

Snout and orbit of Cretaceous Asian multituberculates studied by serial sections

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The orbital wall in *Nemegtbaatar gobiensis* and *Chulsanbaatar vulgaris*, from the Late Cretaceous of the Gobi Desert, Mongolia, comprises a small lacrimal anteriorly, large orbital process of the frontal dorsally, orbitosphenoid posteriorly and maxilla ventrally. *Nemegtbaatar* also possesses an orbital process of the palatine ventrally, not recognized in *Chulsanbaatar*. Large frontal sinuses of both taxa are interpreted as related to lack of the sagittal crest. Other anatomical characters found in this study, such as orbital process of the frontal, ossified turbinals, ossified ethmoid and vomer, frontal, sphenoidal and maxillary sinuses, and the presence of the orbital process of palatine in *Nemegtbaatar* suggest a close relationship of multituberculates to monotremes and therian mammals. By the new data obtained from the serial sections the diagnostic character: orbital process of the palatine absent in Multituberculata, is no longer valid. Ossified ethmoid and maxillary turbinals, characteristic for Monotremata, *Vincelestes*, Marsupialia and Placentalia, are also present in Multituberculata. The presence of a cribiform plate and the presence of an ossified plate of ethmoid in Multituberculata is shared with Monotremata, *Vincelestes*, Marsupialia and Placentalia.

Key words: Multituberculata, cranial morphology, sinuses, Cretaceous, Mesozoic mammals.

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Introduction

More than half a century ago George Gaylord Simpson stated (1926: p. 228) that the order Multituberculata: 'includes members of the very oldest known mammalian faunas and it subsisted practically from the beginning of reptilian dominance on into that of mammalian ascendancy. What role these small beasts played in that savage medieval world and what peculiar advantage secured their unparalleled longevity are questions which have long excited the imagination'.

Multituberculates were dominant throughout the Mesozoic, ranging from the Late Triassic (Rhaetian; Sigogneau-Russell 1989) through Late Eocene (recognized by Robinson *et al.* 1964 as Late Eocene, by Krishtalka *et al.* 1982 as Early Oligocene, and then again by Swisher & Prothero 1990 as Late Eocene). Cranial materials of multituberculates is scarce, but rather diverse in terms of their chronological, ecological, taxonomic and geographic representation. The multituberculate skull, as summarized by Clemens & Kielan-Jaworowska (1979), is depressed dorsoventrally and is comparatively short and wide. The skull has strong zygomatic arches, a blunt snout and a laterally expanded braincase. The orbit has no floor, but is partially roofed by the maxillary and the frontal bones. The eyes of multituberculates were laterally oriented. Primitive therian skulls differ from multituberculates in that the snout is strongly elongated and the braincase is rather narrow and high in taxa such as the Early Paleocene marsupial *Pucadelphys andinus* (see Muizon 1991) and the Late Cretaceous eutherian *Kennalestes gobiensis* (see Kielan-Jaworowska 1969). The orbit is floored but not roofed in most therians (but not in e. g. *Homo*) and the eyes face more anteriorly.

The oldest known multituberculate cranial material has been found in the Kimmerigidan beds of Guimarota in Portugal (Hahn 1969). The material consists of a crushed skull and mandibles of *Paulchoffatia delgadoi* Kühne 1961 (see reconstruction in Hahn 1969) and a rostrum of *Kuehneodon simpsoni* Hahn 1969. With further findings of fragmental paulchoffatiid crania, Hahn made reconstructions of the snout of *Kuehneodon dryas* Hahn 1977, and described the snout and orbit of *Henkelodon naias* Hahn 1977 and the sphenoid region of *Pseudobolodon oreas* Hahn 1977 (see also references in Hahn & Hahn 1983). All of the above mentioned multituberculates are assigned to the suborder Paulchoffatoidea Hahn 1969. In an abstract, Engelmann *et al.* (1990) mentioned two partial multituberculate skulls from the Late Jurassic Morrison Formation of North America. In both specimens anterior parts of skulls have been preserved, and both are referred to as 'plagiaulacoids'. Simpson (1928) described several incomplete cranial elements of Late Jurassic (Middle Purbeck) multituberculates from Swanage, Dorset in England. The figured specimens belong to *Bolodon osborni* Simpson 1928 — a right maxilla, *Bolodon elongatus* Simpson 1928 — an incomplete palate and *Bolodon crassidens* Owen 1871 — a right premaxilla and maxilla. All the specimens belong to the suborder Plagiaulacoidea Simpson 1925 and the family Plagiaulacidae. Simpson (1929) figured the left maxilla of *Ctenacodon laticeps* Marsh 1881 from the Late Jurassic Morrison Formation, Como Bluff, Wyoming, which belongs to the family Allodontidae, in the suborder Plagiaulacoidea.

Two fragmentary left maxillary bones of the Early Cretaceous multituberculate *Monobaatar mimiscus* Kielan-Jaworowska *et al.* 1987 have been described from the Khovboor beds of the Gobi Desert; while *Arginbaatar dimitrievae* Trofimov 1980 from the same locality yielded seven fragments of maxilla (Kielan-Jaworowska *et al.* 1987).

The Mongolian Late Cretaceous Djadokhta and Barun Goyot formations have yielded numerous well preserved multituberculate skulls. The material consists of *Kryptobaatar dashzevegi* Kielan-Jaworowska 1970 (*Gobibaatar parvus*, Kielan-Jaworowska 1970 being its junior synonym), *Kamptobaatar kuczynskii* Kielan-Jaworowska 1970, *Sloanbaatar mirabilis* Kielan-Jaworowska 1970, *Bulganbaatar nemegtbaataroides* Kielan-Jaworowska 1974, *Nemegtbaatar gobiensis* Kielan-Jaworowska 1974, *Chulsanbaatar vulgaris* Kielan-Jaworowska 1974, *Tugrigbaatar saichaenensis* Kielan-Jaworowska & Dashzeveg 1978 (see also Kielan-Jaworowska 1971, 1980). *Djadochtatherium matthewi* Simpson 1925 (see also Kielan-Jaworowska 1974) and *Djadochtatherium catopsaloides* Kielan-Jaworowska 1974 were assigned by Kielan-Jaworowska & Sloan (1979) to *Catopsalis* Cope 1882, but Simmons & Miao (1986) on the basis of PAUP (Phylogenetic Analysis Using Parsimony) demonstrated paraphyly of *Catopsalis* and suggested that the two Mongolian species belong to different genera. *Catopsalis matthewi* was assigned to *Djadochtatherium*, whereas *Djadochtatherium catopsaloides* has been left in an unnamed genus (Simmons & Miao 1986). Kielan-Jaworowska (1994) erected a new monotypic genus *Catopsbaatar* for the latter species. All Asian Late Cretaceous multituberculates belong to the Taeniolabidoidea (Kielan-Jaworowska 1980). The discussion of multituberculate cranial structure in Clemens & Kielan-Jaworowska (1979) is based largely upon the Mongolian material.

The Paleocene of North America has yielded the skulls of two multituberculate taxa: *Taeniolabis taoensis* Broom 1914 (then called *Polymastodon*) (see also Granger & Simpson 1929; Simpson 1937) and *Ptilodus montanus* Gidley 1909 (see also Broom 1914; Simpson 1937). From the Gobi Desert of Mongolia incomplete skulls of the Late Paleocene multituberculates *Prionessus lucifer* Matthew & Granger 1925 and *Sphenopsalis nobilis* Matthew & Simpson 1928, have been described (see also Kielan-Jaworowska & Sloan 1979). From the Late Paleocene and earliest Eocene of China the skulls of *Lambdopsalis bulla* Chow & Qi 1978 have been described in detail by Miao (1988; see also Miao & Lillegraven 1986). The youngest known multituberculate skull is that of *Ectypodus tardus* Sloan 1979, an Early Eocene ptilodontoid from Wyoming.

My study is based primarily on skulls of two multituberculates from the Late Cretaceous of Mongolia, *Nemegtbaatar gobiensis* and *Chulsanbaatar vulgaris*, collected during the Polish-Mongolian expeditions between 1963 and 1971. *Nemegtbaatar* is a monotypic genus attributed to the Eucosmodontidae Jepsen 1940. *Chulsanbaatar* was attributed to the Chulsanbaataridae Kielan-Jaworowska 1974, but Kielan-Jaworowska (1980) regarded this family as a junior synonym of the Eucosmodontidae (see also Kielan-Jaworowska & Dashzeveg 1978).

The sections used in this study were already used to make a reconstruction of the cranial vasculature and an endocranial cast of *Nemegtbaatar gobiensis* (Kielan-Jaworowska *et al.* 1984, Kielan-Jaworowska *et al.* 1986). Although cranial morphology of the two studied species has been de-

scribed on the basis of nearly complete skulls (Kielan-Jaworowska 1974, 1983, Kielan-Jaworowska *et al.* 1984; Kielan-Jaworowska *et al.* 1986; Hopson *et al.* 1989), numerous details remain unknown. This concerns, in particular, the course of sutures, the extent of bones on the inner side of the skull and the internal structure of the bones. The study of serial sections provides insights into the structure of the cranium that otherwise would be not available. Here, I present a study of the anatomy of the snout and orbit of *Chulsanbaatar vulgaris* and *Nemegtbaatar gobiensis* based on the serial sections. The structure of the braincase will be a subject of a forthcoming paper.

All the specimens studied in this paper are housed in the collection of the Institute of Paleobiology, Polish Academy of Sciences, in Warsaw, abbreviated as ZPAL.

Material

The sectioned skull of *Chulsanbaatar vulgaris* ZPAL MgM-I/84 was found at the locality of Khermeen Tsav II, in the Red beds of Khermeen Tsav, which are a stratigraphical equivalent to the Barun Goyot Formation (Gradziński *et al.* 1977). The sectioned skull of *Nemegtbaatar gobiensis* ZPAL MgM-I/78 derives from the Khulsan locality, from the Barun Goyot Formation. In addition, I investigated several skulls of both *Chulsanbataar vulgaris* and *Nemegtbaatar gobiensis* from the ZPAL collection from the localities of Khulsan, Nemegt (both Barun Goyot Formation) and from Khermeen Tsav (the Red beds of Khermeen Tsav).

The age of the Barun Goyot Formation (and its stratigraphic equivalent, the Red beds of Khermeen Tsav) is in dispute. Gradziński *et al.* (1977), on the basis of an analysis of all the fossils that occur in the Barun Goyot Formation and overlying Nemegt Formation (Fig. 1), and a comparison with other areas, suggested a 'Middle Campanian' age of the Barun Goyot Formation. The age estimates given by Gradziński *et al.* (1977) are tentatively accepted in this paper. Discussions regarding the age of the Barun Goyot Formation are still going on. Fox (1978) argued that it is of Late Campanian age, Lillegraven & McKenna (1986) suggested Late Campanian to Early Maastrichtian; and Jerzykiewicz & Russell (1991) suggested Campanian without further qualification. The sedimentation in this formation has been interpreted to have occurred among dune fields. Intermittent lakes, evidence for simultaneous flooding, eolian dunes and ephemeral stream sedimentation were also found (Jerzykiewicz & Russell 1991).

Gradziński *et al.* (1977) estimated an ?Late Santonian and/or ?Early Campanian age of the Djadokhta Formation, while Jerzykiewicz & Russell (1991) suggested the middle Campanian age.

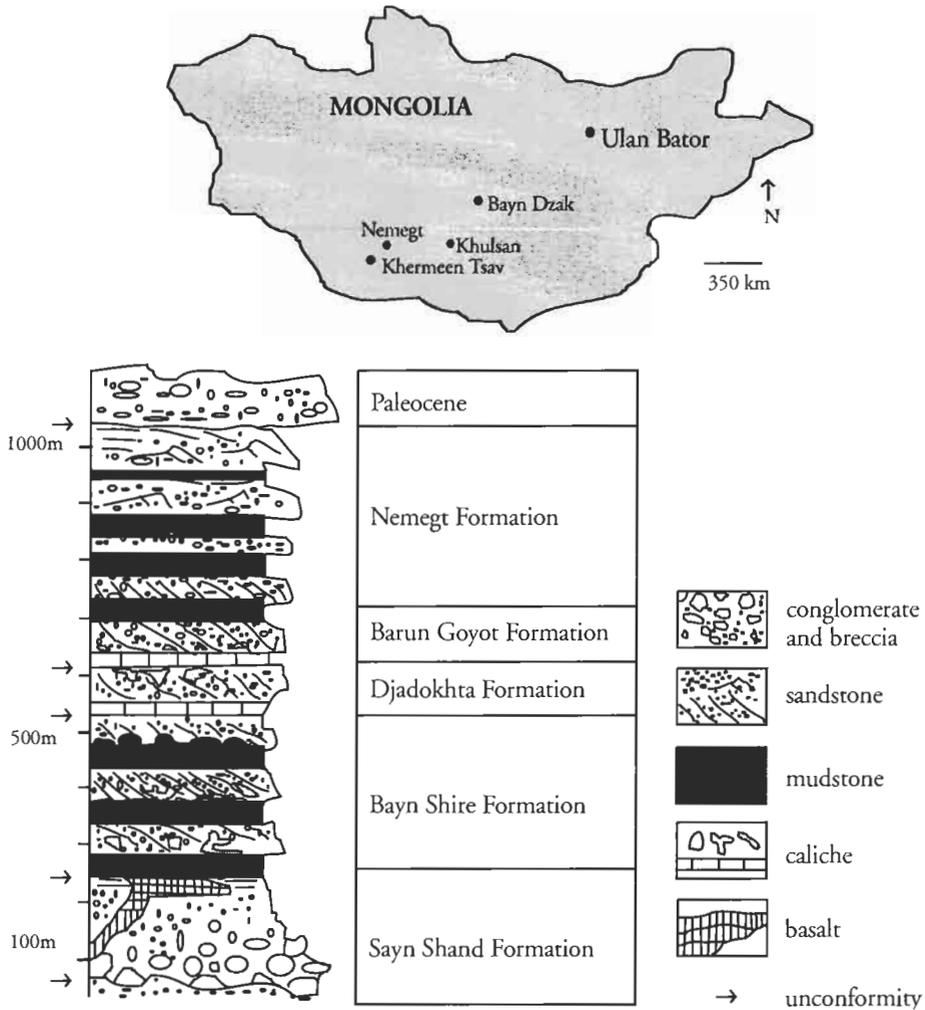


Fig. 1. Map of Mongolia with localities and stratigraphical column of the Upper Cretaceous strata in the Gobi Basin (modified from Jerzykiewicz & Russell 1991).

Methods

The present work is based upon serial sections of skulls made by the use of a Jung Microtome. The original sections are preserved and mounted in glass slides (Poplin & Ricqles 1970). The method was applied for the first time in studies of the cranial anatomy of Carboniferous fish (Poplin 1974, 1977). The common method of obtaining serial sections from fossils is based on serial grinding (see Sollas & Sollas 1914; Simpson 1936; Fourie 1974; Sandy 1989). An actual slice of the specimen is not obtained. A permanent record of each surface can be made by taking acetate peels or by drawings or photographs.

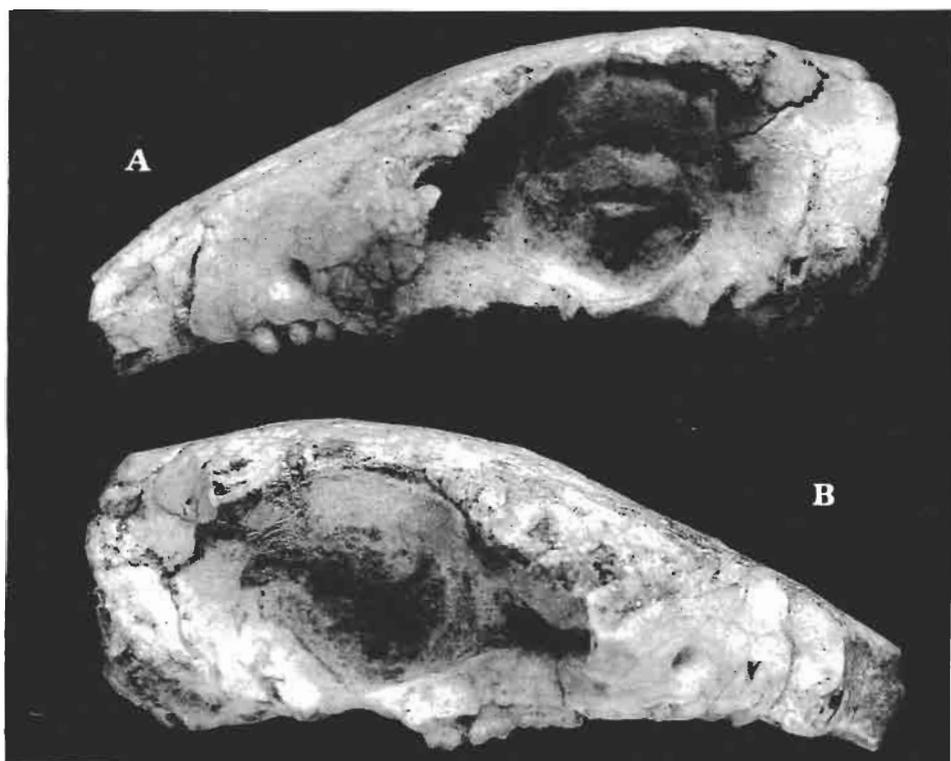


Fig. 2. *Nemegtbaatar gobiensis* Kielan-Jaworowska 1974, skull ZPAL MgM-1/76, before sectioning in left (A) and right (B) lateral views; $\times 3$.

From the *Chulsanbaatar vulgaris* skull (MgM-1/84) sectioned by Jung Microtome (Kielan-Jaworowska *et al.* 1984; Kielan-Jaworowska *et al.* 1986) 885 sections 20 μm thick were obtained, while from the *Nemegtbaatar gobiensis* skull (MgM-1/76) 1370 sections 25 μm thick. The original numbering of the sections, for both specimens, is from back to front.

Every fifth section was photographed under ultraviolet light. The reason for using ultraviolet light in photographing and microscoping the sections is to allow phosphatic bone and organic material to light up, while the sandstone within the specimen remains dark. I used prints of the photographed sections for making the drawings which were transferred to computer using the graphics tablet SummaSketch II and the program Pc3D from Jandel Scientific (see Chapman 1989). For examining the sections I used the microscope Leitz Orthoplan with Leitz Ploemopak 1,25 incident-light fluorescence, 100w Hg lamp and filterblock A2.

For osteological terminology I follow *Nomina Anatomica Veterinaria* (1973); for structures which do not occur in domestic mammals I use Grassé (1967), Starck (1979) and Evans & Christensen (1979). I give the Latin names for particular structures only when I mention them for the first time. Upper teeth are abbreviated as follows: P – premolars, M – molars, with numbers according to their position.

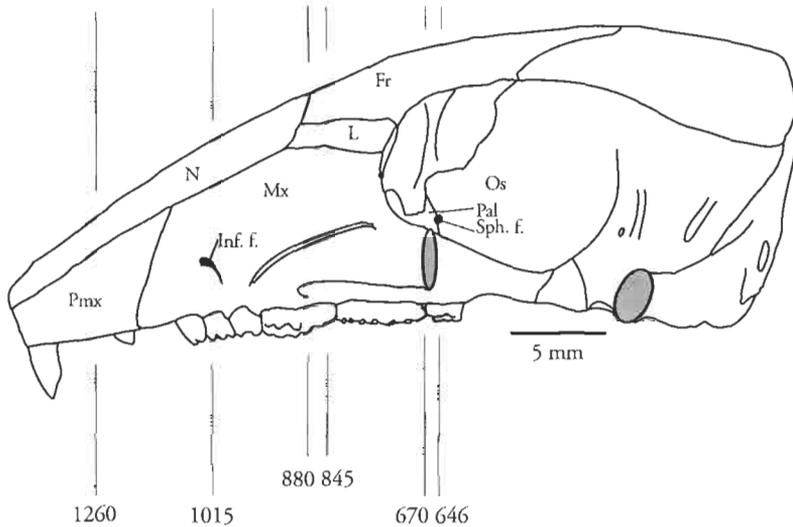


Fig. 3. Lateral view of the skull of *Nemegtbaatar gobiensis* (modified from Kielan-Jaworowska *et al.* 1986) showing positions of sections figured in this paper (Figs 4–9); part of zygomatic arch has been removed, the gray spots denote their sections. Fr – Frontal, Inf. f. – Infraorbital foramen, L – Lacrimal, Mx – Maxilla, N – Nasal, Os – Orbitosphenoid, Pal – Palatine, Pmx – Premaxilla and Sph. f. – Sphenopalatine foramen.

Skull of *Nemegtbaatar gobiensis*

Nasal bone (*Os nasale*). — The nasal bone forms the roof and the dorsal rim of the lateral walls of the nasal cavity. The bone is well exposed and easy to distinguish from the other bones in the sections, but contains numerous cracks on the dorsal surface. Rostrally the nasal forms the dorsal boundary of the piriform aperture. The nasal articulates with the premaxilla rostrrolaterally (*sutura nasoincisiva*), with the maxilla caudolaterally at the nasomaxillary suture (*sutura nasomaxillaris*), with the lacrimal at the nasolacrimal suture (*sutura nasolacimalis*) and with the frontal caudally at the frontonasal suture (*sutura frontonasalis*). The nasal bone, when meeting its fellow in the *sutura internasalis* (*sutura nasoethmoidalis* internally) becomes thicker. In the sections, due to distortion, the nasals are separated from each other. In the *sutura nasoincisiva* the nasal is bifurcated and partially overlying the premaxilla dorsally. *Sutura fronto-nasalis* is well preserved; the nasal covers the frontal bone dorsally (Figs 6–7). *Sutura nasolacimalis* shows that the nasal covers the lacrimal dorsally. There are five 'vascular foramina' or 'nasal foramina' (Simpson 1937; see also discussion in Kielan-Jaworowska 1971; Miao 1988) on the dorsal part of the nasal, arranged symmetrically to those on the opposite bone, the medial foramina being the largest (Kielan-Jaworowska *et al.* 1986). It was impossible to identify all the nasal foramina in the sections, due to the state of preservation, but it seems that they penetrate the bone

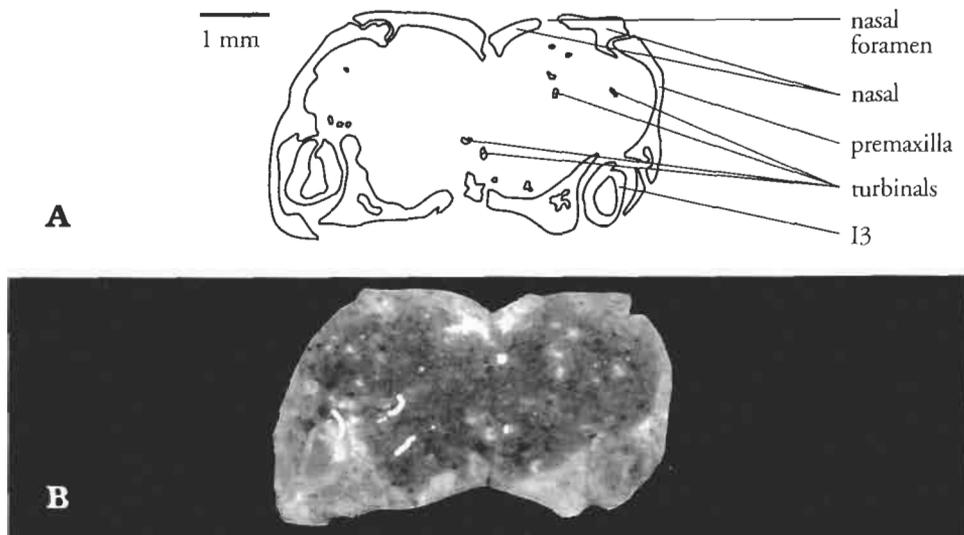


Fig. 4. *Nemegtbaatar gobiensis* Kielan-Jaworowska 1974, skull ZPAL MgM-1/76, section 1260, contour drawing (A) and photograph under ultraviolet light (B), see Fig. 3 for position.

vertically (Figs 4–5). The third nasal foramen is well preserved and penetrates the nasal vertically. Ventrally a few small ridges are present. These ridges are indications of the presence of turbinals. Remnants of the turbinals are also seen in the sections, but are poorly preserved. The nasal contains *sinus frontalis pars nasalis* (Fig. 5), between outer and inner tables of the nasal bone.

Premaxilla (*Os incisivum*). — The premaxilla consists of a horizontal palatal process (*processus palatinus*) and the nasal process (*processus nasalis*) forming the rostralateral and rostroventral parts of the snout. The preservation is good (Fig. 4). Sutures with the maxilla caudally and ventrally (*sutura incisivomaxillaris*) and the nasal dorsally (*sutura nasoincisiva*) are seen in the sections. The bone contains sockets for two incisors and forms the lateral and rostral boundary of the palatine fissure (*fissura palatina*).

Maxilla. — This bone forms most of the lateral and ventral sides of the snout (*facies nasalis* and *facies facialis*), a large part of the secondary palate (*processus palatinus*), the rostral part of the zygomatic arch (*processus zygomaticus*) and the basal part of the orbit (*facies orbitalis*). The tooth-bearing ventral side (*processus alveolaris*) contains sockets (*alveoli dentales*) for four premolars and two molars. The bone is well exposed and easy to identify in all the sections, because it is thicker than the surrounding bones (Figs 5–9). The preservation of *processi palatini* and *facies orbitales* is not the best, they are partly lacking and crushed. Therefore the palatal vacuity is only tentatively placed. The maxilla articulates rostrally with the premaxilla, dorsomedially with the nasal and the lacrimal. In the orbit the bone articulates dorsocaudally with the frontal and ventrocaudally with the palatine. Ventrally, in its rostral two-thirds, it articulates

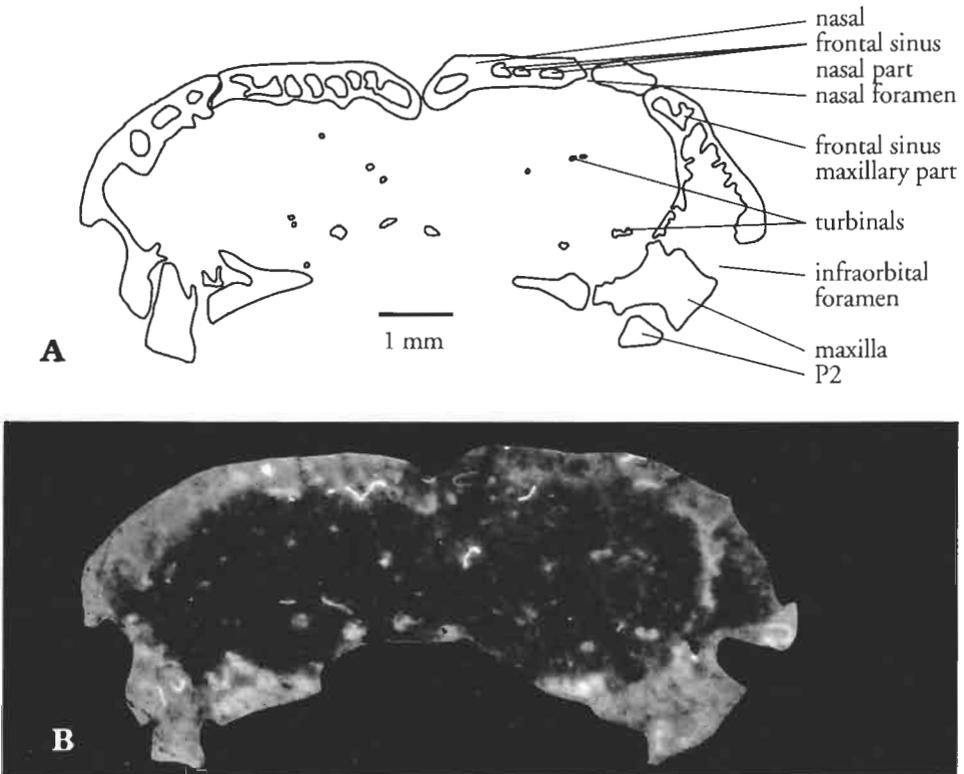


Fig. 5. *Nemegtbaatar gobiensis* Kielan-Jaworowska 1974, skull ZPAL MgM-I/76, section 1015, contour drawing (A) and photograph under ultraviolet light (B), see Fig. 3 for position.

with its fellow in the median palatine suture (*sutura palatina mediana*), and ventrocaudally with the palatine in the palatomaxillary suture (*sutura palatomaxillaris*). The most rostroventral process forms the median margin and dorsal roof of the palatine fissure. This process contains canals for blood vessels. Caudally, the pterygoid process of the maxilla (*processus pterygoideus*) articulates with the sphenoid region, possibly with the alisphenoid. The infraorbital foramen (*foramen infraorbitale*) is large, situated opposite P2 (Fig. 5) (Kielan-Jaworowska 1974). The maxilla contains an extensive infraorbital canal (*canalis infraorbitalis*) seen in sections 880 to 1015 (Fig. 5), not easy to distinguish from the maxillary sinus (*sinus maxillaris*). The maxillary sinus is present. The maxillary part of the frontal sinus is seen in the most dorsomedial part of the bone and is recognized as a part of the frontal sinus because it is in contact with this cavities.

The frontal bone (*Os frontale*). — The frontal is a large, extremely thick and strongly pneumatized bone. It forms a large part of the cranial roof (*facies temporalis* and *squama frontalis*), the caudal part of the snout (*pars nasalis*) and a large part of the orbit (*pars orbitalis*). The preservation of the bone is good (Figs 6–9). The bone articulates with the nasal rostrally and rostromedially where the nasal process (*processus nasalis*) lies under

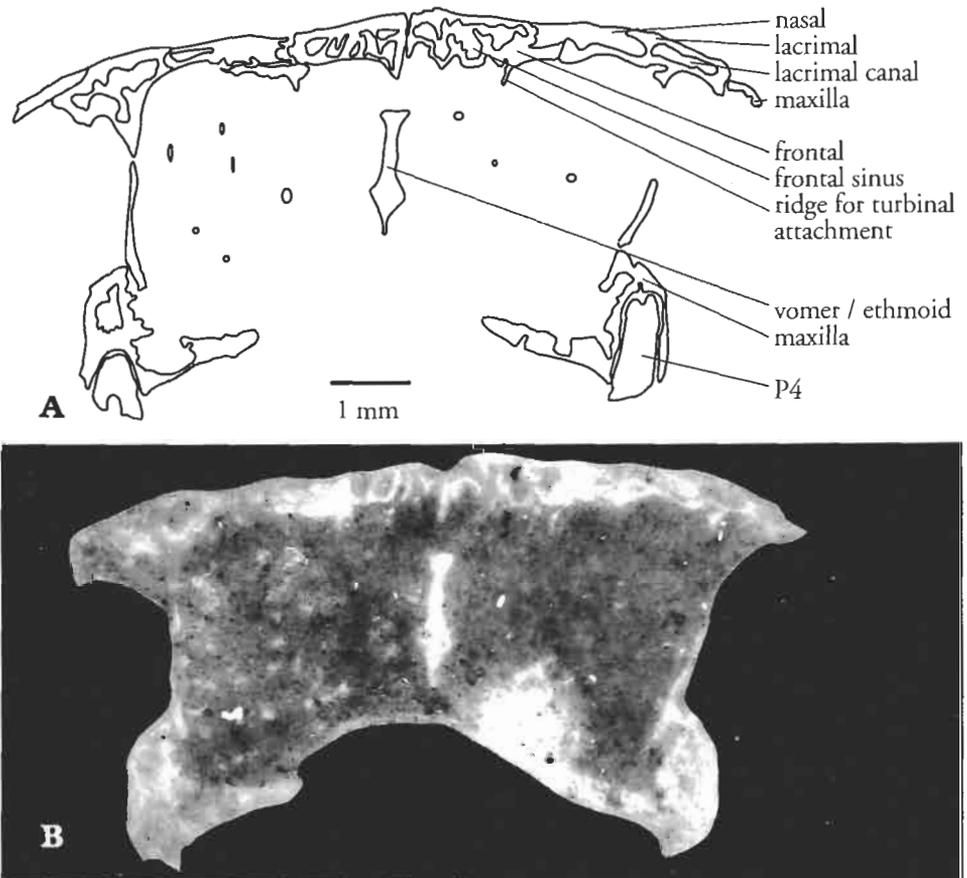


Fig. 6. *Nemegtbaatar gobiensis* Kielan-Jaworowska 1974, skull ZPAL MgM-1/76, section 880, contour drawing (A) and photograph under ultraviolet light (B), see Fig. 3 for position.

and partly between the caudal parts of the nasal (*sutura frontonasalis*). More laterally the frontal articulates with the lacrimal (*sutura frontolacrimalis*). In the orbit the frontal bone articulates with the maxilla rostrally (*sutura frontomaxillaris*), with the palatine ventrally (*sutura frontopalatina*) and ventrocaudally with the orbitosphenoid (*sutura sphenofrontalis*). Mediodorsally the articulation with its fellow (*sutura interfrontalis*) forms a thick septum between the frontal sinuses (*septum sinuum frontaliuum*). Medially, the septum, hidden from external view, makes an internal frontal crest (*crista frontalis interna*) that articulates with the perpendicular plate of the ethmoid at the frontoethmoidal suture (*sutura frontoethmoidalis*). The suture, however, is not seen directly in the sections because the articulation probably was cartilaginous. The dorsocaudal part of the bone articulates with the parietal in the frontoparietal suture (*sutura frontoparietalis*); the suture consist of two branches directed caudally and transversely (Kielan-Jaworowska 1974). *Sinus frontalis pars frontalis* is large (Figs 6–9); the cavity is divided by numerous bony septa.

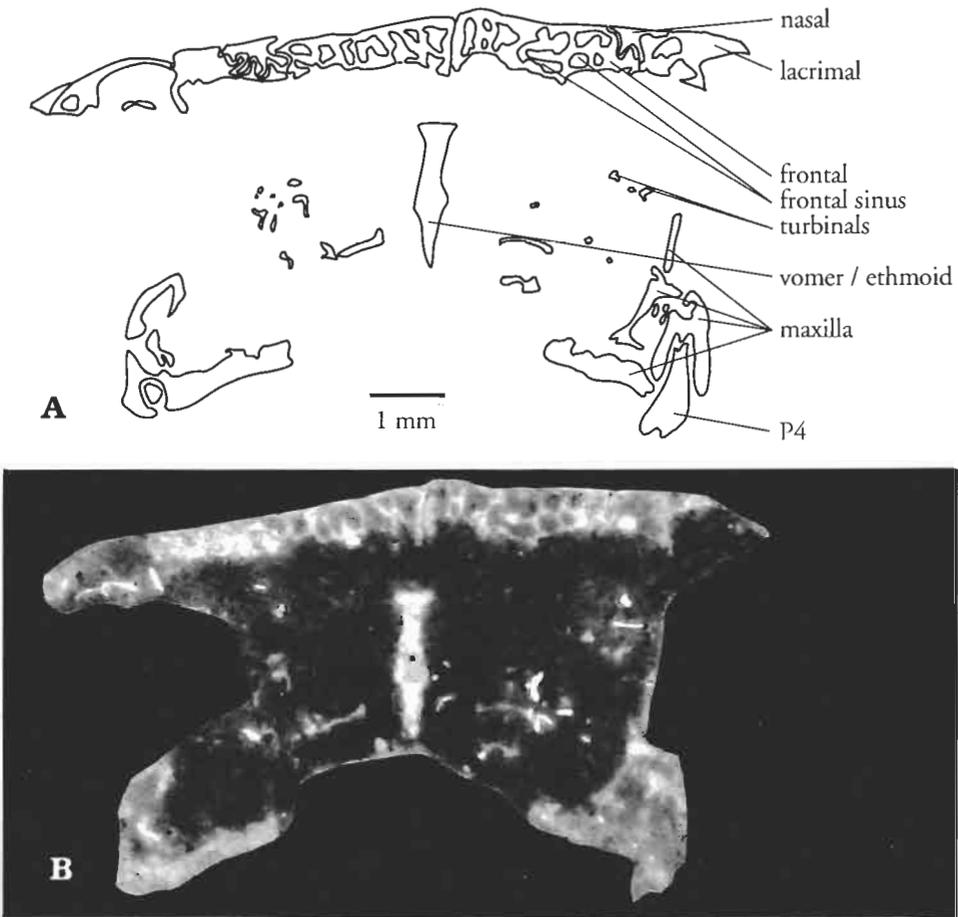


Fig. 7. *Nemegtbaatar gobiensis* Kielan-Jaworowska 1974, skull ZPAL MgM-1/76, section 845, contour drawing (A) and photograph under ultraviolet light (B), see Fig. 3 for position.

Palatine bone (*Os palatinum*). — The palatine consists of two laminae. The horizontal lamina (*lamina horizontalis*) forms the caudal part of the hard palate (*palatum osseum*). The perpendicular lamina (*lamina perpendicularis*) forms the lateral wall of the nasopharyngeal meatus medially, the dorsal roof of the nasopharyngeal meatus (*lamina sphenoeethmoidalis*) and the caudoventral part of the orbit which comprises the maxillary process (*processus maxillaris*) of the lamina. The horizontal lamina is incomplete, only seen as small pieces of bone in the suture with the maxilla and occasional broken parts in the nasopharyngeal meatus. The perpendicular lamina is preserved, both in its orbital part and *lamina sphenoeethmoidalis*. The palatine bone (orbital part of its perpendicular lamina) articulates with the maxilla in rostral and dorsorostral parts at the palatamaxillary suture (*sutura palatamaxillaris*), with the frontal dorsally at the frontopalatine suture (*sutura frontopalatina*) and the presphenoid caudally and medially at the sphenopalatine suture (*sutura sphenopalati-*

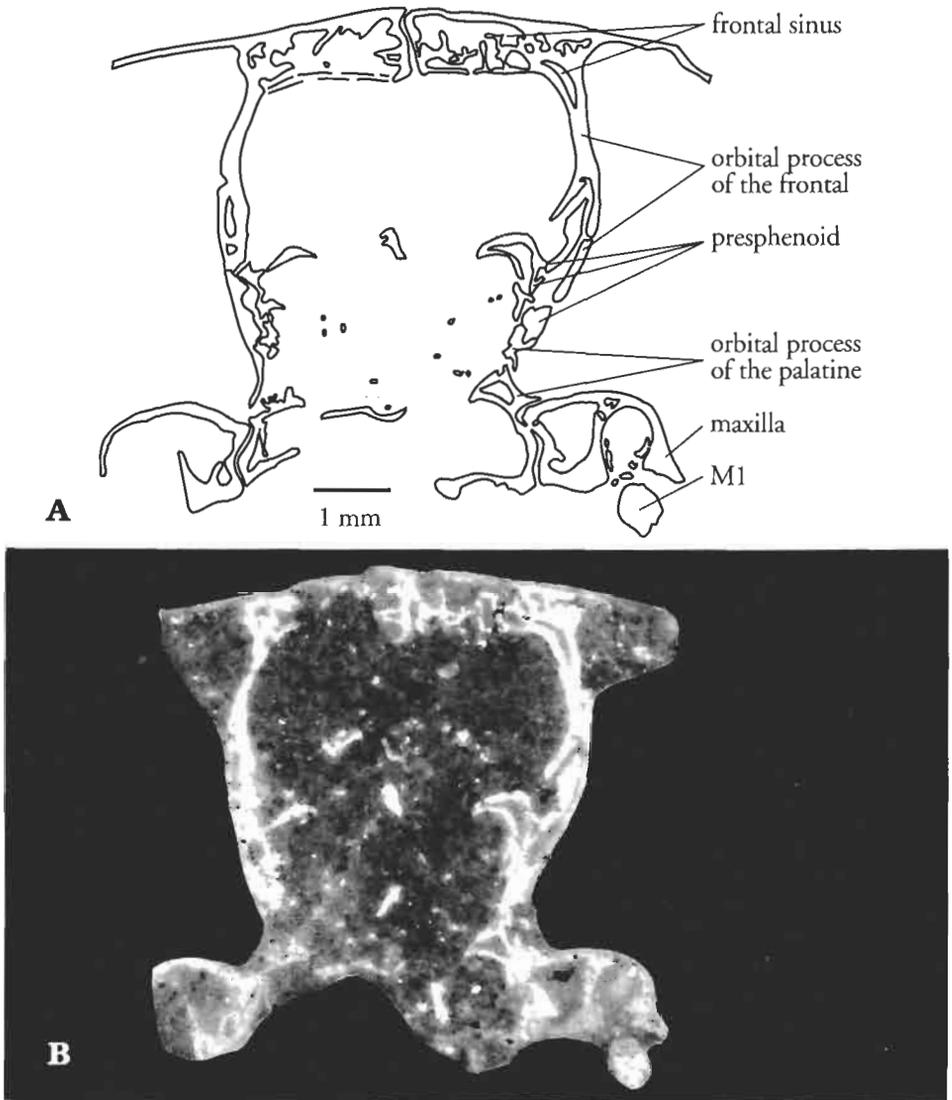


Fig. 8. *Nemegtbaatar gobiensis* Kielan-Jaworowska 1974, skull ZPAL MgM-1/76, section 670, contour drawing (A) and photograph under ultraviolet light (B), see Fig. 3 for position.

na). The horizontal lamina articulates with the maxilla rostrally and laterally, alisphenoid caudolaterally and has a free caudal border. The deep surface of the palatine bone joins rostrally with the ethmoid bone to form the palatoethmoidal suture (*sutura palatoethmoidalis*). The sphenopalatine foramen (Fig. 9) is bordered by the orbital process of the palatine and orbitosphenoid. The horizontal lamina of the palatine is pneumatized ventrally (Fig. 9).

Lacrimal bone (*Os lacrimale*). — The lacrimal bone consists of two parts, the orbital surface (*facies orbitalis*) and the facial surface (*facies*

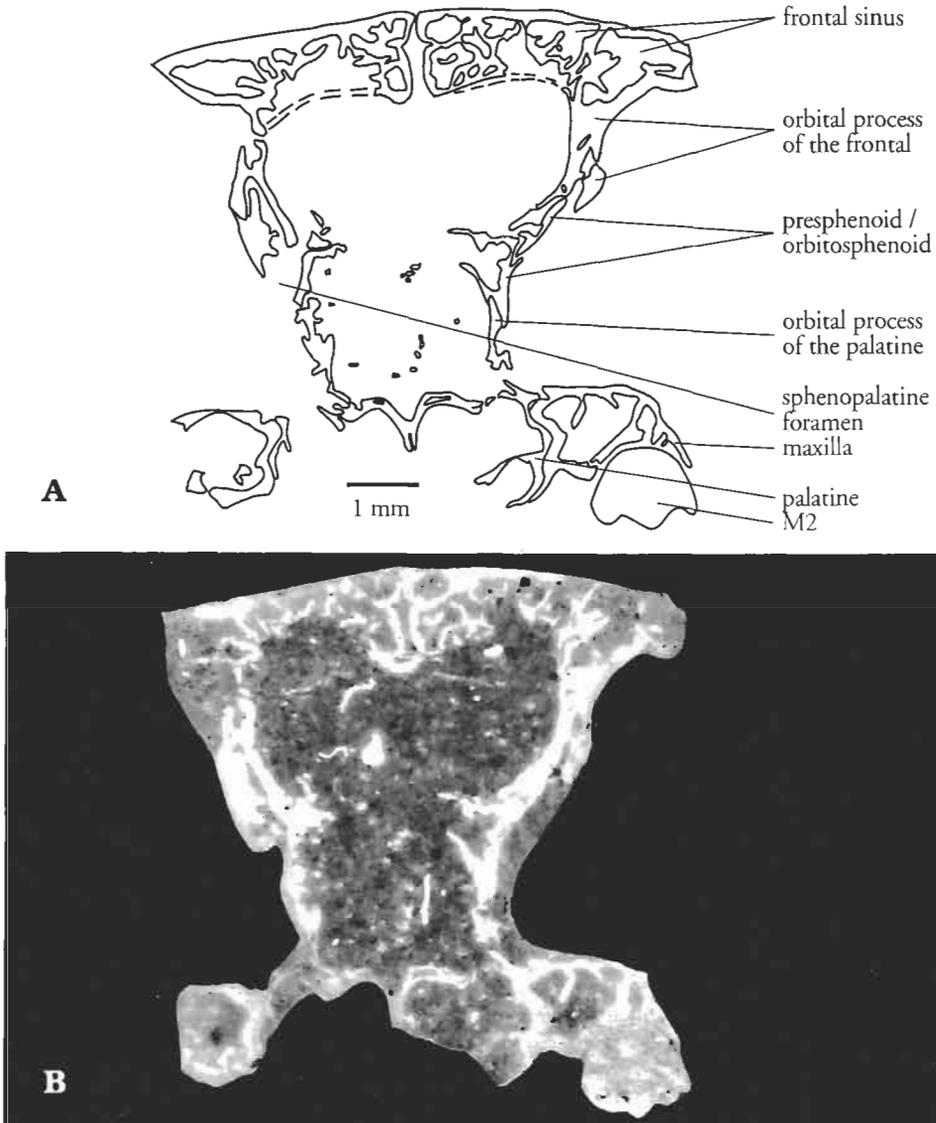


Fig. 9. *Nemegtbaatar gobiensis* Kielan-Jaworowska 1974, skull ZPAL MgM-I/76, section 646, contour drawing (A) and photograph under ultraviolet light (B), see Fig. 3 for position.

facialis) (Figs 6–7). The facial surface is seen in the skull only in dorsal view (Kielan-Jaworowska 1974) and its caudal end forms the rostromedial margin of the orbit. The facial surface articulates with the nasal rostromedially at the nasolacrimal suture (*sutura nasolacrimalis*), with the maxilla laterally at the lacrimomaxillary suture (*sutura lacrimomaxillaris*) and with the frontal medially at the frontolacrimal suture (*sutura frontolacrimalis*). The most rostromedial part of the facial surface is covered by the maxilla. The orbital surface forms the medial margin of the infraorbital canal rostrally and a small part of the orbit caudally. The preservation of the

lacrimal bone is good except for the caudal one fourth of the facial and orbital surface. The orbital surface, not seen in the lateral view of the skull is entirely surrounded by the maxilla, except for the contact with the facial surface of the lacrimal. The lacrimal canal (*canalis lacrimalis*) is observed (Fig. 6). The lacrimal foramen is seen on one side, where the facial surface of the lacrimal bone opens ventrally into the orbit.

The median septum and the cribriform plate (*septum mediale* and *lamina cribrosa*). — It is impossible to distinguish between the perpendicular plate (or mesethmoid) (*lamina perpendicularis*) and the vomer in the sections (Figs 6–7). Therefore these bones are described here as the median septum. The median septum divides the nasal cavity medially. No articulations are seen in the sections, all dorsal articulation with the frontal and nasal were presumably in cartilage. The ventral articulation with the maxilla and palatine is not preserved, due to damage of the specimen. The suture between the vomer and perpendicular septum, the vomeroethmoid suture (*sutura vomeroethmoidalis*) is observed in some sections, but this does not permit separate reconstruction of these bones. Remnants of the lateral lamina of the ethmoid are observed. The cribriform plate (*lamina cribrosa*) is not preserved, but tiny remnants of bone are seen in the sections in the appropriate area (Kielan-Jaworowska *et al.* 1986).

Presphenoid (*Os presphenoidale*) including orbitosphenoid (*ala*). — The bone consists of the median body (*corpus*) and orbitosphenoid or orbital wings (*alae orbitales*). The presphenoid median body which should lie ventrally to the yoke (see below), has not been preserved. The orbitosphenoid contributes to the caudodorsal part of the orbit, while its ventral part, the yoke, forms the rostral base of the neurocranium (Figs 8, 9). In lateral view of the skull the orbitosphenoid is seen in the orbit and has a roughly rectangular shape with a small anterior process. The orbital part articulates rostroventrally with the palatine (*sutura sphenopalatinum*), dorsally with the frontal (*sutura sphenofrontalis*) and ventrally with the maxilla (*sutura sphenomaxillaris*). The orbitosphenoid is much more extensive than it may appear in lateral view of the skull. It starts rostrally as a small bony element medial to the frontal and maxilla and underlies the frontomaxillary suture. The orbitosphenoid lies below the frontal and palatine in the frontopalatine suture. In these sections the bone has a triangular shape, with an acute angle pointing medially and probably forming a yoke (*jugum sphenoidale*) which has not been preserved. The yoke forms the base of the rostral cranial fossa and the dorsal border of the sphenoidal sinus (*sinus sphenoidalis*). The yoke has a median groove, possibly the *fovea hypochiasmatica* (see Hahn 1981). The preservation of the bone is good, but it is partly fused to other bones and the sutures are difficult to identify. The sphenoidal sinus is not preserved, but is possibly present, below the yoke.

Turbinals. — Tiny bony remnants of osseous turbinals are found throughout the nasal region, but due to distortion, they cannot be reconstructed.

Skull of *Chulsanbaatar vulgaris*

Nasal bone. — The nasal bone is not well preserved and the sutures with the frontal and maxilla are only tentatively recognized (Figs 12–14). The suture with the premaxilla is well preserved rostrolaterally. Ventrally, the ridges for attachment of the turbinals are well preserved (Fig. 13).

Premaxilla. — The premaxillary bone is observed with its palatal and nasal processes (Fig. 12). The latter forms the median wall of the maxillary sinus.

Maxilla. — The bone is well preserved except for the median wall of the infraorbital canal on the left side, while the zygomatic arch is not preserved on the right side. The sutures are only tentatively recognized on the basis of an assumption that the maxilla, when it is observed in the sections, is thicker than the surrounding bones (Figs 12–16). The ridges (pointing medially) for attachment of the turbinals are observed. The infraorbital foramen is small and situated opposite P1–P2 (Kielan-Jaworowska 1974; Kielan-Jaworowska *et al.* 1986), but is not seen in the sections due to the poor preservation. The infraorbital canal (Figs 14–15) and the maxillary sinus are seen (Fig. 14). The palatine process sends a single median process, directed dorsally, for the attachment of the median septum (Figs 13–14). It extends for a distance of about 0.4 mm vertically and then divides into two branches directed dorsomedially. Irregular remnants of the turbinals, attached to the process, are seen on both sides.

Frontal bone. — The bone is fused with its fellow of the opposite side and the interfrontal suture is not recognizable. In the area of the suture the bone is about twice as thick as at the sides (Figs 15–17). The preservation of the bone is good, except for the orbital part on the left side. The rostral half of the bone is thin and without pneumatization. In the caudal half of the bone, the frontal sinus is present.

Palatine bone. — The preservation of the horizontal lamina is good on the left side (Fig. 16). The perpendicular lamina is not recognized in any section, it seems that the palatine does not contribute to the orbit. The sutures are tentatively recognized on the assumption that palatine is thinner than maxilla, and by examining the complete skulls. The caudal part of the palatine is pneumatized. The palatonasal notch is seen in the palatomaxillary suture.

Lacrimal bone. — On the left side the lacrimal is missing, while on the right side it is broken (Fig. 14) and in many sections not preserved. The lacrimal canal and foramen are not preserved and the orbital surface is only tentatively reconstructed.

Vomer. — The bone is well preserved and consists of a sagittal and a horizontal part (Fig. 15). The sagittal part lies in the caudal prolongation of the above described median process of the palatine process of the maxilla, and forms the ventral part of the nasal septum. It articulates ventrally with the horizontal lamina of the palatine in sections 416 to 525 and with the presphenoid dorsally. The horizontal part of the vomer forms



Fig. 10. *Chulsanbaatar vulgaris* Kielan-Jaworowska 1974, skull ZPAL MgM-1/84 before sectioning, after some preparation, stereophotograph in lateral view, $\times 3$.

wings (*alae vomeris*) which articulate caudolaterally with the palatine and presphenoid. The wings separate the sphenoidal sinus from the ventrally lying nasopharyngeal meatus and the nasal pharynx. The horizontal part is observed. Rostrally the wings are not strictly horizontal, but are dipping ventrally with an angle of 30° to 40° and articulate laterally with the palatine processes of the maxilla.

Ethmoid. — This bone is not found in any section.

Presphenoid, orbitosphenoid. — The preservation of the presphenoid is better than in *Nemegtbaatar* (Fig. 17). As in *Nemegtbaatar*, the orbitosphenoid starts rostrally as a small bony element medial to the frontal and maxilla. The orbital part of the orbitosphenoid contributes largely to the orbit. The yoke is almost completely preserved and shows a median groove, the *fovea hypochiasmatica* (see Hahn 1981). The sphenoidal sinus is preserved. The median body of the presphenoid is not easy to identify because it is mostly covered by and fused to the vomer rostrally and the pterygoid ventrocaudally. The median body forms the floor and the median septum of the sphenoidal sinuses.

The pterygoid bone (*os pterygoideum*). — The bone is situated in the middle of the choanal channel (Fig. 17) and consists of a thin plate which articulates with the presphenoid in the pterygosphenoid suture (*sutura pterygosphenoidalis*) and covers the median part of the presphenoid ventrally.

Turbinals. — Osseous remnants of turbinals are found in the nasal fossae, but are damaged and impossible to reconstruct.

Paranasal sinuses

In the studied sections of *Nemegtbaatar gobiensis* and *Chulsanbaatar vulgaris* I have found the frontal sinus (*sinus frontalis*), maxillary sinus (*sinus maxillaris*) and sphenoidal sinus (*sinus sphenoidalis*). It proved impossible to follow the numbering of the sinuses introduced by Paulli

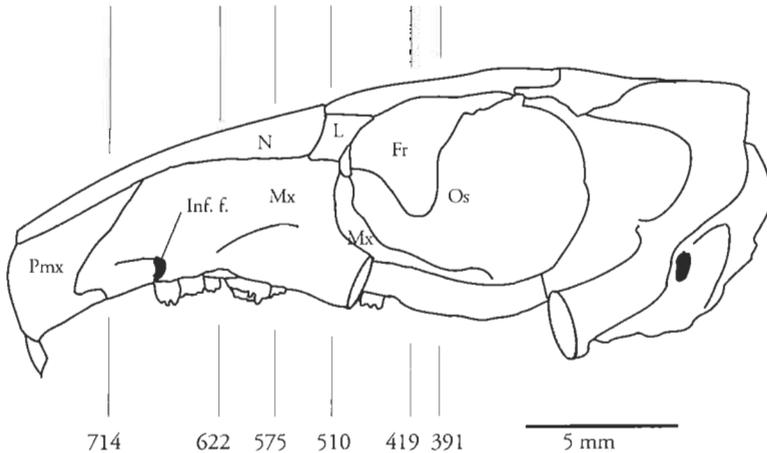


Fig. 11. Lateral view of the skull of *Chulsanbaatar gobiensis* Kielan-Jaworowska 1974 (based on ZPAL MgM-1/84) showing the positions of sections figured in this paper (Figs 12-17): part of the zygomatic arch has been removed, the gray spots denote their sections. Missing parts have been reconstructed, for abbreviations see Fig. 3.

(1900a, 1900b) and adopted by Moore (1981). Paulli numbered the sinuses after their openings into the nasal cavity and their relation to the ethmoturbinals. However, in the studied skulls the turbinals are barely preserved and it was impossible to establish which turbinal was closest to the opening between the sinus and the nasal cavity. I will follow the terminology of Edinger (1950) and Negus (1958).

The nasal part of the frontal sinus (*Sinus frontalis pars nasalis*).

— In *Nemegtbaatar* the frontal sinus is seen in the nasal bone (Fig. 5). In dorsal view the sinus is narrow rostrally, placed medial to the two caudal nasal foramina; it extends laterally in its caudal part. The inner table of the nasal is largely deficient and the turbinals could possibly invade these compartments. There are several bony lamellae dividing the sinus into smaller compartments. The nasal is deepest (0.9 mm) in the internasal suture. The sinus is 0.6 mm high in the same sections.

There is no pneumatization of the nasal bone in *Chulsanbaatar*.

The maxillary part of the frontal sinus (*Sinus frontalis pars maxillaris*). — Pneumatization in *Nemegtbaatar*, not related to the maxillary sinus, is seen in the dorsolateral part of the maxilla (Fig. 5). There are three or four compartments directed antero-caudally, connected caudally with the frontal part of the frontal sinus.

In *Chulsanbaatar* no such compartments are found.

The frontal part of the frontal sinus (*Sinus frontalis pars frontalis*). — In *Nemegtbaatar* the frontal sinus is seen in the frontal bone (Figs 6-9). It is located between the outer and inner tables of the bone and is divided into smaller cavities by numerous bony lamellae. The inner table of the frontal is sometimes deficient, so that the ethmoturbinates can invade the compartments in the nasofrontal opening (*apertura sinus frontalis*). The

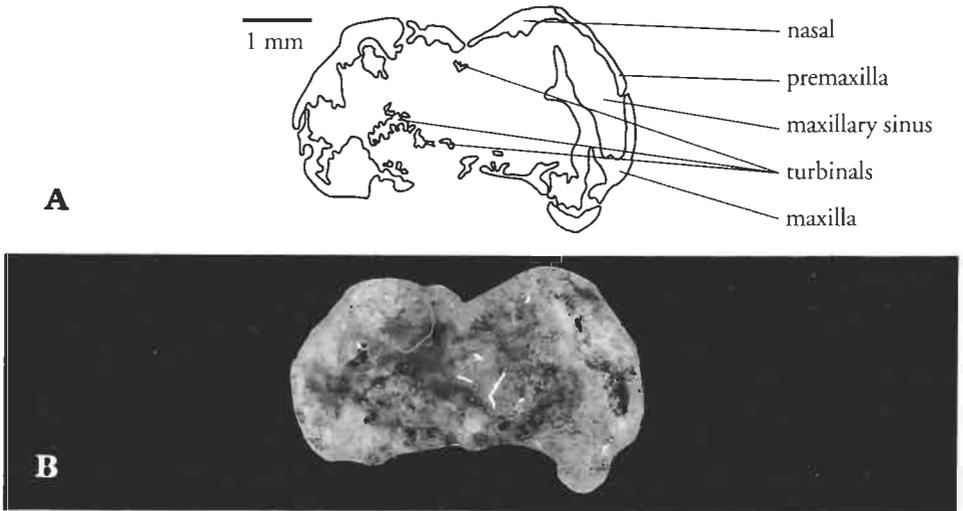


Fig. 12. *Chulsanbaatar vulgaris* Kielan-Jaworowska 1974, skull ZPAL MgM-I/84, section 714, contour drawing (A) and photograph under ultraviolet light (B), see Fig. 11 for position.

preservation is good. In dorsal view (Fig. 18) the sinus is pointed anteriorly and then widens to about one third of its length; in the middle part it is strongly indented laterally; the posterior one third is developed as a large, roughly rectangular, obliquely directed 'wing', which protrudes strongly laterally; the posterior margin of the sinus is concave. The contraction of the middle part of the sinus is caused by the presence of the orbit below the frontal in this region. In the orbital part of the frontal the sinus has a ventrally pointed compartment with a vertical height up to 2.9 mm. The frontal is thickest (1.9 mm), in the interfrontal suture. The sinus has its greatest vertical height (1.4 mm) close to the interfrontal suture. The caudal part of the sinus is divided into a median and a lateral chamber.

In *Chulsanbaatar* the frontal sinus is much less extensive than in *Nemegtbaatar* and it corresponds to the caudal part of the sinus of *Nemegtbaatar*. It consists of a median and a lateral chambers and these are confluent only in some sections (Figs 15–17). The lateral chamber and the median body is observed. The preservation is good and in dorsal view the sinus is H-shaped (Hurum 1992). There is no bony lamella in the sinus and the nasofrontal opening is not found. The frontal is thickest at the interfrontal suture (0.6 mm) and the height of the sinus in the same section is 0.3 mm.

The maxillary sinus. — In *Nemegtbaatar* the sinus is seen dorsally and medially to the premolars and molars (Figs 5–9). A compartment of the sinus is situated laterally to the infraorbital canal and inside the zygomatic process.

In *Chulsanbaatar* the position of the maxillary sinus is the same, but the sinus is only preserved partly (Figs 12, 14). The laterally placed

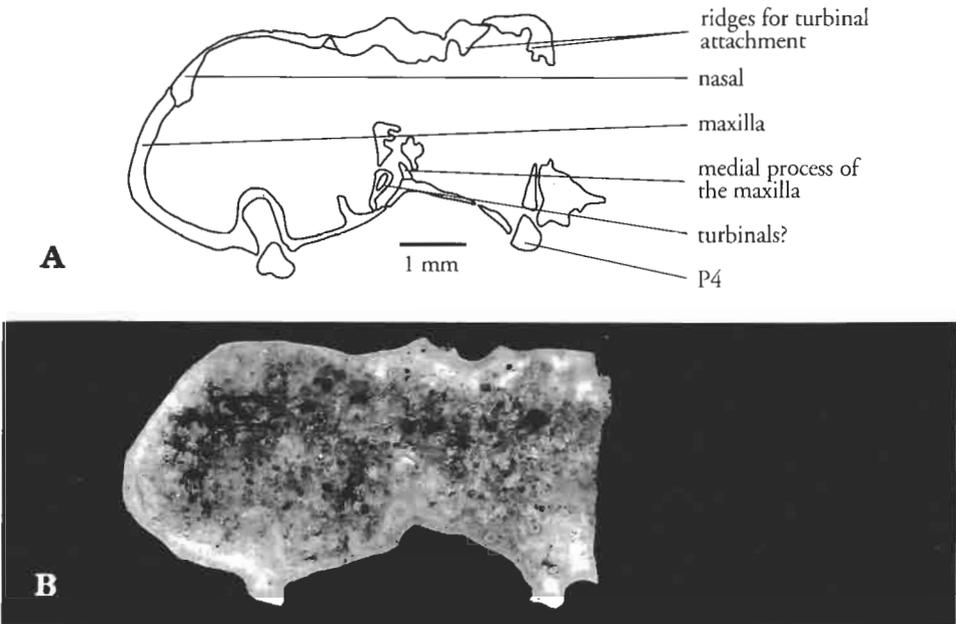


Fig. 13. *Chulsanbaatar vulgaris* Kielan-Jaworowska 1974, skull ZPAL MgM-I/84, section 622, contour drawing (A) and photograph under ultraviolet light (B), see Fig. 11 for position.

maxillary sinus, penetrating into the maxillary part of the zygomatic arch is preserved only on the left side.

The sphenoidal sinus. — The sphenoidal sinus is large in the sections where it is preserved (Figs 8–9, 16–17). The preservation is not good enough to make a detailed reconstruction in either *Chulsanbaatar* or *Nemegtbaatar*.

Comparison with Mesozoic mammals and cynodonts

In the discussion that follows I review the structure of the particular bones of the snout and orbit in different multituberculate taxa in comparison with those of other Mesozoic mammals, some primitive extant therian mammals and some cynodonts (=non-mammalian cynodonts of Wible 1991). The aim of these comparisons is to find out whether there are characters of the multituberculate skull that may be regarded as apomorphies. Comparisons with non-multituberculate mammals are limited because few adequately preserved skulls of Mesozoic mammals are known. These belong to: Early Jurassic morganucodontid *Morganucodon oehleri* Rigney 1963 (Kermack *et al.* 1981); Early Jurassic sinocodontid *Sinoconodon changchiawaensis* Young 1982 (Patterson & Olson 1961; Crompton & Sun 1985), both from the Lufeng beds of China; Kimmeridgian docodont *Haldanodon exspectatus* Küne & Krusat 1972 (Lillegraven & Krusat 1991) from the Guimarota coal mine of Portugal; Kimmeridgian eupantothere

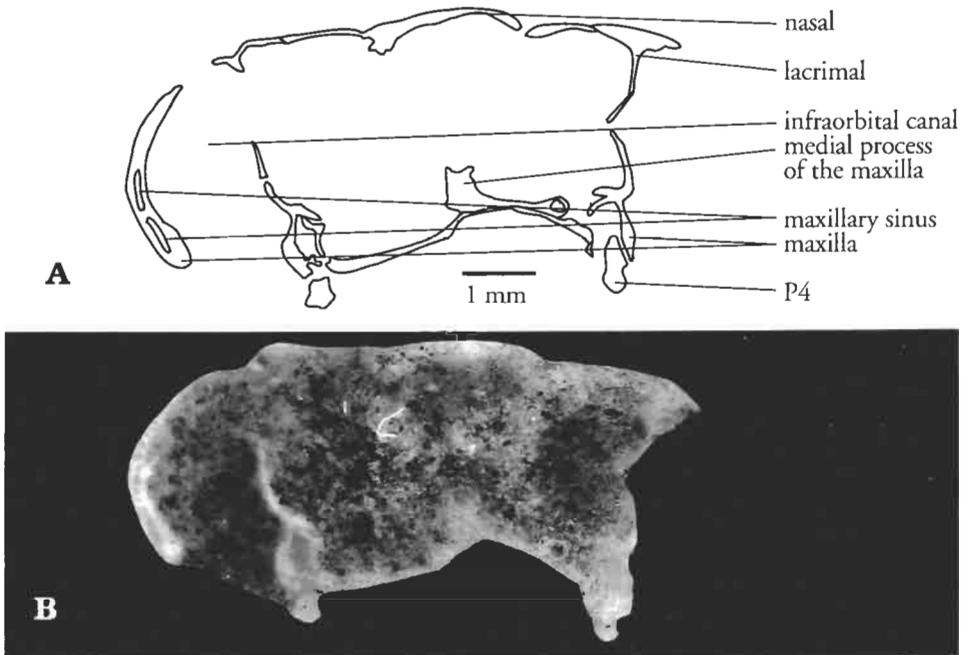


Fig. 14. *Chulsanbaatar vulgaris* Kielan-Jaworowska 1974, skull ZPAL MgM-I/84, section 575, contour drawing (A) and photograph under ultraviolet light (B), see Fig. 11 for position.

Henkelotherium guimarotae Krebs 1991 from the Guimarota coal mine of Portugal; Early Cretaceous eupantothere (possibly peramuran) *Vincelestes neuquenianus* Bonaparte 1986 (Bonaparte & Rougier 1987; Hopson & Rougier 1993 — the latter paper describes only the braincase and provides no data on the structure of the snout and orbit) from the La Amarga Formation of Argentina; Late Cretaceous eutherians from the Gobi Desert *Kennalestes gobiensis* Kielan-Jaworowska 1969 (Kielan-Jaworowska 1981), *Asioryctes nemegtensis* Kielan-Jaworowska 1975 (Kielan-Jaworowska 1981), *Zalambdalestes lechei* Gregory & Simpson 1926 (Kielan-Jaworowska 1969) and *Barunlestes butleri* Kielan-Jaworowska 1975 (Kielan-Jaworowska & Trofimov 1980); Late Cretaceous metatherian deltatheroids *Deltatheridium pretrituberculare pretrituberculare* Gregory & Simpson 1926 and *D. pretrituberculare tardum* (Kielan-Jaworowska 1975) from the Gobi Desert.

I do not compare the studied multituberculates with extant monotremes, because of the extreme specialisation of the monotreme snout (see Zeller 1989; Kuhn 1971).

Cynodonts are represented in the fossil record from the latest Permian. Their evolution throughout the Triassic and until the Early Jurassic shows a significant approach to the mammalian condition in their general morphology. Kielan-Jaworowska *et al.* (1986) made a comparison of the cranial vascular system between multituberculates and some cynodonts. Simpson (1928, 1937) described the Triassic tritylodont *Tritylodon longaeus*

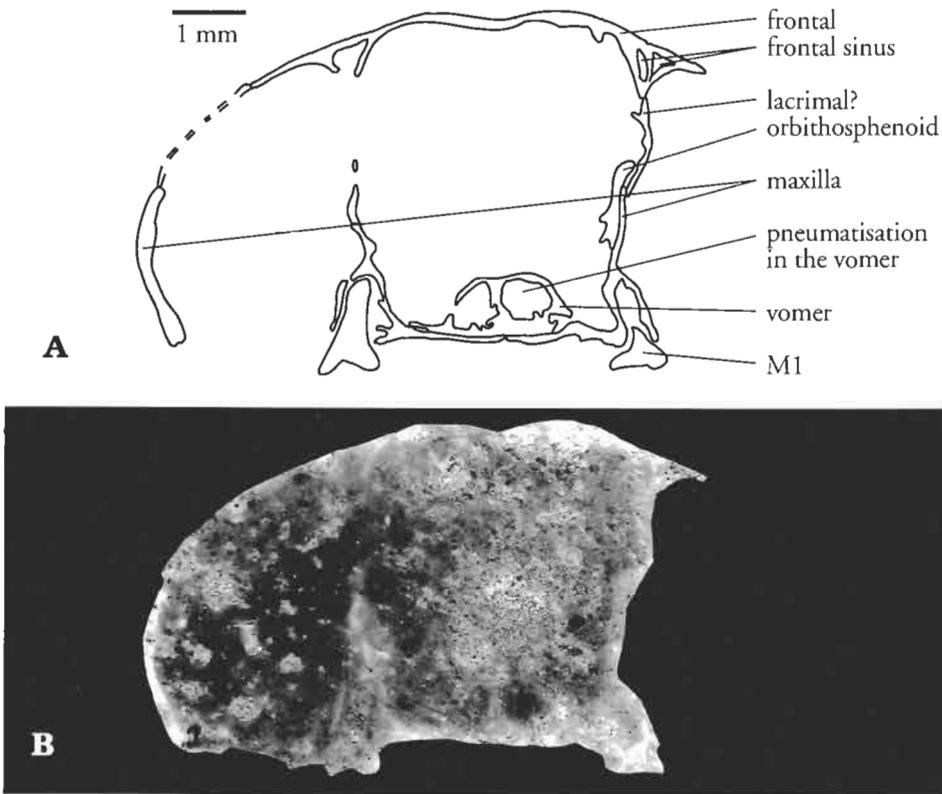


Fig. 15. *Chulsanbaatar vulgaris* Kielan-Jaworowska 1974, skull ZPAL MgM-I/84, section 510, contour drawing (A) and photograph under ultraviolet light (B), see Fig. 11 for position.

which he assigned to multituberculates on the basis of the superficial resemblance of the molars. Several skulls of non-mammalian cynodonts are known and I have chosen to make a comparison with the Middle Triassic traversodontid *Luangwa drysdalli* Brink 1963 (Kemp 1980); the Middle Triassic chiniquodontid *Probainognathus jenseni* Romer 1970; the Early Jurassic tritylodontid *Kayentatherium wellsi* Kermack 1982 (Sues 1986) and the Early Jurassic tritylodontid *Oligokyphus* sp. (Kühne 1956).

Nasal bone. — In multituberculates the nasal is long and slender in the Kimmeridgian *Paulchoffatia delgadoi*, and very wide and expanded posteriorly in the Mongolian Late Cretaceous taxa. In the Early Paleocene *Taeniolabis taoensis* the nasal extends almost to the posterior end of the orbit (Simpson 1937). This is the longest posterior extent of the nasal seen in any multituberculate. In the Paleocene *Ptilodus montanus* the bone is less expanded (Simpson 1937). In *Nemegtbaatar*, in the frontonasal suture, the nasal is overlapped by the frontal, which is the usual condition for multituberculates (except *Lambdopsalis*) and most mammals.

A characteristic feature of multituberculates is the presence of the nasal foramina. In the paulchoffatids the four specimens available that

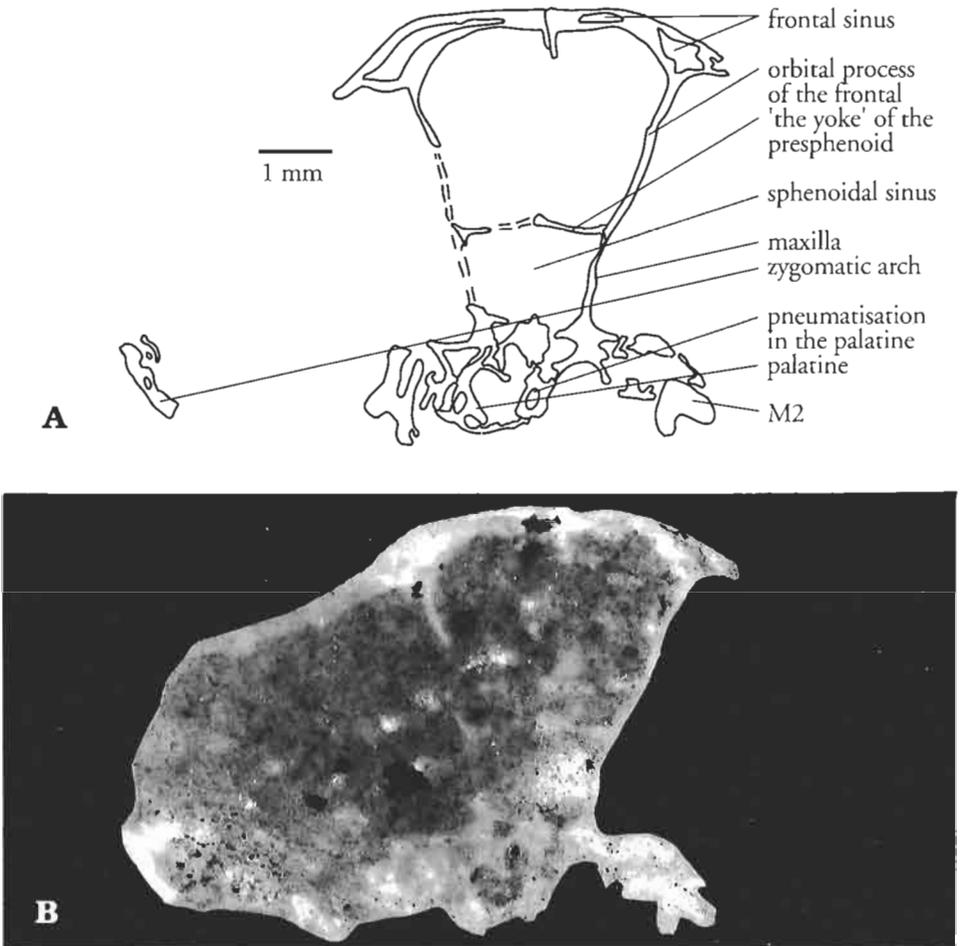


Fig. 16. *Chulsanbaatar vulgaris* Kielan-Jaworowska 1974, skull ZPAL MgM-1/84, section 419, contour drawing (A) and photograph under ultraviolet light (B), see Fig. 11 for position.

have the nasal region preserved are more or less broken and crushed, and the nasal foramina cannot be identified with any certainty. Gerhard Hahn (personal communication) suggested that if these foramina were present in paulchoffatids they must have been very small, and they became enlarged and multiple during the Late Jurassic–Late Cretaceous times. In *Nemegtbaatar* the nasal foramina are arranged symmetrically to those on the opposite bone (Fig. 18). The distribution of these foramina varies in *Chulsanbaatar*, but in most specimens there is a symmetrical pair of larger foramina and another pair of tiny ones in front (Fig. 18). In *Kamptobaatar* there are four small foramina in the left nasal and two in the right, the posterior ones being the largest (Kielan-Jaworowska 1971: Fig. 1). In *Sloanbaatar* the nasal foramina are very indistinct, probably asymmetrically arranged, two in the left nasal and one in the right (Kielan-Jaworow-

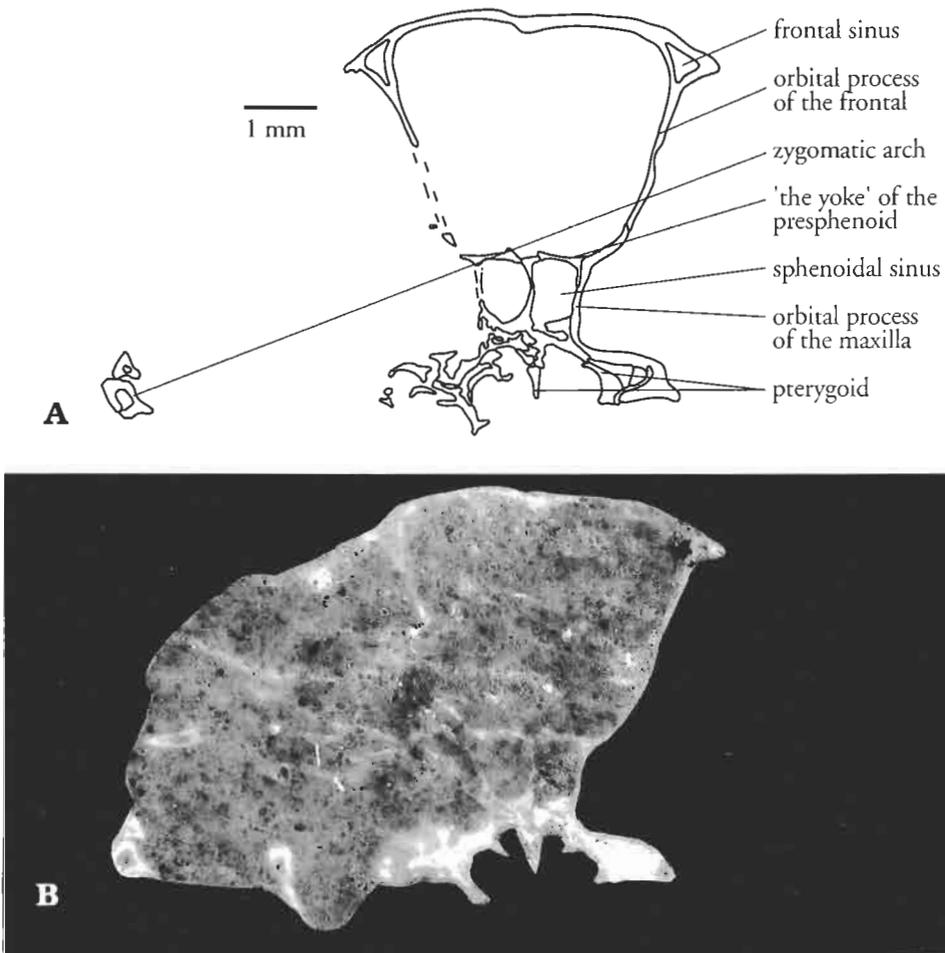


Fig. 17. *Chulsanbaatar vulgaris* Kielan-Jaworowska 1974, skull ZPAL MgM-1/84, section 391, contour drawing (A) and photograph under ultraviolet light (B), see Fig. 11 for position.

ska 1971: Fig. 6). A single foramen arranged symmetrically to the one on the other nasal has been described in *Djadochtatherium* (Gregory & Simpson 1926: Fig. 1). *Kryptobaatar* has one large slitlike foramen symmetrical to the one on the other nasal (Kielan-Jaworowska 1970: Plate XI). *Lambdopsalis* has seven to eight foramina in each nasal, four large ones anteroposteriorly aligned and three to four smaller foramina, the latter lying medial to the larger ones and symmetrical to those on the opposite bone (Miao 1988: Fig. 12). *Ptilodus* has three foramina in the right nasal and two in the left, with some slight difference in position in different specimens (Simpson 1937: Fig. 5). Nasal foramina were found in *Taenio-labis*, but are not described as yet (see Miao 1988). It seems that the nasal foramina, which do not occur in other mammals (except for *Homo* where a single foramen in the nasal bone transmits a branch of the anterior

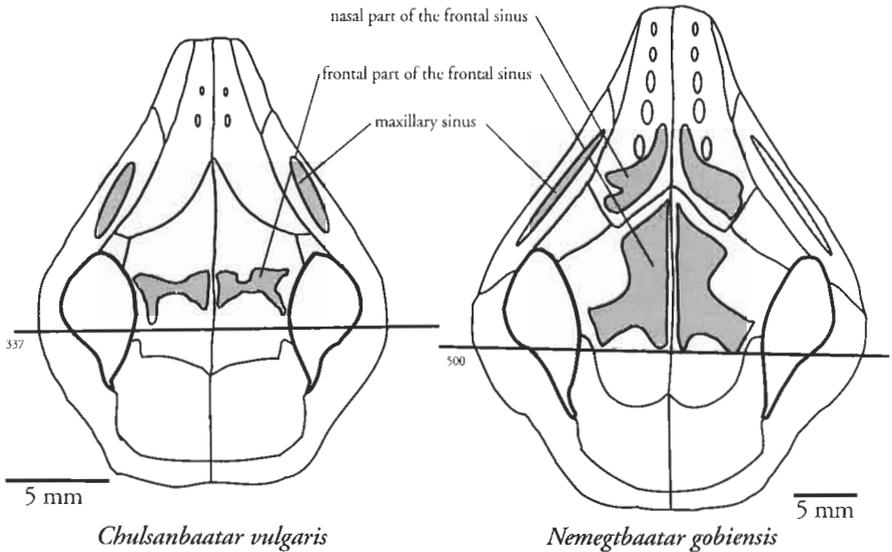


Fig. 18. Location of the frontal and maxillary sinuses (gray) in skulls of *Chulsanbaatar vulgaris* Kielan-Jaworowska 1974 and *Nemegtbaatar gobiensis* Kielan-Jaworowska 1974. The outlines of the skulls in dorsal views are from Kielan-Jaworowska (1983) and Kielan-Jaworowska *et al.* (1986).

ethmoidal nerve, Goodrich 1958; Davies & Davies 1962), are an apomorphy of multituberculates (Miao 1993).

In *Haldanodon* the nasal is the most extensive bone of the skull roof. Lillegraven & Krusat (1991) suggested that this is a primitive character, a retention from cynodont ancestry. In *Haldanodon* the posterior part of the nasal bone is situated well beyond the anterior limit of the orbit. *Morganucodon*, *Haldanodon* and *Vincelestes* have a long nasolacrimal contact as characteristic of *Nemegtbaatar* and *Chulsanbaatar*.

No nasal foramina are present in cynodonts. Expanded nasals occur in all cynodonts. The nasal of *Luangwa* is expanded posteriorly, like in the Late Cretaceous multituberculates; in *Probainognathus* the nasal bone expands only slightly posteriorly; in *Kayentatherium* the nasal becomes much expanded posteriorly between the orbits and has a medio-posteriorly directed process between the frontals; *Oligokyphus* has a flat, thin and long nasal which is only slightly expanded posteriorly (Kemp 1980; Romer 1970; Sues 1986; Kühne 1956). The lateral expansion of the nasals in *Nemegtbaatar* and *Chulsanbaatar* is similar to the expansion seen in *Kayentatherium* and *Probainognathus*. The posterior expansion is shorter in *Chulsanbaatar* and *Nemegtbaatar*, more like that in *Oligokyphus*. The caudally expanded nasals in studied Late Cretaceous and in Tertiary taxa was regarded as a derived feature by Kühne (1961) and Hahn (1969) since in the Late Jurassic multituberculates the nasals were supposed to be narrow, but the nasals of *Paulchoffatia* are expanded

lateral in their posterior part (James A. Hopson personal communication). An explanation for the expanded nasals may be that if multituberculates, as most Mesozoic mammals, were nocturnal (Jerison 1973; Crompton *et al.* 1978, see also the discussion of the orbital structure in this paper) they would be greatly dependent on the sense of smell (Moore 1981) and with an increase of the olfactory bulbs, the nasals will be expanded. Expansion of the nasals also gives more room for turbinals which is an adaptation to the high ventilation rates typical of all mammals (Hillenius 1992). Jenkins (1990) supported the idea that Mesozoic mammals evolved homeothermy and concluded that (1990: p. 25) 'Endothermy and such thermoregulatory structures as fur and sweat glands were already present by Jurassic times (...) Jurassic therians were physiologically adapted for activity in cool ambient temperatures, and therefore could have been either crepuscular or nocturnal in habit, or occupied habitats of dense vegetation.'

Premaxilla. — In all extant mammals the external nares are confluent. The presence of confluent external nares in multituberculates is under debate (Miao 1988). Miao suggested the existence of an internarial bar in *Lambdopsalis*, but this has not been preserved in any specimen. I have not found the internarial process of the premaxilla in *Nemegtbaatar* and *Chulsanbaatar*. In *Sinocodon* and *Haldanodon* the external narial opening is divided by bone into left and right parts (Crompton & Sun 1985; Wible *et al.* 1990; Lillegraven & Krusat 1991). The external nares are not confluent in tritylodonts except maybe in *Oligokyphus* (Kühne 1956). Miao (1988) suggested that the dorsal median process of premaxilla may be present in *Morganucodon*.

Maxilla. — The maxilla in multituberculates is extensive, comparable sometimes with the condition seen in many rodents. The infraorbital canal which transmits the infraorbital branch of the trigeminal nerve, the infraorbital artery and associated veins, pierces through to the surface of maxilla by the infraorbital foramen in all mammals. Two infraorbital foramina were found in the Kimmeridgian Paulchoffatiidae (Hahn 1985) and in the Purbeckian *Bolodon* (James Hopson personal communication contra Hahn 1985). Hahn (1985) suggested that pre-Cretaceous mammals had a tri- or bipartite structure of the infraorbital foramen and this should be regarded as a symplesiomorphy of all pre-Cretaceous mammals, including multituberculates. Miao (1988) stated that the rule is not valid because the Late Cretaceous multituberculate *Meniscoessus robustus* has two foramina, and in one specimen of *Lambdopsalis* there is one foramen on the left side and two on the right side. Miao cited several examples of extant mammals with two infraorbital foramina. Hahn (1985) suggested that the reduction to only one infraorbital foramen took place independently in multituberculates and Metatheria/Eutheria, but Miao argued that the presence of divided foramina is due to the individual variation. In the Early Cretaceous multituberculate *Monobaatar* a single infraorbital foramen positioned above the P3-P4 embrasure was found. In

Arginbaatar two infraorbital foramina are present, the anterior opposite the P3–P4 embrasure and the posterior opposite the posterior part of P4 (Kielan-Jaworowska *et al.* 1987). Among Asian Late Cretaceous multituberculates the infraorbital foramen is single, large, rounded and placed opposite P2 in *Nemegtbaatar* and *Bulganbaatar*. In *Chulsanbaatar* the infraorbital foramen is small and placed opposite P2. In *Kryptobaatar* the foramen is situated on the ventral wall of the maxilla opposite the P1–P2 embrasure. The small infraorbital foramen in *Catopsbaatar* is situated opposite P3 (Kielan-Jaworowska 1970, 1971, 1974). In *Ptilodus montanus* the maxilla is very large and the infraorbital foramen is single situated at the anterior base of the zygomatic root above the posterior end of P3 (Simpson 1937; Krause 1982).

Several Mesozoic mammals have multiple infraorbital foramina. In *Morganucodon* there are three infraorbital foramina. *Henkelotherium* has a relatively long infraorbital canal and the single infraorbital foramen is placed above the last premolar. *Haldanodon* has a tripartite infraorbital foramen, the largest opening preserved opposite P2–P3, the second smaller one dorsally to M1 and the third in the lacrimal. In *Vincelestes* the infraorbital foramen is large, single and situated opposite P2. In *Barunlestes* the infraorbital foramen is situated immediately above the P2–P3 embrasure. The infraorbital foramen in *Kennalestes* is situated above the middle of P3; in *Zalambdalestes* above the P3–P4 embrasure; in *Deltatheridium* above the anterior part of P3 (Kielan-Jaworowska 1975; Kielan-Jaworowska 1981; Kielan-Jaworowska & Trofimov 1980).

In a cynodont *Luangwa* the internal infraorbital foramen is bordered completely by the maxilla and runs into the maxillary sinus, but the external opening has not been preserved. The infraorbital foramen in *Kayentatherium* is split into three slit-like foramina. In *Oligokyphus* the infraorbital foramen is split into two foramina and the maxilla forms the infraorbital canal together with the lacrimal and palatine (Kemp 1980; Romer 1970; Sues 1986; Kühne 1956).

The size of the infraorbital foramen may reflect a more sensitive muzzle. It would be, by this argument, better developed in *Nemegtbaatar* than in *Chulsanbaatar*. The distribution of single, double and triple infraorbital foramina in Mesozoic mammals and cynodonts generally follows Hahn's (1985) suggestion, that cynodonts and pre-Cretaceous mammals developed tri- or bipartite infraorbital foramina, and Cretaceous mammals a single one. The few exceptions from this rule may be individual variants, especially *Lambdopsalis*. The placement of the infraorbital foramen in multituberculates does not follow any regular pattern.

Frontal bone. — The frontal is slender and small in the Kimmeridgian multituberculates, which contrasts with a very extensive frontal in the Cretaceous taxa. This is probably related to the expansion of the olfactory bulbs (see Hahn 1969, 1978; Kielan-Jaworowska 1983; Kielan-Jaworowska *et al.* 1986).

The frontal is excluded from the orbital rim in *Djadochtatherium matthewi* (Simpson 1937). In other Mongolian multituberculates the orbital process of the frontal is large, for example in *Kamptobaatar* (Kielan-Jaworowska 1971), *Chulsanbaatar* and *Nemegtbaatar* (Kielan-Jaworowska *et al.* 1986). In *Taeniolabis* ('*Polymastodon*' of Broom 1914) the frontal is completely excluded from the orbital rim by the nasal and parietal, but forms a part of the medial wall of the orbit. The orbital process of the frontal in *Lambdopsalis* was described by Miao (1988).

In the Jurassic taxa the pointed mediorostral part of the frontal is present in *Paulchoffatia* (Hahn 1969). This is also clearly visible in the Late Cretaceous Mongolian multituberculates *Kamptobaatar*, *Sloanbaatar*, *Nemegtbaatar*, *Catopsbaatar* and *Chulsanbaatar*. Also in *Ptilodus* and *Taeniolabis* the frontals narrow anteriorly to a pointed end inserted between the nasals (Simpson 1937). This anterior pointed end of the frontal is also present, but smaller in *Haldanodon* and *Morganucodon*, but is not present in either *Vincelestes* nor in *Luangwa*, *Oligokyphus*, *Kayentatherium*, and *Probainognathus*.

In *Morganucodon* the orbital process of the frontal bone is less extensive than in *Nemegtbaatar* and *Chulsanbaatar*. The orbital process of the frontal probably contributes to the dorsal half of the orbital wall in *Haldanodon* (Lillegraven & Krusat 1991). In *Henkelotherium* (Krebs 1991) the frontal contributes to the dorsomedial part of the orbit. There is a large orbital process of the frontal in *Barunlestes* (Kielan-Jaworowska & Trofimov 1987).

In *Luangwa* and *Probainognathus* the frontal is a small bone completely shut off from the orbital rim by the laterally placed prefrontal. In *Luangwa* the frontal is exposed within the orbit behind the prefrontal and just below the postorbital, and a ventral flange of the frontal extends down the anterodorsal face of the orbital wall exactly overlapping the prefrontal internally. In *Probainognathus* the frontal extends behind the prefrontal to contact the orbital process of the palatine (James A. Hopson personal communication). The prefrontal is lost in *Kayentatherium* and *Oligokyphus*. The frontal contributes to the orbital wall and the sagittal crest in both, but is still a small bone in dorsal view. In *Kayentatherium* a median crest along the anteroventral surface of the bone presumably supported the internasal septum. The same is observed in *Chulsanbaatar* and *Nemegtbaatar* (this paper).

The orbital process of the frontal is possibly an apomorphic character in mammals and it is found in almost all extant mammals, by this development the frontal bone covers the anterior end of the brain dorsally and laterally. The strength provided by a single bone in this area is more rigid and affords better protection than in the cynodont ancestors that possessed several bones in this region.

The orbit. — The oldest multituberculate orbit has been preserved in *Kuehneodon?* sp. from the Early Kimmeridgian, and it shows the same structure as in younger multituberculates. The medial orbital wall in

Kuehneodon? sp. is formed by the orbitosphenoid, the anteroventral part by the lacrimal and the most anterodorsal part by the frontal (Hahn 1977: Fig. 9). Partly preserved orbital regions are known from *Kuehneodon dryas* and *Henkelodon* from the same locality. The resemblance to younger multituberculates led Hahn (1977: p. 179) to suggest that: 'From Malm to Eocene their [multituberculate] evolution is confined to those parts of the skull which are closely correlated with feeding processes as the dentition and details of the muzzle'. Of the Mongolian Late Cretaceous multituberculates the orbital wall has been described in detail in *Kamptobaatar* (Kielan-Jaworowska 1971). The orbit is very large in all Mongolian multituberculates, largest in relation to the size of the skull, in *Nemegtbaatar*. The orbit of *Nemegtbaatar* does not differ essentially from that of *Kamptobaatar* (Kielan-Jaworowska 1971). In its composition the orbit of *Nemegtbaatar* is formed dorsally by a large orbital process of the frontal, anteriorly by the maxilla, ventrally by the orbital process of palatine and caudally by a large orbitosphenoid. The lacrimal contributes only to a very limited extent to the anterodorsal part of the orbit. The orbit of *Chulsanbaatar* differs from *Nemegtbaatar* in the absence of the orbital process of the palatine. The area occupied by the palatine in the orbit of *Nemegtbaatar* is covered by the maxilla and the orbitosphenoid in *Chulsanbaatar*. The orbit seems to be a conservative area of the skull which underwent only minor changes from advanced non-mammalian cynodonts to the Late Cretaceous mammals (Tab. 1).

The orbital diameter varies in different species and this may allow one to speculate about the activity patterns of early mammals. Kay & Cartmill (1977) plotted orbital diameter against skull length in various species of mammals (83 extant and 17 fossil taxa). In smaller mammals orbital diameter showed positive correlation with the skull length, but negative allometry (larger mammals have absolutely larger, but relative smaller orbits). Krause (1986) used this plot to discuss the activity pattern of multituberculates. He plotted *Ectypodus* and *Ptilodus* and suggested them to be nocturnal with olfaction as the dominant sense. Krause (1986) measured whatever diameter was available on the assumption that the orbits of multituberculates are generally circular in outline (David W. Krause personal communication). The large orbital diameter in *Chulsanbaatar* and *Nemegtbaatar* may be partly due to the lateral expansion of the zygomatic arch, which is related to the strong development of the masticatory musculature and not necessarily related only to the size of the eye. The orbital diameter of multituberculates (without an attempt at reconstruction of the masticatory and facial musculature) may therefore be misleading as evidence of the activity pattern. An analysis of multituberculate orbital diameter in relation to skull size in multituberculates would require a special study.

Palatine bone. — Miao (1988) suggested that the exclusion of the palatine from the orbit might be a synapomorphy for multituberculates. The orbital process of the palatine bone is absent in paulchoffatiids (Hahn

Tab. 1. Bones exposed in the orbit of multituberculates, some Mesozoic mammals and cynodonts. 0 – absent, 1 – present and ? – not preserved, Fr – Frontal, L – Lacrimal, Mx – Maxilla, N – Nasal, Os – Orbitosphenoid, Pal – Palatine, Par – Parietal, Pf – Prefrontal and Po – Postorbital. The taxa cited in the upper rectangle belong to the multituberculates, in the middle rectangle to other Mesozoic Mammals and in the lower rectangle to cynodonts.

	Pf	Po	Fr	L	Mx	Par	Pal	N	Os
<i>Kuehneodon?</i> sp.	0	0	1	1	?	0	0	0	1
<i>Kamptobaatar kuczynskii</i>	0	0	1	1	1	1	1	0	1
<i>Chulsanbaatar vulgaris</i>	0	0	1	1	1	0	0	0	1
<i>Nemegtbaatar gobiensis</i>	0	0	1	1	1	0	1	0	1
<i>Ptilodus montanus</i>	0	0	1	0	1	1	0	0	1
<i>Taeniolabis taoensis</i>	0	0	?	0	1	1	0	0	?
<i>Lambdopsalis bulla</i>	0	0	1	0	1	0	0	0	1
<i>Ectypodus tardus</i>	0	0	1	0	1	1	1	0	1
<i>Morganucodon oehleri</i>	0	0	1	1	1	0	1	0	1
<i>Vincelestes neuquianus</i>	0	0	1	1	1	?	1	0	?
<i>Barunlestes butleri</i>	0	0	1	1	1	0	1	1	?
<i>Asioryctes nemegtensis</i>	0	0	1	1	1	0	1	0	?
<i>Kennalestes gobiensis</i>	0	0	1	1	1	0	1	0	?
<i>Luangwa drysdalli</i>	1	1	0	1	1	0	1	0	0
<i>Kayentatherium wellsi</i>	0	0	1	1	1	0	1	0	1
<i>Oligokyphus</i> sp.	0	0	1	1	1	0	1	0	?

1987), in *Lambdopsalis* and maybe in *Ptilodus montanus*. The orbital process is present, however, in *Nemegtbaatar* (this paper). The presence of an orbital process of the palatine in *Kamptobaatar* and *Ectypodus* (Kielan-Jaworowska 1971; Sloan 1979) shows that the exclusion of the palatine from the orbit cannot be a synapomorphy of multituberculates. The orbit is not well preserved in *Chulsanbaatar*, and an orbital process may be present but is not recognized in this work.

The sphenopalatine foramen occurs in all mammals, but the location of the foramen varies. The foramen is the entry for nerves and vessels and transmits them from the outside to the mucous membranes of the nose and palate. In *Ptilodus montanus* the foramen is bordered by the maxilla and orbitosphenoid; in *Lambdopsalis* by the frontal and maxilla; in *Ectypodus* by the maxilla and palatine; in *Kamptobaatar* it is situated at the junction of the maxilla, the frontal, the orbitosphenoid and the palatine. The foramen in *Nemegtbaatar* was described as being located at the junction of the maxilla, frontal, orbitosphenoid and palatine (Kielan-Jaworowska *et al.* 1986). A close examination of the sections of *Nemegtbaatar* and the finding of the orbital process of the palatine, allows me to state

that the sphenopalatine foramen is placed at the junction between of the palatine and orbitosphenoid.

The palatine bone of *Morganucodon oehleri* is divided into palatine and orbital processes, as in *Nemegtbaatar*. The sphenopalatine foramen in *Morganucodon* is situated between the palatine, maxilla and orbitosphenoid bones. In *Haldanodon* the orbital process of the palatine has not been found; although this may be due to the poor preservation of the orbit. The orbital process of the palatine of *Barunlestes* is large and forms the medial and ventroposterior parts of the orbit. The sphenopalatine foramen is placed low in the orbit, close to the palatino-maxillary suture, just opposite M3 (Kielan-Jaworowska & Trofimov 1980). Kielan-Jaworowska (1981) reconstructed a large orbital process of the palatine in both *Kennalestes* and *Asioryctes*. In *Vincelestes* there is a well exposed orbital process of the palatine (Bonaparte 1986).

The palatine in *Luangwa* consists of a palatal and an orbital process, the orbital process being large and overlapping the medial and ventral parts of the lacrimal. In *Kayentatherium* the orbital process of the palatine is large with two foramina, the exit for a branch of the infraorbital canal anteriorly and the sphenopalatine foramen medially. The bone also contributes to a wall of the infraorbital canal.

The lack of well preserved medial orbital walls in multituberculates may be the reason why the orbital process of the palatine has not been found in several taxa.

Lacrimal. — In the Paulchoffatiinae the lacrimal bone was found in *Paulchoffatia* and in Paulchoffatiinae gen. et sp. indet. (Hahn 1969, 1987). The lacrimal has not been described in Tertiary multituberculates. Kielan-Jaworowska (1974) described the lacrimal in *Nemegtbaatar*, and later in other Mongolian multituberculates (Clemens & Kielan-Jaworowska 1979; Kielan-Jaworowska & Dashzeveg 1978; Kielan-Jaworowska *et al.* 1986). In *Nemegtbaatar* and *Chulsanbaatar* the lacrimal has a large facial surface and a smaller orbital surface. In *Nemegtbaatar* the lacrimal canal and the lacrimal foramen are recognized (this paper). The lacrimal foramen is preserved in the lacrimal bone in *Paulchoffatia* (Hahn 1969). The lacrimal foramen is situated in the maxilla in *Lambdopsalis* (Miao 1988). Miao suggested that the loss of the lacrimal in *Lambdopsalis* and in a number of other multituberculates may be due to dorsal displacement of a large zygomatic root of the maxilla.

The lacrimal in *Morganucodon* possesses a lacrimal duct and two posterior foramina. In both *Morganucodon* and *Haldanodon* the lacrimal makes a contribution to the zygomatic arch, which is not seen in multituberculates (see Lillegraven & Krusat 1991). The lacrimals of *Haldanodon*, *Sinoconodon* and *Morganucodon* are more reminiscent of those in extant primitive therian mammals than in *Nemegtbaatar* and *Chulsanbaatar*.

In *Luangwa* the lacrimal is an extensive bone with a large exposure on the dorsal surface of the snout as well as forming the largest part of the

anterior orbital wall. *Probainognathus* and *Kayentatherium* have large lacrimals which contribute to the snout, the zygomatic arch and the orbit. Kühne (1961) and Hahn (1969) reconstructed the lacrimal in paulchoffatids with small dorsal exposure, not equivalent to the large dorsal lacrimal in cynodonts. According to Prof. James A. Hopson (personal communication) the reconstruction of the lacrimal in paulchoffatids made by Kühne (1961) and used by Hahn (1969) is inaccurate and the lacrimal of *Paulchoffatia* is actually large in dorsal view.

Presphenoid. — This bone has been described briefly only twice in Mesozoic mammals before. The presphenoid was found in *Vincelestes* (Bonaparte & Rougier 1987) and a median process of presphenoid was observed in *Barunlestes* (Kielan-Jaworowska 1975).

Vomer. — Little comparative information on the vomer is available for Mesozoic mammals and cynodonts. The vertical median plate in *Kamptobaatar* was identified tentatively as the vomer (Kielan-Jaworowska 1971). In *Ptilodus montanus* the vomer extends backwards some distance behind the edge of the secondary palate, but it was not described in detail by Simpson (1937).

The vomer was found in *Morganucodon oehleri*, but not described as a separate bone, and mentioned only in connection with the posterior part of the palate (Kermack *et al.* 1981). Kühne (1956) found no parts of the vomer preserved in *Oligokyphus*, but it was probably present in life. The dorsal side of the maxillary should bear an indication of a contact with the vomer but this was not preserved either. In *Kayentatherium* a small fragment of the vomer was figured but not described (Sues 1986: Fig. 9).

Turbinals. — In both *Nemegtbaatar* and *Chulsanbaatar* there are tiny bony remnants of osseous turbinals. In *Lambdopsalis* there is a complex ridge system present on the ventral surfaces of the nasal, frontal and maxilla (Miao 1988). These ridges probably indicate the presence of turbinals. I was unable to reconstruct the ridges in any bones except the nasal in the sectioned skulls of *Nemegtbaatar* and *Chulsanbaatar*. However, I found two longitudinal ridges on the inner side of the maxilla in a crushed skull ZPALMGM-I/66 of ?*Nemegtbaatar*.

Turbinals have not been found in *Morganucodon*, but Kermack *et al.* (1981) reconstructed the turbinals on the basis of the system of ridges on the ventral surface of the nasal, frontal and maxilla. Lillegraven & Krusat (1991) described disordered turbinals in *Haldanodon*. In *Barunlestes* turbinals are present in the frontal sinus (Kielan-Jaworowska & Trofimov 1980). Hillenius (1992) regarded the turbinals as an ancient attribute of mammals that may have evolved among the therapsid ancestors of mammals, in relation to elevated ventilation rates and the evolution of endothermy. In *Oligokyphus* the frontals possess ventrally double ridges supporting the ethmoturbinals, they are also present in *Thrinaxodon* (Fourie 1974), these ridges continue onto the nasal and indicate the presence of turbinals in cynodonts.

Sinuses

The definition of the pneumatic sinuses and the decision when the inner cancellous space in a bone actually turns into a sinus, are difficult to make for fossil material (Armand de Ricqlès, personal communication). Negus (1958) provided an extensive documentation of the distribution of pneumatic sinuses in extant mammals. The paleontological evidence of the evolution of the frontal sinus was given by Edinger (1950).

Maxillary sinuses. — All living mammals, except monotremes, some marsupials and aquatic mammals, have maxillary sinuses. This is the only sinus that occurs in the Insectivora and Chiroptera (Edinger 1950). Lillegraven & Krusat (1991) described the maxillary sinuses in *Haldanodon*. In multituberculates the maxillary sinus has not been as yet described. I found maxillary sinuses in *Nemegtbaatar* and *Chulsanbaatar* which appear confluent with the infraorbital canal, but because of the poor state of preservation it cannot be stated with any certainty that this is not an artifact. If the maxillary sinuses in multituberculates are indeed confluent with the infraorbital canal, this would be similar to the condition in docodonts where the small maxillary sinus is connected posteriorly with the infraorbital canal (Lillegraven & Krusat 1991).

The maxillary sinuses were reported in Diademodontidae (*Diademodon*) (Brink 1955); in Galesauridae (*Thrinaxodon*) (Fourie 1974); some gorgonopsids and in Procynosuchidae (*Procynosuchus*) (Kemp 1979); in Traversodontidae (*Luangwa*) (Kemp 1980); in Tritylodontidae (*Kayentatherium*) (Sues 1985, 1986). The presence of maxillary sinuses in cynodonts, early mammals and in embryos of therian mammals suggests that the maxillary sinus is, as stated by Denhart (1903: p. 48) 'a very old heirloom of the mammals'.

Frontal sinuses. — For a long time a pantodont from the Late Palaeocene was regarded as the oldest mammal with frontal sinuses (Edinger 1950). Kermack *et al.* (1981) found the frontal sinus in the Early Jurassic *Morganucodon*. In multituberculates the frontal sinus has been described in *Lambdopsalis* (Miao 1988).

In *Chulsanbaatar* and *Nemegtbaatar* the frontal sinuses are differently shaped. The frontal part of the frontal sinus is large and extends into the orbital part of the frontal in *Nemegtbaatar* and is restricted to the caudal part of the frontal bone in *Chulsanbaatar*. In *Nemegtbaatar* the frontal sinuses have compartments invading both the maxilla and nasal (Fig. 18). The difference between *Chulsanbaatar* and *Nemegtbaatar* in the development of the frontal sinuses should be considered in relation to size of the two skulls, 17.7 mm and 36 mm respectively. In extant rodents and insectivores there are no frontal sinuses similar to those found in the studied multituberculates (Negus 1958: Fig. 147). Evans & Christensen (1979: Figs 4–42) described and figured the differences in size and shape of the paranasal sinuses in three types of dog skulls. In the mesaticcephalic type (a head of medium proportions) the frontal sinus is developed only in

the frontal bone, as in *Chulsanbaatar*. In the dolicocephalic type (a long narrow head) the frontal sinus occurs in the frontal and maxilla, as in *Nemegtbaatar*. The frontal sinus in *Nemegtbaatar* has an opening into the nasal cavity and is therefore possibly olfactory. The frontal sinus in *Chulsanbaatar* is closed and therefore non-olfactory as in *Morganucodon* (Kermack *et al.* 1981). The connection between the sinus and the cranial cavity as described in *Morganucodon* is not found in the two studied multituberculates. Kermack *et al.* (1981) suggested that the frontal sinus of *Morganucodon* is analogous but not homologous with the internal frontal sinus in placental mammals, because there is no connection between the sinus and the nasal chambers as seen in placentals. The frontal sinus in *Barunlestes* as described by Kielan-Jaworowska & Trofimov (1980) is divided into two main parts. The *sinus frontalis medialis* has two compartments, a large oval posterior one and a smaller anterior one. The *sinus frontalis lateralis* is placed lateral to the medial sinus and is divided longitudinally into two narrow tubular compartments, both of which are subdivided transversely into two parts. This sinus contains complicated turbinals or disordered bony lamellae.

Function of sinuses. — According to Weidenreich (1924, 1941) the basic form of the skull is exclusively determined by the shape of the soft organs. He argued that for functional reasons additional skeletal material has to be developed to compensate for incongruities and to develop the bony buttresses of the masticatory apparatus. The external form of the bones is shaped by the pressure and traction of mechanical stress from the masticatory apparatus and the occipital region. The spaces between the basic and external shapes of the bones are functionless spaces (Weidenreich 1941). These spaces were proved later to be olfactory in some mammals (Negus 1958) by the presence of olfactory epithelium.

In all mammals the *musculus temporalis* originates from the external surface of the frontal, parietal and occipital bones of the braincase. Klatt (1913) argued that the power of the temporal muscle increases proportionally to the plane of its cross section and not proportionally to its volume. The cross section increases with the square and the volume of the muscle increases with the cube. Therefore, if a species doubles its size, the muscle has to increase its volume much more than twice to get the same power, thus in relation to this also the external surface of the skull should increase more than twice. Hofer (1969) suggested two ways of increasing the external surface of the skull, if the skull increases in size by positive allometric growth. The increase is made by forming sagittal and nuchal crests on the frontal, parietal and supraoccipital bones or by inflating the same bones with the frontal sinus. By this, the area of the external surface of the skull changes, but the proportions of the basic form remain the same.

For the purpose of comparison of the volume of the skulls and the volume of the frontal sinuses in *Chulsanbaatar* and *Nemegtbaatar*, one can assume that the shape of the skulls is similar in both species and that

Tab. 2. Measurements of skulls of *Nemegtbaatar gobiensis* and *Chulsanbaatar vulgaris*, measurements in brackets are estimates.

Catalogue numbers in ZPAL collection	Length (mm)	Maximum height (mm)	Maximum interorbital breadth (mm)
<i>Nemegtbaatar gobiensis</i> MgM-1/76	37.6	11.8	16.0
<i>Nemegtbaatar gobiensis</i> MgM-1/65	(33)	12.8	(16.5)
<i>Nemegtbaatar gobiensis</i> MgM-1/81	44.0	(14.5)	14.7
<i>Nemegtbaatar gobiensis</i> MgM-1/57	37.5	13.2	(13.5)
<i>Chulsanbaatar vulgaris</i> MgM-1/139	17.6	6.0	7.3
<i>Chulsanbaatar vulgaris</i> MgM-1/108	16.4	5.9	5.7
<i>Chulsanbaatar vulgaris</i> MgM-1/61	19.8	6.7	(6.8)
<i>Chulsanbaatar vulgaris</i> MgM-1/145	19.3	6.0	8.0
<i>Chulsanbaatar vulgaris</i> MgM-1/157	19.4	6.6	(7.8)
<i>Chulsanbaatar vulgaris</i> MgM-1/168	17.1	5.7	7.2
<i>Chulsanbaatar vulgaris</i> MgM-1/89	20.1	(6.5)	7.0

therefore a simple box will roughly represent the volume of the skulls. The volume of such a 'skull box' can be calculated using the dimensions of the skull length, maximum skull height and maximum interorbital breadth, given in Tab. 2. The average volume of the *Chulsanbaatar* 'skull box' is 922 mm³ and of the *Nemegtbaatar* 'skull box' 7532 mm³, i. e. they differ by a factor of 8. The volume of the frontal sinuses is calculated by multiplying the measured area of the dorsal side of the sinus by the maximum height of the frontal sinus. The frontal sinus box in *Chulsanbaatar* is 14 mm³ and in *Nemegtbaatar* 272 mm³, i. e. the difference is of a factor of 19. Thus, in *Nemegtbaatar* the increase in the volume of the frontal sinus was more than twice (2.4) as great as the increase of the volume of the skull. Both *Nemegtbaatar* and *Chulsanbaatar* are lacking a sagittal crest and therefore an increase of the surface needed for muscle attachment on the external surface of the skull must be made by an increase in the frontal sinus. I suggest that the differences of the mass of the masticatory muscles (not reconstructed in this paper) are the reason for the difference in the shape and size of the frontal sinus of *Chulsanbaatar* and *Nemegtbaatar*.

Many different theories have been put forward to solve the problem of the presence of sinuses in mammals. Are they only unwanted spaces caused by growth or do they have a function?

Negus (1958) gave several examples of functions ascribed to the paranasal sinuses. Moistening of the mucosal surfaces in the nose is essential in the perception of odours. A supply of extra moisture from additional air spaces would be an advantage for entrapping olfactory molecules carried in by diffusion of air. In some mammals this may be a help in olfaction, but, for example, in man there is practically a lack of glandular tissue in the sinuses (Skillern 1920). Sinuses have been suggested to have a vocal function by acting as resonators, but there is no relation between the size of the sinuses and the voice (Negus 1958). Proetz (1953) suggested that the sinuses may be insulators preventing loss of heat from the nasal fossae, but it is more efficient to have large maxillo-turbinal bodies filling the anterior part of the snout (Negus 1958). Direct supply of warmth to the air stream is not possible because of the small openings in and out of the sinus (Negus 1958). Skillern (1920) argued that a lightening of the anterior half of the skull, thus reducing the work of the neck muscles, may be the reason for the origin of the sinuses. However, as argued by Negus (1958), the additional bony walls and septa in the sinus do not lighten the skull but add extra weight to it, but an empty air filled sinus will of course be lightest of all. None of these functions seems more likely than the other for the sphenoid and maxillary sinuses in *Chulsanbaatar* and *Nemegtbaatar*.

Conclusions

Comparisons between the skull structure of *Nemegtbaatar*, *Chulsanbaatar* and other Mesozoic mammals show that the basic patterns of the snout and orbit of all these mammals is essentially the same. The comparison with cynodonts does not indicate any obvious relationships between multituberculates and cynodonts. Any group of cynodonts from which multituberculates evolved is not recognized. The observations in this paper reveal an even closer relationship of multituberculates to monotremes, marsupials and eutherians than accepted in earlier paper by Wible (1991). The orbital processes of the frontal and palatine, ossified turbinals, ethmoid and vomer and the presence of the frontal sinus and maxillary sinus are typical of mammals, while the nasal foramina are probably an apomorphy of multituberculates. The appearance of the frontal sinuses in *Nemegtbaatar* and *Chulsanbaatar* is related to the increase of the external area of the skull needed for attachment of the temporal muscle, because the sagittal crest is not present in these taxa. The function of the maxillary and sphenoid sinuses is not established.

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References

- Bonaparte, J.F. 1986. A new unusual Late Cretaceous Mammal from Patagonia. *Journal of Vertebrate Paleontology* **6**, 264–270.
- Bonaparte, J.F. & Rougier, G. 1987. Mamíferos del Cretácico inferior de Patagonia. *IV Congreso Latinoamericano de Paleontología, Bolivia* **1**, 343–359.
- Brink, A.S. 1955. A study on the skeleton of *Diademodon*. *Palaeontologia Africana* **3**, 3–41.
- Brink, A.S. 1963. Two cynodonts from the Ntawere formation in the Luangwa valley of Northern Rhodesia. *Palaeontologia Africana* **8**, 77–96.
- Broom, R. 1914. On the structure and affinities of the Multituberculata. *Bulletin of the American Museum of Natural History* **33**, 115–134.
- Chapman, R.E. 1989. Computer assembly of serial sections. In: R.M. Feldman, R.E. Chapman, & J.T. Hannibal (eds) *Paleotechniques. The Paleontological Society Special Publication* **4**, 157–165.
- Chow, M. & Qi, T. 1978. Paleocene mammalian fossils from Nomogen Formation of Inner Mongolia. *Vertebrata Palasiatica* **16**, 77–85. (In Chinese, English summary)
- Clemens, W.A. & Kielan-Jaworowska, Z. 1979. Multituberculata. In: J.A. Lillegraven, Z. Kielan-Jaworowska, & W.A. Clemens (eds) *Mesozoic Mammals: The First Two-Thirds of Mammalian History*, 99–149. University of California Press, Berkeley.
- Cope, E.D. 1882. *Mammalia* in the Laramie Formation. *American Naturalist* **16**, 830–831.
- Crompton, A.W., Taylor, C.R. & Jagger, J.A. 1978. Evolution of homeothermy in mammals. *Nature* **272**, 333–336.
- Crompton, A.W. & Sun, A. 1985. Cranial structure and relationships of the Liassic mammal *Sinoconodon*. *Zoological Journal of the Linnean Society* **85**, 99–119.
- Davies, D.V. & Davies, F. 1962. *Gray's Anatomy Descriptive and Applied*. 33-ed. 1632 pp. Longmans, Green & Company Ltd., London.
- Dennhardt, H. 1903. *Ueber die Entwicklung der Nasenhöhle und deren Nebenhöhlen bei einigen Haussäugtieren. Auszüge aus den Inauguraldissertationen*. 51 pp. Zürich.
- Edinger, T. 1950. Frontal sinus evolution (particularly in the Equidae). *Bulletin of the Museum of Comparative Zoology at Harvard College* **103**, 411–496.
- Engelmann, G.F., Greenwald, N.S., Callison, G., & Chure, D.J. 1990. Cranial and dental morphology of a Late Jurassic multituberculate mammal from the Morrison Formation. *Journal of Vertebrate Paleontology* **10**, Abstracts, 22A.

- Evans, H.E. & Christensen, G.C. 1979. *Miller's Anatomy of the Dog*. 1181pp. W.B. Saunders Company, New York.
- Fourie, S. 1974. The cranial morphology of *Thrinaxodon liorhinus* Seeley. *Annals of the South African Museum* **65**, 337–400.
- Fox, R.C. 1978. Upper Cretaceous Terrestrial Vertebrate Stratigraphy of the Gobi Desert (Mongolian People's Republic) and Western North America. *The Geological Association of Canada Special Paper* **18**, 578–594.
- Gidley, J.W. 1909. Notes on the fossil mammalian genus *Ptilodus*, with descriptions of new species. *U.S. National Museum, Proceedings* **36**, 611–626.
- Goodrich, E.S. 1958. *Studies on the Structure and Development of Vertebrates*. 2 vols. 837 pp. Dover Publications, Inc. New York.
- Granger, W. & Simpson, G.G. 1929. A revision of the Tertiary Multituberculata. *Bulletin of the American Museum of Natural History* **56**, 601–676.
- Gradziński, R., Kielan-Jaworowska, Z., & Maryańska, T. 1977. Upper Cretaceous Djadokhta, Barun Goyot and Nemegt Formations of Mongolia, including remarks on previous subdivisions. *Acta Geologica Polonica* **27**, 281–318.
- Grassé, P.P. 1967. *Traité de Zoologie, Anatomie, Systématique, Biologie*. Tome XVI, Fascicule 1, Mammifères: Téguments et Squelette. 1162pp. Paris.
- Gregory, W.K. & Simpson, G.G. 1926. Cretaceous mammal skulls from Mongolia. *American Museum Novitates* **225**, 1–20.
- Hahn, G. 1969. Beiträge zur Fauna der Grube Guimarota Nr 3, die Multituberculata. *Palaeontographica, A* **133**, 1–100.
- Hahn, G. 1977. Neue Schädel-Reste von Multituberculaten (Mamm.) aus dem Malm Portugals. *Geologica et Palaeontologica* **11**, 161–186.
- Hahn, G. 1978. Neue Unterkiefer von Multituberculaten aus dem Malm Portugals. *Geologica et Palaeontologica* **12**, 177–212.
- Hahn, G. 1981. Zum Bau der Schädel-Basis den Paulchoffiidae (Multituberculata; Ober-Jura). *Senckenbergiana Lethaea* **61**, 227–245.
- Hahn, G. 1985. Zum Bau des Infraorbital-Foramens bei den Paulchoffiidae (Multituberculata, Ober-Jura). *Berliner Geowissenschaftliche Abhandlungen* **60**, 5–27.
- Hahn, G. 1987. Neue Beobachtungen zum Schädel- und Gebiss-Bau der Paulchoffiidae (Multituberculata, Ober-Jura). *Paleovertebrata* **17**, 155–196.
- Hahn, G. & Hahn, R. 1983. Multituberculata. In: F. Westphal (ed.) *Fossilium Catalogus, I: Animalia, Pars 127*. 409pp. Kugler Publications, Amsterdam.
- Hillenius, W.J. 1992. The evolution of nasal turbinates and mammalian endothermy. *Paleobiology* **18**, 17–29.
- Hofer, H.O. 1969. The evolution of the brain of primates: its influence on the form of the skull. *Annals of the New York Academy of Sciences* **167**, 341–356.
- Hopson, J.A., Kielan-Jaworowska, Z., & Allin, E.F. 1989. The cryptic jugal of multituberculates. *Journal of Vertebrate Paleontology* **9**, 201–209.
- Hopson, J.A. & Rougier, G.W. 1993. Braincase structure in the oldest known skull of a therian mammal: implications for mammalian systematics and cranial evolution. *American Journal of Science* **293 A**, 268–299.
- Hurum, J.H. 1992. Earliest occurrence of sinus frontalis in Mammalia. In: Á. Geirsdóttir, H. Norddahl, & G. Helgadóttir (eds) *Abstracts: 20th Nordic Geological Wintermeeting, 7–10 January, Reykjavík 1992*. The Icelandic Geoscience Society and the Faculty of Science, University of Iceland, Reykjavik. 77.
- Jenkins, F.A. 1990. Monotremes and the biology of Mesozoic mammals. *Netherlands Journal of Zoology* **40**, 5–31.
- Jepsen, G.L. 1940. Paleocene faunas of the Polecat Bench Formation, Park County, Wyoming. *Proceedings of the American Philosophical Society* **83**, 217–341.
- Jerison, H.J. 1973. *Evolution of the Brain and Intelligence*. xiv + 482pp. Academic Press, New York.
- Jerzykiewicz, T. & Russell, D.A. 1991. Late Mesozoic stratigraphy and vertebrates of the Gobi Basin. *Cretaceous Research* **12**, 345–377.

- Kay, R.F. & Cartmill, M. 1977. Cranial morphology and adaptations of *Palaechthon nacimienti* and other Parymomyidae (Plesiadapoidea, ?Primates), with a description of a new genus and species. *Journal of Human Evolution* **6**, 19–53.
- Kemp, T.S. 1979. The primitive cynodont *Procynosuchus*: Functional anatomy of the skull and relationships. *Philosophical Transactions of the Royal Society of London B* **256**, 1–83.
- Kemp, T.S. 1980. Aspects of the structure and functional anatomy of the Middle Triassic cynodont *Luangwa*. *Journal of Zoology, London* **191**, 193–239.
- Kermack, D.M. 1982. A new tritylodontid from the Kayenta Formation of Arizona. *Zoological Journal of the Linnean Society* **76**, 1–17.
- Kermack, K.A., Mussett, F., & Rigney, H.W. 1981. The skull of *Morganucodon*. *Zoological Journal of the Linnean Society* **53**, 87–175.
- Kielan-Jaworowska, Z. 1969. Preliminary data on the Upper Cretaceous eutherian mammals from Bayn Dzak, Gobi Desert. In: Z. Kielan-Jaworowska (ed.) Results of the Polish-Mongolian Palaeontological Expeditions, pt. I. *Paleontologia Polonica* **19**, 171–191.
- Kielan-Jaworowska, Z. 1970. New Upper Cretaceous multituberculate genera from Bayn Dzak, Gobi Desert. In: Z. Kielan-Jaworowska (ed.) Results of the Polish-Mongolian Palaeontological Expeditions, pt. II. *Paleontologia Polonica* **21**, 35–49.
- Kielan-Jaworowska, Z. 1971. Skull structure and affinities of the Multituberculata. In: Z. Kielan-Jaworowska (ed.) Results of the Polish-Mongolian Palaeontological Expeditions, pt. III. *Paleontologia Polonica* **25**, 5–41.
- Kielan-Jaworowska, Z. 1974. Multituberculate succession in the Late Cretaceous of the Gobi Desert (Mongolia). In: Z. Kielan-Jaworowska (ed.) Results of the Polish-Mongolian Palaeontological Expeditions, pt. V. *Paleontologia Polonica* **30**, 23–44.
- Kielan-Jaworowska, Z. 1975. Preliminary description of two new eutherian genera from the Late Cretaceous of Mongolia. In: Z. Kielan-Jaworowska (ed.) Results of the Polish-Mongolian Palaeontological Expeditions, pt. VI. *Paleontologia Polonica* **33**, 5–16.
- Kielan-Jaworowska, Z. 1980. Absence of ptilodontidean multituberculates from Asia and its palaeogeographic implications. *Lethaia* **13**, 169–173.
- Kielan-Jaworowska, Z. 1981. Evolution of the therian mammals in the Late Cretaceous of Asia. Part IV. Skull structure in *Kennalestes* and *Asioryctes*. In: Z. Kielan-Jaworowska (ed.) Results of the Polish-Mongolian Palaeontological Expeditions, Part IX. *Paleontologia Polonica* **42**, 25–78.
- Kielan-Jaworowska, Z. 1983. Multituberculate endocranial casts. *Palaeovertebrata* **13**, 1–12.
- Kielan-Jaworowska, Z. 1994. *Catopsbaatar*, a new generic name for the multituberculate mammal *Djadochtherium catopsaloides*. *Acta Paleontologica Polonica* **39**, 134–136.
- Kielan-Jaworowska, Z. & Dashzeveg, D. 1978. New Late Cretaceous mammal locality in Mongolia and a description of a new multituberculate. *Acta Palaeontologica Polonica* **23**, 115–130.
- Kielan-Jaworowska, Z., Dashzeveg, D. & Trofimov, B.A. 1987. Early Cretaceous multituberculates from Mongolia and a comparison with Late Jurassic forms. *Acta Palaeontologica Polonica* **32**, 3–47.
- Kielan-Jaworowska, Z., Poplin, C., Presley, R., & de Riquès, A. 1984. Preliminary data on multituberculate cranial anatomy studied by serial sections. In: W.-E. Reif & F. Westphal (eds) *Third Symposium on Mesozoic Terrestrial Ecosystems*, 123–128. Attempto Verlag, Tübingen.
- Kielan-Jaworowska, Z., Presley, R. & Poplin, C. 1986. The cranial vascular system in taeniolabidoid multituberculate mammals. *Philosophical Transactions of the Royal Society of London B* **313**, 525–602.
- Kielan-Jaworowska, Z. & Sloan, Z. 1979. *Catopsalis* (Multituberculata) from Asia and North America and the problem of taeniolabidid dispersal in the Late Cretaceous. *Acta Palaeontologica Polonica* **24**, 187–197.
- Kielan-Jaworowska, Z. & Trofimov, B.A. 1980. Cranial morphology of a Late Cretaceous eutherian mammal *Barunlestes*. *Acta Paleontologica Polonica* **25**, 167–185.
- Klatt, B. 1913. Über den Einfluss der Gesamtgrösse auf das Schädelbild. *Archiv für Entwicklungsmechanik der Organismen*. **36**, 387–471.

- Krause, D.W. 1982. Jaw movement, dental function, and diet in the Paleocene multituberculate *Ptilodus*. *Paleobiology* **8**, 265–281.
- Krause, D.W. 1986. Competitive exclusion and taxonomic displacement in the fossil record: the case of rodents and multituberculates in North America. In: K.M. Flanagan & J.A. Lillegraven (eds) *Vertebrates, Phylogeny, and Philosophy. Contributions to Geology, University of Wyoming, Special paper* **3**, 95–117.
- Krebs, B. 1991. Das Skelett von *Henkelotherium guimarotae* gen. et sp. nov. (Eupantotheria, Mammalia) aus dem Oberen Jura von Portugal. *Berliner Geowissenschaftliche Abhandlungen, A* **133**, 1–110.
- Krishtalka, L., Emry, R.J., Storer, J.E., & Sutton, J.F. 1982. Oligocene multituberculates (Mammalia: Allotheria): youngest known record. *Journal of Paleontology* **56**, 791–794.
- Kuhn, H.J. 1971. Die Entwicklung und morphologie des Schädels von *Tachyglossus aculeatus*. *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft* **528**, 1–192.
- Kühne, W.G. 1956. The Liassic therapsid *Oligokyphus*. 147 pp. British Museum (Natural History), London.
- Kühne, W.G. 1961. Eine Mammaliafauna aus dem Kimeridge Portugals. Vorläufiger Bericht. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* **7**, 374–381.
- Kühne, W.G. & Krusat, G. 1972. Legalisierung des Taxon *Haldanodon* (Mammalia, Docodonta). *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* **5**, 300–302.
- Lillegraven, J.A. & Krusat, G. 1991. Cranio-mandibular anatomy of *Haldanodon exspectatus* (Docodonta; Mammalia) from the Late Jurassic of Portugal and its implication to the evolution of mammalian characters. *Contributions to Geology, University of Wyoming* **28**, 39–138.
- Lillegraven, J.A. & McKenna, M.C. 1986. Fossil mammals from the 'Mesaverde' Formation (Late Cretaceous, Judithian) of Bighorn & Wind River Basins, Wyoming, with definitions of Late Cretaceous North American Land-Mammal 'Ages'. *American Museum Novitates* **2840**, 1–68.
- Marsh, O.C. 1881. New Jurassic mammals. *American Journal of Science* **33**, 326–348.
- Matthew, W.D. & Granger, W. 1925. Fauna and correlation of the Gashato Formation of Mongolia. *American Museum Novitates* **189**, 1–12.
- Matthew, W.D. & Simpson, G.G. 1928. Paleocene multituberculates from Mongolia. *American Museum Novitates* **331**, 1–4.
- Miao, D. 1988. Skull morphology of *Lambdopsalis bulla* (Mammalia, Multituberculata) and its implications to mammalian evolution. *Contribution to Geology, University of Wyoming, Special Paper* **4**, 104 pp.
- Miao, D. 1993. Cranial morphology and multituberculate relationships. In: F.S. Szalay, M.J. Novacek, & M.C. McKenna (eds) *Mammal Phylogeny: Mesozoic Differentiation, Multituberculates, Monotremes, Early Therians, and Marsupials*, 63–74. Springer-Verlag, New York.
- Miao, D. & Lillegraven, J.A. 1986. Discovery of three ear ossicles in a multituberculate mammal. *National Geographic Research* **2**, 500–507.
- Moore, W.J. 1981. *The Mammalian Skull*. 369 pp. Cambridge University Press, Cambridge.
- Muizon, C. 1991. La Fauna de Mamíferos de Tiupampa (Paleoceno Inferior, Formación Santa Lucía), Bolivia. In: R. Suarez-Soruco (ed.) *Fósiles y Facies de Bolivia — Vol. I Vertebrados*.
- Negus, V. 1958. *The Comparative Anatomy and Physiology of the Paranasal Sinuses*. 360 pp. E. & S. Livingstone Ltd. Edinburgh & London.
- Nomina Anatomica Veterinaria*. 1973. International Commission on Veterinary Anatomical Nomenclature. 150 pp. Adolf Holzhausen's Successors, Vienna.
- Owen, R. 1871. Monograph of the fossil Mammalia of the Mesozoic formations. *Palaeontological Society* **24**, 1–115.
- Patterson, B. & Olson, E.C. 1961. A triconodontid mammal from the Triassic of Yunnan. In: G. Vanderbroek (ed) *International Colloquium on Evolution of Lower and Nonspecialized Mammals* **1**, 129–191. Koninklijke Vlaamse Academie voor Wetenschappen, Letteren en Scone Kunsten van België, Klasse der Wetenschappen, Part 1, Paleis der Academi, Brussels.

- Paulli, S. 1900a. Über die Pneumaticität des Schädels bei den Säugenthieren, I. Über den Bau des Seibbeins. Über die Morphologie des Siebbeins und die der Pneumaticität bei den Monotremen und den Marsupialiern. *Gegenbaurs Morphologisches Jahrbuch* **28**, 147–178.
- Paulli, S. 1900b. Über die Pneumaticität des Schädels bei den Säugenthieren, II. Über die Morphologie des Seibbeins und die Pneumaticität bei den Ungulaten und Probosciden. *Gegenbaurs Morphologisches Jahrbuch* **28**, 179–251.
- Poplin, C. 1974. Étude de quelques Paléoniscidés Pennsylvaniens du Kansas. *Cahiers de Paléontologie*. 1–155.
- Poplin, C. 1977. Améliorations de la technique des sections séries au microtome appliquée aux fossiles. *Comptes Rendues Sommaires de la Séance Société Géologique de France* **6**, 342–343.
- Poplin, C. & de Riquès, A. 1970. A technique of serial sectioning for the study of undecalcified fossils. *Curator* **13**, 7–20.
- Proetz, A.W. 1953. *Essays on the Applied Physiology of the Nose*. 2nd ed. 452 pp. St. Louis Annals Publication Company.
- Rigney, H.W. 1963. A specimen of *Morganucodon* from Yunnan. *Nature* **197**, 1122–1123.
- Robinson, P., Black, C., & Dawson, M.R. 1964. Late Eocene Multituberculates and other Mammals from Wyoming. *Science* **145**, 809–811.
- Romer, A.S. 1970. The Chanares (Argentina) Triassic reptile fauna VI, a chiniquodontid cynodont with an incipient squamosal-dentary jaw articulation. *Breviora* **344**, 1–18.
- Sandy, M.R. 1989. Preparation of serial sections. In: R.M. Feldman, R.E. Chapman, & J.T. Hannibal (eds) *Paleotechniques. The Paleontological Society Special Publication* **4**, 146–156.
- Sigogneau-Russell, D. 1989. Haramiyidae (Mammalia, Allotheria) en provenance du Trias supérieur de Lorraine (France). *Palaeontographica A* **206**, 137–198.
- Simmons, N.B. & Miao, D. 1986. Paraphyly in *Catopsalis* (Mammalia: Multituberculata) and its biogeographic implications. In: K.M. Flanagan & J.A. Lillegraven (eds) *Vertebrates, Phylogeny, and Philosophy. Contributions to Geology, University of Wyoming, Special Paper* **3**, 87–94.
- Simpson, G.G. 1925. A Mesozoic mammal skull from Mongolia. *American Museum Novitates* **201**, 1–11.
- Simpson, G.G. 1926. Mesozoic Mammalia. IV. The multituberculates as living animals. *American Journal of Science* **11**, 228–250.
- Simpson, G.G. 1928. *A Catalogue of the Mesozoic Mammalia in the Geological Department of the British Museum*. 215 pp. Oxford University Press, London.
- Simpson, G.G. 1929. American Mesozoic Mammalia. *Peabody Museum (Yale University) Memoirs* **3**, pt. 1, xv + 171 pp.
- Simpson, G.G. 1936. A new fauna from the Fort Union of Montana. *American Museum Novitates* **873**, 1–27.
- Simpson, G.G. 1937. Skull structure of Multituberculata. *Bulletin of the American Museum of Natural History* **73**, 727–763.
- Skillern, R.H. 1920. *The Catarrhal and Suppurative Diseases of the Accessory Sinuses of the Nose*. 3-ed. 418 pp. Lippincott Company, Philadelphia.
- Sloan, R.E. 1979. Multituberculata. In: R.W. Fairbridge & D. Jablonski (eds) *The Encyclopedia of Paleontology*. 492–498. Dowdwen, Hutchinson & Ross Inc., Stroudsburg.
- Sollas, I.B.J. & Sollas, W.J. 1914. A study of the skull of a *Dicynodon* by means of serial sections. *Philosophical Transactions of the Royal Society of London, B* **204**, 201–225.
- Starck, D. 1979. *Vergleichende Anatomie der Wirbeltiere auf evolutionsbiologischer Grundlage. Band 2*. 776pp. Springer-Verlag, Berlin.
- Sues, H.-D. 1985. The relationships of the Tritylodontidae (Synapsida). *Zoological Journal of the Linnean Society* **85**, 205–217.
- Sues, H.-D. 1986. The skull and dentition of two tritylodontid synapsids from the Lower Jurassic of western North America. *Bulletin of the Museum of Comparative Zoology, Harvard University* **151**, 217–268.

- Swisher, C.C. III. & Prothero, D.R. 1990. Single-Crystal $^{40}\text{Ar}/^{39}\text{Ar}$ Dating of the Eocene-Oligocene Transition in North America. *Science* **249**, 760–762.
- Трофимов, В.А. (Трофимов, Б.А.) 1980. Multituberculata и Symmetrodonta из нижнего мела Монголии. *Доклады АН СССР* **243**, 213–216.
- Weidenreich, F. 1924. Über die pneumatischen Nebenräume des Kopfes. Ein Beitrag zur Kenntniss des Bauprinzips der Knochen, des Scädels und des Körpers. (Knochenstudien: III. Teil.). *Zeitschrift für Anatomie und Entwicklungsgeschichte* **27**, 55–93.
- Weidenreich, F. 1941. The brain and it's role in the phylogenetic transformation of the human skull. *Transactions of the American Philosophical Society* **31**, 321–442.
- Wible, J.R. 1991. Origin of Mammalia: The craniodental evidence reexamined. *Journal of Vertebrate Paleontology* **11**, 1–28.
- Wible, J.R., Miao, D., & Hopson, J.A. 1990. The septomaxilla of fossil and recent synapsids and the problem of the septomaxilla of monotremes and armadillos. *Zoological Journal of the Linnean Society* **98**, 203–228.
- Young, C.C. 1982. Two primitive mammals from Lufeng, Yunnan. *Works of Yang Zhongjian (Young Chung-Chien)* 21–26. Beijing Science Press.
- Zeller, U. 1989. Die Entwicklung und Morphologie des Schädels von *Ornithorhynchus anatinus* (Mammalia: Prototheria: Monotremata). *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft* **545**, 1–188.

Streszczenie

W artykule przedstawiono interpretację seryjnych skrawków, uzyskanych przy pomocy mikrotomu Junga, z przednich części czaszek dwu gatunków multituberkulatów z późnej kredy pustyni Gobi. Okazało się, że u *Nemegtbaatar gobiensis* występuje oczodolny wyrostek kości podniebiennej. Jego brak nie może być więc dalej uważany za diagnostyczną cechę multituberkulatów.