

The braincase of two Late Cretaceous Asian multituberculates studied by serial sections

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The braincase structure of two Late Cretaceous Mongolian djadochtatherian multituberculates *Nemegtbaatar gobiensis* and *Chulsanbaatar vulgaris* from the ?late Campanian of Mongolia is presented based on the two serially sectioned skulls and additional specimens. Reconstructions of the floor of the braincase in both taxa are given. The complete intracranial sphenoid region is reconstructed for the first time in multituberculates. Cavum epiptericum is a separate space with the taenia clino-orbitalis (ossified pila antotica) as the medial wall, anterior lamina of the petrosal and possibly the alisphenoid as the lateral wall, and the basisphenoid, petrosal and possibly alisphenoid ventrally. The fovea hypochiasmatica is shallow, tuberculum sellae is wide and more raised from the skull base than it is in the genus *Pseudobolodon*. The dorsal opening of the carotid canal is situated in the fossa hypophyseos. The taenia clino-orbitalis differs from the one described in *Pseudobolodon* and *Lambdopsalis* in possessing just one foramen (metoptic foramen). Compared to all extant mammals the braincase in *Nemegtbaatar* and *Chulsanbaatar* is primitive in that both the pila antotica and pila metoptica are retained. In both genera the anterior lamina of the petrosal is large with a long anterodorsal process while the alisphenoid is small. A review is given of the cranial anatomy in *Nemegtbaatar* and *Chulsanbaatar*.

Key words: Braincase structure, sphenoid complex, cavum epiptericum, Mammalia, Multituberculata, Djadochtatheria, Cretaceous, Mongolia.

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Introduction

Cranial remains of Mesozoic mammals are rare and our understanding of the first two thirds (225–65 MA) of mammalian evolution was for many years based mainly on teeth. In the last 25 years our knowledge of Mesozoic mammals has increased enormously, but there still remain many gaps in our knowledge of the evolution of the

group. Multituberculates, 'the rodents of the Mesozoic', made their appearance in the Jurassic (see Kielan-Jaworowska & Hurum 1997 for review) and became extinct during the Late Eocene possibly as a result of competition with eutherian herbivores (Van Valen & Sloan 1966; Hopson 1967; Krause 1986). Multituberculates resemble morganucodontids, triconodonts and monotremes in having abducted limbs (sprawling posture) and differ in this respect from marsupial and eutherian mammals (Kielan-Jaworowska & Gambaryan 1994; Gambaryan & Kielan-Jaworowska 1997; Kielan-Jaworowska 1998; *contra* Sereno & McKenna 1995).

The multituberculate skull is dorsoventrally compressed with a blunt snout, strong zygomatic arches and a short, laterally expanded braincase (Kielan-Jaworowska 1971; Clemens & Kielan-Jaworowska 1979). The backward masticatory power stroke, unique among mammals (Gingerich 1977; Krause 1982), is responsible for most apomorphies that distinguish the multituberculate skull from those of other mammals (Gambaryan & Kielan-Jaworowska 1995).

The multituberculate basicranium and especially the petrosals have been extensively studied. Simpson (1937) made the first reconstruction of multituberculate basicranium in *Ptilodus*. Kielan-Jaworowska (1970, 1971, 1974) described several Late Cretaceous djadochtatherian multituberculates from Mongolia with complete basicrania. Kielan-Jaworowska & Sloan (1979) reconstructed the skull of the Late Cretaceous djadochtatherian *Catopsbaatar* (referred to as *Catopsalis*), and Kielan-Jaworowska & Dashzeveg (1978) reconstructed the skulls of the Late Cretaceous djadochtatherians *Kryptobaatar saichanensis* (previously assigned to *Tugrigbaatar*, see Kielan-Jaworowska & Hurum 1997) and *Kryptobaatar dashzevegi*. Sloan (1979) figured the basicranium of the Paleocene *Ectypodus*. Kielan-Jaworowska *et al.* (1986) described the petrosal of the Late Cretaceous djadochtatherian *Catopsbaatar catopsaloides* (referred to as *Catopsalis*), an unidentified petrosal from the Hell Creek Formation, Montana, a petrosal of *?Catopsalis joyneri* from the same formation, and the serial sections of the Late Cretaceous djadochtatherians *Chulsanbaatar* and *Nemegtbaatar*. They reconstructed the brain and cranial vasculature of *Nemegtbaatar*, and provided a glossary of the osteological, vascular and neuroanatomical cranial terminology. Hahn (1988) and Lillegraven & Hahn (1993) described isolated petrosals of the Late Jurassic paulchoffatiids. Miao (1988) described the skull of the Paleocene *Lambdopsalis* from China with a well preserved petrosal (see also Miao & Lillegraven 1986). Luo & Ketten (1991) studied isolated petrosals of the Late Cretaceous *?Meniscoessus*, Early Paleocene *?Catopsalis*, and three unidentified ptilodontoid petrosals, and applied computerized tomography (see also Luo 1989) to describe the inner structures. Wible & Hopson (1993) figured the lateral side of the braincase in *Chulsanbaatar* from the Late Cretaceous of Mongolia and an isolated petrosal of *Catopsalis* from the Late Cretaceous (or Early Paleocene) Hell Creek Formation, Montana (for discussion of age see Archibald & Lofgren 1990). Wible & Hopson (1995) illustrated and described petrosals of *Mesodma thompsoni* and *Catopsalis joyneri*. The inner structures of the petrosal have been described in *Lambdopsalis* by Meng & Fox (1995) and Meng & Wyss (1995) and the latter authors described a malleus, ectotympanic bone and a natural endocast of the inner ear of the Paleocene *Lambdopsalis* from China (see also Meng 1992). Meng & Fox (1995) discussed the lifestyle and function of hearing in *Lambdopsalis*. Wible & Hopson (1993) described single petrosals of '*Catopsalis*' and *Mesodma* from

the Late Cretaceous (or Early Paleocene) Hell Creek Formation, Montana. Hurum *et al.* (1996) described ear ossicles (incus and incomplete malleus) in *Chulsanbaatar* and commented on the inner ear structures in multituberculates. Rougier, Wible, & Novacek (1996) described a partial malleus, ectotympanic, stylohyal and a possible stapes of *Kryptobaatar* from the Late Cretaceous of Mongolia. Kielan-Jaworowska & Hurum (1997) published outline reconstructions, including ventral views with basicranial regions, of the skulls of several djadochtatherian taxa and those of *Ptilodus*, *Lambdopsalis* and *Taeniolabis* (the latter three taxa after Simpson 1937, Miao 1988, 1993, and Granger & Simpson 1929) including the petrosal structure. Hurum (in press) described the inner ear of *Chulsanbaatar* and *Nemegtbaatar*, and provided a reconstruction of the latter. Fox & Meng (1997) described the osseous inner ear of three Paleocene multituberculates.

Nemegtbaatar gobiensis Kielan-Jaworowska, 1974 (hereafter *Nemegtbaatar*) and *Chulsanbaatar vulgaris* Kielan-Jaworowska, 1974 (hereafter *Chulsanbaatar*) from the Late Cretaceous (?late Campanian; see Averianov 1997 and Kielan-Jaworowska & Hurum 1997 for age estimates) of Mongolia are the most fully described multituberculates. The skulls of these genera were first described by Kielan-Jaworowska (1974), one skull of each was serially sectioned in 1984 and the cranial vascular system and brain of *Nemegtbaatar* were reconstructed (Kielan-Jaworowska *et al.* 1986). The braincast of *Chulsanbaatar* was prepared and described by Kielan-Jaworowska (1983) and an emended reconstruction was given by Kielan-Jaworowska *et al.* (1986). Hurum (1992, 1994) used the sectioned skulls to reconstruct the sinus system, the snout and the anterior part of the orbit. The postcranial anatomy was described by Kielan-Jaworowska & Gambaryan (1994) and the masticatory musculature and jaw movements by Gambaryan & Kielan-Jaworowska (1995). Hurum *et al.* (1995, 1996) reported the presence of an incus and a small fragment of a malleus in *Chulsanbaatar* and Hurum (in press) has since described the inner ear of both *Nemegtbaatar* and *Chulsanbaatar*. Recently Kielan-Jaworowska & Hurum (1997) have discussed the relationship of these genera to other multituberculates and erected the suborder Djadochtatheria, proposed for most Mongolian Late Cretaceous multituberculates (MLCM).

This work relies on the same serial sections as used in a previous paper (Hurum 1994) in which the following skull bones were described: nasal, premaxilla, maxilla, frontal, palatine, lacrimal, median septum, cribiform plate, and presphenoid of *Nemegtbaatar* and *Chulsanbaatar*; and vomer, incomplete pterygoid and orbitosphenoid of *Chulsanbaatar*. The present paper includes a description of the remaining bones and this allows a summary to be made of the cranial anatomy of *Nemegtbaatar* and *Chulsanbaatar*. The description of the skull bones is from the front backwards (following Simpson 1937 and Kermack *et al.* 1981).

Methods, material and terminology

The serial sections from the skulls of *Chulsanbaatar vulgaris* (ZPAL MgM-1/84) and *Nemegtbaatar gobiensis* (ZPAL MgM-1/76), were made by Prof. Zofia Kielan-Jaworowska using a Jung Microtome, in 1982–1984 at the Institute de Paléontologie,

Muséum National d'Historie Naturelle, Paris and at the Department of Comparative Anatomy, University of Paris VII. The original numbering of the sections is from back to front. From the *Chulsanbaatar* skull, 885 sections 20 µm thick were obtained, and from the *Nemegtbaatar* skull, 1370 sections 25 µm thick. Three reference points were identified through all the sections (Kielan-Jaworowska *et al.* 1984; Kielan-Jaworowska *et al.* 1986; Hurum 1994).

The sections were examined using a Leitz Orthoplan microscope with Leitz Ploemopak 1.25 incident-light fluorescence, 100 W Hg lamp and filterblock A2 (see Hurum 1994 for details). Photographs of every fifth section of *Nemegtbaatar* and *Chulsanbaatar* were enlarged 16 and 20 times, respectively, and these formed the base for models of the basicranial structures. Kielan-Jaworowska *et al.* (1986) produced a 3-D wax model of the brain and cranial vasculature, and one of the inner ear of *Nemegtbaatar* which they did not describe and which is described by Hurum (in press). For the models used here each section was traced onto a 2 mm thick plastic background and individual elements cut out using a heated wire. The cut-outs were then glued to a transparent film, placed over the photographed section and marked with three reference points. The assembled sheets produced a 3-D model for the study.

In order to calculate the volume of the subarcuate fossa, the models were immersed in water.

To aid this study the following comparative material has been used:

1. An unidentified multituberculate petrosal (ZPAL MK-1) and a cast of ?*Catopsalis joyneri* petrosal (MCZ 19176), both from the Hell Creek Formation, Montana (see Kielan-Jaworowska *et al.* 1986: pl. 1: 1; pl. 3: 3).

2. *Chulsanbaatar* skull (ZPAL MgM-1/121a), from the Barun Goyot Formation, (?late Campanian), Nemegt, Gobi Desert, Mongolia, with a dorsally exposed sphenoid complex and partially preserved anterior lamina of the petrosal (this paper, Fig. 13).

3. *Chulsanbaatar* endocranial cast (ZPAL MgM-1/88), from the Red beds of Khermeen Tsav (?late Campanian), Khermeen Tsav II, Gobi Desert, Mongolia (see Kielan-Jaworowska 1983: pl. 1: 1).

4. Holotype skull of *Nemegtbaatar gobiensis* (ZPAL MgM-1/81), from the Red beds of Khermeen Tsav (?late Campanian), Khermeen Tsav II, Gobi Desert, Mongolia, (Kielan-Jaworowska 1974: pls V, VII; fig. 3); Gambaryan & Kielan-Jaworowska 1995: fig. 2B).

5. Skulls of *Ornithorhynchus*, *Didelphis* and several extant insectivores and rodents.

The majority of osteological terms are from *Nomina Anatomica Veterinaria* (1973); otherwise from Grassé (1967), Starck (1979), Evans & Christensen (1979), and Kielan-Jaworowska *et al.* (1986). The terminology of the sphenoid complex follows that of Hahn (1981). The Latin terms for the anatomical parts are mentioned the first time the structures are described in the text.

In the descriptions the numbers in brackets refer to individual serial sections.

Institutional abbreviations: MCZ – Museum of Comparative Zoology, Harvard University, Cambridge, USA; ZPAL – Institute of Paleobiology, Polish Academy of Sciences, Warsaw.

Other abbreviations: MLCM – Mongolian Late Cretaceous multituberculates.

Descriptions

Nemegtbaatar gobiensis (Figs 1–7, 14A)

In the ZPAL collection there are six specimens of *Nemegtbaatar gobiensis*, from the Barun Goyot Formation, localities Khulsan and Nemegt, and from the Red beds of Khermeen Tsav, locality Khermeen Tsav II, Gobi Desert, Mongolia, collected by the Polish-Mongolian Palaeontological Expeditions. The sectioned skull of *Nemegtbaatar* (ZPAL MgM-1/76) is from the Khulsan locality. The adult skull length was estimated to be 40–45 mm (Kielan-Jaworowska *et al.* 1986). In the sectioned skull the anterior part of the snout was missing and the length of the skull was 36 mm.

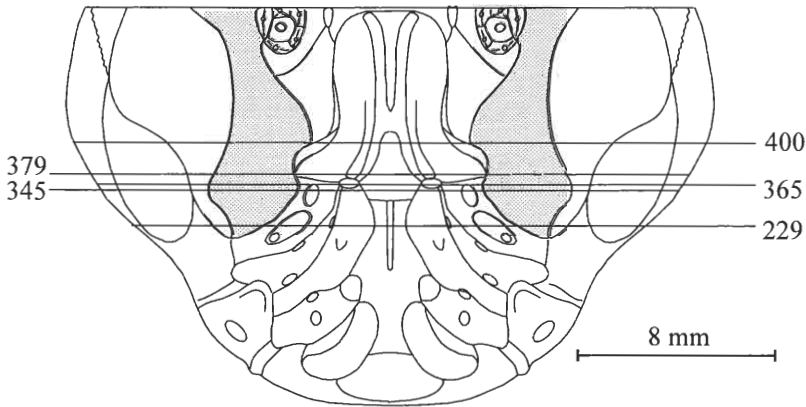


Fig. 1. Basicranial region of *Nemegtbaatar gobiensis*, modified from Kielan-Jaworowska & Hurum (1997), showing positions of sections published in this paper (Figs 2–6).

Sphenoid complex. — *Presphenoid* (*os presphenoidale*) – for description of presphenoid see Hurum (1994).

Alisphenoid (*ala ossis basisphenoidale*). — This bone may be divided descriptively into two parts, the basicranial part consisting of the alisphenoid ridge and the posterior part of the choanal channel (its ventral face partly covered by pterygoid), and the lateral wing which, in its most anterior part, forms the lateral border of the cavum epiptericum (400–350; Fig. 1). The basicranial part is first seen ventrally just anterior to the posterior margin of M2 (595). It covers the medial part of the maxilla and is bordered medially by the palatinum. The maxilla ends posteriorly just to the rear of M2, where the alisphenoid forms the anterior part of the basicranium (500) (Figs 2–5). The lateral wing contacts its basicranial part (379; Fig. 3) anteriorly at the level of the anterior end of the taenia clino-orbitalis, but is only partly preserved. The lateral part covers the anterior lamina of the petrosal at the level of foramen masticatorium and foramen ovale inferium (Fig. 5) until it disappears posterior to these foramina.

Orbitosphenoid (*ala ossis presphenoidale*). — This bone is part of the orbit and the lateral wall of the braincase (Figs 2, 3, 14A). Its most anterior exposure in lateral view is in the orbit at the level of the posterior margin of M2 (Hurum 1994: fig. 3). The bone

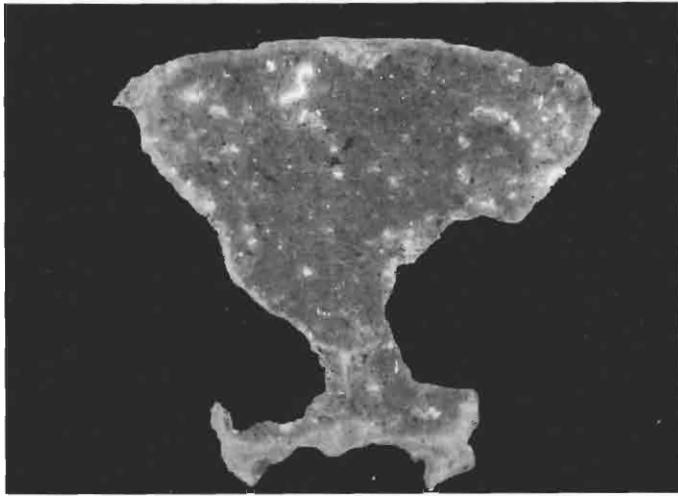
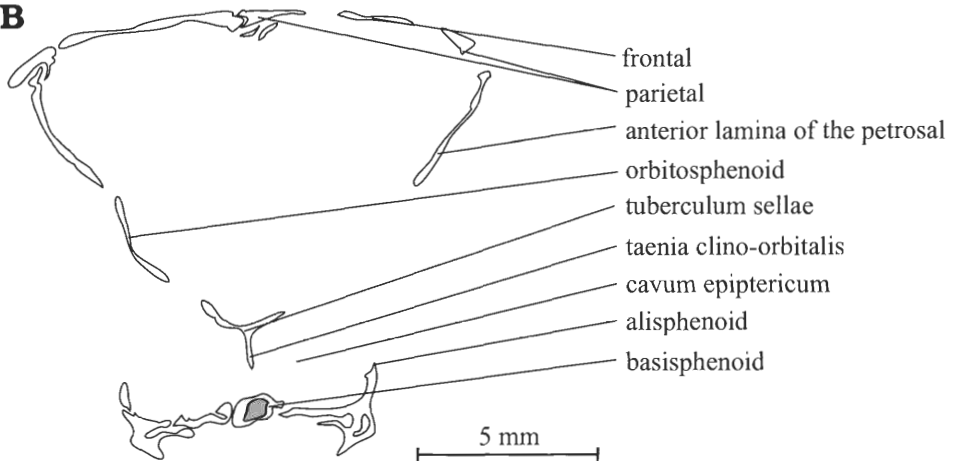
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Fig. 2. *Nemegtbaatar gobiensis* ZPAL MgM-I/76, section 400. **A**. Photograph made in ultraviolet light. **B**. Contour drawing with explanations, see Fig. 1 for position of the section. Grey – sinuses possibly filled with marrow in life.

is bordered anteriorly by the orbital process of the palatine and the orbital process of the frontal. Posteriorly the orbitosphenoid covers the orbital process of the frontal and remains as the only bone in the posterior part of the orbit, bordered dorsally by the parietal, ventrally by the basisphenoid, and most posteriorly by the petrosal. The orbitosphenoid contacts the anterior lamina of the petrosal at the level of the facial canal foramen (*foramen canalis facialis*).

Taenia clino-orbitalis (*taenia clinoorbitalis* = *pila antotica*). — The taenia clino-orbitalis is connected anteriorly to the most posterior part of the orbitosphenoid. The most anterior trace of the taenia clino-orbitalis (410) is as a flat, horizontal structure forming the border between the posterior blind-end of the nasal cavity below, and the brain-cavity above. This is the elevated tuberculum sellae. The bone expands posterior-

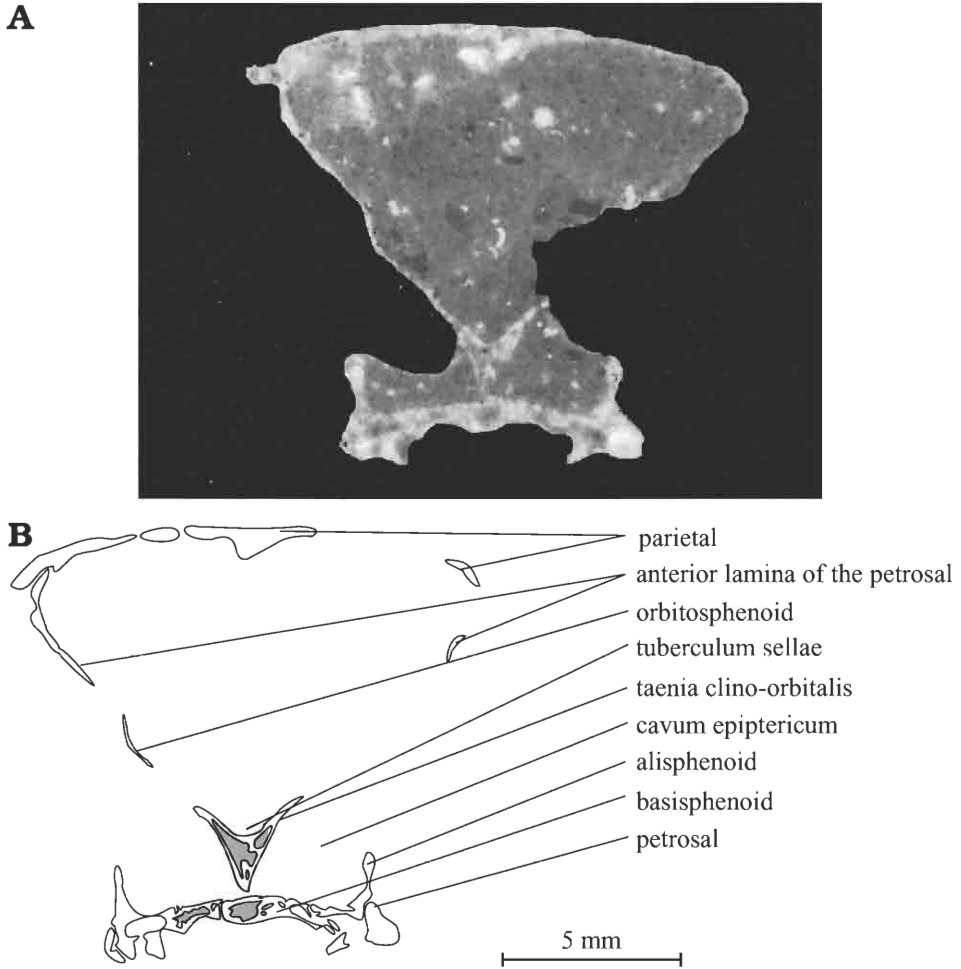


Fig. 3. *Nemegtbaatar gobiensis* ZPAL MgM-I/76, section 379. **A.** Photograph made in ultraviolet light. **B.** Contour drawing with explanations, see Fig. 1 for position of the section. Grey – sinuses possibly filled with marrow in life.

ly becoming T-shaped (400: Fig. 2). A large sinus inside the bone makes the bone V-shaped in the sections 395–379 (Fig. 3). The V-shape splits into two separate bones (375: Fig. 4) which meet the basisphenoid (360) and form the lateral limits of the fossa hypophyseos (Fig. 4). The taenia clino-orbitalis remains as a solid, medial wall in the cavum epiptericum and posteriorly it is hollow with sinuses (350: Fig. 5). At the level of the anterior end of the foramen masticatorium, the most anterior part of the internal carotid canal (*canalis caroticus*) is seen in the contact between the taenia clino-orbitalis and the basisphenoid-petrosal (Fig. 5). The taenia clino-orbitalis is graded into the cochlear housing below and the anterior lamina of the petrosal posteriorly at the level of foramen rotundum (305). The cavum epiptericum opens medially as the fossa for the semilunar ganglion. The lamina is pierced by a small metoptic foramen (*foramen metopticum*) in its posterodorsal part (Fig. 7).

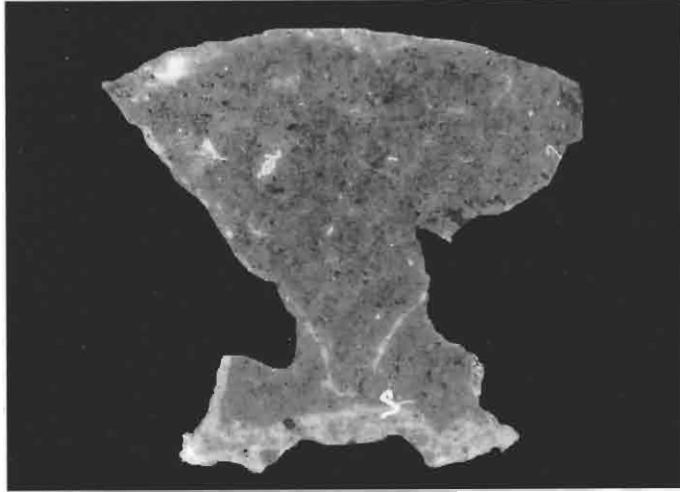
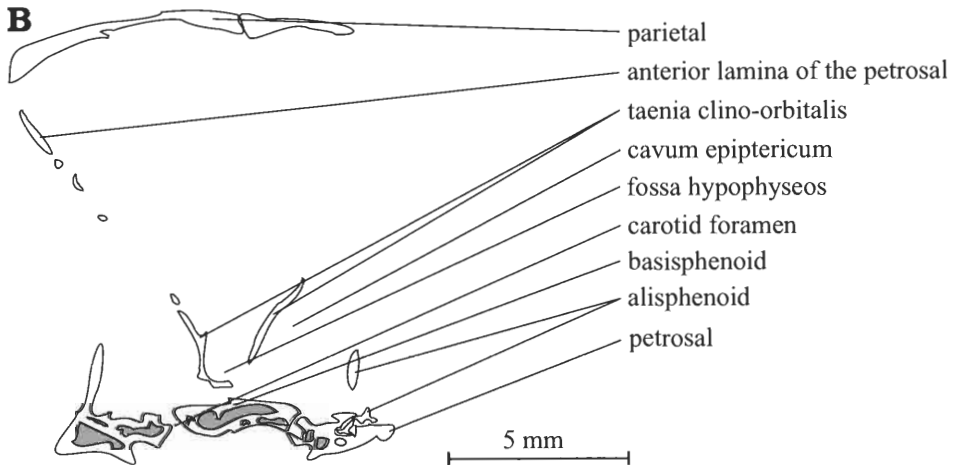
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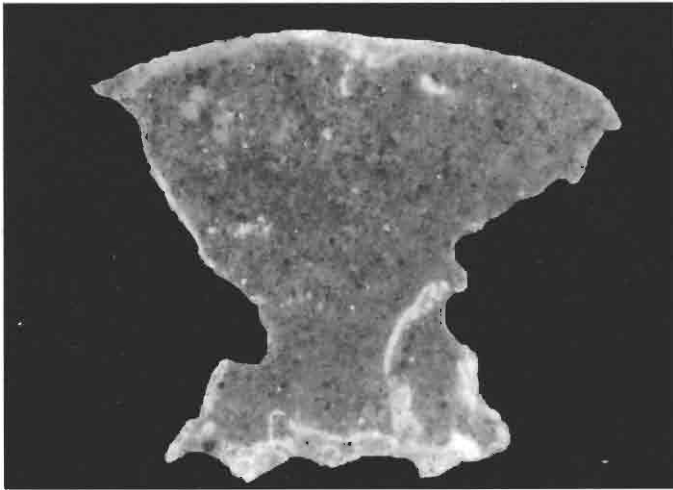
Fig. 4. *Nemegtbaatar gobiensis* ZPAL MgM-I/76, section 365. **A**. Photograph made in ultraviolet light. **B**. Contour drawing with explanations, see Fig. 1 for position of the section. Grey – sinuses possibly filled with marrow in life.

Basisphenoid (*os basisphenoidale*). — This is a robust bone and its sutures are well defined (Figs 2–5). It starts anteriorly at the level of the anterior end of the alisphenoid ridge (420) as a thin wedge separating the alisphenoids. The bone expands laterally and its posterior end is bordered laterally by the petrosal and posteriorly by the basioccipital (320).

Cavum epiptericum. — The cavum epiptericum is bordered medially by the robust wall of taenia clino-orbitalis, ventrally by the basisphenoid and petrosal, and dorsally by the anterior lamina of the petrosal (345: Figs 2–5).

Petrosal (*os petrosum*). — The following description adds to that provided by Kielan-Jaworowska *et al.* (1986). In multituberculates, the petrosal descriptively shows two conjoined parts: the basal part and the anterior lamina (*lamina anterior ossis*

A



B

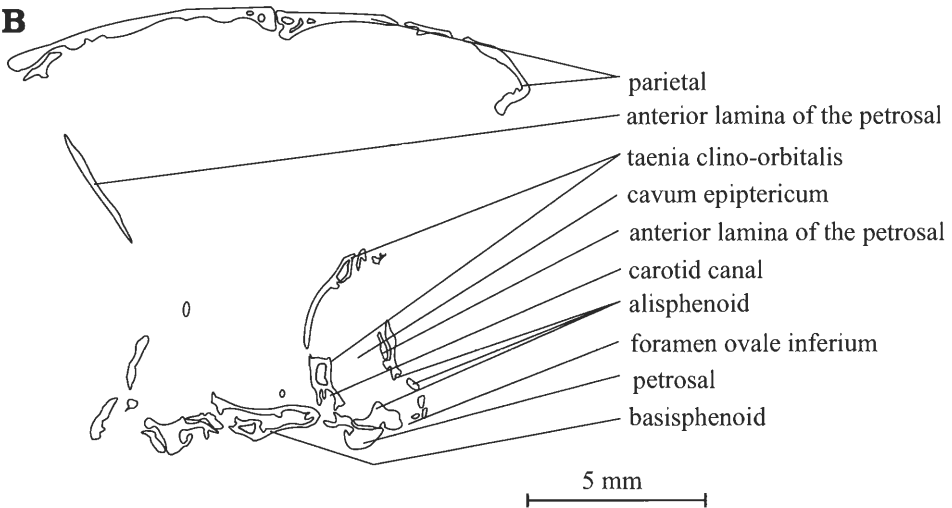


Fig. 5. *Nemegtbaatar gobiensis* ZPAL MgM-1/76, section 345. **A**. Photograph made in ultraviolet light. **B**. Contour drawing with explanations, see Fig. 1 for position of the section. Grey – sinuses possibly filled with marrow in life.

petrosi). The basal part encloses the hearing organs, the organs of balance, and two cranial nerves, the facial nerve (VII) and auditory-vestibular nerves (VIII).

Lateral view. — The anterior lamina in *Nemegtbaatar* is extensive in lateral view. It is first seen dorsoanteriorly as a thin wedge in the orbit between the orbital process of the frontal ventrally and parietal bone dorsally at the level of the posterior alveolus of M2 (435). The dorsal wedge expands ventrally (Figs 2–5, 14) and has a long contact with the orbitosphenoid posteriorly. The ventral part of the bone is incomplete, but is first observed anteriorly as a small fragment medial to the alisphenoid at the level of the most anterior part of the foramen masticatorium (345: Fig. 5). The dorsal wedge and the ventral part grow together and cover the lateroposterior part of the braincase

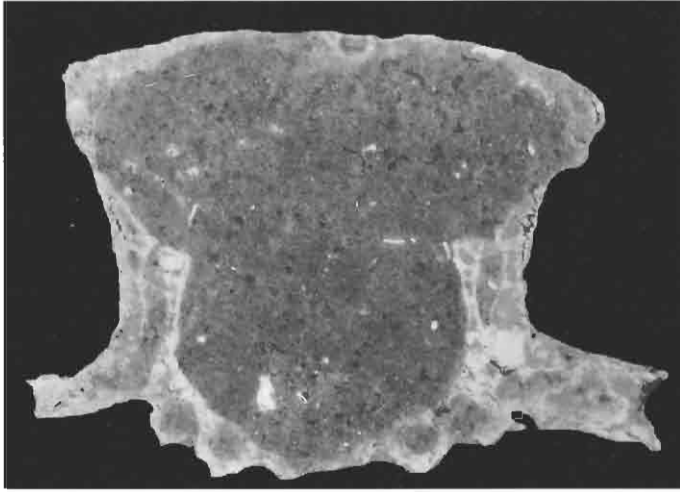
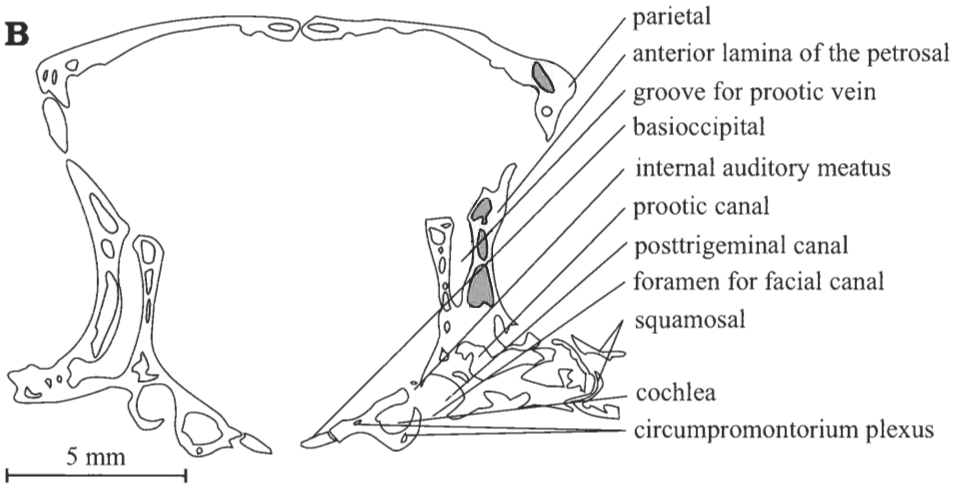
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Fig. 6. *Nemegtbaatar gobiensis* ZPAL MgM-I/76, section 229. **A.** Photograph made in ultraviolet light. **B.** Contour drawing with explanations, see Fig. 1 for position of the section. Grey – sinuses possibly filled with marrow in life.

(Fig. 6). The anterior lamina supports the groove for the tentorial sinus (*sinus tentorii*) and contacts the taenia clino-orbitalis medially at the level of the medial part of the foramen masticatorium (335). The posterior part of the alisphenoid covers the lateroventral part of the anterior lamina (Fig. 5) to the level of the posterior border of the foramen ovale inferium (295) where the alisphenoid tapers out and the anterior lamina remains as the only bone on the lateral wall of the braincase. The lamina is extensive in the posterolateral part of the braincase until it is covered laterally by the squamosal (245–85). The lamina contains the prootic canal (256–234) (*canalis prooticus*; Fig. 6) and the groove for the prootic vein (234–115). In its anterior part it forms the lateral wall of the cavum epiptericum (Fig. 5) and semilunar fossa (*impressio trigeminale*), and posteriorly it forms the lateral wall of the subarcuate fossa (*fossa subarcuata*).

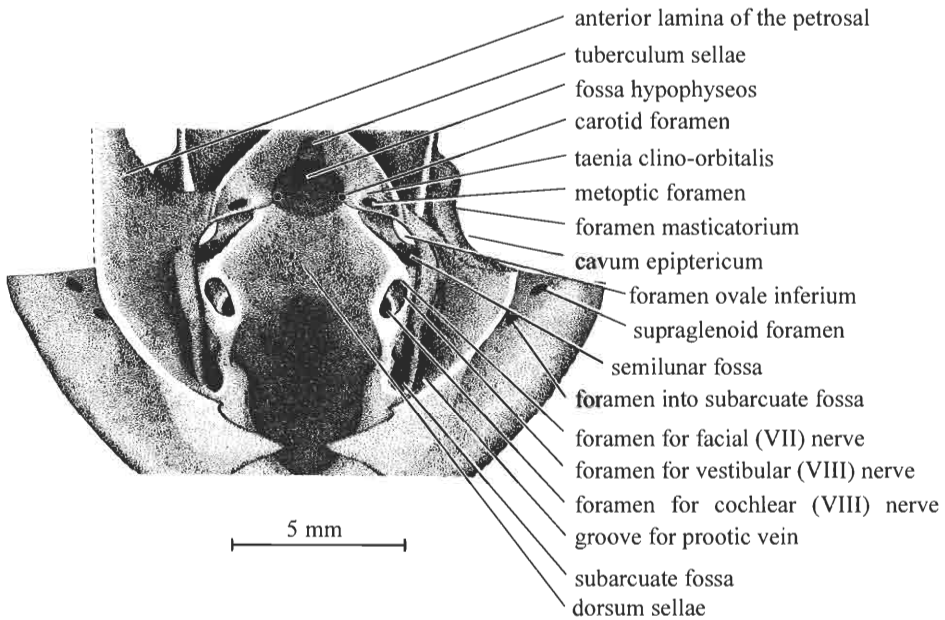


Fig. 7. Reconstruction of the petrosal and sphenoid region in *Nemegtbaatar gobiensis* (dorsal view), sections 55–410. The anterior lamina of the petrosal is removed on the right, along the dotted line, to reveal basicranial detail obscured by the lamina on the left.

There are four tiny, irregular canals inside the petrosal, in addition to the larger and more regular foramina and canals known from the petrosals of multituberculates and other early mammals. The canals are most probably parts of the circumpromontorium plexus and had a nutritive function. The cross-sections of two branches of one of them are visible in Fig. 6.

Dorsal view (cerebellar surface). — There are four major depressions on the dorsal side: semilunar fossa, prootic canal, subarcuate fossa, and the internal auditory meatus (Fig. 7).

The subarcuate fossa (*fossa subarcuata*, floccular fossa of Simpson 1937) (40–200) is the largest recess on the dorsal side of the petrosal and has a posteroventral outlet through the post-temporal fossa (canal). In the most anterior part of the subarcuate fossa there is a small foramen which opens outside as the posterodorsal foramen of the anterior lamina. The volume of the subarcuate fossa in *Nemegtbaatar* is 30.5 mm³.

The internal auditory meatus of *Nemegtbaatar* is oval and contains three foramina. A ridge (transverse septum) separates the posterior foramen for the cochlear nerve (VIII) from the anterior foramina for the vestibular (VIII) and facial nerves (VII).

Squamosal (*os squamosum*). — The bone is only partly preserved and is hollow, and in life may have had sinuses filled with marrow. The bone does not contribute to the inner surface of the braincase. The zygomatic arch (*arcus zygomaticus*) is broken off on both sides of the sectioned specimen. In the sections the squamosal bone is first observed anteriorly as a small part of the zygomatic arch (285–245). In the section 235, in which the anterior border of the hiatus Fallopii is seen, the squamosal covers the

most ventrolateral part of the petrosal. The squamosal remains as a small bone at the tip of the ventrolateral part of the petrosal (Fig. 6) until it expands dorsally at the level of the most anterior part of the fenestra vestibuli and meets the parietal bone (190). In the same section the squamosal forms the lateral wall of the ascending canal (*canalis ascendens*) and continues to do so posteriorly until the canal disappears. The squamosal covers the anterior lamina of the petrosal laterally (Fig. 14). The bone ends at the posterior end of the post-temporal fossa. The passage of the post-temporal canal is between the squamosal on the lateral side and the mastoid portion of the petrosal on the medial. The squamosal is excluded by the anterior lamina of the petrosal and the parietal from the internal surface of the braincase.

Parietal (*os parietale*). — The parietal is the most extensive bone of the skull (Figs 2–6). It is observed in the sections starting anteriorly at the level of the most posterior alveolus for M2 (565). When the skull is viewed dorsally, the most anterior exposure of the parietal is seen as a small splint of bone placed laterally on the skull roof. It is bordered anteriorly by the frontal and anteroventrally by the orbitosphenoid. Posterior to the most anterolateral exposure of the bone a medial process wedges between the two frontals (420: Fig. 2). The lateral and medial parts of the parietal bone join posteriorly at the level of the anterior limit of the dorsal foramen of the anterior lamina (371) (*foramen dorsalis laminae anterioris ossis petrosi*). From this point, to the end of the skull, the parietal remains the only bone in the skull roof (Fig. 4). Laterally the parietal is bordered first by the orbitosphenoid and posteriorly, beginning with the level of the facial canal foramen (224) by the anterior lamina of the petrosal. In the most posterior part, the squamosal covers the parietal laterally (85) and the parietal covers the occipital bone (40).

Basioccipital (*os occipitale, pars basilaris*). — The basioccipital is a single bone posterior to the basisphenoid (320), bordered laterally by the petrosal. The basioccipital is first seen anteriorly at the level of the middle of the foramen ovale inferum (Fig. 6). Posteriorly from the level of the anterior end of the posttemporal fossa and to the last preserved part of the skull only small remnants of the basioccipital are preserved.

Pterygoid (*os pterygoideum*). — The pterygoid is only partly preserved and as for all multituberculates situated in the middle of the choanal channel.

Jugal (*os zygomaticum*). — The zygomatic arches are broken off on both sides.

Chulsanbaatar vulgaris (Figs 8–13, 14B)

Only the type species is known from the Barun Goyot Formation (localities of Khulsan and Nemegt) and the Red beds of Khermeen Tsav (Khermeen Tsav II locality), all of ?late Campanian age, in the Gobi Desert, Mongolia. *Chulsanbaatar* is the most common (36 skulls being collected by the Polish-Mongolian Expeditions) and the smallest multituberculate species in the Barun Goyot Formation, with an adult size of the skull between 17–21 mm. The sectioned skull measured 17.7 mm.

Sphenoid complex. — For description of the presphenoid see Hurum (1994).

Alisphenoid. — This is a poorly preserved bone and difficult to identify in the sections. It extends between the posterior boundary of the maxilla and the petrosal.

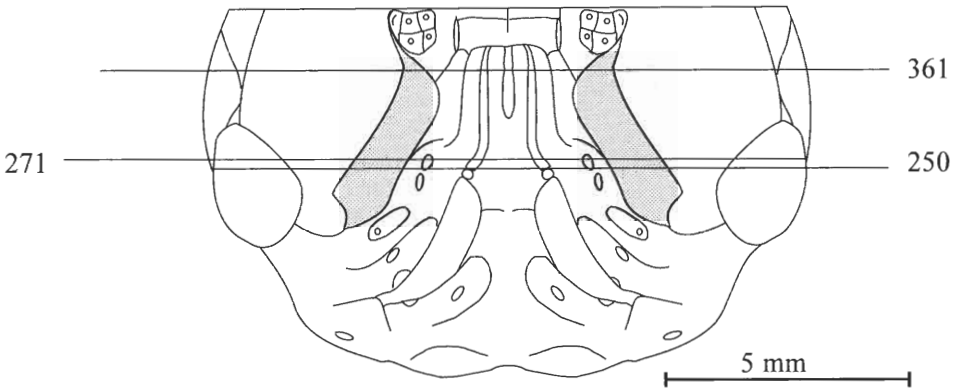
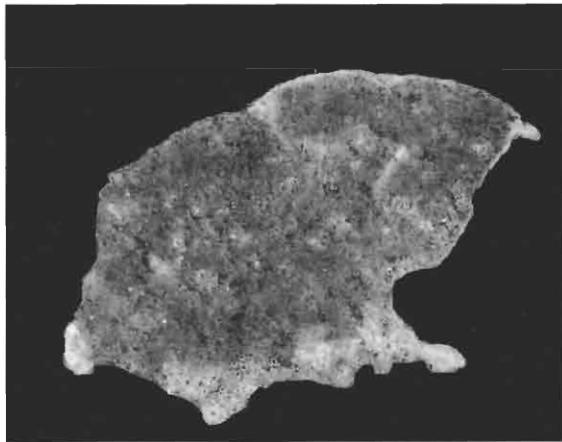


Fig. 8. Basicranial region of *Chulsanbaatar vulgaris*, modified from Kielan-Jaworowska & Hurum (1997), showing positions of sections published in this paper (Figs 9–11).

A



B

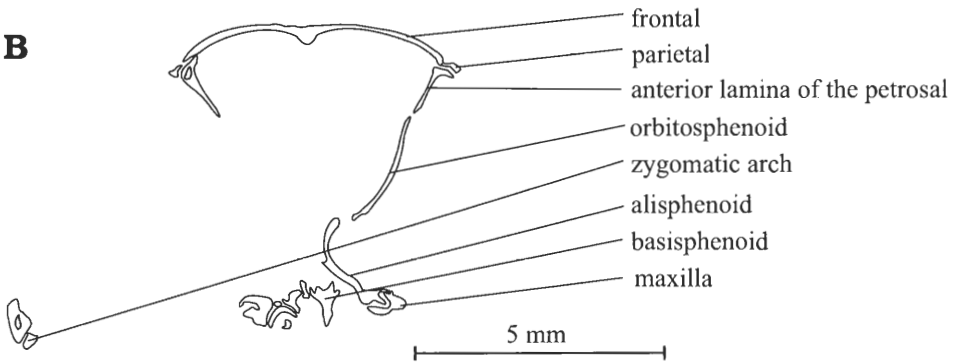


Fig. 9. *Chulsanbaatar vulgaris* ZPAL MgM-I/84, section 361. **A**. Photograph made in ultraviolet light. **B**. Contour drawing with explanations, see Fig. 8 for position of the section. Grey – sinuses possibly filled with marrow in life.

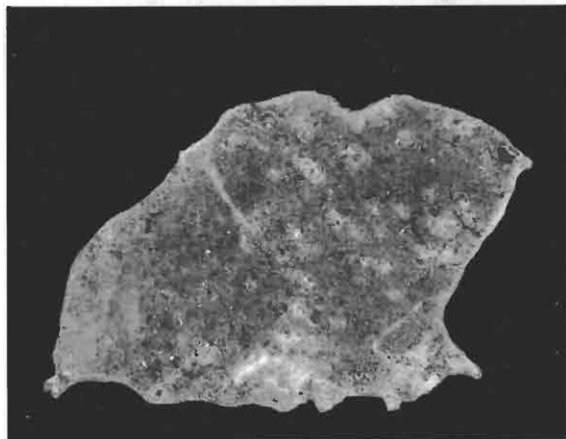
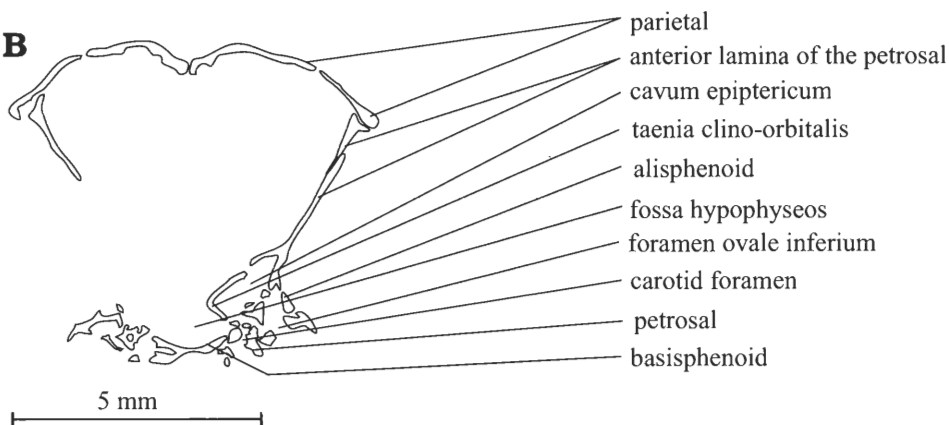
A**B**

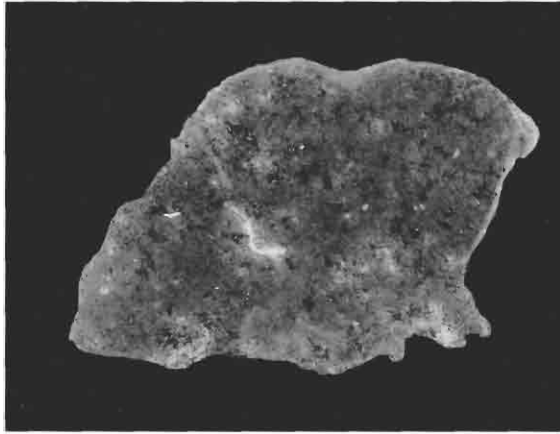
Fig. 10. *Chulsanbaatar vulgaris* ZPAL MgM-I/84, section 271. A. Photograph made in ultraviolet light. B. Contour drawing with explanations, see Fig. 8 for position of the section.

Its dorsal extension (Fig. 10) is difficult to reconstruct, but a dorsal flange limiting the most anterolateral part of the cavum epiptericum is tentatively reconstructed in Fig. 14.

Orbitosphenoid. — This bone is extensive, but not always easily identified in the sections (Fig. 9). It is first seen in the orbit at the level of the embrasure between M1 and M2 and forms the lateral wall of the anterior part of the braincase. The orbitosphenoid is bordered anteriorly by the frontal and dorsally by the frontal and the anterior lamina of the petrosal (Fig. 14B). The anterior lamina and the alisphenoid contact the orbitosphenoid posteriorly and ventrally.

Taenia clino-orbitalis. — The taenia clino-orbitalis is an oblique plate of bone which forms the medial wall of the cavum epiptericum (300–250: Figs 10–12). It begins anteriorly at the level of the anterior edge of the alisphenoid ridge (300), is in contact with the orbitosphenoid and ends at the level of the foramen ovale inferium (250: Fig. 11). The taenia clino-orbitalis meets the anterior lamina of the petrosal

A



B

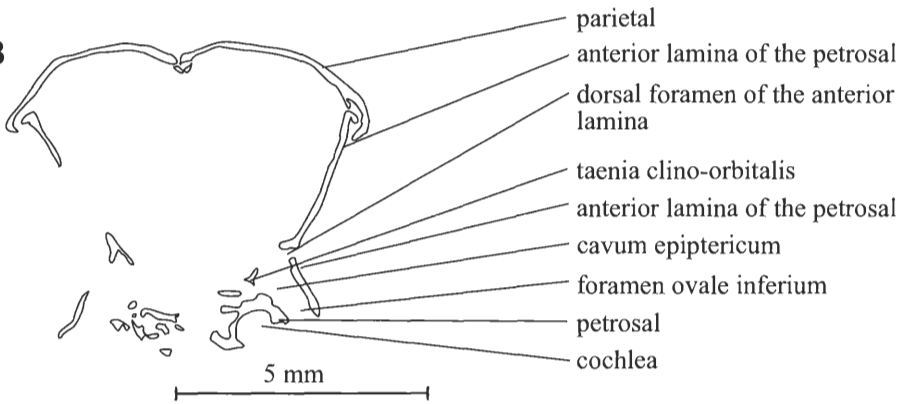


Fig. 11. *Chulsanbaatar vulgaris* ZPAL MgM-I/84, section 250. **A.** Photograph made in ultraviolet light. **B.** Contour drawing with explanations, see Fig. 8 for position of the section.

dorsally and the petrosal and/or alisphenoid ventrally (265). The lamina contains one foramen in its posterodorsal part, the metoptic foramen (Fig. 12).

Basisphenoid. — This bone is not preserved in the sectioned skull due to distortion.

Cavum epiptericum. — This is an extracranial space that extends from the level of the alisphenoid ridge anteriorly to the foramen ovale inferium posteriorly (300–245: Figs 10–12). The cavum epiptericum is laterally bordered by the anterior lamina of the petrosal and possibly by the alisphenoid. Dorsally it is roofed by the anterior lamina and ventrally floored by the alisphenoid anteriorly and the petrosal posteriorly. The preservation is such that it is not possible to identify the boundary between the alisphenoid and the petrosal.

Petrosal. — The petrosal of *Chulsanbaatar*, in ventral view, is bordered anteriorly by the alisphenoid and pterygoid, medially by the basisphenoid, medially and posteriorly by the basioccipital and laterally by the squamosal. The circumpromontorium plexus in the petrosal is less clearly seen in the sections than in *Nemegtbaatar*, due to

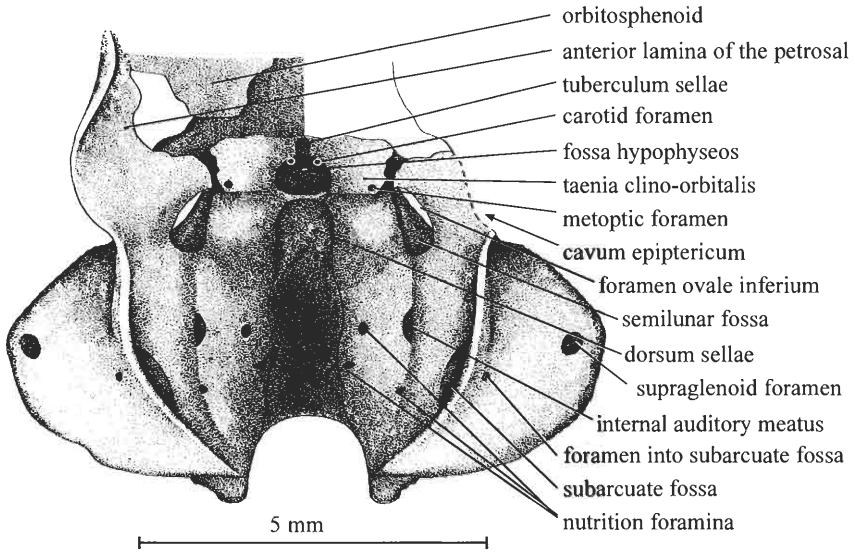


Fig. 12. Reconstruction of the petrosal and sphenoid region in *Chulsanbaatar vulgaris* (dorsal view), sections 30–361.

distortion and poor preservation. Hurum (in press) described briefly three canals in the petrosal and numbered them from 1 to 3.

Lateral view. — The anterior lamina of the petrosal builds most of the posterior half of the lateral wall of the braincase (Figs 9–12). The lamina borders the brain cavity and partly cavum epiptericum laterally. The lamina is first seen dorsoanteriorly in the orbit at the level of the last alveolus of M2 (361: Fig. 9). It continues as a thin wedge dorsal in the orbit at the level of the most anterior exposure of the parietal bone. Dorsally the lamina contacts the parietal, anteriorly the orbitosphenoid and posteriorly the squamosal. Posteriorly the lamina extends ventrally and joins the basal part of the petrosal at the level of the carotid foramen (275: Fig. 10). There is only one foramen in the lamina — the dorsal foramen of the anterior lamina, at the level of the foramen ovale inferium (245–255: Fig. 11).

Dorsal side. — In the internal auditory meatus there are three foramina. These are for the vestibular, cochlear and facial nerves. In dorsal view the meatus is partially hidden by the curved wall between the subarcuate fossa and semilunar fossa (Fig. 12). There are three nutrition foramina posteromedial to the internal auditory meatus.

The volume of the subarcuate fossa is estimated as 2.75 mm^3 .

Squamosal. — The squamosal contributes notably to the zygomatic arch which is incomplete in the sectioned specimen. However, it is seen as a thin bone covering the posterior half of the petrosal laterally (171–105) and is excluded from the inner surface of the braincase. The bone covers only the most lateral part of the petrosal anteriorly and expands posterodorsally to the end of the skull (Fig. 14).

Parietal. — The parietal bone is extensive and builds the whole cranial roof posteriorly (Figs 9–11, 14), covering the posterior part of the brain. It is wedged anteriorly between the anterior lamina ventrally and the frontal medially (361: Fig. 9).

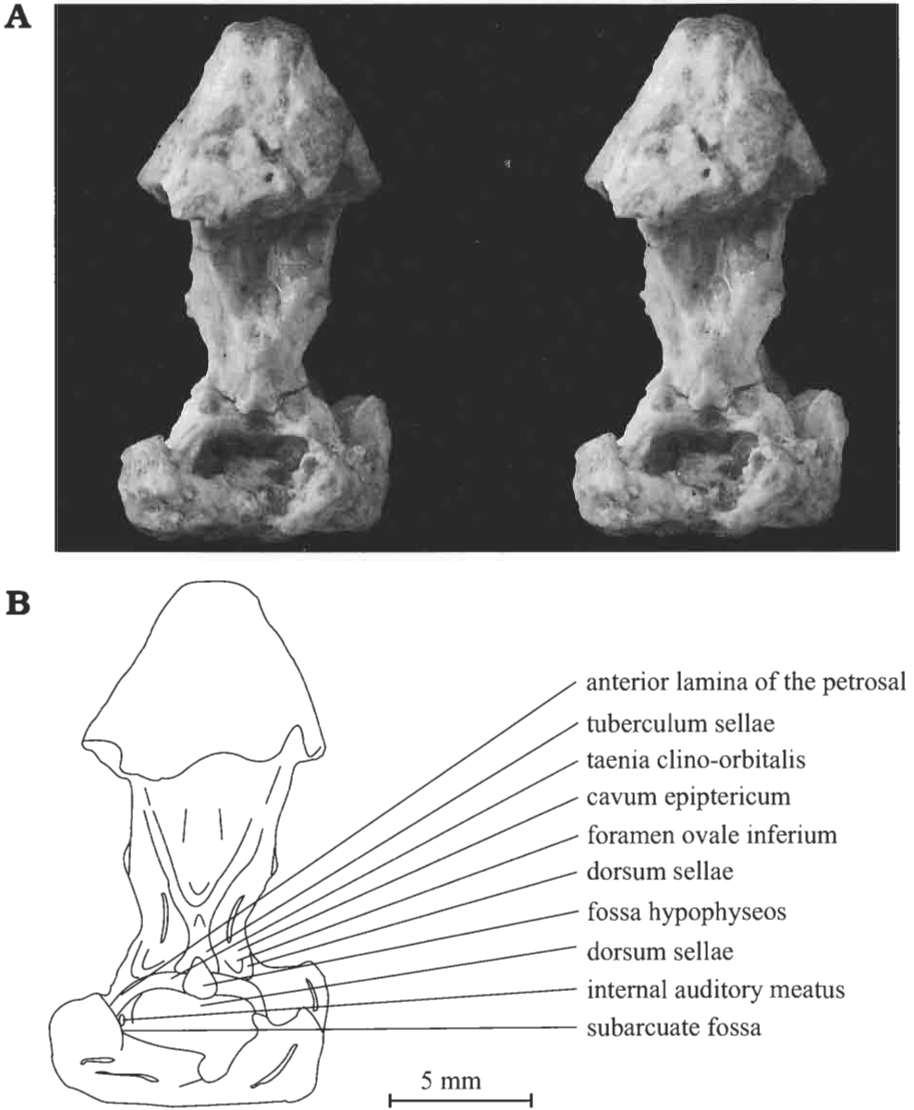


Fig. 13. *Chulsanbaatar vulgaris* ZPAL MgM-I/121a. Dorsal view of sphenoid region with the parietal and frontal bones removed. **A.** Stereo photograph. **B.** Contour drawing with explanations.

Both parietal bones meet each other at the level of the dorsal foramen of the anterior lamina (255). The parietal forms the postorbital process and posteriorly contacts the squamosal (120) ventrally.

Basioccipital. — The basioccipital bone is well preserved and is seen from the level of the posterior edge of the foramen ovale inferium until the end of the skull. It separates the petrosals in the basicranial region and contains sinuses possibly filled with marrow in life.

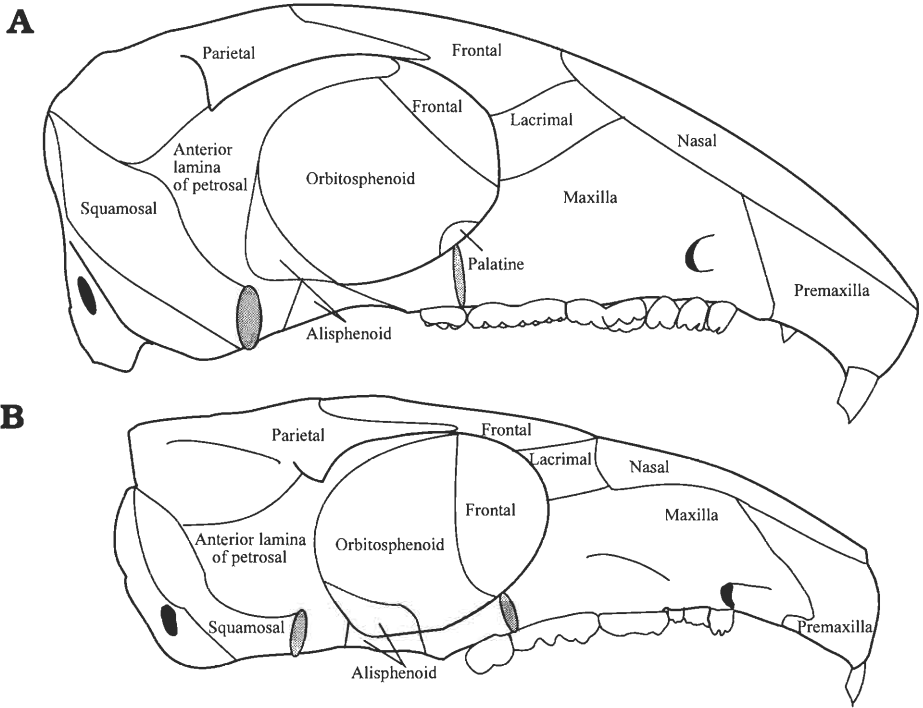


Fig. 14. Reconstructions of skulls of **A.** *Nemegtbaatar gobiensis* (skull length 45 mm) and **B.** *Chulsanbaatar vulgaris* (skull length 21 mm) in lateral view, not to scale.

Pterygoid. — The pterygoid has been preserved only in a few sections and it proved impossible to reconstruct its whole extent.

Jugal. — The jugal has not been preserved in the sections.

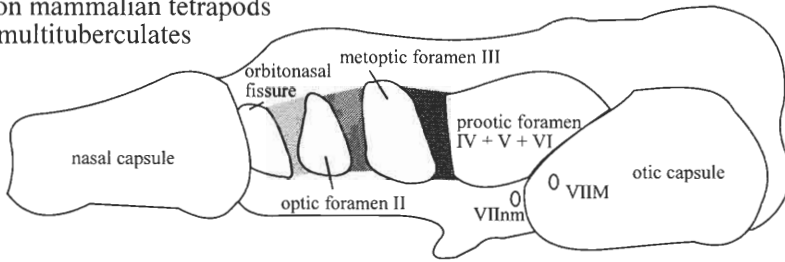
The sphenoid complex of ZPAL MgM-I/121a. — The sphenoid complex has been prepared from the dorsal side and the frontal and parietal bones have been removed (Fig. 13). In both sides the taenia clino-orbitalis is broken off, but the raised tuberculum sellae and the deep fossa hypophyseos are clearly visible. The anterior lamina is broken off on both sides and this makes the cavum epiptericum visible. The foramen ovale inferium is placed in the posterior end of cavum epiptericum. The posteroventral part of the inside of the braincase, to the rear of the fossa hypophyseos, is only partly visible. It is distorted and filled with sediment. The deep pocket just posterior to the fossa hypophyseos is possibly a part of the sphenoid sinus, whose roof is removed.

Reconstruction. — In Fig. 14, I present reconstructions of skulls of *Nemegtbaatar* and *Chulsanbaatar* based on the foregoing descriptions.

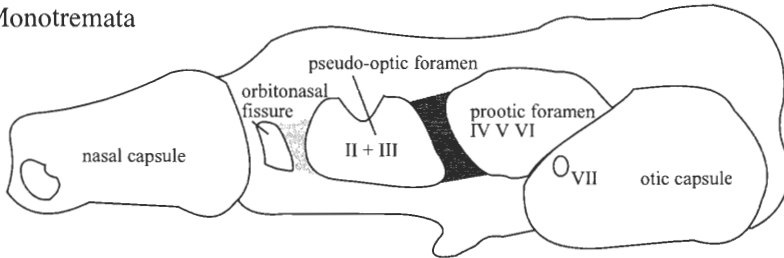
Comparisons

Cavum epiptericum and the sphenoid region. — The cavum epiptericum (Gaupp 1902; Goodrich 1930; DeBeer 1937; Kuhn & Zeller 1987) is an extracranial space in the reptilian skull, situated lateral to the primary side wall of the braincase.

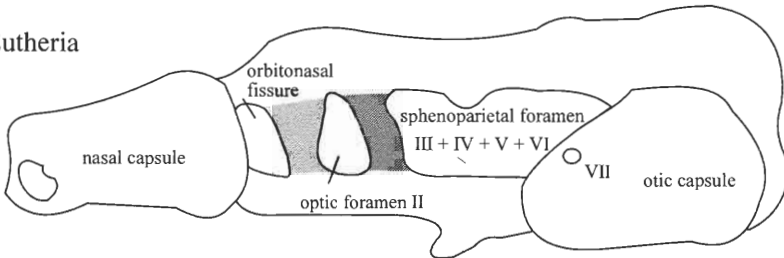
Non mammalian tetrapods
+ multituberculates



Monotremata



Eutheria



Metatheria

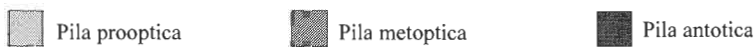
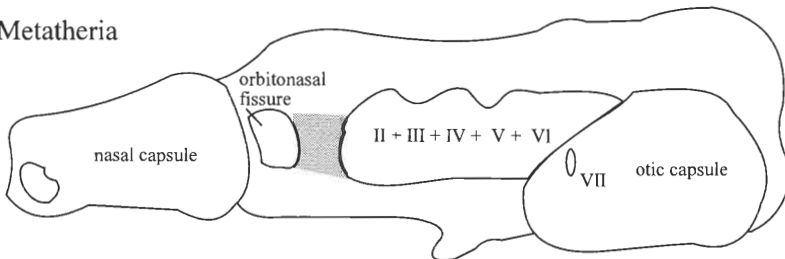


Fig. 15. The cartilaginous braincase in different amniotes, placement of facial nerve (VII) in non-mammalian tetrapods (VIIInm) is different from multituberculates (VIIM) (after Goodrich 1930; Moore 1981).

The space is incorporated into the cranial cavity, although it remains extradural, in all living mammals with the secondary wall of the braincase as its lateral border.

In the primary, cartilaginous braincase of non-mammalian tetrapods there are three pillars running from the cranial base to the margin of the chondrocranium in the

embryo, situated between the nasal capsule and otic capsules. In lateral view (from the front) these are: pila prooptica, pila metoptica and pila antotica (Fig. 15). These pillars contribute to the margins of four foramina: the orbitonasal fissure, optic foramen, metoptic foramen and prootic foramen. All three pillars are retained in non-mammalian tetrapods. The anterior pila prooptica is retained in monotremes, metatherians and eutherians and forms the posterior margin of the inlet to the cavum orbitonasale (Fig. 15). The medial pila metoptica is retained in eutherians, but lost in monotremes and metatherians. Between the pila prooptica and metoptica in non-mammalian tetrapods and eutherians is the optic foramen for the optic nerve (II). In monotremes the optic foramen is confluent with the medial metoptic foramen for the oculomotor nerve (III) forming a pseudo-optic foramen, but the posterior pila antotica is retained. The pila antotica of monotremes forms the posterior margin of the pseudo-optic foramen and the anterior margin of the prootic foramen. The prootic foramen contains the trigeminal (V) and abducens nerves (VI), and there is usually a small separate foramen for the trochlear nerve (IV; Moore 1981). In marsupials and eutherians the pila antotica is lost. In marsupials the optic, metoptic and prootic foramina are confluent, while in eutherians only the metoptic and prootic foramina are confluent.

Older authors used the term *taenia clino-orbitalis* in its literary meaning, as a band between orbitosphenoid and the edge of the dorsum sellae or its neighbourhood, rather than the round-sectioned rod running from basicranium to the skull margin as in squamates. Kielan-Jaworowska *et al.* (1986) favoured '*taenia clino-orbitalis*' over '*pila antotica*' following Gaupp (1902). The completely ossified *taenia clino-orbitalis* (ossified *pila antotica*) is absent in all described Mesozoic mammals except multituberculates (Kielan-Jaworowska *et al.* 1986; Miao 1988) and possibly *Triconodon mordax* (Kermack 1963). A partially ossified *taenia clino-orbitalis* is present in *Adelobasileus* (Lucas & Luo 1993: fig. 10A), *Sinoconodon* and *Megazostrodon* (Lucas & Luo 1993). The presence of *taenia clino-orbitalis* in *Morganucodon* is controversial, Hopson (1964) described it as present, but reduced; Kermack *et al.* (1981: fig. 100A) reconstructed a complete *taenia clino-orbitalis*, while in their fig. 102G they reconstructed it as a membrane only; Crompton & Sun (1985; fig. 6B) figured it as present. Rowe (1988) marked it as present in his character matrix, and Lucas & Luo (1993: table 2) followed this. Wible & Hopson (1993) refuted this opinion and stated that this very weak process in *Morganucodon* is not on the same scale as in non-mammalian cynodonts and multituberculates. The *taenia clino-orbitalis* is absent in *Vincelestes* (Hopson & Rougier 1993).

The cavum epiptericum is variously floored in Mesozoic mammals. Crompton & Sun (1985) stated that the anterior lamina of the petrosal forms a partial floor of the cavum epiptericum in *Morganucodon* and *Sinoconodon* (see also Miao 1988). Wible & Hopson (1993) described a complete floor built of the anterior lamina in *Vincelestes* and in triconodontids. *Haldanodon* has a badly damaged floor (Lillegraven & Krusat 1991). In *Adelobasileus* (Lucas & Luo 1993) the floor is formed by the anterior lamina of the petrosal.

In monotremes the cavum epiptericum is medially bordered by a small remnant of the primary braincase wall, a low ridge that is the ossified base of the *taenia clino-orbitalis*. The lateral, secondary braincase wall is the anterior lamina of the petrosal. The cavum epiptericum is floored by the anterior lamina of the petrosal and the pars

cochlearis of the petrosal in *Ornithorhynchus*, while *Tachyglossus* has a complete floor formed by the anterior lamina of the petrosal, the petrosal, ectopterygoid and palatine (Wible & Hopson 1993; Kuhn & Zeller 1987).

Dr. Zhexi Luo (personal communication, January 1998) drew my attention to the fact, that in MLCM, the taenia clino-orbitalis is different from that in other mammals and reptiles in its connections to other structures of the cranium. In monotremes, the taenia clino-orbitalis has a single posterior connection to the junction of the dorsum sellae and the pars cochlearis (see embryonic condition in *Tachyglossus* illustrated by Kuhn & Zeller 1987: fig. 3 and in *Ornithorhynchus* by Zeller 1989: fig. 5). This condition of monotremes closely resembles the general pattern of the taenia clino-orbitalis in the chondrocrania of diapsids (Goodrich 1930; DeBeer 1937). Although the dorsum sellae is not well developed in non-mammalian cynodonts, because of the generally poor ossification of the entire basicranium, the pila antotica has the same position and pattern of connections as in diapsids.

By contrast, the taenia clino-orbitalis in MLCM has two separate, posterior connections:

- the first is to the dorsum sellae (= posterior wall or slope of fossa hypophyseos) and the pars cochlearis (= 'promontorium');
- the second connection is to the anterior lamina of the petrosal (= lamina obturatoria in embryological terms). In monotremes, there is no such connection between the taenia clino-orbitalis and the lamina obturatoria (Kuhn & Zeller 1987: fig 3 and Zeller 1989: figs 19, 20). This is a very important difference between monotremes and multituberculates that has not received much attention. MLCM have this 'second connection' to the anterior lamina of the petrosal because the taenia is extremely broad.

Hahn (1981) described in dorsal view the first sphenoid complex seen in multituberculates. He interpreted the preserved structures in *Pseudobolodon* as showing a reduced crest of the taenia clino-orbitalis, as in monotremes, and claimed that the cavum epiptericum was completely incorporated into the cranial cavity. This opinion was refuted by Kielan-Jaworowska *et al.* (1986) and Miao (1988) who described the taenia clino-orbitalis in *Nemegtbaatar* and *Chulsanbaatar*, and *Lambdopsalis*, respectively, as much more extensive than in monotremes. The taenia clino-orbitalis is complete in *Nemegtbaatar* and *Chulsanbaatar* (Figs 7, 12) and is very robust in relation to other bones of the skull. The taenia clino-orbitalis is in its most anterior part in contact with the orbitosphenoid, which is a primitive condition shared with cynodonts. Two small perforations of the taenia clino-orbitalis were described in *Pseudobolodon* (Hahn 1981) and *Lambdopsalis* (Miao 1988). Miao interpreted them as metoptic foramina. In *Nemegtbaatar* and *Chulsanbaatar* one foramen is preserved in the posterodorsal part of the anterior lamina (Figs 7, 12).

The intracranial sphenoid complex in *Pseudobolodon* is tripartite in dorsal view; the middle region consists (from the front) of fovea hypochiasmatica, tuberculum sellae, fossa hypophyseos (= pituitary fossa) and dorsum sellae (Hahn 1981). Fovea hypochiasmatica is a deep depression containing the optic foramen. Posteriorly the tuberculum sellae arises from the depression. The two prominent crests arising from the posterior end of tuberculum sellae form the taenia clino-orbitalis. These crests surround the fossa hypophyseos and form the medial walls of the cavum epiptericum.

The dorsum sellae is somewhat raised above the fossa hypophyseos in *Pseudobolodon* and is laterally penetrated by the carotid foramen. The lateral regions are occupied by the cavum epiptericum. The preserved part of the cavum epiptericum in *Pseudobolodon* starts anteriorly at the canalis sphenorbitalis and ends posteriorly at the foramen ovale inferium. The canalis sphenorbitalis is long and opens into the orbit as fissura sphenorbitalis. There is a closed canal in the bottom of the cavum epiptericum. The intracranial sphenoid region of *Nemegtbaatar* and *Chulsanbaatar* is different to that in *Pseudobolodon*, as described by Hahn (1981). In *Nemegtbaatar* the fovea hyposchiastica is not as deep and well defined, but this can be a result of distortion in the relevant sections. The tuberculum sellae in *Nemegtbaatar* is wider and more raised above the base of the skull (Fig. 7). The structure is formed where both sides of the taenia clino-orbitalis grow together forming a V-shaped bone. Posterior to the tuberculum sellae is the fossa hypophyseos which is a shallow, medial groove in the basisphenoid, limited laterally by the taenia clino-orbitalis. In the postero-lateral part of the fossa is the dorsal opening of the carotid canal, but this structure in *Pseudobolodon* is in the dorsum sellae (Hahn 1981: fig. 1b). The dorsum sellae, situated posterior to the fossa hypophyseos, is slightly elevated. In *Chulsanbaatar* the structure of the sphenoid complex is very similar (Fig. 12), except for the placement of the dorsal opening of the carotid canal, which is more anterior in the fossa hypophyseos. As *Chulsanbaatar* is more tiny and delicate than *Nemegtbaatar*, the shape differences in the sphenoid region could be allometric. The taenia clino-orbitalis is not as well ossified in *Chulsanbaatar* as in *Nemegtbaatar* and this may also explain the difference in shape of the most anterior part of the bone as shown in the reconstruction (Figs 7 and 12).

The lateral wall of the cavum epiptericum in *Nemegtbaatar* consists of a large anterior lamina of the petrosal and possibly, most anteriorly, of a small flange of the alisphenoid, but due to the state of preservation, the extent of the alisphenoid is only tentatively recognized. In multituberculates the cavum epiptericum was described as floored by the petrosal (Kielan-Jaworowska *et al.* 1986; Hahn 1988), but this study indicates that a small anterior part of the cavum epiptericum may be floored by the alisphenoid.

In marsupials and eutherians the cavum epiptericum is incorporated into the cranial cavity (Goodrich 1930). The taenia clino-orbitalis is missing and only marked by the cerebral dura mater, while in some forms possible remnants of the original side wall may be found as isolated cartilaginous nodules (DeBeer 1937). The space is laterally bordered by the alisphenoid, which also forms much of the floor (Wible 1990).

The pila metoptica is ossified in multituberculates and the optic foramen is retained as a separate opening and pierces the orbitosphenoid at least in *Lambdopsalis* (Miao 1988), *Pseudobolodon* (Hahn 1981), and possibly also in *Nemegtbaatar* (Kielan-Jaworowska *et al.* 1986), this is similar to eutherians and non-mammalian tetrapods. The pila prooptica is retained in all extant mammals, non-mammalian tetrapods and in multituberculates.

An osseous wall separating the cavum epiptericum from the posterior cavum supracochleare is absent in multituberculates, *Morganucodon*, *Sinoconodon*, *Haldanodon*, and *Ornithorhynchus* and is a synapomorphy of marsupials and eutherians (Wible 1990; Rougier, Wible, & Hopson 1996).

Orbitosphenoid. — The orbitosphenoid forms a large part of the orbital wall and the lateral side of the braincase in *Nemegtbaatar* and *Chulsanbaatar* (Fig. 14). Simpson (1937) tentatively recognized the orbitosphenoid in *Ptilodus* as a large element above the maxillary process in the orbit whilst in *Kamptobaatar*; Kielan-Jaworowska (1971) reconstructed the orbitosphenoid as a large contributor to the orbital wall. Miao (1988), on the other hand, described the orbitosphenoid in *Lambdopsalis* as a small, vertical bone surrounding the optic foramen. In *Lambdopsalis* the orbital process of the frontal occupies a part of the orbital wall that is built by the orbitosphenoid in *Nemegtbaatar*, *Chulsanbaatar* and *Kamptobaatar*. The medial placement of the orbitosphenoid in respect to the alisphenoid in multituberculates is related to the posterior extension of the orbitosphenoid, the taenia clino-orbitalis, which forms the medial wall of the cavum epiptericum medial to the anterior lamina of the petrosal (Kielan-Jaworowska *et al.* 1986).

Alisphenoid. — The alisphenoid in *Nemegtbaatar* and *Chulsanbaatar* may descriptively be divided into two parts: the obvious ventral part and the less obvious lateral, ascending part. In both taxa the bone in ventral view differs from that described by Kielan-Jaworowska *et al.* (1986). These authors described an ectopterygoid bone situated between the alisphenoid posteriorly and maxilla anteriorly. This is not the case as the whole area between the petrosal posteriorly and the maxilla anteriorly is occupied by the alisphenoid.

The embryological development of the anterior lamina of the petrosal and the alisphenoid in extant mammals has been widely debated (see Miao 1988 for references). Presley (1981) maintained that there is no fundamental difference between the monotremes and therians in the development of the membrane bone, lamina obturans, lateral to the cavum epiptericum. According to him, this membrane bone in monotremes in later ontogeny fuses with the petrosal and becomes the anterior lamina, while in marsupials it fuses with the sphenoid and becomes the alisphenoid. This view has been widely accepted by other authors, although questioned by Hopson & Rougier (1993). The alisphenoid has a large exposure in the braincase wall in *Lambdopsalis*, small in *Nemegtbaatar* and *Chulsanbaatar*, and is almost absent in the lateral wall of the braincase of *Kamptobaatar* (Kielan-Jaworowska 1971). The large ascending part of the alisphenoid in *Lambdopsalis* resembles the shape of the anterior lamina of the petrosal in *Nemegtbaatar* and *Chulsanbaatar*. The primitive condition in mammals is probably a similar size of the alisphenoid and the anterior lamina, but in *Lambdopsalis* the condition is secondarily reversed (Miao 1988). In *Sinoconodon*, *Morganucodon*, *Haldanodon*, *Vincelestes*, Marsupialia and Eutheria the alisphenoid is a large element in contact dorsally with the frontal (Wible & Hopson 1993). In the oldest known mammal, *Adelobasileus* (Lucas & Luo 1993), the anterior lamina is extensive compared to non-mammalian cynodonts and the alisphenoid is large and situated similarly to that in *Sinoconodon* and *Morganucodon*.

Petrosal. — The petrosal of monotremes consists of the basal part and the anterolateral wing. The wing, contributing to the lateral wall of the braincase, was designated by Watson (1916) the anterior lamina of the petrosal. The anterior lamina of the petrosal is characteristic also for multituberculates (see discussion in Kielan-Jaworowska 1971

and Miao 1988) and is shared with *Sinoconodon*, morganucodontids, triconodontids and *Vincelestes* (Kermack 1963; Wible 1990; Hopson & Rougier 1993).

The anterior lamina of the petrosal is often broken in isolated petrosals and its whole extent may be studied only when preserved in a skull. The lamina contributes extensively to the lateral wall of the braincase in *Nemegtbaatar* and *Chulsanbaatar* (Fig. 14), forming the lateral wall of the cavum epiptericum and a part of the braincase. In *Nemegtbaatar* and *Chulsanbaatar* the anterior lamina has an extensive anterodorsal process and the general shape of this bone is similar in both taxa. It is prolonged further anteriorly in *Chulsanbaatar* than reconstructed by Wible & Hopson (1993: fig. 5.1.C). *Kamptobaatar* has a similar shape of the anterior lamina except for the anterodorsal part, which is shorter (Clemens & Kielan-Jaworowska 1979). The complete extent of the anterior lamina in multituberculates is not known in other taxa except *Lambdopsalis*, where the anterior lamina forms less of the lateral wall of the braincase than in MLCM. Miao (1988) argued that the small size of the anterior lamina in *Lambdopsalis* is related to the extraordinary expansion of the vestibular apparatus that squeezed the lamina between the large alisphenoid and squamosal bones. Hopson & Rougier (1993) argued that the enlarged anterior lamina and reduced alisphenoid of multituberculates and monotremes are derived traits which may indicate a close relationships; the well developed anterior lamina pierced by V2 and V3 was a primitive feature of all mammals. They concluded further that the loss of the anterior lamina of the petrosal and a posterior expansion of the alisphenoid is a synapomorphy of marsupials and eutherians. The tritheledontid *Pachygenelus*, the morganucodontid *Morganucodon*, and the earliest therian *Vincelestes* all have large anterior laminae (see e.g., Wible & Hopson 1993: fig. 5.1), but also large alisphenoids.

Subarcuate fossa. — The subarcuate fossa in multituberculates is relatively larger than in modern small mammals, because of the differences in the brain structure (Kielan-Jaworowska 1986). In many extant mammals this fossa houses the paraflocculus of the cerebellum (Kielan-Jaworowska *et al.* 1986). Luo (1989) discussed the posteroventral outlet of the subarcuate fossa to the post-temporal fossa (the mastoid fenestration) in several multituberculate petrosals. He suggested a close phylogenetic affinity between the North American pilodontoids and Djadochtatheria on the basis of the presence of this perforation. This derived character is not present in taeniolabidoid multituberculates, *Morganucodon*, *Sinoconodon* or adult extant mammals (see Luo 1989 for discussion). In taeniolabidoid petrosals the subarcuate fossa is smaller than in pilodontoids and djadochtatherians, while the vestibule is more enlarged. In the derived characters concerning the expanded subarcuate fossa and the mastoid fenestration the pilodontoids and djadochtatherians are similar, but in most other cranial characters they differ (see discussion and characters in Kielan-Jaworowska & Hurum 1997).

Parietal. — The parietal bone mainly forms the posterior part of the roof of the cranial cavity rather than the lateral wall of the braincase in *Nemegtbaatar* and *Chulsanbaatar*. The ventral process of the parietal reconstructed for *Kamptobaatar* (Kielan-Jaworowska 1971) later modified by Clemens & Kielan-Jaworowska (1979: fig. 6–2A) is somewhat smaller than in the two multituberculate taxa studied here.

In *Ptilodus*, *Lambdopsalis* and *Taeniolabis* the anterior boundary of the parietal in dorsal view is placed more anteriorly than in MLCM. The frontal in *Lambdopsalis* is a small bone, and the parietal meets the nasal anteriorly (Miao 1988). In MLCM the frontal limits the parietal anteriorly and the frontal is the main contributor to the anterior part of the dorsal orbital rim (Hurum 1994).

Squamosal. — The squamosal is excluded from the inner surface in the posterior part of the braincase in both *Chulsanbaatar* and *Nemegtbaatar*. This is also the condition in all the cynodonts and Jurassic mammals such as *Sinoconodon* and *Morganucodon* (Luo 1994). Zeller (1989: figs 20, 21) described this condition in platypus. This is different from the condition in therian mammals (see e.g., Novacek 1986), where the squamosal is one of the major contributors to the posterolateral wall of the braincase.

Discussion

Study of the sectioned skulls of multituberculates (Kielan-Jaworowska *et al.* 1986; Hurum 1992, 1994, in press, and this paper) shows that analysis of the sections provides insights into the details of the cranial structure that would otherwise have been unavailable. Computer reconstructions of three-dimensional objects have been known for about 20 years. In an earlier paper (Hurum 1994) every photographed section of the snout and anterior part of the orbit was studied and traced for the computer using a graphics tablet and the program Pc3D. The images were viewed on the screen and reproduced with the help of an ink plotter. The reconstructed object may be studied from various angles and rotated accordingly. Due to a complex and time-consuming digitalizing technique and several problems in hardware, the resulting images did not live up to expectations. The awkward processing of the data led to a mistake in the reconstructions of the orbits in Hurum (1994), in which the orbital process of the frontal was placed too far back in both *Nemegtbaatar* and *Chulsanbaatar*.

The anterior lamina of the petrosal is large while the alisphenoid is small in both *Nemegtbaatar* and *Chulsanbaatar*. A long anterodorsal process of the anterior lamina of the petrosal is present in both. The complete intracranial aspect of the sphenoid region is reconstructed here for the first time in multituberculates. The fovea hypochiasmatica is shallow, the tuberculum sellae is wide and more raised from the skull base than in *Pseudobolodon* (Hahn 1981). The dorsal opening of the carotid canal is situated in the fossa hypophyseos. The sinus system is comparable to that in extant mammals in both *Nemegtbaatar* and *Chulsanbaatar* and is divided into a large frontal and an elongated maxillary sinus (Hurum 1994). Rougier *et al.* (1997) described the same pattern of maxillary sinuses in *Tombaatar*, but cautioned against the use of the term sphenoidal sinuses for the posterior expansion of the nasal cavity as no septum separating the sinus from the nasal cavity is found. The definition of a sinus, however, is not clear, and this problem is more of a semantic than of an anatomical nature. Anatomical characters found by Hurum (1994), such as ossified ethmoid and vomer, ossified maxillary and ethmoid turbinals, an orbital mosaic with a small lacrimal anteriorly, large orbital process of the frontal dorsally, orbitosphenoid posteriorly and

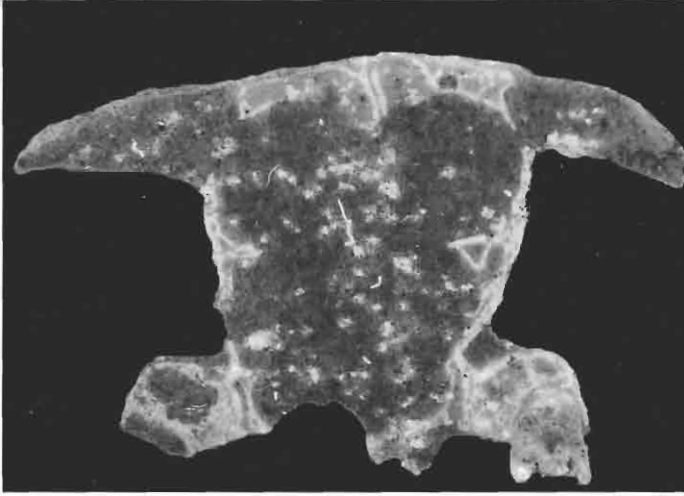
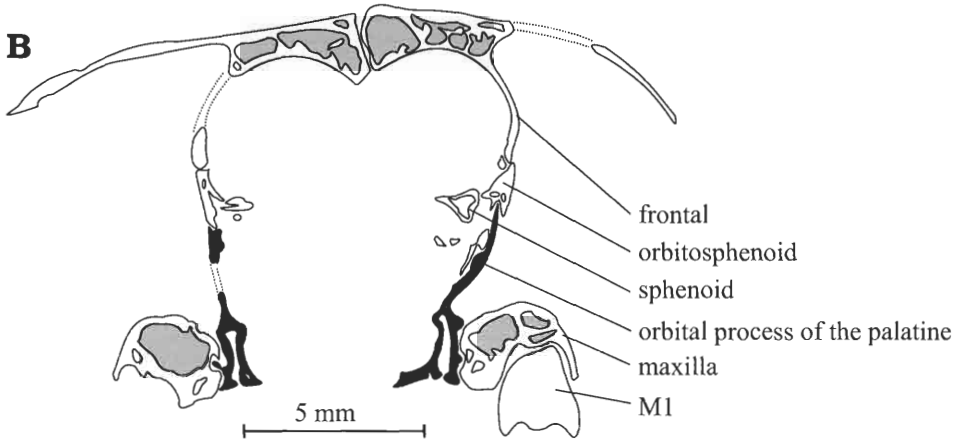
A**B**

Fig. 16. *Nemegtbaatar gobiensis* ZPAL MgM-I/76, section 700. **A**. Photograph made in ultraviolet light. **B**. Contour drawing with explanations. Grey – sinuses possibly filled with marrow in life, black – palatine bone.

maxilla ventrally, and the presence of a cribriform plate in both *Chulsanbaatar* and *Nemegtbaatar* suggest a close relationship of multituberculates to monotremes and therian mammals.

I (Hurum 1994) found an orbital process of the palatine in *Nemegtbaatar* and argued that one of the diagnostic characters of Multituberculata proposed by Wible (1991) – absence of orbital process of the palatine – is not valid. This conclusion has been challenged by Rougier *et al.* (1997) who stated (p. 19) ‘...the sections illustrated are ambiguous, and the bone in that sector might be maxilla, as in comparable sections of *Chulsanbaatar* (cf. figs 9 and 16 of Hurum, 1994)’. However, the finding of the orbital process of the palatine in *Nemegtbaatar* is confirmed by serial sections, where it is observed on both sides of the skull, and the sector is seen to be better preserved in *Nemegtbaatar* than in *Chulsanbaatar*. In Fig. 16 an even better section is shown with

the orbital process of the palatine clearly preserved. It is not possible to interpret this as an orbital process of the maxilla.

In *Nemegtbaatar* and *Chulsanbaatar* (as well as in other MLCM) the lateral expansion of the braincase is associated with the presence of sinuses and development of extensive masticatory musculature, but is not related to the expansion of the vestibule, which is moderately developed (Hurum *et al.* 1996). The expansion of the vestibular apparatus was proposed as a multituberculate apomorphy by Luo & Ketten (1991), but Hurum *et al.* (1996) and Hurum (in press) demonstrated that this character is only present in taeniolabidoid multituberculates as suggested by Miao (1993). The size and proportions of the inner ear of *Nemegtbaatar* and *Chulsanbaatar* as a whole are as expected for extant small mammals (Hurum in press). The semicircular canals of *Nemegtbaatar* and *Chulsanbaatar* are fully developed. The size of the anterior, posterior and lateral canals, and their angles and proportions are comparable to extant mammals (Hurum in press). The anterior semicircular canal of *Nemegtbaatar* forms a smooth half circle and thus is more derived than the angular canal of *Ornithorhynchus* (Hurum in press). The cavum epiptericum in both taxa is an extensive extracranial space, with the taenia clino-orbitalis as the medial wall, the anterior lamina of the petrosal and possibly of the alisphenoid as the lateral wall, and the basisphenoid, petrosal and possibly alisphenoid ventrally. Both the primary braincase wall and the secondary lateral wall of the braincase are present in *Nemegtbaatar* and *Chulsanbaatar*.

The main difference between multituberculates and other mammals in the sphenoid region is the retention of an extensive taenia clino-orbitalis, and hence a robust medial bony wall in the cavum epiptericum. Miao (1988: p. 48) concluded that '...the fact that the bony, primary side wall of the braincase is still fairly complete in multituberculates (even though the secondary side wall also has been completed) implies that their braincase structure seems to be more primitive than in monotremes [...] and provides a morphological intermediate between that of the reptiles and that of the mammals.' On the other hand, Kielan-Jaworowska *et al.* (1986: p. 600) stated that the taenia clino-orbitalis in multituberculates was: 'found to be similar to that of monotremes, but much more extensive, possibly secondarily, in relation to the general robustness of the cranial bones.' The statement of Wible & Hopson (1993) that the weak process of taenia clino-orbitalis in *Morganucodon* is not on the same scale as in multituberculates is supported here. The taenia clino-orbitalis is more heavily ossified in *Nemegtbaatar* and *Chulsanbaatar* than in the oldest cranial remains of a mammal, *Adelobasileus*, and this supports the idea that the ossification may be a secondary specialization.

As demonstrated by Gambaryan & Kielan-Jaworowska (1995) the backward masticatory power stroke shaped the multituberculate skull and dentary differently than in all other mammals. This, together with the cryptomesencephalic brain (Kielan-Jaworowska 1986, 1997) were the two main forces in forming the skull of multituberculates. Multituberculates differ also from other mammals in several other details of the postcranial anatomy, including limb posture and foot structure (Kielan-Jaworowska & Gambaryan 1994; Gambaryan & Kielan-Jaworowska 1997). Kielan-Jaworowska & Gambaryan (1994: pp. 84–85) stated: 'It is [...] interesting that recent thorough analyses of the cranial structure of early mammals by Wible (1991), Wible & Hopson (1993), Hopson & Rougier (1993), Rougier *et al.* (1992) and Lucas & Luo (1993) place the multituberculates closer to other mammals than

the data for the postcranial skeleton do'. The present studies confirm the conclusions of those authors concerning the similarity of the arrangement of the external skull bones in multituberculates and all extant mammals. The difference is in the presence of an extensive cavum epiptericum and extreme ossification of the taenia clino-orbitalis in multituberculates.

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Puszka mózgowa dwóch późnokredowych wieloguzkowców (Multituberculata) badana za pomocą przekrojów seryjnych

JØRN H. HURUM

Streszczenie

Budowa puszek mózgowych dwóch późnokredowych wieloguzkowców z podrzędu Djadochtheria, *Nemegtbaatar gobiensis* i *Chulsanbaatar vulgaris*, z późnego kampanu Mongolii, została zbadana za pomocą seryjnych skrawków dwóch czaszek, ciętych mikrotomem Junga, oraz w oparciu o inne czaszki tych samych gatunków, i pojedyncze kości skaliste innych gatunków. Badane materiały przechowywane są w zbiorach Instytutu Paleobiologii PAN w Warszawie.

Przedstawiono rekonstrukcję podstawy puszek mózgowych obu gatunków. Zrekonstruowano też, po raz pierwszy u wieloguzkowców, budowę kompleksu kości klinowej, widzianą od strony puszek mózgowych. Cavum epiptericum u wieloguzkowców tworzy obszerną przestrzeń, oddzieloną od puszek mózgowych przez taenia clino-orbitalis (skostniała piła antotica), tworzącą jej ścianę przyśrodkową. Ścianę zewnętrzną cavum epiptericum tworzy skrzydło kości podstawnoklinowej, zaś ścianę

dolną kość podstawnoklinowa, kość skalista i przypuszczalnie częściowo skrzydło kości podstawnoklinowej.

Skostnienie wewnętrznej ściany cavum epiptericum jest u wieloguzkowców silniejsze niż u stekowców, co może wskazywać, że wieloguzkowce są pod tym względem prymitywniejsze niż stekowce. Nie jest jednak wykluczone, że skostnienie to jest wtórne, jak to sugerowano wcześniej (Kielan-Jaworowska i wsp. 1986). Fovea hypochiasmatica jest płytka, siodło tureckie jest szerokie i położone wyżej w stosunku do podstawy czaszki niż u jurajskiego rodzaju *Pseudobolodon*. Taenia clino-orbitalis różni się od tej samej struktury opisanej u wieloguzkowców z rodzajów *Pseudobolodon* i *Lambdopsalis* tym, że jest przebita tylko jednym otworem. Puszka mózgowa *Nemegtbaatar* i *Chulsanbaatar* jest bardziej prymitywna niż u wszystkich ssaków współczesnych, ponieważ zachowuje w stadium dorosłym zarówno pila antotica, jak i pila metoptica. U obu rodzajów blaszka przednia kości skalistej (lamina anterior) jest duża, z długim przednio-grzbietowym wyrostkiem, natomiast skrzydło kości podstawnoklinowej jest małe. W pracy przedstawiono również podsumowanie danych o anatomii czaszki *Nemegtbaatar* i *Chulsanbaatar*.