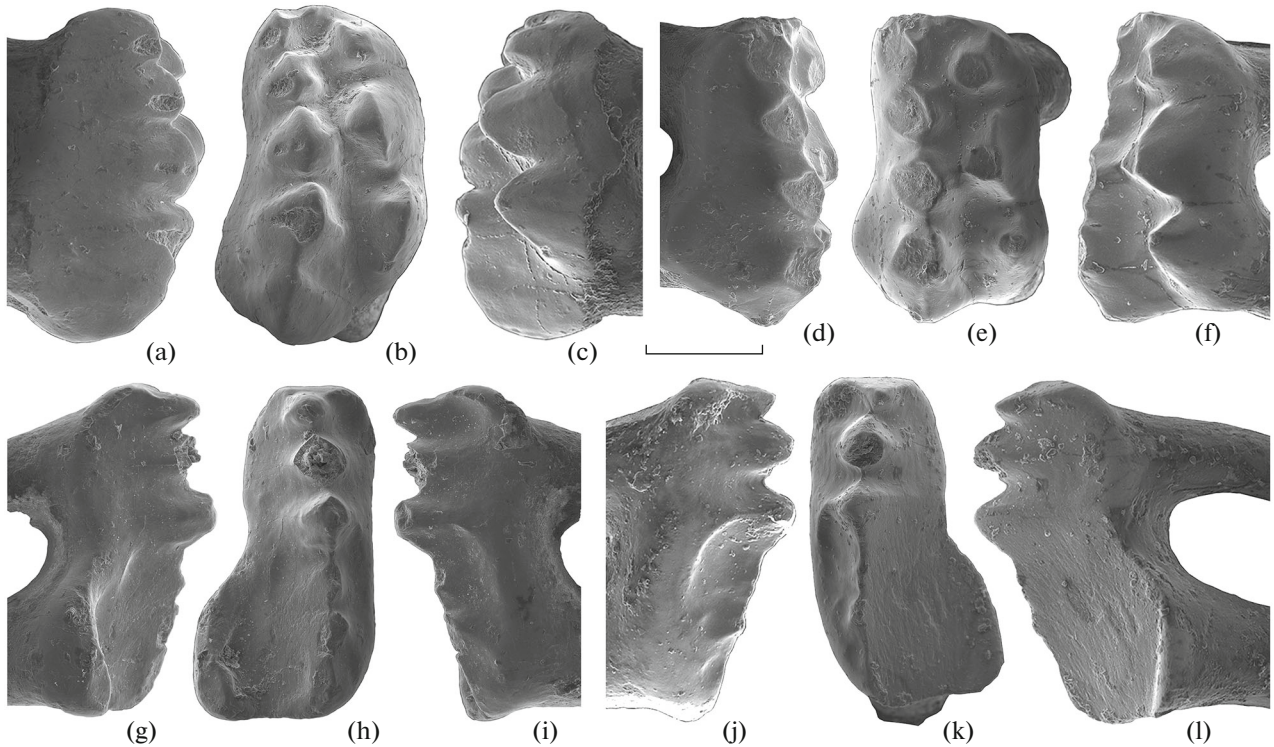


**Fig. 24.** *Arginbaatar dmitrievae* Trofimov, 1980. Khovoor locality, Mongolia; Lower Cretaceous. SEM images of isolated P2, dP3, and P3: (a–c) specimen PIN, no. 3101/625, right P2, in labial (a), occlusal (b), and lingual (c) views; (d–f) specimen PIN, no. 3101/626, right dP3, in labial (d), occlusal (e), and lingual (f) views; (g–i) specimen PIN, no. 3101/621, left P3, in lingual (g), occlusal (h), and labial (i) views. Scale bar, 0.5 mm.

GI PST 10–26 have unworn cusps, while other specimens show variable degree of wear on cusps (Figs. 18, 20g–20k, 22, 25a–25f). The crown is bean-shaped in occlusal view, with convex labial and concave lingual side. The crown is somewhat asymmetrical because of bulging of the crown base at the distal root lingually. There are three labial and four lingual cusps (the cusp formula is 3:4). Also, sometimes there is a minute cuspule on the mesial cingulum between the cusp rows (Fig. 25b). The labial and lingual cusps are conical and labiolingually compressed. The cusp B2 is the largest labial cusp. The other labial cusps are distinctly lower and of similar height (cusp B1 is somewhat larger than cusp B3). The lingual cusps gradually increase in size from L1 to L3. The cusp L4 is distinctly larger than other lingual cusps. Often the cusp L4 continues in a distal ridge-like shoulder (Fig. 25b). The transverse

valleys between the cusps are deeper on the labial side. The longitudinal valley between the cusp rows is shallow between the cusps B1–2 and L1–3 but becomes deeper between the cusps B3 and L4. On PIN 3101/613, there is a wear facet on the lingual side of the crown. This facet becomes more prominent on more worn teeth. The lingual cusps start to wear much earlier than the labial cusps. On early wear stage, the wear facets are separate on lingual cusps (PIN 3101/612; Fig. 25a) and become united on later wear stages. The individual cusps can be still recognizable (PIN 3101/603, PIN 3101/615, PIN 3101/617), or there is a common elliptical wear facet on the lingual cusp row on the later wear stage (PIN 3101/65, PIN 3101/616). Only on the later stage, the labial cusps become significantly worn, but with separate wear facets. The roots are long, at least twice longer than crown, and mesiodistally compressed,





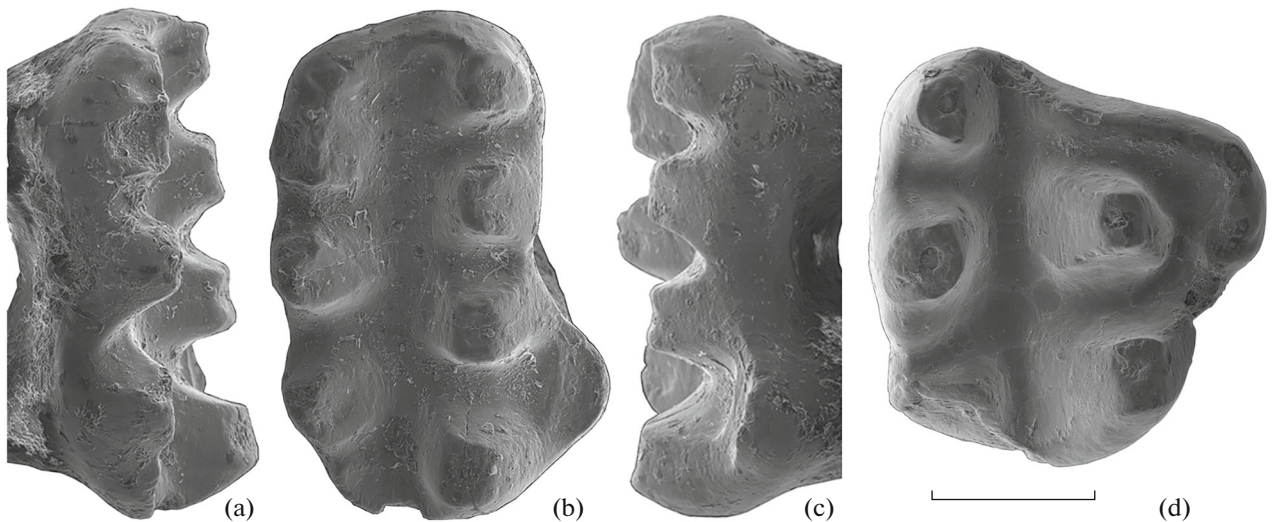
**Fig. 25.** *Arginbaatar dmitrievae* Trofimov, 1980. Khovoor locality, Mongolia; Lower Cretaceous. SEM images of isolated P4 and dP5: (a–c) specimen PIN, no. 3101/612, left P4, in lingual (a), occlusal (b), and labial (c) views; (d–f) specimen PIN, no. 3101/617, left P4, in lingual (d), occlusal (e), and labial (f) views; (g–i) specimen PIN, no. 3101/665, left dP5, in lingual (g), occlusal (h), and labial (i) views; (j–l) specimen PIN, no. 3101/667, right dP5, in labial (j), occlusal (k), and lingual (l) views. Scale bar, 0.5 mm.

with their apices deflected mesially. The mesial root is mesiodistally wider than the distal root. The roots are separated by a space similar in mesiodistal length with that of the distal root.

Four isolated teeth are identified as dP5 of *A. dmitrievae* (Figs. 25g–25l). The tooth is very similar with P5 of *Eobaatar* except in labial cusp row there is a small ridge instead of cusp and the area of the lingual cusp row is more expanded, but with a ridge instead of the cusps. Also, the middle cusp row is not as high as in P5 of *Eobaatar*. The number of cusps in the middle cusp row is variable. In PIN 3101/665, there are five cusps in the middle row (Figs. 25g–25i). The cusps M2 and M3 are the highest. The cusps M4 and M5 are small and ridge-like. In PIN 3101/666, there are four cusp and a ridge distal to the cusp M4. In PIN 3101/667 (Figs. 25j–25l) and PIN 3101/668, there are only three cusps and a long distal ridge. These specimens are worn and the posterior middle cusps, which are already poorly differentiated in PIN 3101/665, could be eliminated by wear. A wide groove separates the middle cusp row from the lingual ridge. The two roots are directed posterodorsally. The mesial root is mesiodistally compressed and has a longitudinal furrow along its distal side. The distal root is more round in cross-section.

Kielan-Jaworowska et al. (1987) considered P5 of *A. dmitrievae* to be identical in morphology with P4. This was questioned by Averianov et al. (2017), who supposed that all these teeth actually represent P4, whereas P5 is unknown for *A. dmitrievae*. This observation is confirmed in present study. All specimens identified as P5 in Kielan-Jaworowska et al. (1987) are actually P4: two isolated teeth, GI PST 10-36 and GI PST 10-44a, and one tooth in maxillary fragment, GI PST 10-15 (Kielan-Jaworowska et al., 1987: pl. 9, fig. 1; pl. 21, figs. 2, 3). The distal end of the supposed P5 in the maxilla fragment GI PST 10-15 is at the posterior root of zygomatic process, as in P4 of other specimens (e.g., PIN 3101/65), while P5 should be posterior to the root of zygomatic process of maxilla. Currently there are no specimens which can be identified as P5 of *A. dmitrievae*.

Four specimens represent M1. Heavily worn PIN 3101/55 and GI PST 10-63 were described as unidentified M1 by Kielan-Jaworowska et al. (1987: p. 34; pl. 6, figs. 1, 2), but nevertheless one of these specimens was used for reconstruction of the upper tooth row in *A. dmitrievae* (Kielan-Jaworowska et al., 1987: text-fig. 3D). PIN 3101/649 is little worn (Figs. 26a–26c). PIN 3101/611 represents distal part of M1 similar in structure and wear stage with the pre-



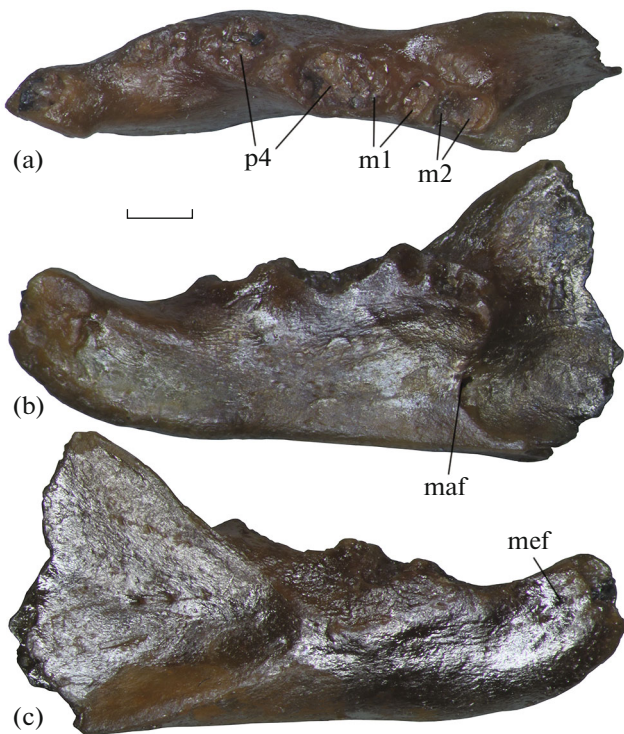
**Fig. 26.** *Arginbaatar dmitrievae* Trofimov, 1980. Khovoor locality, Mongolia; Lower Cretaceous. SEM images of isolated upper molars: (a–c) specimen PIN, no. 3101/649, right M1, in labial (a), occlusal (b), and lingual (c) views; (d) specimen PIN, no. 3101/61, left M2, in occlusal view. Scale bar: 0.5 mm.

vious specimen. The M1 is subrectangular in occlusal view, with parallel labial and lingual margins and convex mesial and distal margins. The M1 has three labial and four lingual cusps and a distolingual wing (the cusp formula is 3:4:Ri). The labial cusps are conical and labiolingually compressed. The cusp B1 is ridge-like and larger than other labial cusps. The cusp B2 is similar in height with the cusp B1. Both cusps are closely spaced. The cusp B3 is smaller than the cusp B2 and separated from the latter by a greater distance. The labial cusps are placed opposite to the transverse valleys separated the lingual cusps. The lingual cusps are pyramidal, gradually increasing in size and height in distal direction. A wide longitudinal valley separates the labial and lingual cusp rows. In PIN 3101/611, there is a short semilunar ridge between the cusps B3 and L4 that closes the longitudinal valley distally. A similar ridge is present also in PIN 3101/649, but there it is very low and the transverse valley is open distally. The distinct semicircular distolingual wing is placed at the level between the cusps L3 and L4 (Fig. 26b). A heavily worn lingual wing in PIN 3101/55 and GI PST 10-63 is distinctly smaller than in PIN 3101/611 and PIN 3101/649. There are two widely separated roots.

Three isolated M2 are attributed here to *A. dmitrievae*. A complete PIN 3101/61 was referred previously to *Monobaatar mimicus* (Kielan-Jaworowska et al., 1987: pl. 7, fig. 3). The M2 crown has slightly (PIN 3101/61; Fig. 26d) to strongly (GI PST 10-20) sinusoidal mesial margin. The labial wing is better developed in PIN 3101/61 compared with GI PST 10-20. There are two labial and three lingual cusps (the cusp formula is 2:3). A strong cingulum surrounds the labial wing and closes the longitudinal valley mesially. Between this cingulum and the labial cusp B1 there is

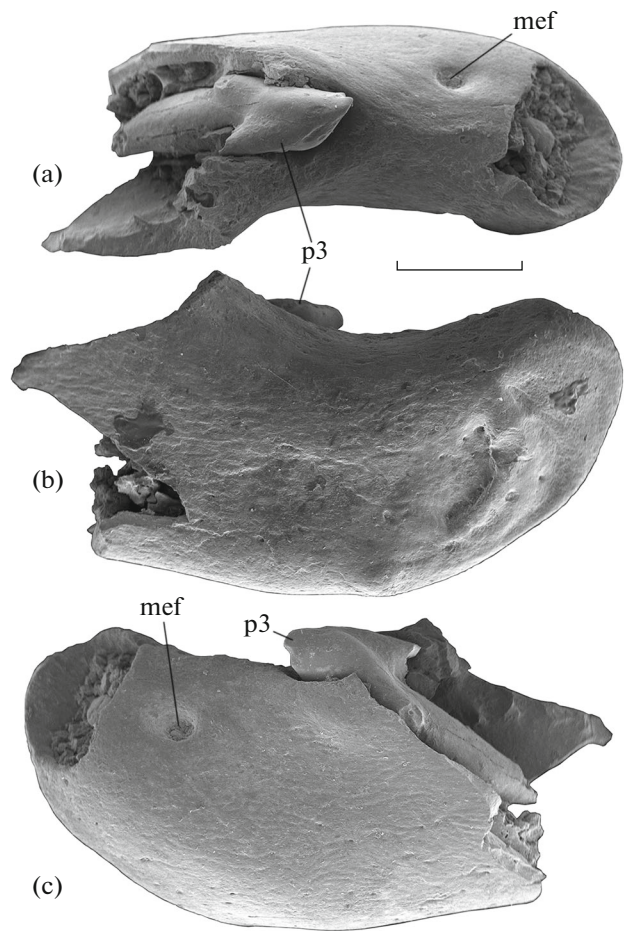
a distinct groove that surrounds the cusp B1 mesially and labially. The labial cusps are pyramidal, with flattened sides adjacent to the transverse groove separating them and with convex opposite sides. The cusp B2 is slightly larger than the cusp B1. The lingual cusps are transversely narrower than the labial cusps and conical. The cusp L2 is slightly larger than the two other lingual cusps. The longitudinal valley separating the cusps rows is similar in width with the transverse grooves separating the cusps. There are two roots. The mesial root is mesiodistally compressed and transversely wide. The distal root is round in cross-section.

The dentary is incomplete on the holotype and all specimens bearing dentition. The most complete specimen is an edentulous dentary PIN 3101/642 which lacks only posterior margin of the mandibular ramus, including the condyloid process and tip of the coronoid process (Fig. 27). The mesial part of the mandibular body is hook-like, curved dorsally in labial and lingual views, and deflected medially in occlusal view. The symphyseal part is flat and short mesiodistally. The symphyseal facet could be rhomboid, occupying anterodorsal half of the symphyseal part (PIN 3101/642; Fig. 27b), or semilunar, occupying all of this space (PIN 3101/640; Fig. 28b). There are tiny symphyseal foramina within the symphyseal facet, closer to its posterior margin. The alveolus for the lower incisor is high and narrow mediolaterally. It occupies all the anterior end of the mandibular body. The height of the mandibular body is gradually increasing posteriorly. The ventral border of the mandibular body has a slight concavity in the middle. The dorsal border of the mandibular body is concave between the alveoli for lower incisor and p4 and deeply excavated by the alveoli for p4. The highest point of the mandibular body is at the bony bar separating the



**Fig. 27.** *Arginbaatar dmitrievae* Trofimov, 1980. Khovoor locality, Mongolia; Lower Cretaceous. Specimen PIN, no. 3101/642, right dentary fragment with alveoli for lower incisor, p2–4, and m1–2, in occlusal (a), lingual (b), and labial (c) views. Abbreviations: maf, mandibular foramen; mef, mental foramen. Scale bar, 1 mm.

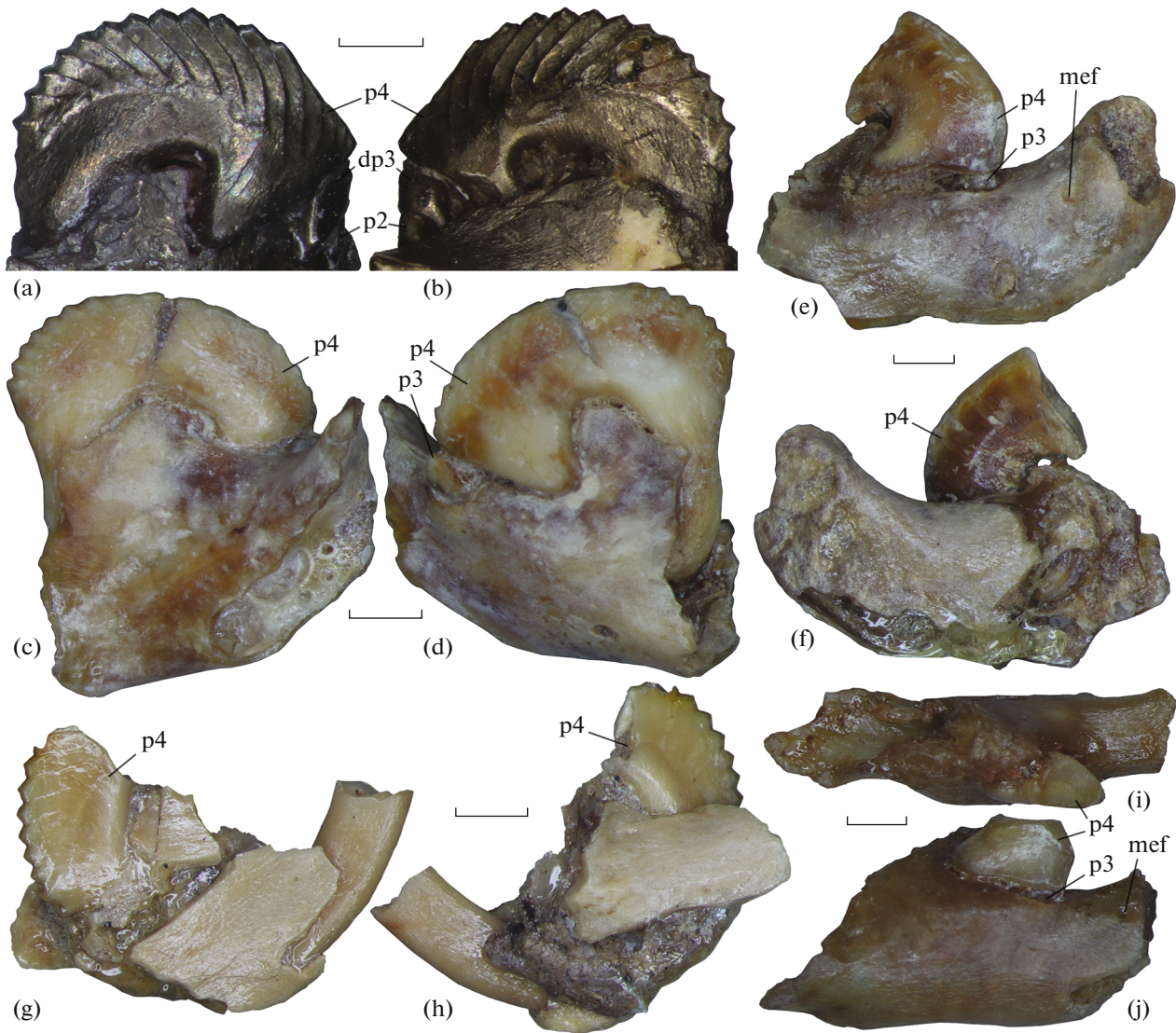
mesial and distal alveoli of m1. In PIN 3101/642, the alveoli for single-rooted p2 and double-rooted p3 are still recognizable but started to plug with the bone. On dorsal side, there is a distinct longitudinal ridge between the alveoli for lower incisor and p2. The alveolus for p2 is set lingual to the line of other cheek teeth alveoli. The pair of alveoli of p4 is the largest among cheek teeth alveoli. It is similar in length with alveoli of m1–2 together. The alveolus for the mesial root of p4 is compressed mesiodistally, while that of the distal root—labiolingually. The space between p4 alveoli is similar in length to the mesial alveolus. The mesial alveolus of p4 is well exposed in labial view of the dentary. The masseteric fossa is shallow, with pointed anterior end reaching the mesial alveolus of p4. There is a distinct ridge extending between the anterior end of the masseteric fossa and dorsal border of the dentary at p3 alveolus. Between this ridge, the masseteric fossa, and alveolar border there is a flat rugose area. A small mental foramen is placed in the diastema region close to the lower incisor alveolus (Figs. 27c, 28c, 29e, 29j). The anterior margin of the coronoid process is placed at the mesial alveolus of m1. There is a large space with depressed bottom between the coronoid process and alveoli of m1–2. The coronoid process is set laterally to the mandibular body, with a consider-



**Fig. 28.** *Arginbaatar dmitrievae* Trofimov, 1980. Khovoor locality, Mongolia; Lower Cretaceous. Specimen PIN, no. 3101/640, left dentary fragment with alveolus of lower incisor and erupting p3, in occlusal (a), lingual (b), and labial (c) views. Abbreviation: mef, mental foramen. Scale bar, 1 mm.

able distance between it and the medial side of the mandibular body. The pterygoid fossa is poorly delimited dorsally, but ventrally it extends on a prominent pterygoid shelf. The mandibular foramen cleft-like, high dorsoventrally and facing posteriorly, almost not visible in medial view (Fig. 27b).

According to Kielan-Jaworowska et al. (1987), the lower incisor in a dentary fragment associated with the holotype dentary (a right dentary fragment PIN 3101/49), comes from a left dentary. However, these authors confused mesiodistal orientation of this incisor. It is actually a right incisor with the mesial part covered by the smooth enamel and the distal “root” section exposed dentine sculptured with fine striae. Most likely, it belongs to the holotype specimen. The posterior part of the lower incisor is preserved in dentary fragments PIN 3101/52 (Kielan-Jaworowska et al., 1987: text-fig. 4P; pl. 18, fig. 4) (Figs. 29g, 29h) and PIN 3101/644. As it is evident from PIN 3101/52 and lower incisor alveolus in PIN 3101/56 (Kielan-



**Fig. 29.** *Arginbaatar dmitrievae* Trofimov, 1980. Khovoor locality, Mongolia; Lower Cretaceous. Dentary fragments: (a, b) specimen PIN, no. 3101/51, right dentary fragment with p2, dp3, and p4, in labial (a) and lingual (b) views; (c, d) specimen PIN, no. 3101/56, left dentary fragment with p4, erupting p3, and alveolus of lower incisor, in lingual (c) and labial (d) views; (e, f) specimen PIN, no. 3101/58, right dentary fragment with p4 and erupting p3, in labial (e) and lingual (f) views; (g, h) specimen PIN, no. 3101/52, left dentary fragment with lower incisor and incomplete p4, in lingual (g) and labial (h) views; (i, j) specimen PIN, no. 3101/638, right dentary fragment with incomplete p4 and erupting p3, in occlusal (i) and labial (j) views. Abbreviation: mef, mental foramen. Scale bars, 1 mm.

Jaworowska et al., 1987: pl. 15, fig. 2b), the lower incisor is relatively short, extending posteriorly to the space between the roots of p4. The lower incisor has oval cross-section, with the dorsoventral diameter about twice greater than the labiolingual diameter. Thin enamel sculptured by fine longitudinal striae completely covers the lower incisor. A little worn anterior end of lower incisor can be seen in PIN 3101/643 (Fig. 30). It gently tapers towards the anterior end. On the lingual side there is a flattened area bordered ventrally by a faint ridge. The dorsal margin of cross section is flat.

The lower premolars undergone tremendous ontogenetic change, as was found previously by Kielan-Jaworowska et al. (1987). The main ontogenetic stages were described by Kielan-Jaworowska et al. (1987). With the new materials, we provide here a more detailed description of the ontogenetic change of lower premolars in *A. dmitrievae*. Four main ontogenetic stages can be recognized based on the available material (Fig. 31).

**Stage 1.** The p4 is little worn, with all serrations intact. Its distal part is partially hidden in the alveolus. The p4 is in vertical position (not rotated), with the

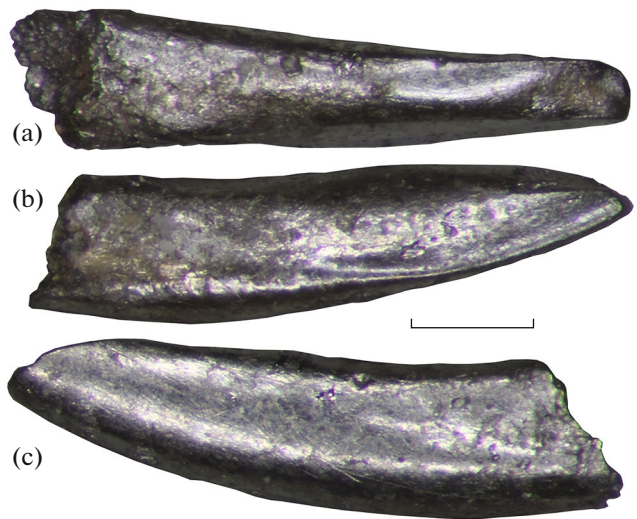
mesial crown margin (including the mesial triangular lobe) oriented at an angle of  $\sim 45^\circ$  to the horizontal axis of the dentary. The p2 and dp3 are present in front of p4. This stage is represented by the holotype (PIN 3101/49; Fig. 31a), GI PST 10-11 (Kielan-Jaworowska et al., 1987: pl. 14, fig. 2) (Fig. 31b), and possibly by PIN 3101/52 (Figs. 29g, 29h). The latter specimen has distal part of the p4 crown hidden in the alveolus, but also has exposed dentine in distal part. Therefore, it is intermediate between this and the next ontogenetic stages. The holotype is not very young ontogenetically because it has a considerably worn m1.

**Stage 2.** The distal part of p4 is completely out of the alveolus with the dentine exposed above the alveolar border in labial view. The first (anteriormost) three to four serrations are eliminated by wear and there is a narrow elliptical wear facet on this place. The dp3 and p2 are still in place. Two specimens are attributed to this stage: PIN 3101/51 (Figs. 29a, 29b, 31c) and GI PST 10-40 (Kielan-Jaworowska et al., 1987: pl. 17, fig. 2) (Fig. 31d).

**Stage 3.** The dp3 and p2 are gone, the p2 alveolus is plugged with bone. The p3 is partially erupted. The wear facet on p4 is still in the mesial part, with individual serrations still recognizable (GI PST 10-12; Fig. 31f; Kielan-Jaworowska et al., 1987: pl. 15, fig. 1), or in the middle of the tooth crown, with most of the serrations gone by the wear (PIN 3101/56; Figs. 29c, 29d, 31e; Kielan-Jaworowska et al., 1987: pl. 15, fig. 2). Also three isolated p4 represent this ontogenetic stage, with the mesial serrations removed by wear and remaining eight (PIN 3101/73a; Figs. 32e, 32f; Kielan-Jaworowska et al., 1987: pl. 16, fig. 3), six (PIN 3101/641; Figs. 33c, 33d), or four distal serrations (PIN 3101/73h; Figs. 33a, 33b).

**Stage 4.** The p4 is fully rotated and heavily worn, with all individual serrations eliminated by wear. The mesial margin of p4 is horizontal ( $0^\circ$  to the horizontal axis of dentary,  $90^\circ$  rotated from the initial position) and overhang partially erupted and impacted p3. PIN 3101/58 (Figs. 29e, 29f, 31g) (Kielan-Jaworowska et al., 1987: pl. 20, fig. 5) represents this stage. A dentary fragment PIN 3101/638 (Figs. 29i, 29j, 31h) with not fully erupted p3 and partial p4 is an abnormal variant of this ontogenetic stage. Here the distal part of p4 was broken and there is an additional polished area (wear facet?) formed on the preserved distal side of the tooth, which is positioned horizontally.

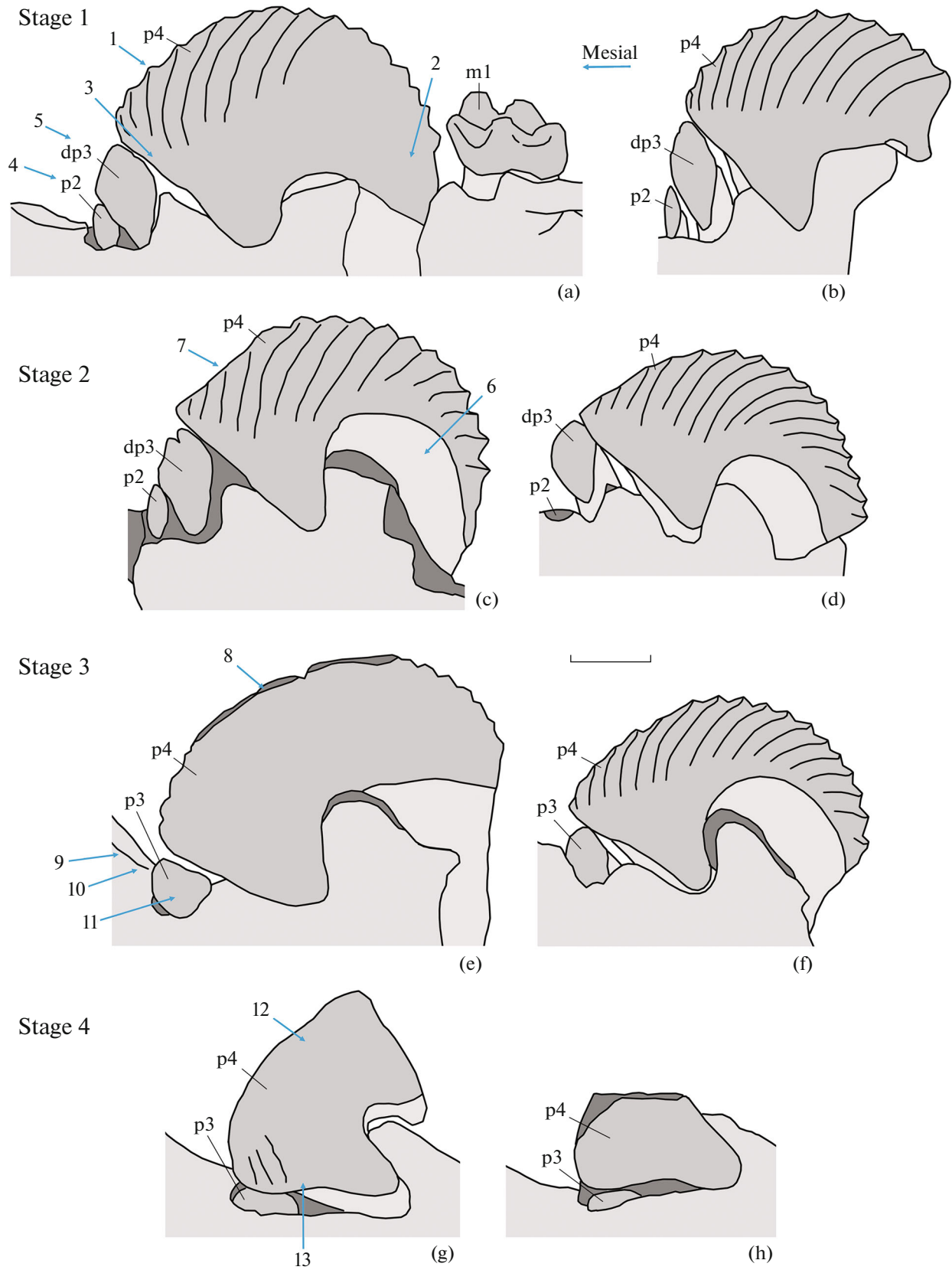
The p2 is a small, peg-like, and single-rooted tooth, known only in three specimens: holotype, PIN 3101/51 (Figs. 29a, 29b), and GI PST 10-11. In GI PST 10-40 there is an alveolus for p2. The dp3 is known from the four specimens mentioned above where it is placed together with p2 and p4. The crown is rhomboid in labial and lingual view, overhanging mesially over p2 and overhang distally by p4. The tooth is likely not functional because it is placed almost completely beneath p4. The crown is bulbous



**Fig. 30.** *Arginbaatar dmitrievae* Trofimov, 1980. Khovoor locality, Mongolia; Lower Cretaceous. Specimen PIN, no. 3101/643, isolated left lower incisor, in dorsal (a), lingual (b), and labial (c) views. Scale bar, 0.5 mm.

at the base and tapers towards a narrow blade-like mesial margin. The crown could be smooth, without serrations (holotype), with two serrations but without ridges (GI PST 10-11 and GI PST 10-40), or with two serrations associated with two short labial ridges (PIN 3101/51; Figs. 29a, 29b). The tooth is single-rooted (holotype and GI PST 10-11), or double-rooted (PIN 3101/51 and GI PST 10-40). The p3 is known from several dentary fragments of the third ontogenetic stage, where it is mostly hidden in the alveolus and fully overhang by rotated p4. Such a p3 is preserved in a dentary fragment PIN 3101/640, missing p4 (Fig. 28). The p3 is double-rooted, with a robust straight mesial root and very short, minute distal root. The crown is likely rhomboid, much higher on the labial side compared with the lingual side (an analogue of the mesial triangular lobe of p4). There are two closely spaced serrations. The mesial serration is associated with a short faint labial ridge.

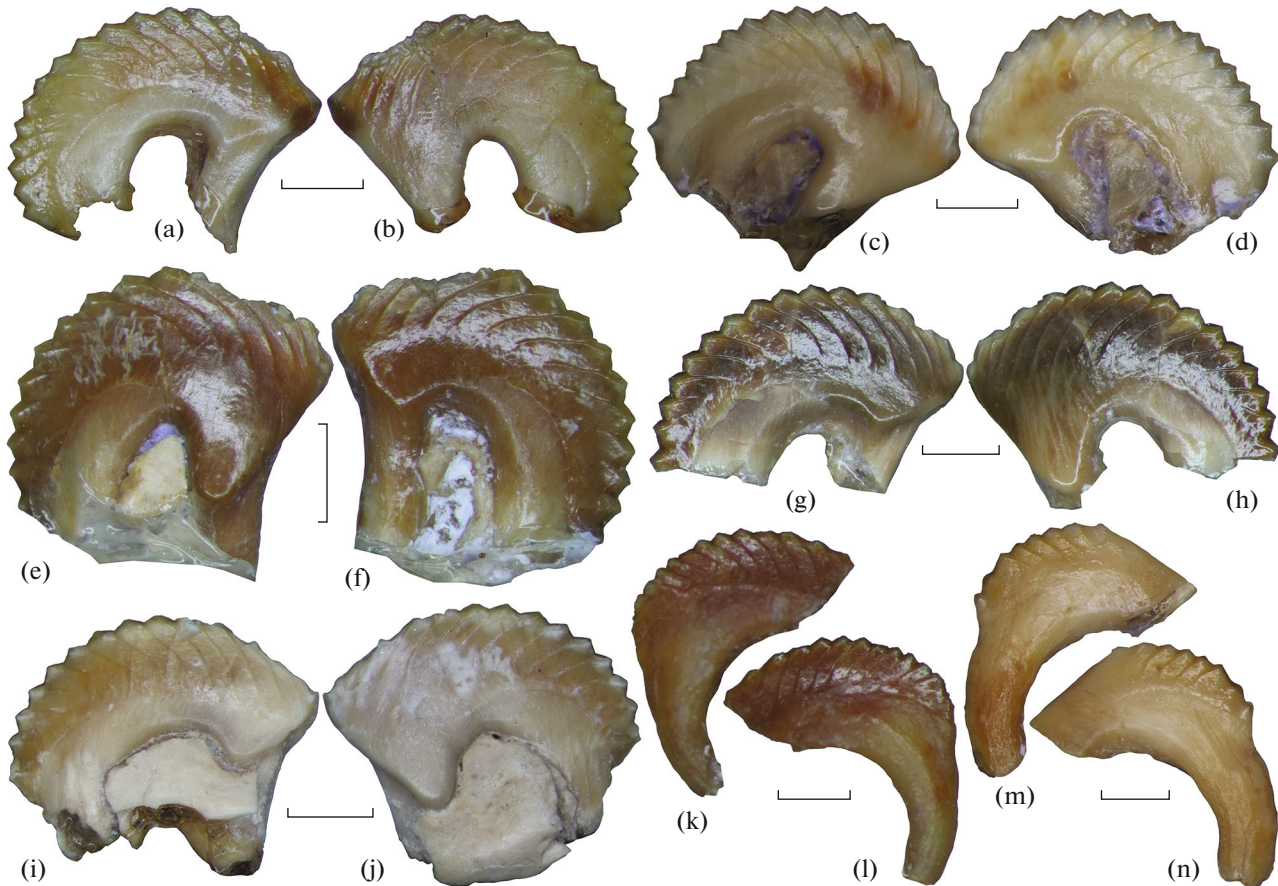
The p4 shows enormous variation in size and shape, as was documented earlier by Kielan-Jaworowska et al. (1987) (Fig. 32). The crown is arcuate, with a long shearing blade. In a circle with the same curvature, the shearing edge would occupy about a half of the circle length. The crown is high mesially, with a voluminous mesial triangular lobe extending more than half the length of the mesial root on labial side. On the lingual side also there is a mesial triangular lobe, but much smaller. The crown height steadily decreases distally, exposing large amount of dentine above the alveolar border on both labial and lingual sides. There are 11–18 serrations, slightly increasing in size distally. The first serration is not associated with the ridges on both sides. The mesial ridges have similar length on labial and distal sides, but distal ridges are



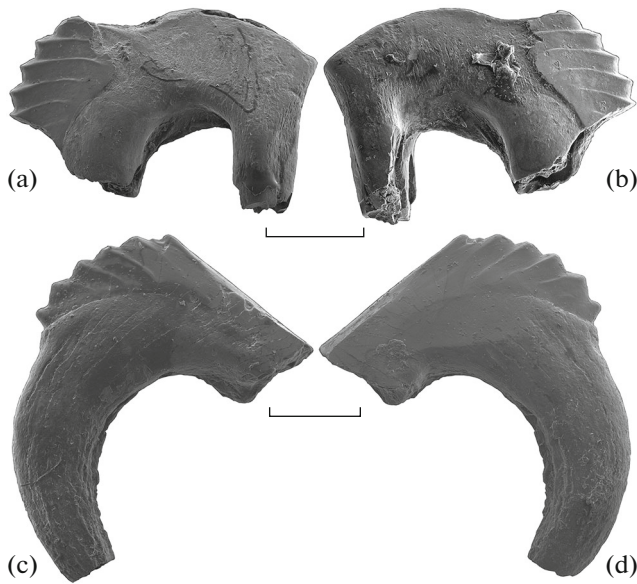
**Fig. 31.** *Arginbaatar dmitrievae* Trofimov, 1980. Khovoor locality, Mongolia; Lower Cretaceous. Dentary fragments showing ontogenetic transformations: (a) holotype PIN, no. 3101/49, right dentary fragment with p2, dp3, p4, and m1, reversed; (b) specimen GI PST 10-11, right dentary fragment with p2, dp3, and p4, reversed; (c) specimen PIN, no. 3101/51, right dentary fragment with p2, dp3, and p4, reversed; (d) specimen GI PST 10-40, right dentary fragment with dp3 and p4, reversed; (e) specimen PIN, no. 3101/56, left dentary fragment with p3-4; (f) specimen GI PST 10-12, left dentary fragment with p3-4; (g) specimen PIN, no. 3101/58, right dentary fragment with p3-4, reversed; (h) specimen PIN, no. 3101/638, right dentary fragment with p3-4, reversed. Ontogenetic markers: 1, p4 little worn, all serrations intact; 2, distal part of p4 crown hidden in the alveolus; 3, mesial margin of p4 crown at  $\sim 45^\circ$  to the horizontal axis of dentary; 4, p2 present; 5, dp3 present; 6, distal part of p4 with exposed dentine; 7, mesial part of p4 crown worn, with 3-4 serrations gone by wear; 8, mesial and central part of p4 crown worn; 9, p2 lost, its alveolus plugged by bone; 10, dp3 shed; 11, p3 partially erupted; 12, all serrations on p4 gone by wear; 13, mesial margin of p4 crown parallel to the horizontal axis of dentary. Figures (b, d, f) are modified from Kielan-Jaworowska et al. (1987: text-figs. 4A, 4C, 4E). Scale bar, 1 mm.

shorter on labial side. In mesial half of the crown, the ridges cover about one third of the crown height. Distally they come close to the crown-root junction. The longest ridges are associated with the serrations 5-8. The mesial root is mesiodistally compressed and has a longitudinal furrow on its distal side. The mesial root is straight or curved slightly mesially. The distal root is labiolingually compressed. Both roots are open.

The holotype dentary (PIN 3101/49) preserves a worn m1 in situ. There are eight isolated m1, four described by Kielan-Jaworowska et al. (1987) and four new specimens (Figs. 34a-34o). There are three labial and two lingual cusps (the cusp formula is 3:2). The m1 crown in occlusal view is intermediate in shape between oval and trapezium, with the lingual side shorter than the labial side. The distal side is convex



**Fig. 32.** *Arginbaatar dmitrievae* Trofimov, 1980. Khovoor locality, Mongolia; Lower Cretaceous. Isolated p4: (a, b) specimen PIN, no. 3101/64, left p4, in lingual (a) and labial (b) views; (c, d) specimen PIN, no. 3101/71b, right p4, in labial (c) and lingual (d) views; (e, f) specimen PIN, no. 3101/71a, right p4, in labial (e) and lingual (f) views; (g, h) specimen PIN, no. 3101/71c, left p4, in lingual (g) and labial (h) views; (i, j) specimen PIN, no. 3101/73b, left p4, in lingual (i) and labial (j) views; (k, l) specimen PIN, no. 3101/646, p4 distal fragment, in two side views; (m, n) specimen PIN, no. 3101/73a, p4 distal fragment, in two side views. Scale bars, 1 mm.



**Fig. 33.** *Arginbaatar dmitrievae* Trofimov, 1980. Khovoor locality, Mongolia; Lower Cretaceous. SEM images of isolated p4: (a, b) specimen PIN, no. 3101/73h, right p4, in labial (a) and lingual (b) views; (c, d) specimen PIN, no. 3101/641, p4 distal fragment, in two side views. Scale bars, 1 mm.

while the mesial side could be convex or concave. The labial and lingual cusps are of similar height but the lingual cusps are placed higher on the crown. Consequently, the enamel is deeper from the labial side compared with the lingual side. The cusp b3 is slightly larger than the cusp b2. The cusp b1 is distinctly smaller than the two other labial cusps. Both lingual cusps have similar height but the cusp l2 is slightly shorter mesiodistally than the cusp l1. The labial cusps are pyramidal with similarly sloping labial and lingual sides. The lingual cusps are more conical, with flattened labial side and convex lingual side. The cusps in the each row are separated by narrow slightly oblique valleys, which usually have the external end more mesial than the internal end. The transverse valley between the cusps b2 and b3 is closed labially by a low ridge. A similarly narrow longitudinal valley separates the labial and lingual cusp rows. The mesial end of this ridge is somewhat deflected lingually because the cusp b1 is slightly displaced lingually from the other labial cusps. PIN 3101/605 differs from other specimens in having cusp b1 in line with other labial cusps, cusp b3 more cone-like and inclining distally, and the longitudinal valley between the cusp rows closed by a short ridge mesially (Figs. 34g–34i). The m1 has two widely separated roots of similar size, which are somewhat compressed mesiodistally.

The m2 was previously unknown for *A. dmitrievae*. Two isolated specimens, which matches closely the m2 alveolus in the holotype dentary (PIN 3101/49), represents m2 in the new material (Figs. 34p–34r). The

roots of m2 are coalesced and deflecting distally, which corresponds to the lack of the interalveolar bony bar in the alveolus of m2 in PIN 3101/49. PIN 3101/633 is slightly larger and unworn compared with PIN 3101/609. The m2 is distinctly shorter than m1. The crown is oval to subrectangular in occlusal view, with convex distal margin and straighter mesial margin. There are three labial cusps and two lingual cusps (the cusp formula is 3:2). The lingual cusps are placed somewhat more mesial compared with the labial cusps. The lingual cusps are higher than the labial cusps. The labial cusps are labiolingually compressed and have similar height. A wide transverse groove separates the distal labial cusp. In PIN 3101/633, the cusps b1 and b2 have distinct apices and are subdivided by a wide lingual groove (Figs. 34p, 34q). In worn PIN 3101/609, the cusps b1 and b2 are united and the lingual groove is nearly absent. The lingual cusps are pyramidal. The cusp l1 is somewhat larger and higher. It is hook-like in lingual view, with convex mesial and concave distal sides. A wide transverse groove separating the lingual cusps is in line with the groove separating the labial cusps b2 and b3. The longitudinal valley separating the cusp rows is very wide and open mesially. Distally a transverse ridge connecting the cusps b3 and l2 closes the longitudinal valley.

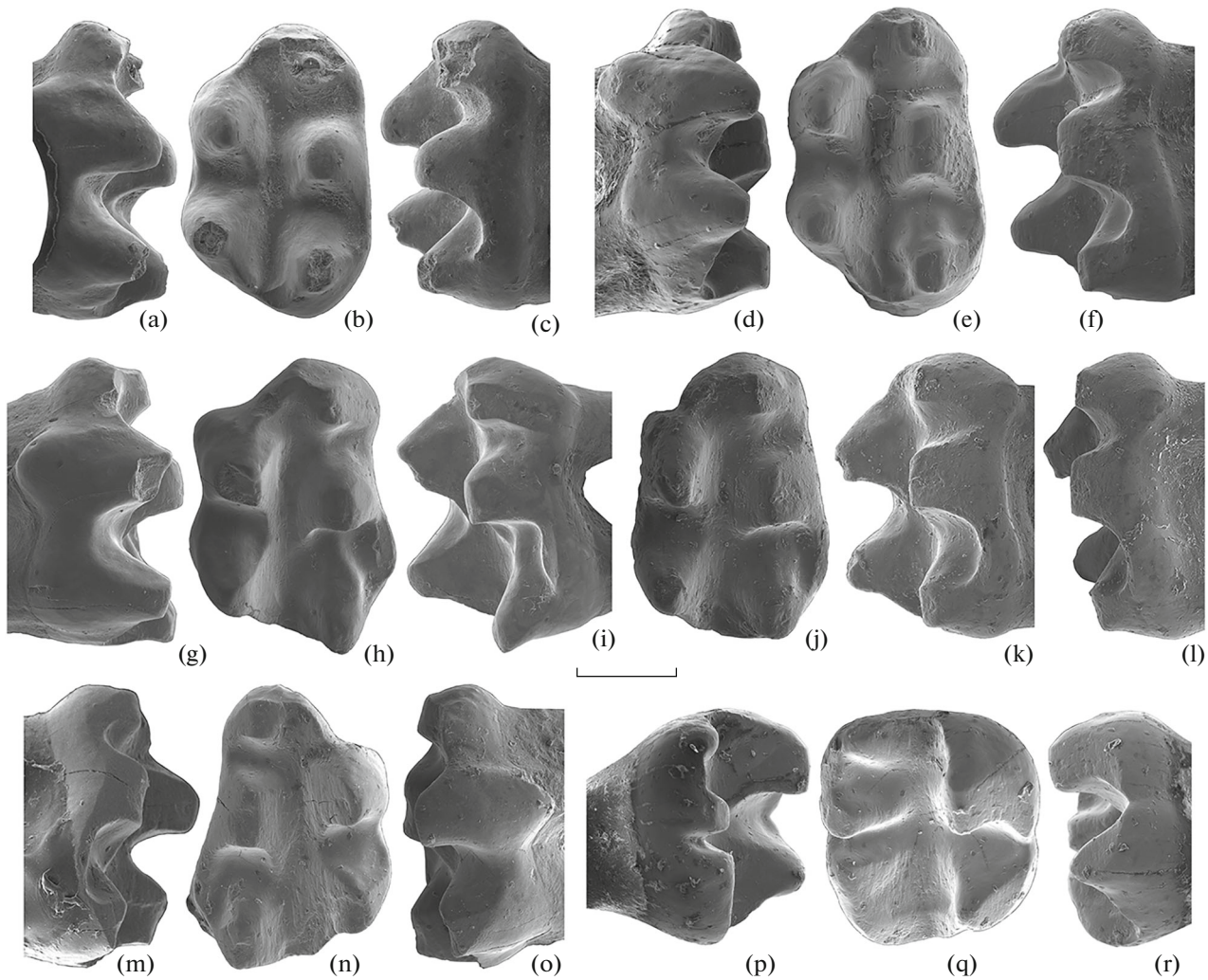
**Measurements.** See Tables 6–8.

**Remarks.** Kielan-Jaworowska et al. (1987, p. 27) consider the upper canine to be present in *A. dmitrievae* based on PIN 3101/68, where “the small broken part of the premaxilla is preserved in front of the maxilla and in the area of the suture a part of the alveolus (possibly for a canine) has been preserved.” We cannot confirm presence of a premaxilla or any alveolus in front of P1 in this specimen. The mesial margin of maxilla in PIN 3101/68 is intact and represents the suture with premaxilla. The upper canine in multituberculates, when present, is within the maxilla, not in the premaxilla or on the premaxillary-maxillary suture (Kielan-Jaworowska et al., 2004). Absence of an alveolus in the maxilla in front of P1 in PIN 3101/68 clearly demonstrates that the upper canine was absent in *A. dmitrievae*.

We identified several specimens of dp5 for *A. dmitrievae*, but no P5 are known for this taxon. It is evident that replacement in the fifth upper premolar locus in *A. dmitrievae* was delayed, similar to a condition in a third premolar locus. The permanent P5 may be absent from the sample due to the preservation artifact, or replacement did not occur in this locus. It should be noted that antagonist of P5 in the lower jaw, the p4, is actually a non-replacing dp4 (Simmons, 1988).

Kielan-Jaworowska et al. (1987) did not recognize replacement in the third lower premolar locus and thought that p4 was rotated over worn p3. This interpretation cannot explain why p3, fully erupted on the stage 2, becomes mostly hidden in the alveolus on the





**Fig. 34.** *Arginbaatar dmitrievae* Trofimov, 1980. Khovoor locality, Mongolia; Lower Cretaceous. SEM images of isolated lower molars: (a–c) specimen PIN, no. 3101/50c, right m1, in lingual (a), occlusal (b), and labial (c) views; (d–f) specimen PIN, no. 3101/607, right m1, in lingual (d), occlusal (e), and labial (f) views; (g–i) specimen PIN, no. 3101/605, right m1, in lingual (g), occlusal (h), and occlusolabial (i) views; (j–l) specimen PIN, no. 3101/608, right m1, in occlusal (j), occlusolabial (k), and labial (l) views; (m–o) specimen PIN, no. 3101/50d, left m1, in labial (m), occlusal (n), and lingual (o) views; (p–r) specimen PIN, no. 3101/633, left m2, in occlusolabial (p), occlusal (q), and lingual (r) views. Scale bar, 0.5 mm.

stage 3. In addition, p3 could not be worn because it is a nonfunctional tooth beneath the p4 crown. The only explanation of this phenomenon is that the tooth present on the stage 2 is dp3, which becomes lost and the tooth on the stage 3 is erupting p3. Its full eruption is impossible because of overhanging rotated p4. This delayed replacement of dp3 is in line with the delayed replacement of dP3 reconstructed here for *A. dmitrievae*.

Kielan-Jaworowska et al. (1987) distinguished *Monobaatar mimicus* from the similarly sized *Arginbaatar dmitrievae* by a single infraorbital foramen and a wider P4 with ornamentation of fine striae. However, this ornamentation is present only in a referred specimen, an isolated P4 (GI PST 10-26) (Kielan-Jaworowska et al., 1987: pl. 9, fig. 2). On the holotype

of *M. mimicus* (PIN 3101/65), the P4 is heavily worn and lack any ornamentation. Kielan-Jaworowska et al. (1987) cited two specimens with a single infraorbital foramen. Nevertheless, in the second maxillary fragment, referred to *M. mimicus*, the infraorbital foramen is incomplete and could be subdivided in a more posterior part which is not preserved. Thus, there is only one specimen in the sample with a single infraorbital foramen (PIN 3101/65, holotype of *M. mimicus*).

Kielan-Jaworowska et al. (1987, p. 20) described fine striations on the cusps and cingulum surrounding the labial wing on the M2 attributed to *M. mimicus* (PIN 3101/61). We cannot confirm this. All enamel in this specimen is smooth (Fig. 26d).

**Table 6.** Measurements (in mm) of anterior upper premolars in *Arginbaatar dmitrievae* (L, crown length; W, crown width)

Specimen	LP1	WP1	LP2	WP2	LdP3	WdP3	LP3	WP3
PIN 3101/68	0.93	0.93	0.92	0.92	0.91	0.84		
PIN 3101/54	0.84	0.93	0.79	0.92	0.91	0.85		
PIN 3101/74	0.96	0.93	0.88	0.91				
PIN 3101/622	0.91	0.79						
PIN 3101/624	0.86	0.84						
PIN 3101/670	0.88	0.87						
PIN 3101/673	0.89	0.86						
PIN 3101/674	0.93	0.79						
PIN 3101/65			0.81	0.92			0.72	0.82
PIN 3101/625			0.81	0.84				
PIN 3101/672			0.90	1.00				
PIN 3101/626					1.00	0.90		
PIN 3101/603					0.69	0.85		
PIN 3101/50a							0.88	1.01
PIN 3101/69							0.90	0.84
PIN 3101/72							0.95	0.86
PIN 3101/620							0.88	0.78
PIN 3101/621							0.88	0.71
PIN 3101/623							0.73	0.77
PIN 3101/671							0.89	0.85
PIN 3101/675							0.82	0.80
Mean	0.90	0.87	0.85	0.92	0.88	0.86	0.85	0.83
Standard error	0.01	0.02	0.02	0.02	0.07	0.01	0.03	0.03

**Table 7.** Measurements (in mm) of posterior upper premolars and upper molars in *Arginbaatar dmitrievae* (L, crown length; W, crown width)

Specimen	LP4	WP4	LdP5	WdP5	LM1	WM1	LM2	WM2
PIN 3101/65	1.53	1.01						
PIN 3101/68	1.44	0.91						
PIN 3101/603	1.46	0.93						
PIN 3101/612	1.55	0.96						
PIN 3101/613	1.32	0.89						
PIN 3101/615	1.48	0.89						
PIN 3101/616	1.47	0.92						
PIN 3101/617	1.38	0.91						
PIN 3101/618	1.33	1.00						
PIN 3101/619	1.36	0.78						
GI PST 10-15*	1.20	0.80						
GI PST 10-26*	1.40	0.86						
GI PST 10-27*	1.60	1.16						
GI PST 10-36*	1.20	0.85						
GI PST 10-44a*	1.20	0.75						
PIN 3101/665			1.52	0.83				
PIN 3101/666			1.44	0.79				
PIN 3101/667			1.55	0.76				
PIN 3101/668			1.65	0.78				
PIN 3101/55					1.48	0.96		
PIN 3101/649					1.65	1.08		
PIN 3101/50a							1.58	1.25
PIN 3101/61							1.28	1.25
GI PST 10-20*							1.30	1.00
Mean	1.40	0.91	1.54	0.79	1.57	1.02	1.39	1.17
Standard error	0.03	0.03	0.04	0.02	0.09	0.06	0.10	0.08

\* Measurements from Kielan-Jaworowska et al. (1987).

**Table 8.** Measurements (in mm) of lower premolars and molars in *Arginbaatar dmitrievae* (L, crown length; W, crown width)

Specimen	Lp2	Wp2	Ldp3	Wdp3	Lp4	Wp4	Lm1	Wm1	Lm2	Wm2
PIN 3101/49*	0.32	0.27	0.66	0.56	4.50	1.56	1.50	1.01		
PIN 3101/51	0.43	0.39	0.67	0.74	4.18	1.43				
PIN 3101/56			0.49	0.51	4.56	1.46				
PIN 3101/64					4.26	1.46				
PIN 3101/71a					3.78	1.38				
PIN 3101/71b					4.10	1.19				
PIN 3101/71c					4.47	1.40				
PIN 3101/73b					4.00	1.50				
PIN 3101/50c							1.53	1.05		
PIN 3101/50d							1.48	0.96		
PIN 3101/605							1.56	1.07		
PIN 3101/606							1.55	1.04		
PIN 3101/607							1.55	1.10		
PIN 3101/608							1.51	1.00		
GI PST 10-42**							1.45	0.90		
GI PST 10-44b**							1.50	0.90		
PIN 3101/609									1.26	1.09
PIN 3101/633									1.30	1.19
Mean	0.38	0.33	0.61	0.60	4.23	1.42	1.51	1.00	1.28	1.14
Standard error	0.06	0.06	0.06	0.07	0.10	0.04	0.01	0.02	0.02	0.05

\* Holotype.

\*\* Measurements after Kielan-Jaworowska et al. (1987).

## VARIATION IN KHOVOOR MULTITUBERCULATES

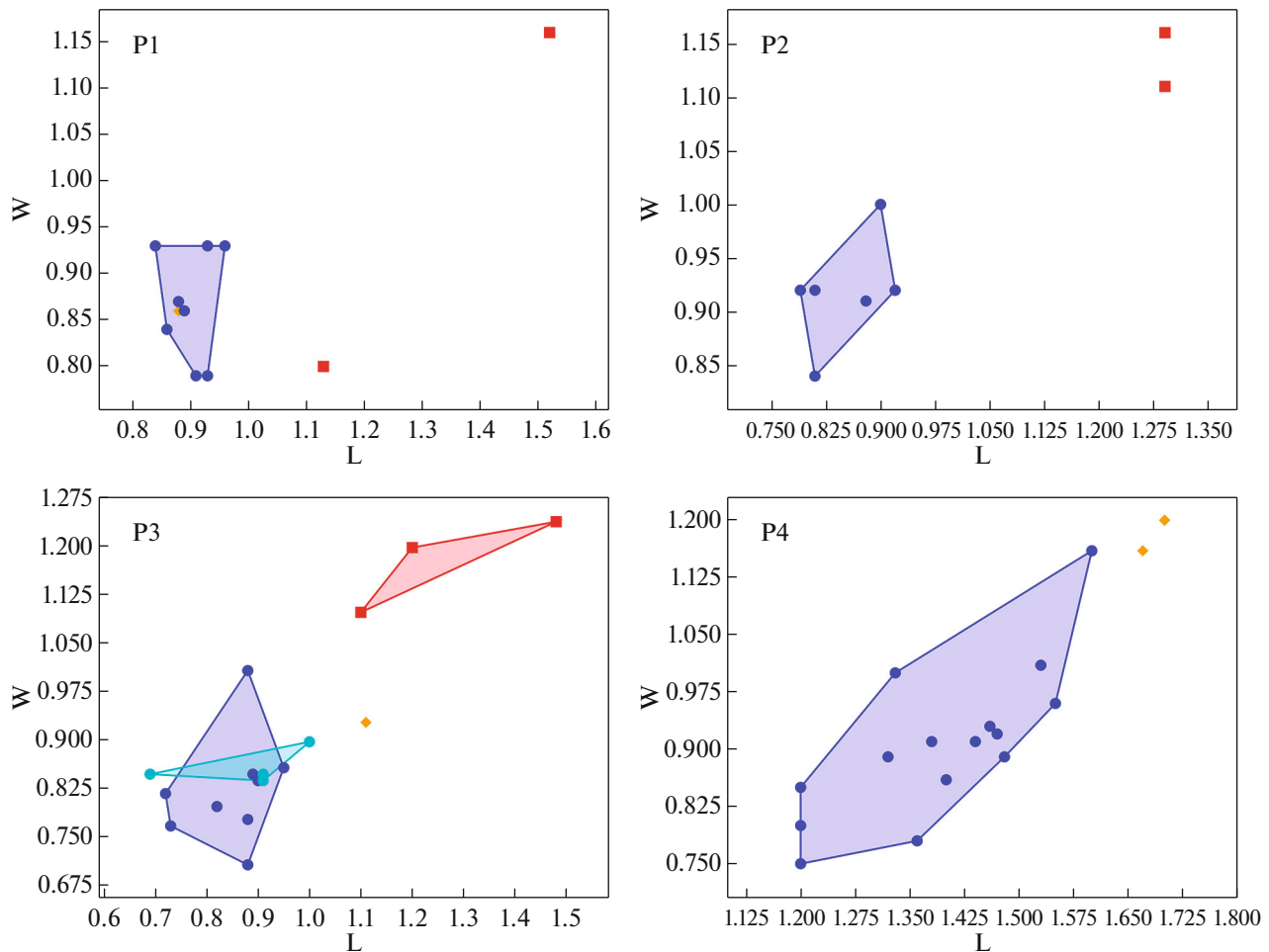
### *Size Variation*

The small size of the most samples prevents use of statistical methods for exploring the variation and estimate reliability of samples distinction. However, most samples are clearly separate in two-dimensional plots (Figs. 35–37). The distinction between the taxa in the size of P1 is not evident as the single known specimen of *Nokerbaatar* falls within the limits of variation of *Arginbaatar* and one of the two specimens of *Eobaatar* has the width identical to that of the smallest specimens of *Arginbaatar* (Fig. 35). Both P2 and P3 of *Eobaatar* and *Arginbaatar* do not overlap in size, while the single known P3 of *Nokerbaatar* differs from the teeth of *Arginbaatar* only by greater length and from *Eobaatar*—by smaller width (Fig. 35). The P5 and upper molars (M1–2) of all three taxa can be clearly differentiated by size (Fig. 36). *Arginbaatar* has unusually large p4 with most specimens exceeding that tooth in *Eobaatar* by size (Fig. 37). The lower molars of *Arginbaatar* and *Eobaatar* also well separated by size (Fig. 37).

### *Morphological Variation*

**Infraorbital foramina.** In *Arginbaatar*, there is a variation in the number of infraorbital foramina, with the two opening present in the majority of specimens. Kielan-Jaworowska et al. (1987) referred the multituberculate specimens with one infraorbital foramen from Khovoor to a distinct taxon, *Monobaatar mimicus*. However, these specimens, as discussed in this paper, do not differ in other respects from *A. dmitrievae*. Thus, we consider difference between the specimens in the number of infraorbital foramina as the individual variation. This variation is expectable for a taxon transitional between the plagiulacidans and cimolodontans. The number of infraorbital foramina varies in the djadochtheroid *Catopsbaatar catopsaloides* from the Late Cretaceous of Mongolia (Kielan-Jaworowska et al., 2005) and the taeniolabidoid *Lambdopsalis bulla* from the Paleocene of China (Miao, 1988).

**Additional cusp on P2–3.** A small additional (fourth) cusp is present on one of two known specimens of P2 in *Eobaatar*. The second specimen, lacking the additional cusp, has an unusually small mesiolingual cusp (PIN 3101/686; Fig. 5). This could be an abnormal specimen and the additional cusp could be



**Fig. 35.** Scatter plot diagrams of length (L) versus width (W) for upper premolars (P1, P2, P3, and P4) in *Eobaatar magnus* (red squares), *Nokerbaatar minor* (orange diamonds), and *Arginbaatar dmitrievae* (blue dots, aqua dots for dP3).

consistently present on P2 of *Eobaatar*. All three known specimens of P3 of *Eobaatar* have the additional cusp. In *Nokerbaatar* P2 is unknown and the single known P3 (or dP3) lacks the additional cusp. Among the four specimens of dP3 and eleven specimens of P3 of *Arginbaatar*, a small additional cusp is present only in one specimen.

**Mesiolingual cusp on P2.** Among two isolated P2 referred to *Eobaatar*, one has normally developed lingual cusps, with the mesiolingual cusp similar in size and somewhat higher than the distolingual cusp (PIN 3101/685; Figs. 4e–4g). The other specimen has abnormally small mesiolingual cusp, which is much smaller than the distolingual cusp (PIN 3101/686; Fig. 5). The latter specimen also lacks an additional small cusp present in PIN 3101/685. There are no other reported specimens of anterior upper premolars of eobaatarids showing such reduced mesiolingual cusp.

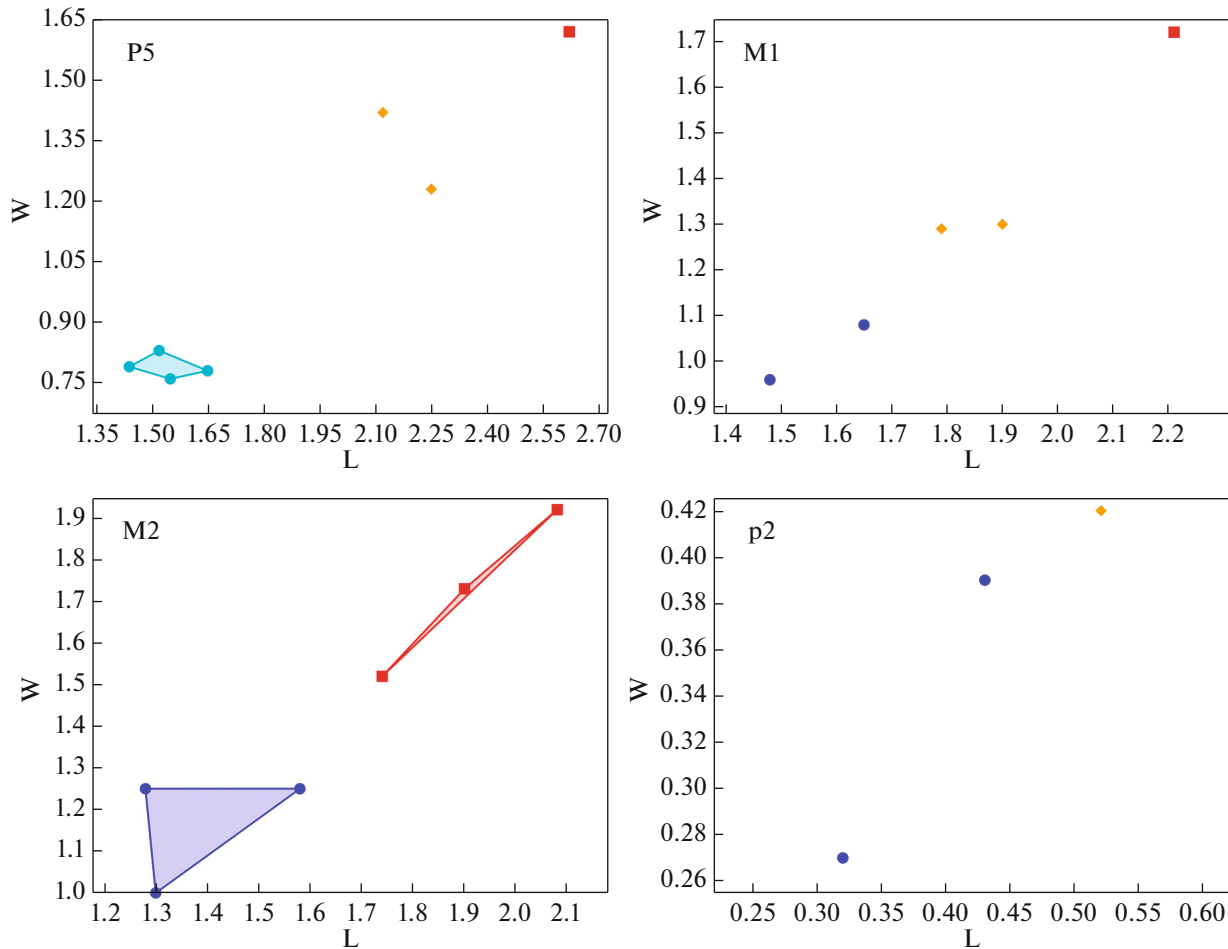
**Lingual cusps of M2.** Among three specimens of M2 of *Eobaatar*, two have three lingual cusps and one has four lingual cusps.

**Serrations on p3.** Among four isolated specimens of p3 referred to *Eobaatar* one specimen has four serrations and two ridges, two specimens have two ridges but no serrations, and one specimen has no serrations or ridges. It is unclear if these differences are accounted for by individual variation, crown wear, or both. The number of serrations on p3 varies from one to three in *Liaobaatar* (Kusuhashi et al., 2009).

**Serrations on p4.** As was discussed in description of *Arginbaatar*, its p4 is highly variable in size and number of serrations, which varies from 11 to 18 ( $M = 15.93 \pm 0.49$ ,  $n = 14$ ). Two known specimens of p4 of *Eobaatar* have the same number of serrations (10).

#### DIAGNOSTIC CHARACTERS OF KHOVOOR MULTITUBERCULATES

**Number of infraorbital foramina.** The number of infraorbital foramina varies in *Arginbaatar*, with most specimens having two foramina (see above). The double infraorbital foramen is present in basal mammaliaformes (Kermack et al., 1981; Lillegraven and Krusat, 1991; Crompton and Luo, 1993) and Jurassic plagiau-

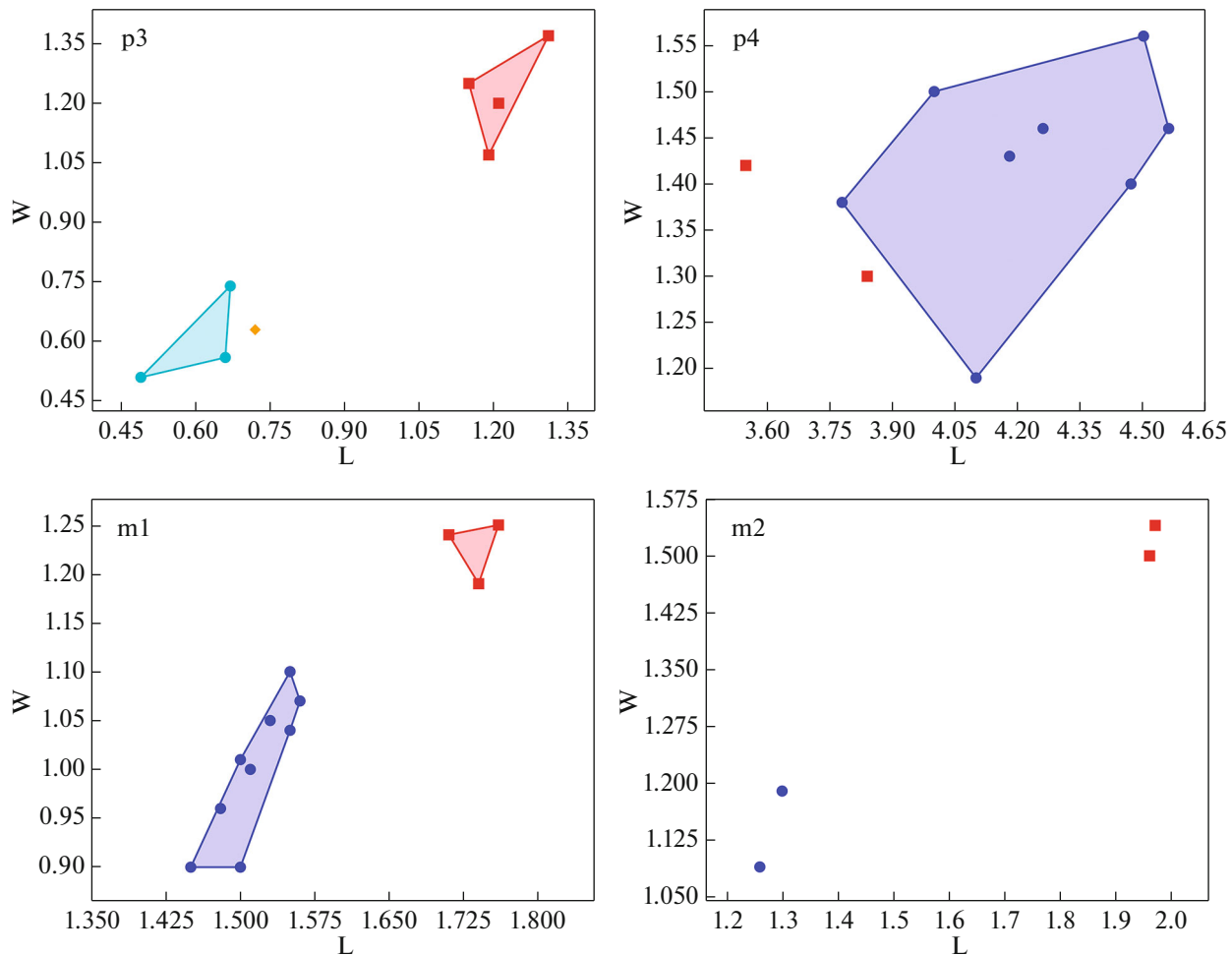


**Fig. 36.** Scatter plot diagrams of length (L) versus width (W) for upper premolar (P5), upper molars (M1 and M2), and lower premolar (p2) in *Eobaatar magnus* (red squares), *Nokerbaatar minor* (orange diamonds), and *Arginbaatar dmitrievae* (blue dots, aqua dots for dP5).

lacidan multituberculates Paulchoffatiidae, *Ctenacodon*, and *Glirodon* (Hahn, 1985; Engelmann and Callison, 1999: text-fig. 13; Engelmann, 2004). In most cimolodontans there is a single infraorbital foramen (Wible and Rougier, 2000). Among cimolodontans, the double infraorbital foramen is known in the djadochtatheroids *Mangasbaatar* and *Guibaatar* (Rougier et al., 2016; Wible et al., 2019). In some cimolodontans the number of infraorbital foramina is variable (see above). This character is poorly known for the Eobaataridae. Particularly, its state is unknown for the Khovoor eobaatarids *Eobaatar* and *Nokerbaatar*. The double infraorbital foramen is present in *Sinobaatar lingyuanensis* (Hu and Wang, 2002: pl. 1c) and ?*Liaobaatar* sp. (Kusuhashi et al., 2019: text-figs. 8a, 8c). The single infraorbital foramen is found in *Sinobaatar pani* (Mao et al., 2020: supplementary text-figs. 1C, 1F).

**Number of cusps on I2.** The upper incisors are unknown for *Eobaatar* and *Nokerbaatar*. Several isolated upper incisors with two-cusped crown are attributed here to *Arginbaatar*. Among multitubercu-

lates, plagiaulacidans except pinheirodontids have two-cusped I2 and sometimes two-cusped I3 (Kielan-Jaworowska et al., 2004). In the Pinheirodontidae I2 is multicusped (Hahn and Hahn, 1999). In the Cimolodonta there are two upper incisors (I1 lost), with I2 (first upper incisor) being single- or two-cusped (Kielan-Jaworowska and Hurum, 2001; Kielan-Jaworowska et al., 2004). Among eobaatarids, the two-cusped I2 is known for *Hakusanobaatar* (Kusuhashi, 2008: text-fig. 3c), *Sinobaatar pani* (Mao et al., 2020: text-figs. 1C, 1D), and *Jeholbaatar* (Wang et al., 2019: extended text-figs. 2f, 2g, 2l). The single cusped I2 is present in *Sinobaatar lingyuanensis* (Hu and Wang, 2002), *S. xiei*, and *S. fuxinensis* (Kusuhashi et al., 2009: text-figs. 5, 14). The two-cusped I2 was reported for a possible eobaatarid *Loxaulax* (Clemens, 1963: text-fig. 5). An isolated two-cusped I2 from the Barremian Wessex Formation of the Isle of Wight, England, may belong to *Eobaatar clemensi* (Butler and Ford, 1977: text-figs. 1D–1F; Sweetman, 2009: text-fig. 2B).



**Fig. 37.** Scatter plot diagrams of length (L) versus width (W) for lower premolars (p3 and p4) and lower molars (m1 and m2) in *Eobaatar magnus* (red squares), *Nokerbaatar minor* (orange diamonds), and *Arginbaatar dmitrievae* (blue dots, aqua dots for dp3).

**Upper canine.** The upper canine is present in the plagiulacidans Paulchoffatiidae, Pinheirodontidae, *Rugosodon*, *Glirodon*, and *Ctenacodon* (Hahn and Hahn, 2002a; Engelmann, 2004; Hahn and Hahn, 2004; Kielan-Jaworowska et al., 2004; Yuan et al., 2013). Kielan-Jaworowska et al. (1987) identified the upper canine in *Arginbaatar* based on the alveolus in a single specimen. As discussed in the description of that taxon, this specimen preserves the intact premaxillary suture and no alveolus for the canine. Thus, upper canine is absent in *Arginbaatar*. The upper canine is unknown for the Eobaataridae, although Mao et al. (2020: text-figs. 1C, 1D) identified a possible upper canine germ in *Sinobaatar pani*. Badiola et al. (2012: text-figs. 23.2, 1e2) described a tooth from the Early Cretaceous of Spain identified as a canine possible referable to the Albionbaataridae. This identification was questioned by Martin et al. (2021).

**Cusp ornamentation on P1–3.** In *Eobaatar* and *Nokerbaatar* the anterior upper premolars (P1–3) are ornamented by pronounced radiating ridges, while in

*Arginbaatar* this ornamentation is poorly developed, or, in most cases, absent. The anterior upper premolars are strongly ornamented in all other known eobaatarids, possibly with exception of *Loxaulax* (Clemens, 1963: text-figs. 3, 4).

**Additional cusp on P2–3.** The additional cusp on P2–3 is present in *Eobaatar*, absent in *Arginbaatar*, and likely absent in *Nokerbaatar* (see the Morphological variation). Among the eobaatarids the additional cusp is present on P2 of *Hakusanobaatar* (Kusuhashi, 2008: text-figs. 2A2, 3A4), P2 of *Jeholbaatar* (Wang et al., 2019: extended text-fig. 2m), P2 of *Liaobaatar* sp. (Kusuhashi et al., 2019: text-figs. 9c1, 2), and on upper premolar attributed to *Loxaulax* (Clemens, 1963: text-figs. 4a, 4b).

**Distal cingulum on P1–3.** The distal cingulum is poorly developed or absent on the anterior upper premolars of *Arginbaatar*. In *Eobaatar* the distal cingulum is present on P2–3, being more pronounced on P3. In *Nokerbaatar* distal cingulum is present on P3 (P2 is unknown in that taxon). The distal cingulum of ante-

rior upper premolars is absent in *Sinobaatar xiei*, *S. pani*, ?*Liaobaatar* sp., *Hakusanobaatar*, *Jeholbaatar*, and *Loxaulax*, while it is well developed in *S. fuxinensis* (Clemens, 1963: text-figs. 3, 4; Kusuhashi, 2008: text-figs. 2, 3; Kusuhashi et al., 2009: text-figs. 4, 17; Kusuhashi et al., 2019: text-fig. 9; Wang et al., 2019: extended text-figs. 2a–2c, 2k; Mao et al., 2020: text-figs. 1C, 1D).

**Labial cusps of P4.** The number of labial cusps on P4 is two for *Nokerbaatar* and three for *Arginbaatar* (the P4 is unknown for *Eobaatar*). Among eobaatarids, the P4 with three labial cusps is known in *Hakusanobaatar*, *S. lingyuanensis*, and *S. pani* (Hu and Wang, 2002; Mao et al., 2020), with two labial cusps—in *Jeholbaatar*, *Sinobaatar xiei*, and *S. fuxinensis* (Kusuhashi et al., 2009; Wang et al., 2019).

**Lingual cusps of P4.** *Nokerbaatar* and *Arginbaatar* have four lingual cusps on P4, although in *Arginbaatar* often there is a ridge-like eminence distal to the fourth lingual cusp. All eobaatarids also have four lingual cusps on P4 (Hu and Wang, 2002; Kusuhashi et al., 2009; Wang et al., 2019; Mao et al., 2020), except of *Hakusanobaatar*, which has five lingual cusps on P4 (Kusuhashi, 2008).

**Labial cusps of P5.** There is a single labial cusp on P5 in *Eobaatar* and *Nokerbaatar* (P5 is unknown for *Arginbaatar*). Two labial cusps and a small additional labial cuspule are present on P5 in *Hakusanobaatar* (Kusuhashi, 2008: text-figs. 3A2, 3A5). In *Sinobaatar lingyuanensis* there are three labial cusps on P5 (Hu and Wang, 2002). Two and one labial cusp on P5 is present in *Jeholbaatar* and *Sinobaatar pani*, respectively (Wang et al., 2019; Mao et al., 2020). In *Sinobaatar xiei* and *S. fuxinensis* there are no labial cusps on P5 (Kusuhashi et al., 2009).

**Middle cusps of P5.** The number of cusps in the middle row of P5 is five in *Nokerbaatar* and six in *Eobaatar*. Among eobaatarids the largest number of the middle cusps on P5 (six) is present in *Hakusanobaatar* (Kusuhashi, 2008: text-figs. 3A2, 3A5). In *Sinobaatar lingyuanensis* and *S. pani* there are five and four middle cusps on P5, respectively (Hu and Wang, 2002; Mao et al., 2020). In *Eobaatar* and *Nokerbaatar* the posterior middle cusp are eliminating at the early wear stages and only three mesial cusps are well recognizable on the middle worn teeth. In *Jeholbaatar*, *Sinobaatar xiei*, and *S. fuxinensis* there are only three cusps in the middle cusp row (Kusuhashi et al., 2009; Wang et al., 2019), which correspond to the first three mesial cusps of *Eobaatar* and *Nokerbaatar*.

**Lingual cusps of P5.** There are three small lingual cusps on P5 of *Eobaatar* and *Nokerbaatar*, which are confined to the distal part of the crown and become obliterated with the early wear. Four lingual cusps on P5 were reported for *Sinobaatar lingyuanensis* (Hu and Wang, 2002). In *Hakusanobaatar* and *Sinobaatar pani* there are two small cusps in the lingual cusp row (Kusuhashi, 2008: text-figs. 3A3, 3A5; Mao et al.,

2020: text-fig. 1D). In *Sinobaatar xiei* and *S. fuxinensis* there are no lingual cusps on P5 (Kusuhashi et al., 2009).

**Cusp ornamentation on M1.** The cusp ornamentation is present on M1 of *Eobaatar*, *Nokerbaatar*, and *Hakusanobaatar* (Kusuhashi, 2008: text-fig. 2B). This ornamentation is absent in *Arginbaatar*, *Sinobaatar xiei*, *S. fuxinensis*, and ?*Liaobaatar* sp. (Kusuhashi et al., 2009, 2019).

**Labial cusps of M1.** There are three labial cusps on M1 in *Arginbaatar* and *Nokerbaatar* and four labial cusps in *Eobaatar*. There are three labial cusps on M1 in *Sinobaatar lingyuanensis* and *S. pani* (Hu and Wang, 2002; Mao et al., 2020), four in *Hakusanobaatar*, *S. xiei* and *S. fuxinensis* (Kusuhashi, 2008; Kusuhashi et al., 2009), and five in *Jeholbaatar* (Wang et al., 2019).

**Cusp ornamentation on M2.** The cusp ornamentation on M2 is absent in *Arginbaatar* and confined to the mesiolabial wing and first two labial cusps in *Eobaatar* (M2 is unknown for *Nokerbaatar*). Similar cusp ornamentation on M2 is present in *Sinobaatar fuxinensis* and *Loxaulax* (Clemens, 1963; Clemens and Lees, 1971; Kusuhashi et al., 2009). The cusp ornamentation on M2 is absent in *Sinobaatar xiei* and ?*Liaobaatar* sp. (Kusuhashi et al., 2009, 2019).

**Labial cusps of M2.** There are two labial cusps on M2 in *Arginbaatar* and three labial cusps in *Eobaatar* and *Nokerbaatar*. Two labial cusps on M2 are found in *Loxaulax* and *Sinobaatar pani* (Clemens, 1963: text-fig. 2; Clemens and Lees, 1971: pl. 1C, E; Mao et al., 2020). In *Sinobaatar* and *Jeholbaatar* there are three labial cusps on M2 (Hu and Wang, 2002; Kusuhashi et al., 2009; Wang et al., 2019).

**Lingual cusps of M2.** The number of lingual cusps on M2 is three for *Arginbaatar*, three to four for *Eobaatar*, and four for *Nokerbaatar*. The four lingual cusps on M2 are present in *Loxaulax*, *Sinobaatar lingyuanensis*, and *S. xiei*, while *S. fuxinensis* and *S. pani* has three lingual cusps on M2 (Hu and Wang, 2002; Kusuhashi et al., 2009; Mao et al., 2020).

**Coronoid process anterior end.** *Arginbaatar* is characteristic by an anterior position of the coronoid process of dentary which anterior end is situated at the distal root of p4. Most eobaatarids have significantly more posterior position of the coronoid process which starts at m2 (*Eobaatar*, *Nokerbaatar*, *Sinobaatar xiei*, *S. fuxinensis*) or at m1 (*Liaobaatar*). The more anterior position of the coronoid process in *Arginbaatar* is evidently related to the great increase in size of p4 in that taxon.

**Lower incisor enamel distribution.** In *Eobaatar* and *Nokerbaatar* the enamel on the lower incisor is restricted to the band covering the ventrolateral side of the incisor. In all other known eobaatarids and *Arginbaatar* the lower incisor is completely covered by enamel (Hu and Wang, 2002; Kusuhashi et al., 2009, 2010, 2019).

**Lingual ridge or groove on lower incisor.** In *Eobaatar* there is a distinct ridge along the ventrolingual margin of the lower incisor, delimiting ventrally a depression on the ventral side of the incisor (Figs. 8c, 8e). In *Nokerbaatar* this ridge is not developed but there is a distinct groove along the ventrolingual margin of the lower incisor (Figs. 16a, 16d). In *Arginbaatar* there is a ridge similar to that of *Eobaatar* but much less pronounced, with flat area rather than depression dorsally (Fig. 30b). A very strong ventrolingual ridge, similar to that in *Eobaatar*, is present in *Dolichoprion* (Kusuhashi et al., 2019: text-figs. 2b, 2c). The ventral margin of the lingual surface of lower incisor is slightly swollen in *Liaobaatar* and *Heishanobaatar* (Kusuhashi et al., 2009, 2010).

**Serrations on p4.** The number of serrations on p4 is highly variable in *Arginbaatar* (11–18). In *Eobaatar*, two specimens of p4 have 10 serrations. Only fragments of p4 are known for *Nokerbaatar*. Among eobaatarids, *Heishanobaatar*, *Jeholbaatar*, and *Dolichoprion* have 8 serrations on p4, *Sinobaatar xiei*—8–9 serrations, *S. fuxinensis*—9 serrations, and *S. lingyuanensis* and *Cheruscodon*—11 serrations (Hu and Wang, 2002; Kusuhashi et al., 2009, 2010, 2019; Wang et al., 2019; Martin et al., 2021).

**Distolabial cusp on p4.** This cusp is present in *Eobaatar*, *Nokerbaatar*, and all other known eobaatarids (Hu and Wang, 2002; Kusuhashi et al., 2009, 2019). The distolabial cusp of p4 is absent in *Arginbaatar*. In *Heishanobaatar* and *Cheruscodon*, the distolabial cusp of p4 is relatively larger than in other eobaatarids (Kusuhashi et al., 2010; Martin et al., 2021).

**Mesioventral rotation of p4.** As was first found by Kielan-Jaworowska et al. (1987) and confirmed by our study (Fig. 31), the p4 in *Arginbaatar* rotates forward about the mediolateral axis of dentary during the ontogeny. This unique feature was considered a specialization of *Arginbaatar* (Kielan-Jaworowska et al., 1987), unparalleled in other mammals. In some diprotodontan marsupials with the plagiaulacoid type of dentition (Simpson, 1933) (*Hypsiprymnodon*, *Bettongia*) the premolars rotate about the long axis of dentary during the ontogeny to maintain the shearing occlusion (Bensley, 1903). In *Hyaenodon* and some other creodonts the carnassial teeth rotate medially about the anteroposterior axis of the dentary (Mellett, 1969, 1977). In *Hyaenodon* the lateral motion of dentary is limited because of fused symphysis and carnassial rotation is needed to maintain a scissors-like contact. In the barbourfelid carnivore *Barbourofelis* the lower carnassial tooth (m1) rotate laterally about the anteroposterior axis of dentary (Baskin, 1981). In *Barbourofelis* the lateral motion of dentary is limited by the long unfused symphysis and the external flange of dentary contacting the large upper canine. In *Arginbaatar* the reason for the p4 mesioventral rotation is likely not the maintaining the shearing occlusion but prolonging the time of shearing during the ontogeny

by bringing new unworn parts of the p4 shearing blade into occlusion. As was already noted, this extreme specialization of *Arginbaatar* is not found in other multituberculates, but the Early Cretaceous eobaatarid *Cheruscodon* from Germany show more limited p4 rotation during the ontogeny (Martin et al., 2021).

**Labial and lingual sides of m1.** The lingual side of m1 is shorter than the labial side in *Arginbaatar* and most eobaatarids, including *Eobaatar* (m1 is unknown for *Nokerbaatar*). However, in *Arginbaatar* the labial side protrudes more mesially compared with the lingual side, while in *Eobaatar* and other eobaatarids the labial side protrudes more distally.

**Labial cusps of m1.** There are three labial cusps on m1 in *Arginbaatar* and four labial cusps in *Eobaatar*. Three labial cusps of m1 are known also for *Loxaulax*, *Dolichoprion*, and *Sinobaatar xiei* (Kusuhashi et al., 2009, 2019). The four labial cusps on m1 are in *S. lingyuanensis* and *S. fuxinensis* (Hu and Wang, 2002). The number of labial cusps of m1 varies in *Liaobaatar* (2–3) (Kusuhashi et al., 2009). *Heishanobaatar* was described and diagnosed as having only two labial cusps on m1 (Kusuhashi et al., 2010). However, on the holotype the labial cusp row of m1 is broken posteriorly and at least three labial cusps can be clearly differentiated on the published photographs of m1 in the referred specimen (Kusuhashi et al., 2010: text-figs. 2b, 3b, 5c).

**Lingual cusps of m1.** There are two lingual cusps on m1 in *Arginbaatar* and three lingual cusps in *Eobaatar*. Two cusps are also present in *Heishanobaatar*, *Dolichoprion*, *Sinobaatar xiei* and *S. fuxinensis*, and three cusps—in *Loxaulax* and *Liaobaatar* (Kusuhashi et al., 2009, 2010, 2019).

**Labial cusps of m2.** There are three separate labial cusps on m2 in *Arginbaatar* and *Sinobaatar lingyuanensis* (Hu and Wang, 2002). In *Eobaatar* and other eobaatarids the cusps in the labial cusp row of m2 are coalesced into a single ridge, with shallow short furrows on the lingual side indicating the limits of formerly individual cusps (Kusuhashi et al., 2009, 2010, 2019).

## CONCLUSIONS

*Arginbaatar dmitrievae* from the Early Cretaceous Khovoor locality in Mongolia was the first Early Cretaceous multituberculate described from Asia (Trofimov, 1980). A large sample of multituberculates from Khovoor locality, including 68 specimens (39 from PIN collection) was described in detail by Kielan-Jaworowska et al. (1987). These authors identified four taxa in the sample, arginbaatarid *Arginbaatar dmitrievae* and three eobaatarids, *Eobaatar magnus*, *E. minor*, and *Monobaatar mimicus*. Using additional 73 multituberculate specimens from Khovoor in PIN collection, we revised this multituberculate assemblage. *Monobaatar mimicus* is considered here to be a



junior subjective synonym of *Arginbaatar dmitrievae*. The number of infraorbital foramina varies in this taxon, with most specimens having two foramina. The previously poorly known *Eobaatar minor* is separated here into a new genus *Nokerbaatar*. It differs from *Eobaatar* by number of cusps on P5 and M1, by a ventrolingual groove instead of ridge on the lower incisor, and by a relatively smaller p3 lacking serrations. *Eobaatar* and *Nokerbaatar* differ from other eobaatarids by having the enamel on lower incisor restricted to ventrolabial side. *Eobaatar* was considered previously as having P4 and P5 of similar morphology. However, we found in new material P5 of both *Eobaatar* and *Nokerbaatar* of shearing type, which are similar to that tooth in other eobaatarids and different from P4. We identified several dP5 for *Arginbaatar* but no one P5. It is likely that in that taxon dP5 was not replacing by P5. According to the previous interpretation, p4 in *Arginbaatar* was rotating ontogenetically over p2 and p3 which become lost. We found that the shed teeth are actually p2 and dp3 and p3 was fully formed but not erupting because it was overhang by p4. The replacement of dP3 by P3 is documented for *Arginbaatar* by differential wear in a series of specimens. Arginbaataridae are currently known only from Khovoor valley in Mongolia, while Eobaataridae were widely distributed in the Early Cretaceous in Asia and Europe.

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#### REFERENCES

- Averianov, A.O., Early Cretaceous "symmetrodont" mammal *Gobiotheriodon* from Mongolia and the classification of "Symmetrodonta," *Acta Palaeontol. Pol.*, 2002, vol. 47, no. 4, pp. 705–716.
- Averianov, A.O., Lopatin, A.V., Skutschas, P.P., Ivantsov, S.V., Boitsova, E.A., and Kuzmin, I.T., An enigmatic multituberculate mammal from the Early Cretaceous of Siberia, Russia, *J. Vertebr. Paleontol.*, 2017, vol. 37, no. 2, e1293070. <https://doi.org/10.1080/02724634.2017.1293070>
- Badiola, A., Canudo, J.I., and Cuenca-Bescós, G., New multituberculate mammals from the Hauterivian/Barremian transition of Europe (Iberian Peninsula), *Palaeontology*, 2008, vol. 51, no. 6, pp. 1455–1469. <https://doi.org/10.1111/j.1475-4983.2008.00822.x>
- Badiola, A., Canudo, J.I., and Cuenca-Bescós, G., A systematic reassessment of Early Cretaceous multituberculates from Galve (Teruel, Spain), *Cretaceous Res.*, 2011, vol. 32, pp. 45–57. <https://doi.org/10.1016/j.cretres.2010.10.003>
- Badiola, A., Canudo, J.I., and Cuenca Bescos, G., New Early Cretaceous multituberculate mammals from the Iberian Peninsula, *Bernissart Dinosaurs and Early Cretaceous Terrestrial Ecosystems*, Godefroit, P., Ed., Indiana Univ. Press, 2012, pp. 409–433.
- Bakker, R.T., Dinosaur mid-life crisis: the Jurassic-Cretaceous transition in Wyoming and Colorado, *New Mexico Mus. Nat. Hist. Sci. Bull.*, 1998, vol. 1998, pp. 67–77.
- Barsbold, R. and Sigogneau-Russell, D., Inventaire des dinosaures et des mammifères de Mongolie, *Dinosaures et mammifères du désert de Gobi, Paris, 1992–1993*, Taquet, P., Ed., Paris: Mus. Natl. Hist. Nat., 1992, pp. 97–126.
- Baskin, J.A., *Barbourofelis* (Nimravidae) and *Nimravides* (Felidae), with a description of two new species from the late Miocene of Florida, *J. Mamm.*, 1981, vol. 62, no. 1, pp. 122–139. <https://doi.org/10.2307/1380483>
- Belyaeva, E.I., Trofimov, B.A., and Reshetov, V.Y., General stages in evolution of late Mesozoic and early Tertiary mammalian faunas in Central Asia, *Tr. Sovmestnoi Sov.-Mongol. Paleontol. Eksp.*, 1974, vol. 1, pp. 19–45.
- Bensley, B.A., On the evolution of the Australian Marsupialia: with remarks on the relationships of the marsupials in general, *Trans. Linn. Soc. London*, 1903, vol. 9, pp. 83–217.
- Butler, P.M. and Ford, R., Discovery of Cretaceous mammals on the Isle of Wight, *Proc. Isle of Wight Nat. Hist. Archaeol. Soc. for 1975, 1977*, vol. 6, no. 10, pp. 662–663.
- Clemens, W.A., Wealden mammalian fossils, *Palaeontology*, 1963, vol. 6, no. 1, pp. 55–69.
- Clemens, W.A. and Kielan-Jaworowska, Z., Multituberculata, *Mesozoic Mammals: The First Two-Thirds of Mammalian History*, Lillegraven, J.A., Kielan-Jaworowska, Z., and Clemens, W.A., Eds., Berkeley: University of California Press, 1979, pp. 99–149.
- Clemens, W.A. and Lees, P.M., A review of English Early Cretaceous mammals, *Early Mammals*, Kermack, D.M. and Kermack, K.A., Eds., *Zool. J. Linn. Soc.*, 1971, vol. 50, suppl. 1, pp. 117–130.
- Crompton, A.W. and Luo, Z.-X., Relationships of the Liasic mammals, *Sinoconodon*, *Morganucodon oehleri*, and *Dinnetherium*, *Mammal Phylogeny: Mesozoic Differentiation, Multituberculates, Monotremes, Early Therians, and Marsupials*, Szalay, F.S., Novacek, M.J., and McKenna, M.C., New York: Springer Verlag, 1993, vol. 1, pp. 30–44. [https://doi.org/10.1007/978-1-4613-9249-1\\_4](https://doi.org/10.1007/978-1-4613-9249-1_4)
- Crusafont, M. and Gibert, J.M., Los primeros Multituberculados de España, Nota preliminar, *Acta Geol. Hisp.*, 1976, vol. 11, no. 3, pp. 57–64.
- Crusafont Pairó, M. and Adrover, R., El primer Mamífero del Mesozoico español, *Publ. Càtedra Paleontol. Univ. Barcelona*, 1966, vol. 13, pp. 28–33.
- Eaton, J.G. and Cifelli, R.L., Multituberculate mammals from near the Early–Late Cretaceous boundary, Cedar Mountain Formation, Utah, *Acta Palaeontol. Pol.*, 2001, vol. 46, no. 4, pp. 453–518.
- Engelmann, G.F., The anterior dentition of the Late Jurassic multituberculate *Ctenacodon*, *Bull. Am. Mus. Nat. Hist.*, 2004, vol. 285, pp. 54–61.
- Engelmann, G.F. and Callison, G.L., *Glirodon grandis*, a new multituberculate mammal from the Upper Jurassic Morrison Formation, *Vertebr. Paleontol. Utah*, Utah Geol. Survey Publ., 1999, vol. 99-1, pp. 161–178.

- Fosse, G., Kielan-Jaworowska, Z., and Skaale, S.G., The microstructure of tooth enamel in multituberculate mammals, *Palaeontology*, 1985, vol. 28, no. 3, pp. 438–449.
- Hahn, G., Neue Schädel-Reste von Multituberculaten (Mamm.) aus dem Malm Portugals, *Geol. Palaeontol.*, 1977, vol. 11, pp. 161–186.
- Hahn, G., Zum Bau des Infraorbital-Foramens bei den Paulchoffatiidae (Multituberculata, Ober-Jura), *Berl. Geowiss. Abh., Reihe A*, 1985, vol. 60, pp. 5–27.
- Hahn, G. and Hahn, R., *Multituberculata, Fossilium Catalogus, I: Animalia, Pars 127*, Amsterdam: Kugler, 1983, pp. 1–409.
- Hahn, G. and Hahn, R., Neue Multituberculaten-Zähne aus der Unter-Kreide (Barremium) von Spanien (Galve und Uña), *Geol. Palaeontol.*, 1992, vol. 26, pp. 143–162.
- Hahn, G. and Hahn, R., Pinheirodontidae n. fam. (Multituberculata) (Mammalia) aus der tiefen Unter-Kreide Portugals, *Palaeontogr., Abt. A: Palaeozool., Stratigr.*, 1999, vol. 253, nos. 4–6, pp. 77–222.
- Hahn, G. and Hahn, R., Multituberculaten-Zähne aus der Unter-Kreide (Barremium) von Pié Pajarón (Prov. Cuenca, Spanien), *Palaeontol. Z.*, 1983, vol. 74, no. 4, pp. 587–589.
- Hahn, G. and Hahn, R., Der Bau der Canini bei den Paulchoffatiidae (Multituberculata; Ober-Jura), *Palaeontol. Z.*, 2002a, vol. 76, no. 2, pp. 235–249.
- Hahn, G. and Hahn, R., Neue Multituberculaten-Zähne aus dem Barremium (Unter-Kreide) von Galve (Spanien), *Palaeontol. Z.*, 2002b, vol. 76, no. 2, pp. 257–259.
- Hahn, G. and Hahn, R., The dentition of the Plagiaulacida (Multituberculata, Late Jurassic to Early Cretaceous), *Geol. Palaeontol.*, 2004, vol. 38, pp. 119–159.
- Hahn, G. and Hahn, R., *Catalogus Plagiaulacidorum cum figuris (Multituberculata suprajurassica et subcretacea)*, *Fossilium Catalogus I: Animalia, Pars 140*, Leiden: Backhuys Publ., 2006.
- Hu, Y. and Wang, Y., *Sinobaatar* gen. nov.: first multituberculate from the Jehol Biota of Liaoning, Northeast China, *Chin. Sci. Bull.*, 2002, vol. 47, no. 11, pp. 933–938.
- Kermack, K.A., Mussett, F., and Rigney, H.W., The skull of *Morganucodon*, *Zool. J. Linn. Soc.*, 1981, vol. 71, no. 1, pp. 1–158.  
<https://doi.org/10.1111/j.1096-3642.1981.tb01127.x>
- Kielan-Jaworowska, Z., Cifelli, R.L., and Luo, Z.-X., *Mammals from the Age of Dinosaurs: Origins, Evolution, and Structure*, New York: Columbia Univ. Press, 2004.
- Kielan-Jaworowska, Z., Dashzeveg, D., and Trofimov, B.A., Early Cretaceous multituberculates from Mongolia and a comparison with Late Jurassic forms, *Acta Palaeontol. Pol.*, 1987, vol. 32, nos. 1–2, pp. 3–47.
- Kielan-Jaworowska, Z. and Ensom, P.C., Multituberculate mammals from the Upper Jurassic Purbeck Limestone Formation of Southern England, *Palaeontology*, 1992, vol. 35, no. 1, pp. 95–126.
- Kielan-Jaworowska, Z. and Hurum, J.H., Phylogeny and systematics of multituberculate mammals, *Palaeontology*, 2001, vol. 44, no. 3, pp. 389–429.
- Kielan-Jaworowska, Z., Hurum, J.H., and Lopatin, A.V., Skull structure in *Catopsbaatar* and the zygomatic ridges in multituberculate mammals, *Acta Palaeontol. Pol.*, 2005, vol. 50, no. 3, pp. 487–512.
- Kielan-Jaworowska, Z. and Nesov, L.A., Multituberculate mammals from the Cretaceous of Uzbekistan, *Acta Palaeontol. Pol.*, 1992, vol. 37, no. 1, pp. 1–17.
- Kielan-Jaworowska, Z., Novacek, M.J., Trofimov, B.A., and Dashzeveg, D., Mammals from the Mesozoic of Mongolia, *The Age of Dinosaurs in Russia and Mongolia*, Benton, M.J., Shishkin, M.A., Unwin, D.M., and Kurochkin, E.N., Eds., Cambridge: Cambridge Univ. Press, 2000, pp. 573–626.
- Kusuhashi, N., Early Cretaceous multituberculate mammals from the Kuwajima Formation (Tetori Group), central Japan, *Acta Palaeontol. Pol.*, 2008, vol. 53, no. 3, pp. 379–390.  
<https://doi.org/10.4202/app.2008.0302>
- Kusuhashi, N., Hu, Y., Wang, Y., Setoguchi, T., and Matsuoaka, H., Two eobaatarid (Multituberculata; Mammalia) genera from the Lower Cretaceous Shahai and Fuxin Formations, Northeastern China, *J. Vertebr. Paleontol.*, 2009, vol. 29, no. 4, pp. 1264–1288.  
<https://doi.org/10.1671/039.029.0433>
- Kusuhashi, N., Hu, Y., Wang, Y., Setoguchi, T., and Matsuoaka, H., New multituberculate mammals from the Lower Cretaceous (Shahai and Fuxin formations), northeastern China, *J. Vertebr. Paleontol.*, 2010, vol. 30, no. 5, pp. 1501–1514.  
<https://doi.org/10.1080/02724634.2010.501435>
- Kusuhashi, N., Wang, Y., and Jin, X., A new eobaatarid multituberculate (Mammalia) from the Lower Cretaceous Fuxin Formation, Fuxin-Jinzhou Basin, Liaoning, Northeastern China, *J. Mamm. Evol.*, 2019.  
<https://doi.org/10.1007/s10914-019-09481-w>
- Lillegraven, J.A. and Krusat, G., Cranio-mandibular anatomy of *Haldanodon exspectatus* (Docodonta; Mammalia) from the Late Jurassic of Portugal and its implications to the evolution of mammalian characters, *Contrib. Geol. Univ. Wyoming*, 1991, vol. 28, no. 2, pp. 39–138.
- Lopatin, A.V., New finds of Early Cretaceous mammals in Mongolia, *Dokl. Biol. Sci.*, 2013, vol. 449, pp. 103–105.
- Lopatin, A.V. and Averianov, A.O., An aegialodontid upper molar and the evolution of mammal dentition, *Science*, 2006a, vol. 313, no. 5790, p. 1092.
- Lopatin, A.V. and Averianov, A.O., Revision of a pretribosphenic mammal *Arguimus* from the Early Cretaceous of Mongolia, *Acta Palaeontol. Pol.*, 2006b, vol. 51, no. 2, pp. 339–349.
- Lopatin, A.V. and Averianov, A.O., *Kielantherium*, a basal tribosphenic mammal from the Early Cretaceous of Mongolia, with new data on the aegialodontid dentition, *Acta Palaeontol. Pol.*, 2007, vol. 52, no. 3, pp. 441–446.
- Lopatin, A.V. and Averianov, A.O., *Gobiconodon* (Mammalia) from the Early Cretaceous of Mongolia and revision of Gobiconodontidae, *J. Mamm. Evol.*, 2015, vol. 22, pp. 17–43.  
<https://doi.org/10.1007/s10914-014-9267-4>
- Lopatin, A.V. and Averianov, A.O., The stem placental mammal *Prokennalestes* from the Early Cretaceous of Mongolia, *Paleontol. J.*, 2017, vol. 51, no. 12, pp. 1293–1374.  
<https://doi.org/10.1134/S0031030117120048>
- Lopatin, A.V. and Averianov, A.O., A new stem placental mammal from the Early Cretaceous of Mongolia, *Dokl. Biol. Sci.*, 2018, vol. 478, pp. 8–11.  
<https://doi.org/10.1134/S0012496618010027>

- Mao, F., Liu, C., Chase, M.H., Smith, A.K., and Meng, J., Exploring ancestral phenotypes and evolutionary development of the mammalian middle ear based on Early Cretaceous Jehol mammals, *Natl. Sci. Rev.*, 2020. <https://doi.org/10.1093/nsr/nwaa188>
- Martin, T., Averianov, A.O., Schultz, J.A., and Schwermann, A.W., First multituberculate mammals from the Lower Cretaceous of Germany, *Cretaceous Res.*, 2021, vol. 1, p. 104699. <https://doi.org/10.1016/j.cretres.2020.104699>
- Mellett, J.S., Carnassial rotation in a fossil carnivore, *Am. Midl. Nat.*, 1969, vol. 82, no. 1, pp. 287–289. <https://doi.org/10.2307/2423840>
- Mellett, J.S., Paleobiology of North American *Hyaenodon* (Mammalia, Creodonta), *Contrib. Vertebr. Paleontol.*, 1977, vol. 1, pp. 1–134.
- Miao, D., Skull morphology of *Lambdopsalis bulla* (Mammalia, Multituberculata) and its implications to mammalian evolution, *Contrib. Geol. Univ. Wyoming, Spec. Pap.*, 1988, vol. 4, pp. 1–104.
- Parmar, V., Prasad, G.V.R., and Kumar, D., The first multituberculate mammal from India, *Naturwissenschaften*, 2013, vol. 100, pp. 515–523. <https://doi.org/10.1007/s00114-013-1047-0>
- Patterson, B., Early Cretaceous mammals and the evolution of mammalian molar teeth, *Fieldiana, Geol.*, 1956, vol. 13, no. 1, pp. 1–105.
- Rougier, G.W., Sheth, A.S., Spurlin, B.K., Bolortsetseg, M., and Novacek, M.J., Craniodental anatomy of a new Late Cretaceous multituberculate mammal from Udan Sayr, Mongolia, *Palaeontol. Pol.*, 2016, vol. 67, pp. 197–248.
- Simmons Greenwald, N., Patterns of tooth eruption and replacement in multituberculate mammals, *J. Vertebr. Paleontol.*, 1988, vol. 8, no. 3, pp. 265–277.
- Simpson, G.G., *A Catalogue of the Mesozoic Mammalia in the Geological Department of the British Museum*, London: British Museum (Natural History), 1928.
- Simpson, G.G., The “plagiaulacoid” type of mammalian dentition, *J. Mamm.*, 1933, vol. 14, pp. 97–107.
- Sweetman, S.C., A new species of the plagiaulacoid multituberculate mammal *Eobaatar* from the Early Cretaceous of southern Britain, *Acta Palaeontol. Pol.*, 2009, vol. 54, no. 3, pp. 373–384. <https://doi.org/10.4202/app.2008.0003>
- Trofimov, B.A., Mammals from the Lower Cretaceous of Mongolia, *Session Devoted to the Hundred's Anniversary of the Academichian A.A. Borissiak*, Moscow: Paleontol. Inst., Akad. Nauk SSSR, 1972, pp. 65–67.
- Trofimov, B.A., Multituberculata and Symmetrodonta from the Lower Cretaceous of Mongolia, *Dokl. Akad. Nauk SSSR*, 1980, vol. 251, pp. 209–212.
- Wang, H., Meng, J., and Wang, Y., Cretaceous fossil reveals a new pattern in mammalian middle ear evolution, *Nature*, 2019. <https://doi.org/10.1038/s41586-019-1792-0>
- Wible, J.R. and Rougier, G.W., The cranial anatomy of *Kryptobaatar dashzevegi* (Mammalia, Multituberculata), and its bearing on the evolution of mammalian characters, *Bull. Am. Mus. Nat. Hist.*, 2000, vol. 247, pp. 1–124.
- Wible, J.R., Shelley, S.L., and Bi, S., New genus and species of djadochtatheriid multituberculate (Allotheria, mammalia) from the Upper Cretaceous Bayan Mandahu Formation of Inner Mongolia, *Ann. Carnegie Mus.*, 2019, vol. 85, no. 4, pp. 285–327.
- Woodward, A.S., On some mammalian teeth from the Wealden of Hastings, *Q. J. Geol. Soc. London*, 1911, vol. 67, pp. 278–281. <https://doi.org/10.1144/GSL.JGS.1911.067.01-04.11>
- Yuan, C.-X., Ji, Q., Meng, Q.-J., Tabrum, A.R., and Luo, Z.-X., Earliest evolution of multituberculate mammals revealed by a new Jurassic fossil, *Science*, 2013, vol. 341, no. 6147, pp. 779–783.