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A new species of *Kryptobaatar* (Multituberculata): the first Late Cretaceous mammal from Inner Mongolia (P. R. China)¹

by Thierry SMITH, Dian-Yong GUO & Yan SUN

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Abstract

Multituberculates are the best represented mammals of the Late Cretaceous in Asia and most of them are from Outer Mongolia. The djadochtatherioidean multituberculate *Kryptobaatar mandahuensis* n. sp. is described on the basis of two skulls from the Upper Cretaceous locality of Bayan Mandahu (Inner Mongolia, People's Republic of China). The main characters that differentiate it from the type species *K. dashzevegi* KIELAN-JAWOROWSKA, 1970 are: the base of the zygomatic arch situated at the level of the anterior root of the P4 and the narrow anterior extent of the orbit, the "V" shape of the palatomaxillary suture between the two major palatine foramina, the high and thick part of the dentary under the mandibular diastema, the long and low part of the dentary under the mandibular notch, the anteroposteriorly short coronoid process, the presence of 5 cusps on the middle row of M1 and on the labial row of m1, the long p4, the high ratio p4:m1 length, and the robust i1. The presence of this species in Inner Mongolia extends the palaeogeographical distribution area of the djadochtatherioideans to the southern part of the Gobi Basin. Nevertheless, morphological differences between *K. mandahuensis* from Inner Mongolia and *K. dashzevegi* from Outer Mongolia suggest a palaeogeographical isolation within the Djadochtatherioidea group during the Campanian.

Key words: Mammals, Multituberculata, Djadochtatherioidea, Late Cretaceous, Inner Mongolia.

Résumé

Les multituberculés sont les mammifères les mieux représentés du Crétacé supérieur d'Asie et la plupart d'entre eux sont connus de Mongolie extérieure. Le multituberculé djadochtatherioïde *Kryptobaatar mandahuensis* n. sp. est décrit sur base de deux crânes découverts dans le Crétacé supérieur de Bayan Mandahu (Mongolie intérieure, République Populaire de Chine). Les caractères principaux qui différencient cette espèce de l'espèce-type *K. dashzevegi* KIELAN-JAWOROWSKA, 1970 sont: la base de l'arcade zygomatique située au niveau de la racine antérieure de la P4 et la partie antérieure de l'orbite étroite, la forme en V de la suture palatomaxillaire entre les deux foraments palatins majeurs, le dentaire haut et épais sous le diastème mandibulaire, le dentaire long et bas sous l'incisure mandibulaire, le processus coronoïde court antéro-postérieurement, la présence de 5 cuspidés sur la rangée médiane de la M1 et sur la rangée labiale de la m1, la longue p4, le rapport longueur p4/m1 élevé et la robuste i1. La présence de cette espèce en Mongolie intérieure permet d'étendre l'aire de répartition paléogéographique des djadochtatherioïdeans jusqu'au sud du Bassin du Gobi. Toutefois, les différences morphologiques entre *K. mandahuensis* de Mongolie intérieure et *K. dashzevegi* de Mongolie extérieure sont en faveur d'un isolement paléogéographique au sein du groupe des Djadochtatherioidea durant le Campanien.

Mots-clés: Mammifères, Multituberculés, Djadochtatherioidea, Crétacé supérieur, Mongolie intérieure.

Introduction

Many Cretaceous mammal species were described from the Mongolian part of the Gobi desert (see KIELAN-JAWOROWSKA *et al.*, 2000, for an overview), most of them collected from the Djadokhta Formation at Bayn Dzak (American-Mongolian expeditions in 1920s, see SIMPSON, 1925, 1928; Polish-Mongolian expeditions in 1963 to 1971, see KIELAN-JAWOROWSKA, 1970, 1974) and from Ukhaa Tolgod (American-Mongolian expeditions since the 1990s, see ROUGIER *et al.*, 1997; WIBLE & ROUGIER, 2000). However, knowledge on Late Cretaceous mammals from the Chinese portion of the Gobi desert was based on an axis of *Khuduklestes bohlini* NESSOV *et al.*, 1994 discovered in 1929-1930 by the Sino-Swedish expedition at Tsondolein-Khuduk in the Gansu Province (BOHLIN, 1953, p. 41-42, fig. 20). More recently, the Sino-Canadian expedition (1987 to 1990) reported the discovery of several mammalian skulls in Bayan Mandahu, Inner Mongolia (DONG, 1993, p. 2000; JERZYKIEWICZ *et al.*, 1993, p. 2188-2189) 250 km north-east from Tsondolein-Khuduk (Fig. 1). The specimens are yet undescribed so far.

The two skulls of multituberculate mammals described below were discovered during the Sino-Belgian expedition in Inner Mongolia at Bayan Mandahu in 1996 (Fig. 1). A nearly complete skeleton of a large multituberculate and four other skulls and postcranial remains have also been found at Bayan Mandahu, in 1995 and in 1999 respectively, and will be described later.

The monophyletic order Multituberculata is represented by 86 genera belonging to at least 17 families (see KIELAN-JAWOROWSKA & HURUM, 2001) distributed in the whole world except the Australian region and Antarctica. Two large groups are distinguished within the Multituberculata: the paraphyletic suborder "Plagiaulacida" *sensu* KIELAN-JAWOROWSKA & HURUM (2001) which is distributed from the Middle Jurassic (Bathonian of England, FREEMAN, 1976, 1979; see also BUTLER, 2000) to the Early Cretaceous, and the apparently monophyletic suborder Cimolodonta which is distributed from the Early Cretaceous to the Late Eocene

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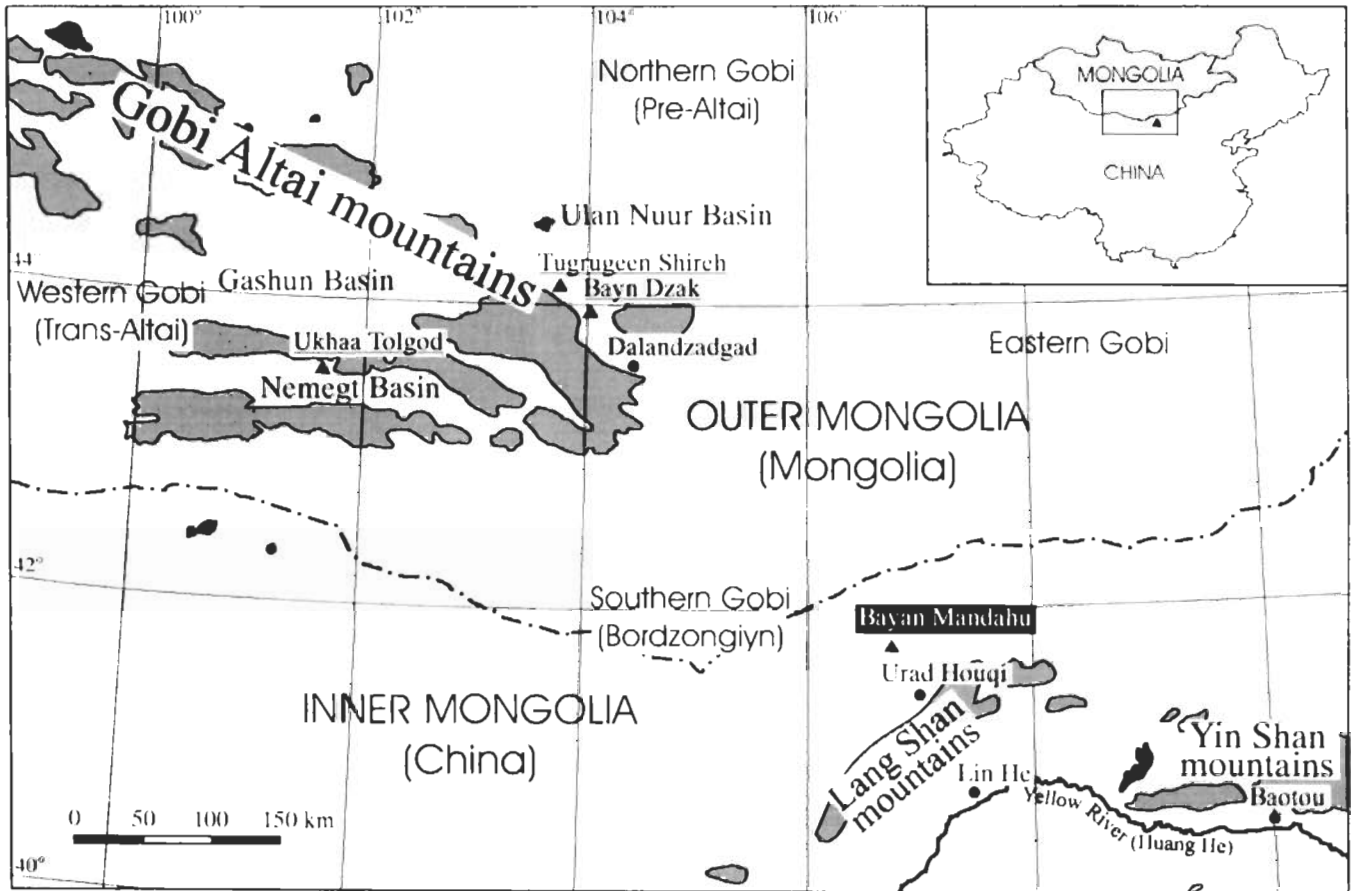


Fig. 1 — Map of the Gobi Basin showing the Inner Mongolian locality of Bayan Mandahu, which has provided the material of *Kryptobaatar mandahuensis* and the Outer Mongolian localities of Bayn Dzak, Tugrugeen Shireh and Ukhaa Tolgod, which have provided the material of *K. dashzevegi*.

(specifically Priabonian, “Chadronian” of Wyoming and Saskatchewan, KRISHTALKA *et al.*, 1982; “Chadronian” of Nebraska, OSTRANDER, 1984). The plagiulacidan multituberculates possess many plesiomorphic characters such as, notably, three upper incisors, an upper premolariform canine (if present), five to four upper premolars, four to three lower premolars, and the absence of the third lingual row of cusps in M1 but an incipient postero-lingual ridge may be present. On the other hand, the cimolodont multituberculates differ by several apomorphies, the most typical of which are: loss of the first upper incisor, a maximum of four upper premolars, loss of the two first lower premolars, third lower premolar peg-like or lost, increase or reduction in size of p4, and development of a third lingual row of cusps in M1. Most of the genera are known only from isolated teeth or fragments of jaws, and thus, during many years, the phylogenetic relationships of the multituberculates, which share several homoplastic characters with rodents, were poorly understood. The study of skulls and postcranial bones of Mongolian Late Cretaceous cimolodontan multituberculates, essentially during the last thirty years by Zofia KIELAN-JAWOROWSKA and co-workers, has permitted to describe more precisely the particular anatomy of this order (e.g. KIELAN-JAWOROWSKA, 1969, 1971, 1979, 1998; KIELAN-JAWOROWSKA & GAMBARYAN, 1994). Exceptional discoveries and new detailed anatomical studies have permitted recently to better understand the multituberculate rela-

tionships (SERENO & MCKENNA, 1995; KIELAN-JAWOROWSKA, 1996; ROUGIER *et al.*, 1996; GAMBARYAN & KIELAN-JAWOROWSKA, 1997; BUTLER, 2000; WIBLE & ROUGIER, 2000; KIELAN-JAWOROWSKA & HURUM, 2001). Multituberculates are generally considered as more basal than archaic therians, symmetrodonts, marsupials and placentals, but more derived than monotremes. What some authors disagree about is the relative position of the triconodonts in comparison with the multituberculates. The same anatomical characters treated in phylogenetic analyses are considered as homoplasies or synapomorphies according to the authors. Triconodonts are situated between multituberculates and symmetrodonts (ROUGIER *et al.*, 1996, WIBLE & ROUGIER, 2000) or considered as more primitive than multituberculates and also monotremes (HU *et al.*, 1997; Ji *et al.*, 1999) in the early mammal phylogeny.

With the exception of the genus *Buginbaatar* KIELAN-JAWOROWSKA & SOCHAVA, 1969, all the Mongolian Late Cretaceous multituberculates belong to one monophyletic group: the Djadochtatherioidea KIELAN-JAWOROWSKA & HURUM, 2001. This superfamily includes the genera: *Djadochtatherium* SIMPSON, 1925; *Kryptobaatar* KIELAN-JAWOROWSKA, 1970; *Kamptobaatar* KIELAN-JAWOROWSKA, 1970; *Sloanbaatar* KIELAN-JAWOROWSKA, 1971; *Chulsanbaatar* KIELAN-JAWOROWSKA, 1974; *Bulganbaatar* KIELAN-JAWOROWSKA, 1974; *Nemegtbaatar* KIELAN-JAWOROWSKA, 1974; *Catopsbaatar* KIELAN-JAWOROWSKA, 1994; *Tom-*

baatar ROUGIER *et al.*, 1997; and *Nessovbaatar* KIELAN-JAWOROWSKA & HURUM, 1997. The two skulls described here from the southern Gobi desert in China belong to the genus *Kryptobaatar*. The comparison with material from different localities of Mongolia (Fig. 1) gives us new information about the anatomy and the phylogeny of this Asiatic group, but also about the palaeogeography of the Gobi desert area during the Late Cretaceous.

Geographic and geological setting

The Gobi Basin (term redefined by JERZYKIEWICZ & RUSSELL, 1991, p. 346) is a large plateau in east central Asia, between 900 and 1500 metres high. It is bordered by the Altai, Khangai and Khentei mountains to the north in Outer Mongolia (Mongolia) and by the Lang Shan and Yin Shan mountains to the south in Inner Mongolia (North China). The Bayan Mandahu fossil locality takes its name from the nearest village, a small shepherd station situated 50 km north-west from the city of Urad Houqi in the southern part of the Gobi Basin near the Lang Shan mountains in China (Fig. 1).

Exposures of the Bayan Mandahu redbeds extend over 12 km length and 2 km width ($41^{\circ} 43-48' N$, $106^{\circ} 42-45' E$; Fig. 2) and are generally correlated with the Campanian age Djadokhta Formation of south-central Mongolia, 350 km to the north-west (JERZYKIEWICZ *et al.*, 1993). These more or less horizontal red sandstone deposits have been interpreted as the result of an eolian sedimentary environment which dominated in both areas (JERZYKIEWICZ *et al.*, 1993). In Bayan Mandahu, EBERTH (1993) showed also locally an alluvial and lacustrine component representing a proximal to distal depositional gradient in a semi-arid climate (EBERTH, 1993). Further information on the locality can be found in GODEFROIT *et al.* (1999).

Abbreviations

- BM: Bayan Mandahu.
 GI: Geological Institute, Mongolian Academy of Sciences, Ulaan Baatar.
 IMM: Inner Mongolian Museum, Hohhot.
 IRSNB: Institut royal des Sciences naturelles de Belgique / Koninklijk Belgisch Instituut voor Natuurwetenschappen, Brussels.
 PSS (SPS): Palaeontological and Stratigraphic Section of the Geological Institute, Mongolian Academy of Sciences, Ulaan Baatar.
 MAE: Mongolian-American Museum Expedition.
 SBDE: Sino-Belgian Dinosaur Expedition.
 ZPAL: Institute of Paleobiology, Polish Academy of Sciences, Warsaw.

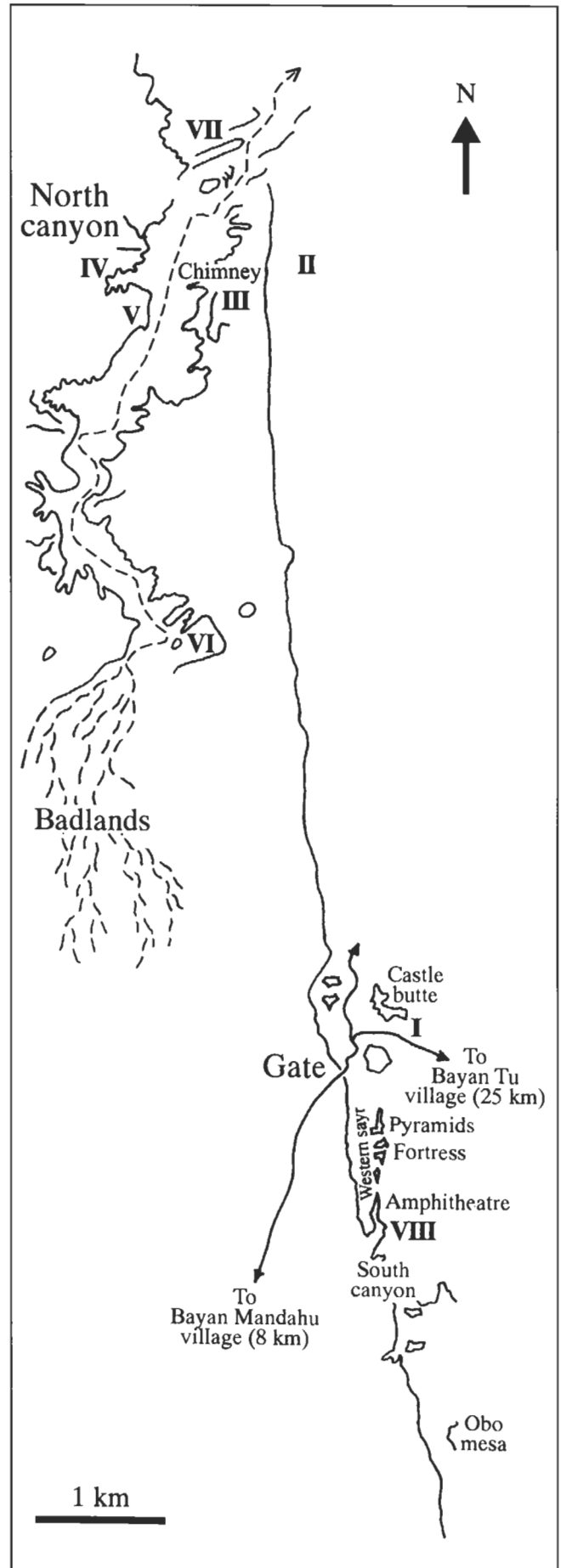


Fig. 2 — The Bayan Mandahu area (modified from JERZYKIEWICZ *et al.*, 1993; EBERTH, 1993) with the precise fossil localities (indicated by roman numerals, see also GODEFROIT *et al.*, 1999). The two *Kryptobaatar mandahuensis* specimens have been discovered in 1996 in the locality I (IMM 96BM-I/4) and in locality II (IMM 96BM-II/3).

Systematic palaeontology

Class Mammalia LINNAEUS, 1758
 Subclass Allotheria MARSH, 1880
 Order Multituberculata COPE, 1884
 Suborder Cimolodonta MCKENNA, 1975
 Superfamily Djadochtatherioidea KIELAN-JAWOROWSKA
 & HURUM, 2001
 Family Djadochtatheriidae KIELAN-JAWOROWSKA &
 HURUM, 1997
 Genus *Kryptobaatar* KIELAN-JAWOROWSKA, 1970
 Type species *Kryptobaatar dashzevegi* KIELAN-
 JAWOROWSKA, 1970

Kryptobaatar mandahuensis n. sp.

HOLOTYPE

IMM 96BM-II/3, complete skull (Pl. 1, Figs. 1-3; Pl. 2, Figs. 1-3; Pl. 5; Pl. 9, Figs. 5-6). A cast of the specimen (IRSNB M1837) is housed in Brussels.

TYPE LOCALITY

15 km north of Bayan Mandahu village (41° 47.874' N, 106° 44.197' E; altitude: 1226 m), quarry SBDE 96BM-II (see fig. 2 in GODEFROIT *et al.*, 1999), Urad Houqi Banner, Bayan Nor League, Inner Mongolia Province, P. R. China.

	Left		Right			
	Length	Max. width	Min. width	Length	Max. width	Min. width
IMM 96BM-II/3						
P1	—	—	—	—	—	—
P2	0.95	0.95	—	0.95	0.90	—
P3	1.15	0.80	—	0.95	0.80	—
P4	—	—	—	2.40	0.95	—
P1-4	—	—	—	6.00*	—	—
M1	2.80	—	—	2.80	1.65	—
M2	—	—	—	1.90	1.75	—
M1-2	—	—	—	4.60	—	—
IMM 96BM-I/4						
P1	1.70	1.45	—	1.70	1.15	—
P2	1.35	1.20	—	1.40	1.15	—
P3	1.45	1.15	—	1.20	0.90	—
P4	—	—	—	2.55	1.15	—
P1-4	—	—	—	6.80	—	—
M1	—	—	—	2.95	1.85	1.45
M2	2.15	2.05	1.45	—	—	—
M1-2	—	—	—	—	—	—
p4	3.50	1.25	—	3.65	1.20	—
m1	2.40	1.45	—	2.45	1.45	—
m2	—	—	—	1.65	1.55	—

Table 1 — Dental measurements (in mm) of *Kryptobaatar mandahuensis* n. sp. from the Upper Cretaceous of Bayan Mandahu (Inner Mongolia, P. R. China). *: estimated value.

Table 2 — Cranial measurements (in mm) of *Kryptobaatar mandahuensis* n. sp. from the Upper Cretaceous of Bayan Mandahu (Inner Mongolia, P. R. China). *: estimated value.

STRATOTYPE

Bayan Mandahu redbeds, correlative to the Djadokhta Formation of Bayn Dzak in Outer Mongolia, Campanian, Upper Cretaceous.

REFERRED MATERIAL

IMM 96BM-I/4, nearly complete skull associated with complete lower jaw from the Bayan Mandahu redbeds (41° 44.494' N, 106° 44.765' E; altitude: 1192 m), quarry SBDE 96BM-I (Fig. 3; Pl. 3, Figs. 1-3; Pl. 4, Figs. 1-3; Pl. 6; Pl. 7, Figs. 1-3; Pl. 8, Figs. 1-3; Pl. 9, Figs. 1-4 and 7-9). A cast of the specimen (IRSNB M1838) is housed in Brussels.

DERIVATION OF NAME

From the locality of Bayan Mandahu where the specimens were discovered.

DIAGNOSIS

The skull differs from the one of *K. dashzevegi* KIELAN-JAWOROWSKA, 1970 in having the base of the zygomatic arch at the level of the anterior root of the P4 (rather than the posterior root) and the anterior extent of the orbit (in ventral view) narrower. The palatomaxillary suture has a "V" shape between the two major palatine foramina whereas *K. dashzevegi* has a straight palatomaxillary suture. The dentary is higher and thicker under the mandibular diastema. The part of the dentary under the

	IMM 96BM	
	II/3	I/4
Length of skull	30.5	32.4
Width of skull	24.1	26.8
Width of snout (contact premax.-maxillary suture and alveolar border in ventral view)	7.2	8.4
Width of snout (at the level of I1)	4.3	5.5
Length of premaxilla (alveolar border)	4.4	5.2
Length of premaxilla (nasal suture)	7.2	7.7
Length of premaxilla (palatine process)	7.0	7.6
Maximum length of maxilla (palatal view)	11.9	13.1
Length of palate	17.1	18.0
Width of palate (between P4)	7.2	7.7
Depth of skull (above I2)	5.0	5.4
Depth of skull (above M2)	10.5	10.5
Maximum length of nasal	13.5	*14.9
Minimum length of nasal	10.5	*12.0
Length of frontal	12.7	13.4
Length of lower jaw (from i1 base)	—	21.0 (R)
—	—	21.3 (L)
Depth of lower jaw (below p3)	—	5.3 (R)
—	—	5.4 (L)
Depth of lower jaw (below m1)	—	6.5 (R)
—	—	6.6 (L)

mandibular notch is longer and lower. The coronoid process is shorter anteroposteriorly. The teeth differ in having 5 cusps on the middle row of M1 and 5 cusps on the labial row of m1 (rather than 4). The p4 is longer. The ratio p4:m1 length is higher. The i1 is more robust.

MEASUREMENTS

See Tables 1 and 2.

COMPARATIVE DESCRIPTION

The description of the genus *Kryptobaatar* was based originally on the holotype of *K. dashzevegi*, a rostrum associated with a right and left incomplete dentary (ZPAL MgM-I/21) from Bayn Dzak (KIELAN-JAWOROWSKA, 1970). KIELAN-JAWOROWSKA & DASHZEVEG (1978) completed the description of *Kryptobaatar* with a skull associated with both dentaries and the incomplete postcranial skeleton of a specimen from Toogreeg (= Tugrueen Shireh). The diagnosis of the genus has also been revised and the morphological variability of *K. dashzevegi* has been discussed (KIELAN-JAWOROWSKA & HURUM, 1997). WIBLE & ROUGIER (2000) described in detail the cranial anatomy of *K. dashzevegi* on the basis of well-preserved complete skulls and dentaries from Ukhaa Tolgod and Tugrueen Shireh, and completed the diagnosis of *Kryptobaatar*. Thus, a bone-by-bone description of the Inner Mongolian specimens collected by us in Bayan Mandahu is not warranted. Indeed, several cranial bones of *K. mandahuensis* seem very similar to those of *K. dashzevegi*, such as the frontal, squamosal, parietal, petrosal and the occipital complex. In addition, some cranial sutures are not well preserved in *K. mandahuensis* so that the jugal limits are not completely visible. Other bones are damaged or missing, such as the vomer, pterygoid and the sphenoid complex. For these reasons, the following morphological description is primarily focused on the differences with the *Kryptobaatar* species from Outer Mongolia.

Before describing the new species based on skull and dentition, the characters allowing to attribute the two Chinese specimens to the middle-sized djadochtatheriid *Kryptobaatar* have to be underlined. The length of the skull is 30.5 mm for IMM 96BM-II/3 and 32.4 mm for IMM 96BM-I/4 respectively (between 25 and 32 mm for *K. dashzevegi*, see KIELAN-JAWOROWSKA & HURUM, 1997). The snout is subtrapezoidal in dorsal view. The parietal postorbital process is relatively long. There are no palatal vacuities. The infraorbital foramen is dorsoventrally compressed and situated dorsally to P2. The alveolus for I3 is placed on the palatal part of the premaxilla. Four upper double-rooted premolars are present. P4 is not reduced but somewhat shorter than M1. The length of the M1 inner row is about the half of the tooth length. On the lower jaw, the p4 is arcuate.

The skull

The morphology and the size of the rostrum of the specimen IMM 96BM-II/3 (Pl. 1, Fig. 1; Pl. 2, Fig. 1; Pl. 5) are close to those of the holotype ZPAL MgM-I/21 of *K. dashzevegi* (see KIELAN-JAWOROWSKA, 1970). The maxillary sinuses are well developed and give, in dorsal view, a subtrapezoidal shape to the snout, as in other djadochtatheriids (see HURUM, 1994). Indeed, the antero-

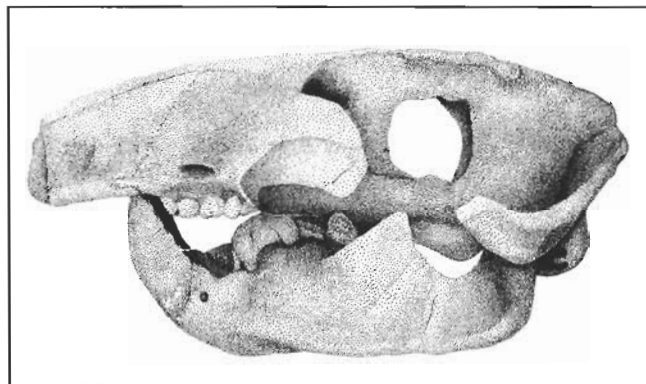


Fig. 3 — *Kryptobaatar mandahuensis* n. sp. (specimen IMM 96BM-I/4) from the Upper Cretaceous of Bayan Mandahu (Inner Mongolia, P. R. China) in left lateral view.

lateral borders of the snout are confluent with the zygomatic arches, and the infraorbital foramina are dorsoventrally compressed (Pl. 1, Fig. 2; Pl. 2, Fig. 2). However, the anterolateral borders of the snout are slightly incurved in front of the arches on IMM 96BM-I/4 (Pl. 3, Fig. 1) and the infraorbital foramina are also less compressed than on IMM 96BM-II/3 (Pl. 3, Fig. 2; Pl. 4, Fig. 2). The same morphological details are observed in the specimen ZPAL MgM-I/6 of *K. dashzevegi* called “wide snout” (KIELAN-JAWOROWSKA & HURUM, 1997, p. 211). Moreover, the snout of IMM 96BM-I/4 has the same width as that of ZPAL MgM-I/6.

In ventral view, the anterior extent of the orbit located between the base of the zygomatic arch and the alveoli is narrower on IMM 96BM-II/3 (Pl. 5) and IMM 96BM-I/4 (Pl. 6) than in *K. dashzevegi*. The base of the zygomatic arch as marked by the posterior edge is at the level of the anterior root of the P4 in *K. mandahuensis*, while it is at the level of the posterior root of the P4 in the holotype of *K. dashzevegi* and the other Outer Mongolian specimens. The zygomatic ridges seem similar in both species. Only, in the specimen IMM 96BM-I/4, the first zygomatic ridge (on the maxilla) is relatively better developed (Pl. 3, Fig. 2) than in IMM 96BM-II/3.

Anteriorly each nasal has two vascular foramina in *K. mandahuensis*. These pairs of nasal foramina are not exactly symmetrically arranged between the two sides in IMM 96BM-I/4 (Pl. 3, Fig. 1). The posterior nasal foramen is slightly anterior to the contact point of the premaxilla, maxilla and nasal (Fig. 4). This is different from *K. dashzevegi* where the second nasal foramen is more anterior (see specimens ZPAL MgM-I/6 from Bayn Dzak, KIELAN-JAWOROWSKA & HURUM, 1997, fig. 2 and PSS-MAE 101 from Ukhaa Tolgod, WIBLE & ROUGIER, 2000, fig. 8).

The shape of the nasal-frontal suture is similar to that of *K. dashzevegi* but more pointed in the middle of the cranial roof (Pl. 3, Fig. 1; Fig. 4).

On the palate, between the two major palatine foramina, the palatomaxillary suture has a “V” shape (Fig. 5). This character, clearly visible on IMM 96BM-II/3 (Pl. 5), is different in *K. dashzevegi* which has a straight palatomaxillary suture between the two major palatine foramina. In lateral view, the premaxillary-maxillary suture is oblique and approximately straight from the

palatal margin to the contact with the nasal (Fig. 6). In *K. dashzevegi*, the suture is vertical near the palatal margin and curves posteriorly near the nasal (see KIELAN-JAWOROWSKA & HURUM, 1997, fig. 3; WIBLE & ROUGIER, 2000, p. 16-17, fig. 26) excepted in GI SPS 8-2 PST where the suture extends almost vertically along the lateral wall of the snout (KIELAN-JAWOROWSKA & DASHZEVEG, 1978, p. 119).

The posterior part of the skull is somewhat dorso-ventrally compressed in IMM 96BM-I/4 which allows to visualise easily the suture between the squamosal and the anterior lamina (Pl. 3, Fig. 1). The maxillary-frontal suture is also well visible on the left lateral side of this specimen because the maxilla and the frontal are not fused anymore and the sphenopalatine foramen is consequently completely open (Pl. 4, Fig. 2). The basicranium shows a large and deep jugular fossa separated from an elongated epitympanic recess by the promontorium. The perilymphatic foramen (sensu Wible & Rougier, 2000, fig. 14, p. 39) and the fenestra vestibuli (oval window) are visible on each side of the promontorium (Pl. 4, Fig. 1; Pl. 6).

The dentary

The shape and the general morphology of the mandible are relatively similar in *K. mandahuensis* and in *K. dashzevegi*. The differences result from the proportions

of the different parts of the dentary (Fig. 8). The part of the dentary under the mandibular diastema (between the incisor and the P3) of *K. mandahuensis* is higher, thicker and anteroposteriorly shorter (Pl. 7, Figs. 2-3; Pl. 8, Figs. 2-3) in comparison with *K. dashzevegi* (see KIELAN-JAWOROWSKA, 1970, pl. 15, figs. 1b-d; WIBLE & ROUGIER, 2000, p. 14, fig. 5; p. 26, fig. 12). This character makes the depression of the mandibular diastema deeper in *K. dashzevegi*. On the other hand, the part of the dentary under the mandibular notch (between the coronoid process and the condyle) of *K. mandahuensis* is longer and less high. The coronoid process is also shorter anteroposteriorly in *K. mandahuensis*.

The dentition

The teeth are damaged and their enamel is not preserved. They are worn, in particular on IMM 96BM-I/4, but several important characters can be identified, such as their shape, size, proportions and number of cusps.

Upper teeth: The two large anterior incisors (I2) are preserved on IMM 96BM-II/3 (Pl. 1, Fig. 3). Only the root of the right I3 is preserved on IMM 96BM-I/4, the other incisors are missing. The P1, which is somewhat larger than P2 and P3, presents a triangular shape with three cusps, one anterior and two posterior (Pl. 6; Pl. 9, Fig. 8). The P2 is rounded and also has 3 cusps. The P3 possesses four

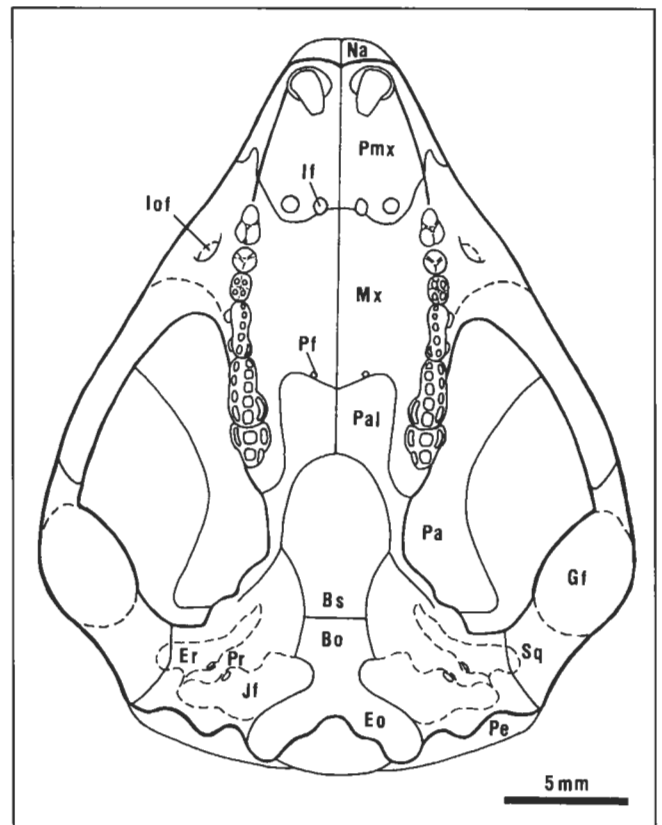
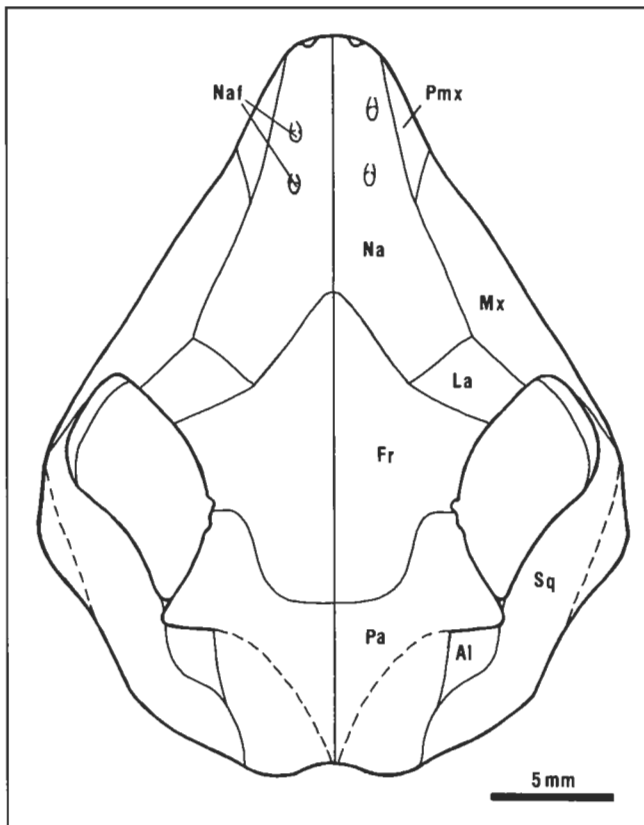


Fig. 4 — *Kryptobaatar mandahuensis* n. sp. Reconstruction of the skull in dorsal view. Al: anterior lamina; Fr: frontal; La: lacrimal; Mx: maxilla; Na: nasal; Naf: nasal foramina; Pa: parietal; Pmx: premaxilla; Sq: squamosal.

Fig. 5 — *Kryptobaatar mandahuensis* n. sp. Reconstruction of the skull in ventral view. Bo: Basioccipital; Bs: Basisphenoid; Eo: exoccipital; Er: epitympanic recess; Gf: glenoid fossa; If: incisive foramen; Iof: infraorbital foramen; Jf: jugular fossa; Mx: maxilla; Na: nasal; Pa: parietal; Pal: palatine; Pe: petrosal; Pf: palatine foramen (major); Pmx: premaxilla; Pr: promontorium; Sq: squamosal.

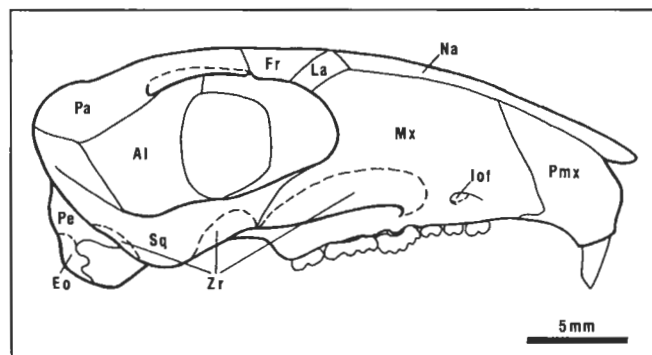


Fig. 6 — *Kryptobaatar mandahuensis* n. sp. Reconstruction of the skull in lateral view. Al: anterior lamina; Eo: exoccipital; Fr: frontal; Iof: infraorbital foramen; La: lacrimal; Mx: maxilla; Na: nasal; Pa: parietal; Pe: petrosal; Pmx: premaxilla; Sq: squamosal; Zr: zygomatic ridges (anterior, intermediate, posterior).

small cusps and is somewhat anteroposteriorly elongated which differs from the rounded P3 of *K. dashzevegi*. The P4 is long and narrow, and the cusp formula seems to be 0:5:2. Four cusps or part of cusps are visible on the middle row and the broken anterior part of the tooth bore probably a fifth cusp (Pl. 9, Fig. 5). The M1 has a length/width ratio similar to that of *K. dashzevegi* but its anterior part is proportionally elongated (Pl. 9, Figs. 5-7). The distance between the anterior border of the M1 and the beginning of the lingual row is 46% (1.3 mm) of the tooth length (2.8 mm) on the holotype IMM 96BM-II/3. The M1 cusp formula is 4:5:?. The fourth cusp on the labial row (the most posteriorly situated) is elongated. The five cusps of the middle row are visible in the specimen IMM 96BM-II/3. The first cusp (the most anterior cusp) of IMM 96BM-I/4 is not preserved because it is completely worn, leaving a space at the anterior part of the tooth. In *K. dashzevegi*, only 4 cusps are present on the middle row of the M1. The M2 cusp formula of *K. mandahuensis* is probably 1:2:2 (Pl. 9, Figs. 5 and 9). Only two long cusps seem to exist on the lingual row, whereas *K. dashzevegi* has three smaller cusps on its lingual row.

Lower teeth: The very large incisor (i1) is approximately of the same length but more robust than that of *Kryptobaatar dashzevegi* (Pls. 7-8). A peg-like p3 is also present (Pl. 8, Fig. 2). The p4 is arcuated and longer than the p4 of *K. dashzevegi* (Figs. 7-8; Pl. 9, Figs. 1-4). The ratio p4:m1 length is 1.46 (left) and 1.49 (right) which is also significantly higher than for the Outer Mongolian species. It is 1.29 in the holotype of *K. dashzevegi* MgM-I/21 (see KIELAN-JAWOROWSKA, 1970, table 2) and in PSS-MAE 113 (see WIBLE & ROUGIER, 2000, table 1), 1.13 in GISPS 8-3PST (see KIELAN-JAWOROWSKA & DASHZEVEG, 1978, p. 119), 1.35 in MgM-I/10 (see KIELAN-JAWOROWSKA, 1970, table 2), and 1.30 in GI SPS 8-2 PST (see KIELAN-JAWOROWSKA & DASHZEVEG, 1978, p. 119). The m1 cusp formula is 5:3 (Pl. 9, Figs. 2 and 4) rather than 4:3. The m2 cusp formula is 3:2 (Pl. 9, Fig. 2) which is the same from *K. dashzevegi* excepted in GI SPS 8-2 PST (4:2). Nevertheless, the anterior cusp of the labial row is somewhat different in *K. mandahuensis* because it is labio-lingually elongated.

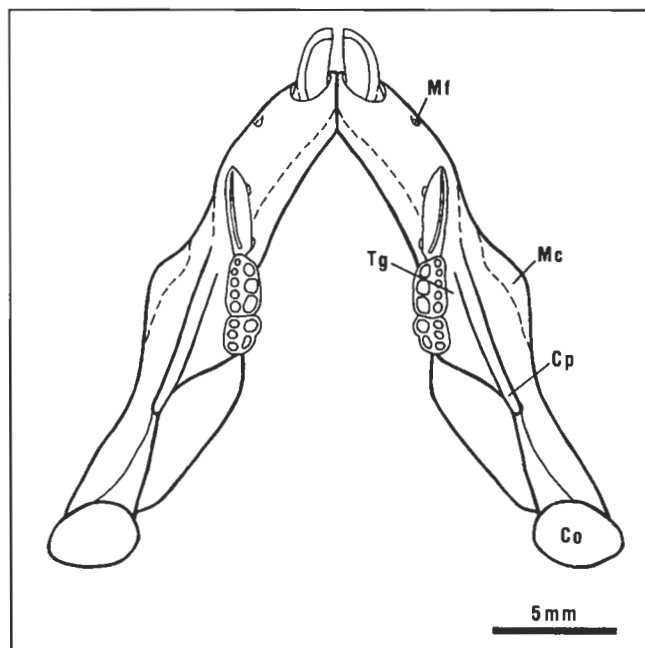


Fig. 7 — *Kryptobaatar mandahuensis* n. sp. Reconstruction of the lower jaw in dorsal view. Co: condyle; Cp: coronoid process; Mc: masseteric crest; Mf: mental foramen; Tg: temporal groove.

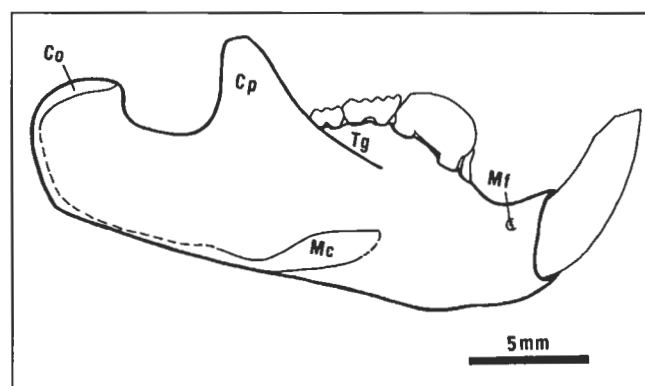


Fig. 8 — *Kryptobaatar mandahuensis* n. sp. Reconstruction of the mandible in labial view. Co: condyle, Cp: coronoid process; Mc: masseteric crest; Mf: mental foramen; Tg: temporal groove.

Analysis of osteological characters

The differences in the shape of the snout of some *Kryptobaatar* specimens may result from the state of preservation or from ontogenetic variation as argued by KIELAN-JAWOROWSKA & HURUM (1997). These authors observed that the older specimens are relatively wider than the others and they called the rostrum ZPAL MgM-I/6 of *K. dashzevegi* from Bayn Dzak "wide snout", by opposition to the "narrow snout" of the holotype and most of the specimens. We confirm this observation on the skulls of *K. mandahuensis* from Bayan Mandahu. IMM 96BM-II/3 has a narrow snout and IMM 96BM-I/4 has the typical characters of a wide snout. IMM 96BM-I/4 represents probably an old animal, as suggested by its very worn teeth. This argumentation may also be used for the specimens of *K. dashzevegi* PSS-MAE 101 from

Ukhaa Tolgod and PSS-MAE 113 from Tugrugen Shireh (illustrated by WIBLE & ROUGIER, 2000, figs. 3-4). They could represent a young adult with a narrow snout and an old adult with a wide snout respectively.

Some morphological differences between the two specimens of *K. mandahuensis* cannot be explained by ontogenetic variation, as for example the cusp formula of the teeth. Indeed, the M1 of IMM 96BM-II/3 presents four cusps on the labial row, whereas the M1 of IMM 96BM-I/4 seems to have only three cusps. The long anterior cusp could result from the fusion of the first and the second cusp or may be caused by the wear of the two first cusps. This is why we consider that both specimens belong to the same species. This observation is in favour of an intraspecific morphological variability in the population of *K. mandahuensis* from Inner Mongolia as is the case for *K. dashzevegi* from Outer Mongolia. WIBLE & ROUGIER (2000, p.11) recognize *K. saichanensis* as a junior synonym of *K. dashzevegi* because the differences between the two species are relatively minor, except the cusp formula of the m2. Their argument is that, after inspection of the holotype GI SPS 8-2 PST of *K. saichanensis*, they found three cusps in the labial row on the left M2 and three cusps plus an accessory cusp on the right m2. The authors listed other intraspecific differences present on the specimens of *K. dashzevegi* collected by the American-Mongolian expeditions.

One of the osteological particularities of the multituberculates is the composition of the zygomatic arch. This arch superficially resembles that of rodents but this is evidently a homoplastic character as is also the single pair of long lower incisors or the diastema due to the loss of the canines and the anterior premolars. SIMPSON (1937) already showed that the zygomatic arch is formed by the association of long processes from the maxilla anteriorly and the squamosal posteriorly in the Paleocene multituberculates *Ptilodus* and *Taeniolabis*. The jugal that forms a large part of the zygomatic arch in the therian mammals is reduced to a plate-like bone not exposed laterally in the multituberculates (HOPSON *et al.*, 1989). In a detailed study of the masticatory musculature of the djadochtatherioidean multituberculates, GAMBARYAN & KIELAN-JAWOROWSKA (1995) showed that the insertion of the muscles was more anterior in the multituberculates than in any other mammal group. They completed the studies of GINGERICH (1977) and KRAUSE (1982) made on North American multituberculates, and concluded to a mode of chewing with a backward power stroke. GAMBARYAN & KIELAN-JAWOROWSKA (1995, p. 50) identified three zygomatic ridges (for the insertion of the masseteric muscles) on the zygomatic arch. WIBLE & ROUGIER (2000, p.104) consider in their amended diagnosis of *Kryptobaatar* that this genus differs from *Nemegtbaatar*, *Chulsanbaatar* and *Catopsbaatar* in that the anterior and intermediate zygomatic ridges are confluent and that the posterior ridge is absent.

Only the posterior part of the intermediate zygomatic ridge is preserved in the Inner Mongolian specimens, which shows it is present. It is true that in *Kryptobaatar* the intermediate zygomatic ridge is closer to the anterior one than in *Nemegtbaatar*, but it seems not closer than in *Catopsbaatar* and *Chulsanbaatar* (see GAMBARYAN &

KIELAN-JAWOROWSKA, 1995, fig. 2). The difficulty for giving more precise outlines of the muscular insertions may come from the fact that in *Kryptobaatar*, the limit between the anterior and the intermediate zygomatic ridges coincides also with the limit between the maxilla and the squamosal. It is thus probable that in some specimens the bases of the ridges are touching each other. The term "confluent" used by WIBLE & 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 (see WIBLE & ROUGIER, 2000, fig. 2). Also in ZPAL MgM-I/41 (see KIELAN-JAWOROWSKA & 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 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 the impression that is a depression. Nevertheless, this does not exclude that it is a ridge. In conclusion, the three zygomatic ridges seem present in *Kryptobaatar mandahuensis* as in the other djadochtatherians.

The position of nasal foramina, which are different in *K. mandahuensis* and *K. dashzevegi*, is a variable character. In the specimens of *K. dashzevegi* ZPAL MgM-I/10 and ZPAL MgM-I/21 (KIELAN-JAWOROWSKA, 1969, pl. 10, fig. 1b and pl.14, fig. 1c), and ZPAL MgM-I/6 (KIELAN-JAWOROWSKA & HURUM, 1997, fig. 2) from Bayan Dzak, the posterior nasal foramen is large and elongated, while in the specimen PSS-MAE 101 from Ukhaa Tolgod (WIBLE & ROUGIER, 2000, fig. 8) nasal foramina are very small. Not only in the specimens of *K. dashzevegi* but also in other djadochtatherians, the position, the size and the number of nasal foramina can be different from one specimen to another (see KIELAN-JAWOROWSKA, 1971, p. 25; HURUM, 1994, p. 201-205; WIBLE & ROUGIER, 2000, p. 76).

The interpretation of the osteological characters of *K. mandahuensis* in comparison with *K. dashzevegi* seems not to give direct evidence of a precise evolutive stage (more primitive or advanced) in the phylogenetical relationships of the djadochtatherioidean multituberculates. *K. mandahuensis* is relatively close to *K. dashzevegi* and the differences between them constitute a mosaic of both possibly synapomorphic and symplesiomorphic characters. Indeed, the following characters of *K. mandahuensis* are generally considered as more derived: the presence of five cusps on the middle row of M1 and on the labial row of m1, and the higher ratio p4:m1 length. The presence of two long cusps on the lingual row of M2, rather than three as in many Cretaceous multituberculates, could be a reversion, but we cannot totally exclude that it could result from the bad preservation of the M2. Other characters are regarded as more primitive: the base of the zygomatic arch situated more anteriorly and the anterior extent of the orbit narrower. It should be noted that if the cusp number of the teeth does change a little, the size of teeth in both species is the same.

Several characters which separate *K. mandahuensis* from *K. dashzevegi* result from a differentiation affecting the maxilla: position of the base of the zygomatic arch, shape of the palatomaxillary suture and the premaxillary-maxillary suture, width of the anterior extent of the orbit, morphology of the upper teeth. Among these characters, the "V" shape of the palatomaxillary suture between the two major palatine foramina is remarkable. This autapomorphic character differs not only from *K. dashzevegi* but also from all the other djadochtatherioidean genera from Outer Mongolia, which have a straight palatomaxillary suture. Other characters concern the mandible: height of the dentary, shape of the coronoid process, morphology of the lower teeth. During the mastication the maxilla and the mandible are closely related. Moreover, the morphology of the posterior part of the dentary forms a different surface for the insertion of the masseteric muscle in comparison with *K. dashzevegi*. The robust anterior part of the dentary and the large p4 in *K. mandahuensis* are additional arguments in favour of a relatively different diet from that of *K. dashzevegi*.

These characters may suggest that *K. mandahuensis* evolved independently from other djadochtatherioidean species known from the Djadokhta Formation of Outer Mongolia.

Biostratigraphical and palaeogeographical significance

The presence of the multituberculate mammal *Kryptobaatar* in the Bayan Mandahu redbeds combined with that of the typical dinosaur assemblage such as the neoceratopsian *Protoceratops* (see LAMBERT *et al.*, 2001), the ankylosaurid *Pinacosaurus* (see GODEFROIT *et al.*, 1999), and the theropods *Oviraptor* (see DONG & CURRIE, 1996) and *Saurornithoides* (see CURRIE & PENG, 1993), confirms the biostratigraphical correlation with the Bayn Dzak deposits of the Djadokhta Formation proposed by JERZYKIEWICZ *et al.* (1993). Moreover, 10 species of squamates have been recognized as common to Bayan Mandahu and Bayn Dzak (GAO & HOU, 1996). The biostratigraphic correlation is not established only on the presence of taxa common to the two areas, but also on the abundance of some genera in the two areas. The middle-sized multituberculate *Kryptobaatar* is the most abundant mammal in Outer Mongolia (WIBLE & ROUGIER, 2000) which seems also to be the case in Inner Mongolia. Out of six skulls and one skeleton discovered by the Sino-Belgian expeditions in Bayan Mandahu, three belong to the genus *Kryptobaatar*. GAO & HOU (1996, p. 594) noted that the most abundant lizard is the scincomorphan teiid *Adamisaurus* which is also the case at Bayn Dzak. Among the dinosaurs, *Protoceratops* is the most abundant genus in both areas. The Djadokhta Formation also shows a lithofacies similar with that of the Bayan Mandahu redbeds (see JERZYKIEWICZ & RUSSELL, 1991; JERZYKIEWICZ *et al.*, 1993). EBERTH (1993) underlined the similarities between the Bayn Dzak and Bayan Mandahu palaeoenvironments and fossil assemblages and concluded to a consistency in climate and depositional processes across the Gobi Basin during the Campanian. Sandstorms have been proposed to explain the death of several ani-

mals discovered in ventral position at Bayan Mandahu (JERZYKIEWICZ *et al.*, 1993), whereas rainstorms with a rapid deposition on dune-sand alluvial fans have been proposed for the specimens from the Nemegt Basin (LOOPE *et al.*, 1998).

Nevertheless, the Outer and Inner Mongolian specimens of *Kryptobaatar* do not belong to the same species. The analysis of the anatomical characters does not demonstrate biostratigraphic differences between *Kryptobaatar dashzevegi* and *K. mandahuensis*. The morphological differences are at a relatively low level and probably result more from a palaeobiogeographical isolation of the populations. Both species show a high degree of relationship, which is also observed in other vertebrates. Indeed, morphometrical and morphological studies of *Protoceratops* skulls from Bayan Mandahu and Bayan Dzak indicate slight specific differences (GODEFROIT *et al.*, 1999; LAMBERT *et al.*, 2001). *Pinacosaurus mephistocephalus* GODEFROIT *et al.*, 1999 from Bayan Mandahu is closely related to *P. grangeri* GILMORE, 1933 from Outer Mongolia (GODEFROIT *et al.*, 1999). The trionychoid turtles *Zangerlia neimongoliensis* BRINKMAN & PENG, 1996 from Bayan Mandahu and *Z. testudinimorpha* MLYNARSKI, 1972 from the Barun Goyot Formation of Outer Mongolia are closely similar (BRINKMAN & PENG, 1996).

The Late Cretaceous multituberculates of Outer Mongolia come essentially from two large tectonic depressions (grabens or semigrabens) which were formed after the Triassic in the Gobi Basin (BERKEY & MORRIS, 1927): the Ulan Nur subordinate Basin with the localities of Bayn Dzak and Tugrugeen Shireh and the Nemegt subordinate Basin with the Ukhaa Tolgod locality (Fig. 1). These three localities are situated near the Altai mountains. The Inner Mongolian locality Bayan Mandahu is 350 km distant from Bayn Dzak and 470 km from Ukhaa Tolgod, and is situated in a semigraben to the north of the Lang Shan mountains. Its redbed deposits could be derived from a southerly source in the palaeo-Lang Shan mountains (EBERTH, 1993, p. 2208). This geographic segregation could be at the origin of the morphological differences resulting of the speciations between vertebrate populations of Outer and Inner Mongolia within the Gobi Basin. In this case, the faunas from both areas were geographically isolated: one close to the Altai in the north and the second to the Lang Shan in the south. A geographical barrier such as a desert could have already isolated them. Besides, the Asian Late Cretaceous multituberculates inhabited semi-deserts and were probably terrestrial and constructed burrows (KIELAN-JAWOROWSKA & GAMBARYAN, 1994). Also, the small to medium size of the dinosaurs and the low diversity of the vertebrate assemblage witness to a stressed palaeoenvironment (JERZYKIEWICZ *et al.*, 1993).

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PLATE 1

Stereo-photographs of the skull of *Kryptobaatar mandahuensis* n. sp. (specimen IMM 96BM-II/3) from the Upper Cretaceous of Bayan Mandahu (Inner Mongolia, P. R. China). Specimen coated with ammonium chloride.

- Fig. 1 — Dorsal view.
Fig. 2 — Right lateral view.
Fig. 3 — Anterior view.

PLATE 2

Stereo-photographs of the skull of *Kryptobaatar mandahuensis* n. sp. (specimen IMM 96BM-II/3) from the Upper Cretaceous of Bayan Mandahu (Inner Mongolia, P. R. China). Specimen coated with ammonium chloride.

- Fig. 1 — Ventral view.
Fig. 2 — Left lateral view.
Fig. 3 — Posterior view.

PLATE 3

Stereo-photographs of the skull and the lower jaw of *Kryptobaatar mandahuensis* n. sp. (specimen IMM 96BM-I/4) from the Upper Cretaceous of Bayan Mandahu (Inner Mongolia, P. R. China). Specimen coated with ammonium chloride.

- Fig. 1 — Dorsal view.
Fig. 2 — Right lateral view.
Fig. 3 — Anterior view.

PLATE 4

Stereo-photographs of the skull and the lower jaw of *Kryptobaatar mandahuensis* n. sp. (specimen IMM 96BM-I/4) from the Upper Cretaceous of Bayan Mandahu (Inner Mongolia, P. R. China). Specimen coated with ammonium chloride.

- Fig. 1 — Ventral view.
Fig. 2 — Left lateral view.
Fig. 3 — Posterior view.

PLATE 5

Skull of *Kryptobaatar mandahuensis* n. sp. (specimen IMM 96BM-II/3) from the Upper Cretaceous of Bayan Mandahu (Inner Mongolia, P. R. China), in ventral view.

PLATE 6

Skull of *Kryptobaatar mandahuensis* n. sp. (specimen IMM 96BM-I/4) from the Upper Cretaceous of Bayan Mandahu (Inner Mongolia, P. R. China), in ventral view.

PLATE 7

Right mandible of *Kryptobaatar mandahuensis* n. sp. (specimen IMM 96BM-I/4) from the Upper Cretaceous of Bayan Mandahu (Inner Mongolia, P. R. China).

- Fig. 1 — Stereo-photograph in occlusal view.
Fig. 2 — Labial view.
Fig. 3 — Lingual view.

PLATE 8

Left mandible of *Kryptobaatar mandahuensis* n. sp. (specimen IMM 96BM-I/4) from the Upper Cretaceous of Bayan Mandahu (Inner Mongolia, P. R. China).

- Fig. 1 — Stereo-photograph in occlusal view.
Fig. 2 — Labial view.
Fig. 3 — Lingual view.

PLATE 9

SEM photographs of the dentition of *Kryptobaatar mandahuensis* n. sp. from the Upper Cretaceous of Bayan Mandahu (Inner Mongolia, P. R. China).

- Fig. 1 — Left p4 and m1-2 in occlusal view (specimen IMM 96BM-I/4).
Fig. 2 — Right p4 and m1-2 in occlusal view (specimen IMM 96BM-I/4).
Fig. 3 — Left p3-4 and m1-2 in labial view (specimen IMM 96BM-I/4).
Fig. 4 — Right p4 and m1-2 in labial view (specimen IMM 96BM-I/4).
Fig. 5 — Right P4 and M1-2 in occlusal view (specimen IMM 96BM-II/3).
Fig. 6 — Left M1-2 in occlusal view (specimen IMM 96BM-II/3).
Fig. 7 — Right P4 and M1 in occlusal view (specimen IMM 96BM-I/4).
Fig. 8 — Left P1-3 in occlusal view (specimen IMM 96BM-I/4).
Fig. 9 — Left M2 in occlusal view (specimen IMM 96BM-I/4).

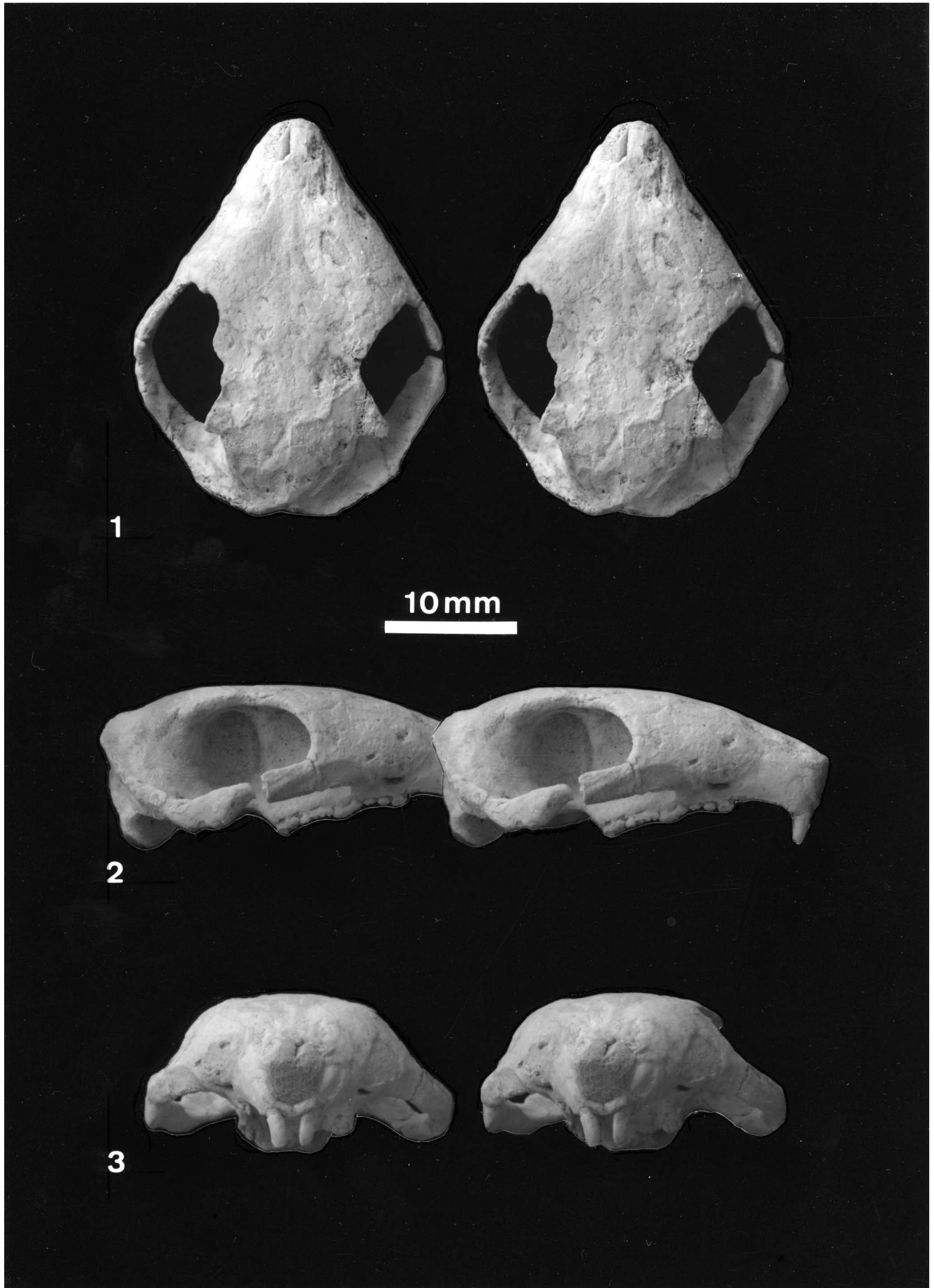


PLATE 1



PLATE 2



PLATE 3

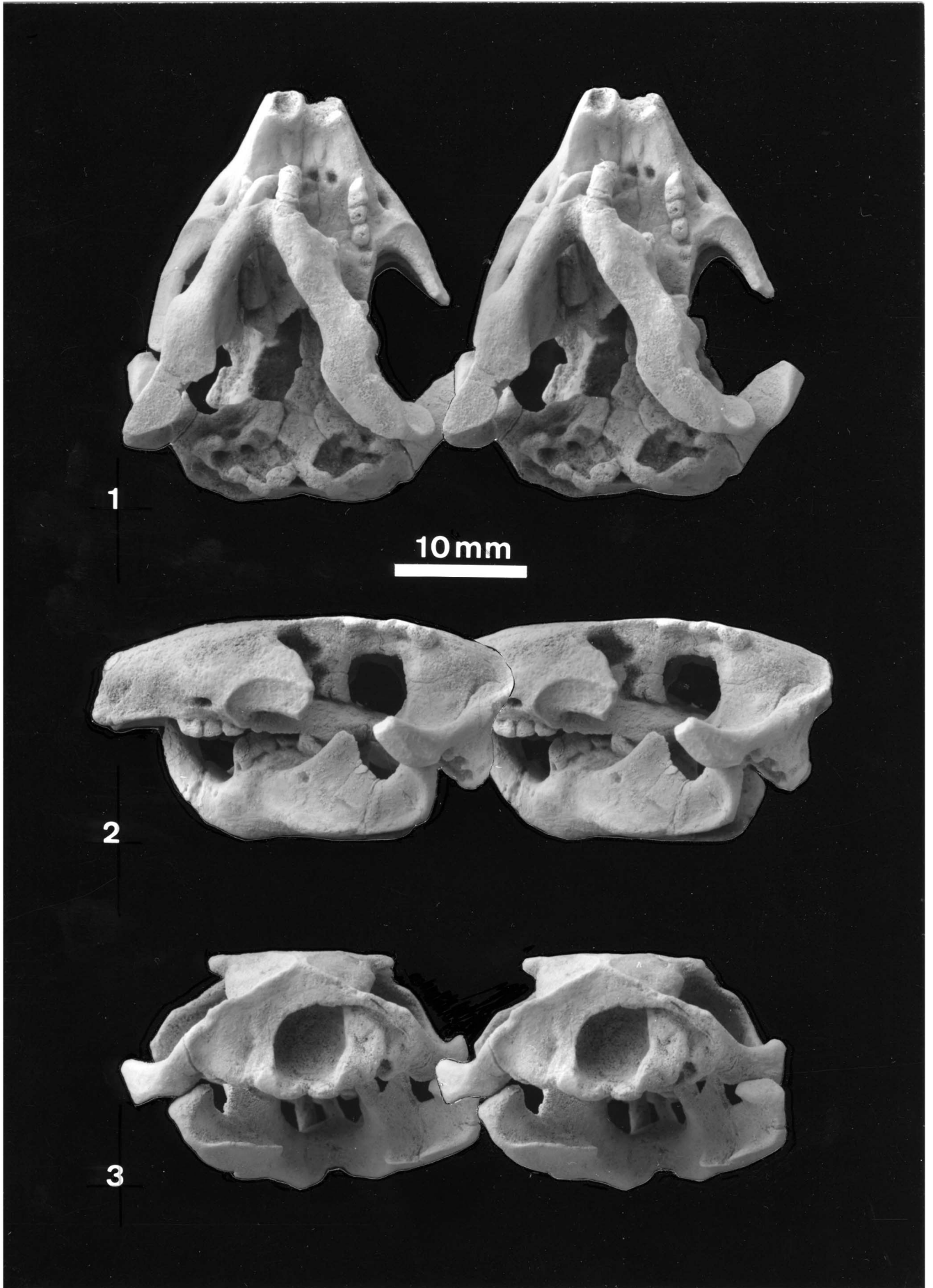


PLATE 4



PLATE 5





PLATE 7



PLATE 8

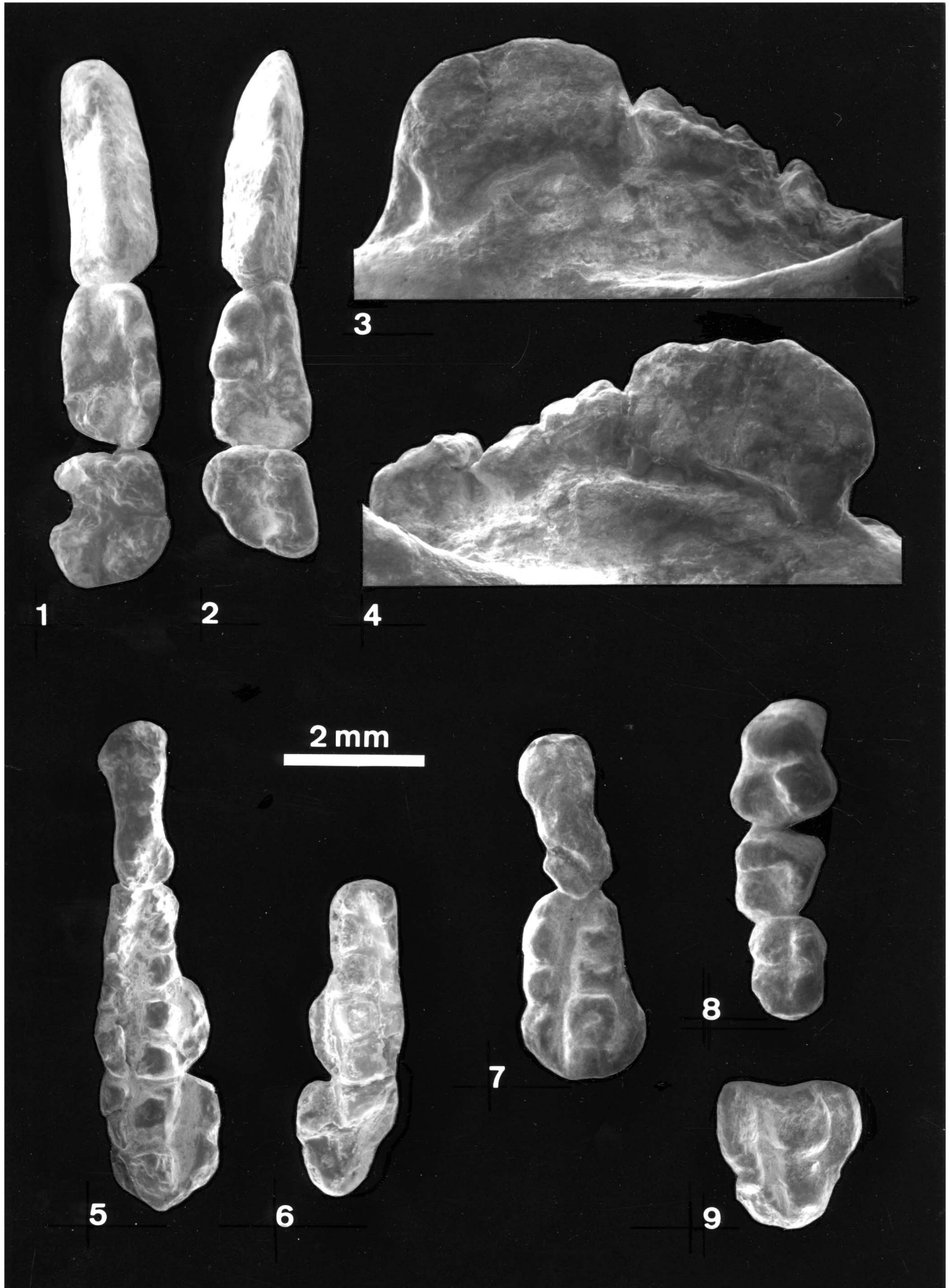


PLATE 9