

Revision of a pretribosphenic mammal *Arguimus* from the Early Cretaceous of Mongolia

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Lopatin, A.V. and Averianov, A.O. 2006. Revision of a pretribosphenic mammal *Arguimus* from the Early Cretaceous of Mongolia. *Acta Palaeontologica Polonica* 51 (2): 339–349.

Arguimus khosbajari is redescribed, based on five additional specimens from the topotypic Early Cretaceous (Aptian–Albian) Höövör locality in Mongolia. The teeth preserved in the holotype of *A. khosbajari* are interpreted as p4–5, m1–3. The original identification of the teeth preserved in the holotype and single specimen of *Arguitherium cromptoni* from Höövör as p4–5, m1 is confirmed and this specimen is considered conspecific with *A. khosbajari*. Thus *Arguitherium cromptoni* Dashzeveg, 1994 and *Arguitheriidae* Dashzeveg, 1994 are junior subjective synonyms of *Arguimus khosbajari* Dashzeveg, 1979 and *Arguimuridae* Dashzeveg, 1994 respectively (syn. nov.). *Arguimus* is a stem-lineage zatherian characterized by the lower postcanine formula p1–5, m1–4, a premolariform p5, a “partially molariform” m1 having a widely open trigonid basin, trigonid cusps less angulated than in m2–4, a low and small paraconid, and a small but distinct metaconid, a single cusped talonid with an incipient talonid basin on m1–4, a distinct labial mandibular foramen, and total lack of the Meckel’s groove. A similar “partially molariform” m1 was apparently characteristic also for the stem-lineage zatherian *Nanolestes* from the Late Jurassic of Portugal, based on reinterpretation of the isolated tooth Gui Mam 1005, considered previously to be a deciduous premolar, and for *Chunnelodon* from the Early Cretaceous of England, described originally as an indeterminate dryolestoid, but referred here to as a stem-lineage zatherian.

Key words: *Arguimus*, *Arguitherium*, Zatheria, dental formula, Early Cretaceous, Höövör, Mongolia.

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Introduction

An Early Cretaceous mammal assemblage from Höövör in Northern Gobi, Mongolia, is unique in the combination of mammals of different evolutionary levels: various multituberculates, “triconodont” *Gobiconodon*, “symmetrodon” *Gobiotheriodon*, pretribosphenic mammal *Arguimus*, primitive tribosphenic mammal *Kielantherium*, and eutherian *Prokennalestes* (Kurochkin et al. 1970; Barsbold et al. 1971; Kalandadze and Reshetov 1971; Trofimov 1972, 1978, 1980, 1997; Belyaeva et al. 1974; Kalandadze and Kurzanov 1974; Dashzeveg 1975, 1979, 1994; Reshetov and Trofimov 1980, 1984; Dashzeveg and Kielan-Jaworowska 1984; Kielan-Jaworowska et al. 1987, 2000, 2004; Dashzeveg et al. 1989; Kielan-Jaworowska and Dashzeveg 1989, 1998; Reshetov 1989; Nessov and Kielan-Jaworowska 1991; Sigogneau-Russell et al. 1992; Wible et al. 1995; Rougier et al. 1996). In 1969–1972 an extensive collection of mammals from Höövör has been assembled by the Soviet Mongolian expedition and housed in the Moscow Paleontological Institute, but only a small part of this collection has been studied and published (Trofimov 1978, 1980, 1997; Kielan-Jaworowska et al. 1987; Averianov 2002; Lopatin et al. 2005).

The remaining part of this collection is currently under study by the authors. In this report we describe five additional specimens of *Arguimus khosbajari* Dashzeveg, 1979 from Höövör and discuss its phylogenetic position as well as the validity of *Arguitherium cromptoni* Dashzeveg, 1994 from the same locality.

Institutional abbreviations.—BMNH, Natural History Museum, London; PIN, Paleontological Institute, Russian Academy of Sciences, Moscow; PSS, Paleontology and Stratigraphic Section of the Geological Institute, Mongolian Academy of Sciences, Ulaanbaatar.

Measurements.—L, length; W, width. All measurements are in mm.

In classification of Mesozoic mammals and morphological terminology we follow Kielan-Jaworowska et al. (2004), except the identification of a single talonid cusp in pretribosphenic mammals as hypoconid rather than hypoconulid. In *Arguimus* this cusp is connected to the distal metaconid and is labial to the incipient talonid basin, as the hypoconid in *Peraurus* and *Kielantherium*, and thus considered here as homologous to the hypoconid of Zatheria (see also Butler 1990; Martin 2002). Wear facet nomenclature is after Crompton (1971).

Systematic paleontology

Mammalia Linnaeus, 1758

Stem-lineage of Zatheria McKenna, 1975

Arguimus Dashzeveg, 1979

= *Arguitherium* Dashzeveg, 1994

Type species: *Arguimus khosbajari* Dashzeveg, 1979. Mongolia, Early Cretaceous.

Included species: Type species only.

Revised diagnosis.—Differs from crown-group Zatheria in having four rather than three molars and in lack of a hypoculid. Additionally, differs from *Peramus* Owen, 1871 in the deeper dentary lacking Meckel's groove and from *Tendagurutherium* Heinrich, 1998 by lack of Meckel's groove and coronoid. Differs from *Amphitherium* de Blainville, 1838 in having smaller number of molars (four *versus* six-seven), incipient talonid basin on lower molars, and lack of Meckel's groove. Differs from *Nanolestes* Martin, 2002 in having four rather than five lower molars, in having an incipient talonid basin, and in a deeper dentary lacking Meckel's groove. Differs from *Minimus* Sigogneau-Russell, 1999 by longer talonid on lower molars. Differs from *Chunnelodon* Ensom and Sigogneau-Russell, 1998 in having a shorter talonid with incipient talonid basin and lower metaconid on m1. Differs from *Vincelestes* Bonaparte, 1986 in having a larger number of lower premolars (five *versus* two) and molars (four *versus* three), the last premolar smaller than m1, and longer molar talonids.

Arguimus khosbajari Dashzeveg, 1979

Figs. 1–6.

1979 *Arguimus khosbajari* sp. nov.; Dashzeveg 1979: 200, fig.1, pl.1.

1994 *Arguimus khosbajari* Dashzeveg, 1979; Dashzeveg 1994: 5, figs. 2, 5, 6.

1994 *Arguitherium cromptoni* sp. nov.; Dashzeveg 1994: 2, figs. 1, 3, 4.

1990 *Arguimus khosbajari* Dashzeveg, 1979; Butler 1990: fig. 3.

1999 *Arguimus khosbajari* Dashzeveg, 1979; Sigogneau-Russell 1999: fig. 5.

1999 *Arguitherium cromptoni* Dashzeveg, 1994; Sigogneau-Russell 1999: fig. 6.

2000 *Arguimus khosbajari* Dashzeveg, 1979; Kielan-Jaworowska et al. 2000: 598, fig. 29.16B.

2000 *Arguitherium cromptoni* Dashzeveg, 1994; Kielan-Jaworowska et al. 2000: 598, fig. 29.16A.

2001 *Arguimus khosbajari* Dashzeveg, 1979; Butler and Clemens 2001: fig. 8E.

2004 *Arguimus khosbajari* Dashzeveg, 1979; Kielan-Jaworowska et al. 2004: 397, fig. 10.13A.

2004 *Arguitherium cromptoni* Dashzeveg, 1994; Kielan-Jaworowska et al. 2004: 399, fig. 10.13B.

Holotype: PSS 10-15, left dentary fragment with p4–5, m1–3, and alveoli for p2–3 and m4 (see discussion for interpretation of the dental formula).

Type locality and horizon: Höövör (Khoboor), Mongolia; Aptian–Albian, Early Cretaceous.

Material.—PSS 10-31, right dentary fragment with p4–5, m1, and alveoli for p1–3, and m2–3 (holotype of *Argui-*

Table 1. Trigonid angle in molars of *Arguimus khosbajari* Dashzeveg, 1979. Höövör, Mongolia; Early Cretaceous. The specimens are arranged according to progressive wear.

Specimen	m1	m2	m3	m4
PIN 3101/364	130°	86°		
PIN 3101/400	134°			
PIN 3101/106	130°	86°		
PSS 10-31	118°*			
PSS 10-15	102°*	65°	52°	
PIN 3101/108			56°	87°
PIN 3101/107		50°*		

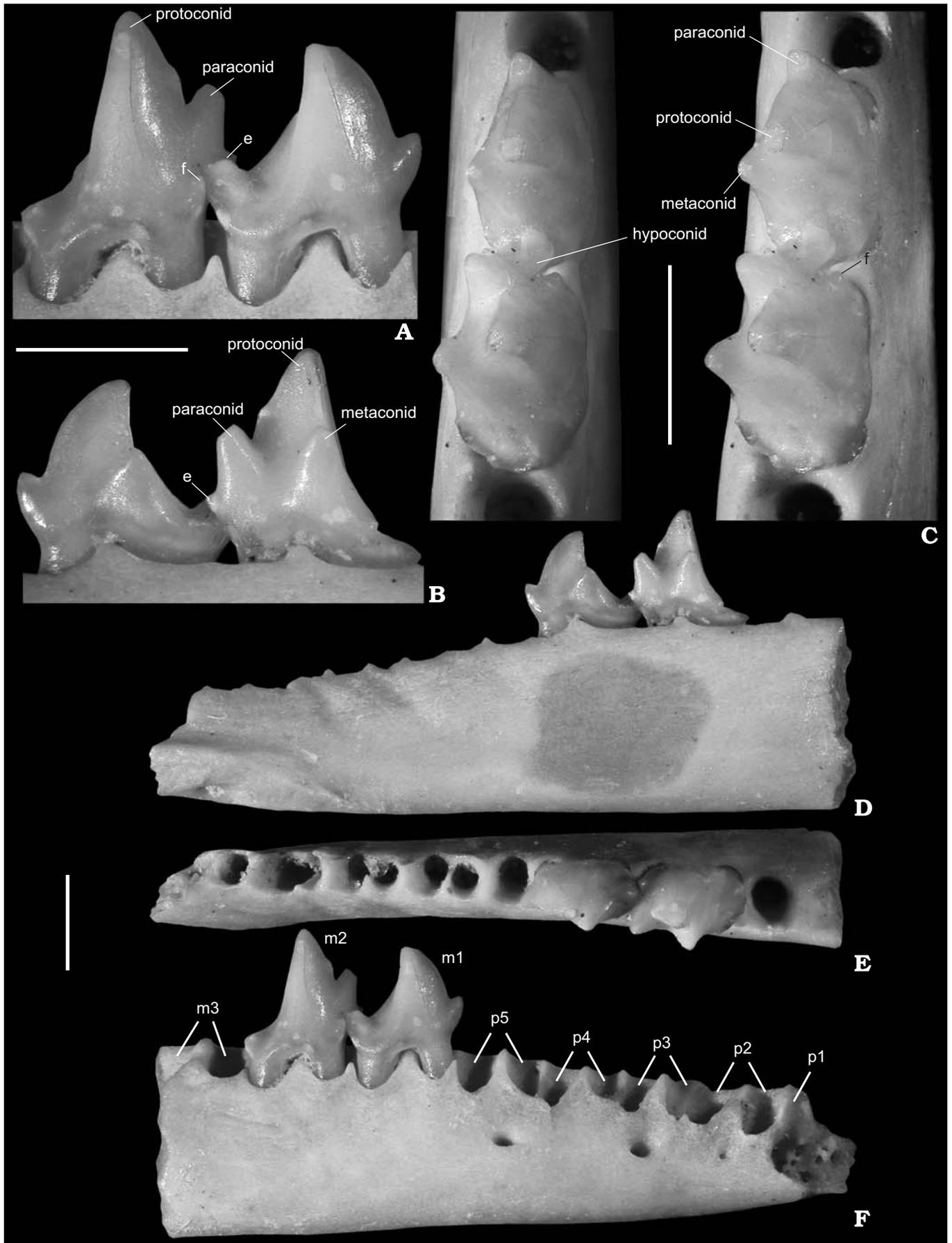
* Approximate estimate on a heavily worn tooth.

therium cromptoni Dashzeveg, 1994); PIN 3101/364, right dentary fragment with m1–2 and alveoli for p1–5, and m3; PIN 3101/400, left dentary fragment with m1 and alveoli for p2–5 and m2–3; PIN 3101/106, right dentary fragment with m1–2 and alveoli for m3–4; PIN 3101/107, right dentary fragment with worn m2 and alveoli for m3–4; PIN 3101/108, left dentary fragment with m3–4, alveoli for m2, and partial coronoid process.

Diagnosis.—As for genus.

Description.—The dentary was apparently elongate, with the mandibular symphysis terminating between p3 and p4 (PSS 10-15 and 10-31) or under the anterior root of p4 (PIN 3101/364 and 400; Figs. 1D and 2D). There is a distinct nutrient foramen within the mandibular symphysis in PIN 3101/364 (Fig. 1D). The dentary deepens considerably in the molar region, being approximately twice as deep as the unworn m2 in PIN 3101/364 (Fig. 1D and F). The labial margins of the tooth alveoli are distinctly lower than their lingual margins, and this height differential increases anteriorly (Figs. 1D, F, 2D, F, 3A, B, 4A₃, A₄, B₃, B₄). The posterior mental foramen is situated under the anterior root of p4 (PIN 3101/400; Fig. 2F), posterior root of p4 (PSS 10-31), anterior root of p5 (PSS 10-15), between the roots of p5 (PIN 3101/364; Fig. 1F), or between the roots of m1 (PIN 3101/106; Fig. 3A). There are two anterior mental foramina: under the anterior root of p4 (PSS 10-15) or the posterior root of p3 (PIN 3101/364; Fig. 1F), and under the posterior root of p2 (PSS 10-15, PIN 3101/364; Fig. 1F). In all specimens there are no traces of the Meckel's groove. The coronoid process (partially preserved only in PIN 3101/108, Fig. 4A) is rather steep and close to m4, with a strong coronoid crest. Inside the masseteric fossa, at the base of the posterior side of the coronoid crest in PIN 3101/108, is a cleft-like depression with a labial mandibular foramen at the alveolar level leading to the mandibular canal (Fig. 5). The mandibular canal is large, as evident from its section in several specimens. On

Fig. 1. *Arguimus khosbajari* Dashzeveg, 1979. PIN 3101/364, right dentary fragment with m1–2 and alveoli for p1–5, and m3. Höövör, Mongolia; Early Cretaceous. A–C. The m1–2 in labial (A), lingual (B), and occlusal (C, stereopair) views. D–F. The whole specimen in lingual (D), occlusal (E), and labial (F) views. Scale bars 1 mm. →



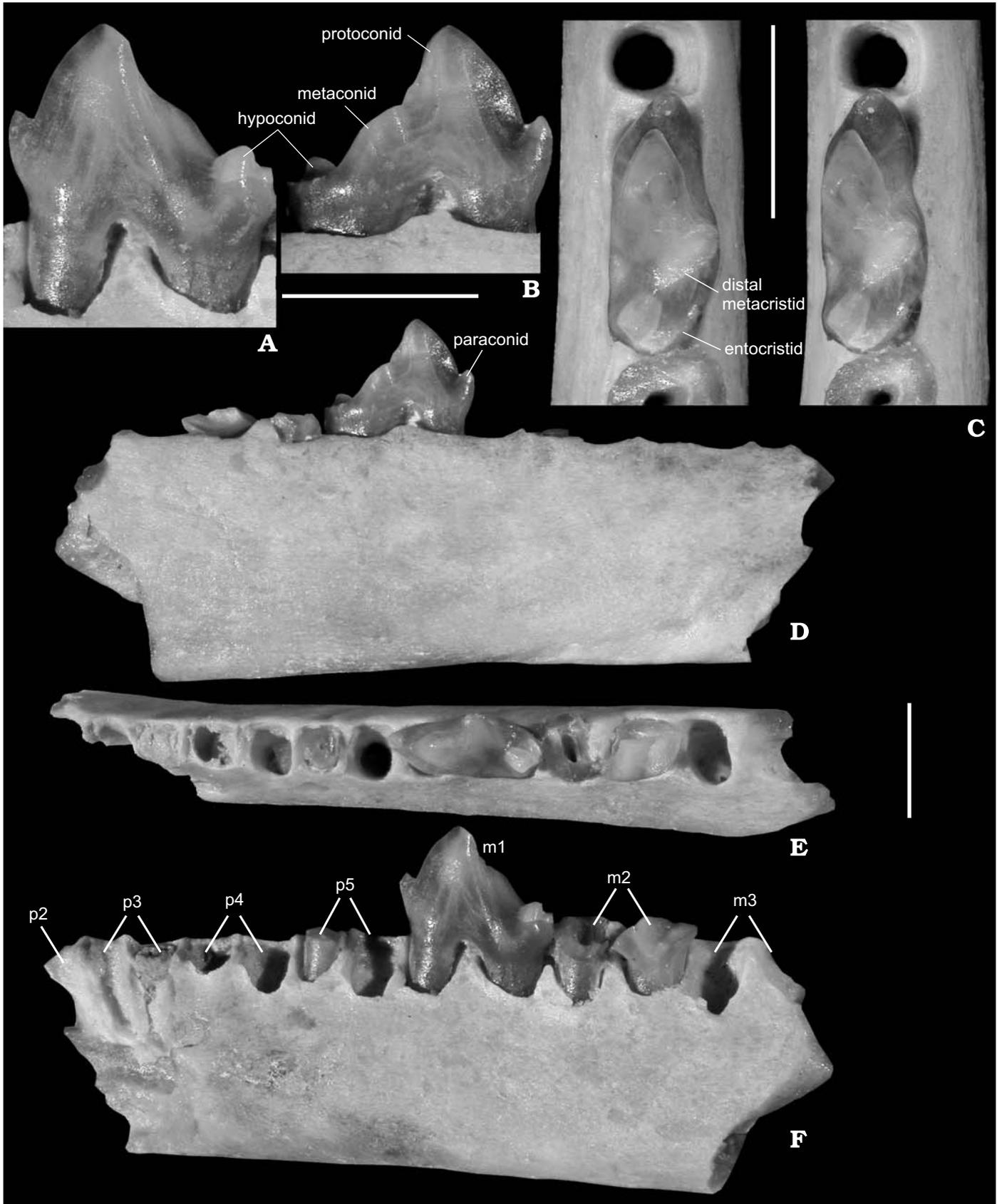


Fig. 2. *Arguimus khosbajari* Dashzeveg, 1979. PIN 3101/400, left dentary fragment with m1 and alveoli for p2–5 and m2–3. Höövör, Mongolia; Early Cretaceous. A–C. The m1 in labial (A), lingual (B), and occlusal (C, stereopair) views. D–F. The whole specimen in lingual (D), occlusal (E), and labial (F) views. Scale bars 1 mm.



Fig. 3. *Arguimus khosbajari* Dashzeveg, 1979. PIN 3101/106, right dentary fragment with m1–2 and alveoli for m3–4 in labial (A), lingual (B), and occlusal (C, stereopair) views. Höövör, Mongolia; Early Cretaceous. Scale bars 1 mm.

PIN 3101/108 (Fig. 4A₄) there is neither a coronoid bone preserved, nor a distinct facet for this bone, but there is a very faint bump-like structure on the medial side of the coronoid process at the alveolar level, which is referred to as a rugosity of uncertain meaning after Wible et al. (2004).

Anterior premolars are not known, their alveoli are best preserved on PSS 10-31 and PIN 3101/364 (Fig. 1E, F), and interpreted as double-rooted p1–3. Judging from the alveoli on PIN 3101/364, p2 was larger than p1 and p3. The p4–5 are preserved on the holotype and PSS 10-31 and are heavily worn in both specimens. Both posterior premolars are similar premolariform in structure. The p5 is intermediate in height between p4 and m1. The anterior accessory cusp was apparently present on both premolars (better developed on p4) but worn in known specimens. The posterior accessory cusp is distinct. The p5 widens considerably posteriorly, p4 is of similar width through out its entire length. The lingual cingulid is not distinct but the bulbous lingual base of the crown is worn on p4 and especially on p5.

The roots of all cheek teeth are set vertically in the dentary. On molars the labial side of the crown is higher than the lingual and the crowns are tilted somewhat lingually from the vertical plane. The trigonid angle of molars is largest on m1, decreases on m2 and m3 and slightly increases on m4 (Table 1). This angle decreases considerably with wear by the removing of dentine from the paracristid anteriorly and protocristid posteriorly, as evident from m1 and m2 (Table 1). Lower molars have a short talonid with a single cusp (hypoconid) and variably developed interlocking system. The best developed interlocking is between m1 and m2 on PIN 3101/364 (Fig. 1C), where the m1 talonid is deeply inserted between the well developed cusps *e* (anterolingual) and *f* (anterolabial). A less pronounced interlocking is present between m1 and m2 on PIN 3101/106 and between m2 and m3 on PIN 3101/108 (Figs. 3C and 4A₁). Cuspule *e* is small and ridge-like in both specimens and cuspule *f* is absent on PIN 3101/106.

The m1 is the most distinctive tooth of the lower molars, being “partially molariform”. The protoconid is lower than

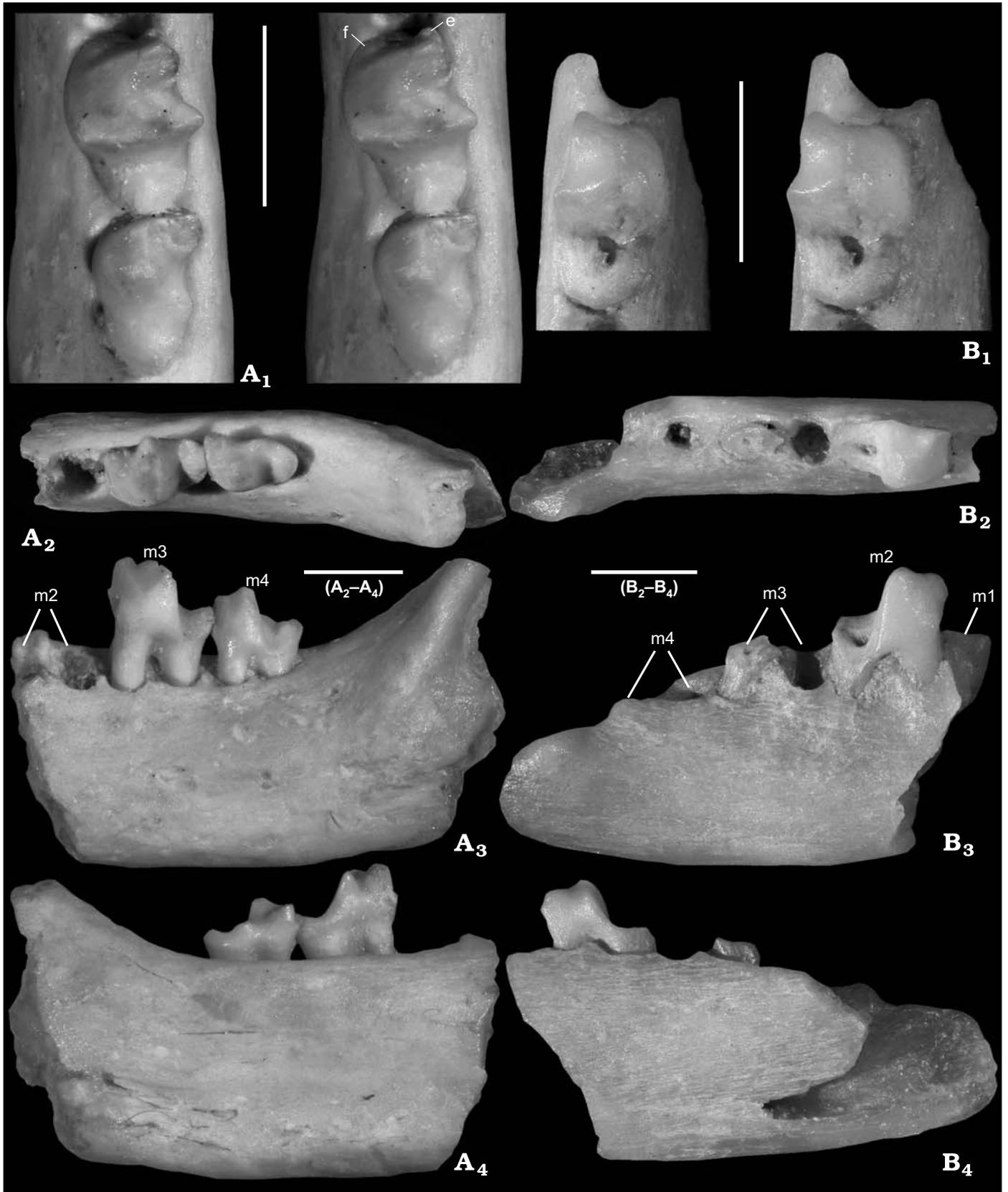


Fig. 4. *Arguimus khosbajari* Dashzeveg, 1979. Höövör, Mongolia; Early Cretaceous. **A.** PIN 3101/108, left dentary fragment with m3–4, alveoli for m2, and partial coronoid process (A₁, m3–4 in occlusal view, stereopair; A₂–A₄, the whole specimen in occlusal, labial, and lingual views). **B.** PIN 3101/107, right dentary fragment with worn m2 and alveoli for m3–4 (B₁, in occlusal view, stereopair; B₂–B₄, the whole specimen in occlusal, labial, and lingual views). Scale bars 1 mm.

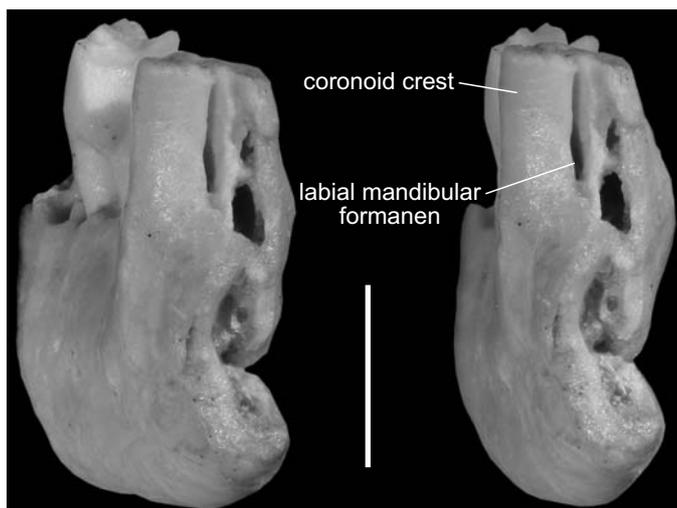


Fig. 5. *Arguimus khosbajari* Dashzeveg, 1979. PIN 3101/108, left dentary fragment with m3–4, alveoli for m2, and partial coronoid process in posterior view. Höövör, Mongolia; Early Cretaceous. Scale bar 1 mm.

on m2. The paraconid is very small and low, placed almost anteriorly to the protoconid. The metaconid is higher, but still small and placed posterolingually to the protoconid. There is a short and almost vertical distal metacristid. It is seen only on unworn specimens (PIN 3101/364 and 400, Figs. 1C and 2C) and rapidly becomes obliterated by wear. On PIN 3101/400 the talonid of m1 is relatively longer and with a better developed hypoconid than on m1 of PIN 3101/364. A small incipient talonid basin is preserved only in unworn m1's of PIN 3101/364 and 400 (Figs. 1C and 2C) and partially preserved on the worn m1 of PIN 3101/106 (Fig. 3C). The entocristid, bordering the talonid basin posteriorly and lingually, is distinct on PIN 3101/400, but much weaker on PIN 3101/364 (Figs. 1C and 2C).

On m2–4 (m2 is unworn in PIN 3101/364; Fig. 1) the paraconid and metaconid are of similar height and distinctly higher than on m1. The talonid of m2–4 is relatively shorter than on m1. The m4 is distinctly lower and somewhat shorter than m3 (PIN 3101/108; Fig. 4A).

The known specimens show progressive wear of molars and can be grouped into several stages:

(1) PIN 3101/364 (m1–2): completely unworn molars (Fig. 1).

(2) PIN 3101/400 (m1): wear facet 3 produced by the postparacrista of upper molar is developed along the distal metacristid and at the bottom of hypoflexid; there are no wear facets 1 or 2 (Fig. 2C).

(3) PIN 3101/106 (m1–2), PSS 10-15 (m2–3), and PSS 10-31 (m1): vertical wear facet 3 along the distal metacristid is extensive, removing a considerable part of the labial tooth crown and coming down the crown to near the crown-root junction (on m2 of PIN 3101/106 the pulp cavity is visible through a thin dentine layer); protocristid and paracristid are worn by more horizontal wear facets 1 and 2 produced respectively by the preparacrista and postmetacrista of the upper molar. On m1 of PSS 10-31 the horizontal component of wear facet 1 is extensive, while the paracristid is almost unworn. On m1 of PIN 3101/106 the paracristid is little worn (Fig. 3C).

(4) PIN 3101/108 (m3–4): there are extensive vertical wear facets 1 and 3 along the protocristid and distal metacristid, occupying almost all the space of the hypoflexid and coming down to the root labially; a horizontal wear facet 2 is extensive and a vertical component of this facet appears on the labial side along the paracristid. Along the posterolabial side of the hypoconid on m4 of PIN 3101/108 there is a distinct wear facet 4 produced by the premetacrista of M4 (Fig. 4A₁).

(5) PIN 3101/107 (m2) and PSS 10-15 (m1): trigonid cusps are almost completely worn down, the hypoflexid is deeply excavated by the vertical wear facets 1 and 3 (exposing the pulp cavity on PIN 3101/107; Fig. 4B₁).

None of the studied specimens shows unequivocal attritional wear facets within the talonid on the lingual slope of the hypoconid. This would suggest the absence of a well developed protocone on upper molars.

Measurements.—See Table 2.

Discussion

Arguimus khosbajari Dashzeveg, 1979 was originally described on a single dentary fragment with five teeth, interpreted as p2–4, m1–2, and referred to the Peramuridae.

Table 2. Dental measurements in *Arguimus khosbajari* Dashzeveg, 1979. Höövör, Mongolia; Early Cretaceous. The specimens are arranged according to progressive wear.

Specimen	p4		p5		m1		m2		m3		m4	
	L	W	L	W	L	W	L	W	L	W	L	W
PIN 3101/364					1.40	0.65	1.25	0.75				
PIN 3101/400					1.50	0.70						
PIN 3101/106					1.35	0.80	1.40	0.90				
PSS 10-31*	0.96	0.46	0.97	0.61	1.32	0.74						
PSS 10-15*	1.02	0.51	0.95	0.58	1.30	0.76	1.27	0.84	1.23	0.87		
PIN 3101/108									1.25	0.85	1.05	0.70
PIN 3101/107							1.30	0.75				

* After Dashzeveg (1994).

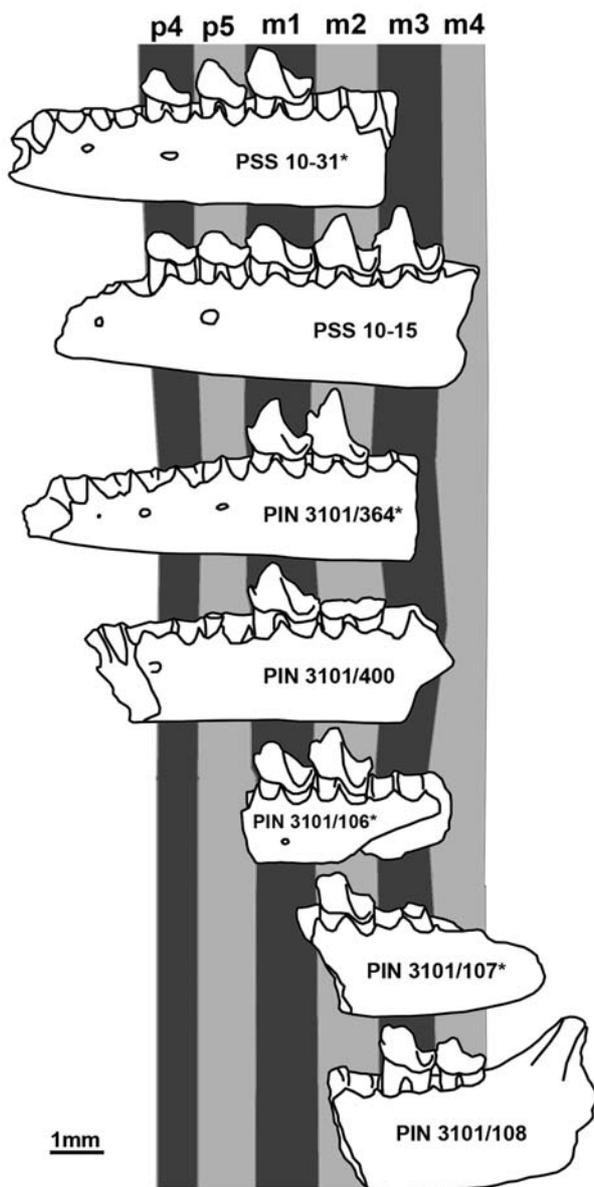


Fig. 6. Known specimens of *Arguimus khosbajari* Dashzeveg, 1979 (Höövör, Mongolia; Early Cretaceous) drawn at the same scale in labial view, with interpretation of preserved dentition. Reversed images are marked by asterisk.

Later Dashzeveg (1994) changed premolar count to p3–5 according to McKenna's (1975) interpretation of the post-canine dental formula as p1–5, m1–3 for *Peramus tenuirostris* Owen, 1871 from the earliest Cretaceous Purbeck Limestone in England. In the same paper he erected the family Arguimuridae for *Arguimus* and then unnamed "eupantotherian" represented by a lower molar from the Late Jurassic of Porto Pinheiro, Portugal (Krusat 1969). He also described *Arguitherium cromptoni*, based on a single dentary fragment with three teeth (interpreted as p4–5, m1), and referred it to the monotypic family Arguitheriidae. Dashzeveg (1994: fig. 8) believed that Arguimuridae were related to the Amphitheriidae and Arguitheriidae were related to the Peramuridae.

McKenna and Bell (1997) referred both the Arguitheriidae and Arguimuridae to the subregion Zatheria and infralegion *incertae sedis*.

Sigogneau-Russell (1999) accepted Dashzeveg's interpretation of *Arguitherium* and noted that this taxon might be related to the primitive tribosphenic mammal *Kielantherium*.

Butler and Clemens (2001) argued that the dental formula of the holotype of *Arguimus khosbajari* was more probably p1–4, m1–4, because the fifth postcanine tooth is distinctly more worn than the following molars and thus cannot be the ultimate premolar.

Martin (2002) reinterpreted the teeth preserved on the holotype of *Arguitherium cromptoni* as p3–5, based on comparison with the stem-lineage zatherian *Nanolestes drescherae* Martin, 2002, from the Late Jurassic Guimarota coal mine in Portugal. This conclusion has been reached earlier by Sigogneau-Russell (1999). Martin (2002) also referred the "Porto Pinheiro molar" to *Nanolestes krusati* Martin, 2002. Both *Arguimus* and *Arguitherium* were considered as having a semimolariform ultimate premolar (p5) by Kielan-Jaworowska et al. (2002) and Tsubamoto et al. (2004). But later Kielan-Jaworowska et al. (2004) followed Butler and Clemens (2001) in their interpretation of the dental formula for *Arguimus* (p1–4, m1–4), while accepting Martin's (2002) identification of the preserved dentition of *Arguitherium* as p3–5.

The foregoing review shows considerable confusion in interpretation of the dentition in *Arguimus* and *Arguitherium*. Although additional materials from the PIN collection are not unconditionally conclusive, study of all available specimens allows us to make the following observations:

(1) The third preserved tooth on the *Arguimus khosbajari* holotype and the last preserved tooth on the *Arguitherium cromptoni* holotype represent the same tooth locus (m1; Fig. 6). This tooth, termed here the "partially molariform" tooth, is characterized by small and widely separated paraconid and metaconid, so the trigonid angle is noticeably greater than in the following molars, and the talonid is compatible in size with that of the following molars. Anterior to this tooth in both specimens are typical premolars, lacking a metaconid, without or with a very small "paraconid", and having a short, cusp-like "talonid". Posterior to this tooth on PSS 10-15 are typical molars with more angulated trigonids. Thus *Arguimus* and *Arguitherium* cannot be differentiated by the degree of molarization of this tooth; it is similarly "semimolariform" in both taxa. Moreover, the "partially molariform" tooth is almost identical in size on the holotypes of both taxa: L = 1.30, W = 0.76 for "p5" in *Arguimus* and L = 1.32, W = 0.74 for "m1" in *Arguitherium* (Dashzeveg 1994: tables. 1, 2) and on the PIN sample (Table 2). Two other characters used for differentiation of *Arguitherium* and *Arguimus* by Dashzeveg (1994), absence of a talonid basin and presence of additional talonid cusps (entoconid and hypoconulid) on the molars of *Arguimus*, are misinterpretations due to the heavily worn teeth (the talonid is worn labially by the posterior side of the paracone; wear facet 3). Sigogneau-Russell (1999) also observed only a

single talonid cusp in both taxa. Thus we find no morphological or dimensional grounds for referring PSS 10-15 and 10-31 to different taxa and consider *Arguitherium cromptoni* Dashzeveg, 1994 a junior subjective synonym of *Arguimus khosbajari* Dashzeveg, 1979 (syn. nov.). All PIN specimens described in this paper are referable to the same taxon.

(2) The postcanine teeth in *Arguimus* are basically similar to postcanine teeth in *Peramus*, now almost universally interpreted as p1–5, m1–3 (Kielan-Jaworowska et al. 2004). In both taxa three undoubted molars are separated from the undoubted premolars by a “partially molariform” tooth with a widely open trigonid angle. However, in *Peramus* this tooth (p5) has nothing but a metaconid swelling on the protocristid in contrast to the real albeit small metaconid in *Arguimus*. None of the known pretribosphenic mammals have a “semi-molariform” ultimate premolar with a distinct metaconid, and even in the basal eutherian *Prokennalestes* p5 is not molariform (Kielan-Jaworowska and Dashzeveg 1989). This suggests that the “partially molariform” tooth in *Arguimus* is the m1. A marked difference in triangulation between this tooth and the following molars might be a primitive trait, seen for example in the Late Jurassic *Tinodon* from North America (e.g., Sigogneau-Russell 2003: pl. 1: 9). In *Nanolestes* none of the lower molars is associated with a dentary. Martin (2002: fig. 4) described three lower deciduous premolars of *Nanolestes drescheriae*, all having an elongate crowns and a widely lingually open trigonid basins, recalling the morphology of the “partially molariform” tooth in *Arguimus*. However, one tooth (Gui Mam 1005; Martin 2002: 336, fig. 4A–C), considered as coming “from a more posterior position” (dp?2–3), differs in a number of details from the two remaining deciduous teeth. It has a relatively smaller and less anteriorly procumbent paraconid, a relatively higher metaconid, a narrower talonid, and lacks a characteristic ridge-like cuspule along the lingual edge of the trigonid basin between the paraconid and metaconid. This tooth (Gui Mam 1005) may be actually a m1 of *Nanolestes*, and if this is correct, both *Nanolestes* and *Arguimus* would be similar in having m1 with a widely open trigonid basin, that is less angulated than remaining molars. Two very similar “partially molariform” teeth from the Berriasian Purbeck Limestone of England have been described as a new dryolestoid *Chunnelodon alopekoides* Ensom et Sigogneau-Russell, 1998 (Ensom and Sigogneau-Russell 1998; Kielan-Jaworowska et al. 2004). These teeth may be actually m1’s of a stem-lineage zatherian similar in size to *Minimus richardfoxi* Sigogneau-Russell, 1999 from the Berriasian of Morocco (Sigogneau-Russell 1999).

(3) In *Peramus* the posterior mental foramen is situated under the posterior root of p4 (BMNH M21888, M47739), or the anterior root of p5 (BMNH M47744). In *Nanolestes* the posterior mental foramen is under posterior root of p5 (Martin 2002: fig. 7C). In *Arguimus* this foramen is between the roots of the “partially molariform” tooth (PIN 3101/106), under the ultimate undoubted premolar (PSS 10-15, PIN 3101/108 and 364), or the penultimate undoubted premolar (PSS 10-31, PIN

3101/400). Thus, position of the posterior mental foramen predominantly under the undoubted premolars also suggests that the “partially molariform” tooth in *Arguimus* is the m1.

(4) As previously noted by Butler and Clemens (2001), the “partially molariform” tooth in PSS 10-15 is more worn than the following molars and thus cannot be the ultimate premolar. In trechnotherians, the first molar is fully erupted long before replacement at the last premolar locus and thus the ultimate premolar cannot be more worn than m1 (Kielan-Jaworowska et al. 2004). The same wear pattern is observed on PIN 3101/106, where the “partially molariform” tooth is distinctly more worn than the following molar (Fig. 3). This further supports our interpretation that the tooth in question on the holotype of *Arguimus khosbajari* is the m1.

(5) None of the known dentary specimens of *Arguimus* is complete anteriorly and the claim that the canine alveoli are preserved on the holotype (Dashzeveg 1994) cannot be confirmed. Material of *Nanolestes* (Martin 2002) and *Prokennalestes* (collection PIN 3101) demonstrate that the dentaries in pretribosphenic and early eutherian mammals could be long. Pretribosphenic mammals with a known dental formula (*Nanolestes*, *Peramus*) have five premolars and this number of premolars is postulated here for *Arguimus*. In *Nanolestes*, anterior premolars are widely separated by diastemata and p2 is smaller than p1, resembling dryolestids (Martin 2002), while in *Peramus* the diastemata are reduced and p1 is smaller than p2. In *Arguimus* premolars are closely packed, without diastemata, and judging from alveoli in PSS 10-31 and PIN 3101/364, p2 was larger than p1 and 3, resembling *Prokennalestes* (Sigogneau-Russell et al. 1992; collection PIN 3101).

Summarizing, the lower postcanine dental formula of *Arguimus* is interpreted here as p1–5, m1–4, which is intermediate between *Nanolestes* (p1–5, m1–5) and *Peramus* (p1–5, m1–3). One of the peculiarities of *Arguimus* is the labially oblique tooth row, with a great difference in height between the labial and lingual margins of the alveoli, so alveoli for cheek teeth are well exposed on the labial side but not on the lingual side (Figs. 1D, F, 2D, F, 3A, B, 4A₃, A₄, B₃, B₄, and 6). A similar condition is apparently characteristic of *Nanolestes* (Martin 2002: fig. 5), but not of *Peramus* (personal observations by AA). The phylogenetic significance of this character is unclear. It is characteristic also for dryolestids and spalacotheriids and may be correlated with the rotation of the mandibular ramus during occlusion and, thus, acquired independently in different groups. *Arguimus* apparently occupies phylogenetic position intermediate between *Nanolestes* and *Peramus*, being transitional in dental formula, similar to *Peramus* but more derived than *Nanolestes* in having an incipient talonid basin, and possibly sharing with *Nanolestes* a plesiomorphic m1 with a widely open trigonid basin that is less angulated than on the following molars (see above). *Arguimus* differs from both *Nanolestes* and *Peramus* in the total absence of the Meckel’s groove, which may be an autapomorphy of this taxon. The synonymy of *Arguimus* and *Arguitherium*, established in this paper, im-

plies synonymy of Arguimuridae Dashzeveg, 1994 and Arguitheriidae Dashzeveg, 1994 (syn. nov.). However, as pointed out by Martin (2002) and confirmed by this study, “Arguimuridae” differ from Peramuridae Kretzoi, 1946 only in plesiomorphic characters (less advanced dental formula and single cusped talonid) and thus recognition of this family is not warranted. Zatheria McKenna, 1975 are diagnosed by reduction of molars to three [the presence of four molars in metatherians was secondarily acquired by lack of replacement of the last deciduous tooth], basined talonids, and presence of both the hypoconid and hypoconulid (Prothero 1981; Kielan-Jaworowska 2004). *Arguimus* has four molars and lacks the hypoconulid and thus it belongs to the stem-lineage representatives of Zatheria (Martin 2002; Kielan-Jaworowska et al. 2004).

Acknowledgments

We thank Profs. William Clemens (Museum of Paleontology, University of California, Berkeley) and Denise Sigogneau-Russell (Muséum national d'Histoire naturelle, Paris) for reading of the manuscript and critical comments. This work was supported by the Russian Fund of Basic Research (RFBR) grants 04-04-49637, 04-04-49113, 04-05-64805, and 02-04-48458, President's of Russia grants MD-255.2003.04 and NSH-1840.2003.4, and Russian Science Support Foundation. The US Civilian Research and Development Foundation (CRDF) grant #RUG1-2571-ST-04, which supported study of various Mesozoic mammals in Natural History Museum (London), American Museum of Natural History (New York), Peabody Museum of Yale University (New Haven), and National Museum of Natural History (Washington) by AA, is also gratefully acknowledged.

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