Kielantherium, a basal tribosphenic mammal from the Early Cretaceous of Mongolia, with new data on the aegialodontian dentition

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Two additional specimens of the basal tribosphenid mammal *Kielantherium gobiense*, the first known aegialodont upper molar (possibly M2) and a dentary fragment with m1, are described from the Early Cretaceous Höövör locality in Mongolia. The upper molar shows an initial stage of the protocone development. *Kielantherium gobiense* has been known from two specimens only, and thus the new material doubles the hypodigm of this species. *Kielantherium* is clearly not a junior synonym of *Aegialodon*, as it differs from the latter in having a cusp-like mesiolabial cingulid cuspule *f* rather than prominent ridge-like precingulid. *Kielantherium*'s lower postcanine dental formula (with four or more premolars and four molars) is distinctive and more primitive than in *Peramus* and Eutheria which have five premolars and three molars, and Metatheria which have three premolars and four molars.

Key words: Mammalia, Tribosphenida, Aegialodontia, *Kielantherium*, Cretaceous, Mongolia.

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Introduction

The Early Cretaceous was crucial for the establishment of therian mammals (placentals and marsupials), the dominant mammalian group in the subsequent epochs. The ancestry of the Theria is among poorly known groups of basal tribosphenic mammals, one of them being the Aegialodontia, which have been found in just a few Early Cretaceous localities of Eurasia.

This paper adds new information to an important Early Cretaceous mammal fauna from Höövör in the northern Gobi Desert, Mongolia, which was collected by the Soviet-Mongolian expeditions in the late 1960s and early 1970s and deposited in the Paleontological Institute of the Russian Academy of Sciences in Moscow (see Lopatin and Averianov 2006a). In this report we describe two additional specimens of the rarest species in the collected fauna, a basal tribosphenic (aegialodontid) mammal, *Kielantherium gobiense* Dashzeveg, 1975. This species has previously been known only from two specimens, the holotype lower molar and a dentary fragment with four molars (Dashzeveg 1975; Dashzeveg and Kielan-Jaworowska 1984). Thus the two additional specimens described here double the known sample of the species. One of these specimens, PIN 3101/110, is an upper molar, found by the authors in June 2005 in an unsorted sample of mammalian teeth from Höövör (Lopatin and Averianov 2006b). This tooth, at present the only known aegialodont upper molar, preserves a small but unmistakable protocone. Another specimen, a dentary fragment PIN 3101/32 has been known to exist for as long as the holotype of *K. gobiense*, but has never been described.

Institutional abbreviations.—PIN, Paleontological Institute, Russian Academy of Sciences, Moscow, Russia; PSS, Paleontology and Stratigraphic Section of the Geological Institute, Mongolian Academy of Sciences, Ulaanbaatar, Mongolia.

Other abbreviations.—L, length; Ltal, talonid length; W, width; Wtal, talonid width. All measurements are in mm.

Systematic paleontology

In classification of Mesozoic mammals and morphological terminology, we follow Kielan-Jaworowska et al. (2004). Nomenclature for wear facet is after Crompton (1971).

Mammalia Linnaeus, 1758

Tribosphenida McKenna, 1975

Aegialodontia Butler, 1978

Aegialodontidae Kermack, 1967

Genus *Kielantherium* Dashzeveg, 1975

Type species: *Kielantherium gobiense* Dashzeveg, 1975. Höövör, Mongolia, Aptian–Albian, Early Cretaceous.

Included species: Type species only.

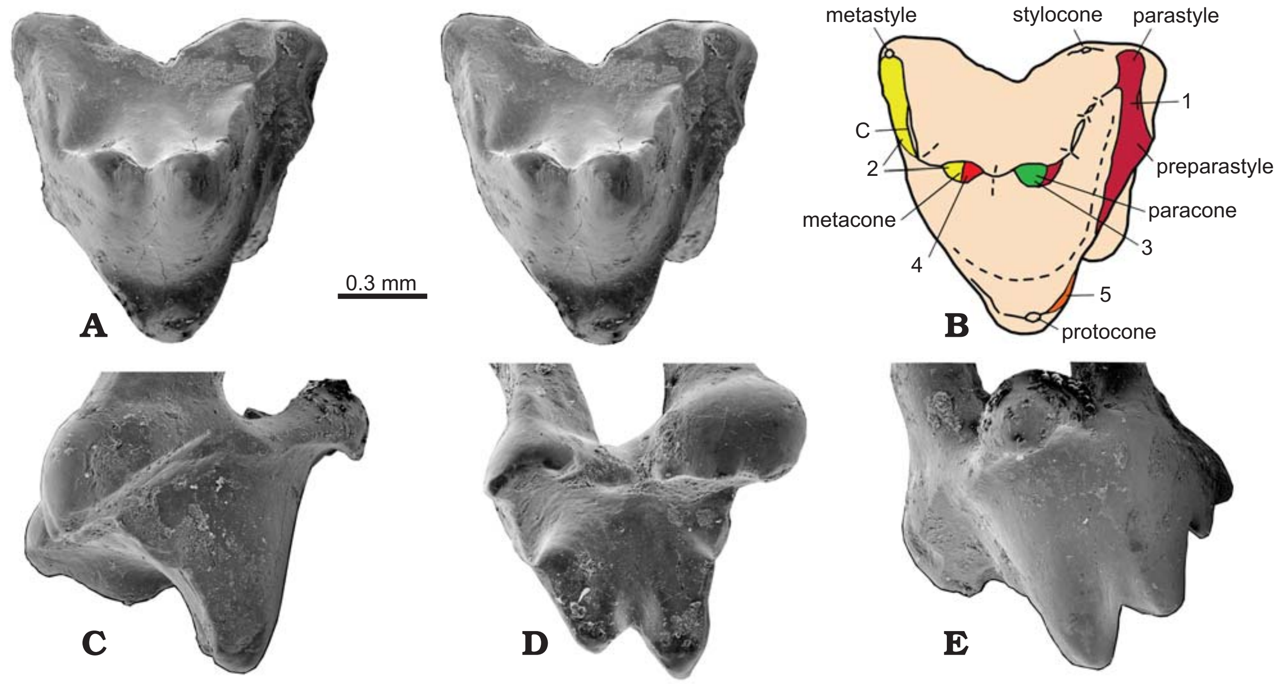

Fig. 1. Tribosphenic mammal *Kielantherium gobiense* Dashzeveg, 1975. PIN 3101/110, right upper molar, possibly M2. Höövör, Mongolia; Early Cretaceous. SEM micrographs. In occlusal view (**A**, stereopair); explanatory drawing of occlusal view (**B**), posterior (**C**), labial (**D**), and lingual (**E**) views.

Revised diagnosis.—Differs from *Aegialodon* Kermack, Lees and Mussett, 1965 in having cusp-like mesiolabial cingulid cuspule *f*, rather than prominent ridge-like precingulid. Differs from *Tribactonodon* Sigogneau-Russell, Hooker, and Ensom, 2001 in lacking entoconid and lingual cingulid, and having much smaller mesial cingulid cuspules *e* and *f*. Differs from *Hypomylos* Sigogneau-Russell, 1992 in having larger and higher paraconid, well developed mesial cingulid cuspules, relatively shorter talonid with a more horizontal, and less sloping lingually talonid basin bordered lingually by a more prominent entocristid. Differs from crown-group Theria in having a distinctly smaller protocone, and smaller and shorter talonid basin with only two cusps. Differs from *Peramus* Owen, 1971 by having protocone and four molars. Additionally differs from Eutheria in having four molars and from Metatheria in having at least four premolars.

Kielantherium gobiense Dashzeveg, 1975

Figs. 1–3.

1975 [cf.] *Aegialodon* [sp.]; Kielan-Jaworowska 1975: 105, 106.
1975 *Kielantherium gobiensis* Dashzeveg, 1975: 402, figs. 1, 2.
1976 *Aegialodon gobiensis*; Fox 1976: 1117.
1978 *Kielantherium gobiensis*; Crompton and Kielan-Jaworowska 1978: 257, figs. 2, 3.
1979 *Kielantherium gobiensis*; Kielan-Jaworowska et al. 1979: 183, fig. 10-1.
1984 *Prodelttheridium* [lapsus calami for *Prodeltatheridium*] *kalandadzei* [nomen nudum]; Reshetov and Trofimov 1984: 12.
1984 *Kielantherium gobiensis* Dashzeveg, 1975; Dashzeveg and Kielan-Jaworowska 1984: 219, figs. 1, 2.
1990 *Kielantherium gobiensis*; Butler 1990: fig. 3.
1992 *Kielantherium*; Butler 1992: fig. 1.
1995 *Kielantherium*; Sigogneau-Russell 1995: fig. 7C.
2000 *Kielantherium gobiensis* Dashzeveg, 1975; Kielan-Jaworowska et al. 2000: 599, fig. 29.17.
2001 *Kielantherium gobiensis*; Kielan-Jaworowska and Cifelli 2001: fig. 5A.
2001 *Kielantherium*; Luo et al. 2001: fig. 2.
2004 *Kielantherium gobiensis* Dashzeveg, 1975; Kielan-Jaworowska et al. 2004: 419, fig. 11.4A.
2006 *Kielantherium gobiense* Dashzeveg, 1975; Lopatin and Averianov 2006b: 1092, fig. 1 [correction of the species name according to the neuter gender of the generic name].

Holotype: PSS 10-14, right lower molar, possibly m2.

Type locality: Höövör (variously spelled Khoboor, Khobur, Khoobur, and Khovboor), northern Gobi Desert, Mongolia.

Type horizon: Züünbayan [= Dzun Bayan, = Dzunbain] Svita (alternatively referred to as Khulsangol [= Khulsyngol] or Döshuul [= Dushuul, = Dushi Ula] Svita), Aptian–Albian, Early Cretaceous.

Material.—PIN 3101/110, right upper molar, possibly M2; PSS 10-16, right dentary fragment with m1–4 and alveoli or roots of four double-rooted premolars, and broken alveolus for another premolar or the canine; PIN 3101/32, right dentary fragment with m1.

Diagnosis.—As for genus.

Description.—The outline of the upper molar, probably an M2 (PIN 3101/110; Fig. 1), forms a near isosceles triangle dominated by the paracone and metacone, with an extensive stylar shelf and a very small protocone. The paracone and metacone closely approximate each other and are connate, with a very short and shallow centrocrista; the paracone is distinctly higher than the metacone. The lingual slopes of the paracone and metacone are slightly convex while their labial slopes are slightly concave. The preparacrista is mesiolabially directed and connects with the parastyle rather than with a minute

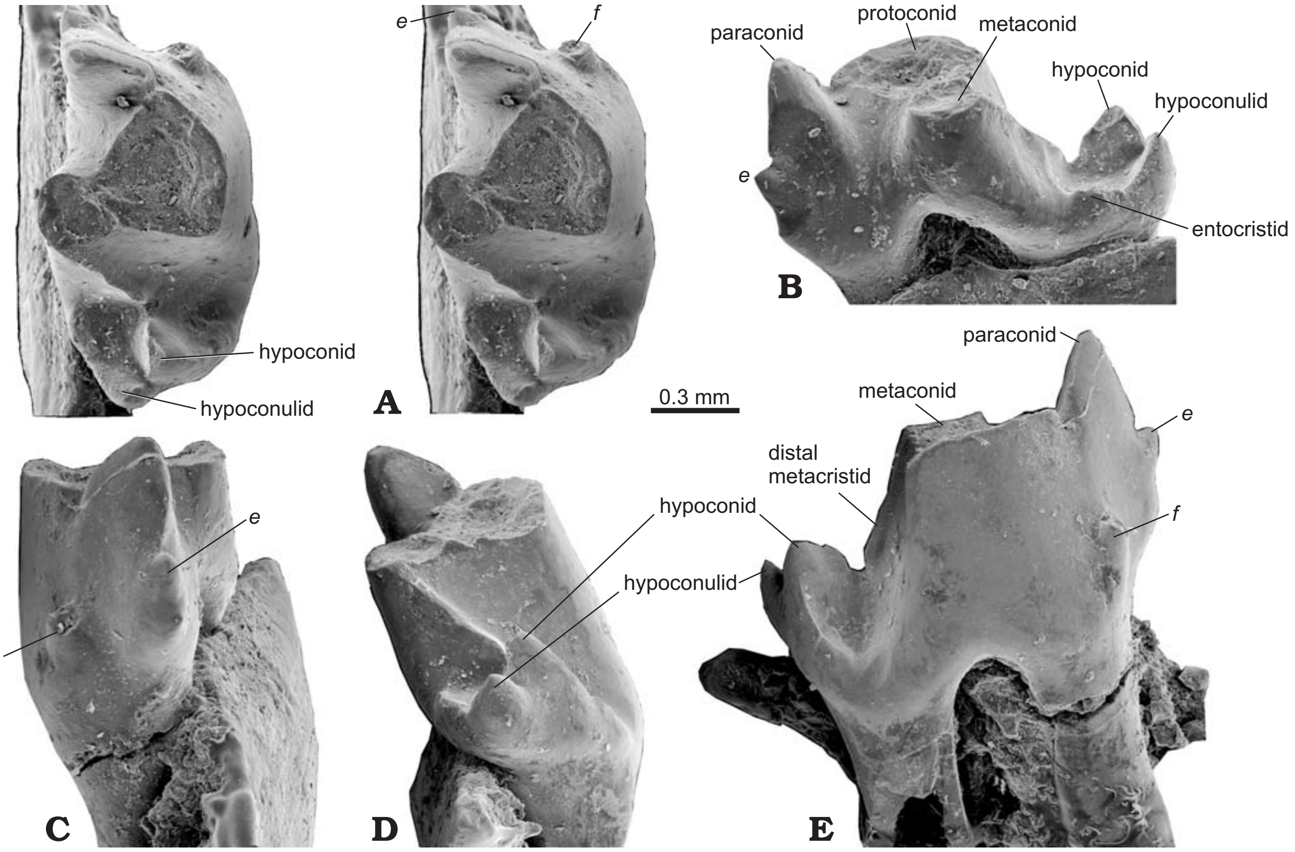

Fig. 2. Tribosphenic mammal *Kielantherium gobiense* Dashzeveg, 1975. PIN 3101/32, right dentary fragment with m1 as now preserved. Höövör, Mongolia; Early Cretaceous. SEM micrographs. In occlusal (**A**, stereopair), lingual (**B**), anterior (**C**), posterior (**D**), and labial (**E**) views.

stylocone; in the centre of the preparacrista there are two small cusp-like eminences. The parastylar wing (Kielan-Jaworowska et al. 2004) is well developed. A distinct preparastyle is present lingual to the parastyle. The parastylar groove is well developed. The ectoflexus is distinct and of moderate depth. There are three small stylar cusps distal to the stylocone on the ectocingulum. The postmetacrista is more transverse than the preparacrista and bears a well developed postmetacrista cusp (cusp "*c*" in Crompton 1971, emended as "*C*" in Kielan-Jaworowska et al. 2004). There is a very small, ridge like metastyle. The protocone is a small, distinct but very low cusp; it is about one-fourth the height of the paracone. The protocone is narrow labiolingually and slightly elongate mesiodistally. The preprotocrista is rather long, extending mesiolabially towards the preparastyle. This labially extended preprotocrista and the preparacrista provide for double-rank prevallum/postvallid shearing, a distinctive synapomorphic feature of Tribosphenida (Fox 1975; Luo et al. 2002; Kielan-Jaworowska et al. 2004). The postprotocrista is much shorter, terminating at the lingual base of the metacone. There are no conules. The crown is slightly worn, with prominent wear facet 1 along the preparacrista, on the mesial slope of the paracone apex, and along the parastylar groove and wear facet 2 along the postmetacrista and on the metacone apex. On the centrocrista the small wear facets 3 and 4 are confined to the paracone and metacone, respectively. There is also a distinct wear facet 5 along the preprotocrista. There are three roots; the preserved labial roots are rather long. The not preserved lingual root, supporting the protocone, apparently was distinctly smaller than the labial roots.

The lower molar (PIN 3101/32; Figs. 2, 3) is identified as m1 because the protocristid is almost transverse to the long axis of the dentary, as in m1 of PSS 10-16 (Dashzeveg and Kielan-Jaworowska 1984: fig. 2B), whereas in the holotype (m2; Crompton and Kielan-Jaworowska 1978: fig. 3B) and in m2–4 of PSS 10-16, it is more oblique, with the metaconid placed somewhat posterior to the protoconid. The crown is dominated by a large trigonid, whereas the talonid is much smaller, some 24% of the trigonid length. The crown is higher labially than lingually because the crown basal margin is distinctly lowered labially. The apices of the protoconid and metaconid are broken off. In the trigonid the protoconid is the most massive and was almost certainly the tallest cusp, with its base (which is somewhat triangular in cross section) occupying most of the trigonid area. The trigonid basin is small and widely open lingually, with the bases of the paraconid and the metaconid well separated. The paraconid is a distinct, ridge like cusp, almost vertically directed. The paraconid is mesiodistally compressed, with a sharp paracristid, while the metaconid is more rounded at the base. On the anterior side at the base of the paraconid there are two prominent cingulid cusps, the mesiolingual cuspule *e* and the mesiolabial cuspule *f*. These cusps are well separated and apparently abutted against the distal margin of the ul-

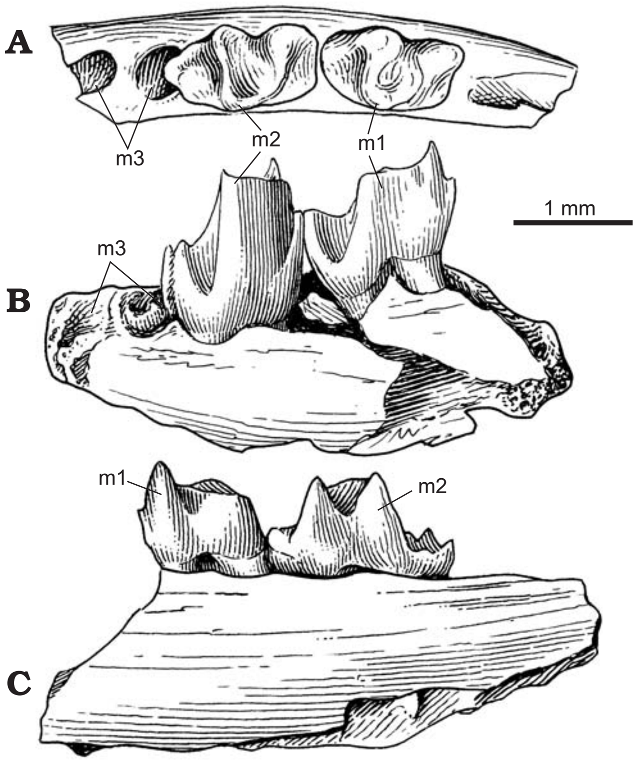

Fig. 3. *Kielantherium gobiense* Dashzeveg, 1975. PIN 3101/32, right dentary fragment with m1–2 and alveoli for the ultimate premolar, and m3. Original unpublished drawing by Konstantin P. Meshkov of the specimen from the PIN archive before damage. Höövör, Mongolia; Early Cretaceous. This drawing should be considered with caution as the tooth proportions are not always exact, particularly wrong is depicting of the m1 talonid in lingual view (**C**), showed as a part of the m2 crown. In occlusal (**A**), labial (**B**), and lingual (**C**) views.

timate premolar. The mesiolingual cuspule *e* is a continuation of a sharp vertical crest along the mesiolingual edge of the paraconid, but separated from the latter crest by a distinct notch. The distal metacristid (Fox 1975) is a distinct, sharp crest, extending from the lingual side of the metaconid (possibly from its apex) towards the base of the hypoconid. The hypocristid is also high and sharp, separated from the distal metacristid by a distinct notch. The talonid is two-cusped, with the hypoconid about twice as large as the hypoconulid and placed midway along the width of the talonid, relatively close to the level of the protocristid notch. The talonid cusps are positioned close to one another. The lingual side of the hypoconid is almost vertical, sloping into the relatively small talonid basin. The hypoconulid is lower than the hypoconid and forms a short posterior wall of the talonid basin; it bears a sharp postcristid on its labial slope. The talonid basin is widely open lingually, without even an incipient entoconid; although bordered lingually by a distinct ridge (entocristid). The entocristid bears at least one crenulation, similar to that described for the *K. gobiense* holotype (Dashzeveg 1975). The crown is at a very early stage of wear, showing only an incipient wear facet 3 in the hypoflexid produced by the paracone, the highest upper crown cusp. The two roots are almost equal in length.

Measurements.—See Table 1.

Remarks.—When found, PIN 3101/32 was a dentary fragment with two molars (m1–2) and alveoli for the ultimate premolar and m3 (Fig. 3). Kielan-Jaworowska (1975) noted a similarity of this specimen to *Aegialodon* and subsequently it was included in the material of *K. gobiense* in the original description of this species, established upon a single lower molar from the Ulaanbaatar collection (Dashzeveg 1975). Subsequently, this specimen suffered serious damage, and now only m1 adherent to a small piece of the dentary is preserved (Fig. 2). Apparently it was broken along the crack seen on this specimen in a drawing from the PIN archive (Fig. 3B) and the posterior part of the specimen is now missing. This specimen was attributed to "*Prodeltatheridium kalandadzei*" [nomen nudum] by Boris A. Trofimov (Paleontological Institute, Moscow), according to the label accompanying this drawing.

The lower molar (m1) in PIN 3101/32 appears to be somewhat larger than previously known lower molars of *Kielantherium* (Table 1). However, the actual measurements of the teeth in the previously known specimens of *Kielantherium* (PSS 10-14 and 10-16) were never published. Our values for these specimens as given in Table 1 were taken from the published figures of them, so whether the differences in dimensions between PIN 3101/32 and these teeth are real is not entirely certain.

Discussion

When first described, *Kielantherium* was referred to the Aegialodontidae and considered as "almost identical" with *Aegialodon* from the Valanginian of Great Britain (Dashzeveg 1975: 402). Indeed, the similarity is so striking that some authors synonymized the genera (Fox 1976; McKenna and Bell 1997). We think that *Kielantherium* is clearly different (more plesiomorphic) than *Aegialodon* in having a small, cusp-like

Table 1. Dental measurements in *Kielantherium gobiense* Dashzeveg, 1975. Höövör, Mongolia; Early Cretaceous.

Specimen	M2		m1				m2				m3				m4			
	L	W	L	Ltal	W	Wtal	L	Ltal	W	Wtal	L	Ltal	W	Wtal	L	Ltal	W	Wtal
PIN 3101/110	1.25	1.30																
PSS 10-16*			1.18	0.31	0.69	0.38	1.19	0.31	0.71	0.49	1.13	0.28	0.71	0.49	0.93	0.28	0.58	0.41
PIN 3101/32			1.65	0.45	0.80	0.80												
PSS 10-14**							1.28	0.41	0.76	0.57								

* calculated after Dashzeveg and Kielan-Jaworowska (1984: figs. 1, 2); ** calculated after Crompton and Kielan-Jaworowska (1978: fig. 2).

mesiolabial cingulid cuspule *f*, while in *Aegialodon* it is transformed into a prominent ridge, the precingulid, like that in more derived therian mammals. No upper molar is known for *Aegialodon*, but Crompton (1971: fig. 4) provided a hypothetical reconstruction. PIN 3101/110 is generally similar to this reconstruction, differing mostly in having a more transverse postmetacrista and in lacking the paraconule.

Dashzeveg and Kielan-Jaworowska (1984) described PSS 10-16, a dentary fragment with four molars and alveoli for at least four double-rooted premolars, the most nearly complete specimen of *Kielantherium* known so far. The dentary bears a relatively deep Meckel's groove posteriorly and a labial mandibular foramen within the masseteric fossa posterior to the coronoid crest; a similar foramen has been recently reported for the pretribosphenic mammal *Arguimus* Dashzeveg, 1979 from the same Höövör fauna (Lopatin and Averianov 2006a). This specimen is crucial for postulating that the primitive molar count for Tribosphenida is four, not three, as suggested by McKenna (1975; see also Prothero 1981), based on the interpretation of the postcanine dental formula of the pretribosphenic (zatherian) mammal *Peramus* from the Berriasian of Great Britain as P1–5 M1–3 / p1–5 m1–3. In stem-lineage zatherians, the number of molars varies from five (*Nanolestes* Martin, 2002) to four (*Arguimus*).

Interestingly, *Peramus* possesses lower molars with a two-cusped talonid and with an incipient talonid basin, while the protocone on its upper molars is totally lacking (Clemens and Mills 1971; personal observations by AA). Similarly, a well developed talonid is present in Australosphenida, while their upper molars, still not known, may lack the protocone (Woodburne 2003; Martin and Rauhut 2005). Thus, an incipient talonid basin is not necessarily indicative for the presence of the protocone on upper molars. Besides, Li et al. (2005) recently reinvestigated PSS 10-16 and did not find wear facet 5, a product of shearing against the protocone lingual to the distal metacristid. They therefore questioned the presence of a functional protocone in *Kielantherium*. Discovery of PIN 3101/110 shows for the first time that a functional protocone was indeed developed in at least one aegialodontid (Lopatin and Averianov 2006b). Based upon the upper molars known for *Peramus* and *Deltatheridium* Gregory and Simpson, 1926, PIN 3101/110 is likely M2 of *Kielantherium*. In overall appearance, the labial part of the *Kielantherium* upper molar is very similar to upper molars of *Peramus*, but lingually it is strikingly dissimilar in having a distinct protocone. Structurally, the upper molar of *Kielantherium* is truly intermediate between pretribosphenic *Peramus* and basal tribosphenic mammals such as *Pappotherium* Slaughter, 1965.

Tribactonodon, known from a single isolated lower molar from the Berriasian of Great Britain, is a basal tribosphenic mammal provisionally referred to the Aegialodontia (Sigogneau-Russell et al. 2001; Kielan-Jaworowska et al. 2004). In this taxon the talonid is relatively longer and the mesial cingulid cuspules *e* and *f* are hypertrophied compared with the condition in *Kielantherium*. Also, in contrast to *Kielantherium*, the hypoconulid is distinctly larger than the hypoconid, which may be a positional variation because the only known specimen of *Tribactonodon* is apparently an ultimate molar (Sigogneau-Russell et al. 2001). Another striking feature of *Tribactonodon* is a lingual cingulid, totally absent in *Kielantherium* (a faint lingual cingulid might be present in *Aegialodon*, see Sigogneau-Russell et al. 2001). The talonid of *Tribactonodon* is three-cusped, with an incipient entoconid, while two-cusped in *Kielantherium*. Sigogneau-Russell and Ensom (1994) described two fragments of two-cusped talonids also coming from the Berriasian of England. In these specimens the hypoconulid is only slightly smaller, or even somewhat larger than the hypoconid, closer to the condition in *Tribactonodon* than *Kielantherium*.

Hypomylos from the Berriasian of Morocco is another stem tribosphenidan taxon known from isolated lower molars classified into two-three species (Sigogneau-Russell 1992, 1995). These molars are structurally similar to those of *Kielantherium*, but clearly different in having a reduced paraconid, a relatively longer talonid with the talonid basin sloping lingually and not bordering by the entocristid. In *Hypomylos* also the mesiolabial cingulid cuspule *f* is less developed while the mesiolingual cuspule *e* is totally lacking; both cuspules are well developed in *Kielantherium*.

Marshall and Kielan-Jaworowska (1992) and Kielan-Jaworowska (1992: fig. 1) proposed that Aegialodontia are structurally ancestral to Metatheria but not Eutheria, based on similarity between aegialodontids and stem metatherians (Deltatheridia) in having four molars, a similarly shaped trigonid with the paraconid higher or subequal to the metaconid, and a low, narrow and short talonid set on the lingual side of the trigonid. But *Kielantherium* is distinctly different from Deltatheridia in having at least four premolars, not three as in metatherians (Cifelli 1993; Kielan-Jaworowska and Cifelli 2001). The upper molar of *Kielantherium* described herein is inconsistent with this hypothesis. By having the preparastyle PIN 3101/110 is reminiscent of early eutherians, such as *Prokennalestes* Kielan-Jaworowska and Dashzeveg, 1989 and *Murtoilestes* Averianov and Skutschas, 2001, but not metatherians. Discovery of a *Kielantherium* upper molar suggests that divergence of metatherian and eutherian lines took place at a more derived morphological stage than that exemplified by *Kielantherium*.

Acknowledgments

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