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Two Previously Unknown Eupantotheres (Mammalia, Eupantotheria)[1]

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ABSTRACT

Two new families of Eupantotheria, Arguitheriidae and Arguimuridae, are described from the Early Cretaceous Khoobur locality in Mongolia. The Arguitheriidae are represented by a new genus and species, *Arguitherium cromptoni*. The Arguimuridae are represented by *Arguimus khosbajari* Dashzeveg, 1979, from the Early Cretaceous of Mongolia, and are also known by an unnamed genus from the Jurassic of Porto Pinheiro, Portugal (Krusat, 1969). This paper discusses the general dental features of earliest therians within the Eupantotheria; these features relate to the evolution of molar cusps.

INTRODUCTION

In recent years there have been many discoveries of specimens assigned to Eupantotheria. The remains of this group are known from the Late Jurassic of Portugal and Western Europe (Krebs, 1991), as well as the Early Cretaceous of Morocco in North Africa (Sigogneau-Russell et al., 1990) and Patagonia in South America (Bonaparte, 1986). The collections of 1965 from the Early Cretaceous Khoobur (sometimes Khovrboor) locality, Mongolia, contained, apart from Symmetrodonta, Triconodonta, Multituberculata, and Eutheria, some fragments that represent more primitive mammals (Dashzeveg, 1979). The present paper gives a brief description of two new eupantotherid families that contribute significantly to our knowledge of Mesozoic mammals.

The age of the Khoobur fauna of Mongolia is tentatively dated as Aptian-Albian within the lower Cretaeous (Kielan-Jaworowska and Dashzeveg, 1987). The institutional abbreviation used here is PSS for specimens from the Paleontology and Stratigraphic Section of

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the Geological Institute of the Mongolian Academy of Sciences.

SYSTEMATICS

CLASS MAMMALIA LINNAEUS, 1758

SUBCLASS THERIA PARKER AND HASWELL, 1897

INFRACLASS PANTOTHERIA SIMPSON, 1929

ORDER EUPANTOTHERIA KERMACK AND MUSSETT, 1958

SUBORDER AMPHITHERIA KERMACK, KERMACK AND MUSSETT, 1968

Arguitheriidae, new family

DIAGNOSIS: p5 is premolariform, lacking a distinct talonid basin. m1 has a poorly developed trigonid basin and a distinct cristid obliqua. Except for the hypoconulid (?), cusps on the m1 talonid are not yet differentiated, but a basin exists. The labial side of m1 shows an anterior cingulum.

INCLUDED GENERA: *Arguitherium,* n. gen.

COMPARISONS: Arguitheriidae differ from Amphitheriidae by the presence of a talonid basin and a better-developed cingulum on the labial side of m1. They differ from Peramuridae in having a nonmolariform p5, and a less-developed cristid obliqua and undifferentiated cusps on the m1 talonid.

Arguitherium, new genus

ETYMOLOGY: The name is derived from that of the Argui River near the Khoobur locality.

TYPE SPECIES: *Arguitherium cromptoni,* n. sp.

DIAGNOSIS: Same as for family.

Arguitherium cromptoni, new species

(Figures 1, 3, 4; table 1)

ETYMOLOGY: The species is named after Professor A. W. Crompton to mark his valuable contribution to Mesozoic mammalian studies.

HOLOTYPE: PSS no. 10-31, a fragment of the right lower jaw with p4-5 and m1; the Valley of Lakes, Ubur-Khangai county, Guchin Us, Khoobur locality.

AGE: Lower Cretaceous—Aptian-Albian.

DIAGNOSIS: Same as for family.

DESCRIPTION: Dental formula: i? c1 p5, m3.

TABLE 1
Measurements (mm) of *Arguitherium cromptoni*

	p4	p5	m1
Length	0.96	0.97	1.32
Width	0.46	0.61	0.74

The jaw shows the preserved p4-5 and m1, while the alveoli available indicate the presence of c1, p1, p2, p3, m2, and part of m3. The canine is comparatively small; its length is about one-half its width. Judged by the alveolus p1 has one root. All the premolars after p1 are double-rooted. The p4 is asymmetrical; the frontal slope of the main cusp is steep, while the rear one is gentle; the talonid is poorly outlined. The fifth lower premolar is slightly larger than p4 and is unmolarized except for an incipient metaconid, while its talonid is quite distinct. The first lower molar is larger than p5. The trigonid of m1 consists of three cusps of unequal size: the protoconid is the highest and most massive; the metaconid is much smaller and lower than the protoconid; and the paraconid is the smallest trigonid cusp. The meta- and paraconids are linked with the protoconid by weak cristids. The trigonid basin is comparatively poorly developed. The talonid is well developed, and is much lower than the trigonid. Its cristid obliqua is well expressed. The talonid basin is not well developed and is comparatively narrow. The talonid cusps are undifferentiated except for a small hypoconulid (?) which lies at the distal end of the talonid.

The m1 talonid shows distinct facets. Facet 3 (after Crompton, 1971) is quite pronounced at the rear base of the protoconid, at the trigonid and talonid juncture. Facet 4 is very pronounced at the labial side of the talonid, and has a distinctly triangular shape. Thus, the metacone on the respective upper molars was probably well developed.

Arguimuridae, new family

DIAGNOSIS: No talonid basin developed on the lower molars. The fifth lower premolar tends to be molariform. The paraconid and metaconid on m2 are much lower than the

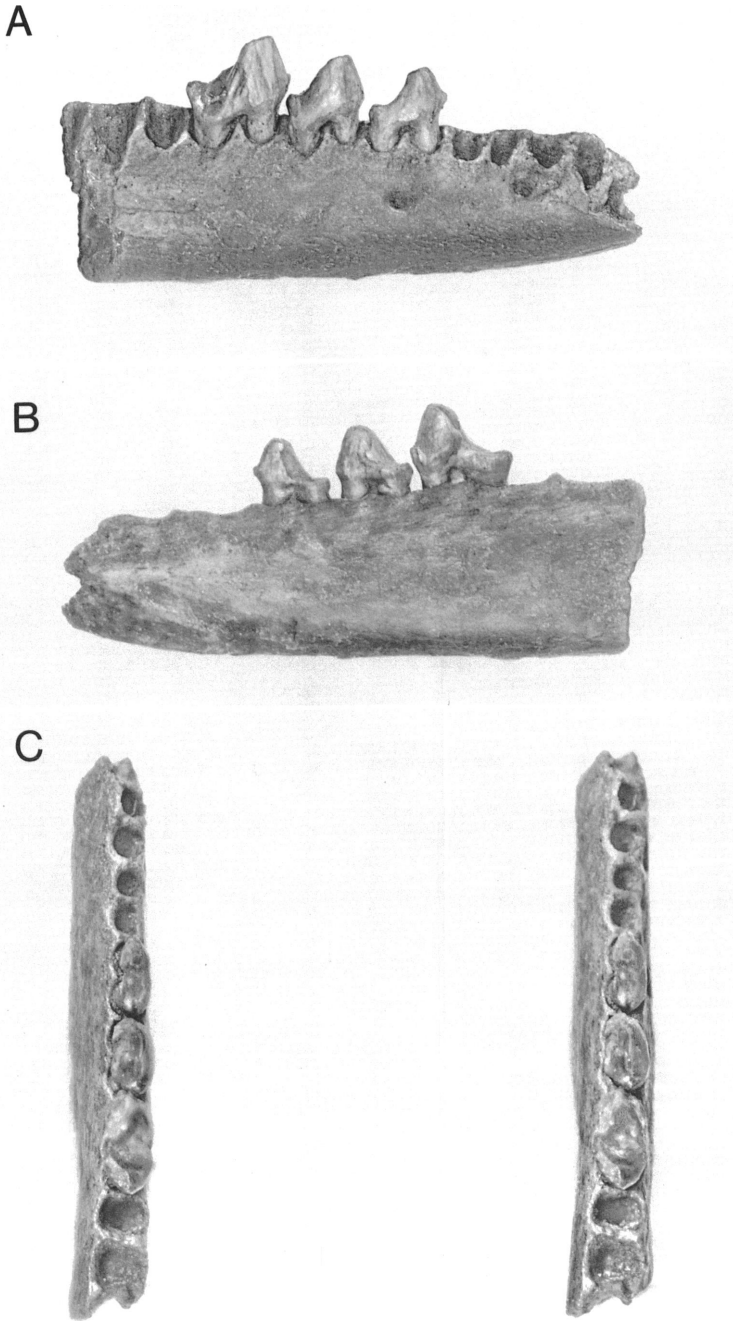

Fig. 1. *Arguitherium cromptoni,* new genus and species, right lower jaw with p4-M1, PSS no. 10-31. **A,** Labial view, **B,** lingual view, **C,** occlusal view. Stereophotograph.

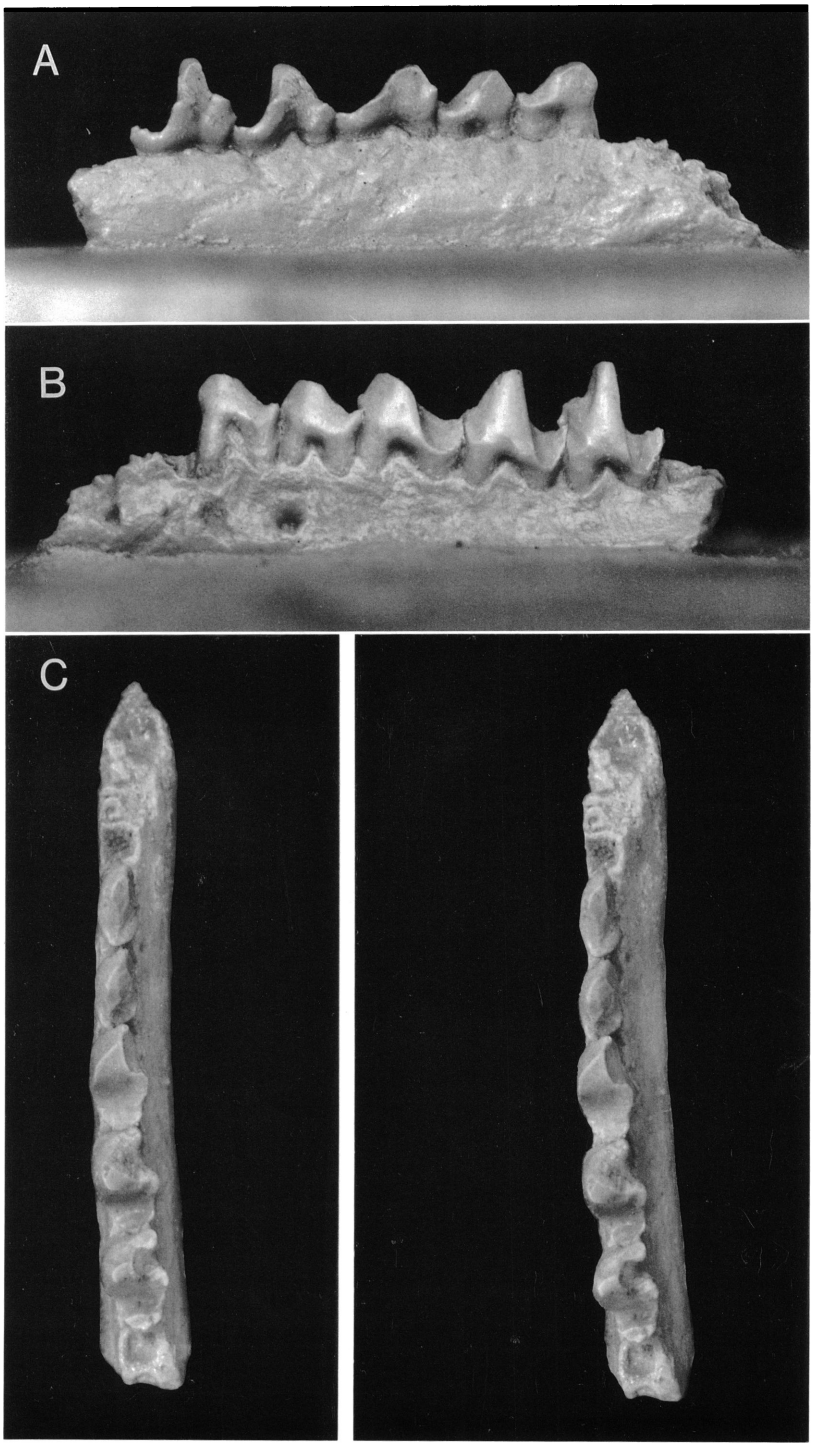

Fig. 2. *Arguimus khosbajari* Dashzeveg, fragment of left jaw with p3-M2, PSS no. 10-15. **A,** Labial view, **B,** lingual view, **C,** occlusal view. Stereophotograph.

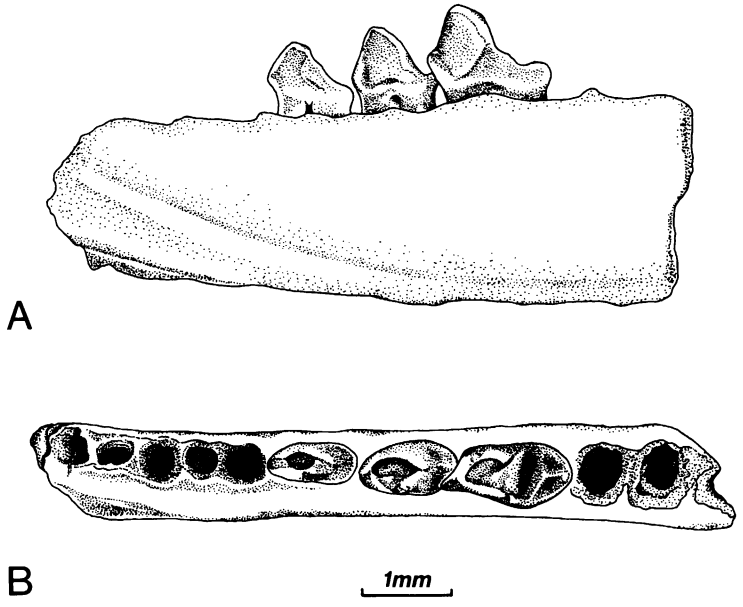

Fig. 3. *Arguitherium cromptoni,* new genus and species. Holotype, PSS no. 10-31. Right lower jaw with p4-m1. Mongolia, Ubur-Khangai county, Guchin Us, locality Khoobur; Early Cretaceous, Aptian-Albian. **A,** Lingual view, **B,** occlusal view.

protoconid (less than half the height of the latter). The hypoconulid is very well pronounced, an "entoconid" is present, and the hypoconid is barely outlined.

INCLUDED GENERA: *Arguimus* Dashzeveg, 1979, and an unnamed eupantothere known by a lower molar (fig. 7A, B, C) from the Jurassic of Porto Pinheiro, Portugal (Krusat, 1969).

COMPARISON: Members of the Arguimuridae differ from Amphitheriidae and Paurodontidae by possession of a comparatively large talonid with a well-developed hypoconulid on the lower molars. They differ from Peramuridae, Arguitheriidae, and Aegialodontidae in that the talonid basin is absent on arguimurid molars, yet a large hypoconulid is present.

Arguimus Dashzeveg, 1979

TYPE SPECIES: *Arguimus khosbajari* Dashzeveg, 1979.

DIAGNOSIS: Same as for family.

Arguimus khosbajari Dashzeveg, 1979
(Figures 2, 5, 6; table 2)

Arguimus khosbajari; Dashzeveg, 1979: 200–201; pl. 1, fig. 1a, b, c.

HOLOTYPE: PSS, no. 10-15, a fragment of the right lower jaw with p3-m2; the Valley of Lakes, Ubur-Khangai County, Guchin Us, Khoobur locality.

AGE: Lower Cretaceous—Aptian-Albian.

DIAGNOSIS: Same as for family.

DESCRIPTION. Judged by the alveolus, the canine tooth is comparatively big, with its depth almost 1.3 times the width. Alveoli indicate that the first lower premolar has one root, and p2 has two roots. The third, fourth, and fifth premolars are distinctly asymmetrical, while p5 and m1 are similar in shape and form. The fifth lower premolar shows a tendency toward molarization; its trigonid is weakly expressed, in contrast to the rather indistinct talonid. The first lower molar differs from p5 in its better-developed trigonid and taller protoconid. The second lower molar is slightly bigger than m1. The wide trigonid has a triangular shape in plan view. The protoconid is massive while the paraconid and metaconid are almost equal in size, though the former is definitely taller than the latter. The talonid has an oblong and low shape, and is clearly separated from the rear wall of the protoconid by a deep depression presumably for reception of a large paracone. The talonid shows two distinct cusps: a hy-

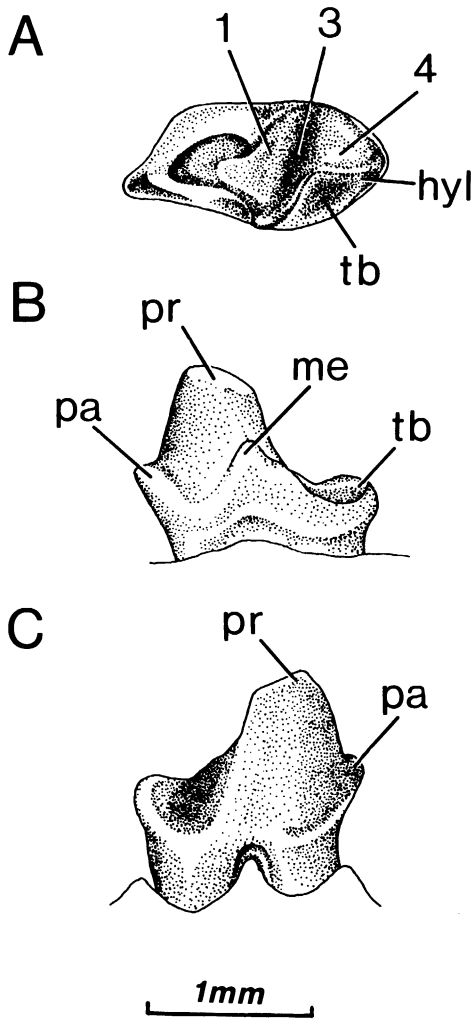

Fig. 4. *Arguitherium cromptoni,* new genus and species. Right m1 (from holotype). **A,** Occlusal view, **B,** lingual view, **C,** labial view. Wear surfaces (1–4) are numbered according to the scheme of Crompton (1971). hyl, hypoconulid, me, metaconid, pa, paraconid, pr, protoconid, tb, talonid basin.

poconulid and a tiny cusp that I conditionally call an entoconid. The former is much bigger than the latter and has a more posterior position. The "entoconid" is situated at the posterolingual end of the talonid, close to the hypoconulid. The cristid obliqua is distinct. The hypoconid (?), if present, is very indistinct. The talonid basin is not developed. The mesial cuspule is well pronounced at the frontal base of the paraconid. The second lower molar has clear wear facets. Facet 1 (after Crompton, 1971) has a distinctly transverse position on the rear slope of the protoconid, and is bounded lingually by a metaconid crista, while facet 2 is fixed at the frontal slope of the protoconid and occupies part of the frontal slope of the paraconid along the paracristid. Facet 3 is smaller than facet 1 and is well pronounced. Facet 4 has not been traced, because it is obviously too minute.

TABLE 2
Measurements (mm) of *Arguimus khosbajari*

	p3	p4	p5	m1	m2
Length	1.02	0.95	1.30	1.27	1.23
Width	0.51	0.58	0.76	0.84	0.87

DISCUSSION

Clemens and Mills (1971) believed that *Peramus tenuirostris* possessed four lower premolars and four lower molars. This opinion was shared by Clemens and Lillegraven (1986). A new interpretation of the dental formula of primitive Tribosphenida was provided by McKenna (1975), who argued that *Peramus tenuirostris* typically has five premolars and three molars. This latter opinion is supported by the observation that m1 and M1 of *Peramus tenuirostris* differ considerably from m2 and M2 both in the structure and the shape of the tooth crown (Dashzeveg and Kielan-Jaworowska, 1984).

According to McKenna's hypothesis, *Arguimus khosbajari* should have five premolars and three molars. The tooth that I identify as m1 (Dashzeveg, 1979) is intermediate in morphology between p5 and m2; it is distinguished by greater molarization in comparison with the former, and has a less-developed talonid and a less-perfect trigonid than the latter. In *Arguitherium cromptoni,* the p5 to m1 transition is rather abrupt; the former is identified as a premolar due to its similarities with that of other eupantotheres. Thus, the new Mongolian data support McKenna's (1975) interpretation.

The following tentative vertical evolutionary series that typify the eupantothere history within Amphitheria are here recognized as

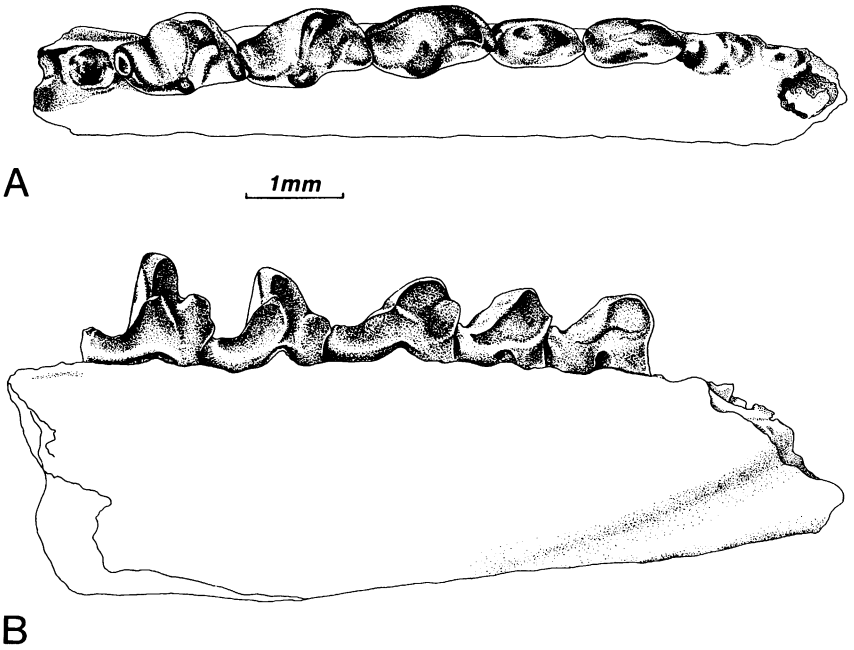

Fig. 5. *Arguimus khosbajari* Dashzeveg. Holotype, PSS no. 10-15. Left lower jaw with p3-m2. Mongolia, Ubur Khangai county, Guchin Us, locality Khoobur, Early Cretaceous, Aptian-Albian. **A,** Occlusal view, **B,** lingual view.

follows: Amphitheriidae → Peramuridae → Arguitheriidae and Amphitheriidae → Arguimuridae. The most distinctive and diagnostic feature of Amphitheria is the progressive growth and differentiation of the talonid on the lower molars, which appears to be a parallel feature in various phyletic branches of this suborder. Within the above taxa, the basal line is believed to be represented by *Amphitherium* or a closely related form; it is characterized by a comparatively small talonid on the lower molars, consisting only of the hypoconulid. According to Prothero (1981), *Amphitherium* is the earliest (and most primitive?) member of the Theria.

The Amphitheriidae → Peramuridae relationship is suggested by the presence in both groups of a small talonid basin emerging on the lower molars. The earliest evidence of

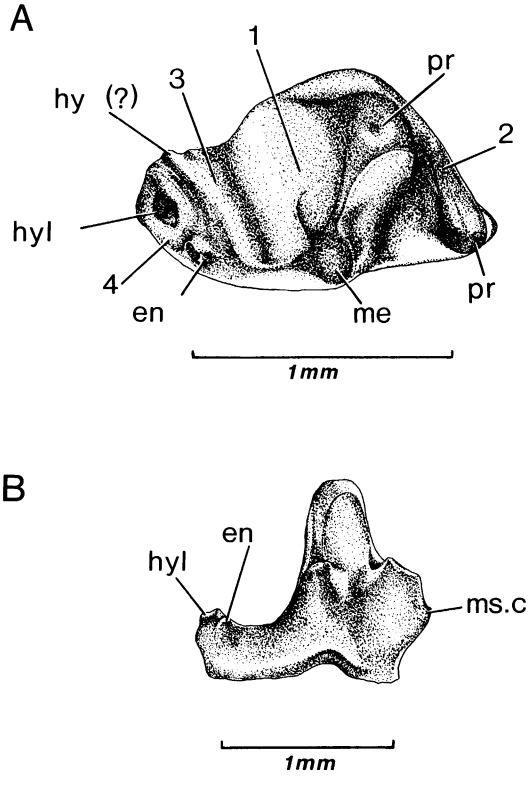

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Fig. 6. *Arguimus khosbajari* Dashzeveg. Left m2 (from holotype). **A,** Occlusal view, **B,** lingual view. en, entoconid, hy, hypoconid, ms. c, mesial cuspule; other abbreviations as in fig. 4.

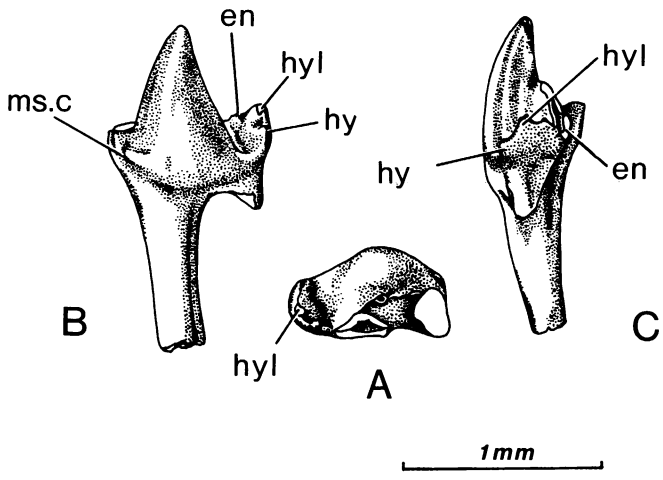

Fig. 7. *Eupantothere.* Left lower molar, Porto Pinheiro (Portugal), Kimmeridgian. **A,** Occlusal view, **B,** labial view, **C,** distal view (from Krusat, 1969). Abbreviations as in figs. 4 and 6.

this basin is recorded in the Middle-Jurassic *Palaeoxonodon ooliticus* from England (Freeman, 1976a, 1976b). The rear edges of the talonid basin on m1 and m2 of *P. ooliticus* clearly show a hypoconulid and an emergent hypoconid.

Talonid differentiation and cusp development become more obvious in the Late Jurassic *Peramus.* The latter is known as the most advanced form of non-tribosphenic Theria (Mills, 1964; Clemens and Mills, 1971; Crompton, 1971).

Arguitheriidae is phylogenetically related to Peramuridae, and the development of the talonid basin on the molars of both families is a feature that unites them. Despite its young geological age, this family shows such primitive features as premolariform p5 and imperfect m1 trigonid structure, which are not typical of Peramuridae.

In the lines Amphitheriidae → Arguimuriidae (an unnamed genus known by lower molars from the Jurassic of Portugal → *Arguimus*), the growth of the talonid is the result of entoconid and hypoconid differentiation from the original cusp, the hypoconulid. The second lower molar of *Arguimus* from Mongolia shows a striking resemblance to its counterpart from Porto Pinheiro, Portugal (fig. 7) and differs only in its somewhat broader and more massive hypoconulid. In the course of phyletic differentiation of the above line, there is a specific type of non-tribosphenic molar structure. This structure, in contrast to other, earlier Theria, is marked by a lack of the talonid basin on the lower molars; instead, the talonid is tubercular and is composed exclusively of transverse cusps dominated by the hypoconulid. In general, there are two distinctly independent lines in the eupantotherid evolution within Amphitheria. The first line is characterized by the formation of the talonid basin on lower molars, while the second one is characterized by a basin-free talonid.

Which cusp is the first to form on the lower molar talonid of early therian mammals? There is no consensus among researchers on that question. Some believe that the first talonid cusp of primitive Theria was the hypoconulid, while others think it was the hypoconid (see Slaughter, 1971; Freeman, 1979). In the center of the talonid of the eupantothere lower molar from the Jurassic of Porto Pinheiro, Portugal (Krusat, 1969), there is a distinct hypoconulid and a developed entoconid, while a hypoconid is only vaguely outlined (fig. 7) The same may be said about m2 of *Arguimus khosbajari* from Mongolia where the hypoconulid is the dominant cusp and the hypoconid (?) is rudimentary. I interpret the first cusp on the talonid of early Theria to be the hypoconulid, not the hypoconid.

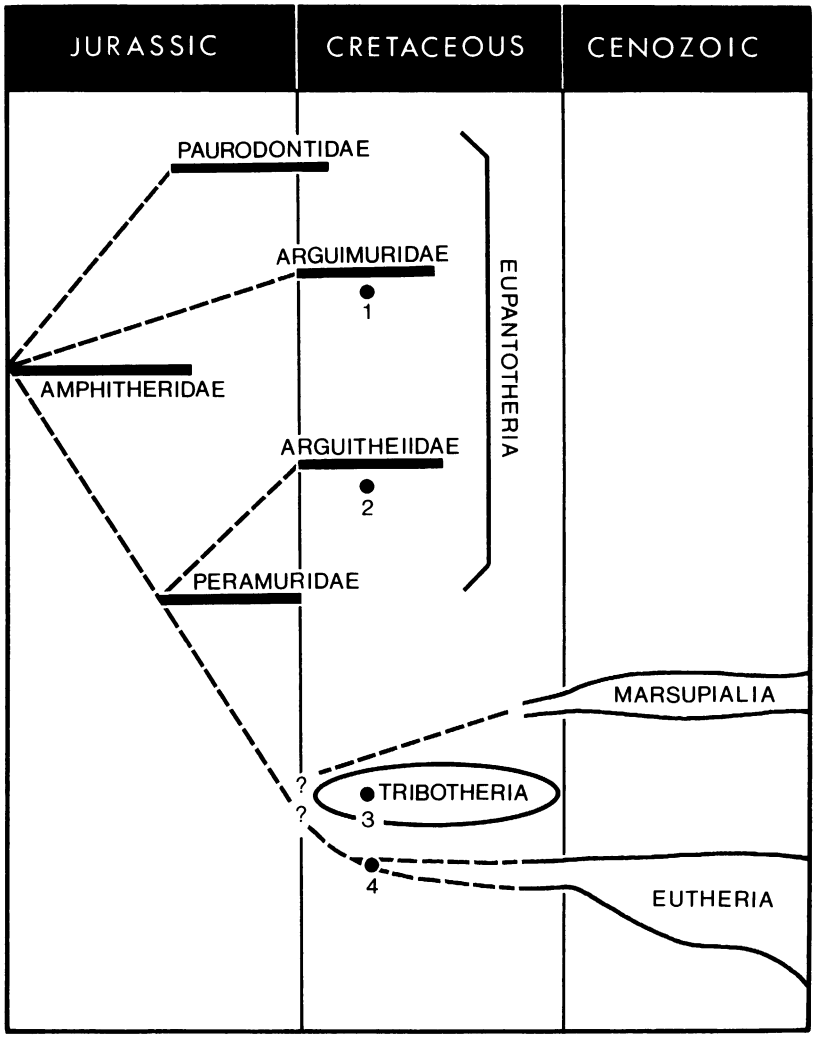

Fig. 8. Affinities of early therians. Numbers refer to approximate age of occurrence in the Khoobur locality for the following genera: **1.** *Arguimus,* **2.** *Argutherium,* **3.** *Kielantherium,* **4.** *Prokennalestes.*

Which is formed earlier, the hypoconid or the entoconid, subsequent to the appearance of the hypoconulid on the talonid of primitive Theria? In Theria with tribosphenic molars, formation of the entoconid on lower molars correlates with the emergence of the protocone on the upper molars. The entoconid on lower molars in various phylogenetic lines usually forms after the hypoconulid and hypoconid, as seen on *Kielantherium, Deltatheridium,* etc. (Crompton, 1971; Crompton and Kielan-Jaworowska, 1978; Kielan-Jaworowska et al., 1987; Butler, 1990).

A different case is the sequence in the formation of an entoconid-like cusp on lower molars of tubercular eupantotheres (without a talonid basin). In *Arguimus khosbajari* the "entoconid," not the hypoconid, is well developed. Such an early appearance of the entoconid-like cusp in this group remains poorly understood. Thus, the hypoconulid on the lower molars of early Theria is the first talonid cusp to have appeared, while the entoconid and hypoconid are to be regarded as more specialized or "advanced" developments relative to the hypoconulid.

In terms of tritubercular nomenclature, the hypoconulid is viewed as a supplementary conule. According to that system, the primary cusps of lower molars should have roots of their own, while the supplementary ones should be termed conules and regarded as subordinate to the primary ones (Osborn, 1907). This tritubercular concept was based largely on later forms of the tuberculo-sectorial, buno-, and bunolophodont forms of early Tertiary mammals. The Mongolian material, combined with the respective literature, has made it possible to define more precisely the general trends in the adaptive radiation of "non-tribosphenic Theria" that were advanced by Prothero (1981). While the dichotomous evolution of marsupials and placentals relates to Eupantotheria, these groups must be linked more directly with that line of non-tribosphenic Theria that is characterized by the presence of a talonid basin on the lower molars. It should be noted that the evidence is too poor to allow a realistic evaluation of the relationships of Eupantotheria with the divergent lineages of Metatheria, Eutheria, and Tribotheria (fig. 8).

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