Skull structure in *Catopsbaatar* and the zygomatic ridges in multituberculate mammals

ZOFIA KIELAN-JAWOROWSKA, JØRN H. HURUM, and ALEXEY V. LOPATIN

Kielan-Jaworowska, Z., Hurum, J.H., and Lopatin, A.V. 2005. Skull structure in *Catopsbaatar* and the zygomatic ridges in multituberculate mammals. *Acta Palaeontologica Polonica* 50 (3): 487–512.

The late Campanian djadochtatherioid multituberculate *Catopsbaatar catopsaloides* was originally known from three skulls from Hermiin Tsav in the Gobi Desert (Mongolia). Three more skulls from Hermiin Tsav are now available, associated with parts of the previously unknown postcranial skeleton, which will be described separately. We describe herein the skull and dentition of *C. catopsaloides*, based on all available material, housed in PIN, PM, and ZPAL collections. The genera *Catopsbaatar*, *Djadochtatherium*, and *Kryptobaatar* share several characters, unknown in *Tombaatar*, such as very long postorbital processes directed postero-laterally and downwards, parietal ridges extending from the posterior margins of the postorbital processes postero-medially, and nuchal crests with prominent lateral wings, incurved anteriorly in the middle, so that the skull in dorsal view is shorter in the middle than laterally. *Catopsbaatar* shares with *Djadochtatherium* a very high and prominent anterior zygomatic ridge, and presence of the masseteric protuberance, but differs from it and from other djadochtatherioid genera in having the orbit situated more posteriorly, the intermediate zygomatic ridge adhering to the anterior ridge, and a smaller trapezoidal (rather than crescent-shaped) p4 without ridges; it differs from *Kryptobaatar* and *Djadochtatherium* in having three upper premolars (P2 being lost) and shares this last character with *Tombaatar*. *Catopsbaatar* is known not only from Hermiin Tsav, but also from Baruungoyot Formation of Khulsan, represented there by a single m2. We demonstrate that the separation of the masseter superficialis into two parts, the origins of which leave scars on the lateral wall of the zygomatic arch surrounded by zygomatic ridges, occurs in all the multituberculates (beginning with Paulchoffatiidae), and is regarded as a multituberculate autapomorphy.

Key words: Mammalia, Multituberculata, Djadochtatheriidae, *Catopsbaatar*, *Djadochtatherium*, *Kryptobaatar*, zygomatic ridges, Cretaceous, Gobi Desert.

Zofia Kielan-Jaworowska [zkielan@twarda.pan.pl], Instytut Paleobiologii, Polska Akademia Nauk, ul. Twarda 51/55, PL-00-818 Warszawa, Poland;
Jørn H. Hurum [j.h.hurum@nhm.uio.no], Naturhistorisk Museum, Boks 1172 Blindern, N-0318 Oslo, Norway;
Alexey V. Lopatin [alopat@paleo.ru], Paleontological Institute, Russian Academy of Sciences, Profsojuznaya 123, 117997 Moscow, Russia.

Introduction

In 1997 Kielan-Jaworowska and Hurum erected the multituberculate family Djadochtatheriidae to include four Late Cretaceous Gobi Desert genera: *Djadochtatherium* Simpson, 1925, *Kryptobaatar* Kielan-Jaworowska, 1970, *Catopsbaatar* Kielan-Jaworowska, 1994, and *Tombaatar* Rougier, Novacek, and Dashzeveg, 1997. The family is well-defined and differs not only from all other multituberculates, but also from all other mammals in having an unusual shape of the snout. While in mammals in general, the lateral margins of the snout are incurved medially in front of the zygomatic arches, in Djadochtatheriidae the anterior margins of the snout are confluent with the zygomatic arches, which results in a subtrapezoid shape of the snout in dorsal view.

The material of *Catopsbaatar*, which is a monotypic genus represented by *Catopsbaatar catopsaloides* (Kielan-Jaworowska, 1974), housed in three museums (ZPAL, PIN, and PM, in Warsaw, Moscow and Ulaanbaatar respectively), derives almost exclusively from the locality of Hermiin Tsav situated some 50 km south-westward from Naran Bulak in the Gobi Desert (Barsbold et al. 1971; Gradziński and Jerzykiewicz 1972; Kielan-Jaworowska and Barsbold 1972; Kielan-Jaworowska et al. 2000). The only exception is the single m2 from Khulsan (ZPAL MgM-I/159, see description of the dentition).

The Polish-Mongolian Expedition of 1971, when collecting mammals at Hermiin Tsav, recognized within the Upper Cretaceous outcrops there two localities, designated Hermiin Tsav I and Hermiin Tsav II (Gradziński and Jerzykiewicz 1972: 27, figs. 6, 7; Kielan-Jaworowska and Barsbold 1972: 11). Of three *C. catopsaloides* skulls found by members of the Polish-Mongolian Expeditions in 1971, two (ZPAL MgM-I/78 and /79) were found at Hermiin Tsav I and one (ZPAL MgM-I/80) at Hermiin Tsav II. Specimen PM 120/107 derives from Hermiin Tsav I. The exact location of the two skulls (PIN 4537/4 and 4537/5) found by members of the South Gobi Group of the Soviet-Mongolian Expedition in 1975 is not known, and we refer to them as Hermiin Tsav, without further qualification (see also Kurochkin and Bars-

Acta Palaeontol. Pol. 50 (3): 487–512, 2005

http://app.pan.pl/acta50/app50-487.pdf

bold 2000). For lists of mammals found at the two localities see Kielan-Jaworowska et al. (2003: table 2).

In the present paper we re-describe the skull of *Catopsbaatar catopsaloides*, mostly on the basis of three new, fairly complete specimens. The masticatory musculature of the specimen PIN 4537/5 has been reconstructed by Gambaryan and Kielan-Jaworowska (1995). Specimen PM 120/107, found during the 1999 Nomadic Expedition at the locality of Hermiin Tsav I, was briefly reported by Kielan-Jaworowska et al. (2002). The red beds of Hermiin Tsav yielding these skulls are regarded as a stratigraphic equivalent of the Baruungoyot Formation, which is apparently of early or late Campanian age (Gradziński and Jerzykiewicz 1972; Gradziński et al. 1977; Averianov 1997; Kielan-Jaworowska et al. 2003). In addition to the three new skulls mentioned above, we figure in this paper the two specimens from the 1971 Polish-Mongolian Expedition, mentioned by Kielan-Jaworowska (1974: 41), but not figured previously. These are the skull ZPAL MgM-I/80 from Hermiin Tsav and the single m2 from Khulsan (ZPAL MgM-I/159).

The new skulls described herein are more complete than those previously known and allow us to recognize some structures not known previously in *Catopsbaatar*. Nonetheless the state of preservation of all the skulls of *Catopsbaatar* is not exquisite, and often we base our interpretations on a comparison with better preserved material of *Kryptobaatar* recently described in meticulous detail by Wible and Rougier (2000). Comparisons with *Kryptobaatar* and *Djadochtatherium* (the latter based on the holotype AMNH 20440; photographs of a specimen from Tögrög, kindly sent by Dr. Mahito Watabe to ZK-J in 1996; and the photograph of a skull, collected by Mongolian-American Museum Expeditions at Ukhaa Tolgod, figured by Webster 1996) show that the three genera in question are closer to one another than previously thought, which allows us to enlarge the diagnosis of the family Djadochtatheriidae. The relevant details of skull structure are, however, not known in *Tombaatar*, which is less complete than other djadochtatheriid taxa.

The genus *Catopsbaatar* has a long history. Originally *Catopsbaatar catopsaloides* was referred to *Djadochtatherium* (Kielan-Jaworowska 1974) and then to *Catopsalis* (Kielan-Jaworowska and Sloan 1979; Kielan-Jaworowska et al. 1986). Cladistic analysis of *Catopsalis* and related forms allowed Simmons and Miao (1986: 87) to demonstrate the paraphyly of *Catopsalis*, which is "composed of no fewer than five independent monophyletic lines". Results of this analysis induced Kielan-Jaworowska (1994) to erect the separate genus *Catopsbaatar*, for "*Djadochtatherium*" *catopsaloides*.

Kielan-Jaworowska and Hurum (1997) assigned Djadochtatheriidae to their new suborder Djadochtatheria. Four years later, Kielan-Jaworowska and Hurum (2001) revised the high rank systematics of Multituberculata and divided the multituberculate suborders Plagiaulacida and Cimolodonta into superfamilies. To maintain consistent systematic division they replaced the suborder Djadochtatheria by the superfamily Djadochtatherioidea within Cimolodonta. We follow this division in the present paper.

As most of the djadochtatherioidean genera are monotypic (*Kryptobaatar* being an exception), in the descriptions that follow, for the sake of brevity we often use only generic names.

Institutional abbreviations.—HMNS, Hayashibara Museum of Natural Sciences, Okayama, Japan; IMM, Inner Mongolian Museum, Hohhot, China; PIN, Paleontological Institute, Russian Academy of Sciences, Moscow, Russia; PM, Paleontological Center of the Mongolian Academy of Sciences, Ulaanbaatar, Mongolia; PSS-MAE, Mongolian-American Museum Expeditions (the collections are for the time being housed at the American Museum of Natural History in New York, USA); PU, Princeton University, Princeton, New Jersey, USA; ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

Other abbreviations.—We use abbreviations I, P, M, and i, p, m, for upper and lower incisors, premolars and molars respectively; m, muscle.

Terminology

Wherever possible we use the terminology of *Nomina Anatomica Veterinaria* (Schaller 1992) and Evans (1995). For osteological characters, which do not occur in extant mammals we follow Kielan-Jaworowska et al. (1986) and Wible and Rougier (2000), with the exception of usage of "minor palatine foramen" by the latter. With respect to "lateral flange" we use this term differently than Wible and Hopson (1995).

The term lateral flange was introduced by Crompton (1958) for *Diarthrognathus,* and then adopted by Kermack (1963) for Mesozoic mammals ("triconodonts"). Of the specimens described by Kermack (1963) it is best seen in *Trioracodon ferox* extending parallel to the lateral boundary of the lateral trough, which adjoins the promontorium (pl. 2: 3 of Kermack's paper). Kielan-Jaworowska (1971: fig. 12) compared the ventral view of the petrosals in two multituberculate taxa, *Kamptobaatar* and *Sloanbaatar*, with that of *Trioracodon* and identified the multituberculate lateral flange placed exactly as in *Trioracodon*. Wible and Hopson (1993: fig. 5.3C of *Catopsalis joyneri*) placed the lateral flange medial to the epitympanic recess, although the notation "lateral flange" was placed posterior to the recess. The structure identified in this figure as "lf" bifurcates anteriorly, its medial branch being medial to the epitympanic recess, and lateral branch lateral to it. Wible and Hopson (1995) in fig. 7A of "*Catopsalis joyneri*", placed "lf" lateral to the epitympanic recess, as in *Mesodma thompsoni* in their fig. 8A. In response to our enquiry James Hopson (letter of 6 January, 2004) wrote: "[...] the lateral flange in multis is the entire descending sheet of bone forming the outer wall of the lateral trough and, where the sheet bends medially to contact the promontorium, the floor of the lateral trough. In other early mammaliaforms, such as *Morganucodon* and triconodontids, the lateral flange is vertical and the lateral trough is open below. We interpret the lateral flange in *Morganucodon* and triconodontids to correspond to that part of the lateral flange forming the lateral wall of the lateral trough in multis. What is different about multis is that the lateral flange has grown inward to contact the promontorium and form a floor to the lateral trough. But it is ALL lateral flange. The epitympanic recess thus lies on the ventral surface of the lateral flange."

Fully aware of these two somewhat different usages, we prefer, for consistency with our earlier descriptions of multituberculate skulls, to follow our more restricted usage of this term of Kielan-Jaworowska (1971), accepted also recently by Wible and Rougier (2000: 40, 94).

We introduce two new osteological terms. In all the Djadochtatherioidea, at the boundary between the palatal and facial parts of the premaxilla, there occurs a sharp ridge, which we designate the premaxillary ridge (*crista premaxillaris*). This ridge is probably an apomorphy of Djadochtatherioidea; to our knowledge it does not occur in other multituberculates. The function of the ridge is not known, however, in some rodents a similar ridge marks the lower boundary of the insertion of part of the buccinator muscle (Meinertz 1941).

In *Catopsbaatar* and in *Djadochtatherium*, at the anterior end of the masseteric crest, there occurs a swollen protuberance, which we designate the masseteric protuberance (*protuberantia masseterica*). Gambaryan and Kielan-Jaworowska (1995) regarded the swollen masseteric crest in *Catopsbaatar* as the place for insertion of the enormous masseter superficialis pars anterior.

Kielan-Jaworowska et al. (1986) demonstrated on the basis of the sectioned skull of *Nemegtbaatar gobiensis* ZPAL MgM-I/76, that the slit-like "foramen" situated at the end of the postpalatine torus, does not pierce the bone and designated it the "palatonasal notch" (previous palatonasal foramen of Kielan-Jaworowska 1971). We refer to a similar structure in *Catopsbaatar* as the palatonasal notch, *contra* Wible and Rougier (2000) who called it in *Kryptobaatar* the minor palatine foramen. We also do not accept their usage of accessory foramina for minor palatine foramina. For the terminology related to muscular reconstructions, we follow Gambaryan and Kielan-Jaworowska (1995).

We follow the transcription of Mongolian names proposed by Benton (2000), and hence we use e.g., Hermiin Tsav locality and beds, rather than previously used Khermeen Tsav.

Systematics

Order Multituberculata Cope, 1884

Suborder Cimolodonta McKenna, 1975

Superfamily Djadochtatherioidea Kielan-Jaworowska and Hurum, 2001

Family Djadochtatheriidae Kielan-Jaworowska and Hurum, 1997

Revised diagnosis.—Well-defined family, which includes the largest Djadochtatherioidea. Differ from all other multituberculates (and from 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 Djadochtatherioidea in having the snout extending for almost 50 percent or more of the skull length. They have very long postorbital processes directed postero-laterally and downwards, and parietal ridges extending from them postero-medially. The parietal apparently sends a lateral process along the upper margin of the orbit (character well-documented in *Kryptobaatar*, but is less certain in other genera). The nuchal crest is very prominent, incurved anteriorly in the middle, so that the skull in dorsal view is shorter in the middle than laterally. They share with *Chulsanbaatar*, *Kamptobaatar*, and Taeniolabididae lack of palatal vacuities.

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

Distribution.—Late Cretaceous (?early and ?late Campanian) formations Djadokhta, Bayan Mandahu, Baruungoyot, and their stratigraphic equivalents in the Gobi Desert.

Genus *Catopsbaatar* Kielan-Jaworowska, 1994

Type species: *Catopsbaatar catopsaloides* (Kielan-Jaworowska, 1974); Hermiin Tsav I, Gobi Desert (Mongolia), Red beds of Hermiin Tsav, ?upper Campanian.

Revised diagnosis.—*Catopsbaatar* differs from other djadochtatheriid genera in having the orbit situated far posteriorly and in consequence a more elongated snout, extending for about 65 percent of the skull length. Differs from *Kryptobaatar* in being distinctly larger and from *Djadochtatherium* in being slightly larger. Differs from *Djadochtatherium* and *Kryptobaatar* in having subtrapezoidal and smaller p4 (rather than crescent-shaped), devoid of ridges, and in having only three upper premolars (P2 being lost), sharing this character with *Tombaatar*. Shares with *Djadochtatherium* a very high anterior zygomatic ridge, but differs from it in the shape of the ridge, which is semi-circular, rather than roughly trapezoidal, and in having the intermediate zygomatic ridge contacting the anterior ridge. Differs from *Tombaatar* in having the I3 alveolus formed exclusively by the premaxilla, rather than by both premaxilla and maxilla, and in having less prominent postpalatine torus. Differs from *Djadochtatherium*, *Kryptobaatar,* and *Tombaatar* in having the naso-frontal suture less pointed anteriorly in the middle. Shares with *Kryptobaatar* the fronto-parietal suture composed of a widely U-shaped, convex posteriorly (but relatively less deep than in *Kryptobaatar*) middle part, and small lateral parts, each of which forms a U-shaped structure, situated more anteriorly than the middle part. Differs in this respect from *Djadochtatherium*, in which the fronto-parietal suture consists of the middle V-shaped part, narrower than the U-shaped part in *Kryptobaatar* and *Catopsbaatar*.

Distribution.—Known from the red beds of Hermiin Tsav, stratigraphic equivalent of the ?late Campanian Baruungoyot Formation, localities Hermiin Tsav I and II, south-western part of the Gobi Desert, Mongolia, and from the Baruungoyot Formation at Khulsan in the Nemegt Valley.

Catopsbaatar catopsaloides (Kielan-Jaworowska, 1974)

Figs. 1–10, 11C.

Djadochtatherium catopsaloides sp. nov.; Kielan-Jaworowska (1974: 40; text-fig. 6; pl. V: 9; pl. XVII: 2; pls. XVIII–XXI).

Catopsalis catopsaloides (Kielan-Jaworowska); Kielan-Jaworowska and Sloan (1979: 188, fig. 2B).

Catopsalis catopsaloides (Kielan-Jaworowska); Kielan-Jaworowska et al. (1986: pl. 1: 2, pl. 2: 3).

Catopsbaatar catopsaloides (Kielan-Jaworowska); Kielan-Jaworowska (1994: 134).

Catopsbaatar catopsaloides (Kielan-Jaworowska); Gambaryan and Kielan-Jaworowska (1995: 62, figs. 2A, 7B, 17B).

Catopsbaatar catopsaloides (Kielan-Jaworowska); Kielan-Jaworowska and Hurum (1997: figs. 10I, 11I, and 12K).

Catopsbaatar catopsaloides (Kielan-Jaworowska); Kielan-Jaworowska et al. (2000: 592, fig. 29.11).

Catopsbaatar catopsaloides (Kielan-Jaworowska); Kielan-Jaworowska et al. (2002: 557, figs. 1, 2).

Catopsbaatar catopsaloides (Kielan-Jaworowska); Kielan-Jaworowska et al. (2004: 324, figs. 8.9, 8.38I, 8.39F, 8.40K).

Holotype: ZPAL MgM-I/78. Nearly complete skull, associated with both dentaries of a juvenile individual, figured by Kielan-Jaworowska (1974: text-fig. 6, pl. V: 9, pl. XVII: 2, pls. XVIII–XX), by Kielan-Jaworowska et al. (1986: fig. 2), re-figured by Kielan-Jaworowska et al. (2000: fig. 29.11); we figure herein (Fig. 10A) the SEM micrographs of the dentition of the holotype specimen. Originally the right zygomatic arch was broken and has been glued back. A comparison with PIN 4537/5 and PM 120/107, in which both zygomatic arches have been preserved, shows that apparently it has been glued too far laterally, with the glenoid fossa retaining an antero-posterior position, rather than antero-lateral–postero-medial, as characteristic of PIN 4537/5 and PM 120/107.

Type horizon and locality: Red beds of Hermiin Tsav (stratigraphic equivalent of the ?late Campanian Baruungoyot Formation), locality Hermiin Tsav I, south-western part of the Gobi Desert, Mongolia.

Material.—In addition to the holotype specimen, there are:

ZPAL MgM-I/79, Hermiin Tsav I, incomplete skull of an adult individual, figured by Kielan-Jaworowska (1974: pl. XXI).

ZPAL MgM-I/80, Hermiin Tsav II, incomplete damaged skull, associated with anterior parts of damaged dentaries; the skull is figured herein (Fig. 5), and the left dentary (Fig. 9A).

ZPAL MgM-I/159, Khulsan, Nemegt Valley, right, slightly worn m2, figured herein (Fig. 10B).

PIN 4537/4, Hermiin Tsav (no further data), skull without zygomatic arches and with damaged basicranial region of a juvenile individual, associated with both fragmentary dentaries, figured herein (Figs. 1A and 4).

PIN 4537/5, Hermiin Tsav (no further data), nearly complete skull of a juvenile individual, associated with both dentaries, figured by Gambaryan and Kielan-Jaworowska (1995: figs. 2A, 7B, and 17B), and herein (Figs. 1B and 3).

PM 120/107, Hermiin Tsav I, almost complete, but somewhat depressed skull of an adult individual, with damaged basicranial region and partly damaged occipital region, associated with both dentaries and a large part of the postcranial skeleton, figured by Kielan-Jaworowska et al. (2002: figs. 1, 2) and herein (Figs. 1C, 2, and 9B).

Diagnosis and distribution.—As for the genus.

Description

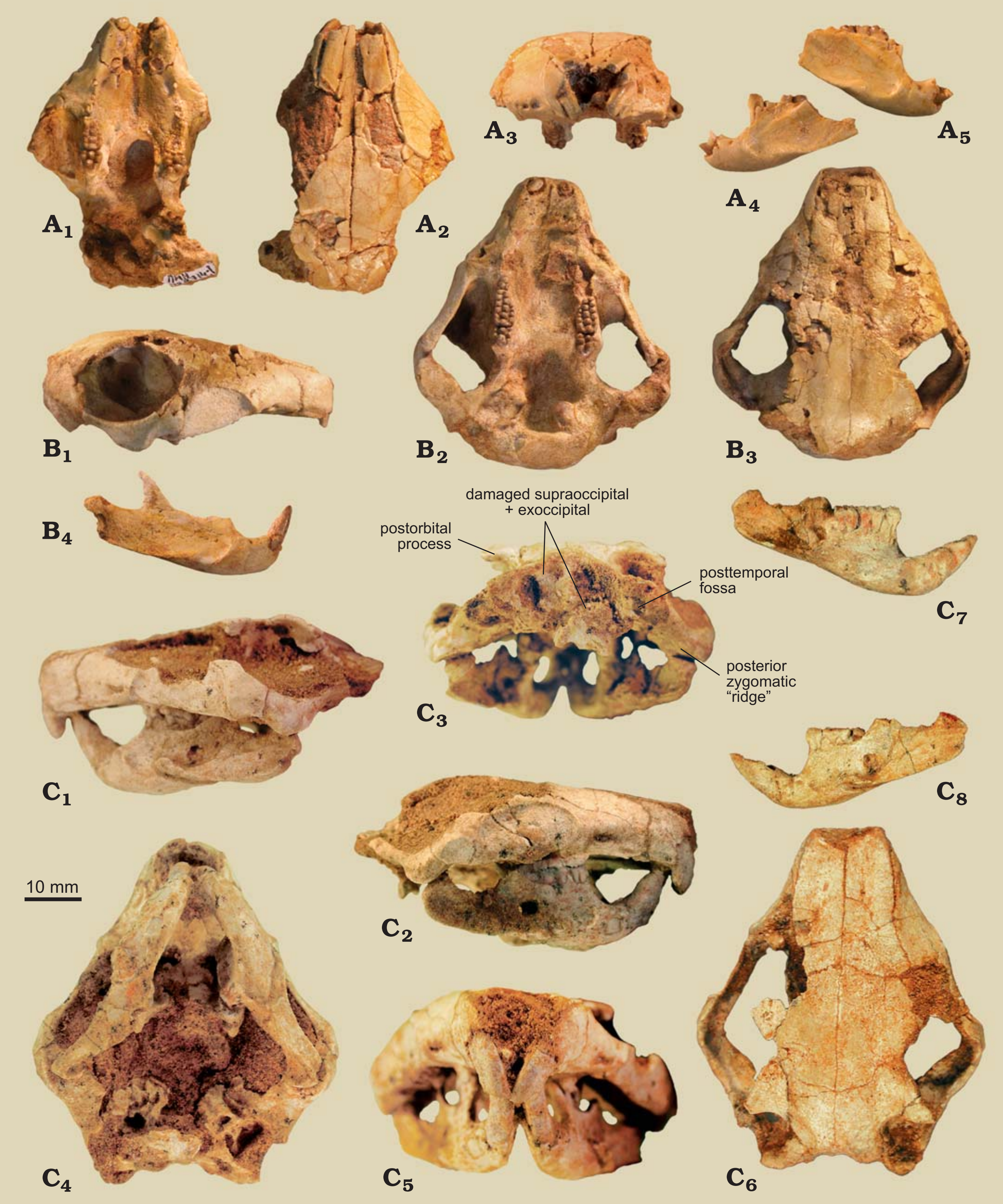
We describe the skull not by regions, as often done (e.g., Simpson 1937; Kielan-Jaworowska 1971), but bone by bone (as e.g., Kielan-Jaworowska et al. 1986; Miao 1988; Wible and Rougier 2000). We follow the description sequence of Wible and Rougier (2000), in order to facilitate a comparison with *Kryptobaatar*, which is the best known djadochtatheriid.

Skull as a whole.—The skull is massive, with a wide transverse anterior margin; it is shorter in the middle than laterally, due to the middle incurvature of the nuchal crest, best seen in PM 120/107 (see reconstructions in Figs. 6–8). In PIN 4537/5 (Figs. 1B and 3), the posterior margin of the skull appears rounded, which is due to its incompleteness, the lateral parts of the nuchal crests being missing; however, the middle part apparently corresponds to the real skull length. The zygomatic arches are strongly expanded laterally—the skull width across the zygomatic arches in PIN 4537/5 is about 85 percent of its length (measured in dorsal view),

Table 1. Measurements of the skull and lower jaw of *Catopsbaatar catopsaloides* in mm. The specimens numbered MgM-I/# belong to ZPAL collection.

	skull length	skull width	length lower jaw
PM 120/107	63	55	41
MgM-I/78	about 53	56	35.0 35.3
MgM-I/79	about 70	?	?
MgM-I/80	about 58	?	?
PIN 4537/4	about 48	?	?
PIN 4537/5	about 52.3	45.2	36.5

Fig. 1. *Catopsbaatar catopsaloides*. Three skulls and dentaries from Hermiin Tsav, Gobi Desert, Mongolia, ?upper Campanian, showing size variation related to the age of individuals. PM 120/107 is from Hermiin Tsav I; detailed localization of PIN 4537/4 and PIN 4537/5 is not known. **A**. PIN 4537/4, incomplete skull of juvenile individual, zygomatic arches and posteriormost part not preserved, in ventral (A_1), dorsal (A_2), and anterior (A_3) views; incomplete left dentary of the same in lateral view (A_4), and incomplete right dentary of the same in lateral view (A_5). **B**. PIN 4537/5, almost complete skull of juvenile individual in right lateral (B_1), ventral (B_2), and dorsal (B_3) views; the right dentary of the same in lateral view (B_4). **C**. PM 120/107, almost complete skull →



associated with both dentaries of adult individual in left lateral (C_1), right lateral (C_2), occipital (C_3), ventral (C_4), and anterior (C_5) views; isolated skull of the same in dorsal view (C_6); left dentary of the same in medial (C_7) and lateral (C_8) views. All in the same scale. Note the tripartite infraorbital foramen (right side of PIN 4537/4, A_3); double (right side of PIN 4537/5, B_1, B_2); and single (both sides of PM 120/107, C_1, C_2, C_5). The structures seen in C_3 are explained. For explanation of structures in other figures, see Figs. 2–4, 9, and reconstructions in Figs. 6–8.

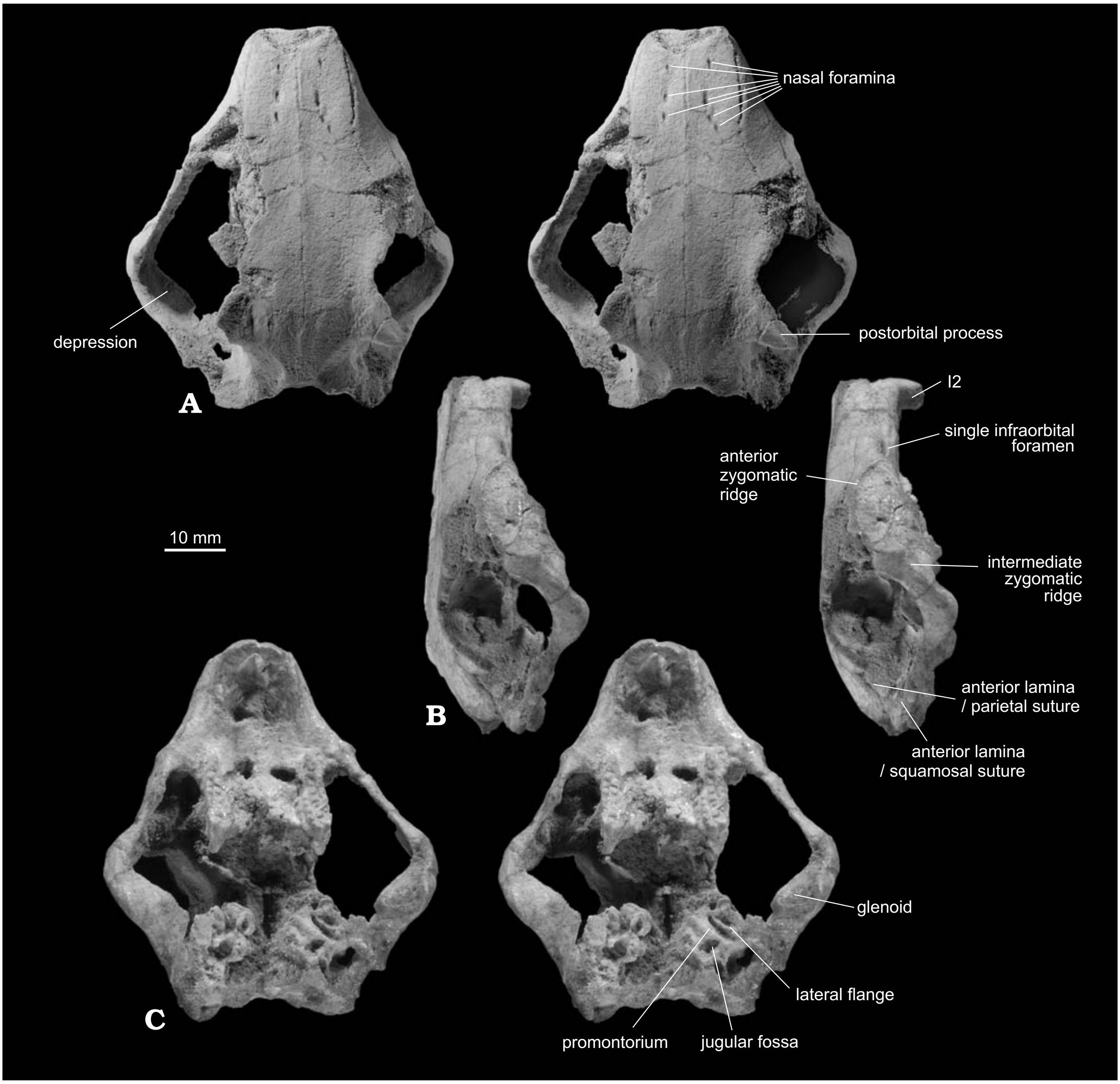


Fig. 2. *Catopsbaatar catopsaloides*, PM 120/107, Hermiin Tsav I, Gobi Desert, Mongolia, ?upper Campanian, stereo-photographs of the skull of an adult individual, with missing choanal and damaged basicranial regions, in dorsal (**A**), right lateral (**B**), and ventral (**C**) views. In A on the left side of the specimen a depression is seen medially, at the posterior part of zygomatic arch. In comparison with *Ptilodus*, *Nemegtbaatar*, and *Kryptobaatar*, it is situated too far posteriorly to house the jugal bone (not preserved). The premaxillary ridge is seen in C; the P1 and P3, present in juvenile individuals (best seen in Figs. 4E and 10A) have been resorbed. In B the suture between the maxilla and squamosal is discernible along the posterior margin of the anterior zygomatic ridge.

while in PM 120/107 it is about 90 percent of the length along the middle line (Table 1). It cannot be excluded that the unusually high width/length ratio of PM 120/107 has in part been caused by the slight dorso-ventral flattening of the specimen. In dorsal view the anterior parts of the orbits are situated more posteriorly than in other djadochtatheriids, which results in a very long snout and a small orbit. The occipital plate, as fragmentarily preserved in PM 120/107, was arranged almost vertically, but it appears slightly concave and it is not seen in dorsal view of the skull (being obscured by the prominent nuchal crest). Although the most complete skull of *Catopsbaatar* is depressed and the occipital plate has been badly damaged, we assume (Figs. 7 and 11C) that the position of the occipital plate with respect to the rest of the skull was apparently as in e.g., *Kamptobaatar*, *Sloanbaatar*, and *Nemegtbaatar*, in which the occipital plate slopes

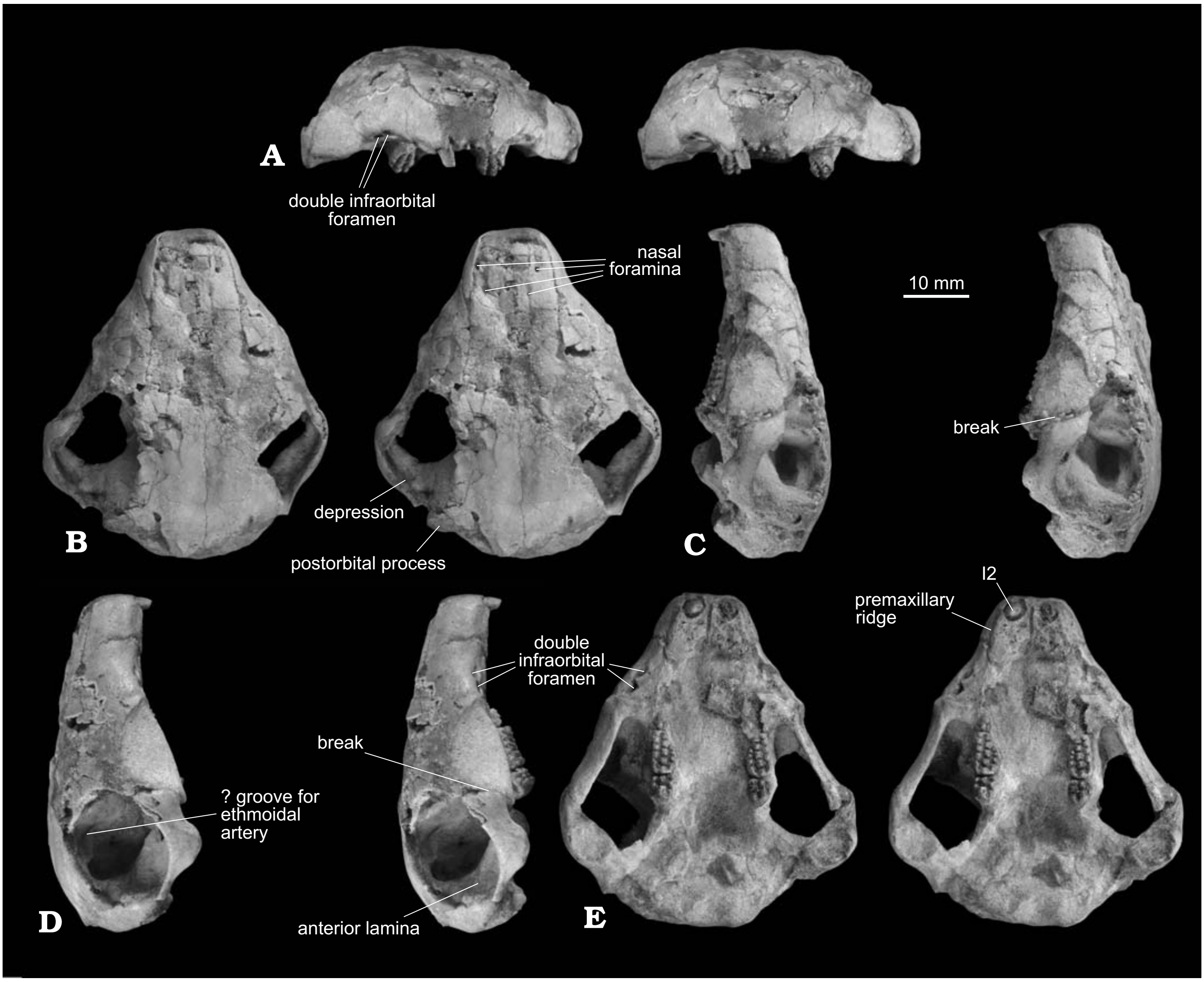


Fig. 3. *Catopsbaatar catopsaloides*, PIN 4537/5, Hermiin Tsav, Gobi Desert, Mongolia, ?upper Campanian, stereo-photographs of an almost complete, but damaged skull of a juvenile individual in anterior (**A**), dorsal (**B**), left lateral (**C**), right lateral (**D**), and ventral (**E**) views. The premaxillary ridge is poorly discernible in C and D, and well visible in E. Note the double infraorbital foramen visible on the right side of the specimen (A and E); on both sides (C and D) the zygomatic arch has been broken along the maxilla-squamosal suture, and the posterior parts of the arches have been slightly displaced dorsally.

postero-dorsally from the condyles (see e.g., Kielan-Jaworowska 1970, 1971, and Kielan-Jaworowska et al. 1986).

Premaxilla.—As usual, the premaxilla consists of facial and palatal parts, at the boundary of which in Djadochtatherioidea there is a distinct ridge designated herein the premaxillary ridge (see e.g., Kielan-Jaworowska 1970: pl. 1: 2b, and Kielan-Jaworowska 1974: pl. XXI: 1b, and Figs. 2C, 3C–E, 4E, and 8 herein). In palatal view the premaxillary ridge is not situated at the margin of the skull, but extends longitudinally and leaves a triangular ventral portion of the facial part of the premaxilla lateral to it. In ZPAL MgM-I/79 the premaxillary ridges on both sides are especially prominent, and have a narrow, flat ventral surface, covered with longitudinally arranged rows of minute foramina (Kielan-Jaworowska 1974: pl. XXI: 1b).

Wible and Rougier (2000: 18) stated that in *K. dashzevegi*: “[...] extending posteriorly from the anterior part of the premaxillary-maxillary suture is a small horizontal furrow, perhaps representing an attachment for facial musculature (‘muf’ in fig. 14). The most probable occupant of such a furrow was the musculus incisivus superioris, which raised the upper lip [...]”. Examination of fig. 14 in their paper shows that the furrow in question was arranged longitudinally and was situated anterior to the premaxillary-maxillary suture, rather than posterior as stated by the authors. In most *Catopsbaatar* specimens this region is damaged; however, on the left side of ZPAL MgM-I/79 (Kielan-Jaworowska 1974: pl. XXI: 1b), on the right side of PIN 4537/4 (Fig. 4E), and right side of PIN 4537/5 (Fig. 3E) in front of the premaxillary-maxillary suture, there is a distinct longitudi-

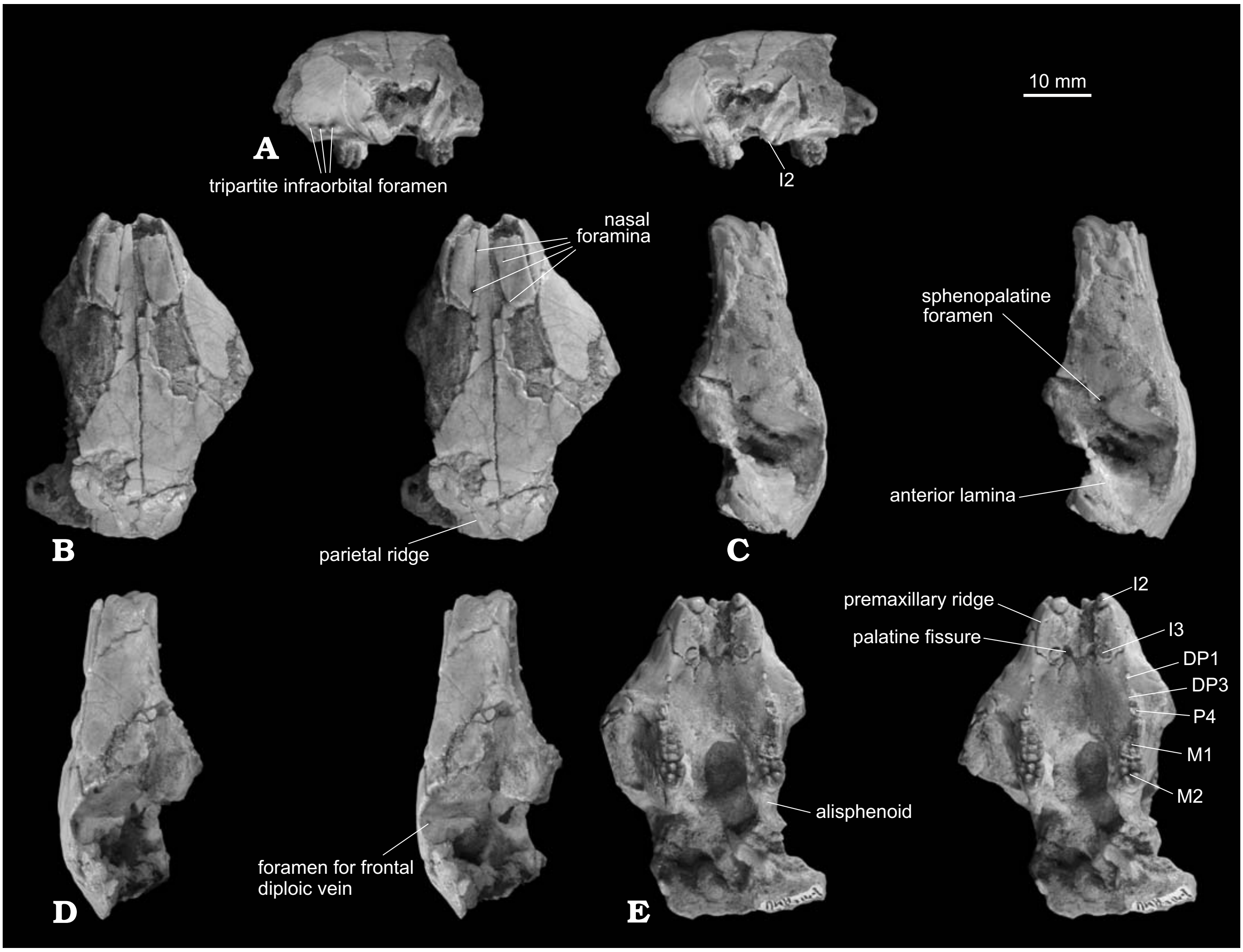


Fig. 4. *Catopsbaatar catopsaloides*, PIN 4537/4, Hermiin Tsav, Gobi Desert, Mongolia, ?upper Campanian, stereo-photographs of an incomplete, severely damaged skull of a juvenile individual in anterior (**A**), dorsal (**B**), left lateral (**C**), right lateral (**D**), and ventral (**E**) views.Anterior upper premolars preserved on both sides of this specimen are recognized as deciduous, as they are single-rooted, rather than double-rooted as in specimens of more mature individuals. The tripartite infraorbital foramen is seen on the right side in A and the premaxillary ridge on the right side in E; single-rooted DP1 and DP3 (replaced in ontogeny by double-rooted P1, and P3, which disappear in adult individuals), are preserved in this specimen (E).

nally directed facet, which may correspond to muscle attachment, similar to that recognized by Wible and Rougier (2000) for *Kryptobaatar*. This facet is situated opposite the anterior part of the premaxillary ridge.

The premaxillary-maxillary suture in lateral view extends in the dorsal part roughly horizontally, along the narrow posterodorsal process, which increases in width anteriorly, then the suture turns in a bow downwards, extending almost vertically, and then near the ventral margin of the snout it turns posteriorly again (Figs. 1B_1, C_1–C_2, 2B; 3C, D, 4C, D). The palatal part of the premaxillary-maxillary suture is perhaps best preserved in PIN 4537/4 (Fig. 4E); it extends a short distance lateral to the premaxillary ridge, then turns, crosses the ridge and extends postero-medially. It turns around I3 (or the alveolus for it), some distance to the rear of it, reaches the incisive foramen, extends transversely along its posterior boundary and reaches its counterpart from the other side The palatal part of the premaxilla is concave, but the distinct thickenings, characteristic of *Kryptobaatar* (Wible and Rougier 2000) and *Tombaatar* (Rougier et al. 1997) are not recognizable. There are depressions on the palatal part, situated between I2 and I3; in PIN 4537/4 on the left side the depression houses a large vascular foramen. In ZPAL MgM-I/79 (Kielan-Jaworowska 1974: pl. XX: 1b) and PIN 4537/5 (Fig. 3E), the palatal part is pierced by numerous nutrient foramina distributed at random; these are present but less distinct in other specimens (see our reconstruction in Fig. 8). The premaxilla is relatively smaller than in *Kryptobaatar*, extending for less than one third of the preorbital part of the snout (Figs. 5 and 7).

Nasal.—The nasal in *Catopsbaatar* is a relatively wide bone, moderately widening posteriorly in the posterior half of its length. Along the lateral border the nasal contacts the pre-

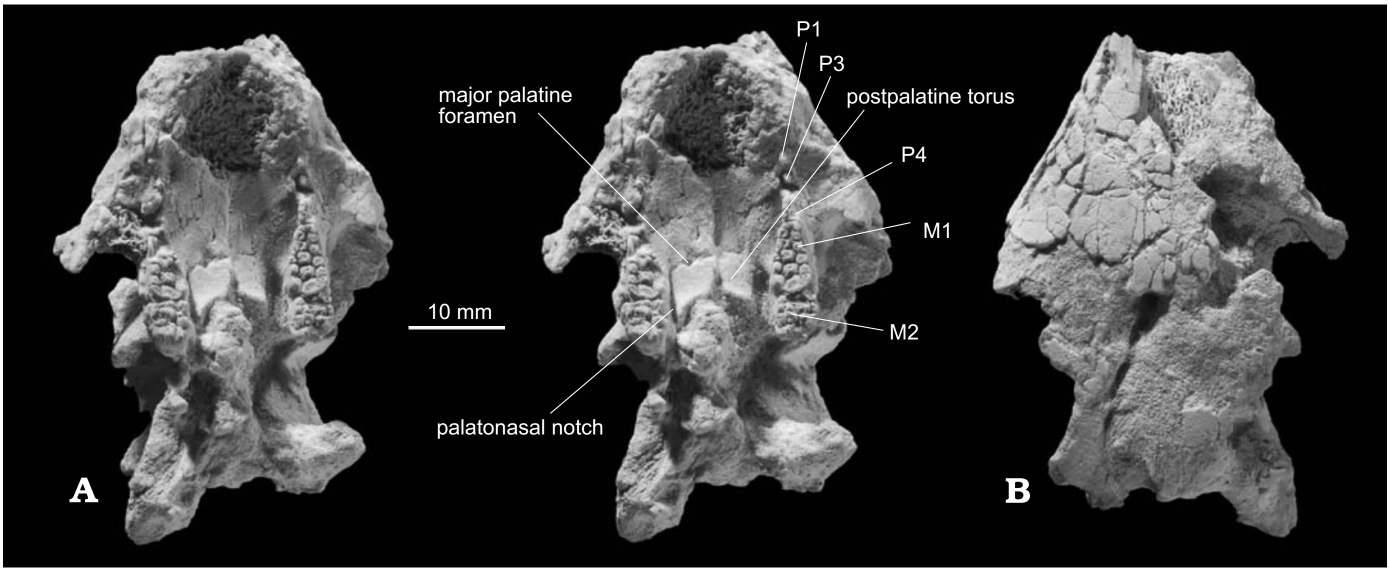


Fig. 5. *Catopsbaatar catopsaloides*, ZPAL MgM-I/80, Hermiin Tsav II, Gobi Desert, Mongolia, ?upper Campanian, severely damaged skull of a juvenile individual; stereo-photograph in ventral view (**A**), dorsal view of the same (**B**). The palatine bone, damaged in other specimens, has been preserved, showing major palatine foramina and palatonasal notches. The roots (in A) designated P1 and P3 might either belong to deciduous premolars, or might represent the posterior root of P1 and anterior root of P3 respectively. The latter interpretation appears more probable as the skull MgM-I/78 figured here is slightly bigger (see Table 1) than that of the holotype MgM-I/78, in which there are double-rooted P1 and P3.

maxilla and maxilla, and posteriorly the lacrimal and frontal. The naso-frontal suture is not pointed anteriorly in the middle, as tentatively reconstructed by Kielan-Jaworowska and Sloan (1979: fig. 1A), Kielan-Jaworowska and Hurum (1997: fig. 10I), and Kielan-Jaworowska et al. (2004: fig. 8.39F), but rather rounded. Reconstruction of the postero-lateral margin of the nasals, as given in Fig. 6, is only tentative, due to the uncertainty of the size and shape of the lacrimal (see below). On the anterior two-thirds of the nasals' length in PM 120/107, there are four irregularly arranged vascular nasal foramina on the right side and apparently only three on the left side (Fig. 6), the second from anterior being larger than the others on both sides. In other specimens there may be only two pairs of vascular foramina (see section "Variation" below for discussion on distribution of nasal foramina in various specimens).

Lacrimal.—Reconstruction of the size and shape of the facial wing of the lacrimal bone in *C. catopsaloides* poses difficulties, as the relevant region in three skulls ZPAL MgM-I/79, /80 and PM 120/107 is missing or devoid of the bones, while in the three remaining skulls ZPAL MgM-I/78, PIN 4537/4, and PIN 4537/5 it has been preserved, but damaged. Kielan-Jaworowska and Sloan (1979: fig. 1) reconstructed the facial wing of the lacrimal bone in *Kryptobaatar dashzevegi* (1979: fig. 1A) as a very large, rectangular bone, extending from the anterior end of the orbit up to the contact with nasal; this reconstruction was accepted by Kielan-Jaworowska and Hurum (1997: fig. 10I) and Kielan-Jaworowska et al. (2004: fig. 8.39F). Wible and Rougier (2000: fig. 32) reconstructed a smaller facial wing in *K. dashzevegi* from Ukhaa Tolgod, where it invades the maxilla laterally, which we regard as correct. In *Djadochtatherium* (Webster 1996: photo on p. 84), however, which is very close to *Catopsbaatar*, the facial wing of the lacrimal is relatively larger, and apparently sub-rectangular. In *Catopsbaatar*, in ZPAL MgM-I/78 on the right side, the bone is missing around the orbit, but on the matrix preserved there is an imprint of a presumed lacrimal, which invades the maxilla and has a rounded anterior margin. Similar structure has been preserved on the right side of PIN 4537/4 and the right side of PIN 4537/5. On the basis of these three specimens, and a comparison with *Kryptobaatar* and *Djadochtatherium* we tentatively reconstruct the facial wing of the lacrimal as a relatively elongated bone, with a rounded anterior margin (Fig. 6). The orbital wing of the lacrimal in all the skulls available is not sufficiently well preserved to allow a reconstruction of its shape and size, although in PIN 4537/4, on the right side of the skull a very large lacrimal foramen appears to be present. In Fig. 11C we reconstruct tentatively the orbital wing of the lacrimal, based on a comparison with *Kryptobaatar* (Wible and Rougier 2000).

Frontal.—The frontal is a large bone consisting of a horizontal component, building the large part of the cranial roof, and a vertical component, contributing to the medial wall of the orbit. The horizontal part (e.g., Fig. 2A, and reconstruction in Fig. 6) is very wide, roughly trapezoidal in shape; the left and right parts of the frontals meet one another along the midline in an irregular suture. Anteriorly the frontals contact the nasals, with a suture that is slightly convex anteriorly; laterally they contact the lacrimals and form the margin of part of the orbit, and posteriorly the parietals. The frontal-parietal suture is U-shaped as in almost all djadochtatherioid genera (see Kielan-Jaworowska and Hurum 1997: fig. 10, and the description

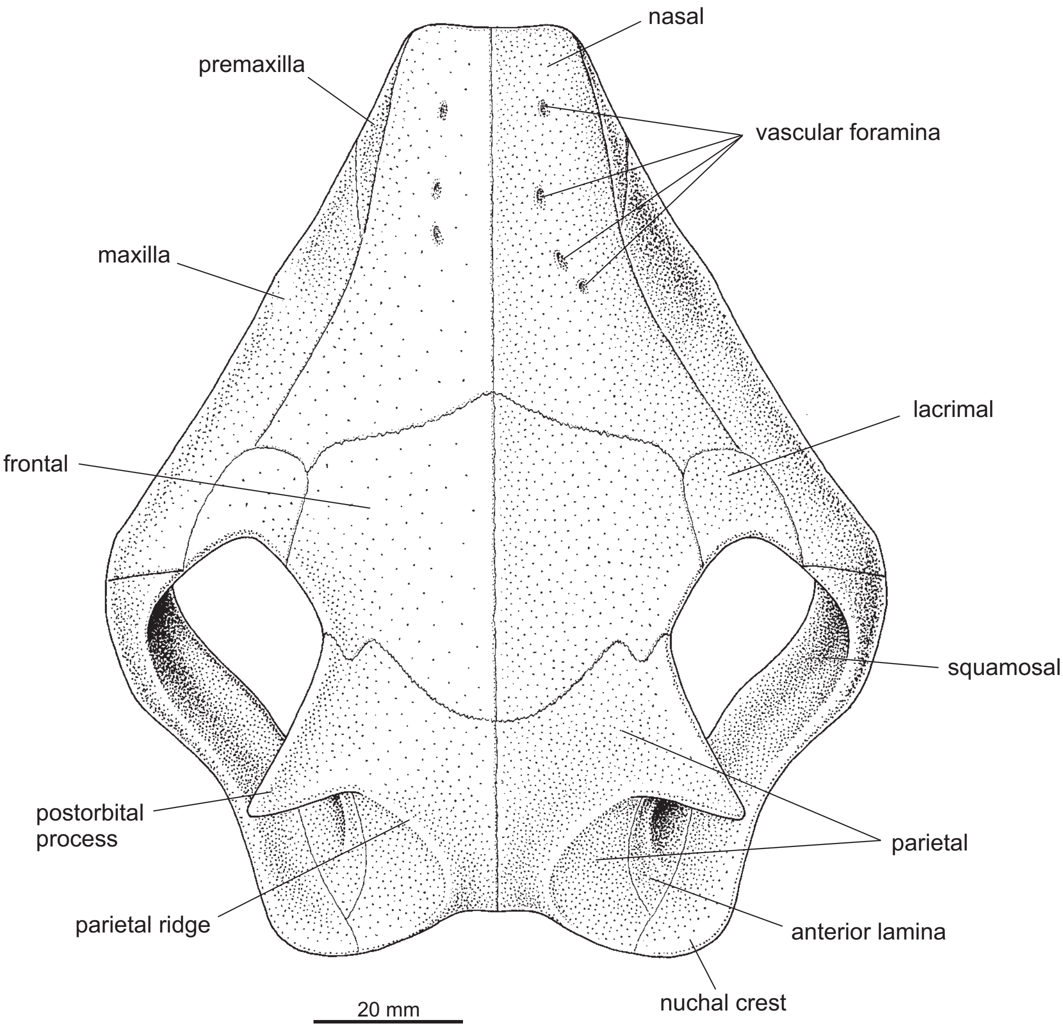


Fig. 6. *Catopsbaatar catopsaloides,* reconstruction of the skull, based on all available specimens, in dorsal view. The nasal vascular foramina are shown as preserved in PM 120/107. In other specimens there may be only two pairs of nasal vascular foramina.

below). The suture in *Catopsbaatar* apparently resembles most that in *Kryptobaatar* (Wible and Rougier 2000: fig. 32), but forms a relatively narrower and shallower arc. This arc is somewhat more convex in the holotype ZPAL MgM-I/78 (Kielan-Jaworowska 1974: pl. XVIII: 1c) than in the others, but even in the holotype it is less deep and narrower than in *Kryptobaatar*. Similar to *Kryptobaatar*, the lateral part of the suture on each side forms a small bow convex posteriorly. These bows in *Catopsbaatar* are relatively larger, deeper, and wider transversely than in *Kryptobaatar*. The suture is different from that in *Djadochtatherium*, where in the specimen from Tögrög provisionally numbered HMNS 94-10-278 (see Acknowledgements for details, personal communication from Mahito Watabe to ZK-J, October, 1996), the middle part is V-shaped rather than U-shaped, and the lateral bows on the suture are wider transversely in *Djadochtatherium* than in *Catopsbaatar*. The supraorbital notch, which has been described in *Kryptobaatar* by Wible and Rougier (2000) at the boundary between the vertical and horizontal components of the parietal, apparently was also present in *Catopsbaatar*, as may be inferred from examination of the relevant region in ZPAL MgM-I/78, PM 120/107, and the left side of PIN 4537/4 (Fig. 7). The structure of the orbit partly preserved in PIN 4537/4 and PIN 4537/5 suggests that the vertical component of the frontal is relatively longer in *Catopsbaatar* than *Kryptobaatar*. In PIN 4537/4 on the right side the foramen for frontal diploic vein (see Wible and Rougier 2000: fig. 36A) is preserved in the upper part of the frontal (Fig. 4D). The suture between the vertical portions of the maxilla and frontal as well as the sphenopalatine foramen are visible on left side of PIN 4537/4 (Fig. 4C). In PIN 4537/5, the deep, vertically directed groove in the anterior part of the orbit (Fig. 3D) might be for ethmoidal artery.

Maxilla.—The maxilla (Figs. 6, 7, 8, 11) is a very extensive bone; its facial process (lateral view) comprises most of the lateral wall of the snout and is seen at the lateral parts of the snout in dorsal view; the palatal process contributes to a large part of the palate (ventral view); and the alveolar process, lateral to it, bears all the upper teeth except for the incisors. The zygomatic process of the maxilla forms the anterior part of the zygomatic arch, up to the suture with the squamosal, situated at the boundary between the anterior and the intermediate zygomatic ridges. Finally, the orbital process, poorly preserved in all available specimens, constitutes part of the vertical wall, forming the medial wall of the orbit. The facial process contacts the premaxilla anteriorly (with the suture described above) and the nasal and lacrimal dorsally. The infraorbital foramen as preserved in ZPAL MgM-I/78 (Kielan-Jaworowska 1974: pl. XVIII: 1a, d), and in PM 120/107 (Figs. 1C$_1$, C$_2$, C$_5$, and 2B) is single, relatively small, slit-like (dorso-ventrally compressed), and visible in anterior, ventral and lateral views; its posterior margin is situated opposite P3 in ZPAL MgM-I/78, but more anteriorly (opposite of the missing P1, or even in front of it) in PM 120/107. It is not preserved in ZPAL MgM-I/79 and /80. In PIN 4537/5, the infraorbital foramen, preserved on the right side of the skull, is double (Figs. 1B$_1$, B$_2$, 3A, D), while in PIN 4537/4 (Figs. 1A$_3$, 4A, D), preserved on the right side, it is tripartite, the anteriormost foramen being the largest, the others decreasing in size posteriorly. In contrast to ZPAL Mg-I/78 and PM 120/107, where the infraorbital foramina are slit-like, in two PIN specimens the double or tripartite foramina are rounded.

The most characteristic feature of the facial and zygomatic processes of the maxilla in *Catopsbaatar* is the enormous anterior zygomatic ridge (Gambaryan and Kielan-Jaworowska 1995; and Fig. 7 herein), which is relatively much higher than the corresponding ridges in other djadochtatherioidean taxa, except for *Djadochtatherium* (Fig. 11). In *Catopsbaatar* the anterior zygomatic ridge encircles almost half a circle, rather than half of an ellipse as in most genera, e.g., *Nemegtbaatar*, *Chulsanbaatar* (see Gambaryan and Kielan-Jaworowska 1995: fig. 2B, C) and *Kryptobaatar* (Fig. 11A). The anterior margin of the anterior zygomatic ridge in *Catopsbaatar* is strongly thickened, producing a bulge on the lateral margin of the snout seen in both ventral and dorsal views (as characteristic also of *Kryptobaatar*, see e.g., PSS-MAE 113, figured by Wible and Rougier 2000: figs. 4—two upper photographs, and 15). See description of the intermediate zygomatic ridge and the maxilla-squamosal suture under "Squamosal" below. The lower part of the maxilla-squamosal suture, as examined in lateral view, extends along the posterior boundary of the anterior zygomatic ridge and has a sigmoid shape; however, the uppermost part of the suture is poorly recognized (see section "Comparisons" and Fig. 11C below).

Gambaryan and Kielan-Jaworowska (1995: fig. 7B$_1$) reconstructed the masseter superficialis pars anterior as originating from the anterior zygomatic ridge. The upper margin of the zygomatic arch forms a bow around the lower margin of the orbit. The anterior part of the zygomatic arch (built by the maxilla) is high, but relatively thin latero-medially, and because of this (e.g., in PM 120/107) it is undulating, deformed by preservation.

The palatal processes of the maxilla are extensive, forming most of the palate. Right and left components form together a concave surface. The transverse suture with the horizontal part of the palatine bone is best preserved in ZPAL MgM-I/80 (Fig. 5A), where it extends opposite the anterior half of M1. The major palatine foramina are well-preserved; shallow grooves extend from them anteriorly, along the palatal part of the maxilla (Figs. 5 and 8). In ZPAL MgM-I/78 the horizontal part of the palatine bone has not been preserved, but still the suture shows the presence of the major palatine foramina (Kielan-Jaworowska 1974: pl. XVIII: 1d). In PM 120/107 on the palatine process of the maxilla there are two relatively large foramina created by damage. In PIN 4537/4 the right major palatine foramen is preserved, situated opposite the anterior part of M1 (Fig. 4E). The palatine has not been preserved, but the posterior margins of both palatal processes of the maxilla have the shape of an overturned letter U, and apparently correspond to the maxillary-palatine suture. The suture between the palatal part of the maxilla and the alisphenoid is seen on the left side of PIN 4537/4 (Fig. 4E); it is placed relatively more close to M2 than in *Kryptobaatar* (Wible and Rougier 2000: fig. 34), see also the reconstruction in Fig. 8.

Palatine.—The palatine bone in multituberculates, as in other mammals, consists of two parts: the horizontal lamina and the perpendicular lamina (Evans 1995). The horizontal lamina in multituberculates forms a roughly rectangular plate surrounded as usually from anterior and lateral sides by the maxilla, its posterior border (often with a thickened postpalatine torus) forming the anterior margin of the choanae. Among the Late Cretaceous Asian multituberculates the horizontal lamina is perhaps best preserved in the juvenile skull of *Kamptobaatar kuczynskii* ZPAL MgM-I/33 (Kielan-Jaworowska 1971: fig. 4 and pl. I: 2b) and a juvenile specimen of *Chulsanbaatar vulgaris*, ZPAL MgM-I/168 (Kielan-Jaworowska et al. 1986: fig. 14A). In *Kamptobaatar* there is a pair of major palatine foramina situated slightly in front of the maxilla-palatine suture, and two pairs of minor palatine foramina within the horizontal lamina (accessory palatine foramina of Wible and Rougier 2000); there is a moderately prominent postpalatine torus and the palatonasal notches at the lateral sides of it. In *Chulsanbaatar* the horizontal lamina is similarly built as in *Kamptobaatar*, the difference concerning presence of only one, rather than two pairs of minor palatine foramina.

In *Catopsbaatar* the horizontal lamina has not been preserved in ZPAL MgM-I/78, PIN 4537/4, and PIN 4537/5. It is almost completely preserved in ZPAL MgM-I/80 (Fig. 5A), in which the postpalatine torus is present but very weak. In ZPAL MgM-I/79 (Kielan-Jaworowska 1974: pl. XXI, 1b) a small part of the horizontal lamina has been preserved on the right side of the skull, including an indistinct postpalatine notch and a tiny fragment of the postpalatine torus (see section "Terminology" above). In PM 120/107 (Fig. 2C) the horizontal part of the palatine bone has been preserved, but the suture between it and the palatine process of the maxilla is poorly seen, situated opposite the second and the third

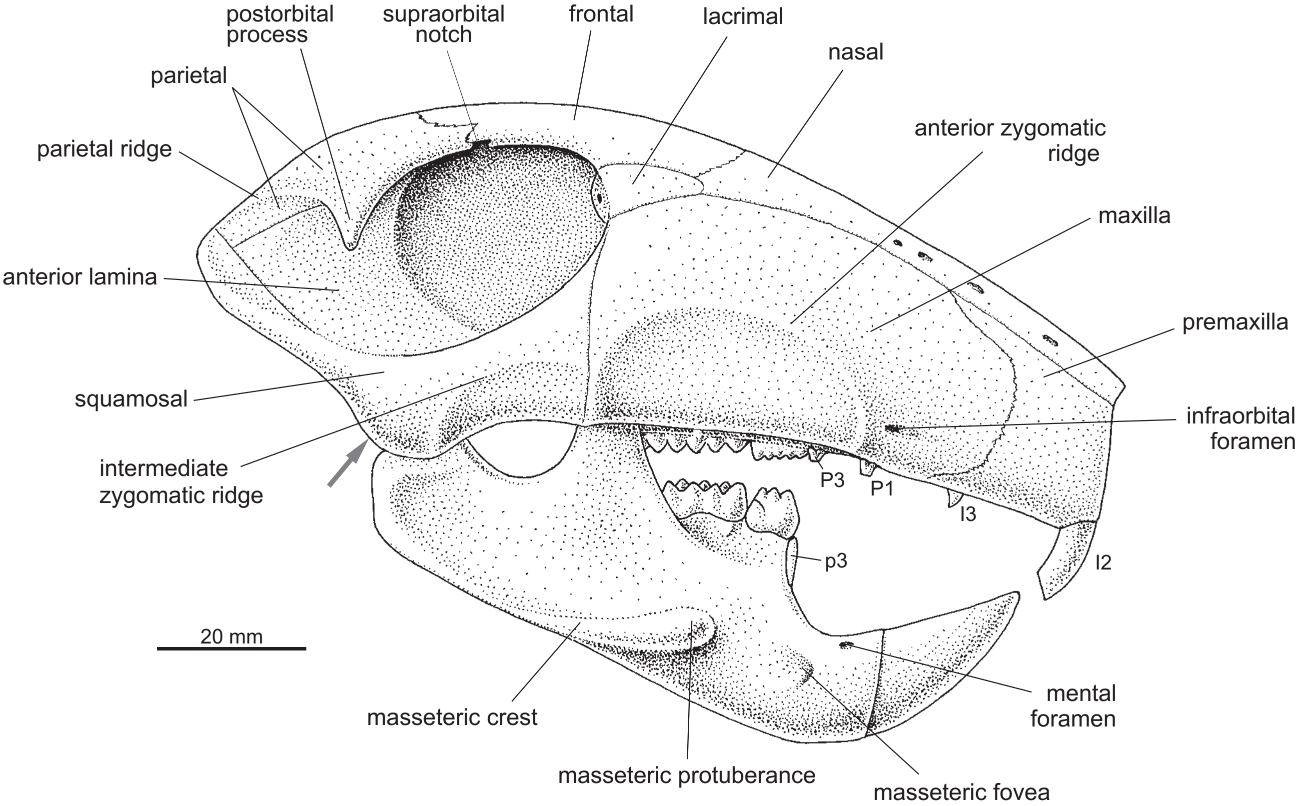


Fig. 7. *Catopsbaatar catopsaloides*, reconstruction of the skull, based on all available specimens, in lateral view. The reconstruction is of an adult individual, but the upper premolars P1 and P3, which disappear during ontogeny, are reconstructed. The bones of the orbit, not preserved in ZPAL and PM specimens and very fragmentarily preserved only in PIN 4537/4 and /5, have not been reconstructed. The dorsal part of the maxilla/squamosal suture is tentatively reconstructed on the basis of PIN 4537/5 (Fig. 3C, D) and a comparison with *Djadochtatherium* (Fig. 11B). The arrow points to the posterior zygomatic "ridge" (muscle scar), preserved on the squamosal above the glenoid fossa and discernible in occipital view. The teeth not marked on the dentary are p4 and m1, on maxilla P4 and M1.

cusps of the middle row of M1, as in ZPAL MgM-I/80 (see also Fig. 8).

There is controversy concerning the exposure of the perpendicular lamina of the palatine bone in the orbit in multituberculates. Kielan-Jaworowska (1971: fig. 3) recognized the exposure of the palatine within the ventral part of the orbit of *Kamptobaatar*. Miao (1988) demonstrated that the palatine is wholly excluded from the orbit in *Lambdopsalis bulla*, while Wible and Rougier (2000) demonstrated the same for *Kryptobaatar dashzevegi*. Miao (1988) argued that the lack of the palatine exposure in the orbit should be regarded as the autapomorphy of Multituberculata. On the other hand, Hurum (1994, 1998a) demonstrated its presence in the sectioned skull of *Nemegtbaatar* (see Kielan-Jaworowska et al. 1986), while Sloan (1979: fig. 1) reconstructed it in the orbit of *Ectypodus*.

In *Catopsbaatar*, as far as can be judged from the poorly preserved orbital walls (best seen in ZPAL MgM-I/78), the palatine bone was apparently not exposed in the orbit.

Wible and Rougier (2000: 79) concluded: "If Hurum's (1994, 1998a) interpretations of the orbital sutures in *Nemegtbaatar* are correct, then the Mongolian Late Cretaceous taxa would be polymorphic regarding the presence of the palatine in the orbit."

Pterygoid and vomer.—Kielan-Jaworowska (1971) argued that multituberculates differ from all other mammals in the position of the pterygoids, which do not form parts of the lateral walls of the choanae, but are situated between the vomer and the lateral walls of the choanae, the latter apparently built by the alisphenoids. The sutures between the pterygoids and other bones, however, have not been recognized. Since that time similar structure of the choanal region has been recognized in numerous multituberculate taxa, especially in representatives of the exquisitely preserved Late Cretaceous djadochtatherioideans. Wible and Rougier (2000) described this region in *Kryptobaatar* in detail. They referred to the two channels on each side of the choanal region as the pterygopalatine troughs; the medial one, situated between the vomer and the pterygopalatine ridge (pterygoid of Kielan-Jaworowska 1971: fig. 4), as the medial pterygopalatine trough; and the lateral one (?scaphoid fossa of Kielan-Jaworowska 1971) as the lateral pterygopalatine trough. The term pterygopalatine ridge was introduced by Barghusen (1986: fig. 1B) for the ridge of the pterygoid bone in *Thrinaxodon*, and used by him in interpreting the choanal structure in *Kamptobaatar* (fig. 6B in his paper). Barghusen also identified a notch in the ridge of the pterygoid bone in *Kamptobaatar*, marked by Kielan-Jaworowska (1971: fig. 4) with a question mark, as

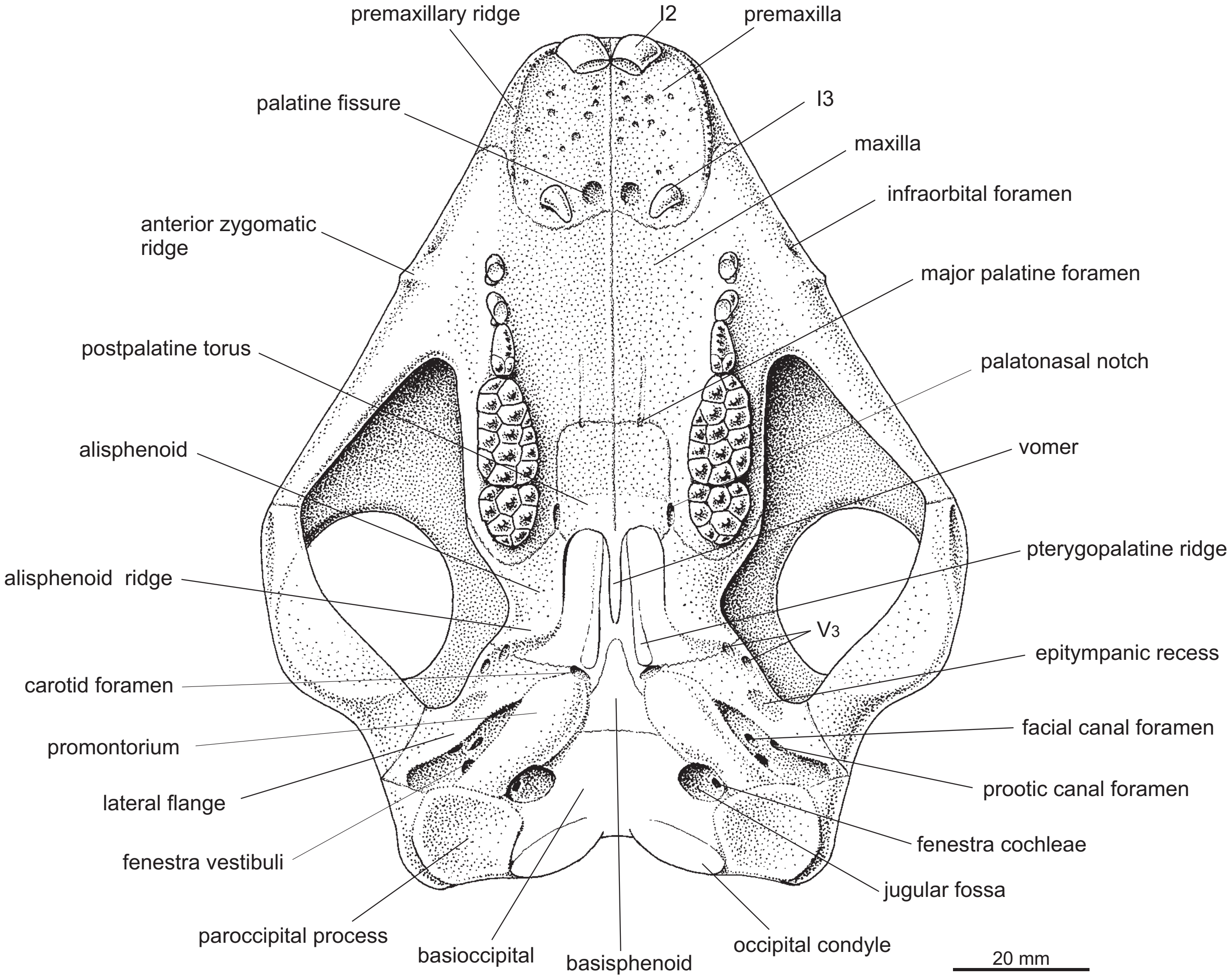


Fig. 8. *Catopsbaatar catopsaloides*, reconstruction of the skull, based on all available specimens, in ventral view. The reconstruction is of an adult individual, but the upper premolars P1 and P3, which disappear during ontogeny, have been reconstructed. The teeth in maxilla are P1, P3, P4, M1, and M2. The choanal region and the middle part of the basicranial region (diagrammatical), including recognition of most of the foramina not preserved or poorly preserved in *Catopsbaatar* (see text for details), have been reconstructed on the basis of other djadochtatherioid genera, especially *Kamptobaatar* (Kielan-Jaworowska 1971), *Nemegtbaatar* (Kielan-Jaworowska et al. 1976), and *Kryptobaatar* (Wible and Rougier 2000).

an incisure connecting the lateral nasopharyngeal passage with the internal naris. In the skulls of *Catopsbaatar* housed in ZPAL, PIN, and PM the choanal region has been damaged and does not provide information on the structure of the pterygoids and the vomer in this taxon.

Kielan-Jaworowska (1971) suggested that in multituberculates the pterygoids do not form the lateral walls of the choanae, but are situated in the middle of the choanal channel on each side. In light of Barghusen (1986) and Wible and Rougier (2000) papers it is now possible to speculate that in multituberculates the pterygoids apparently form the lateral walls of the choanae, as in all other mammals, being in contact with alisphenoids, and form the roof of the lateral parts of the choanal channels. They differ from those in other mammals in producing a medial longitudinal crest, designated by Wible and Rougier (2000) the pterygopalatine ridge (pterygoid of Kielan-Jaworowska 1971). Our reconstruction of the pterygoids and the whole choanal region in *Catopsbaatar*, presented in Fig. 8, is entirely tentative, based on comparisons with *Kamptobaatar* (Kielan-Jaworowska 1971), *Nemegtbaatar* (Kielan-Jaworowska et al. 1986), and *Kryptobaatar* (Wible and Rougier 2000).

Sphenoid complex.—The details of the sphenoid complex are difficult to recognize in multituberculates because of the early fusion of the presphenoid, basisphenoid, orbitosphenoid, and alisphenoid. In the juvenile skull of *Kamptobaatar* ZPAL MgM-I/33, Kielan-Jaworowska (1971: fig. 3) recognized a very large, fan-shaped orbitosphenoid, less certainly a small alisphenoid, and the anterior lamina of the petrosal. The extent of the latter bone has been subsequently corrected by Kielan-Jaworowska et al. (1986: figs. 20b, 14B, C) on the basis of better preserved braincases in *Nemegtbaatar* and *Chulsanbaatar*, showing a very extensive anterior lamina, apparently characteristic for multituberculates as a whole. The large, fan-shaped orbitosphenoid, small alisphenoid, and extensive anterior lamina of the petrosal with a large antero-dorsal process have subsequently been confirmed in *Nemegtbaatar* and *Chulsanbaatar* by Hurum (1994, 1998a), who, on the basis of the sectioned skulls, reconstructed their reliable lateral aspects in both genera (Hurum 1998a: fig. 14).

In *Kryptobaatar* Wible and Rougier (2000) reconstructed an orbitosphenoid, relatively smaller than in *Kamptobaatar*, with the ethmoid foramen situated at the boundary with frontal, rather than within the orbitosphenoid, as in *Kamptobaatar* (Kielan-Jaworowska 1971), and the anterior lamina of the petrosal without an antero-dorsal process, present in *Nemegtbaatar* and *Chulsanbaatar* (Hurum 1998a: fig. 14). We were unable to recognize the extent of these bones in *Catopsbaatar*.

The mesocranial region has been damaged in all the available skulls of *Catopsbaatar*, and no traces of the presphenoid and basisphenoid have been preserved. The orbital wall has been fragmentarily, but apparently best preserved in PIN 4537/4 and PIN 4537/5, and has been discussed above under the description of the frontal bone. It has been partly preserved also on the left side of the holotype ZPAL MgM-I/78 and on the right side of PM 120/107, but in both specimens no sutures or foramina are recognized. Our reconstruction of this region, presented in Fig. 8, is entirely tentative, based on comparisons with the genera discussed above.

Petrosal.—The petrosal is one of the most complicated bones in the mammalian skull, housing the organs of hearing and balance. It has been studied preserved *in situ* in multituberculate skulls by Simpson (1937), followed by Kielan-Jaworowska (1971, 1974), Miao (1988), Rougier, Wible, and Hopson (1992), Rougier, Wible, and Novacek (1996), Hurum (1998a, b), and Wible and Rougier (2000). Because of its robustness and resistance, the multituberculate petrosal is rather well-known, as it has often been preserved not only in skulls, but also in isolation and described in detail (e.g., Kielan-Jaworowska et al. 1986; Wible and Hopson 1993, 1995; Fox and Meng 1997). The meticulous works by Rougier, Wible, and Hopson (1992) and Wible and Hopson (1993, 1995) resulted not only in the description of the osteology of the basicranial region and the lateral wall of braincase, but also in reconstruction of the cranial vasculature. The multituberculate cranial vasculature was earlier studied by Kielan-Jaworowska et al. (1986) on the basis of sectioned skulls belonging to the genera *Chulsanbaatar* and *Nemegtbaatar*, but Wible and Hopson (1995) challenged part of the conclusions of these authors and offered a somewhat different interpretation.

Wible and Rougier (2000) provided a detailed description of the petrosal in *Kryptobaatar dashzevegi*, accompanied by reconstruction of the cranial vasculature.

The material of *Catopsbaatar* studied by us is much less complete and not as well preserved as that of *K. dashzevegi* studied by Wible and Rougier. Fragments of the petrosal preserved in ZPAL MgM-I/78 and /79 have been figured and described by Kielan-Jaworowska et al. (1986). In ZPAL MgM-I/80 and PIN 4537/4 the petrosal region has not been preserved; in PIN 4537/5, the hardly discernible right epitympanic recess, promontorium, and jugular fossa may be tentatively identified. In PM 120/107 the basicranial region is poorly preserved, with the middle part (basisphenoid and basioccipital) almost entirely missing (see reconstruction in Fig. 8, largely based on a comparison with better preserved basicranial region in other genera).

Kielan-Jaworowska et al. (1986: 534) described the promontorium in ZPAL MgM-I/78 as follows: “In front of the fenestra cochleae the promontorium is roughly rectangular with a swollen, rounded and slightly pointed anterior margin.” The left promontorium in PM 120/107 (Figs. 2C, 8) has a similar structure (ventral view), being associated on the medial side with a fragment of basisphenoid-basioccipital. At the postero-lateral part the promontorium strongly narrows, its medial part being occupied by a jugular fossa, which appears relatively smaller than in other djadochtatheriid genera, while on the lateral part there is a distinct fenestra vestibuli, better seen in a ventro-lateral view of the skull. The fenestra cochleae is not discernible, possibly being confluent with the jugular fossa (as tentatively reconstructed in Fig. 8). Lateral to the promontorium a relatively wide horizontal part of the anterior lamina of the petrosal has been preserved (see Kielan-Jaworowska 1971: 12 for discussion concerning the notion of the “anterior lamina of the petrosal” in multituberculates, and the section “Terminology” above). The horizontal part of the anterior lamina is divided by a ridge of the lateral flange (which extends roughly parallel to the promontorium turning laterally in the posterior part) into a narrow medial trough, housing the foramina and the wider lateral part. The foramina situated in the trough (see reconstruction of *Nemegtbaatar* skull by Kielan-Jaworowska et al. 2004: fig. 8.4B) cannot be recognized in *Catopsbaatar*. Lateral to the lateral flange, there is a very deep and wide epitympanic recess (which houses the ear ossicles) and anterior to it at the suture with the alisphenoid and at the edge between the horizontal and vertical parts of the anterior lamina, traces of two V_3 foramina are tentatively recognized. The carotid foramina have not been preserved.

The vertical wall of the anterior lamina of the petrosal is almost completely preserved on the left side of PIN 4537/4 (Fig. 4C), where the suture with the squamosal is recognizable; the concave anterior margin of the anterior lamina apparently corresponds to its original contact with the orbitosphenoid, as in other multituberculate genera the anterior margin of the anterior lamina is concave (see e.g. Kielan-Jaworowska 1971; Kielan-Jaworowska et al. 1986; Wible and Rougier 2000). The anterior lamina has been also partly preserved on the right side of ZPAL MgM-I/78 and less completely on the left side of the same specimen (Kielan-Jaworowska 1974: pl. XIX: 1d, 1e); it has been preserved on the left side of ZPAL MgM-I/79 (Kielan-Jaworowska 1974: pl. XXI: 1d) and partly on the right side of the same specimen. Finally the anterior lamina has been preserved, but strongly cracked on both sides of PM 120/107 (Fig. 2B); in this specimen on the left side, below the postorbital process, a foramen has been preserved (Fig. $1C_1$). It is probably the opening of the orbitotemporal canal (Wible and Rougier 2000: figs. 12 and 36), referred to by Kielan-Jaworowska et al. (1986: fig. 20b) as the postorbital foramen. This foramen in *Catopsbaatar* is situated more posteriorly than the opening of the orbitotemporal canal, identified by Wible and Rougier in *Kryptobaatar*. On the right side the sutures with the parietal and squamosal are tentatively recognized (Fig. 2B, see also Fig. 7), but the orbitosphenoid has not been preserved and the contacts with that bone (and alisphenoid ventrally) are not discernible.

The occipital exposure of the petrosal (preserved only in PM 120/107, where it is strongly damaged) is similar to that in *Kryptobaatar*, the petrosal (mastoid) being pierced by a posttemporal canal of moderate size (Fig. $1C_3$). In Fig. 8 we tentatively reconstruct a relatively large paroccipital process, with a ?rounded anterior margin, similarly placed as in other djadochtatherioidean genera.

Jugal.—The jugal in multituberculates was reported for the first time by Hopson et al. (1989), who recognized its presence in *Ptilodus*, *Ectypodus*, *Nemegtbaatar*, and *Chulsanbaatar*, and suggested (based on scars) its presence also in the Late Jurassic paulchoffatiids. In all cases the jugal is placed on the medial side of the zygomatic arch. The largest is the well-preserved jugal in *Ptilodus*, which extends between the floor of the orbit and the glenoid. Wible and Rougier (2000) described a well-preserved jugal in *Kryptobaatar*, which is a very delicate, regularly oval bone, distinctly smaller than in *Ptilodus*.

The jugal has not been preserved in studied specimens of *Catopsbaatar*, but in PIN 4537/5 (Figs. $1B_3$, 3B) on the medial side of the right zygomatic arch, and of both sides in PM 120/107 (Figs. $1C_6$, 2A), there is a depression on the squamosal, in the posterior part of zygomatic arch, which possibly could have accommodated the jugal. This depression is, however, situated more posteriorly than in all other multituberculate genera in which the jugal has been preserved.

Squamosal.—Wible and Rougier (2000) divided the squamosal bone into two parts for descriptive purposes: the zygomatic process and the dorsal flange. In *Catopsbaatar* the dorsal flange is similarly built as in *Kryptobaatar*. The zygomatic part differs from that in *Kryptobaatar* in having the zygomatic arch relatively higher and the zygomatic ridges differently arranged. These are best preserved in PIN 4537/5 (see Gambaryan and Kielan-Jaworowska 1995: fig. 2A, and our Figs. $1B_1$, 3C, D, 11C), but also well seen in PM 120/107 (Figs. $1C_1$, C_2, 2B). The intermediate zygomatic ridge, which contacts the anterior zygomatic ridge anteriorly, is well-preserved in PIN 4537/5 and PM 120/107 (Figs. $1B_1$, 3C, D and $1C_1$, C_2, 2B respectively). It is much smaller and lower than the anterior one. The maxilla-squamosal suture extends along the posterior boundary of the anterior zygomatic ridge, but its upper part has not been preserved. We reconstruct the dorsal part of the maxilla-squamosal suture (Figs. 7, 11C), based mostly on PIN 4537/5 (Fig. $1B_1$, 3D) and a comparison with *Djadochtatherium*, as extending antero-dorsally and reaching the lacrimal. On both sides of PIN 4537/5 the zygomatic arch was slightly displaced along the posterior margin of the anterior zygomatic ridge, the lower margin of the arch to the rear of the anterior zygomatic ridge being placed higher than it originally was.

The posterior zygomatic "ridge" in *Catopsbaatar* is the weakest of the three ridges and the muscle scar related to it is as a rule marked only as a depression (arrow in Fig. 7). This depression is recognizable in PIN 4537/5 in lateral view (Figs. $1B_1$, 2D) and in PM 120/107 (Fig. $1C_1$, C_3, on the left side), above the posterior part of the glenoid fossa.

The contact of the squamosal with the petrosal (mastoid) (Fig. $1C_3$) seen in occipital view appears as in *Kryptobaatar* (Wible and Rougier 2000: figs. 16, 17, 35). The glenoid fossa preserved in ZPAL MgM-I/78, PM 120/107, and PIN 4537/5, when examined in lateral view slopes posteriorly (as characteristic of multituberculates, see Gambaryan and Kielan-Jaworowska 1995). The glenoid fossa (Figs. $1B_2$, 2C, 3E; see also Kielan-Jaworowska 1974: pl. XVIII: 1d, where it has been wrongly glued, as discussed under "Holotype" above), may be characterized as roughly semicircular, with its base arranged antero-medially (towards the orbit), and the margins of the semicircle developed as rounded ridges, protruding downwards (Fig. 8). The greatest downward protrusion is at the antero-medial corner of the glenoid, where the surrounding ridge forms a bulge.

The glenoid fossa resembles that in *Kryptobaatar dashzevegi*, from which it differs in having an almost straight antero-medial margin, rather than more convex, which allowed Wible and Rougier to describe it in *Kryptobaatar* as tear-drop shaped.

Parietal.—The parietal bones, as with most bones of the cranial roof, consist of dorsal and lateral components. The dorsal components, which form the whole cranial roof posteriorly, have been preserved partly in the holotype (ZPAL MgM-I/78, see Kielan-Jaworowska 1974: pl. XVIII: 1c), PIN 4537/4 (Figs. $1A_2$, 4b) and PIN 4537/5 (Figs. $1B_3$, 3B). In these three specimens the posteriormost part of the parietal is missing. The parietal is completely preserved only in PM 120/107 (Figs. $1C_6$, 2A, see also Fig. 6). The fronto-parietal suture has been described above under "Frontal". According to the reconstruction of the dorsal component of the parietal bone in *Kryptobaatar dashzevegi* by Wible and Rougier (2000: 46): "Anteriorly, they [the parietals] contact the frontals as a broad U-shaped suture; lateral to the arms of the U, a narrow anterior process of the parietals extends forwards, nearly to the lacrimal on the orbital rim, to form the posterior part of the supraorbital notch and supraorbital crest." The pattern of bone arrangement in *Catopsbaatar* resembles very closely that in *Kryptobaatar dashzevegi*; the state of preservation of all the skulls of *Catopsbaatar* does not allow us, however, to state with any certainty whether the similar anterior process of the parietal was also present in *Catopsbaatar catopsaloides*. Exceptions are the two juvenile skulls PIN 4537/4 and 4537/5, in which the small anterior processes are tentatively recognized.

The postorbital processes are very long. The parietal ridges extend from the posterior margin of the postorbital processes postero-medially, not reaching one another, but leaving a broad middorsal ridge between them. In this respect, the parietals of *Catopsbaatar* resemble those in *Kryptobaatar dashzevegi* (Wible and Rougier 2000: figs. 9 and 32), but not in *K. mandahuensis* (Smith et al. 2001: pl. 3: 1 and text-fig. 4), in which the parietal ridges meet at the end of the parietal. Lateral to the parietal ridges the parietals slope steeply latero-ventrally, giving the impression that the skull strongly narrows in the posterior part, which is not the case. Such structure of the parietals is shared with both species of *Kryptobaatar* (Wible and Rougier 2000; Smith et al. 2001) and with *Djadochtatherium*, as observed on the specimen HMNS 94-10-278.

Along the posterior margin the parietals contact the supraoccipital medially and the petrosals (mastoids) laterally, forming together a very prominent nuchal crest (Fig. 6). The nuchal crest extends transversely a short distance in the middle and then slopes postero-latero-ventrally, producing the extensive wings of the nuchal crest, which are convex posteriorly. Within the lateral parts of the nuchal crest the parietal contacts the squamosal.

The lateral component of the parietal contacts the frontal anteriorly; in the middle it has a long contact with the anterior lamina. The suture between the bones is generally straight, directed obliquely antero-dorsally/postero-ventrally. In the most posterior part the parietal contacts the squamosal.

Supraoccipital.—The supraoccipital of *Catopsbaatar* has been preserved only in PM 120/107, where it is partly distorted (Fig. 1C_3). It is limited to the occipital plate and, as in *Kryptobaatar dashzevegi* (Wible and Rougier 2000: figs. 7, 17, 35) and *K. mandahuensis* (Smith et al. 2001: pl. 2: 3 and pl. 6: 3), it is hexagonal and contacts the parietal dorsally, the petrosals laterally, and the exoccipitals ventro-laterally. It contributes to the middle part of the upper margin of the foramen magnum ventrally.

Exoccipital.—Wible and Rougier (2000) divided the exoccipital in *K. dashzevegi* for descriptive purposes into: the occipital plate, the condyle, and contribution to the jugular fossa. In PM 120/107 and in ZPAL and PIN specimens all these elements are badly damaged, except perhaps for parts of the jugular fossae preserved in ZPAL MgM-I/78, described above under "Petrosal".

Basioccipital.—The basioccipital is badly damaged in all ZPAL, PIN specimens and in PM 120/107; its reconstruction in Fig. 8 is based on a comparison with other djadochtatherioidean genera and is entirely tentative.

Endocranium.—The studied skull material of *Catopsbaatar catopsaloides* does not provide information on the endocranial structure in this taxon, except for some fragments preserved in ZPAL MgM-I/79, discussed and figured by Kielan-Jaworowska et al. (1986: 535 and pl. 2: 3).

Mandible.—Both dentaries have been preserved in the holotype (ZPAL MgM-I/78, figured by Kielan-Jaworowska 1974: pl. V: 9, pl. XVII: 2, and pl. XX). Here we figure the fragmentary left mandible of ZPAL MgM-I/80 (Fig. 9A), fragmentary mandibles of juvenile PIN 4537/4 (Fig. 1A_4, A_5), the right mandible of juvenile PIN 4537/5 (Fig. 1B_4), and both right and left complete mandibles of adult PM 120/107 (Fig. 9B).

In *Catopsbaatar* the mandible is robust and strongly elongated. The angle between the ventral border and the horizontal line (measured along the upper margin of p4 and the molars) varies around 17 degrees. In lateral view the diastema, which is distinctly concave dorsally, extends for 20 percent of the dentary length (measured without the incisor). The small mental foramen, plainly visible in ZPAL MgM-I/78, PM 120/107, PIN 4537/5, and PIN 4537/4, is situated close to the upper margin of the diastema, about the middle of the diastema length. The coronoid process has been most completely preserved in the right dentary of ZPAL MgM-I/78 (Kielan-Jaworowska 1974: pl. V: 9, pl. XVII: 2, pl. XX: 1) and the right dentary of PIN 4537/5. In the latter specimen (Fig. 1B_4) it apparently shows its complete height, but its posterior part is damaged, giving the process a needle-like appearance. It appears very long, possibly relatively the longest among all djadochtatherioideans and narrower than in other djadochtatherioidean taxa (compare Kielan-Jaworowska et al. 2004: fig. 8.40 and our reconstructions, Figs. 7 and 11C), based on all available specimens. The coronoid process starts opposite m1 and rises at an angle of around 45 degrees to the horizontal, less steeply than in *Kryptobaatar dashzevegi* (Wible and Rougier 2000: 60, and figs. 29 and 30, where it is about 60 degrees). It is distinctly separated from the alveolar process, which contains the teeth, by a wide temporal groove.

The condyle is situated only slightly above the upper level of the molars. It is devoid of a neck as in most djadochtatherioidean genera; it is oval in dorsal view and slopes posteriorly and slightly medially. The masseteric fossa is roughly triangular, extending anteriorly to below the m1. In the anterior part it is very sharply delimited ventrally by the masseteric crest, which is very prominent in its anterior course, where it forms a bulge, designated herein the masseteric protuberance (especially well-seen in the left dentary of PM 120/107, Fig. 9B_1). In poorly preserved dentaries (worn) the masseteric protuberance is hardly discernible (see e.g., Fig. 1A_4, A_5, and B_4). The masseteric crest is relatively more robust than in closely related *Kryptobaatar*, which does

Fig. 9. *Catopsbaatar catopsaloides*, Gobi Desert, Mongolia, ?upper Campanian. **A**. Stereo-photographs of the partial left dentary of ZPAL MgM-I/80 from Hermiin Tsav II, in medial (A_1), lateral (A_2), and dorsal (A_3) views. **B**. PM 120/107, Hermiin Tsav I. Stereo-photographs of the left dentary in lateral view (B_1), in medial view (B_2) and in occlusal view (B_3); stereo-photographs of the right dentary of the same specimen in dorsal (B_4) medial (B_5), and lateral (B_6) views. Note large masseteric protuberance at the anterior end of the masseteric crest in B_1, damaged but discernible in B_6 and A_2. →

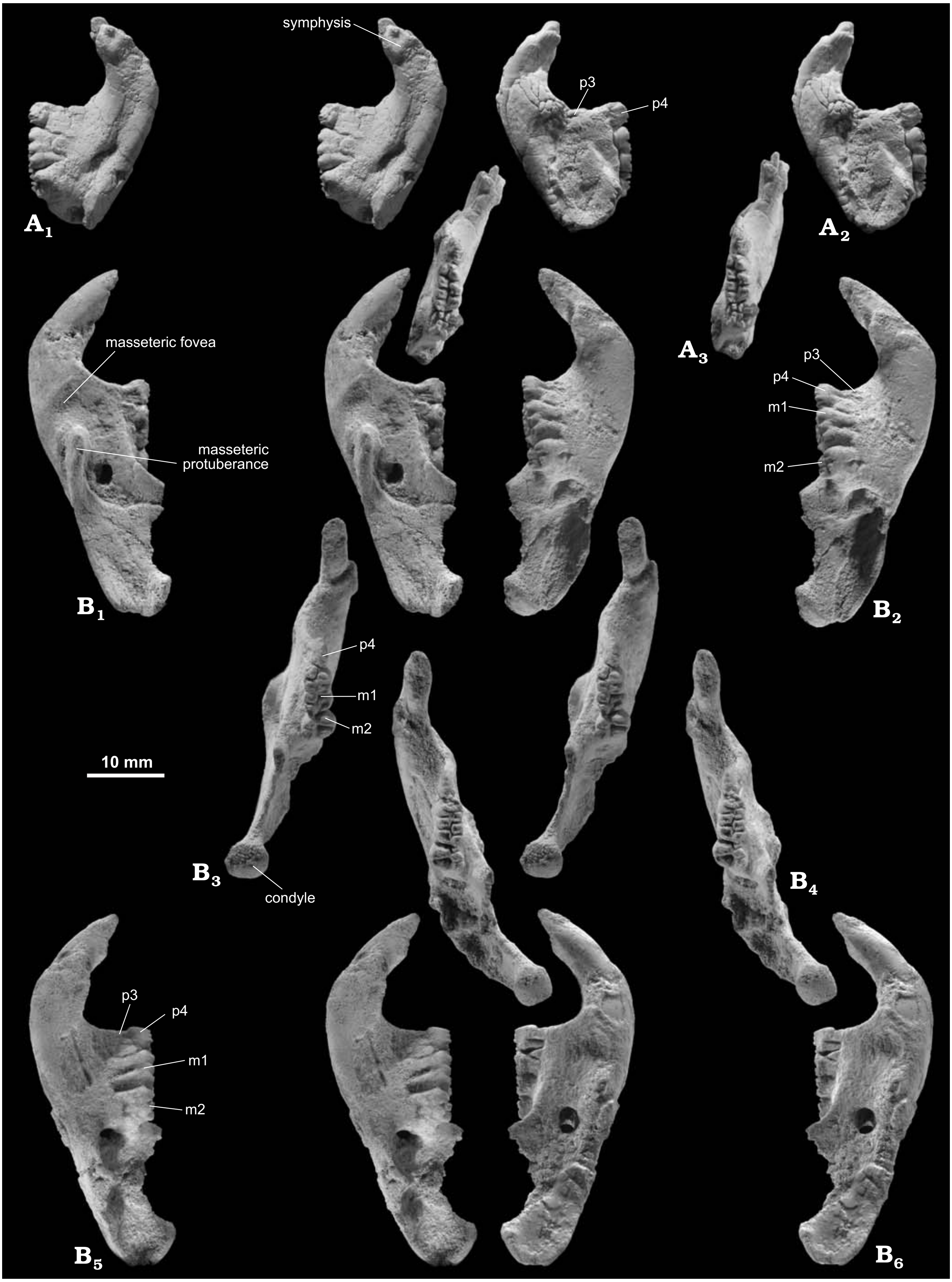

A_1
symphysis
p3
p4
A_2
A_3
masseteric fovea
masseteric protuberance
B_1
p3
p4
m1
m2
B_2
p4
m1
m2
10 mm
B_3
condyle
B_4
p3
p4
m1
m2
B_5
B_6

Table 2. Measurements of the dentition of *Catopsbaatar catopsaloides* in mm. The specimens numbered MgM-I/# belong to ZPAL collection.

	l. P4	l. M1	w. M1	l. M2	w. M2	l. p4	l. m1	w. m1	l. m2	w. m2	lenght upper toothrow	lenght lower toothrow
PM 120/107	4.2	7	4.1	4.3	4.5	3.3	5.8	3.5	3.4	4.2	P4-M2 15.5	12.5
MgM-I/78	3.5	7.1	4.2	4.2	4.5	3.6	5.6	3.5	3.3	3.8	P4-M2 14.8 (whole 19.3)	12.5
MgM-I/79	?	6.6	3.9	4.2	4.5	?	?	?	?	?	P4-M2 18 (whole about 23)	?
MgM-I/80	ca 4.0	7.5	4.2	5	4.5	3.5	5.7	3.4	3.5	3.7	P4-M2 16.5 (whole 19.5)	12.7
PIN 4537/4	ca. 2.1	6.9	3.9	4.2	4.2	3.2	5.4	3.3	3.2	3.7	P4-M2 13.2	11.3
PIN 4537/5	3	6.9	4	4.4	4.2	3.2	5.8	3.4	3.3	3.7	P4-M2 14.1	?
MgM-I/159	?	?	?	?	?	?	?	?	3.2	3.5	?	?

not develop the masseteric protuberance (Kielan-Jaworowska 1971; Gambaryan and Kielan-Jaworowska 1995; Wible and Rougier 2000). A robust masseteric crest apparently ending with the masseteric protuberance occurs in *Djadochtatherium matthewi* (observed by ZK-J in the holotype specimen AMNH 20440) and in the fragmentary dentary from Ukhaa Tolgod (GI 5/301) figured by Kielan-Jaworowska and Hurum (1997: fig. 5). The masseteric protuberance apparently occurs also in *Taeniolabis taoensis* (Granger and Simpson 1929: fig. 4; Simmons 1987: fig. 4.4).

The masseteric fovea is situated in front of the masseteric fossa (Gambaryan and Kielan-Jaworowska 1995: fig. 1); the fovea is well-visible in both fragmentary dentaries of PIN 4537/4 (Fig. 1A$_4$, A$_5$) and in PIN 4537/5 (Fig. 1B$_4$); it is probably more distinct in *Catopsbaatar* than in other djadochtatherioidean genera (see also Fig. 9B$_1$, B$_6$).

On the medial side the symphysis is best seen on the left dentary of ZPAL MgM-I/80 (Fig. 9A$_1$) and on the right dentary of PM 120/107 (Fig. 9B$_2$, B$_5$) where it forms a tear drop-shaped structure, vertically directed and narrowing ventrally.

The pterygoid fossa is very large, occupying the whole posterior surface of the middle part of the dentary to the rear of m2. In both dentaries of PM 120/107 (Fig. 9B$_2$, B$_5$) the fossa appears to be divided by a vertical ridge into two parts, the smaller of which is the anterior one. The division of the fossa is not discernible in the holotype specimen figured by Kielan-Jaworowska (1974: pl. XVII: 2c and pl. XX: 1b), nor in PIN 4537/5 (not figured). On the other hand, Gambaryan and Kielan-Jaworowska (1995) divided the pterygoid fossa in *Nemegtbaatar* into two parts, the anterior one deeper, designated the pterygoid fossa (for m. pterygoideus medialis), and the shallower and smaller posterior one, which they designated the pterygoid fovea (for m. pterygoideus lateralis), which would correspond to the division observed by us in PM 120/107.

In *Catopsbaatar* the pterygoid fossa is bounded ventrally by an extensive pterygoideus shelf, which narrows posteriorly. The shelf was referred to by Simpson (1926) as the pterygoid crest, but we follow Miao (1988), who designated it the pterygoideus shelf.

In dorsal view (Fig. 9B$_3$, B$_4$) the area of the diastema forms a wide shelf, which gently slopes downwards medially. On both sides a ridge protrudes; laterally it is the masseteric protuberance at the anterior part of the masseteric crest, and on the medial side the pterygoideus shelf.

Dentition.—The dental formula of *Catopsbaatar catopsaloides* is 2032/1022.

Upper teeth: In the holotype ZPAL MgM-I/78 the I2 are broken, only the roots are preserved; in ZPAL MgM-I/80 I2 and I3 are missing; in ZPAL MgM-I/79, the left I2 has been preserved (Kielan-Jaworowska 1974: pl. XXI), but it is now broken, only the roots are exposed dorsally, the right root measured on this specimen is 10.3 mm long and extends further posteriorly, hidden in the alveolus. Both I2 have been preserved in PM 120/107; are very robust, with a sharply limited enamel band, and converge slightly medially, touching one another (Figs. 1C$_4$, C$_5$, 2C). In PIN 4537/4 there are the roots of both I2, while in PIN 4537/5 the root of right I2 and complete left I2 (Figs. 1B$_2$, 3E) are preserved.

The I3 are poorly known. The right I3 has been preserved in the holotype ZPAL MgM-I/78 (Kielan-Jaworowska 1974: pl. XVIII: 1d) and is cone-like with a broken tip; on the left side it is broken. The right I3 is also present in PIN 4537/4 (Figs. 1A$_1$, 4E). The broken I3 is well seen on the right side of ZPAL MgM-I/79 (Kielan-Jaworowska 1974: pl. XXI: 1b), while on the left side only the alveolus has been preserved. In ZPAL MgM-I/80 and PM 120/107 both I3 are missing. In PIN 4537/5 this region is badly damaged and both I3 are missing.

The anterior upper premolars P1 and P3 are present only in juvenile individuals, in the older ones they are lost and even the alveoli disappear. In the holotype ZPAL MgM-I/78, which belongs to a young individual, all the upper premolars and molars have been preserved, the M2s are still erupting (Kielan-Jaworowska 1974: text-fig. 6; pl. XVIII: 1b, d; Kielan-Jaworowska et al. 1986: pl. 1: 2a; and our Fig. 10A$_5$). On the left side the P1 appears to have two uncertain cusps; no cusps have been preserved on P3. In PIN 4537/4 (Figs. 1A$_1$, 4E) the right DP1 is single-rooted, with a cone-like blunt crown. On the left side there is the single root of DP1 in its alveolus. The roots of the right and left DP3 are preserved.

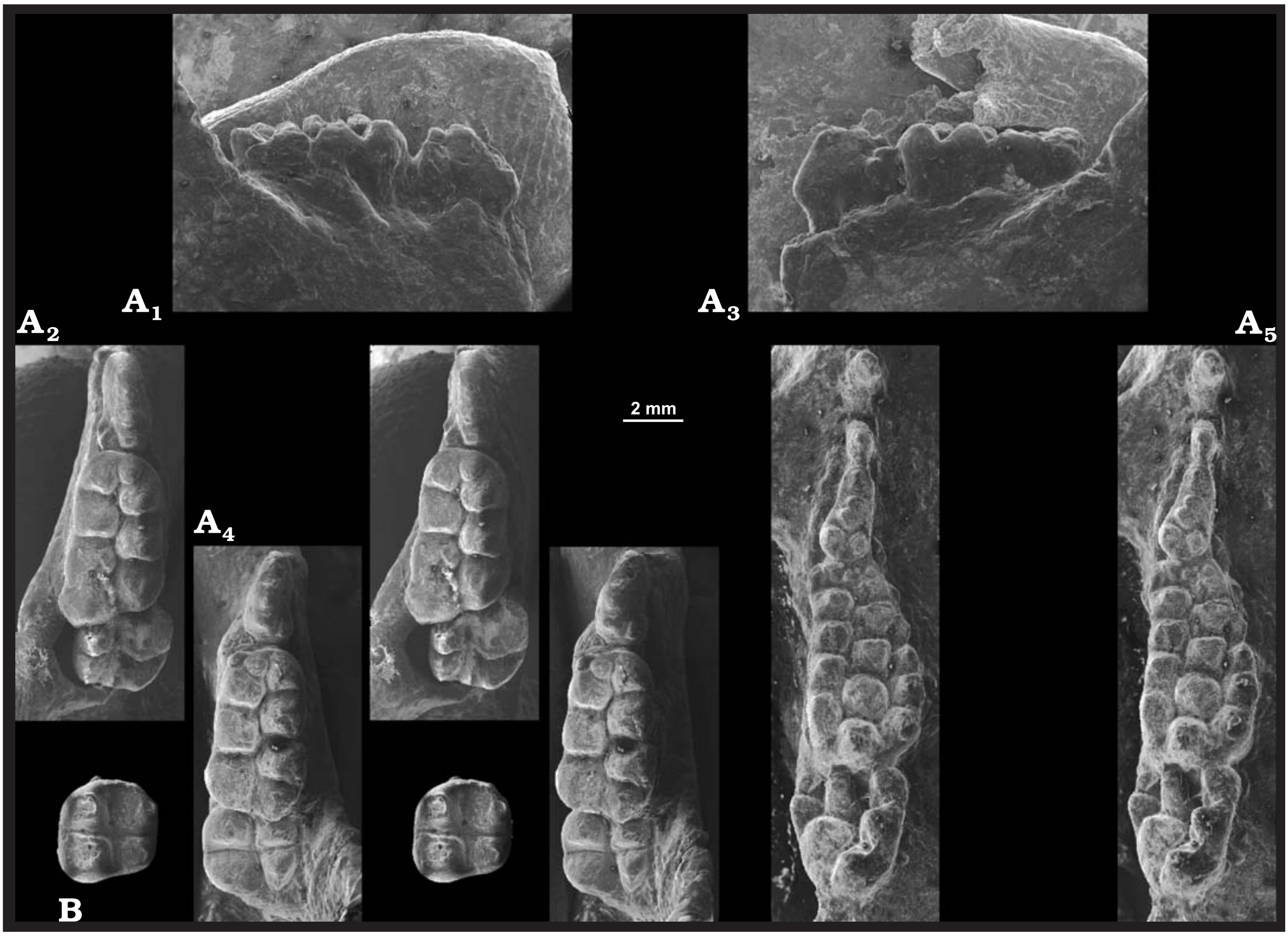


Fig. 10. *Catopsbaatar catopsaloides*, Gobi Desert, Mongolia, ?upper Campanian. **A**. ZPAL MgM-I/78, holotype (juvenile individual) from Hermiin Tsav I. SEM micrographs of the dentition. Fragment of the right dentary in lateral view, showing p3 (peg-like adhering the wall of the dentary), p4 and m1 (A_1). Stereo-micrographs of p4, m1, and m2 of the same in dorsal view (A_2). Fragment of the left dentary of the same specimen, showing p4 and m1, the p3 is broken, only its lower part has been preserved (A_3). Stereo-photograph of the complete right side of the upper dentition, showing P1, P3, P4, M1, and erupting M2 (A_5); P1 and P3 are double-rooted. **B**. ZPAL MgM-I/159, Khulsan, Nemegt Valley, right m2 in occlusal view.

Judging from them, DP3 is single-rooted and smaller than DP1. In PIN 4537/5 this region is badly damaged, and P1 and P3 are not preserved. In ZPAL MgM-I/79, which belongs to an adult individual, roots of P1 and P3 are preserved on both sides (Kielan-Jaworowska 1974: pl. XXI: 1b.) In ZPAL MgM-I/80 (Fig. 5A), which belongs to a relatively young individual (the m2 on the left side is still erupting, and cusps on the molars are moderately worn), only two roots (P1 and P3) have been preserved on the left side (though less certain on the right side). For interpretation of these roots see caption to Fig. 5. In PM 120/107 (Fig. 2C) no traces of the roots of P1 or P3 are preserved.

The P4 cusp formula is 5-4:1. The P4 has been preserved on both sides of ZPAL MgM-I/78 (Fig. 10A_5) and has been schematically figured by Kielan-Jaworowska (1974: fig. 6). In PM 120/107 the P4 is preserved on both sides (Fig. 2C). In PIN 4537/5 it is preserved on the right side and with cusp formula 4:1, the central cusp being distinctly larger than the others (Fig. 3E). In PIN 4537/4 the P4 is damaged on both sides. In ZPAL MgM-I/79 the P4 is missing on the left side and badly damaged on the right; in ZPAL MgM-I/80 it is preserved only on the left side. Our reconstruction in Fig. 8 has been based on all the specimens.

Both M1 have been preserved (at least partially) in all ZPAL, PM and PIN skulls. The cusp formula of M1 is 5-6:5-6:4. The inner ridge extends for about 75 percent of the tooth length. In juvenile individuals (ZPAL MgM-I/78 and PIN 4537/5) the cusps are sharp and not worn, moderately worn in ZPAL MgM-I/80 and PIN 4537/4, while in ZPAL MgM-I/79 and PM 120/107 they are strongly worn and concave. The same concerns M2s.

The M2 has also been preserved in all the specimens. The cusp formula is 2:2-3:2-3. In ZPAL MgM-I/78 both M2 are erupting.

Lower teeth: The single pair of the lower incisors, characteristic of all Multituberculata, is very strong and compressed laterally in *Catopsbaatar*. It has a sharply limited enamel band and was ever-growing. It is best preserved in the right dentary of the holotype ZPAL MgM-I/78 (Kielan-Jaworowska 1974: pl. XVII: 2a, pl. XX: 1a, b) and PM 120/107 (Fig. 9B), in which in dorsal view the large, oval, worn surface is clearly seen on its posterior surface.

Of the two premolars, the p3 is very small entirely adhering to the posterior wall of the diastema and hidden under p4. It has been preserved in the right dentary of ZPAL MgM-I/78 (Fig. 10A$_1$) and partly in the left dentary (Fig. 10A$_3$). In the badly damaged anterior portions of the dentaries of ZPAL MgM-I/80 (Fig. 9A) the p3s are poorly preserved; while in PM 120/107 only the upper part of p3 has been preserved in the right dentary, but is missing from the left (Fig. 9B). In PIN 4537/4 the single root of p3 is preserved on both sides (Fig. 1A$_4$, A$_5$). The p4 has been well preserved in both dentaries of ZPAL MgM-I/78 (Kielan-Jaworowska 1974: pl. XVII: 2, pl. XX; and our Fig. 10A, B), in left ZPAL MgM-I/80 (Fig. 9A), in left PIN 4537/4 (Fig. 1A$_4$), in left PIN 4537/5 (not figured), and in both PM 120/107 (Fig. 9B). The p4 is roughly trapezoidal in lateral view, blade-like, with three cusps along the straight, horizontal upper margin and a single postero-labial cusp. The labial and lingual ridges, characteristic of p4s of most multituberculates, including *Kryptobaatar* and *Djadochtatherium*, are absent in *Catopsbaatar*.

The m1 (Fig. 10A$_1$–A$_4$) is almost symmetrical with cusp formula 4:4. The size of the cusps varies even between right and left teeth of the same specimen; e.g., in the right dentary of ZPAL MgM-I/78 the cusps in the outer row are larger than in the inner row, while in the left dentary those of the inner row are larger. In both rows the size of cusps decreases anteriorly.

The cusp formula of m2 is 2-3:2; however, in most specimens it is 2:2, except for the right dentary of PM 120/107, in which it is 3:2. The cusps of the medial row are distinctly wider than in the lateral row, the medial row of cusps is shorter than the lateral one, and the posterior margin of the tooth is obliquely arranged. The single right m2 from Khulsan (ZPAL MgM-I/159) is more worn than all the m2s preserved in dentaries, and because of wear, may appear on first sight different, e.g., from that in the holotype specimen (Fig. 10A$_4$ and 10B respectively). It is insignificantly wider than the m2s preserved in dentaries associated with skulls (Table 2); however, we believe that there is no reason to assign it to species other than *Catopsbaatar catopsaloides*. We figure the Khulsan specimen herein (Fig. 10B) in order to demonstrate that *C. catopsaloides* was not restricted to Hermiin Tsav (which yielded most of its specimens), but occurred also in the Baruungoyot Formation at an other Gobi Desert locality, being very rare there.

Variability

In addition to the variation in number of tooth cusps and their size, which is characteristic of all multituberculates, the variation in *Catopsbaatar* specimens studied herein concerns first of all the overall size. Three of the studied skulls (ZPAL Mg-MI/78, PIN 4537/4, and PIN 4537/5) belong to juvenile individuals. The size differences between the juveniles and adults are quite dramatic, e.g., estimated length of PIN 4537/5 skull is 52 mm, which is about 80 percent of the most complete adult skull PM 120/107, which measures about 63 mm (Table 1). However, although all the teeth are erupted in the skull PM 120/107, the heads of the femora are not ossified to the necks, indicating presence of juvenile cartilage in this region (Kielan-Jaworowska and Hurum in preparation), so the length of skulls of the completely grown individuals may be still larger.

Other variations concern the number of infraorbital foramina and the vascular nasal foramina.

Hahn (1985) described a double infraorbital foramen in Kimmeridgian Paulchoffatiidae and a single one in Berriasian *Bolodon*. He was of the opinion that the double infraorbital foramen was plesiomorphic and regarded a single one as a synapomorphy of stratigraphically younger groups. Miao (1988) challenged the conclusion of Hahn and argued for variation of infraorbital foramina even within the same specimen. In one specimen of *Lambdopsalis bulla*, he found two infraorbital foramina on one side and a single on the other side of the same specimen.

In this paper we describe still greater variation in the number of infraorbital foramina. Out of six described skulls of *Catopsbaatar catopsaloides* four (housed in ZPAL and PM) have single, slit-like infraorbital foramina, while the juvenile skull PIN 4537/4 has two infraorbital foramina (preserved only on one side), and finally PIN 4537/5 has three infraorbital foramina, again preserved only on one side, the other being damaged (see references to the respective figures under description of the "Maxilla" above). To our knowledge the tripartite infraorbital foramen reported herein has for the first time been found in multituberculates.

As far as the nasal foramina are concerned, Kielan-Jaworowska (1971) demonstrated that they are subject to very great variability (e.g., there are two foramina on the right nasal of *Kamptobaatar kuczynskii* ZPAL MgM-I/33, and four on the left nasal of the same specimen.) She argued that they may transmit cutaneous branches of the lateral ethmoid nerve, as in lizards and man.

In PM 120/107 the nasal foramina are small and reminiscent in proportion to those occurring in *Kryptobaatar dashzevegi* from Ukhaa Tolgod (Wible and Rougier 2000: fig. 32). The similarity does not concern the holotype of *K. dashzevegi* and other specimens from Bayan Zag, as in all specimens of this species housed at ZPAL there are only two nasal foramina, the second pair being deep, strongly elongated, and decidedly larger than the first one, and than those in the specimens from Ukhaa Tolgod (see Kielan-Jaworowska 1970: pl. X: 1b, pl. XV: 1c; and Kielan-Jaworowska and Hurum 1997: fig. 2). In GI PST 8-2 from Tögrög, originally described as *Tugrigbaatar saichanensis* (Kielan-Jaworowska and Dashzeveg 1978), in which the anteriormost part of the snout is missing, on the left nasal there is an elongated vascular foramen, reminiscent of the second foramen present in *K. dashzevegi* from Bayan Zag. In PIN 4537/4 there are three foramina on the left side (the middle is the largest), and one on the right side (Fig. 4). In PIN 4537/5 there are three nasal foramina on the right side, of which the anterior is the largest; because of damage only one middle foramen is recognizable on the left side (Fig. 3).

Comparisons

Members of the family Djadochtatheriidae share many characters in common (see diagnosis of the family above). Among the family members, *Catopsbaatar* is most similar to *Djadochtatherium* Simpson, 1925, from which it is only insignificantly larger. The similarities concern (Fig. 11B, C) the presence of a very large and high anterior zygomatic ridge, which, however, in *Catopsbaatar* is almost half-circular, while in *Djadochtatherium*, as figured by Webster (1996: photo on p. 84), is roughly trapezoidal (almost rectangular). The skull from Ukhaa Tolgod, figured by Webster as *Djadochtatherium* (unfortunately not yet described), in our opinion, belongs in all probability to *Djadochtatherium matthewi* Simpson, 1925. Examination of an enlarged figures by Webster allowed us to recognize most of the sutures observable in the lateral aspect of the skull. Another difference between *Catopsbaatar* and *Djadochtatherium* concerns the intermediate zygomatic ridge, which in *Catopsbaatar* contacts the anterior zygomatic ridge, while in *Djadochtatherium* it is placed a small distance to the rear of it.

In Fig. 11A we reconstruct also the position and shape of the anterior and intermediate ridges in *Kryptobaatar*. Our reconstruction shows that the ridges differ considerably from those in *Catopsbaatar* and *Djadochtatherium*. In *Kryptobaatar* the anterior ridge is low (which is related to the low zygomatic arch) and is asymmetrical, slightly higher anteriorly than posteriorly, while the intermediate one is almost symmetrical, and as usual, is smaller and lower, placed some distance to the rear of the anterior ridge.

The greatest difference between the skull of *Catopsbaatar* and other djadochtatheriidids, as well as other known well-preserved djadochtatherioidean genera, concerns the small size of the orbit and its posterior position in *Catopsbaatar*. In *Catopsbaatar* the snout (measured from the anteriormost part of the orbit in lateral view) extends for about 65 percent of the skull length, in *Djadochtatherium* for 58 percent, in *Kryptobaatar* 49–50 percent, in *Nemegtbaatar* 48 percent, in *Kamptobaatar* 46 percent, in *Sloanbaatar* and *Chulsanbaatar* 41 percent.

As may be seen in Fig. 11, the posterior position of the eye results in different proportions between the particular bones of the skull. In all djadochtatherioideans the suture between the maxilla and squamosal extends obliquely across the zygomatic arch, to the rear of the anterior zygomatic ridge. The anterior ridge is situated on the maxilla, while the intermediate ridge on the squamosal. In taxa with a narrow zygomatic arch and the orbit placed relatively anteriorly, the suture extends obliquely postero-ventrally/antero-dorsally and reaches the ventral part of the orbital margin (e.g., in *Kryptobaatar*, Fig. 11A).

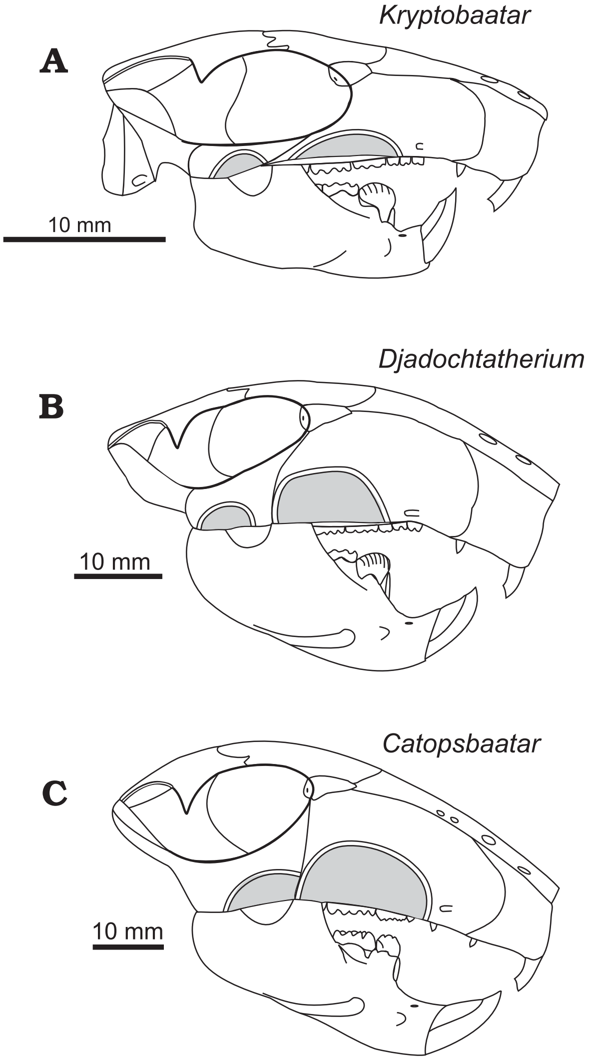


Fig. 11. Comparison of three djadochtatheriid skulls in lateral view, rendered to approximately the same length. The muscle scars surrounded by the anterior and intermediate zygomatic ridges are shaded. The details of the structure of the orbit have been omitted. **A**. *Kryptobaatar dashzevegi* Kielan-Jaworowska, 1969, based on photographs and reconstruction of the specimens from Ukhaa Tolgod, figured by Wible and Rougier (2000), and skulls from Bayan Zag housed in ZPAL. The vascular nasal foramina as preserved in the holotype ZPAL MgM-I/21. **B**. *Djadochtatherium matthewi* Simpson, 1925, tentative reconstruction based on: the holotype AMNH 20440 (rostral part of the skull and both dentaries from Bayan Zag); HMNS 94-10-278 (fairly complete skull with incomplete dentaries from Tögrög, examined on the photographs); GI 5/301 (partial dentary from Ukhaa Tolgod); and the photograph of the complete skull with both dentaries from Ukhaa Tolgod, figured by Webster (1996, the number not available). **C**. *Catopsbaatar catopsaloides* (Kielan-Jaworowska, 1994), reconstruction of the skull in lateral view, based on all known specimens. Orbital wings of the lacrimal, not preserved in *Djadochtatherium* (B) and *Catopsbaatar* (C) have been reconstructed on the basis of comparisons with *Kryptobaatar* (A).

In *Djadochtatherium* and *Catopsbaatar*, in which the zygomatic arch is very high and the eye placed fairly posteriorly, the maxilla-squamosal suture extends differently. In *Djadochtatherium*, after leaving the posterior boundary of the anterior zygomatic ridge, the suture runs antero-dorsally along the antero-ventral part of the orbit and reaches the lacrimal. This results in the thin, tapering antero-dorsally strip of squamosal building part of the antero-ventral margin of the orbit, which is unusual for mammals (see Webster 1996: photo on p. 84 and our reconstruction in Fig. 11B). Along the upper margin of the squamosal, which encircles the ventral and antero-ventral margin of the orbit, there extends in *Djadochtatherium* a thread-like furrow (Webster 1996: photo on p. 84), which might correspond to the origin of the masseter superficialis pars anterior and pars posterior, as reconstructed by Gambaryan and Kielan-Jaworowska (1995: fig. 6B) for *Nemegtbaatar*. The lacrimal in *Djadochtatherium* (examined only in the photograph of Webster 1996, in lateral view) is possibly relatively longer than reconstructed by Wible and Rougier (2000: fig. 32) for *Kryptobaatar*, and apparently more similar in size to that reconstructed by us for *Catopsbaatar* (Fig. 6). It is not certain whether the apparent lateral widening of the posteriormost part of the lacrimal (at the margin of the orbit), observable in the photograph of Webster (1996), is due to damage, or reflects the real structure of the lacrimal.

Catopsbaatar is also similar to *Djadochtatherium* in the structure of the dentary, in which the masseteric crest is unusually strong and provided with a masseteric protuberance, absent from *Kryptobaatar* and other djadochtatherioid genera. The lower margin of the dentary, where the masseteric crest leaves the ventral margin of the dentary and turns antero-dorsally, is slightly incurved in grown specimens of *Catopsbaatar* (e.g., Fig. 9A_1, and less obvious in A_6) and *Djadochtatherium* (Webster 1996: fig. on p. 84).

An important difference between *Catopsbaatar* and *Djadochtatherium* concerns the dentition. *Djadochtatherium* shares the conservative dental formula of 2042/2022, with most djadochtatherioidean genera, except for *Catopsbaatar* and *Tombaatar* (Rougier et al. 1997), in both of which the P2 is missing and hence the upper teeth formula is 2032. In addition, in *Catopsbaatar*, in grown individuals the P1 and P3 disappear (the condition is not known in *Tombaatar*, which is represented by a single specimen). Another difference concerns the structure of p4, which in all the djadochtatherioidean taxa (but not in *Catopsbaatar*, unknown in *Tombaatar*) is traditionally crescent-shaped and provided with ridges. The p4 in *Djadochtatherium* is relatively smaller than in other djadochtatherioid genera (Fig. 11B), but still crescent-shaped and provided with five or so ridges (recognized by us on the photograph of poorly preserved p4 in the left dentary of HMNS 94-10-278 from Tögrög, in which the top part of p4 is missing). In *Catopsbaatar* the reduction of p4 is still more advanced; the p4 is relatively small, roughly trapezoidal in shape, with three cusps along its dorsal margin, and is devoid of ridges.

In *Catopsbaatar* one observes a tendency, known otherwise in the Taeniolabididae (assigned to a superfamily of their own—Taeniolabidoidea, see Kielan-Jaworowska et al. 2004), of disappearance of the premolars, with their function usurped by enlarged molars. However, we know only the Campanian episode of the history of Djadochtatherioidea, while the known distribution of Taeniolabididae is limited to the Maastrichtian–early Paleocene (McKenna and Bell 1997; Kielan-Jaworowska et al. 2004). Known Taeniolabididae are more advanced than the Djadochtatherioidea in the process of losing premolars, which in Taeniolabididae are represented by one upper and one lower tooth. The two Paleocene Gobi Desert multituberculate genera *Prionessus* Matthew and Granger, 1925 and *Catopsalis* Matthew, Granger, and Simpson, 1928 have traditionally been assigned (Matthew et al. 1929, McKenna and Bell 1997) to the Taeniolabididae. As long as their skulls are not known, they should remain in this family, especially given the p4 of *Prionessus lucifer*, reconstructed by Matthew and Granger (1925: 6 and fig. 6) on the basis of the alveoli in the holotype AMNH 20423, is very small, with two connate roots, reminiscent more of those of the Taeniolabididae, than the Djadochtatherioidea. On the other hand, the upper molars of *Prionessus lucifer* (Matthew et al. 1928: fig. 2) are reminiscent more of those in the Djadochtatherioidea, than in the Taeniolabididae.

Multituberculate zygomatic ridges

In their revised diagnosis of *Kryptobaatar*, Wible and Rougier (2000: 104) stated: "[...] differs from *Nemegtbaatar, Chulsanbaatar*, and *Catopsbaatar* in that the anterior and intermediate zygomatic ridges are confluent and the posterior zygomatic ridge is absent". This statement has been challenged by Smith et al. (2001: 36), who stated: "The term 'confluent' used by Wible and Rougier (2000) seems not adequate because it could imply that the two ridges form finally one large ridge, which is not the case. The specimen PSS-MAE 101 shows the two first zygomatic ridges well arched and individualized (Wible and Rougier 2000: fig. 2). Also in ZPAL MgM-I/41 (see Kielan-Jaworowska and Gambaryan 1994: figs. 1D, E) the separate zygomatic ridges are distinctly seen. Concerning the posterior zygomatic ridge, well preserved in the specimen IMM 96BM-I/4 [of *Kryptobaatar mandahuensis*] from Bayan Mandahu (Inner Mongolia), it has not exactly the same aspect as the first two. It has a somewhat more ventral position, posteriorly to the glenoid fossa. It is shorter and relatively less marked than in *Nemegtbaatar*, *Chulsanbaatar*, and *Catopsbaatar*, and therefore gives an impression that it is a depression. [...] In conclusion the three zygomatic ridges seem present in *Kryptobaatar mandahuensis* as in other djadochtatherians."

We agree with the criticism of Smith et al. (2001) and we wish to explain that the statement of Wible and Rougier (2000) on the absence of the posterior zygomatic ridge in *Kryptobaatar* may be related to terminological confusion.

The term zygomatic ridge was introduced by Kielan-Jaworowska (1971) for the anteriormost ridge that occurs on the zygomatic arch in multituberculates and is well visible in ventral and lateral views of well-preserved multituberculate skulls, in which the anterior part of the zygomatic arch is preserved.

Gambaryan and Kielan-Jaworowska (1995) designated the anterior ridge on the zygomatic arch the "anterior zygomatic ridge", the next one "intermediate zygomatic ridge", and the third (the smallest of all, situated on the posterior wall of the skull above the glenoid fossa, and often hardly discernible) the "posterior zygomatic ridge". They interpreted all of these as related to the masseter musculature (see our Fig. 7).

The separation of the origin of the superficial masseter into two parts (anterior and posterior), characteristic of multituberculates, is unique among mammals (Gambaryan and Kielan-Jaworowska 1995). In multituberculates the scars of the origin of these two muscles form distinct semicircles or half-ovals, surrounded by rounded ridges (anterior and intermediate zygomatic ridges), which do not occur in other mammals.

The third "ridge" recognized by Gambaryan and Kielan-Jaworowska (1995), designated the posterior zygomatic ridge, is a muscle scar, rarely surrounded by a distinct ridge-like structure and may be recognized only as a slight concavity, as often are the muscle scars in other mammals. It has been recognized only as a concavity in *Kryptobaatar mandahuensis* by Smith (2001). Therefore the statement of Wible and Rougier (2000) on the absence of the posterior zygomatic ridge in *Kryptobaatar* may be related to the terminological confusion, as indeed the posterior zygomatic "ridge" in *Kryptobaatar* is only a muscle scar, in which the surrounding ridge may be absent. That is why in the caption to Fig. 7, when referring to the posterior zygomatic "ridge" we use quotation marks. This muscle scar is present in all well-preserved djadochtatherioid skulls in which the relevant region has been preserved.

The complete zygomatic arches in multituberculates have only rarely been preserved except for the Djadochtatherioidea. Anterior and intermediate zygomatic ridges are clearly present in all the members of Djadochtatherioidea, in which the zygomatic arches are preserved. They are the weakest in *Sloanbaatar mirabilis* (Kielan-Jaworowska 1971) and most prominent in *Catopsbaatar catopsaloides,* described by Gambaryan and Kielan-Jaworowska (1995) and herein (Figs. 7, 11C), as well as in *Djadochtatherium matthewi* (Fig. 11B).

The anterior zygomatic ridge has often been preserved and figured in various multituberculate skulls, beginning with Marsh (1887: pl. VII: 1 and 4, who figured it for *Allodon* [now *Ctenacodon*] *laticeps*). In the 20th century it has been figured, for example: by Simpson (1929: pl. II: 3 and pl. III: 1 for *Ctenacodon laticeps*); by Sloan and Van Valen (1965: fig. 3 for *Mesodma thompsoni*, and fig. 5 for *Stygimys kuszmauli*); by Hahn (1969: fig. 9 and pl. 6 for *Meketichoffatia krausei*—referred to as *Paulchoffatia delgadoi*); by Hahn (1977: fig. 2 and pl. 1: 1a for *Pseudobolodon oreas*, and Hahn 2001: several photographs of the same species); by Kielan-Jaworowska et al. (1987: pl. 3: 3c for *Monobaatar mimicus*, and pl. 21: 2a, 2c for *Arginbaatar dimitrievae*); by Miao (1988: fig. 18 for *Lambdopsalis bulla*); by Hahn and Hahn (1998: pl. 1: 2a for *Kielanodon hopsoni*); by Engelmann and Callison (1999: several photographs and drawings of *Glirodon grandis*); by Hahn (2001: pl. 3: 2 for *Renatodon amalthea*), and in several others.

Anterior and intermediate zygomatic ridges have been preserved also in other multituberculate groups. Broom (1914: pls. XI and XII) figured the skull of *Taeniolabis taoensis*, in which the two zygomatic ridges are present. These have also been observed by Yaoming Hu (personal communication, letter of 15 January 2005), who examined the specimen of *T. taoensis* AMNH 16321 on our request, and confirmed the presence of two zygomatic ridges. The first author recognized the two zygomatic ridges in the holotype skull of *Kogaionon ungureanui* from Romania, which on the request of the late Costin Rădulescu was photographed in ZPAL in Warsaw in June 1997.

The presence of two zygomatic ridges in Ptilodontoidea requires a study. James Hopson, who on our request examined the type of *Ptilodus montanus* (AMNH 35490), wrote (letter of April 7, 2005): "This specimen [AMNH 35490] definitely lacks the anterior zygomatic ridge on the lateral face of the maxilla behind the infraorbital foramen. Rather it has a broad ventral shelf on the maxilla, which is bounded on the ventrolateral margin of the zygoma by a distinct ridge [...] I interpret the above as indicating that the anterior superficial masseter attached to the ventral surface of the zygoma, but did not extend on to its lateral surface.[...] Concerning the intermediate zygomatic ridge [...] on both sides of the type of *P. montanus* there is a possible ridge, actually more of a change in angulation of the lateral surface, that begins at the posterolateral margin of the glenoid and extends forward to a position shortly in front of the glenoid." Examination of the exquisite cast of AMNH 35490 in ZPAL cast collections, and figures of this specimen in Hopson et al. (1989) convinced us that there are indeed two zygomatic ridges in this taxon, albeit somewhat differently distributed than in other multituberculates. The anterior zygomatic ridge is very obvious on the right side of the cast of the AMNH 35490 and the muscle scar is situated more ventrally than in djadochtatherioideans, but a small part of the scar enters the lower part of the lateral wall of the zygomatic arch; the anterior zygomatic ridge is observable in the lateral views of the skull, placed very low on the zygomatic arch. In *Ectypodus tardus* figured by Sloan (1979: fig. 1, PU 14724), the two zygomatic ridges might be present. James A. Hopson, who examined this skull on our request (letter of 7 April, 2005) informed us that the arrangement of zygomatic ridges in *Ectypodus* is similar to that in *Ptilodus.* According to James A. Hopson the third zygomatic "ridge" is not discernible in *Ptilodus* and *Ectypodus*.

Given that the masticatory strategy of Ptilodontoidea was very different from those in other multituberculate lines

(Krause 1982; Wall and Krause 1992) there is no wonder that the two parts of the superficial masseter acted differently.

The most important was, however, the information received from Gerhard Hahn (letters of 18 and 30 January, 2005), who on our request examined some undescribed fragments of paulchoffatiid skulls from the Kimmeridgian of Portugal. In one of them, with provisional working number Mam 149/76, the zygomatic arch is relatively well preserved, showing the anterior and intermediate zygomatic ridges. The anterior one is large and delimited by the zygomatic ridge as in other paulchoffatiid genera discussed above. The intermediate "zygomatic ridge" is a half-oval concave scar, restricted to the ventral half of the zygomatic arch, and not delimited by an obvious ridge. Gerhard Hahn (in the first mentioned letter) commented that in the Paulchoffatiidae pars posterior of masseter superficialis was apparently less strongly developed than in cimolodontan multituberculates, but the basic arrangement of the muscles was the same.

Gambaryan and Kielan-Jaworowska (1995), who studied the masticatory musculature in several genera of Djadochtatherioidea (referred to by them as Taeniolabidoidea) stated (p. 52): "The prominent anterior and intermediate zygomatic ridges, on the zygomatic process of maxilla and squamosal respectively are unique for multituberculates and we regard the possession of them as a multituberculate autapomorphy. In therian mammals if a ridge occurs, it is single and it is placed on the jugal, rather than on the maxilla or squamosal (e.g., as in *Canis*, see Evans and Christensen 1979)." In the course of this study we examined the skulls or illustrations of multituberculate zygomatic arches belonging to various groups and in all of them (in which the zygomatic arches have been preserved) we confirmed the presence of two distinct muscle scars for two parts of masseter superficialis. Only in the oldest (Kimmeridgian) Paulchoffatiidae, is the posterior of the two scars devoid of a distinct ridge.

In light of the above discussed data we confirm and extend the conclusion of Gambaryan and Kielan-Jaworowska (1995) that the presence of anterior and intermediate zygomatic ridges, on the outer surface of the zygomatic arch, is an autapomorphy of Multituberculata. We regard the separation of the masseter superficialis into two parts, the origins of which leave on the lateral (or ventrolateral) wall of the zygomatic arch the scars more prominent than in any other mammal group, as another multituberculate autapomorphy.

Acknowledgements

Rinchen Barsbold (Paleontological Center of the Mongolian Academy of Sciences, Ulaanbaatar) lent us the specimen of *Catopsbaatar* PM 120/107, described in this paper. Mahito Watabe (Hayashibara Museum of Natural Sciences, Okayama, Japan) sent to ZK-J, in October, 1996, the photographs of the skull of *Djadochtatherium* found at the locality of Tögrög during the 1994 Joint Palaeontological Expedition of the Hayashibara Museum of Natural Sciences and Mongolian Paleontological Center, with permission to comment on this specimen. Robert Presley, John R. Wible, and Richard L. Cifelli, reviewed the submitted manuscript and offered most useful suggestions. Their comments and discussion with them greatly contributed to the improvement of the paper. Gerhard Hahn, James A. Hopson, and Yoaming Hu examined some specimens at our request and provided useful information, used in this paper. The conventional photographs of the specimens housed in ZPAL, as well as part of the photographs of PM 120/107 were taken by Marian Dziewiński (ZPAL), some of the photographs of PM 120/107 by JHH, while the specimens housed in PIN were taken by AL with the technical assistance of Pavel Parkhaev and Alexander Mazin. The SEM micrographs were taken by Cyprian Kulicki, while Aleksandra Hołda (both from ZPAL) mounted all the figures and processed them in the computer; Bogusław Waksmundzki (Warsaw) made the drawings published as Figs. 6–8, after pencil sketches by ZK-J, and Aleksandra Hołda made the drawing in Fig. 11, after our pencil sketches. The work of ZK-J was funded by the Institute of Paleobiology, Polish Academy of Sciences, Warsaw, that of JHH by the University of Oslo, and that of AL by the Paleontological Institute, Russian Academy of Sciences, Moscow, and grants of the Russian Foundation for Basic Research (project no. 04-04-49637), the Board of the President of the Russian Federation (project nos. NSh-1840.2003.4 and MK-726.2004.4), and Russian Foundation for Science Support. To all these persons and institutions we express our sincere thanks and gratitude.

References

Averianov, A.O. 1997. New Late Cretaceous mammals of southern Kazakhstan. *Acta Palaeontologica Polonica* 42: 243–256.

Barghusen, H. 1986. On the evolutionary origin of the therian tensor veli palatini and tensor tympani muscles. *In*: N. Hotton, P.D. MacLean, J.J. Roth, and E.C. Roth (eds.), *The Ecology and Biology of Mammal-like Reptiles*, 253–262. Smithsonian Institution Press, Washington, D.C.

Barsbold, R., Voronin, J., and Zhegallo, V.I. [Žegallo, V.I.] 1971. On the work of the Soviet-Mongolian Palaeontological Expeditions in 1969–1970 [in Russian]. *Paleontologičeskij žurnal* 2: 139–143.

Benton, J.M. 2000. Mongolian place names and stratigraphic terms. *In*: M.J. Benton, M.A., Shishkin, D.M. Unwin, and E.N. Kurochkin (eds.), *The Age of Dinosaurs in Russia and Mongolia*, xxii–xxviii. Cambridge University Press, Cambridge.

Broom, R. 1914. On the structure and affinities of the Multituberculata. *Bulletin of the American Museum of Natural History* 33: 115–134.

Cope, E.D. 1884. The Tertiary Marsupialia. *American Naturalist* 18: 686–697.

Crompton, A.W. 1958. The cranial morphology of a new genus and species of ictidosauran. *Proceedings of the Zoological Society of London* 130: 183–215.

Engelmann, G.F. and Callison, G. 1999. *Glirodon grandis*, a new multituberculate mammal from the Upper Jurassic Morrison Formation. *In*: D.D. Gillette (ed.), *Vertebrate Paleontology in Utah*, 161–177. Utah Geological Survey, Miscellaneous Publication 99-1, Salt Lake City.

Evans, A.R. 1995. *Miller's Anatomy of the Dog, 3rd Edition*. 1113 pp. W.B. Saunders Company, Philadelphia.

Evans, H.E. and Christensen, G.C. 1979. *Miller's Anatomy of the Dog*. 1181 pp. W.B. Saunders Company, Philadelphia.

Fox, R.C. and Meng, J. 1997. An X-radiographic and SEM study of the osseous inner ear of multituberculates and monotremes (Mammalia): implications for mammalian phylogeny and evolution of hearing. *Zoological Journal of the Linnean Society* 121: 249–291.

Gambaryan, P.P. and Kielan-Jaworowska, Z. 1995. Masticatory musculature of Asian taeniolabidoid multituberculate mammals. *Acta Palaeontologica Polonica* 40: 45–108.

Gradziński, R. and Jerzykiewicz, T. 1972. Additional geographical and geological data from the Polish-Mongolian Palaeontological Expeditions. *In*: Z. Kielan-Jaworowska (ed.), Results of the Polish-Mongolian Palaeontological Expeditions, part IV. *Palaeontologia Polonica* 27: 17–30.

Gradziński, R., Kielan-Jaworowska, Z., and Maryańska, T. 1977. Upper Cretaceous Djadokhta, Barun Goyot and Nemegt formations of Mongolia, including remarks on previous subdivisions. *Acta Geologica Polonica* 27: 281–318.

Granger, W. and Simpson, G.G. 1929. A revision of the Tertiary Multituberculata. *Bulletin of the American Museum of Natural History* 56: 601–676.

Hahn, G. 1969. Beiträge zur Fauna der Grube Guimarota nr. 3. Die Multituberculata. *Palaeontographica Abteilung A* 133: 1–100.

Hahn, G. 1977. Neue Schädel-Reste von Multituberculaten (Mamm.) aus dem Malm Portugals. *Geologica et Paleontologica* 11: 161–186.

Hahn, G. 1985. Zum Bau des Infraorbital-Foramens bei den Paulchoffatiidae (Multituberculata, Ober-Jura). *Berliner geowissenschafliche Abhandlungen A* 60: 5–27.

Hahn, G. 2001. Neue Beobachtungen an Schädel-Resten von Paulchoffatiidae (Multituberculata; Ober-Jura). *Geologica et Paleontologica* 35: 121–143.

Hahn, G. and Hahn, R. 1998. Neue Beobachtungen an Plagiaulacoidea (Multituberculata) des Ober-Juras 1. Zum Zahn-Wechsel bei *Kielanodon*. *Berliner geowissenschafliche Abhandlungen E* 28: 1–7.

Hopson, J.A., Kielan-Jaworowska, Z., and Allin, E.F. 1989. The cryptic jugal of multituberculates. *Journal of Vertebrate Paleontology* 9: 201–209.

Hurum, J.H. 1994. The snout and orbit of Mongolian multituberculates studied by serial sections. *Acta Palaeontologica Polonica* 39: 181–221.

Hurum, J.H. 1997. *Cranial Structure and Relationships of Mongolian Late Cretaceous multituberculate mammals*. 169 pp. Ph.D. dissertation, Paleontological Museum, University of Oslo, Oslo.

Hurum, J.H. 1998a. The braincase of two Late Cretaceous Asian multituberculates studied by serial sections. *Acta Palaeontologica Polonica* 43: 21–52.

Hurum, J.H. 1998b. The inner ear of two Late Cretaceous multituberculate mammals, and its implications for multituberculate hearing. *Journal of Mammalian Evolution* 5: 65–94.

Hurum, J.H., Presley, R., and Kielan-Jaworowska, Z. 1996. The middle ear in multituberculate mammals. *Acta Palaeontologica Polonica* 41: 253–275.

Kermack, K.A. 1963. The cranial structure of the triconodonts. *Philosophical Transactions of the Royal Society of London* 246: 83–103.

Kielan-Jaworowska, Z. 1970. New Upper Cretaceous multituberculate genera from Bayn Dzak, Gobi Desert. *In*: Z. Kielan-Jaworowska (ed.), Results of the Polish-Mongolian Palaeontological Expeditions, part II. *Palaeontologia Polonica* 21: 35–49.

Kielan-Jaworowska, Z. 1971. Skull structure and affinities of the Multituberculata. *In*: Z. Kielan-Jaworowska (ed.), Results of the Polish-Mongolian Palaeontological Expeditions, part III. *Palaeontologia Polonica* 25: 5–41.

Kielan-Jaworowska, Z. 1974. Multituberculate succession in the Late Cretaceous of the Gobi Desert (Mongolia). *In*: Z. Kielan-Jaworowska (ed.), Results of the Polish-Mongolian Palaeontological Expeditions, part V. *Palaeontologia Polonica* 30: 23–44.

Kielan-Jaworowska, Z. 1994. A new generic name for the multituberculate mammal "*Djadochtatherium*" *catopsaloides*. *Acta Palaeontologica Polonica* 39: 134–136.

Kielan-Jaworowska, Z. and Barsbold, R. 1972. Narrative of the Polish-Mongolian Palaeontological Expeditions 1967–1971. *In*: Z. Kielan-Jaworowska (ed.), Results of the Polish-Mongolian Palaeontological Expeditions, part IV. *Palaeontologia Polonica* 27: 5–16.

Kielan-Jaworowska, Z. and Dashzeveg, D. 1978. New Late Cretaceous locality in Mongolia and a description of a new multituberculate. *Acta Palaeontologica Polonica* 23: 115–130.

Kielan-Jaworowska, Z. and Gambaryan, P.P. 1994. Postcranial anatomy and habits of Asian multituberculate mammals. *Fossils & Strata* 36: 1–92.

Kielan-Jaworowska, Z. and Hurum, J.H. 1997. Djadochtatheria—a new suborder of multituberculate mammals. *Acta Palaeontologica Polonica* 42: 201–242.

Kielan-Jaworowska, Z. and Hurum, J.H. 2001. Phylogeny and systematics of multituberculate mammals. *Palaeontology* 44: 389–429.

Kielan-Jaworowska, Z. and Sloan, R.E. 1979. *Catopsalis* (Multituberculata) from Asia and North America and the problem of taeniolabidid dispersal in the Late Cretaceous. *Acta Palaeontologica Polonica* 24: 187–197.

Kielan-Jaworowska, Z., Cifelli, R.L., and Luo Z.-X. 2004. *Mammals from the Age of Dinosaurs: Origins, Evolution, and Structure*. 630 pp. Columbia University Press, New York.

Kielan-Jaworowska, Z., Dashzeveg, D., and Trofimov, B.A. 1987. Early Cretaceous multituberculates from Mongolia and a comparison with Late Jurassic forms. *Acta Palaeontologica Polonica* 32: 3–47.

Kielan-Jaworowska, Z., Hurum, J.H., and Badamgarav, D. 2003. An extended range of multituberculate *Kryptobaatar* and the distribution of mammals in the Upper Cretaceous of the Gobi Desert. *Acta Palaeontologica Polonica* 49: 161–166.

Kielan-Jaworowska, Z., Hurum, J.H., Currie, P.J., and Barsbold, R. 2002. New data on anatomy of the Late Cretaceous multituberculate mammal *Catopsbaatar*. *Acta Palaeontologica Polonica* 47: 557–560.

Kielan-Jaworowska, Z., Novacek, M.J., Trofimov, B.A., and Dashzeveg, D. 2000. Mammals from the Mesozoic of Mongolia. *In*: M.J. Benton, M.A. Shishkin, D.M. Unwin, and E.N. Kurochkin (eds.), *The Age of Dinosaurs in Russia and Mongolia*, 573–626. Cambridge University Press, Cambridge.

Kielan-Jaworowska, Z., Presley, R., and Poplin, C. 1986. The cranial vascular system in taeniolabidoid multituberculate mammals. *Philosophical Transactions of the Royal Society of London B* 313: 525–602.

Krause, D.W. 1982. Jaw movement, dental function, and diet in the Paleocene multituberculate *Ptilodus*. *Paleobiology* 8: 265–281.

Kurochkin, E.N. and Barsbold, R. 2000. The Russian-Mongolian expeditions and research in vertebrate palaeontology. *In*: M.J. Benton, M.A. Shishkin, E.N. Kurochkin, and D.M. Unwin (eds.), *The Age of Dinosaurs in Russia and Mongolia*, 235–255. Cambridge University Press, Cambridge.

Marsh, O.C. 1887. American Jurassic mammals. *American Journal of Science* 33: 326–348.

Matthew, W.D. and Granger, W. 1925. Fauna and correlation of the Gashato Formation of Mongolia. *American Museum Novitates* 189: 1–12.

Matthew, W.D., Granger, W., and Simpson, G.G. 1928. Paleocene multituberculates from Mongolia. *American Museum Novitates* 331: 1–4.

Matthew, W.D., Granger, W., and Simpson, G.G. 1929. Additions to the fauna of the Gashato Formation of Mongolia. *American Museum Novitates* 376: 1–12.

McKenna, M.C. 1975. Toward a phylogenetic classification of the Mammalia. *In*: W.P. Luckett and F.S. Szalay (eds.), *Phylogeny of the Primates*, 21–46. Cambridge University Press, Cambridge.

McKenna, M.C. and Bell, S.K. 1997. *Classification of Mammals Above the Species Level*. 631 pp. Columbia University Press, New York.

Miao, D. 1988. Skull morphology of *Lambdopsalis bulla* (Mammalia, Multituberculata). *Contributions to Geology, University of Wyoming, Special Paper* 4: 1–104.

Meinertz, T. 1941. Das oberflächliche Facialisgebiet der Nager. *Zoologische Jahrbucher, Abteilung für Anatomie und Ontogenie der Tiere* 67: 119–270.

Rougier, G.W., Novacek, M.J., and Dashzeveg, D. 1997. A new multituberculate from the Late Cretaceous locality Ukhaa Tolgod, Mongolia. Considerations on multituberculate relationships. *American Museum Novitates* 3193: 1–26.

Rougier, G.W., Wible, J.R., and Hopson, J.A. 1992. Reconstruction of the cranial vessels in the Early Cretaceous mammal *Vincelestes neuquenianus*: implications for the evolution of the mammalian cranial system. *Journal of Vertebrate Paleontology* 12: 188–216.

Rougier, G.W., Wible, J.R., and Novacek, M.J. 1996. Middle-ear ossicles of *Kryptobataar dashzevegi* (Mammalia, Multituberculata): implications for mammaliamorph relationships and evolution of the auditory apparatus. *American Museum Novitates* 3187: 1–43.

Schaller, O. (ed.) 1992. *Illustrated Veterinary Anatomy Nomenclature*. 614 pp. Ferdinand Enke Verlag, Stuttgart.

Simmons, N.B. 1987. A revision of *Taeniolabis* (Mammalia, Multituberculata) with a new species from the Puercan of Eastern Montana. *Journal of Paleontology* 61: 794–808.

Simmons, N.B. and Miao, D. 1986. Paraphyly of *Catopsalis* (Mammalia: Multituberculata) and its biogeographic implications. *Contributions to Geology, University of Wyoming, Special Paper* 3: 87–94.

Simpson, G.G. 1925. A Mesozoic mammal skull from Mongolia. *American Museum Novitates* 201: 1–11.

Simpson, G.G. 1926. Mesozoic Mammalia. IV. The multituberculates as living animals. *American Journal of Science* 11: 228–250.

Simpson, G.G. 1929. American Mesozoic Mammalia. *Memoirs of the Peabody Museum of Yale University* 3: 1–235.

Simpson, G.G. 1937. Skull structure of the Multituberculata. *Bulletin of the American Museum of Natural History* 73: 727–763.

Sloan, R.E. 1979. Multituberculata. *In*: R.W. Fairbridge and D. Jablonski (eds.), *The Encyclopedia of Paleontology*, 492–498. Dowden, Hutchinson & Ross, Stroudsburg.

Sloan, R.E. and Van Valen, L. 1965. Cretaceous mammals from Montana. *Science* 148: 220–227.

Smith, T., Guo, D.-Y., and Sun, Y. 2001. A new species of *Kryptobaatar* (Multituberculata): the first Late Cretaceous mammal from Inner Mongolia (P.R. China). *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre*, Supplement 71: 29–50.

Wall, C.E. and Krause, D.W. 1992. A biomechanical analysis of the masticatory apparatus of *Ptilodus* (Multituberculata). *Journal of Vertebrate Paleontology* 12: 172–187.

Webster, D. 1996. Dinosaurs of the Gobi. Unearthing a fossil trove. *National Geographic* 190 (1): 70–89.

Wible, J.R. and Hopson, J.A. 1993. Basicranial evidence for early mammal phylogeny. *In*: F.S. Szalay, M.J. Novacek, and M.C. McKenna (eds.), *Mammal Phylogeny: Mesozoic Differentiation, Multituberculates, Monotremes, Early Therians, and Marsupials*, 45–62. Springer-Verlag, New York.

Wible, J.R. and Hopson, J.A. 1995. Homologies of the prootic canal in mammals and non-mammalian cynodonts. *Journal of Vertebrate Paleontology* 15: 331–336.

Wible, J.R. and Rougier, G. 2000. The cranial anatomy of *Kryptobaatar dashzevegi* (Mammalia, Multituberculata), and its bearing on the evolution of mammalian characters. *Bulletin of the American Museum of Natural History* 247: 1–124.