Djadochtatheria – a new suborder of multituberculate mammals

ZOFIA KIELAN-JAWOROWSKA and JØRN H. HURUM

Mongolian Late Cretaceous multituberculates (except *Buginbaatar*) form a monophyletic group for which the suborder Djadochtatheria is proposed. Synapomorphies of Djadochtatheria are: large frontals pointed anteriorly and deeply inserted between the nasals, U-shaped fronto-parietal suture, no frontal-maxilla contact, and edge between palatal and lateral walls of premaxilla. Large, rectangular facial surface of the lacrimal exposed on the dorsal side of the cranial roof is present in all djadochtatherians, but may be a plesiomorphic feature. It is also possible that in djadochtatherians the postglenoid part of the braincase is relatively longer than in other multituberculates. Djadochtatherians have an arcuate p4 (secondarily subtrapezoidal in *Catopsbaatar*) that does not protrude dorsally over the level of the molars (shared with Eucosmodontidae), I3 placed on the palatal part of the premaxilla (shared with the eucosmodontid *Stygimys* and the cimolomyid *Meniscoessus*). The small number of cusps on the upper and lower molars and no more than nine ridges on p4 are possibly plesiomorphies for Djadochtatheria. The djadochtatherian *Nessovbaatar multicostatus* gen. et sp. n., family *incertae sedis* from the Barun Goyot Formation is proposed. New specimens of the djadochtatherian genera *Kryptobaatar*, ?*Djadochtatherium*, and *Kamptobaatar* are described and revised diagnoses of these taxa and *Sloanbaatar* are given. A cladistic analysis of Mongolian Late Cretaceous multituberculates (MLCM), using Pee-Wee and NONA programs and employing 43 dental and cranial characters, 11 MLCM taxa, five selected Late Cretaceous or Paleocene multituberculate genera from other regions, and a hypothetical ancestor based on the structure of Plagiaulacoidea, is performed. The Pee-Wee program yielded two equally fit trees that confirm the monophyly of MLCM excluding *Buginbaatar*. *Kryptobaatar*, *Djadochtatherium*, *Catopsbaatar*, and *Tombaatar* form a clade, for which the family Djadochtatheriidae is proposed. *Chulsanbaatar* is the sister taxon of this clade. *Bulganbaatar* and *Nemegtbaatar* are the sister group of all other djadochtatherians. *Kamptobaatar*, *Sloanbaatar*, and *Nessovbaatar* form a separate clade in the Pee-Wee tree. The NONA program yielded thirty equally parsimonious trees and a strict consensus tree with a poor resolution.

Key words: *Djadochtatherium, Kamptobaatar, Kryptobaatar, Nessovbaatar, Sloanbaatar*, Multituberculata, Late Cretaceous, Mongolia.

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Introduction

Djadochtatherium matthewi Simpson, 1925 from the Djadokhta Formation of Bayn Dzak, Mongolia, was the first mammal found in the Mesozoic rocks of Asia. The holotype specimen on which Simpson's new species was based (AMNH 20440) is a poorly preserved anterior part of the skull associated with both dentaries with damaged teeth (Simpson 1925). Subsequently, Simpson (1928a) described some post-cranial fragments (see also McKenna 1961) belonging to the same individual. An additional Djadokhta Formation specimen, AMNH 21703, attributed by Gregory & Simpson (1926) to *Djadochtatherium matthewi*, does not belong to this taxon (Kielan-Jaworowska 1970; Rougier *et al.* 1997).

For 45 years *Djadochtatherium* was the only multituberculate known from the Late Cretaceous of Mongolia. Between 1963 and 1971 Polish-Mongolian Palaeontological Expeditions conducted extensive field work in the Gobi Desert and assembled a large collection of Late Cretaceous mammals, including numerous multituberculates. Of this collection Kielan-Jaworowska (1970, see also 1971) described from the Djadokhta Formation four new multituberculate monotypic genera: *Kryptobaatar*, *Gobibaatar*, *Kamptobaatar*, and *Sloanbaatar*, all based on almost complete skulls associated with dentaries. Subsequently, Kielan-Jaworowska (1980) demonstrated that *Gobibaatar parvus* was based on juvenile individuals of *Kryptobaatar dashzevegi* and regarded *Gobibaatar* as a junior synonym of *Kryptobaatar*.

During the 1970 and 1971 Polish-Mongolian Expeditions a new collection of mammals was assembled from the Late Cretaceous Barun Goyot Formation (strati-graphically younger than the Djadokhta Formation) and its stratigraphic equivalent – the Red beds of Khermeen Tsav. Kielan-Jaworowska (1974) described *Bulganbaatar*, a new monotypic genus from the Djadokhta Formation and two new monotypic genera *Chulsanbaatar, Nemegtbaatar*, and a new species *Djadochtatherium catopsaloides* from the Barun Goyot Formation and Red beds of Khermeen Tsav. Kielan-Jaworowska & Sloan (1979) assigned *D. catopsaloides* to *Catopsalis* Cope. Simmons & Miao (1986) demonstrated the paraphyly of *Catopsalis* and finally Kielan-Jaworowska (1994) erected for *Djadochtatherium catopsaloides* a new monotypic genus *Catopsbaatar*.

Kielan-Jaworowska & Dashzeveg (1978) erected *Tugrigbaatar saichanensis* for the specimen from the Toogreeg beds equivalent to the Djadokhta Formation (Gra-dziński *et al.* 1977) at Toogreeg (Toogreegeen Shireh), in the Gobi Desert. *Tugrig-baatar* is generally similar to *Kryptobaatar* but appeared at that time to differ from it in lacking the so called basioccipital box, a structure characteristic of *Kryptobaatar*, but unknown to occur in other mammals. Kielan-Jaworowska *et al.* (1986), however, demonstrated that the basioccipital box is an artefact (see also Kielan-Jaworowska & Gambaryan 1994: fig. 1D). It follows that the differences between *Kryptobaatar* and *Tugrigbaatar* are of specific rather than of generic rank and we include *Tugrigbaatar* in the synonymy of *Kryptobaatar*, the conclusion reached also by Rougier *et al.* (1997). Kielan-Jaworowska & Sochava (1969, see also Trofimov 1975) described *Buginbaatar transaltaiensis* from the region of Bugeen (= Bugin) Tsav in Trans-Altai Gobi, from beds apparently equivalent to the Nemegt Formation (?early Maastrichtian). This specimen was collected by a Soviet-Mongolian Geological Expedition.

Between 1990 and 1996 the American Museum of Natural History and the Mongolian Academy of Sciences organized seven palaeontological expeditions to Mongolia known as the Mongolian Academy of Sciences-American Museum of Natural History Paleontological Expeditions (MAE); the project will continue. They discovered the Ukhaa Tolgod locality in the Nemegt Basin of the Gobi Desert, which yielded more than 250 specimens of Late Cretaceous mammals. Rougier *et al.* (1997) described the new multituberculate *Tombaatar sabuli* from the Ukhaa Tolgod beds. The Ukhaa Tolgod beds resemble those belonging to the Djadokhta Formation at the type section (see also Novacek *et al.* 1994 and Dashzeveg *et al.* 1995). The only specimen of *Tombaatar sabuli* PSS-MAE 122 is a well preserved rostrum, with dentition. Sereno & McKenna (1995) briefly described the postcranial skeleton and figured the complete skull associated with dentaries of *Bulganbaatar nemegtbaataroides* from the Djadokhta Formation at Bayn Dzak.

In 1994, members of the Japanese-Mongolian Expedition (organized by the Hayashibara Museum of Natural Sciences and the Geological Institute of the Mongolian Academy of Sciences) collected mammals at Toogreeg. They found an almost complete skull of *Djadochtatherium matthewi*, associated with both dentaries. Mahito Watabe, the leader of the Japanese group, kindly sent us color photographs of this skull and allowed us to refer to them in this paper.

In 1995 a small Polish-Mongolian team visited the Gobi Desert, among others the Ukhaa Tolgod locality. They assembled 10 specimens of mammals, one of which is an incomplete dentary of ?*Djadochtatherium* which we describe in this paper. We describe also the new multituberculate taxon *Nessovbaatar multicostatus* gen. et sp. n. from the Red beds of Khermeen Tsav, based on material collected by members of the Polish-Mongolian expedition in 1971.

It follows that the hitherto known collection of the Mongolian Late Cretaceous multituberculates (MLCM) contains 12 species: *Buginbaatar transaltaiensis* Kielan-Jaworowska & Sochava, 1969, *Bulganbaatar nemegtbaataroides* Kielan-Jaworowska, 1974, *Catopsbaatar catopsaloides* (Kielan-Jaworowska, 1974), *Chulsanbaatar vulgaris* Kielan-Jaworowska, 1974, *Djadochtatherium matthewi* Simpson, 1925, *Kamptobaatar kuczynskii* Kielan-Jaworowska, 1970, *Kryptobaatar dashzevegi* Kielan-Jaworowska, 1970, *Kryptobaatar saichanensis* (Kielan-Jaworowska & Dashzeveg, 1978), *Nemegtbaatar gobiensis* Kielan-Jaworowska, 1974, *Nessovbaatar multicostatus* gen. et sp. n., *Sloanbaatar mirabilis* Kielan-Jaworowska, 1971, and *Tombaatar sabuli* Rougier *et al.*, 1997.

We started to work on the revision of the systematics of MLCM in 1995. When the first draft of our paper was prepared, our colleagues Guillermo W. Rougier, Michael J. Novacek, and Demberlyin Dashzeveg sent us their manuscript on *Tombaatar* (Rougier *et al.*, 1997). These authors used a slightly corrected character list of Simmons (1993) to establish relationships of *Tombaatar* and concluded that most of the MLCM belong to an endemic monophyletic group, that falls outside Cimolodonta (Ptilodontoidea and Taeniolabidoidea). They did not name the relevant MLCM high rank taxa.

Our conclusions on the uniqueness of MLCM generally agree with those of Rougier *et al.* (1997), although the results of the cladistic analysis that we present below, using Pee-Wee program (Goloboff 1993a, 1996), differ in detail. As the paper by Rougier *et*

al. (1997) includes 'Considerations on multituberculate interrelationships', we refrain from publishing extensively on this subject, preferring to wait until their more comprehensive paper (in preparation) is published. In agreement with Guillermo W. Rougier, Michael J. Novacek, and Demberlyin Dashzeveg, however, we propose and diagnose in this paper the suborder Djadochtatheria nov. for most MLCM, and the family Djadochtheriidae nov.

Gradziński *et al.* (1977) estimated as 'best guesses' the ages of three Late Cretaceous Mongolian formations as: Djadokhta Formation–?upper Santonian and/or ?lower Campanian; Barun Goyot Formation–?middle Campanian; Nemegt Formation–?lower Maastrichtian. Fox (1978) concluded that the Djadokhta and Barun Goyot formations are Campanian in age, and in his fig. 1 he correlated the Djadokhta Formation with middle Campanian and Barun Goyot with upper Campanian. Lillegraven & McKenna (1986) regarded the Djadokhta Formation as an equivalent of the Judith River and Oldman formations of North America, while the Barun Goyot and Nemegt Formations, and poorly known Bugeen Tsav beds, as compressed into an interval of time equivalent to the Judithian and/or Lancian North American land mammal ages. Jerzykiewicz & Russell (1991: p. 360) stated: 'The vertebrate assemblages of Djadokhta, Barun Goyot and Nemegt time can be considered as representative of a single middle Campanian through middle Maastrichtian faunal complex in central Asia'. Jerzykiewicz *et al.* (1993) claimed that the Djadokhta Formation and its Chinese equivalent Bayan Mandahu red beds are of middle to late Campanian age, while Jerzykiewicz (1996: fig. 2) correlated Djadokhta Formation with the middle Campanian. Averianov (1997) reported the finding of early Campanian (dated on the basis of shark teeth) mammal teeth in Kazakhstan. He stated (p. 244) that Campanian is '[...] a marine stage established in Europe and divided on the basis of ammonites and other marine invertebrates into two substages (Harland *et al.* 1989). In view of this, the tripartite division of the Campanian in Asia or North America is not appropriate'. He concluded that the assemblage from Kazakhstan is at the generic level strikingly similar to that of the Djadokhta Formation, suggesting the early Campanian age for the latter.

On the basis of all these data, in the present paper we tentatively accept the age of the Djadokhta Formation as ?early Campanian, that of the Barun Goyot Formation as ?late Campanian and the Nemegt Formation as ?early Maastrichtian. We agree, however, with comment of Michael J. Novacek (letter of March 17, 1997), who wrote: 'The evidence thus far is hardly satisfactory, being based on little in the way of marine correlations and entirely lacking any relevant geochrons based on radiometrics or palaeomagnetics.'

The Ukhaa Tolgod beds discovered by MAE yielded a mammalian assemblage generally similar to that of the Djadokhta Formation, in addition to some taxa (*Chulsanbaatar* and *?Nemegtbaatar*) known from the Barun Goyot Formation (personal information from Demberlyin Dashzeveg, Michael J. Novacek and Guillermo W. Rougier). The stratigraphic position of these beds remains open.

Measurements: We measured all the teeth, except p4, (Fig. 1) in occlusal view at the horizontal position of the molars and premolars; the length of p4 was measured in labial view (Jepsen 1940: fig. 1a).
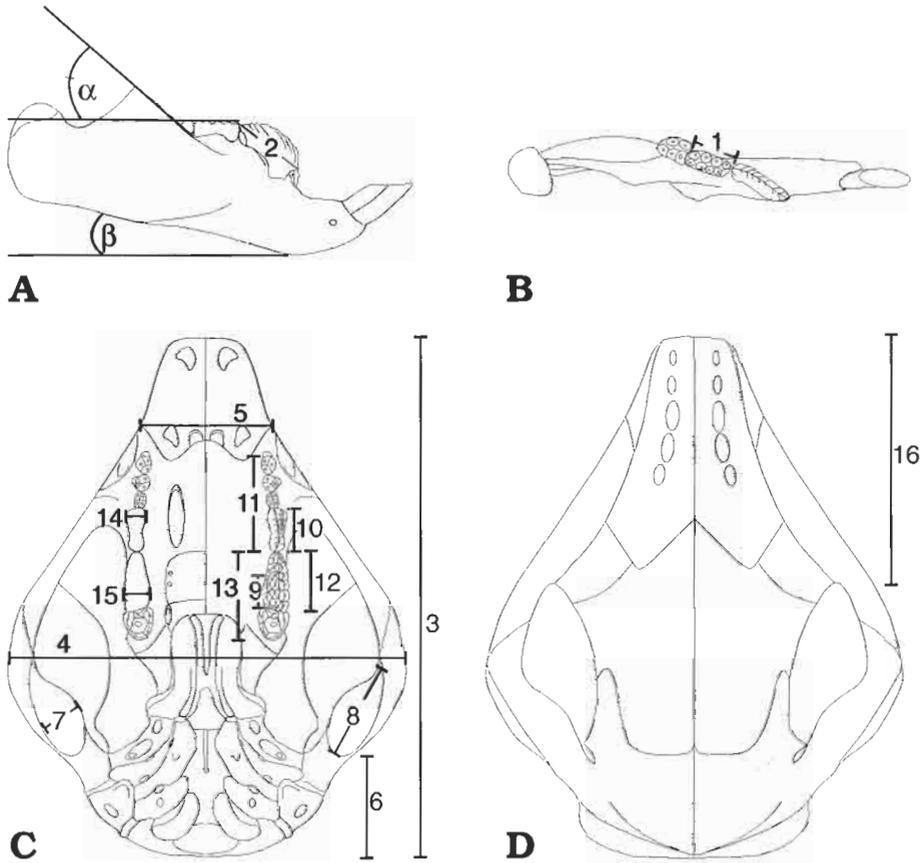
Fig. 1. Diagram showing distances of measurements (based on *Nemegtbaatar gobiensis* ZPAL MgM-I/81). **A**, **B**. Lateral and dorsal views of the right dentary. **C**, **D**. Ventral and dorsal views of the skull. α – angle of the coronoid process; β – angle between the lower margin of the dentary and the occlusal level of the molars; 1 – length of m1; 2 – length of p4; 3 – length of the skull; 4 – width of the skull; 5 – width of the snout; 6 – length of the postglenoid region of the braincase; 7 – width of the glenoid fossa; 8 – length of the glenoid fossa; 9 – length of the inner ridge or the inner row of cusps in M1; 10 – length of P4; 11 – length of the upper premolars; 12 – length of M1; 13 – length of the upper molars; 14 – width of P4; 15 – width of M1; 16 – length of the snout.

Institutional abbreviations: AMNH – Department of Vertebrate Paleontology, American Museum of Natural History, New York; GI – Geological Institute, Mongolian Academy of Sciences, Ulan Bator; HMNS – Hayshibara Museum of Natural Sciences, Hayshibara, Japan; PSS – Palaeontological and Stratigraphical Section of the Geological Institute, Mongolian Academy of Sciences, Ulan Bator (abbreviated also sometimes as SPS); ZPAL – Institute of Paleobiology, Polish Academy of Sciences, Warsaw.

Other abbreviations: IPM/ipm – upper and lower incisors, premolars and molars respectively; MAE – Mongolian Academy of Sciences-American Museum of Natural History Paleontological Expeditions; MLCM – Mongolian Late Cretaceous multi-tuberculates.

Systematic Palaeontology

Suborder Djadochtatheria nov.

Families and genera included. — Sloanbaataridae Kielan-Jaworowska, 1974 (*Sloanbaatar* Kielan-Jaworowska, 1974); Djadochtatheriidae nov. (*Djadochtatherium* Simpson, 1925, *Kryptobaatar* Kielan-Jaworowska, 1970, *Catopsbaatar* Kielan-Jaworowska, 1994, *Tombaatar* Rougier, Novacek & Dashzeveg, 1997); five *incertae sedis* genera: *Chulsanbaatar* Kielan-Jaworowska, 1974, *Bulganbaatar* Kielan-Jaworowska, 1974, *Nemegtbaatar* Kielan-Jaworowska, 1974, *Kamptobaatar* Kielan-Jaworowska, 1970, *Nessovbaatar* nov.; and tentatively assigned: *Paracimexomys* Archibald, 1982 and *Pentacosmodon* Jepsen, 1940.

Stratigraphic and geographical range. — Late Cretaceous Djadokhta and Barun Goyot formations (?early and ?late Campanian respectively), Red beds of Khermeen Tsav, and Ukhaa Tolgod beds, Gobi Desert, Mongolia. As North American taxa are only tentatively assigned, we restrict the stratigraphic and geographical range to the Asian formations.

Diagnosis. — A clade of multituberculates with skull length varying between 20 and 70 mm, dental formula 2 0 3–4 2 / 1 0 2 2, unicuspid I2 and double-rooted upper premolars. Djadochtathcrians are characterized by the following synapomorphies: large frontals, pointed anteriorly in the middle, deeply inserted between the nasals; U-shaped fronto-parietal suture; a sharp edge between the lateral and palatal walls of premaxilla (rounded in other multituberculates). A large roughly rectangular facial surface of the lacrimal, exposed on the cranial roof, separating the frontal from the maxilla is also characteristic for Djadochtatheria, but this may be a plesiomorphy.

Differential diagnosis. — In Djadochtatheria the postglenoid region of the braincase is apparently longer, compared to the skull length, than in all other multituberculates. They differ from multituberculates in which the occipital region is known (but not from *Ptilodus* and *Catopsalis*) in having a large posttemporal fossa (canal). Differ from all other multituberculates except *Stygimys* and *Meniscoessus* in having I3 placed on the palatal part of prcmaxilla (it is slightly shifted from the labial margin in *Lambdopsalis*). Differ from Plagiaulacoidea (*sensu* Hahn 1993) in having two upper incisors rather than three, single-cuspid I3, two lower premolars rather than three or four, in having only one basal cuspule on p4 rather than a row of cuspules, and in having arcuate p4 rather than rectangular (secondarily subtrapezoidal in *Catopsbaatar*). Djadochtatheria have sharply limited enamel band on the lower incisor, except *Sloanbaatar* and *Kamptobaatar* in which the enamel is thicker on the ventrolateral surface, but not sharply limited. The sharply limited enamel band occurs also in Taeniolabidoidea, Cimolomyidae, North American 'plagiaulacoid' (Engelmann *et al.* 1990), and *Eobaatar* sp. a (Kielan-Jaworowska *et al.* 1987). Share with most Taeniolabidoidea, Cimolomyidae and a few *incertae sedis* multituberculate genera gigantoprismatic enamel. Differ from Taeniolabididae in having two lower premolars instead of one, arcuate p4 (secondarily subtrapezoidal in *Catopsbaatar)* rather than triangular, three or four upper premolars rather than one, and smaller number of cusps on the upper and lower molars. Share with Eucosmodontidae a low p4, which does not protrude dorsally over the level of the molars, but differ from it in having smaller number of serrations (up to ten) on p4 and smaller number of cusps on the lower and upper molars. Differ

from Ptilodontoidea in having a more robust lower incisor, with a limited enamel band, and in having a smaller p4 that does not protrude dorsally over the level of the molars (it strongly protrudes in Ptilodontoidea). Differ from *Uzbekbaatar* and Arginbaataridae in having a basal cuspule on p4 (Kielan-Jaworowska & Nessov 1992), and from Arginbaataridae in having less arcuate crown of p4, completely covered with enamel and not rotating during ontogeny (Kielan-Jaworowska *et al.* 1987). Differ from Gond-wanatheria in having rounded rather than rectangular p4, in the presence of p3, and in lacking transverse ridges between the cusps of the upper and lower molars (Krause *et al.* 1992; Kielan-Jaworowska & Bonaparte 1996).

Remarks. — For diagnoses of: *Buginbaatar* – see Kielan-Jaworowska & Sochava (1969) and Trofimov (1975); *Chulsanbaatar*, *Bulganbaatar* and *Nemegtbaatar* – Kielan-Jaworowska (1974); *Catopsbaatar* – Kielan-Jaworowska (1994); *Tombaatar* – Rougier *et al.* (1997).

Family Sloanbaataridae Kielan-Jaworowska, 1974

Type genus by monotypy: *Sloanbaatar* Kielan-Jaworowska, 1970.

Diagnosis. — As for the type genus.

Genus *Sloanbaatar* Kielan-Jaworowska, 1970

Figs 10F, 11F, 12F.

Revised diagnosis. — The skull (known only in a single specimen of *Sloanbaatar mirabilis*) differs from all other djadochtatherians in having a very narrow and rectan-gular snout, slender zygomatic arches strongly expanded laterally, one pair of the vascular foramina on the nasals and two pairs of palatal vacuities. The snout/skull width ratio (see Fig. 1 for method of measurements) is in *Sloanbaatar* the lowest among djadochtatherians. The relatively narrow snout is characteristic also of *Chul-sanbaatar*; however, *Sloanbaatar* differs from *Chulsanbaatar* in having the zygomatic arches more strongly expanded laterally, one pair of vascular foramina on the nasals and two pairs of palatal vacuities. The facial surface of the lacrimal is possibly roughly quadrangular and relatively smaller than in other djadochtatherians, except *Chulsan-baatar*. *Sloanbaatar* shares with *Catopsbaatar* the incisive foramen placed entirely within the premaxilla. It shares with *Catopsbaatar* a relatively large angle between the lower margin of the dentary and the occlusal level of the molars. Shares with *Kampto-baatar* and *Nessovbaatar* a small and laterally flared coronoid process. Shares with *Kamptobaatar*, *Djadochtatherium, Catopsbaatar*, and *Nessovbaatar* the position of the condyle above the level of the molars and differs in this respect from other djadochtatherians. Differs from other djadochtatherians in having a high (but smaller than in *Nessovbaatar*) ratio between p4:m1 length. Shares with *Kryptobaatar* a rela-tively high (eight) number of serrations on p4, but smaller than in *Nessovbaatar* (ten).

Remarks. — The skull in *Sloanbaatar* is known only from a single specimen of *S. mirabilis* (ZPAL MgM-I/20), the cranial roof of which is strongly cracked. There-fore, the reconstruction of the course of the naso-frontal suture poses difficulties. We reconstruct (Fig. 10F) the frontal as more pointed anteriorly than drawn by Kielan-Jaworowska (1970: fig. 1 and 1971: fig. 6) and contacting the maxilla along a longer distance. The facial surface of the lacrimal is possibly roughly quadrangular and apparently larger than it may appear from previous reconstructions.

Family Djadochtatheriidae nov.

Type genus: *Djadochtatherium* Simpson, 1925.

Genera included. — *Djadochtatherium* Simpson, 1925; *Kryptobaatar* Kielan-Jaworowska, 1970; *Catopsbaatar* Kielan-Jaworowska, 1994; *Tombaatar* Rougier, Novacek & Dashzeveg, 1997.

Diagnosis. — Family of Djadochtatheria that differs from all other multituberculates (and all other mammals) in having a subtrapezoidal snout in dorsal view, with wide anterior margin and lateral margins confluent with zygomatic arches rather than incurved in front of the arches. Djadochtatheriidae differ from other members of Djadochtatheria in having the snout extending for 50% or more of the skull length, anterior part of promontorium (*sensu* Hurum *et al.* 1996) irregular, with incurvatures on both sides, rather than oval (a character shared with *Lambdopsalis*). They share with *Chulsanbaatar* two pairs of vascular foramina on the nasals and share with *Chulsanbaatar, Kamptobaatar*, and Taeniolabididae lack of palatal vacuities.

Genus *Kryptobaatar* Kielan-Jaworowska, 1970

Synonyms: *Gobibaatar* Kielan-Jaworowska, 1970 and *Tugrigbaatar* Kielan-Jaworowska & Dashzeveg, 1978.

Revised diagnosis. — The smallest member of the Djadochtatheriidae nov. (skull length 25–32 mm), most similar to *Djadochtatherium*, with which it shares an arcuate (rather than trapezoidal as in *Catopsbaatar*) p4. The p4 in *Kryptobaatar* is relatively longer than in *Djadochtatherium* and has eight serrations (number unknown in *Djadochtatherium*). Differs from *Catopsbaatar* in having relatively smaller facial surface of the lacrimal; differs from *Djadochtatherium* and *Catopsbaatar* in having a shorter postorbital process. Shares with all MLCM except *Tombaatar* the alveolus for I3 formed by premaxilla, rather than by both premaxilla and maxilla (autapomorphy of *Tombaatar*). Differs from *Catopsbaatar* and *Tombaatar* in having four upper premolars. Differs from *Catopsbaatar* in having an inner row of cusps in M1 extending for less than a half, or a half of the tooth length, rather than a long row; shares short inner row of cusps in M1 with *Tombaatar* and the North American *Paracimexomys* (Lillegraven 1969; Archibald 1982). Differs from *Chulsanbaatar* and *Sloanbaatar* in having cusps on the inner ridge in M1, rather than a smooth ridge. Differs from *Tombaatar* in having M1 cusp formula 4–5:4:3–5 rather than 5:5:2. Differs from *Djadochtatherium* and *Catopsbaatar* in having a shorter snout (but longer than in non-djadochtatheriid djadochtatherians), a relatively less robust lower incisor, and less prominent masseteric and parietal crests.

Species assigned. — *Kryptobaatar dashzevegi* Kielan-Jaworowska, 1970 (type species) and *Kryptobaatar saichanensis* (Kielan-Jaworowska & Dashzeveg, 1978).

Kryptobaatar dashzevegi Kielan-Jaworowska, 1970

Figs 2–4, 10H, 11H, 12I.

Holotype: ZPAL MgM-I/21, rostrum associated with right and left incomplete dentary, figured by Kielan-Jaworowska (1970: plates 14, 15).

Type horizon and locality: Djadokhta Formation (?early Campanian), Bayn Dzak, Gobi Desert, Mongolia.

Remarks. — For description of *K. dashzevegi* see Kielan-Jaworowska (1970, 1980), Kielan-Jaworowska & Dashzeveg (1978), Kielan-Jaworowska *et al.* (1986),
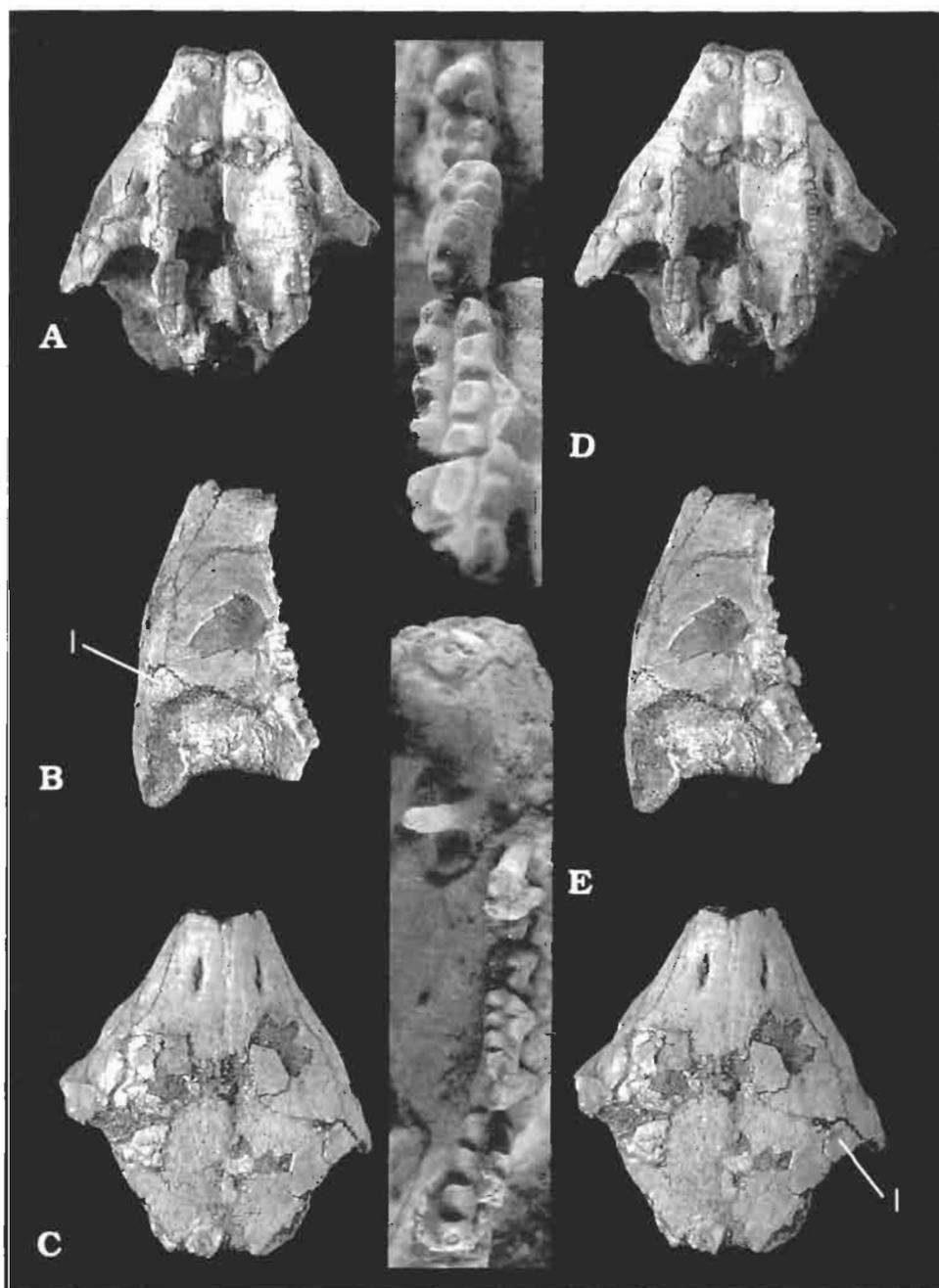
Fig. 2. *Kryptobaatar dashzevegi* Kielan-Jaworowska, 1970. **A–D**. ZPAL MgM-I/6. **A**. Rostral part of the skull 'wide snout', ventral view. **B**. The same, lateral view. **C**. The same, dorsal view. **D**. Right P2–M2 of the same in occlusal (slightly medial) view. **E**. ZPAL MgM-I/17, left upper dentition, broken off I2, I3–M2 in occlusal view; M2 incomplete, showing 3 cusps in the inner row. Upper Cretaceous, Djadokhta Formation, Bayn Dzak, Gobi Desert, Mongolia. **A–C**, stereo-photographs, × 2.2; **D**, × 18; **E**, × 16. **D** coated with ammonium chloride; l – lacrimal.

Kielan-Jaworowska & Gambaryan (1994), Gambaryan & Kielan-Jaworowska (1995), Rougier *et al.* (1996), and Rougier *et al.* (1997). In the diagnosis of *K. dashzevegi*, Kielan-Jaworowska (1970) did not mention the presence of a lacrimal. In several specimens of *K. dashzevegi* collected after the diagnosis of Kielan-Jaworowska (1970) was published, we recognized the facial surface of the lacrimal (e.g., Figs 2B, C; 10H), which is roughly trapezoidal in shape, with a slightly convex medial margin. Kielan-Jaworowska (1970) described the naso-frontal suture as gently sigmoid, directed subtransversely in the middle, but in several well preserved specimens found or prepared subsequently, the frontals taper together anteriorly to a pointed end, deeply inserted between the nasals. The cusp formula in M1 was originally identified as 4:4:ridge, because of the poor state of preservation of the holotype specimen (ZPAL MgM-I/21). It is now recognized as 4–5:4:3–5, as in several specimens (e.g., Fig. 2A, D, E) and in PSS MAE-113 from Toogreeg figured by Rougier *et al.* (1996: fig. 1) it is 4:4:3, and 5:4:5 in ZPAL MgM-I/52 (associated with a dentary) and MgM-I/19 (Fig. 4).

Revised diagnosis. — Type species of *Kryptobaatar* that differs from *K. saichanensis* in having the mandibular condyle placed at the level of the molars and facing postero-dorsally, the palatal part of the premaxillary-maxillary suture placed at the level of P2, and consequently a longer premaxilla. The M1 is shorter than in *K. saichanensis* and there are 3:2 cusps in m2.

Variability. — *K. dashzevegi* is known from the Djadokhta Formation at Bayn Dzak, Toogreeg beds at Toogreeg, and Ukhaa Tolgod beds at Ukhaa Tolgod in the
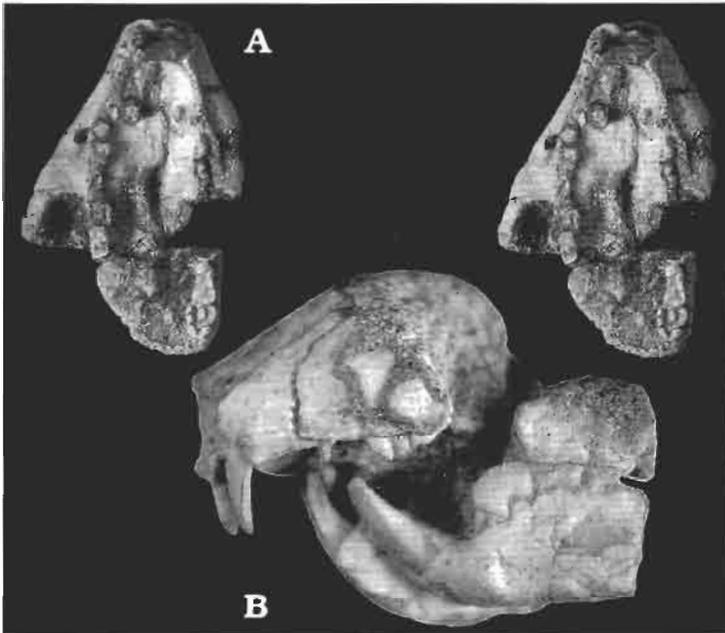
Fig. 3. *Kryptobaatar dashzevegi* Kielan-Jaworowska, 1970. ZPAL MgM-I/9, 'narrow snout'. Upper Cretaceous, Djadokhta Formation, Bayn Dzak, Gobi Desert, Mongolia. **A**. Stereo-photograph in ventral view. **B**. Left lateral view of the same, before separation of the dentaries. × 2.2.

Nemegt Basin. The collection of *K. dashzevegi* from Bayn Dzak housed in ZPAL consists of 22 specimens (some of which are very fragmentary) that show some variation. The differences in the shape of the snout may be in part caused by the state of preservation (lateral *versus* dorsoventral compression), and in part by the ontogenetic variation – older specimens are relatively wider, e.g., ZPAL MgM-I/6 (Fig. 2A–C) referred to as 'wide snout' and ZPAL MgM-I/9 (Fig. 3), referred to as 'narrow snout'. The dentition in all the studied specimens identified as *K. dashzevegi* shows a relatively small range of variability (except M1 cusp formula), falling within the range of one species.
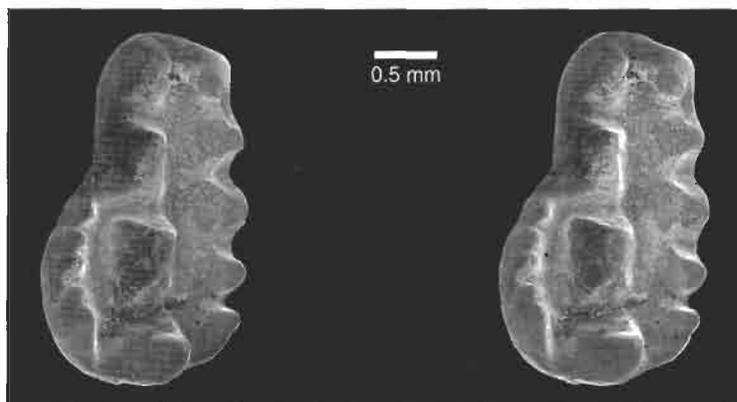
Fig. 4. *Kryptobaatar dashzevegi* Kielan-Jaworowska, 1970. ZPAL MgM-I/19. Stereo-photograph of left M1, occlusal view, showing 5 cusps in the inner row. Upper Cretaceous, Djadokhta Formation, Bayn Dzak, Gobi Desert, Mongolia.

There are nine specimens of *Kryptobaatar* from Ukhaa Tolgod in the GI collection, available to us for examination, which have not been prepared as yet. Our impression is that, on average, the *Kryptobaatar* specimens from Ukhaa Tolgod are smaller than those from Bayn Dzak and Toogreeg. A large collection of multituberculates from Ukhaa Tolgod assembled by the MAE team is currently being studied by American and Mongolian colleagues.

Kryptobaatar saichanensis (Kielan-Jaworowska & Dashzeveg, 1978)

Holotype: GI SPS 8–2 PST, skull associated with both dentaries and incomplete postcranial skeleton, figured by Kielan-Jaworowska & Dashzeveg (1978: text-figs 1–5 and plates 1–4).

Type horizon and locality: Toogreeg beds, equivalent of the Djadokhta Formation (?early Campanian), Bayn Dzak, Gobi Desert, Mongolia.

Revised diagnosis. — Differs from *K. dashzevegi* in having M1 slightly longer and 4:2 cusps in m2 (3:2 in *K. dashzevegi*), in having the palatal part of the premaxillary-maxillary suture in front of P1 rather than at the level of P1, possibly a smaller glenoid fossa, placed more laterally, on a longer stem, and in having a smaller mandibular condyle, facing more dorsally, with its ascending ramus longer and directed more laterally.

Remarks. — Kielan-Jaworowska & Dashzeveg (1978) described a small foramen of unknown function in the middle of the palatal part of the premaxilla of *K. saichanensis* skull, which does not occur in *K. dashzevegi* specimens in ZPAL

collection. Guillermo W. Rougier, however, informed us (letter of January 30, 1997) that a similar foramen occurs on one side of the premaxilla in a skull of ?*Kryptobaatar* from Ukhaa Tolgod. It follows that it cannot be a diagnostic character for *K. saichanensis*.

Genus *Djadochtatherium* Simpson, 1925
Fig. 12J.

Type species by monotypy: *Djadochtatherium matthewi* Simpson, 1925.

Remarks. — Until recently *D. matthewi* was known only from the holotype, AMNH 20440, which is a damaged anterior part of the skull, associated with both dentaries with incisors and p3 preserved on both sides. Upper and lower molars are not preserved. The badly damaged right p4 has since been lost.

During the 1994 Japanese-Mongolian Expedition a complete skull of *Djadochtatherium matthewi*, associated with dentaries was found in Toogreg beds, in Toogreeg. This specimen is provisionally registered as HMNS 94-10-178 (ultimately to be registered in GI collections). HMNS 94-10-178 is about 55 mm long. It shares with the holotype specimen similar size and shape of the skull (having the snout slightly narrower), the presence of four upper premolars (only the P1–P3 are preserved in the holotype specimen), the alveolus for I3 formed by the premaxilla (not by premaxilla and maxilla as in *Tombaatar*), and the identical size and shape of the second pair of the vascular foramina on the nasals. The small difference in the shape of the snout between the holotype and Toogreeg specimens may be attributed to the dorsoventral compression of the holotype. We have observed even greater variation in the shape of the snout in other djadochtatherian taxa, e.g., in *Kryptobaatar dashzevegi* (Figs 2A–C and 3), described above. In the holotype specimen, the anterior part of the nasals, that may have one more pair of vascular foramina, has not been preserved. The anterior part of the nasals is more complete in the Toogreeg specimen, preserving the lateral margin of the anterior vascular foramen. This shows that two pairs of nasal vascular foramina were present in *Djadochtatherium*. The postorbital process, not known previously, is well preserved in the Toogreeg specimen, and is almost as long as in *Catopsbaatar*. The well preserved p4 is only insignificantly longer than m1 and has an arcuate shape, as originally reconstructed by Simpson (1925: fig. 2, *contra* reconstruction of Kielan-Jaworowska & Sloan 1979: fig. 2A). In Simpson's (1925) reconstruction the p4 is almost as long with respect to m1 as in HMNS 94-10-178, but protrudes dorsally over the level of the molars (a characteristic feature of Ptilodontoidea), which is not the case. We base the revised diagnosis of *Djadochtatherium* presented below on the above data and on an examination of the photographs of HMNS 94-10-178.

Revised diagnosis. — Skull length about 50–55 mm, m1 cusp formula 4:3. Differs from *Kryptobaatar* in being distinctly larger; shares with *Kryptobaatar* and *Catopsbaatar* similar shape of the snout. Shares with *Kryptobaatar* presence of four upper premolars and arcuate p4. The p4 is only insignificantly longer than m1. Differs from *Catopsbaatar* and *Tombaatar* in having four, rather than three upper premolars. Shares with *Catopsbaatar* very long postorbital process and robust lower incisor, but differs from it in having the orbit placed somewhat more anteriorly, and relatively larger and arcuate p4 (subtrapezoidal in *Catopsbaatar*).

?*Djadochtatherium matthewi* Simpson, 1925
Fig. 5.

Remarks. — An incomplete right dentary, GI 5/301, was found in a sandstone nodule by the Mongolian-Polish team in September 1995 at the Ukhaa Tolgod locality. The site is situated northwest of the main collecting area of the MAE (Rougier *et al.* 1997).
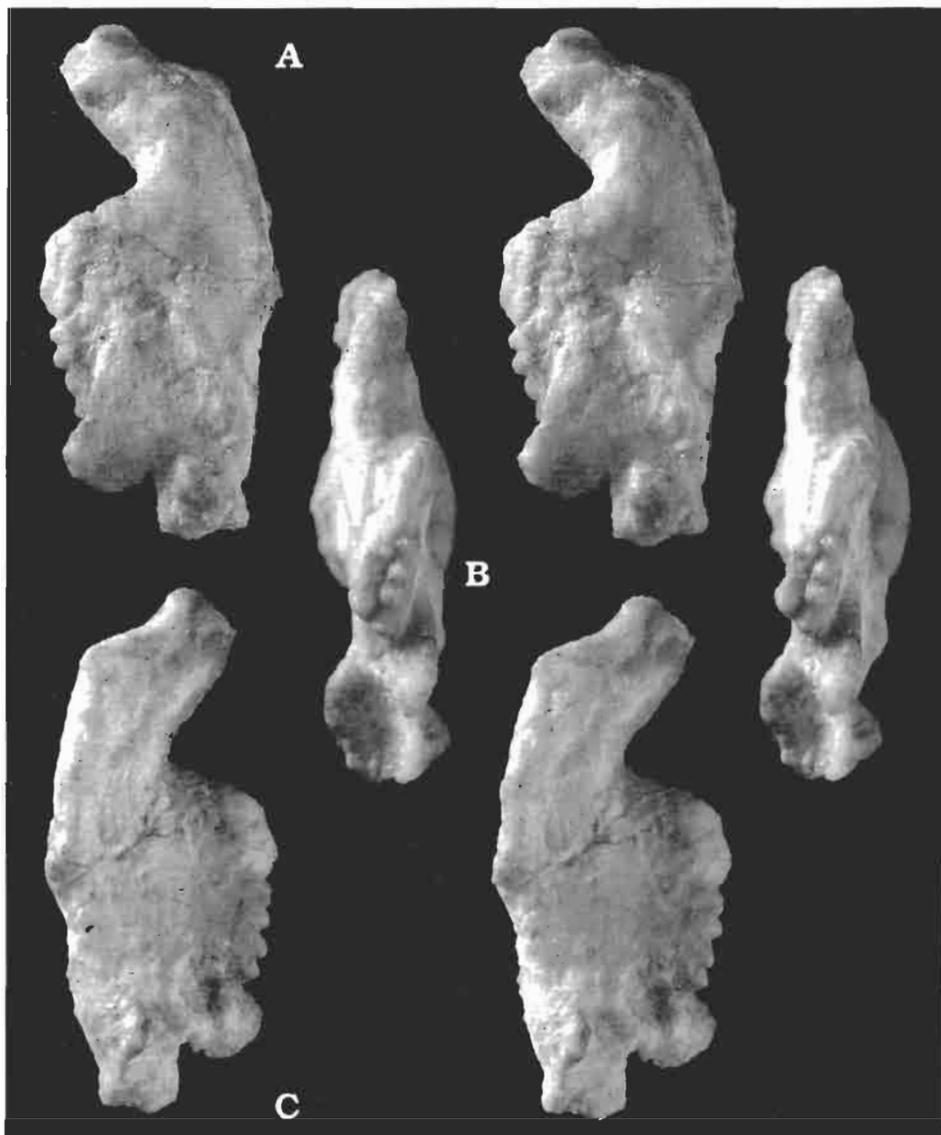
Fig. 5. ?*Djadochtatherium matthewi* Simpson, 1925. GI 5/301. Incomplete right dentary of the juvenile individual with broken deciduous incisor, broken p3, p4 and m1. Upper Cretaceous, Ukhaa Tolgod beds, Ukhaa Tolgod, Nemegt Basin, Gobi Desert, Mongolia. A. Lateral view. B. The same dorsal view. C. The same medial view. All stereo-photographs × 3.

GI 5/301 has a similar size and proportions of the dentary and p4 as HMNS 94-10-178, and we believe that they are conspecific. However, GI 5/301 is damaged, and since we have not seen the original of the Toogreeg skull, we identify our dentary as ?*D. matthewi.*

Description and comments. — GI 5/301 is a large anterior portion of the right dentary of a juvenile individual, with broken deciduous incisor, p3, p4, m1, and damaged alveolus for m2. Part of the dentary below the root of the incisor is missing on the lateral side, but is preserved on the medial side. The coronoid process begins opposite the anterior margin of m1 and rises at the beginning relatively gently, the angle between it and the occlusal level of m1 being about 58°. It appears from the preserved fragment that posteriorly the coronoid crest rises more steeply. The masseteric crest is very prominent with an inflation at its most anterior part. In front and slightly dorsal to it there is a shallow deepening, the masseteric fovea (Gambaryan & Kielan-Jaworowska 1995). On the lingual side there is a deep but poorly preserved pterygoid fossa, the anterior margin of which is at the level of the middle of the alveolus for m2.

The surface of the preserved part of the incisor is badly damaged and we were unable to recognize the enamel band, characteristic of all the members of MLCM. We identify the incisor in GI 5/301 as a deciduous one, as it is less robust than the permanent incisor in the holotype and in HMNS 94-10-178, which clearly shows a limited enamel band. The vertical diameter of the incisor in GI 5/301 is 2.5 mm, the transverse one 1.5 mm (measured at the boundary with the dentary); p3 is peg-like, poorly preserved; p4 has its labial and lingual surfaces damaged, and part of the top is missing. Originally p4 was arcuate; its length is 4.3 mm. The number of serrations and ridges cannot be recognized, but the prominent and relatively large basal cuspule has been preserved. The m1 is 4.2 mm long, with a cusp formula 4:3, and p4:m1 length ratio is 1.02.

The dentaries in AMNH 20440 are badly damaged and, of the teeth, only the incisors, both p3, and incomplete right p4 (now lost) have been preserved. This latter tooth appears in the photograph of Simpson (1925: fig. 7B) as belonging to the left dentary. Because of the incomplete state of preservation, the p4 was reconstructed by Kielan-Jaworowska & Sloan (1979: fig. 2A) as much shorter and having a different shape than it really has (Figs 5 and 12J). The incisors in AMNH 20440 have been broken and apparently glued back more horizontally than originally preserved (Simpson 1925: fig. 7). They are procumbent (personal information from Guillermo W. Rougier, letter of January 30, 1997), but less so than figured by Simpson.

The dentary GI 5/301 described by us is smaller than the corresponding part of AMNH 20440, which may be due to the younger individual age of our specimen.

Family *incertae sedis*
Genus *Kamptobaatar* Kielan-Jaworowska, 1970
Kamptobaatar kuczynskii Kielan-Jaworowska, 1970
Figs 6, 7, 10E, 11E, 12E.

Holotype: ZPAL MgM-I/33, skull of a juvenile individual without zygomatic arches, figured by Kielan-Jaworowska 1970: fig. 2 and pl. 17, and Kielan-Jaworowska 1971: figs 1–5 and plates 1–4, and refigured in various text-books and papers.

Type horizon and locality: Djadokhta Formation (?early Campanian), Bayn Dzak, Gobi Desert, Mongolia.

Revised diagnosis. — Member of Djadochtatheria with a relatively wide and rectangular anterior part of the snout and anterior part of the zygomatic arches varying in position from roughly transverse to posterolateral. Differs from other djadochtatherians in having up to five, asymmetrically arranged pairs of vascular foramina on the nasals and the foramen ovale divided into five foramina. Differs from all the djadochtatherians in having M1 with a smooth inner ridge extending along the length of the tooth, rather than a short
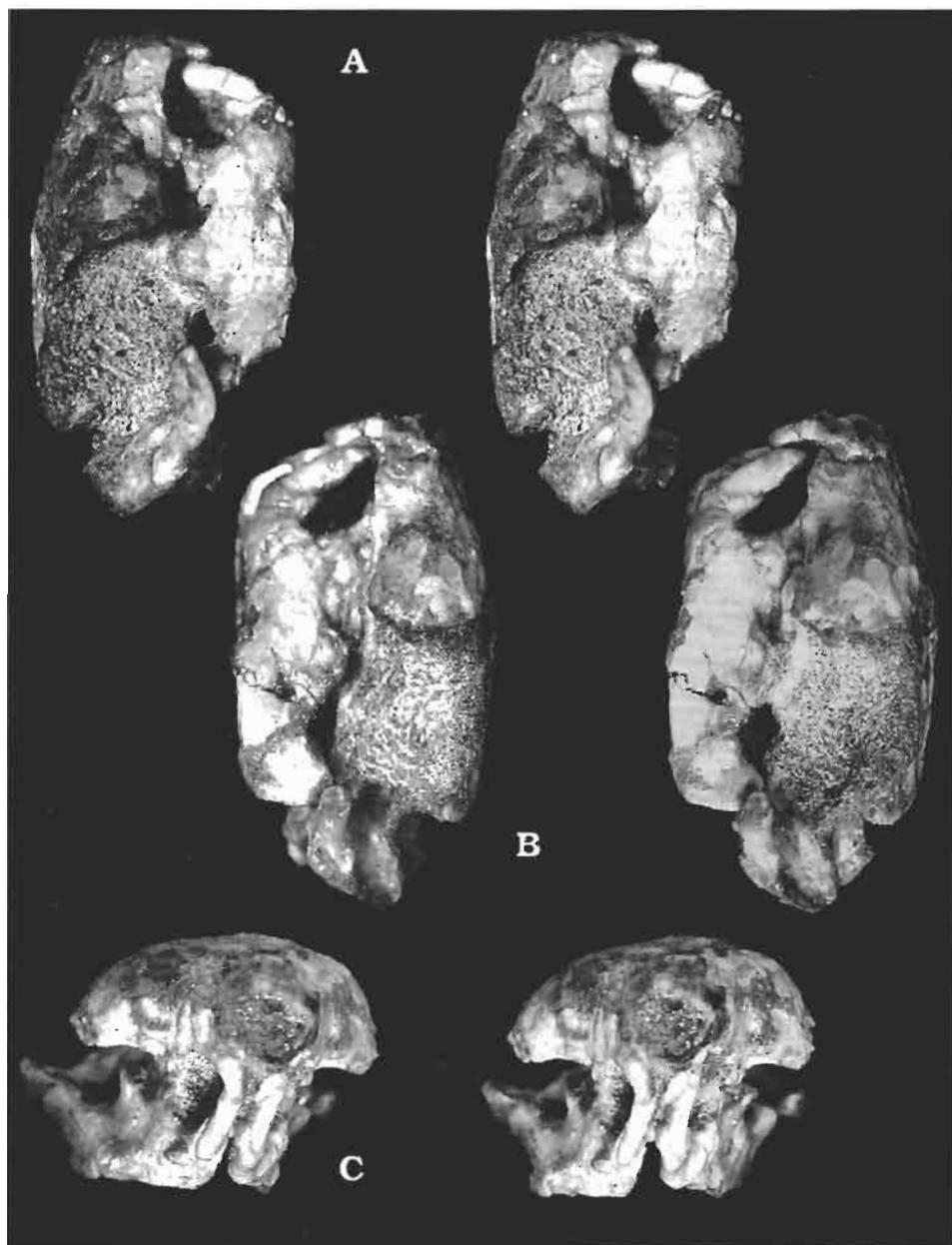
Fig. 6. *Kamptobaatar kuczynskii* Kielan-Jaworowska, 1970. ZPAL MgM-I/49, incomplete skull associated with both dentaries in occlusion (see also Fig. 7), Upper Cretaceous, Djadokhta Formation, Bayn Dzak, Gobi Desert, Mongolia. **A**. Right lateral view. **B**. Left lateral view. **C**. Anterior view. All stereo-photographs × 3.

ridge extending for a half of the tooth length, or a row of cusps. Differs from *Sloanbaatar* and Djadochtatheriidae in having the zygomatic arches moderately expanded laterally
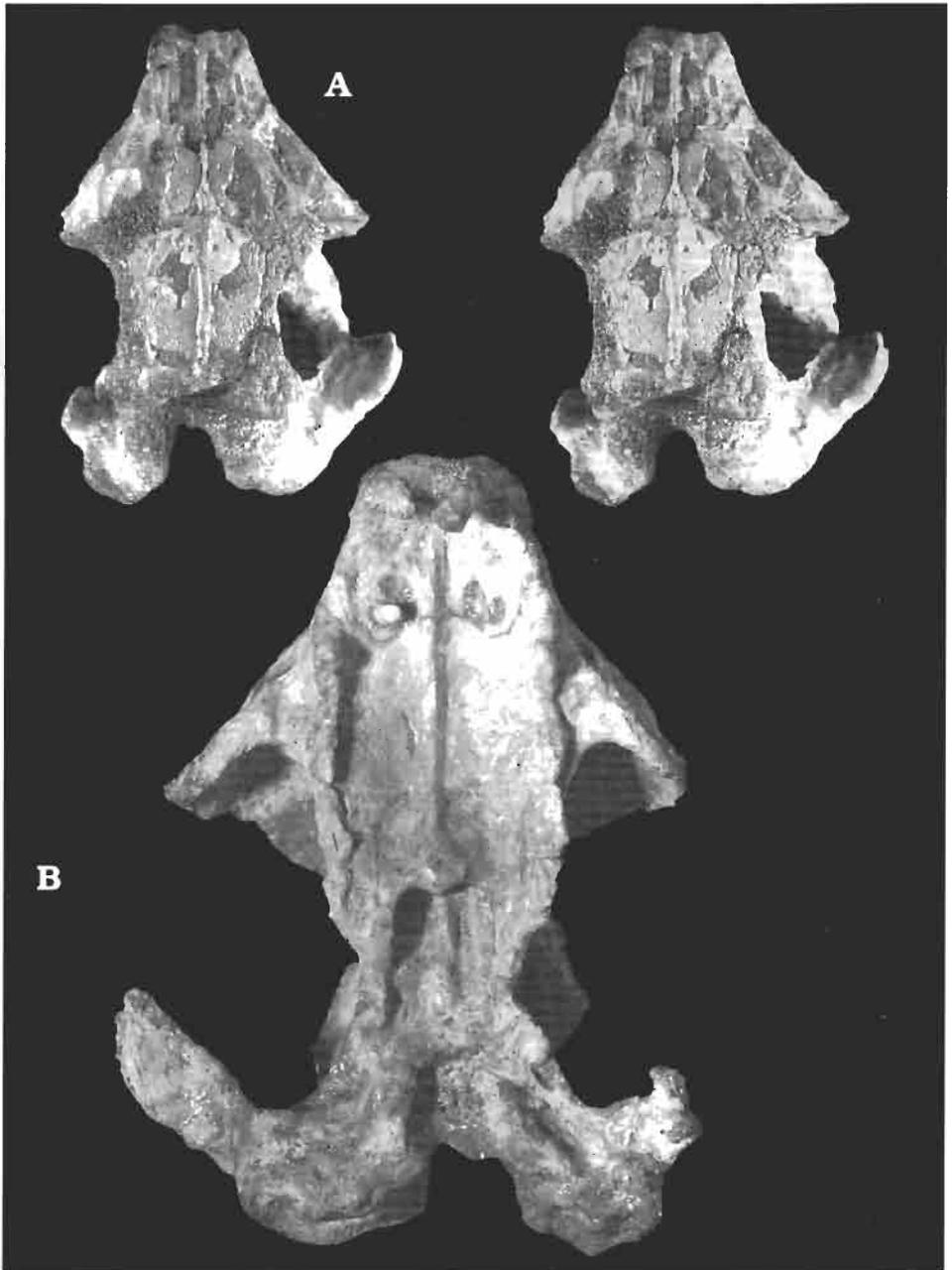
Fig. 7. *Kamptobaatar kuczynskii* Kielan-Jaworowska, 1970. ZPAL MgM-I/49, partial skull (see also Fig. 6), Upper Cretaceous, Djadokhta Formation, Bayn Dzak, Gobi Desert, Mongolia. **A**. Dorsal view, stereophotograph × 3. **B**. The same, ventral view, × 5.

and in this respect it resembles *Nemegtbaatar* and *Chulsanbaatar*. Shares with *Sloanbaatar* and *Nemegtbaatar* a relatively narrow glenoid fossa, although the details of its

shape are different than in these taxa (Fig. 11). Shares with *Sloanbaatar* and *Nessovbaatar* a relatively low coronoid process, that flares laterally. Shares with most djadochtatherians, except for *Kryptobaatar*, *Nemegtbaatar*, and *Chulsanbaatar*, the mandibular condyle situated above the occlusal level of the molars and facing dorsally.

Description and comments. — *Kamptobaatar kuczynskii* from the Djadokhta Formation, Bayn Dzak, Gobi Desert, the only species of *Kamptobaatar*, was erected by Kielan-Jaworowska (1970) on the basis of two specimens ZPAL MgM-I/33 and ZPAL MgM-I/39. Kielan-Jaworowska (1971) described one more specimen ZPAL MgM-I/38 and offered a detailed description of skull anatomy of *Kamptobaatar*, based mostly on exquisitely preserved, although incomplete ZPAL MgM-I/33. One more specimen of *Kamptobaatar*, ZPAL MgM-I/49, was subsequently found at Bayn Dzak, and it is figured in this paper. Although showing a damaged dentition and bone surface, it is more complete than in the previously known specimens; it preserves incomplete zygomatic arches with right glenoid fossa and a complete dentary. In spite of the fact that the upper and lower teeth are strongly damaged, it is possible to assign MgM-I/49 to *K. kuczynskii* with certainty, as it shows identical general shape, size and proportions of upper and lower teeth as previously described specimens, the same structure of the palatal region and details of the cranial sutures. The skull of MgM-I/49 is 20 mm long (18 mm in MgM-I/33, which is a juvenile specimen). The glenoid fossa is narrow, half-oval in shape, and anterolaterally elongated. ZPAL MgM-I/49 differs from MgM-I/33 and MgM-I/38 in having the anterior part of the zygomatic arches directed posterolaterally, rather than laterally, which is probably a manifestation of individual variation. Therefore, our new reconstruction of the skull (Figs 10E and 11E) differs slightly in shape of the snout from previous reconstructions (Kielan-Jaworowska 1970: fig. 2; 1971: figs 1 and 4). The vascular foramina on the nasals, irregularly arranged in MgM-I/33, cannot be recognized in MgM-I/49. It cannot be stated with any certainty whether foramen ovale, divided in MgM-I/33 into five foramina, was similarly divided in MgM-I/49.

Only the anterior part of the dentaries has been preserved in ZPAL MgM-I/38 and MgM-I/39. The dentaries, as preserved in MgM-I/49, show a relatively low coronoid process, flaring laterally, a strong masseteric crest and a condyle situated slightly above the level of the molars and facing dorsally rather than posterodorsally. Because of the poor state of preservation of ZPAL MgM-I/49, we continue to reconstruct *Kamptobaatar* mostly on the basis of ZPAL MgM-I/33, combined with information provided by the new specimen.

Genus *Nessovbaatar* nov.

Type species by monotypy: *Nessovbaatar multicostatus* sp. n.

Nessovbaatar multicostatus sp. n.

Figs 8, 9, 12G.

Derivation of the name: named in honor of the late Dr. Lev A. Nessov from St. Petersburg University, in recognition of his contribution to the knowledge of the Mesozoic mammals of Asia; Mongolian *baatar* – a hero; Lat. *multum* – many, *costa* – rib, ridge – alludes to relatively many (9) ridges on p4.

Holotype and only known specimen: ZPAL MgM-I/103, both dentaries with incisors partly broken. The right dentary is almost complete, with broken coronoid process, broken incisor and missing m2. In the left one all the premolars and molars are preserved, the coronoid process is broken and the posterior part is missing.

Type horizon and locality: Red beds of Khermeen Tsav (equivalent of the Barun Goyot Formation, ?late Campanian), Khermeen Tsav II, Gobi Desert, Mongolia.

Remarks. — It cannot be excluded that *Nessovbaatar* is a member of the Sloanbaataridae. However, without the skull, it is provisionally assigned to a family *incertae sedis*. **Generic and specific diagnosis.** — Small member of the Djadochtatheria, family *incertae sedis*, known only from the dentaries of a single individual. Differs from *Sloanbaatar* in being smaller, but shares with it and with *Kamptobaatar* a relatively
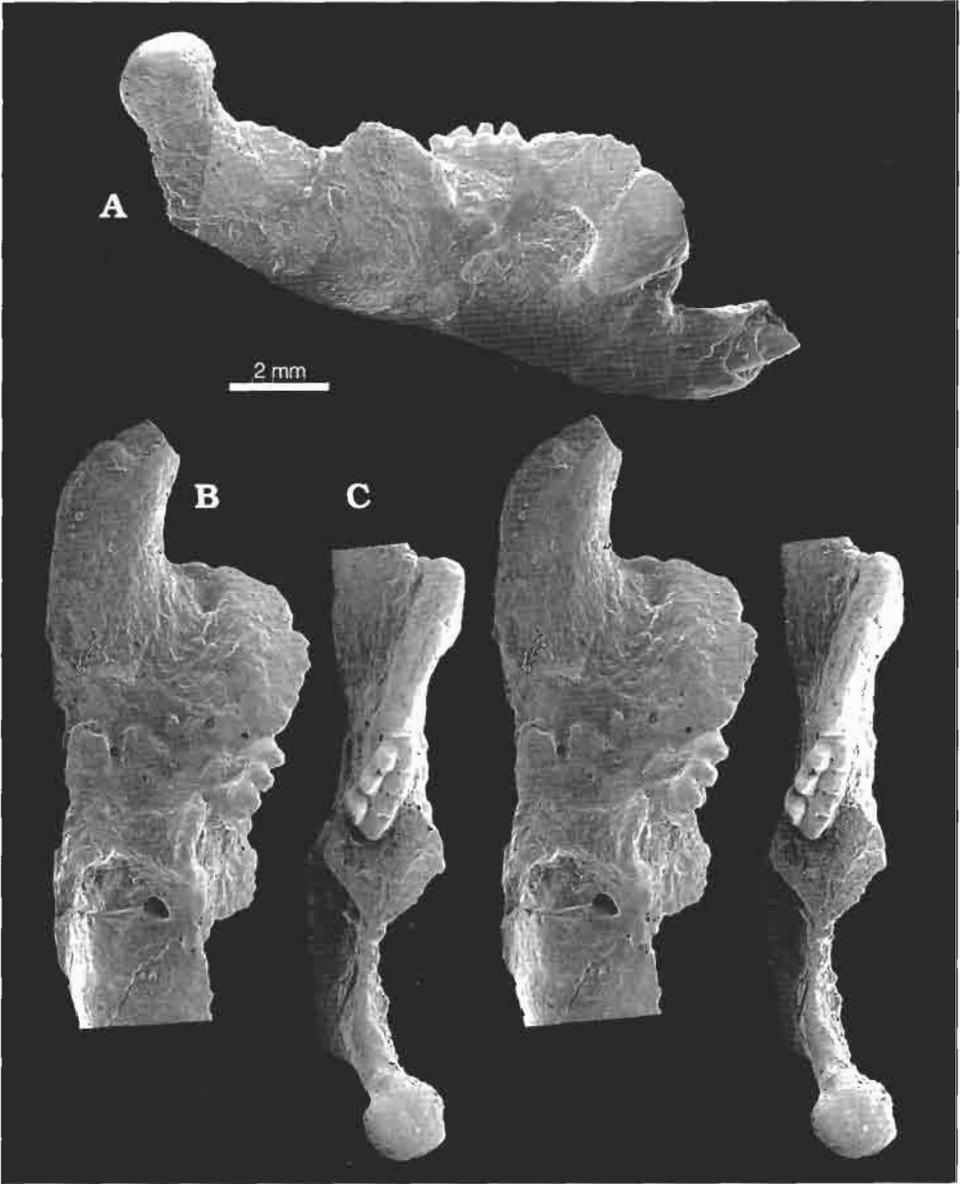
Fig. 8. *Nessovbaatar multicostatus* gen. et sp. n., ZPAL MgM-I/103, holotype (see also Fig. 9). Upper Cretaceous, Red beds of Khermeen Tsav, Khermeen Tsav II, Gobi Desert, Mongolia. **A**. Right dentary, lateral view. **B**. Stereo-photograph of the teeth of the same, occlusal view. **C**. Stereo-photograph of the anterior part of the same, medial view. All SEM micrographs.

small coronoid process that flares laterally. Shares with *Sloanbaatar, Kamptobaatar, Djadochtatherium,* and *Catopsbaatar* the condyle placed above the occlusal level of the molars and facing dorsally (a possible homoplasy). Differs from all djadochtathe-rians in having a very large fan-shaped p4 with 10 serrations, nine of which are
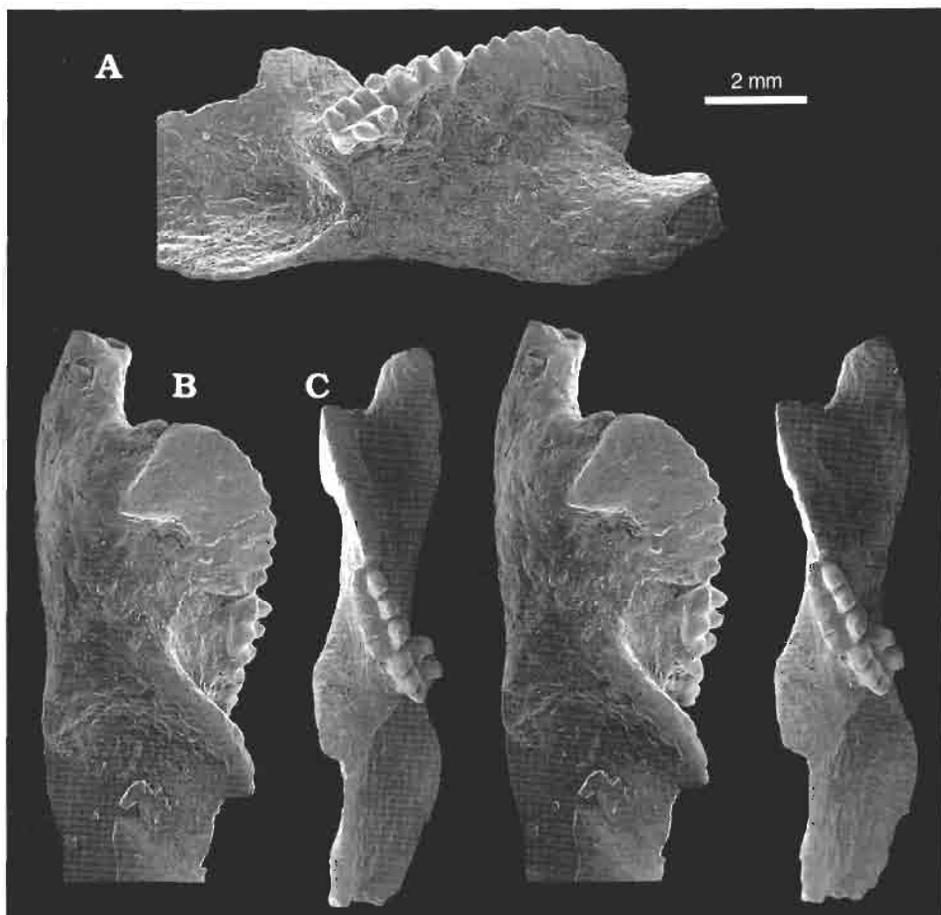
Fig. 9. *Nessovbaatar multicostatus* gen. et sp. n. ZPAL MgM-I/103, holotype (see also Fig. 8). Upper Cretaceous, Red beds of Khermeen Tsav, Khermeen Tsav II, Gobi Desert, Mongolia. **A**. Incomplete left dentary, medial view. **B**. Stereo-photograph of the lateral view of the same. **C**. Stereo-photograph of the dorsal view of the same. All SEM micrographs.

provided with weak ridges. Approaches *Sloanbaatar* in having 4:3 cusps on m1. Differs from *Sloanbaatar* in having angle of 18° between the ventral margin of the dentary and the occlusal level of the molars, rather than 28° or even more; in having 3:2 cusps on m2, rather than 2:2. It has similar size and cusp formulae in lower molars as *Chulsanbaatar*, from which it differs in structure of p4 and in lack of the distinct masseteric fovea with a rounded ridge in front of it. The p4 resembles that of Mongolian Early Cretaceous *Arginbaatar* in being fan-shaped with a large triangular lobe over the first root (exodaenodont lobe of Krause 1977), but differs from it in being less vaulted, having a smaller number of serrations with ridges and being completely covered with enamel.

Description. — The length of the dentary from the base of the incisor to the posterior margin of the condyle is about 13.5 mm. At the middle of the diastema between the incisor and p3, close to the base of the incisor there is a small mental foramen. The angle between the occlusal level of the

molars and the lower margin of the dentary is about 18°. The masseteric crest is weak and does not extend high across the jaw; it ends opposite the middle of m1. In the posterior part of the dentary, between the masseteric and coronoid crests there is a distinct, deep masseteric fossa, the anterior margin of which is convex and rounded anteriorly opposite the middle of m1; the masseteric fovea is not recognizable. The coronoid crest starts below the middle of m1 and forms an angle of about 43° with the occlusal level of the molars. Its upper part is broken off, but the preserved part shows that it flares outwards. The mandibular condyle, as preserved in the right jaw, is situated on a relatively long stem, above the level of the occlusal surface of the molars. It faces generally dorsally, but is rounded both anteriorly and posteriorly. It does not prolong onto the posterior margin of the jaw, as in many djadochtatherians, but it is rather similar in shape and position to that in *Sloanbaatar.* It cannot be stated with any certainty whether the posterior margin of the dentary as preserved on the right side is a real one, or has been broken off. The pterygoid fossa is deep as in other multituberculates, its anterior margin being just below the posterior margin of m2.

The incisors are broken off in both dentaries. In the right dentary one can see a thick layer of enamel in the ventral part of the broken tooth, but because of breakage one cannot be sure whether the enamel was sharply limited or only somewhat thicker ventrally than dorsally; therefore in Table 2 we score it as a question mark. The p3 preserved in both dentaries is partly obscured by the overhanging anterior margin of p4 but it is clearly narrow and peg-like, as in all other djadochtatherians. The p4 is fan-shaped (Figs 8, 9 and 12G); its maximum length in lateral view, measured obliquely is 3.5 mm, and the p4:m1 length ratio is 1.75. The serrations on the upper margin are sharp in the posterior, unworn part, and worn out in the anterior part. Therefore the number of serrations cannot be recognized with any certainty; it seems that there were 10 serrations, nine of which are provided with ridges (lack of one ridge may be due to the state of preservation). In the posterior part there is a small basal cuspule, poorly recognizable. In labial view the anterior part of the tooth forms a large triangular lobe. The crown is much shallower in lingual view than in labial one. The m1 is 2.0 mm long, with cusp formula 4:3; the anterior cusp in the labial row is somewhat larger than the remaining ones and in the left jaw, because of wear, it looks like it is divided into two cusps. The m2 is 1.1 mm long; its cusp formula is 3:2.

Comments on djadochtatherians

The MLCM taxa differ from those known from other continents and/or other strati-graphical units in their state of relatively complete preservation. The majority of MLCM taxa is represented by incomplete or entire skulls (Figs 10D–I, 11D–I, 12D–K), often associated with postcranial skeletons, while the taxa known from other parts of the world are, as a rule, represented by isolated teeth or jaw fragments with teeth (see Clemens & Kielan-Jaworowska 1979 and Hahn & Hahn 1983 for reviews). Dentaries and large fragments of multituberculate skulls have been preserved in the Kimmerid-gian Guimarota fauna of Portugal (Hahn 1969, 1977, 1987, 1993 and references therein), but some details of the skull morphology, such as structure of the orbit, most of the cranial sutures, details of the structure of the basicranial region and the occipital plate remain unknown. The same holds true for the Purbeck multituberculates from England (Simpson 1928b; Kielan-Jaworowska & Ensom 1992). In the North American Late Jurassic Morrison Formation there occur isolated teeth and jaw fragments (Simpson 1929), but two multituberculate skulls have been found which still require description (Engelmann *et al.* 1990). The Early Cretaceous faunas of the world are rare. The best known is that from the ?Albian Khoboor beds of Mongolia (Trofimov 1980; Kielan-Jaworowska *et al.* 1987), again represented by isolated teeth and jaw fragments.

The Early Cretaceous multituberculates from Great Britain and Spain are represented by isolated teeth (see Canudo & Cuenca-Bescós 1996 for references). The Albian multituberculate fauna of Texas, although discovered some 40 years ago (Patterson 1956; Krause *et al.* 1990) still awaits description. Multituberculates from the Late Albian Cedar Mountain Formation of Utah are represented by several species of *Paracimexomys* and teeth of uncertain affinity. Eaton & Nelson (1991) assigned *Paracimexomys* to ?Ptilodontoidea and concluded (p. 11): 'Comparison of the material from Asia and Utah provided no evidence of multituberculate exchange between Asia and North America during the late Early Cretaceous'.

Mammals from the early part of the Late Cretaceous have not been recorded in Mongolia and mammalian faunas from this period of earth's history are rare and generally poorly known, although in the last two decades new discoveries have been made in North America and Asia. North American Cenomanian and Turonian multituberculates from Utah were described by Eaton and Cifelli (1988) and Eaton (1995). They contain representatives of Ptilodontoidea, *Paracimexomys* assigned to a suborder and family *incertae sedis*, and uncertain representatives of Taeniolabidoidea.

Nessov published a series of papers with descriptions of mammalian faunas from vast territory of southwestern Asia (Uzbekistan, Kazakhstan and Tajikistan, often referred to as 'Middle Asia' in Soviet literature). The Cretaceous beds in these areas range from Aptian to Maastrichtian (see Nessov *et al.* 1994 for summary and Averianov 1997). Few multituberculates were encountered in the Coniacian of Uzbekistan (Kielan-Jaworowska & Nessov 1992).

In the North American Late Cretaceous faunas no skull has been preserved (e.g., Clemens 1963; Lillegraven 1969; see also Clemens & Kielan-Jaworowska 1979 for review). One skull is known from the Late Cretaceous of Europe (Rădulescu & Samson 1996). The Late Cretaceous multituberculates from Gondwana are poorly known and represented by isolated teeth (Bonaparte 1990; Sigogneau-Russell 1991; Krause *et al.* 1992), with a single exception of an incomplete dentary (Kielan-Jaworowska & Bonaparte 1996). In the Paleocene rocks multituberculates are more common (e.g., Jepsen 1940; Krause 1977; Sloan 1981), and skulls belonging to *Taeniolabis*, *Ptilodus*, and *Ectypodus* in North America (Granger & Simpson 1929; Simpson 1937; Sloan 1979; Krause 1982) and *Lambdopsalis* in Asia (Miao 1988) have been described (Figs 10A–C, 11A–C, 12A–C). These skulls, except perhaps *Ectypodus tardus*, figured by Sloan (1979: fig. 1), and *Lambdopsalis bulla*, figured by Miao (1988: fig. 3), are less complete than those from the Late Cretaceous of Mongolia (Figs 10D–I, 11D–I, 12D–K).

As no complete skulls of Plagiaulacoidea have been described and only that of *Paulchoffatia* was reconstructed (Hahn 1969, 1987), it is difficult to venture an opinion which of the djadochtatherian characters are primitive or derived. The posterior position of the glenoid fossa (or of the mandibular joint) is primitive for mammals. The mandibular joint is placed posteriorly in cynodonts, *Morganucodon*, *Sinoconodon*, and monotremes (Brink 1982; Kermack *et al.* 1981; Crompton & Luo 1993). As may be seen in Fig. 11, the glenoid fossa is apparently placed in all the djadochtatherians more anteriorly than in *Ptilodus* and *Taeniolabis*. Hahn (1969, 1987) reconstructed the glenoid fossa in a relatively posterior position in *Paulchoffatia*, placed somewhat more anteriorly than reconstructed for *Ptilodus* and *Taeniolabis* (Simpson 1937). The gle-
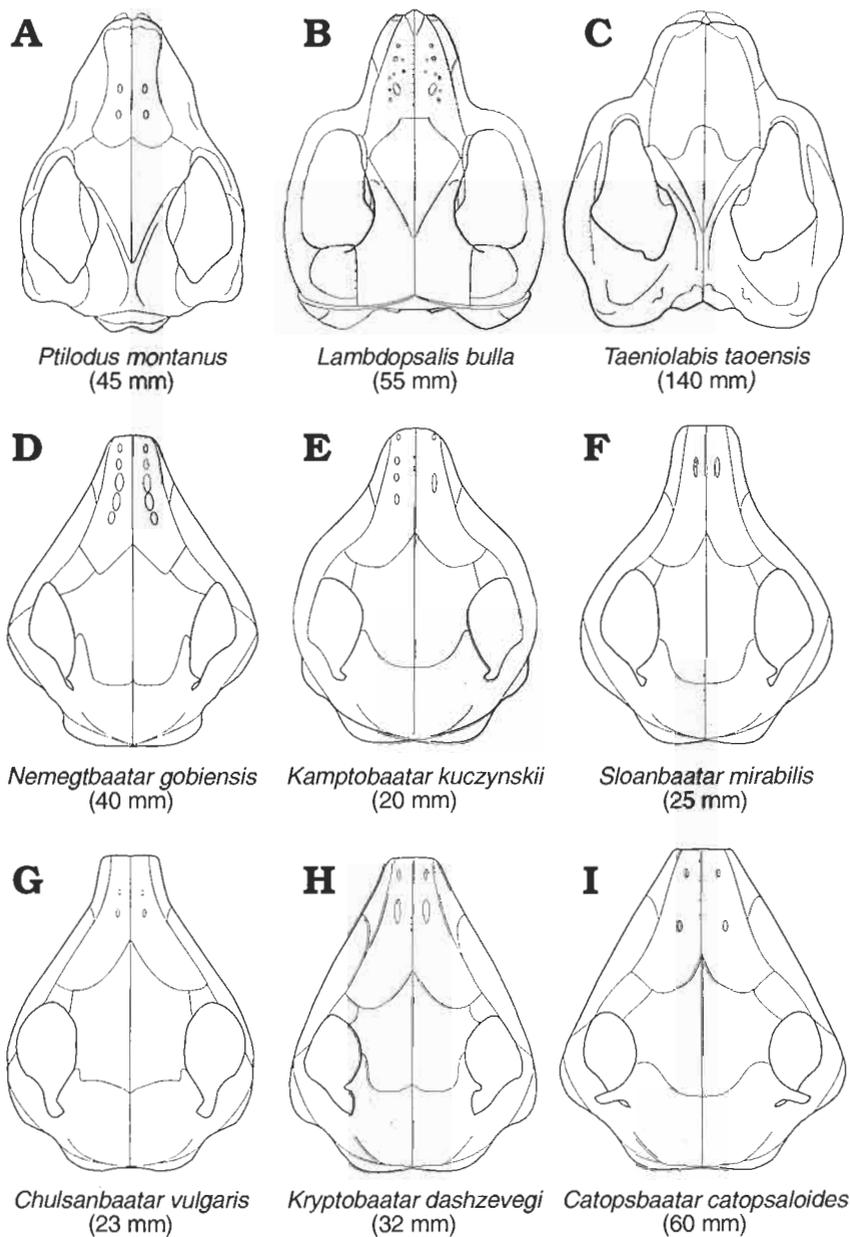
Fig. 10. Diagrammatic drawings of selected Late Cretaceous and Tertiary multituberculate skulls, rendered to the same length, dorsal views. The numbers in brackets refer to the estimated maximum length of the skull. Modified from: **A**. Simpson (1937), **B**. Miao (1988, 1993), **C**. Granger & Simpson (1929), **D**. Kielan-Jaworowska *et al.* (1986), **E**, **F**. Kielan-Jaworowska (1971), **G**. Hurum (1994), **H**. Original, **I**. Kielan-Jaworowska & Sloan (1979). The zygomatic arches in **B** and **E** are reconstructed.

noid fossa has not been preserved in *Lambdopsalis*, but was reconstructed by Miao (1988). The only non-djadochtatherian multituberculate with the glenoid fossa placed
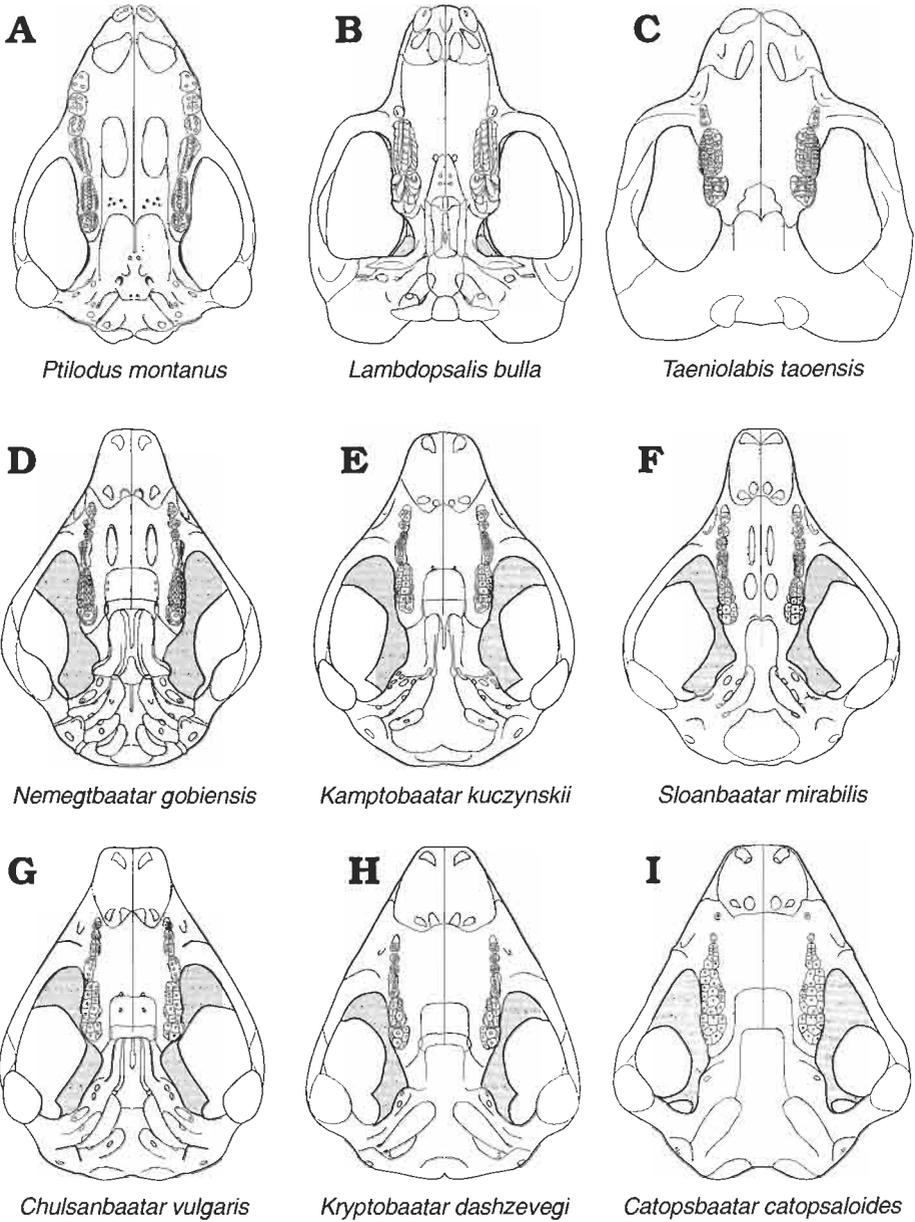
Fig. 11. Diagrammatic drawings of selected Late Cretaceous and Tertiary multituberculate skulls, rendered to the same length, ventral views. Modified from: **A**. Simpson (1937), **B**. Miao (1988, 1993), **C**. Granger & Simpson (1929), **D**, **G**. Kielan-Jaworowska *et al.* (1986), **E**, **F**. Kielan-Jaworowska (1971), **H**. Kielan-Jaworowska & Dashzeveg (1978), **I**. Kielan-Jaworowska & Sloan (1979). The zygomatic arches in **B** and **E** are reconstructed.

relatively anteriorly is *Ectypodus tardus*, reconstructed by Sloan (1979). In that reconstruction the glenoid fossa is placed as in therian mammals and the posterior part of the

skull in lateral view has a somewhat therian appearance (Sloan 1979: figs 2, 3). As a photograph of the *Ectypodus* skull has not been published, it is difficult to venture an opinion to what extent Sloan's reconstruction is reliable. Because of the scarcity of figured skulls belonging to non-djadochtatherian taxa, the conclusion that the djadoch-tatherians are more advanced than other multituberculates, in having a longer braincase to the rear of the glenoid fossa (Figs 10 and 11), must be regarded as tentative.

Djadochtatherians differ from other multituberculates in having a large, roughly rectangular facial surface of the lacrimal (Figs 1D, 2 and 10). Large dorsal exposure of the lacrimal is characteristic for cynodonts (in addition to the lacrimal there occurs also the prefrontal), *Morganucodon* and *Sinoconodon* (Brink 1982; Kermack *et al.* 1981; Crompton & Luo 1993). In view of this, the large dorsal exposure of the lacrimal should be regarded as a primitive character. On the other hand, the lacrimal is absent in monotremes and has been reconstructed as small in *Paulchoffatia* (Hahn 1969). However, Guillermo W. Rougier, has examined the Guimarota collection and informed us (letter of January 30, 1997) that the lacrimal may be relatively extensive in *Paulchoffatia.* In *Ptilodus* and *Taeniolabis* (not found in *Ectypodus*) the dorsal expo-sure of the lacrimal is small (Simpson 1937; Sloan 1979). We tentatively regard a large, rectangular facial surface of the lacrimal as a synapomorphy of djadochtatherians, but it cannot be excluded that this is a plesiomorphic character. As may be seen in Fig. 10, the frontal contacts the maxilla in *Ptilodus*, while in the Taeniolabididae (*Taeniolabis* and *Lambdopsalis*) the frontal is separated from the maxilla by the nasal and parietal and not by the lacrimal as in djadochtatherians. Hahn (1969) reconstructed the frontals in *Paulchoffatia* as pointed anteriorly and rounded posteriorly. If this reconstruction is reliable, then the shape of the frontal characteristic of djadochtatherians may be regarded as a primitive feature. Another djadochtatherian synapomorphy is the U-shaped fronto-parietal suture. This suture was reconstructed in *Paulchoffatia* as consisting of two parts convex posteriorly, the parietal being slightly inserted medially between the frontals (Hahn 1969: fig. 15). Because of the ambiguity related to this suture, we score it as a question mark in a hypothetical ancestor in Table 2. If it turns out that this suture was U-shaped in Plagiaulacoidea, retention of this character in Djadochtatheria should be regarded as a plesiomorphy.

The presence of a large posttemporal fossa (canal) is characteristic of all the djadochtatherians in which the skulls have been preserved; it is placed in the middle of the petrosal exposed on the occipital plate. In non-djadochtatherian multituberculates, the posttemporal fossa has been described only in isolated petrosals of *Catopsalis* (Kielan-Jaworowska *et al.* 1986; Wible & Hopson 1993), where it is relatively small and placed more laterally than in djadochtatherians. In consequence, the vascular system of the posterior part of the head was apparently different in djadochtatherians (as exemplified by *Nemegtbaatar*) from that in *Catopsalis* (Kielan-Jaworowska *et al.* 1986: figs 32 and 33). Recently James A. Hopson informed us (letter of September 10, 1996) that the *Ptilodus* skull being redescribed by him has a large posttemporal fossa placed close to the lateral margin of the occiput. If so, a large posttemporal fossa is not a synapomorphy of djadochtatherians, although it is apparently absent in *Taeniolabis* and *Lambdopsalis*. The occipital plate in *Ectypodus* has not been described. The sharp ridge between lateral and ventral parts of the premaxilla is apparently unique for djadochtatherians and is a derived character.
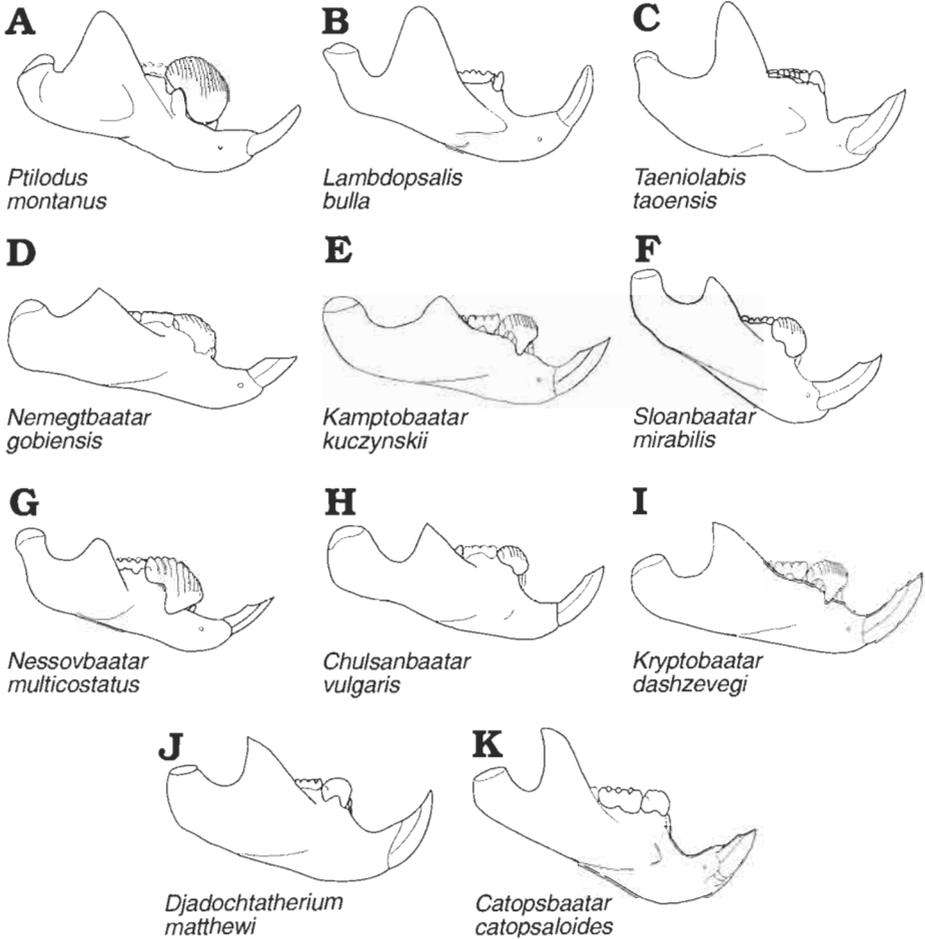
Fig. 12. Diagrammatic drawings of selected Late Cretaceous and Tertiary multituberculate dentaries. rendered to the same length, lateral views. Modified from: **A**, Simpson (1937), **B**. Miao (1993). C. Granger & Simpson (1929), coronoid process based on *Taeniolabis lamberti* Simmons, 1987. **D**. Kielan-Jaworowska *et al.* (1986), **E**, **F**. Kielan-Jaworowska (1971), **K**. Kielan-Jaworowska & Sloan (1979). **G–J**. Original. The coronoid processes in **B**, **G**, **J**, and lower incisor in **G** are reconstructed.

The small number of cusps on the upper and lower molars and premolars, characteristic of djadochtatherians, and the small number of ridges on p4, are features primitive for multituberculates. The arcuate form of the p4 is, however, a derived feature, as it is rectangular in Plagiaulacoidea. An arcuate p4 is characteristic of the Late Cretaceous and Paleocene multituberculates, except for Taeniolabididae and Gondwanatheria (Granger & Simpson 1929; Kielan-Jaworowska & Bonaparte 1996). Djadochtatherians share with Eucosmodontidae an arcuate p4 that does not protrude dorsally above the level of the molars, whereas it protrudes strongly in Ptilodontoidea (a ptilodontoidean autapomorphy). The limited enamel band on the lower incisor is an advanced feature, which occurs in an undescribed multituberculate from the Morrison Formation, eobaatarids, djadochtatherians (except for *Sloanbaatar* and *Kampto-*

baatar), eucosmodontids and taeniolabidids. The medial position of I3 is a derived character, but in addition to djadochtatherians, it also occurs in the eucosmodontid *Stygimys* and the cimolodontid *Meniscoessus*. In *Lambdopsalis*, I3 is positioned slightly medially from the lateral margin of the premaxilla (Miao 1986, 1988). The above comparisons show that djadochtatherians are a separate line of multituberculates, which shows a mosaic of primitive and advanced characters.

Other cranial features found in all djadochtatherians, such as e.g., presence of vascular foramina on the nasals, the jugal situated on the medial side of the zygomatic arch (Hopson *et al.* 1989), pterygoids placed in the middle of choanal channels (Kielan-Jaworowska 1971), division of foramen ovale into at least two foramina (Simpson 1937), conspicuous zygomatic ridges, anterior position of the masseteric and coronoid crests, large, flat glenoid fossa, sloping down and backwards and placed well lateral of the braincase (Gambaryan & Kielan-Jaworowska 1995), backward power stroke (Krause 1982), cryptomesencephalic type of brain (Kielan-Jaworowska 1986), and several others, are apparently synapomorphies for multituberculates as a whole.

Cladistic analysis

Simmons (1993) provided a comprehensive phylogenetic analysis to resolve the relationships of all multituberculate groups. She made a list of 67 characters (41 dental and 26 cranial) and examined 49 taxa and a hypothetical ancestor. Rougier *et al.* (1997) adopted Simmons' list with small alterations and examined 49 multituberculate taxa (the new genus, *Tombaatar*, being added and *Tugrigbaatar* removed), and a hypothetical ancestor.

We constructed a Character list (Table 1) different from those of Simmons (1993) and Rougier *et al.* (1997); our Taxon-character matrix (Table 2) contains 17 taxa and 43 characters and all the characters are considered as unordered. Ten characters employed by us in Table 1 (nos. 1, 2, 5, 11, 12, 22, 27, 28, 30 and 34) are taken from Simmons (1993) and Rougier *et al.* (1997), while two (nos. 23 and 33) are emended by us. We do not use other characters from the Character descriptions of Simmons (1993, Appendix 2 in her paper), or her corrected list, proposed by Rougier *et al.* (1997, Appendix 1 in their paper), for the following reasons (if not stated otherwise, numbers in brackets refer to numbers in Appendix 1 of the paper by Rougier *et al.*):

— We do not use the enamel microstructure (no. 1), as all the taxa employed by us (except for *Ptilodus*, which has small arcuate prisms), show the same type of gigantoprismatic enamel (the character not known in *Buginbaatar*), while the ancestor apparently had a preprismatic enamel, different from those in the taxa studied.

— We do not use the metric characters (nos. 10, 14, 16, 36, 39, 41), as they may be possibly used in phylogenetic analyses of low rank taxa, such as species of the same genus, but are not appropriate for high rank taxa, such as genera, families, infraorders, suborders etc. The polarization of metric characters in high rank taxonomy may be misleading, as, e.g., P4 has approximately the same length in *Chulsanbaatar* and *Lambdopsalis*, which obviously belong to different clades (and there are many examples).

— As we confine our analysis to the MLCM taxa, we do not use representatives of Plagiaulacoidea (except for construction of an ancestor). That is why we do not employ

the characters that differentiate the Plagiaulacoidea from all later taxa (nos. 2, 5, 6, 8, 12, 15, 17, 18, 19, 21, 23, 24, 25, 26, 40), and we replace them in Table 1 by other characters.

— We do not use characters that in our opinion occur in all the multituberculates (nos. 4, 47, 50, 51, see Gambaryan & Kielan-Jaworowska 1995) and we replace them by other characters.

— We employ several characters that may have phylogenetic value and have not been used by Simmons (1993) and Rougier *et al.* (1997), (nos. 13, 19, 20, 26, 38, 39, 40, 41, 42, 43 in Table 1). Other characters (nos. 15, 16, and 29 in Table 1) are replaced by us by characters differently defined.

In the phylogenetic analysis presented below we make an attempt to verify the relationships among the eleven established MLCM genera: *Bulganbaatar, Buginbaatar, Catopsbaatar, Chulsanbaatar, Djadochtatherium, Kamptobaatar, Kryptobaatar, Nemegtbaatar, Nessovbaatar, Sloanbaatar,* and *Tombaatar.* Ten of these genera are monotypic, while *Kryptobaatar* is represented by two species, *K. dashzevegi* and *K. saichanensis.* We have chosen *K. dashzevegi* for our cladistic analysis, as it is more complete than *K. saichanensis.*

As the diagnostic characters of the MLCM are based on both the skull structure and dentition, we have chosen for comparison the taxa that are known from relatively complete skulls. We selected the following Paleocene or Late Cretaceous genera: *Lambdopsalis, Ptilodus, Stygimys,* and *Taeniolabis.* In addition, we also use *Eucosmodon,* which is less completely known. As our analysis concerns the MLCM taxa and selected Paleocene and Late Cretaceous members of Cimolodonta (*sensu* McKenna 1975) from other continents, we constructed a hypothetical ancestor of all these forms on the basis of characters that occur in Late Jurassic Plagiaulacoidea (Simpson 1928b, 1929; Hahn 1969, 1977, 1987, 1993 and references therein; Kielan-Jaworowska & Ensom 1992).

In our Taxon-character matrix (Table 2) the ancestor is 60% complete, *Nemegtbaatar* 100%, *Chulsanbaatar* 100%, *Catopsbaatar* 98%, *Kamptobaatar* 95%, *Kryptobaatar* 100%, *Djadochtatherium* 61%, *Bulganbaatar* 44%, *Sloanbaatar* 98%, *Buginbaatar* 35%, *Nessovbaatar* 21%, *Tombaatar* 49%, *Lambdopsalis* 88%, *Taeniolabis* 77%, *Stygimys* 60%, *Eucosmodon* 35%, and *Ptilodus* 98%. Novacek *et al.* (1988) argued that when 30% or more of relevant data are missing, the use of such taxa for reflecting true evolutionary relationships is limited. We agree, but still use e.g., *Nessovbaatar,* which is only 21% complete, being aware that when the skull of this taxon is found, its position in a phylogenetic tree may be changed.

In an attempt at cladistic analysis we employed two different programs, using the same Character list (Table 1) and Taxon-character matrix (Table 2) for both. These are: Pee-Wee (Goloboff 1993a, 1996) and NONA (Goloboff 1993b). From the Pee-Wee program we obtained a tree with better resolution (Fig. 13) than from the NONA program (Fig. 14). Therefore we discuss the NONA results only briefly. The high rank taxa proposed in this paper: Djadochtatheria nov. and Djadochtatheriidae nov. are based on Pee-Wee results.

Pee-Wee results (Tables 1–4 and Fig. 13). — Using the Pee-Wee program (Goloboff 1993a, 1996) we obtained two trees with the best fit (353.7; 63%, for fit of every

character, see Table 3), with lengths of 103 and 104 steps. We chose the shorter of these trees (Fig. 13) which differs from the longer one only in the relationship of the group *Nemegtbaatar–Bulganbaatar* to the group of *Kamptobaatar–Sloanbaatar–Nessov-baatar.*

Results of the cladistic analysis presented in this paper, based on the Pee-Wee program (Fig. 13), show the monophyly of MLCM taxa (except *Buginbaatar*). This agrees with the results of Rougier *et al.* (1997), based on a PAUP analysis and employing a different Character list.

For the monophyletic group (MLCM taxa except *Buginbaatar*) we propose the suborder Djadochtatheria (Fig. 13, node 9). Rougier *et al.* (1997) included the North American Paleocene genus *Pentacosmodon* in this clade and placed the Early–Late Cretaceous *Paracimexomys* close to it. We agree that *Pentacosmodon* and *Paracimexo-mys* may be close to Djadochtatheria, or even members of it, which is supported by enamel microstructure (Carlson & Krause 1985; Krause & Carlson 1987). We have not included, however, these two taxa into our analysis, because of their incompleteness. As Djadochtatheria are defined mostly on cranial characters and the skulls of these North American genera are not known, their attribution to a new suborder cannot be demonstrated with any certainty.

Several characters that we use to diagnose the Djadochtatheria, based on the uniqueness of their skull (characters 19 and 26–29 in Table 1), are not preserved in known Eucosmodontidae (exemplified in our tree by *Stygimys* and *Eucosmodon*). The program did not use these characters to show the monophyly of the Djadochtatheria, as it is not known whether the characters in question made their appearance at node 7 or 9 in Fig. 13. Still the monophyly of the Djadochtatheria is shown in our tree (Fig. 13, node 9).

In Fig. 13 (node 18), the four genera: *Kryptobaatar, Djadochtatherium, Catops-baatar* and *Tombaatar* form a clade for which the new family Djadochtatheriidae is proposed. In this respect our results differ from those of Rougier *et al.* (1997) who place *Kryptobaatar* between *Chulsanbaatar* and *Bulganbaatar.* The four genera assigned by us to Djadochtatheriidae share a subtrapezoidal shape of the snout, a character that is unique not only among multituberculates, but also among mammals. We hypothesize that this character arose only once in multituberculate evolution. The difference between our and Rougier's *et al.* (1997) results concerning the position of *Krypto-baatar* is related to the different Character lists used. The djadochtatheriid genera *Djadochtatherium, Catopsbaatar,* and *Tombaatar* are placed by Rougier *et al.* (1997) close to one another, which agrees with our results.

In our tree (Fig. 13, node 16), *Chulsanbaatar* is a sister taxon of the Djadochtathe-riidae, from which it differs in having the snout incurved in front of the anterior part of zygomatic arches, a character which we evaluate as an important one. *Chulsanbaatar* shares with Djadochtatheriidae two pairs of vascular foramina on the nasals, lack of palatal vacuities and a relatively long snout. The snout in *Chulsanbaatar,* however, extends for less than a half of the skull length, while for a half or more in djadochtathe-riids. *Bulganbaatar* and *Nemegtbaatar* (Fig. 13, node 10) form a clade, which is the sister group of all other djadochtatherians. *Nessovbaatar* in Fig. 13 is in a trichotomy with *Sloanbaatar* and *Kamptobaatar* and they form a sister group of *Chulsanbaatar* + Djadochtatheriidae. In these respects our tree differs from results of Rougier *et al.* (1997).

Table 1. Character list. Characters nos. 1, 2, 5, 11, 12, 22, 27, 28, 30 and 34 are as in Simmons 1993 and Rougier *et al.* 1997; nos. 23, 33 and 38 are emended after these authors.

1. Enamel covering of lower incisor of uniform thickness (0), thicker on labial surface than on lingual surface (1), completely restricted to labial surface of tooth (2).
2. p3 present (0), absent (1).
3. p4 serrations count 5 or less (0), 6–10 (1), more than 10 (2).
4. p4 in lateral view rectangular (0), arcuate (1), trapezoidal (2), triangular (3).
5. m1 cusp formula 4:3 (0), 4:4 (1), 5:4–5 (2), 7:4 or higher (3).
6. Ratio of p4:m1 length less than 0.6 (0), 0.6–1.7 (1) above 1.7 (2).
7. m2 cusp formula 2:2 (0), more (1).
8. I2 bicuspid (0), single-cuspid (1).
9. I3 located on margin of palate (0), slightly shifted from the labial margin (1), in about the middle of the palatal part of premaxilla (2).
10. Upper premolars five (0), four (1), three (2) one (3).
11. P3 double-rooted (0), single-rooted (1).
12. P4 double-rooted (0), single-rooted (1).
13. Length of upper premolar tooth row:molar tooth row more than 1.5 (0), 1.5–0.5 (1), 0.5–0.1 (2).
14. P4 cusp formula 0–5:1–4:0–5 (0), 0–5:5–10:0–5 (1), 5–7:5–8:2–5 (2).
15. M1 cusp formula 4–5:4–5:0–5 (0), 5–7:5–8:2–5 (1), 5–11:7–10:6–11 (2).
16. M1 inner ridge length:length of M1 0.5 or less (0), more than 0.5 (1).
17. Width of P4:M1 ratio more than 0.9 (0), 0.9–0.6 (1), 0.6–0.45 (2), 0.45–0.2 (3).
18. M2 cusp formula 1:2:2 (0), 1:2:3 (1), more (2).
19. Ridge between the palate and lateral walls of premaxilla absent (0), present (1).
20. Shape of the snout in dorsal view: incurved in front of the zygomatic arches with anterior part directed posterolaterally (0), incurved with anterior part of zygomatic arches directed transversely (1), trapezoidal, not incurved in front of zygomatic arches (2),
21. Number of pairs of vascular foramina on nasal: 1 (0), 2 (1), more (2).
22. Infraorbital foramen positioned dorsal to P1 (0), dorsal to P2 (1), dorsal to P3 or P4 (2).
23. Base of zygomatic arch as marked by posterior edge directly dorsal to P4 (0), dorsal or posterior to P4/M1 embrasure (1).
24. Postorbital process short (0), long (1).
25. Snout length 49%or less of total skull length (0), 50% or more of skull length (1).
26. Frontals pointed anteriorly and not deeply inserted between the nasals (0), pointed anteriorly and deeply inserted between the nasals (1), with subtransversal anterior margins (2).
27. Frontal-parietal suture V-shaped (0), U-shaped (1).
28. Contacts between nasal and parietal absent (0), present (1).
29. Facial surface of lacrimal very small and arcuate (0), large, roughly rectangular (1).
30. Thickening in palatal process of premaxilla absent (0), present (1).
31. Incisive foramen situated within premaxilla (0), limited posteriorly by maxilla (1).
32. Palatal vacuities absent (0), single (1), double (2).
33. Foramen ovale inferium placed medial to foramen masticatorium (0), posterior to foramen masticatorium (1).
34. Jugular fossa small and shallow (0), large and deep (1).
35. Anterior part of promontorium (*sensu* Hurum *et al.* 1996) oval (0), irregular with incurvatures on both sides (1).
36. Glenoid fossa (anterolateral to posteromedial) length:width ratio more than 1.7 (0), below 1.69 (1).
37. Angle of coronoid process relative to tooth row steep 45° or >45° (0), low <45° (1).
38. Coronoid process parallel to the rest of the outer wall of the dentary (0), flared laterally (1).
39. Posttemporal fossa large (0), reduced to a small foramen (1).
40. Angle between the lower margin of the dentary and the occlusal level of the molars between 11–20° (0), above 20° (1).
41. Mandibular condyle opposite or below the level of the molars (0), above the level of the molars (1).
42. Width of the snout:skull length ratio below 0.3 (0), 0.3–0.39 (1), above 0.4 (2).
43. Skull width:skull length ratio 0.79 and below (0), above 0.8 (1).

Table 2. Taxon-character matrix.

	1. Enamel on i1 uniform thickness(0), thicker on labial (1), restricted to labial (2)	2. p3 present (0), absent (1)	3. p4 serrations count 5 or less (0), 6-10 (1), more than 10 (2)	4. p4 in lateral view rectangular (0), arcuate (1), trapezoidal (2), triangular (3)	5. m1 cusp formula 4:3 (0), 4:4 (1), 5:4-5 (2), 7:4 or more (3)	6. Ratio of p4:m1 less than 0.6 (0), 0.6-1.7 (1), above 1.7 (2)	7. m2 cusp formula 2:2 (0), more (1)	8. I2 bicuspid (0), single-cuspid (1)	9. I3 on margin of palate (0), slightly shifted (1), medial position (2)	10. Upper premolars five (0), four (1), three (2), one (3)	11. P3 double-rooted (0), single-rooted (1)	12. P4 double-rooted (0), single-rooted (1)	13. Upper premolar row:molar row more than 1.5 (0), 1.5-0.5 (1), 0.5-0.1 (2)	14. P4 cusp formula 0-5:1-4:0-5 (0), 0-5:5-10:0-5 (1), 5-7:5-8:2-5 (2)	15. Cusp formula on M1 4-5:4-5:0-5 (0), 5-7:5-8:2-5 (1), 5-11:7-10:6-11 (2)	16. M1 inner ridge length:length of M1 0.5 or less (0), more than 0.5 (1)	17. Width of P4:M1 more than 0.9 (0), 0.9-0.6 (1), 0.6-0.45 (2), 0.45-0.2 (3)	18. Cusp formula on M2 1:2:2 (0), 1:2:3 (1), more (2)	19. Ridge between the palate and lateral walls of premaxilla absent (0), present (1)	20. Snout shape incurved, anterior part of zygomatic arches posterolateral (0), incurved, anterior part of zygomatic arches transverse (1), trapezoid (2)	21. Numbers of pairs of vascular foramina on nasals 1 (0), 2 (1), more (2)
ancestor	0	0	0	0	0	?	?	0	0	0	0	0	0	?	?	0	0	?	0	0	?
Nemegtbaatar	2	0	1	1	2	1	1	1	2	1	0	0	1	1	1	1	1	2	1	0	2
Chulsanbaatar	2	0	1	1	0	1	0	1	2	1	0	0	1	1	0	0	2	0	1	0	1
Catopsbaatar	2	0	0	2	1	1	0	1	2	2	0	0	1	1	1	1	2	2	1	2	1
Kamptobaaatar	1	0	1	1	0	1	?	1	2	1	0	0	1	1	0	1	2	1	1	0	2
Kryptobaatar	2	0	1	1	0	1	1	1	2	1	0	0	1	1	0	0	2	1	1	2	1
Djadochtatherium	2	0	?	1	0	1	?	1	2	1	?	?	?	0	?	?	?	?	1	2	?
Bulganbaatar	?	?	?	?	?	?	?	1	2	1	0	0	1	1	0	1	1	0	1	0	?
Sloanbaatar	1	0	1	1	0	1	0	1	2	1	0	0	1	1	0	0	2	1	1	0	0
Buginbaatar	0	1	0	1	3	0	1	?	?	?	?	0	?	1	2	1	3	2	?	?	?
Nessovbaatar	?	0	1	1	0	2	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Tombaatar	?	?	?	?	?	?	?	1	2	2	0	0	1	1	0	0	2	1	1	?	1
Lambdopsalis	2	1	0	3	2	0	1	1	1	3	?	1	2	0	2	1	3	2	0	1	2
Taeniolabis	2	1	0	3	3	1	1	1	0	3	?	1	2	0	2	1	3	2	0	1	?
Stygimys	2	1	2	1	3	2	1	0	2	1	1	0	1	1	1	0	2	?	?	0	?
Eucosmodon	2	1	2	1	3	2	1	0	?	?	1	0	?	?	1	0	?	?	?	?	?
Ptilodus	0	0	2	1	2	2	1	1	0	1	0	0	0	2	2	1	0	2	0	0	1

The three genera *Kamptobaatar*, *Sloanbaatar*, and *Nessovbaatar* share the coronoid process flared laterally and a high position of the mandibular condyle. We believe that these characters could develop in parallel (homoplasy) in various multituberculate groups (Gambaryan & Kielan-Jaworowska 1995). The enamel band on the lower incisor is less sharply limited in *Sloanbaatar* and *Kamptobaatar* than in other djadochtatherians, eucosmodontids and taeniolabidiids. This character is not known in *Nessovbaatar*. *Sloanbaatar* and *Kamptobaatar* differ from one another in many important cranial and dental characters (nos. 16, 21, 22, 31, 32, 37, 40, 42, and 43 in Table 1). *Nessovbaatar* is

Character descriptions:

22. Infraorbital foramen dorsal to P1 (0), P2 (1), P3 or P4 (2)
23. Base of zygomatic arch dorsal to P4 (0), dorsal or posterior to P4/M1 embrasure (1)
24. Postorbital process short (0), long (1)
25. Snout length 49% or less of skull length (0), 50% or more (1)
26. Frontals pointed (0), pointed and deeply inserted between nasals (1), sub transverse (2)
27. Frontal-parietal suture V-shaped (0), U-shaped (1)
28. Contacts between nasals and parietals absent (0), present (1)
29. Lacrimal dorsal part very small arcuate (0), large roughly rectangular (1)
30. Thickening in palatal process of premaxilla absent (0), present (1)
31. Incisive foramen situated within premaxilla (0), limited posteriorly by maxilla (1)
32. Palatal vacuities absent (0), single (1), double (2)
33. Foramen ovale inferium placed medial to foramen masticatorium (0), posterior (1)
34. Jugular fossa small and shallow (0), large and deep (1)
35. Anterior part of promontorium oval (0), irregular (1)
36. Glenoid fossa ratio of length:width 1.7 or more (0), 1.69 or below (1)
37. Angle of coronoid process relative to tooth row more than 45° (0) less than 45° (1)
38. Coronoid process parallel to the outer wall of the dentary (0), flared laterally (1)
39. Posttemporal fossa large (0), reduced to a small foramen (1)
40. Angle of lower margin of the dentary to occlusal level of molars 11-20° (0), above 20° (1)
41. Mandibular condyle opposite or below the level of the molars (0), above (1)
42. Width of the snout:skull length ratio below 0.3 (0), 0.3-0.39 (1), above 0.4 (2)
43. Skull width:skull length ratio 0.79 and below (0), 0.8 and above (1)

22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	Taxon
?	?	?	0	0	?	0	0	0	?	?	?	0	0	?	0	0	?	0	0	?	?	ancestor
1	0	0	0	1	1	0	1	1	1	1	0	1	0	0	1	0	0	0	0	1	0	*Nemegtbaatar*
0	0	0	0	1	1	0	1	1	1	0	1	1	0	1	1	0	0	0	0	0	0	*Chulsanbaatar*
2	1	1	1	1	0	1	1	0	0	?	1	1	1	?	0	0	1	1	?	2	1	*Catopsbaatar*
0	0	0	0	1	1	0	1	1	1	0	?	1	0	0	1	1	0	0	1	1	0	*Kamptobaaatar*
1	0	0	1	1	1	0	1	1	1	0	1	1	1	1	1	0	0	0	0	2	1	*Kryptobaatar*
1	0	1	1	1	1	0	1	1	1	?	?	?	?	?	0	0	0	0	1	?	?	*Djadochtatherium*
1	0	?	?	?	?	?	1	1	?	1	?	?	?	?	?	?	?	?	?	?	?	*Bulganbaatar*
1	0	0	0	1	1	0	1	1	1	0	2	0	?	0	0	0	1	0	1	1	0	*Sloanbaatar*
?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	0	?	?	?	*Buginbaatar*
?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	0	1	?	?	?	*Nessovbaatar*
1	0	?	?	1	?	0	1	1	1	0	?	?	?	?	?	?	?	?	?	?	?	*Tombaatar*
2	1	?	0	2	0	1	0	0	1	0	?	1	1	?	0	?	1	0	1	1	1	*Lambdopsalis*
2	?	?	0	2	0	1	0	0	?	0	?	?	?	?	0	0	1	?	1	1	1	*Taeniolabis*
0	0	?	?	?	?	?	?	1	1	1	?	?	?	?	1	0	?	0	?	?	?	*Stygimys*
?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	0	0	?	?	*Eucosmodon*
2	0	?	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	1	0	*Ptilodus*

apparently more similar to *Sloanbaatar* than to *Kamptobaatar*, however, as long as its skull is not known, its relationships must remain unresolved.

In a second Pee-Wee run, *Nessovbaatar* was removed from the matrix, because of its incompleteness. This gave a tree identical (except for lack of *Nessovbaatar*) to the shorter tree in our complete Pee-Wee run. The grouping of *Kamptobaatar* + *Sloanbaatar* was maintained.

The Pee-Wee program (with complete Taxon-character matrix, including *Nessovbaatar*) recognized 27 homoplasies (Table 4) in the tree presented in Fig. 13. We regard

Fig. 13. Shorter tree (103 steps), obtained from Pee-Wee (Goloboff 1996), using 43 characters (Table 1) and 17 taxa in Taxon-character matrix (Table 2). Diagnoses of nodes (the numbers in brackets refer to character numbers):

1. The node containing all except ancestor: (4) p4 in lateral view changes from rectangular to arcuate; (8) I2 changes from bicuspid to single-cuspid; (10) upper premolars change from 5 to 4; (16) length ratio of M1 inner ridge:length of M1, changes from 0.5 or less to more than 0.5.

2. The node containing *Ptilodus*: (3) p4 serrations count 5 or less changes to more than 10.

3. The node containing all except ancestor and *Ptilodus*: (2) p3 present changes to absent; (17) width ratio of P4:M1 changes from more than 0.9 to 0.45–0.2.

4. The node containing all taxa except ancestor, *Ptilodus* and *Buginbaatar*: (1) enamel covering of lower incisor changes from uniform thickness to completely restricted to labial surface of the tooth.

5. The node containing *Lambdopsalis* and *Taeniolabis*: (4) p4 in lateral view changes from arcuate to triangular; (10) number of upper premolars changes from 4 to 1; (12) P4 changes from double-rooted to single-rooted; (14) P4 cusp formula changes from 0–5:5–10:0–5 to 0–5:1–4:0–5; (20) shape of the snout in dorsal view changes from incurved in front of the zygomatic arches with anterior part directed posterolaterally to incurved with anterior part of zygomatic arches directed transversely; (28) contacts between nasal and parietal change from absent to present; (32) palatal vacuities change from single to absent; (39) posttemporal fossa changes from large to reduced to a small foramen; (41) mandibular condyle changes from opposite or below the level of the molars to condyle above the level of the molars; (43) skull width:length ratio changes from 0.79 and below to above 0.80.

6. The node containing *Lambdopsalis*: (9) I3 located on margin of palate changes to slightly shifted from the labial margin.

7. The node containing all taxa except ancestor, *Ptilodus*, *Buginbaatar*, *Lambdopsalis*, and *Taeniolabis*: (9) I3 changes from located on margin of the palate to medial position near midline; (17) width of P4:M1 changes from 0.45–0.2 to 0.6–0.45; (30) thickening on palatal process of premaxilla changes from absent to present; (37) angle of coronoid process relative to tooth row changes from steep > 45° to low < 45°.

8. The node containing *Stygimys* and *Eucosmodon*: (8) I2 changes from single-cuspid to bicuspid, (11) P3 changes from double-rooted to single-rooted.

9. The node containing all MLCM taxa except for *Buginbaatar*: (2) p3 changes from absent to present.

10. The node containing *Nemegtbaatar* and *Bulganbaatar*: (17) P4:M1 width ratio changes from 0.6–0.45 to 0.9–0.6.

11. The node containing *Bulganbaatar*: (18) cusp formula of M2 changes from more than 1:2:3 to 1:2:2.

12. The node containing *Kamptobaatar, Sloanbaatar, Nessovbaatar, Chulsanbaatar, Djadochtatherium, Catopsbaatar*, and *Tombaatar*: (18) cusp formula of M2 changes from more than 1:2:3 to 1:2:3; (32) palatal vacuities change from single to absent.

13. The node containing *Kamptobaatar, Sloanbaatar*, and *Nessovbaatar* (trichotomy): (1) enamel covering of lower incisor changes from completely restricted to labial surface of tooth to thicker on labial surface than on lingual surface; (38) coronoid process changes from parallel to the rest of the outer wall of the dentary to flared laterally; (41) mandibular condyle changes from placed opposite or below the level of the molars to placed above the level of the molars.

14. The node containing *Sloanbaatar*: (21) number of pairs of vascular foramina in nasals changes from more than one to one; (31) incisive foramen changes from limited posteriorly by maxilla to situated within premaxilla; (32) palatal vacuities change from absent to double; (37) angle of coronoid process changes relative to tooth row from < 45° to steep > 45°; (40) angle between the lower margin of the dentary and the occlusal level of the molars changes from between 11–20° to above 20°; (42) ratio between width of the snout and skull length changes from 0.3–0.39 to below 0.3; (43) skull width:length ratio changes from 0.79 and below to above 0.8.

15. The node containing *Nessovbaatar*: (6) length ratio of p4:m1 changes from 0.6–1.7 to above 1.7.

16. The node containing *Chulsanbaatar, Kryptobaatar, Djadochtatherium, Catopsbaatar*, and *Tombaatar*: (21) number of pairs of vascular foramina on nasals changes from more than 2 to 2; (33) foramen ovale inferium changes from placed medial to foramen masticatorium to posterior to foramen masticatorium.

17. The node containing *Chulsanbaatar*: (18) cusp formula of M2 changes from 1:2:3 to 1:2:2; (42) ratio between width of the snout and skull length changes from 0.3–0.39 to below 0.3.

18. The node containing *Kryptobaatar, Djadochtatherium, Catopsbaatar*, and *Tombaatar*: (20) shape of the snout in dorsal view changes from incurved in front of the zygomatic arches, with anterior part of zygomatic arches directed posterolaterally, to trapezoidal, not incurved in front of zygomatic arches; (25) snout length changes from < 49% of skull length to > 50% of skull length; (35) anterior part of promontorium *sensu* Hurum *et al.* (1996) changes from oval to irregular with incurvatures on both sides (42) ratio between of width of the snout:skull length changes from 0.3–0.39 to above 0.4; (43) skull width:length ratio changes from above 0.8 to 0.79 and below.

19. The node containing *Djadochtatherium, Catopsbaatar*, and *Tombaatar*: (24) postorbital process changes from short to long; (37) angle of coronoid process relative to tooth row changes from low <45° to steep > 45°; (41) mandibular condyle changes from opposite or below the level of the molars to condyle above the level of the molars.

20. The node containing *Djadochtatherium*: (14) P4 cusp formula changes from 0–5:5–10:0–5 to 0–5:1–4:0–5.

21. The node containing *Catopsbaatar* and *Tombaatar*: (10) the number of upper premolars changes from 4 to 3.

22. The node containing *Catopsbaatar*: (15) cusp formula of M1 changes from 4–5:4–5:0–5 to 5–7:5–8:2–5; (16) M1 inner ridge length ratio to length of M1 changes from 0.5 or less to more than 0.5; (18) cusp formula of M2 changes from 1:2:3 to more; (22) infraorbital foramen positioned dorsal to P2 changes to dorsal to P3 or P4; (23) base of zygomatic arch as marked by posterior edge, changes from placed directly dorsal to P4 to dorsal or posterior to P4/M1 embrasure; (31) incisive foramen limited posteriorly by maxilla changes to situated within premaxilla.

one of these homoplasies (presence of p3) as an undoubted plesiomorphy, its absence being a homoplasy. Four others (bicuspid I2, steep coronoid process, small angle between the lower margin of the dentary and occlusal level of the molars, and mandibular condyle placed opposite or below the level of the molars) are possible plesiomorphies. Other homoplasies agree with ideas on parallel evolution in multi-tuberculates and some of them have been explained on functional grounds. For example, Gambaryan & Kielan-Jaworowska (1995) argued that a high position of the

Table 3. Fit (weighting) for every character in the tree selected after the run of Pee-Wee (length 103). Lower value – more homoplasy.

character	1	2	3	4	5	6	7	8	9	10	11
fit	10	7.5	6	10	5	5	6	7.5	10	10	10
character	12	13	14	15	16	17	18	19	20	21	22
fit	10	10	7.5	6	4.2	10	6	10	10	7.5	5
character	22	23	24	25	26	27	28	29	30	31	32
fit	5	7.5	10	10	10	10	10	10	10	7.5	7.5
character	33	34	35	36	37	38	39	40	41	42	43
fit	10	10	7.5	7.5	6	10	10	7.5	6	7.5	6

condyle (scoring 1 for character 41 in Table 1) may make its appearance in parallel in different groups of multituberculates as an adaptation for crushing hard seeds.

The position of *Buginbaatar*, which is the only MLCM that falls outside Djadoch-tatheria remains unresolved. It was assigned to ?Cimolomyidae by Kielan-Jaworowska & Sochava (1969) and to Eucosmodontidae by Trofimov (1975). Hahn & Hahn (1983) placed it in a separate subfamily Buginbaatarinae within Eucosmodontidae. In the tree obtained by us (Fig. 13), *Buginbaatar* is close to *Lambdopsalis* and *Taeniolabis*. It should be, however, stressed that members of Cimolomyidae have not been used in our analysis. In a more extended PAUP run with 49 taxa, employed by Rougier *et al.* (1997), *Buginbaatar* is placed in a polytomy between *Essonodon, Neoliotomus* + *Boffius* and the Taeniolabididae (figs 6A and 6B in their paper), or as a sister group of the Taeniolabididae (fig. 6C). As long as the number of upper premolars in *Buginbaatar* is not known (only P4 has been preserved), its attribution to the Cimolomyidae or any other known multituberculate family cannot be done with any certainty.

Sloan & Van Valen (1965) erected the suborder Taeniolabidoidea to include the Eucosmodontidae, Taeniolabididae and Cimolomyidae and defined it (p. 222): 'as including multituberculates in which the enamel of the lower incisor is restricted to the ventrolateral surface of the tooth, producing a self-sharpening tooth similar to that of rodents'. Clemens & Kielan-Jaworowska (1979) and Archibald (1982) assigned Cimo-lomyidae to a suborder *incertae sedis*.

Carlson & Krause (1985) and Fosse *et al.* (1985) demonstrated the presence of two types of enamel in advanced multituberculates referred to by Carlson & Krause as: (1) small circular prisms – characteristic of Ptilodontoidea (with few exceptions), and (2) large, arcade-shaped prisms (gigantoprismatic enamel of Fosse *et al.* 1985), characteristic for Taeniolabidoidea and Cimolomyidae. This points to the affinity of the Cimolomyidae with Taeniolabidoidea. The Djadochtatheria, members of which were previously assigned to Eucosmodontidae or Taeniolabididae, have gigantoprismatic enamel and share this character with Taeniolabidoidea and Cimolomyidae. As the only taeniolabidoid synapomorphy recognized by Sloan & Van Valen (1965), the limited enamel band of the lower incisor, is not unique for the Taeniolabidoidea (see above), the taeniolabidoid monophyly requires revision (Kielan-Jaworowska 1974; Krause & Carlson 1987; see also Stevens 1988). This is beyond the scope of the present paper.

Table 4. Steps and extra steps for the characters (Fig. 13). The characters not listed fit the tree perfectly – no extra steps, fit = 10, see Table 2. Our opinion in brackets.

Character 2	p3 present appears twice: node 0 and node 9 (plesiomorphy).
Character 3	p4 serration count 5 or less appears three times: node 0, node 5 and *Catopsbaatar* (node 22).
Character 5	Cusp formula of m1 4:3 appears twice: node 0 and node 12; cusp formula 5:4–5 appears three times: *Ptilodus* (node 2), *Lambdopsalis* (node 6), and *Nemegtbaatar*.
Character 6	Ratio of p4:m1 less than 0.6 appears two times: *Lambdopsalis* (node 6) and *Buginbaatar*; ratio 0.6–1.7 appears three times: *Ptilodus* (node 2), node 8 and *Nessovbaatar* (node 15); ratio 0.6–1.7 appears two times: *Taeniolabis* and node 9.
Character 7	m2 cusp formula 2:2 appears three times: *Sloanbaatar* (node 14), *Chulsanbaatar* (node 17), and *Catopsbaatar* (node 22).
Character 8	I2 bicuspid appears twice: node 0 and node 8 (possibly plesiomorphy).
Character 14	P4 cusp formula 0–5:1–4:0–5 appears twice: node 5 and *Djadochtatherium* (node 20).
Character 15	Cusp formula of M1 5–7:5–8:2–5 appears three times: node 8, *Catopsbaatar* (node 22) and *Nemegtbaatar*.
Character 16	Ratio M1 inner ridge length:M1 length more than 0.5 appears four times: node 1, node 10, *Catopsbaatar* (node 22) and *Kamptobaatar*.
Character 18	Cusp formula in M2 1:2:2 appears twice: *Bulganbaatar* (node 11) and *Chulsanbaatar* (node 17); more than 1:2:3 appears twice: node 1 and *Catopsbaatar* (node 22).
Character 21	Two pairs of vascular foramina on nasals appear twice: *Ptilodus* (node 2) and node 16.
Character 22	Infraorbital foramen positioned dorsal to P1 appears three times: *Stygimys*, *Kamptobaatar*, and *Chulsanbaatar* (node 17); dorsal to P3 or P4 appears twice: node 1 and *Catopsbaatar* (node 22).
Character 23	Base of zygomatic arch, as marked by posterior edge, dorsal or posterior to P4/M1 embrasure appears twice: *Lambdopsalis* (node 6) and *Catopsbaatar* (node 22).
Character 31	Incisive foramen situated within premaxilla appears twice: *Sloanbaatar* (node 14) and *Catopsbaatar* (node 22).
Character 32	Palatal vacuities absent appears twice: node 5 and node 12.
Character 35	Anterior part of promontorium (*sensu* Hurum *et al.* 1996) irregular with incurvatures on both sides appears twice: *Lambdopsalis* (node 6) and node 18.
Character 36	Glenoid fossa length:width ratio below 1.69 appears twice: *Ptilodus* (node 2) and node 16.
Character 37	Angle of the coronoid process relative to tooth row steep 45° or > 45° appears three times: node 0, *Sloanbaatar* (node 14) and node 19.
Character 40	Angle between the lower margin of the dentary and the occlusal level of the molars above 20° appears twice: *Sloanbaatar* (node 14) and *Catopsbaatar* (node 22).
Character 41	Mandibular condyle above the level of the molars appears three times: node 5, node 13 and node 19.
Character 42	Ratio of width of the snout:skull length below 0.3 appears twice: *Chulsanbaatar* (node 17) and *Sloanbaatar* (node 14).
Character 43	Skull width:length ratio below to above 0.8 appears three times: node 5, *Sloanbaatar* (node 14) and node 18.

In our tree (Fig. 13), *Ptilodus* is closest to the ancestor. We are aware of the high specialization of Ptilodontoidea and its important autapomorphies, which we do not use in Table 1, as they do not appear in other taxa. Our tree (Fig. 13) suggests that Djadochtatheria are more closely related to Eucosmodontidae (the skulls of which are not known, except for a rostrum of *Stygimys*) and to Taeniolabididae, than they are to
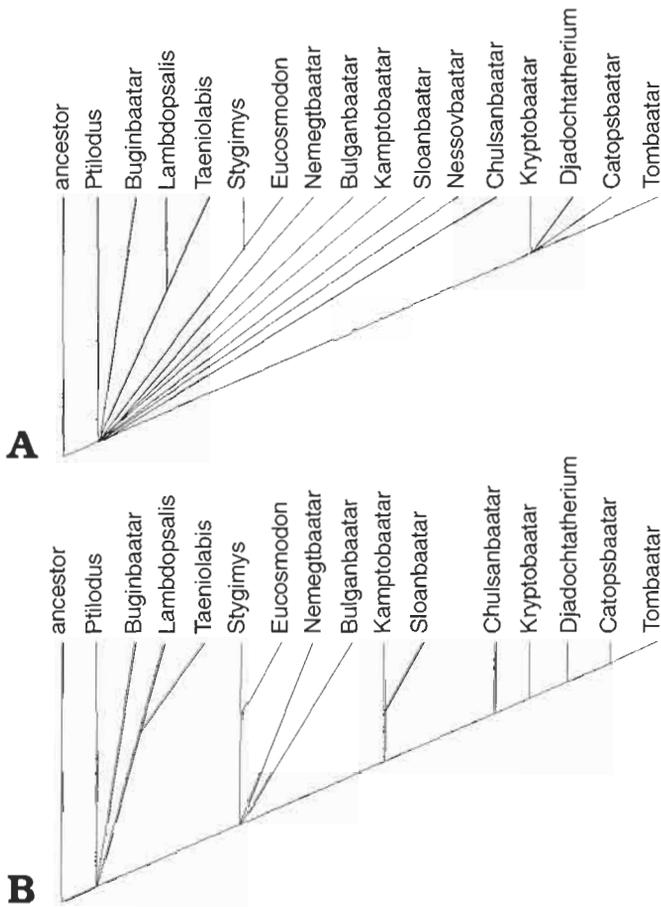
Fig. 14. Results of the NONA program (Goloboff 1993b), using 43 characters (Table 1) and 17 taxa in Taxon-character matrix (Table 2). A. Strict consensus tree obtained from 30 equally parsimonious trees of 103 steps. B. Strict consensus tree obtained from nine equally parsimonious trees after removing *Nessovbaatar* from the Taxon-character matrix, length 101 steps.

Ptilodontoidea. They are apparently also related to Cimolomyidae, which we do not use in our analysis because of their incompleteness.

As skulls of the Late Jurassic and Early Cretaceous multituberculates are hardly known and as Djadochtatheria are defined mostly on the basis of cranial characters, we refrain from speculating on the origin of Djadochtatheria.

NONA results (Tables 1, 2 and Fig. 14). — In the NONA program (Goloboff 1993b) calculations are made on the same basis as in PAUP (Swofford 1993). The NONA run yielded 30 equally parsimonious trees with a length of 103 steps. The relation of *Kamptobaatar*, *Sloanbaatar*, and *Nessovbaatar* changes in these trees. The strict consensus tree gave an unresolved polytomy after the ancestor (Fig. 14A). The groupings: *Lambdopsalis + Taeniolabis; Stygimys + Eucosmodon; Kryptobaatar + Djadochtatherium + Catopsbaatar + Tombaatar*, present in the 30 trees, are maintained in the strict consensus tree. The positions of *Sloanbaatar, Nemegtbaatar, Bul-*

ganbaatar, Kamptobaatar, and *Chulsanbaatar* are unresolved. Because of lack of data the position of *Nessovbaatar* is mobile.

By removing *Nessovbaatar* from our analysis, NONA produced nine trees with the length of 101 steps and a strict consensus tree (Fig. 14B) with more resolution than the previous consensus tree (Fig. 14A). Both strict consensus trees produced by NONA (Fig. 14) do not confirm the monophyly of MLCM (excluding *Buginbaatar)*, but confirm the monophyly of Djadochtatheriidae shown by Pee-Wee (Fig. 13, node 18).

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Djadochtatheria – nowy podrząd multituberkulatów

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Streszczenie

Na podstawie porównań anatomicznych popartych analizą filogenetyczną wykazano, że późnokredowe multituberkulaty (wieloguzkowce) Mongolii, z wyjątkiem rodzaju *Buginbaatar*, tworzą monofiletyczną grupę, dla której zaproponowano nowy podrząd Djadochtatheria. Podrząd Djadochtatheria charakteryzuje się następującymi synapomorfiami: kości czołowe są proporcjonalnie duże i wcinają się głęboko w formie zaostrzonego szpica między kości nosowe; szew czołowo-ciemieniowy jest U-kształtny; kość czołowa nie kontaktuje się ze szczęką; wzdłuż kontaktu między podniebienną i boczną powierzchnią kości przedszczękowej występuje ostra krawędź. U wszystkich Djadochtatheria część twarzowa kości łzowej jest duża, w przybliżeniu prostokątna, umieszczona na dachu czaszki, co być może jest cechą symplezjomorficzną. Jest również możliwe, że tylna część czaszki, położona za dołemu żuchwowym jest u Djadochtatheria dłuższa w stosunku do całej czaszki niż u innych multituberkulatów. Djadochtatheria mają łukowaty p4 (wtórnie trapezoidalny u *Catopsbaatar*), który nie wystaje ponad poziom powierzchni żującej trzonowców (cecha wspólna z Eucosmodontidae), oraz I3 umieszczony na podniebiennej części kości przedszczękowej (cecha występująca również u eukosmodontida *Stygimys* i u cimolomyida *Moeniscoessus*). Mała liczba guzków na dolnych i górnych trzonowych, oraz nie więcej niż dziewięć grzebieni na p4 są przypuszczalnie cechami symplezjomorficznymi. Z formacji Barun Gojot opisano przedstawiciela Djadochtatheria *Nessovbaatar multicostatus* gen. et sp. nov., zaliczonego do rodziny *incertae sedis*. Zaproponowano nową rodzinę Djadochtatheriidae dla rodzajów *Kryptobaatar*, *Djadochtatherium*, *Catopsbaatar* i *Tombaatar*, a w oparciu o nowe materiały przedstawiono zrewidowane diagnozy czterech rodzajów Djadochtatheria: *Sloanbaatar*, *Kryptobaatar*, *Djadochtatherium* i *Kamptobaatar*.

W celu przeprowadzenia analizy filogenetycznej późnokredowych multituberkulatów Mongolii zaproponowano listę 43 cech (różniącą się, z wyjątkiem dziesięciu cech, od list używanych dotychczas przy analizach filogenetycznych multituberkulatów) oraz matrycę taksonów i cech, obejmująca 17 taksonów. Taksony uwzględnione

w analizie obejmują 11 późnokredowych rodzajów z Mongolii, pięć najkompletniej poznanych późnokredowych i paleoceńskich rodzajów z Ameryki Północnej i Azji, oraz hipotetycznego przodka, skonstruowanego na podstawie cech występujących u jurajskich multituberkulatów z rzędu Plagiaulacoidea. W analizie kladystycznej zastosowano dwa różne programy komputerowe: Pee-Wee (Goloboff 1993a, 1996) oraz NONA (Goloboff 1993b), oparty na tej samej zasadzie co powszechnie używany PAUP (Swofford 1993). Program Pee-Wee przedstawił dwa drzewa. Fig. 13 przedstawia krótsze z tych drzew, które potwierdza odrębność *Buginbaatar* i monofiletyzm Djadochtatheria. Analiza przeprowadzona za pomocą tego programu wykazuje również monofiletyzm rodziny Djadochtatheriidae ustanowionej w pracy (Fig. 13, węzeł 18). Program NONA zaproponował 30 jednakowo oszczędnych drzew. Dwa drzewa ścisłej zgodności (Fig. 14A and 14B) wykazują znacznie gorszą rozdzielczość niż drzewo zaproponowane przez program Pee-Wee, na którym oparto wnioski filogenetyczne.