

The middle ear in multituberculate mammals

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Hurum, J.H., Presley, R., & Kielan-Jaworowska, Z. 1996. The middle ear in multituberculate mammals. *Acta Palaeontologica Polonica* **41**, 3, 253–275.

The ear ossicles, preserved in skulls of a tiny Late Cretaceous multituberculate *Chulsanbaatar vulgaris* from Mongolia are arranged as in modern mammals. This makes the idea of an independent origin of the multituberculates from other mammals unlikely. We report the finding of ear ossicles in Mesozoic multituberculates. Three almost complete incudes and two fragments of malleus are described and compared with those reported in the Paleocene *Lambdopsalis* and in non-multituberculate mammals. In these Late Cretaceous multituberculates lateral expansion of the braincase is associated with the presence of sinuses and development of extensive masticatory musculature, but not by the expansion of the vestibule, which is moderately developed. It is argued that because of the lateral expansion of the multituberculate braincase, the promontorium is arranged slightly more obliquely with respect to the sagittal plane than in other mammals and the fenestra vestibuli faces anterolaterally, rather than laterally. This results in a corresponding alteration in orientation of the stapes. The epitympanic recess is situated more anteriorly with respect to the fenestra vestibuli than in other mammals. The recess is deep, and the incus must therefore be oriented somewhat vertically. The incus is roughly A-shaped, with crus breve subparallel to the axis of vibration of the malleus. This axis, approximately connecting the anterior process of the malleus and the crus breve of the incus, lies at 45–55° to the sagittal plane in *Chulsanbaatar*. Probably most multituberculates were similar in this respect. The fragments of the malleus show a very long anterior process, which agrees with the reconstruction of the malleus in *Lambdopsalis* by Meng & Wyss (1995), and with the partial malleus of *Kryptobaatar*, described by Rougier *et al.* (in press).

Key words: Multituberculata, ear ossicles, promontorium, vestibule, evolution.

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Introduction

The origin and evolution of the mammalian middle ear has been studied by embryologists and comparative anatomists from the first half of the 19th century, but it is only since the middle of the 20th century that this problem has been addressed in any detail by paleontologists. During almost two hundred years of investigation a vast literature has been published on the subject, which is considered a classic in comparative anatomy (see Allin 1975 and Lombard & Bolt 1979 for reviews). In all jawed vertebrates except mammals, the jaw joint is between the quadrate above and the articular, derived from Meckel's cartilage, below. In mammals, except for the earliest Late Triassic and some Jurassic forms (which have a double jaw joint), there is a single jaw joint between the dentary and squamosal.

It has been demonstrated on embryological evidence, beginning with the classical work of Reichert (1837) and Gaupp (1913), that the mammalian ear ossicles: stapes, incus and malleus, are, respectively, homologous to the reptilian columella auris, quadrate, and articular plus prearticular, while the ectotympanic bone of mammals is homologous to the angular of reptiles. In a very thorough study, Allin (1975) explained on palaeontological evidence how the transformation of the reptilian jaw elements into mammalian ear ossicles and tympanic bone could have occurred. According to this theory, the development of the dentary-squamosal articulation was important for both auditory function and increase of mandibular strength (see Allin & Hopson 1992 and Novacek 1993 for reviews). Rowe (1995) argued that heterochronic acceleration of brain development was the driving force producing both the mammalian neocortex and middle ear.

The Late Triassic-Early Jurassic *Morganucodon* is the oldest mammal in which the jaw-joint can be confidently reconstructed (K.A. Kermack *et al.* 1973, 1981; see also Graybeal *et al.* 1989). *Morganucodon* has a double jaw joint, in which the reptilian articulation (between quadrate and articular) and the mammalian articulation (between squamosal and dentary) function together as one compound joint. As may be inferred from the presence of the trough on the medial side of the dentary, in which the so called reptilian bones are housed, a double jaw joint occurred in all the Late Triassic-Early Jurassic mammals in which lower jaws are known. A double jaw joint has been reconstructed in the early mammal *Sinoconodon* (Crompton & Sun 1985) in which the stapes has been illustrated by Crompton & Luo (1993), in the Jurassic docodont *Haldanodon* in which a dentary groove, a coronoid fragment, an articular complex and the foot-plate of the stapes are known (Lillegraven & Krusat 1991), and in the earliest therian, *Kuehneotherium* (D.M. Kermack *et al.* 1968), known only from a dentary with an extensive trough and isolated teeth. Crompton & Luo (1993) reported a remnant of the quadrate (incus) of the Early Jurassic triconodont *Dinnetherium*.

The ear ossicles and tympanic bone, if released from the lower jaw and not associated with a bony bulla, have a reduced chance of preservation in fossil state. They have not been found in Late Jurassic and Early Cretaceous mammals. Archibald (1979) described a stapes associated with an eutherian petrosal from the latest Cretaceous Hell Creek Formation of Montana. Horseshoe-shaped ectotympanics have been preserved in Late Cretaceous (possibly Campanian) skulls of early eutherians from Mongolia, *Kennalestes* and *Asioryctes* (Kielan-Jaworowska 1981). In a juvenile eutherian skull from the Coniacian of Uzbekistan found by Dr. Lev A. Nessov, malleus and incus have been preserved *in situ*, with the ectotympanic bones displaced. This unique specimen has still to be described (McKenna, Kielan-Jaworowska, Meng, & Nessov, unpublished).

In contrast to all other mammalian lines, evidence of a double jaw joint has not been found as yet in multituberculates. Multituberculata is an early group of mammals, the relationships of which are debated (see Miao 1993 and Kielan-Jaworowska *in press* for reviews). The oldest multituberculate lower jaws and skulls (belonging to the Paulchoffatiidae) are known from beds as young as the Upper Jurassic (Kimmeridgian or Oxfordian) of Portugal (Hahn 1993 and references therein). Isolated teeth of the Haramiyidae, regarded previously as the earliest multituberculates (Hahn 1973; see also Sigogneau-Russell 1989) are known from the Late Triassic and Early Jurassic. Butler & MacIntyre (1994) regarded the haramiyids as a sister group of multituberculates (see also Sigogneau-Russell & Hahn 1994). The oldest purported multituberculate may be *Mojo*, represented by a partial tooth from the Late Triassic of Belgium (Hahn *et al.* 1987). Other possible pre-Kimmeridgian multituberculates are represented by isolated teeth (K.A. Kermack 1988 and personal communication). The time span between *Mojo* and the Paulchoffatiidae is about 70 million years, during which important changes in the structure of the jaw joint apparently occurred. In the paulchoffatiids the dentary-squamosal joint is completely developed and there is no trace of the reptilian postdentary bones (Hahn 1978), nor is there a trough on the medial side of the dentary. The only postdentary lower jaw bone preserved in any multituberculate is the coronoid of the Kimmeridgian *Kuehneodon* (Hahn 1977).

Sloan (1979: fig. 1) illustrated the tympanic of the multituberculate *Ectypodus*, but did not describe it. Allin (1986) mentioned the presence of a tympanic ring in *Ectypodus*, referring to the personal communication of R.E. Sloan. However, the orientation and the shape of the tympanic in *Ectypodus* remain undescribed.

Miao & Lillegraven (1986) described the first multituberculate ear ossicles preserved in association in a right half of the basicranial region of the highly specialized Paleocene multituberculate *Lambdopsalis* from China. The cranial anatomy of *Lambdopsalis* was subsequently described in detail by Miao (1988). He published (Miao 1988: fig. 26) a composite reconstruction of the *Lambdopsalis* skull in ventral view including the ear ossicles, and reconstructed a tympanic ring, not known at that time.

Although the ear ossicles of *Lambdopsalis* have an essentially similar arrangement to those in modern mammals, according to Miao's interpretation they differ in orientation. While in modern mammals the manubrium of the malleus primitively points anteromedially (see e.g., Fleischer 1973; Maier 1989, 1990), in *Lambdopsalis* it has been reconstructed as pointing posterolaterally. The ear ossicles of *Lambdopsalis* are rather robust. As observed by Allin & Hopson (1992) the entire middle ear of *Lambdopsalis* is reoriented so that its morphologic lateral aspect is anterior. They argued that this reorientation was a result of the great expansion of the vestibule of the inner ear, characteristic of *Lambdopsalis* (Miao 1988).

The stapes of *Lambdopsalis* was described by Meng (1992) as small and columelliform, slim shafted, with a slit-like stapedial foramen, a distinct head, and a well-developed, nearly circular footplate. Meng (accepting the interpretation of Miao & Lillegraven 1986) argued that in contrast to the condition in other mammals, the stapes runs anteriorly to articulate with the incus (rather than laterally, as in most therians). He regarded this contact as a possible autapomorphy of multituberculates.

Hurum *et al.* (1995) also accepted the interpretations of Miao & Lillegraven (1986) and Miao (1988) and reconstructed the ear ossicles in *Chulsanbaatar* with the manubrium pointing posteromedially. They reported a stapes in ZPAL MgM-I/108, but this cannot now be unequivocally demonstrated. New discoveries demonstrate that the reconstructions of Miao & Lillegraven (1986) and Miao (1988) and consequently of Hurum *et al.* (1995) require revision. Meng & Wyss (1995) found a partial tympanic and partial malleus of *Lambdopsalis*. They reconstructed the ear ossicles in *Lambdopsalis* oriented as in modern mammals, and argued that four characters of ear ossicles ally multituberculates with monotremes. Three of these characters have been challenged by Rougier *et al.* (1996). First, the incus articulating dorsally with the malleus in monotremes has not been documented for multituberculates. Second, a horizontal ectotympanic, characteristic of monotremes and *Lambdopsalis*, is not characteristic for other multituberculates, as inferred from oblique position of fenestra vestibuli (Wible 1991). Third, as put by Rougier *et al.* (1996, p. 406): "...the 'contact' between the ectotympanic and 'pterygoid' purported for *Lambdopsalis* is between two broken pieces, one from the ectotympanic, the other from the pterygoid... In addition, the free monotreme 'pterygoid' is a neomorph under any recent phylogenetic scheme; therefore its homology with the multituberculate pterygoid is suspected."

Rougier *et al.* (in press) described a partial malleus, ectotympanic, stylohyal and a fragment of a possible stapes in the Late Cretaceous *Kryptobaatar* from Mongolia and equated their arrangement with that in modern mammals. They also argued that a part of the ossicle in *Lambdopsalis* which was identified by Miao & Lillegraven (1986) as a manubrium represents a fragment of the ectotympanic.

Although well-preserved skulls of multituberculates from the Late Cretaceous of Mongolia have been described in detail (Kielan-Jaworowska 1970 and references therein, 1971, 1974; Clemens & Kielan-Jaworowska 1979; Kielan-Jaworowska *et al.* 1986; Hurum 1994; Gambaryan & Kielan-Jaworowska 1995), except for the recent discovery of Rougier *et al.* (in press) their ear ossicles have not previously been found. In the present paper we report the discovery of three incomplete incudes, one fragment of incus and two fragments of the malleus in the small multituberculate *Chulsanbaatar vulgaris* from the Late Cretaceous of Mongolia. We discuss the multituberculate ear region in comparison to that in other mammals, and as an introduction to the region of multituberculates we describe briefly the exquisitely preserved basicranium of *Kamptobaatar*.

Material

In the collection of the Late Cretaceous multituberculates from the Gobi Desert, housed in the Institute of Paleobiology of the Polish Academy of Sciences in Warsaw (abbreviated as ZPAL), the ear ossicles have been preserved in four specimens of *Chulsanbaatar vulgaris* Kielan-Jaworowska 1974: ZPAL MgM-I/108 (not described in this paper), MgM-I/86, MgM-I/160 and MgM-I/140; all of which are from the Red beds of Khermeen Tsav (?middle Campanian), Khermeen Tsav II, Gobi Desert, Mongolia. For comparisons we studied skulls of other multituberculate taxa from the Late Cretaceous of the Gobi Desert, in ZPAL collections and figure part of the basicranial region of *Kamptobaatar kuczynskii* Kielan-Jaworowska 1970 ZPAL MgM-I/33 from the Djadokhta Formation (?early Campanian), Bayn Dzak, Gobi Desert.

The stereo photograph of *Kamptobaatar kuczynskii* was made in Institute of Paleobiology, Polish Academy of Sciences in Warsaw, Poland under normal light, while the photographs of the three specimens of *Chulsanbaatar vulgaris* were made under ultraviolet light at the Institut for Energiteknikk, Kjeller, Norway (IFE). Conventional quantitative microscopic luminescence spectrometry on macro fossils, micro fossils and hydrocarbon fluid inclusions hosted in minerals has hitherto been limited to fluorescence emission spectroscopy of approximately 400 nm wavelength and above. IFE have expanded the use of well established luminescence techniques of excitation spectroscopy and synchronous excitation-emission spectroscopy into the microscopic domain by using a luminescence spectrometer adapted to a microscope via quartz fiber optics (Kihle 1995a, 1995b). These techniques were developed to obtain non-destructive fingerprinting of individual hydrocarbon fluid inclusions by use of quantitative parameters, and are used here for the first time on fossil vertebrates. The serial section in Fig. 7 was photographed under ultraviolet light at the Institut de Paléontologie, Paris (Kielan-Jaworowska *et al.* 1986).

Descriptions

Kamptobaatar basicranium

ZPAL MgM-I/33. — The whole skull was described and illustrated by Kielan-Jaworowska (1971). The promontorium and epitympanic recess (*recessus epitympanicus*) are exquisitely preserved on the right hand side of the specimen (Fig. 1). The epitympanic recess is an ovoid hollow running backwards and outwards at about 45° with respect to the sagittal plane from just caudolateral to the foramen ovale inferium. The long axis of the recess measures approximately 1.2 mm and the maximal diameter at right angles to it is approximately 0.7 mm. It is limited laterally by a shallow rounded margin, but medially a much more prominent ridge forms a steeper margin overhanging the sulcus facialis. This ridge turns steadily more laterally to become a tall, almost vertical, posterior crest. This crest ends abruptly by falling to a shallow ridge which blends into the squamosal anterior to the stylomastoid notch.

The anterior three-fifths of the promontorium, separated from the epitympanic recess by the sulcus facialis, has a long axis at about 45° to the sagittal plane. This part of the promontorium is 2 mm long and runs from the level of the foramen ovale inferium to that of the anterior margin of the jugular fossa, where it flares into the posterior two-fifths. Also at this point the ventral crest on the promontorium shows a distinct tubercle. The posterior portion of the promontorium, which lies at 72° to the sagittal plane (Table 1), is approximately 1.3 mm long, but an ill-distinguished junction with the paroccipital process (*processus paroccipitalis*) makes measurement arbitrary. The middle third of this part of the promontorium carries the fenestra vestibuli on its anterolateral face, with the fenestra cochleae on the opposite face. The promontorium is continued outward, as the crista interfenestralis (Wible *et al.* 1995), between the fenestrae and beyond them with only slight narrowing relative to the proximal part. This is also the case in the other taeniolabidoid multituberculates studied by us, in contrast to e.g., *Morganucodon* (K.A. Kermack *et al.* 1981). The diameter of the distal extension from the promontorium in *Kamptobaatar*, beyond the fenestra vestibuli and fenestra cochleae, is about a half of the diameter of the proximal part and its sides are parallel as it reaches the paroccipital process posterior to the sulcus facialis (Kielan-Jaworowska 1971).

Chulsanbaatar ear ossicles

ZPAL MgM-1/140. — A large fragment of incus is observed *in situ* in the epitympanic recess on the right side of the specimen (Fig. 2). The bone is flat, the preserved part is roughly A-shaped, and its lateral leg (*crus breve*) is longer and more robust than the more gracile but incomplete *crus longum*. In ultraviolet light, demarcation of this structure from the surrounding borders of the epitympanic recess is clearly visible, and between the preserved ends of the *crus breve* and *crus longum* there is an oval

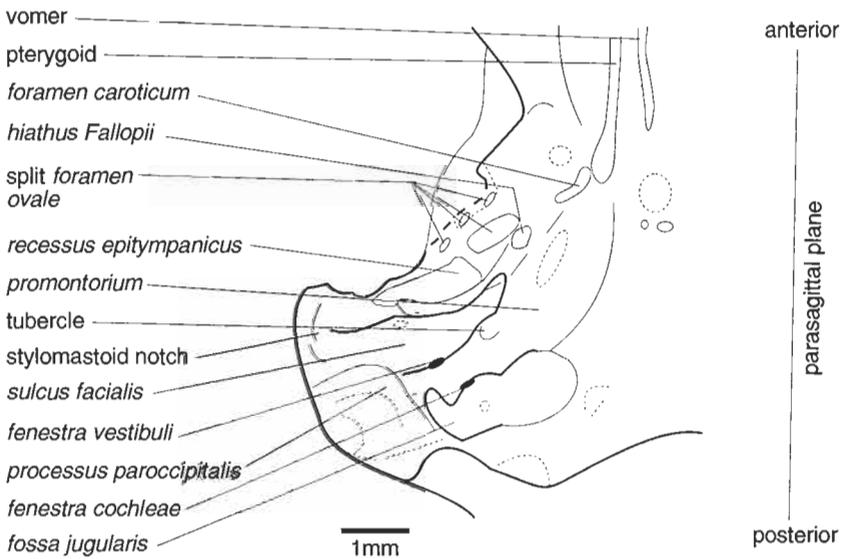
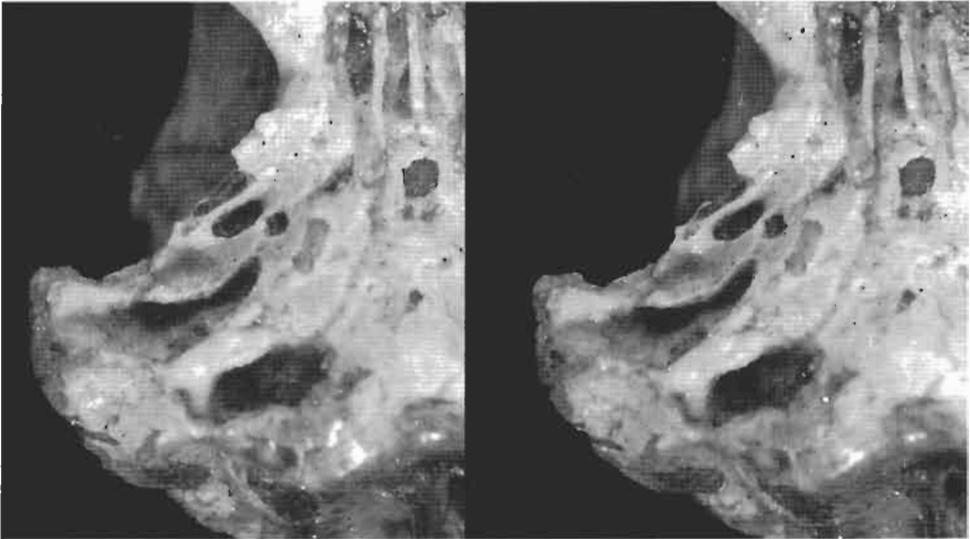


Fig. 1. *Kamptobaatar kuczynskii* ZPAL MgM-I/33 from the Late Cretaceous Djadokhta Formation, Bayn Dzak, Gobi Desert, Mongolia. Stereophotograph of the right side of the basicranium in ventral view. Note the flaring of the promontorium, the orientation of the epitympanic recess and the steepness of its medial wall, especially posteriorly. Key to features mentioned in the text.

depression. The incus is 1.25 mm at its longest axis and its maximum width is 0.62 mm.

On the left side of this specimen (not photographed) a smaller fragment of the incus is preserved, in the epitympanic recess. It has a notch facing posterolaterally which divides the incus posteriorly into two very short,

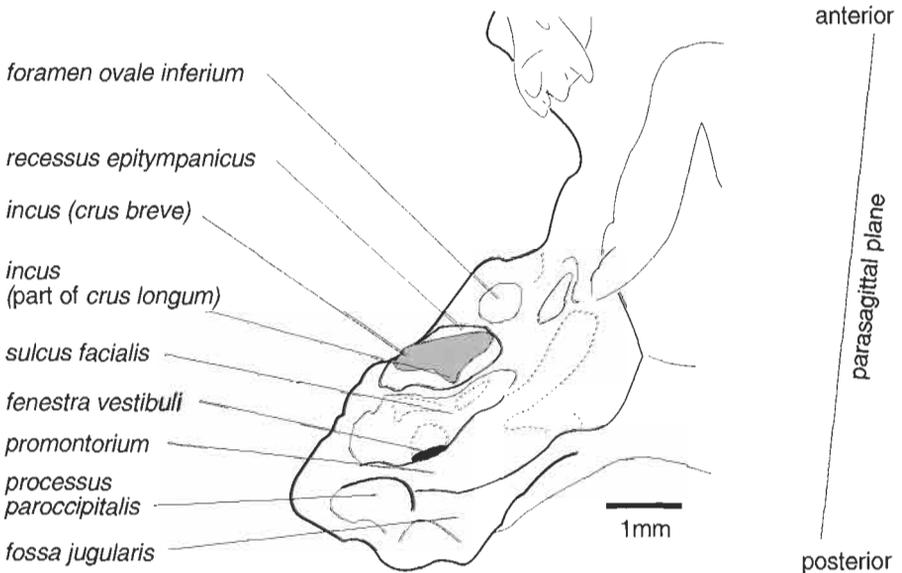
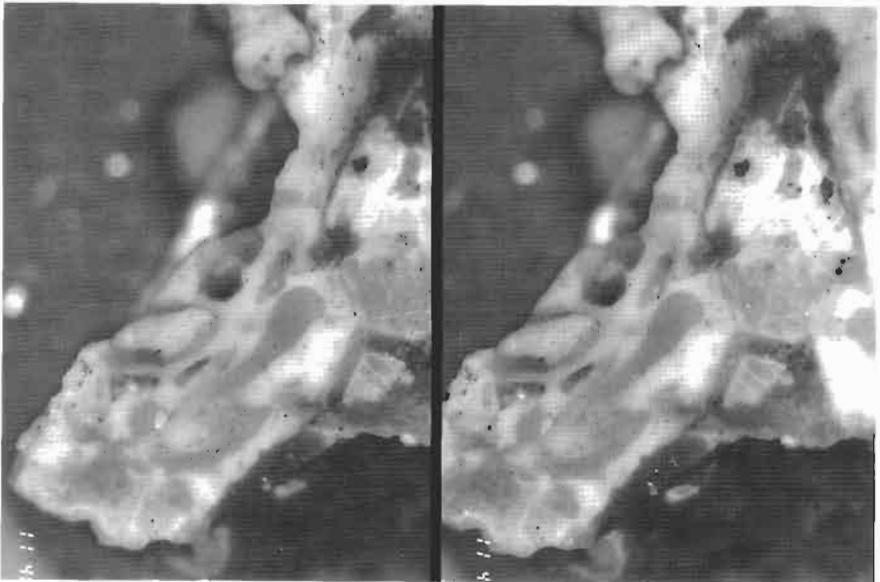


Fig. 2. *Chulsanbaatar vulgaris* ZPAL MgM-I/140 from the Red beds of Khermeen Tsav (?middle Campanian), Khermeen Tsav II, Gobi Desert, Mongolia. Stereophotograph made in ultra violet light of the right side of the basicranium in ventral view and explanation of features seen on the photograph, showing incus in epitympanic recess.

broken processes. The lateral process (a small part of *crus breve*) is directed posterolaterally and the medial, small part of *crus longum* is weaker and directed posteriorly. The incus fragment is 0.5 mm at its longest and 0.64 mm in maximum width. Posterior to the fragment of incus, two additional bony fragments are present. These do not correspond

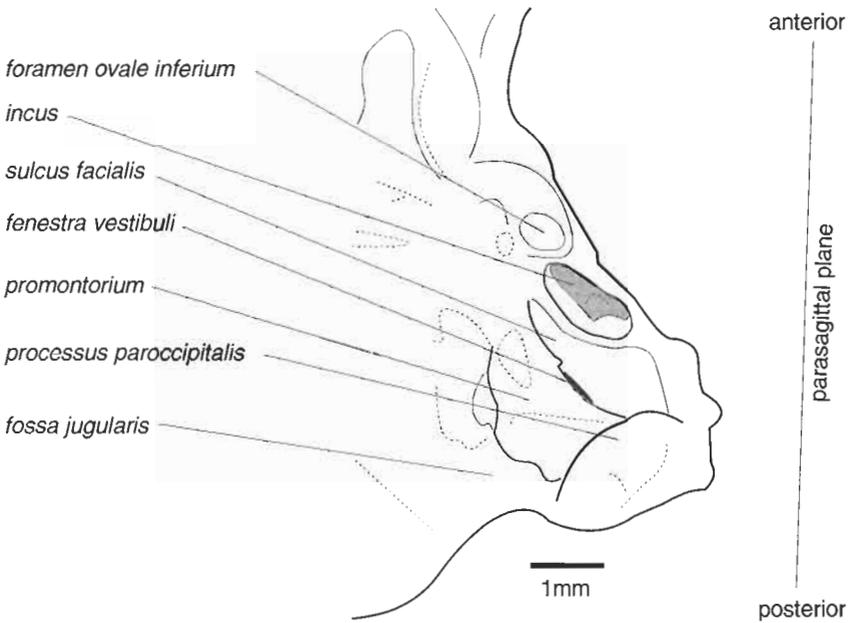
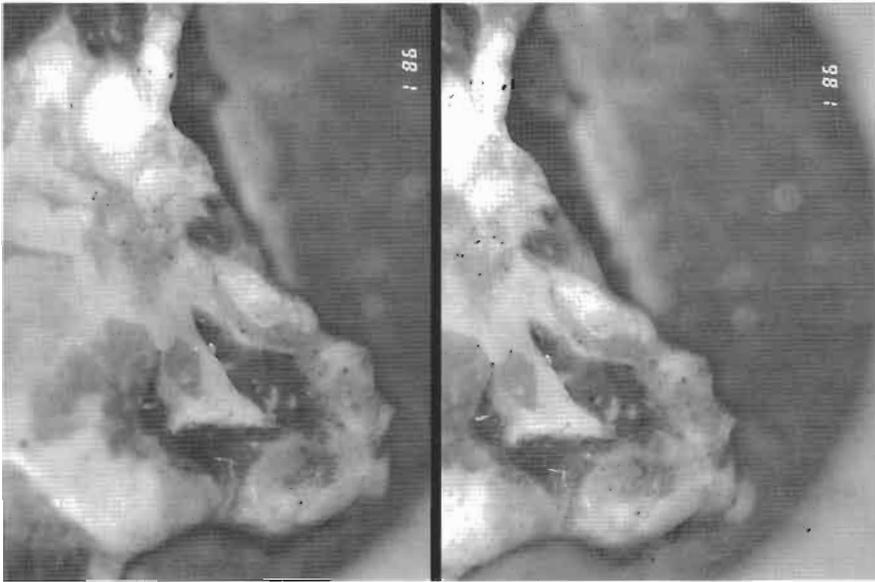


Fig. 3. *Chulsanbaatar vulgaris* ZPAL MgM-I/86 from the Red beds of Khermeen Tsav (?middle Campanian), Khermeen Tsav II, Gobi Desert, Mongolia. Stereophotograph made in ultraviolet light of the left side of the basicranium in ventral view and explanation, showing a fragment of incus in the epitympanic recess.

in size and shape to parts of the incus or stapes, and therefore may possibly be part of the malleus or ectotympanic. The lateral fragment is a small triangular-shaped bone with a distinct edge (0.4 × 0.5 mm). The

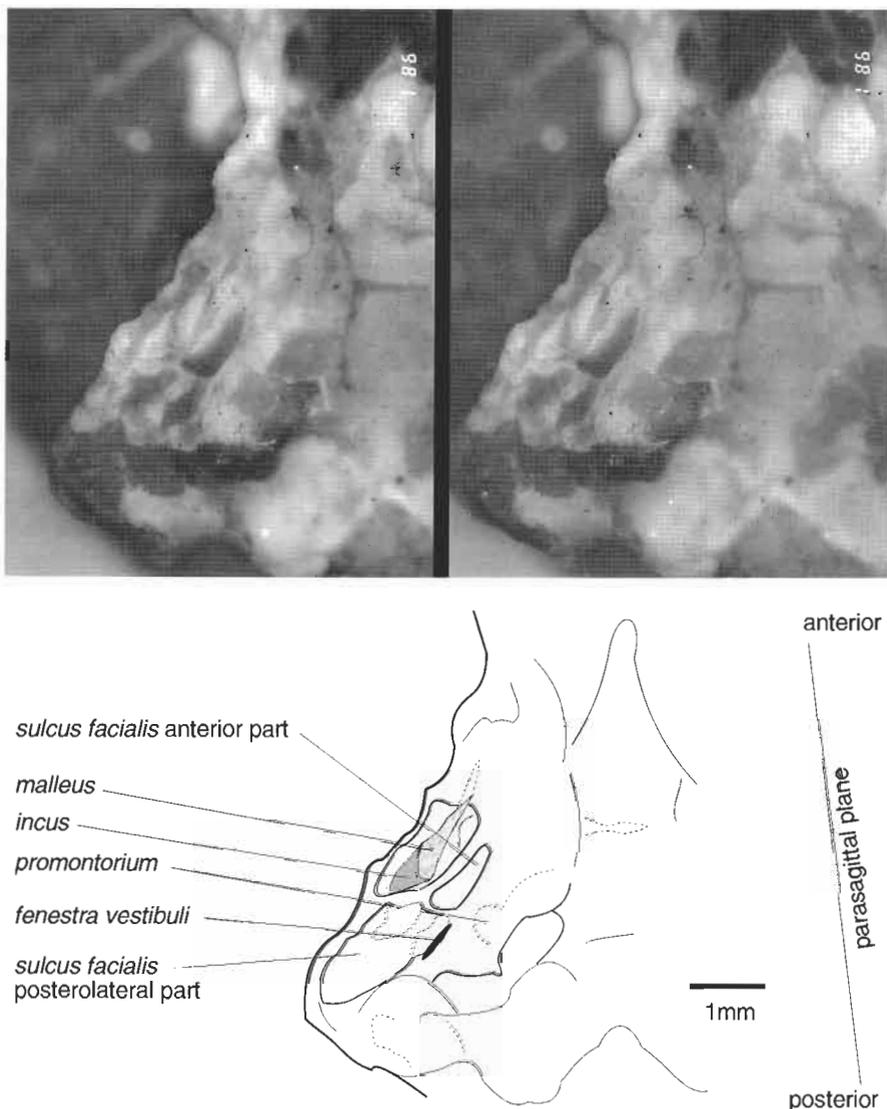


Fig. 4. *Chulsanbaatar vulgaris* ZPAL MgM-1/86 from the Red beds of Khermeen Tsav (?middle Campanian), Khermeen Tsav II, Gobi Desert, Mongolia. Stereophotograph made in ultraviolet light of the right side of the basicranium in ventral view and explanation, showing a fragment of incus posterolaterally in the eptympanic recess and a fragment of malleus at the medial border.

medial, larger fragment is a more oval bone with a lateromedial orientation (0.75×0.25 mm).

ZPAL MgM-I/86. — A partial incus (Fig. 3) is preserved in the eptympanic recess on the left side. The posterior end is divided into two processes, as in the left incus fragment in MgM-I/140. The maximum length and width are 1.0 mm and 0.5 mm. On the right side of the same

specimen (Fig. 4), a rod-like fragment is found in the epitympanic recess. The epitympanic recess is partly filled with sediment, but with examination under ultraviolet light the fragment in the recess can be described. We interpret the rounded posterior part as the head of the malleus (*caput mallei*) and the tapering anterior part as the posterior part of the anterior process. The malleus as preserved matches the shape of the medial border of the epitympanic recess. The posterior end possibly represented the base of the manubrium, but the inclination of the manubrium is impossible to reconstruct exactly from this specimen. Posterodorsal to the fragment of malleus, a broken fragment of incus is preserved, placed exactly as the incus in MgM-I/140. The articulation between the incus and malleus is not possible to reconstruct due to damage of the incus during preparation.

ZPAL MgM-I/160. — In this specimen the right side of the basicranium has been preserved (Fig. 5). The bone of the promontorium in the posterior part is missing, leaving a calcite cast, which appears black on the photograph taken in ultraviolet light. Lateral to the posterior end of the promontorium is a log-shaped bone, which might be a part of a stapes. Lateral to and along the promontorium there is an extensive facial sulcus which is not prepared in this specimen.

The facial sulcus in eucosmodontid multituberculates is divided into two parts, referred to by Kielan-Jaworowska *et al.* (1986: fig. 6) in *Chulsanbaatar* ZPAL MgM-I/168 as the anterior and posterolateral parts. In front of the anterior part there is a depression for the hiatus Fallopii, while medial to the posterolateral part there is the fenestra vestibuli. In well preserved skulls, e.g., in *Chulsanbaatar* MgM-I/168, on the left side, the bridges of bone between these depressions and sulci are well preserved; they are also seen, but are less obvious in *Nemegtbaatar* skulls ZPAL MgM-I/81 and MgM-I/82 (Kielan-Jaworowska 1974; Kielan-Jaworowska *et al.* 1986). In most cases these delicate bridges of bone are destroyed during preservation or preparation and there is a big sulcus facialis lateral to the promontorium. The roof of this sulcus is not smooth, but is covered by ridges which are the remnants of broken bones, e.g., *Kamptobaatar* (Fig. 1, see also Kielan-Jaworowska 1971: pl. 2).

In MgM-I/160 within the extensive facial sulcus, there are two tiny pieces of bone arranged obliquely anteromedially, which may be displaced remnants of the bridges that originally separated parts of the facial sulcus, or ridges in its roof (Fig. 5).

Lateral to the facial sulcus there is an extensive lateral flange, arranged parallel to the promontorium, the bone of which is cracked in the anterior part.

The epitympanic recess situated lateral and parallel to the lateral flange is filled with small pieces of bone (Fig. 5). We interpret the thin, longitudinal bone lying parallel to the lateral flange and adhering to it as the anterior process of the malleus preserved *in situ*. Posteriorly, it meets a well-preserved smaller bone, with rounded posterolateral margin that occupies the most posterior part of the epitympanic recess and might be

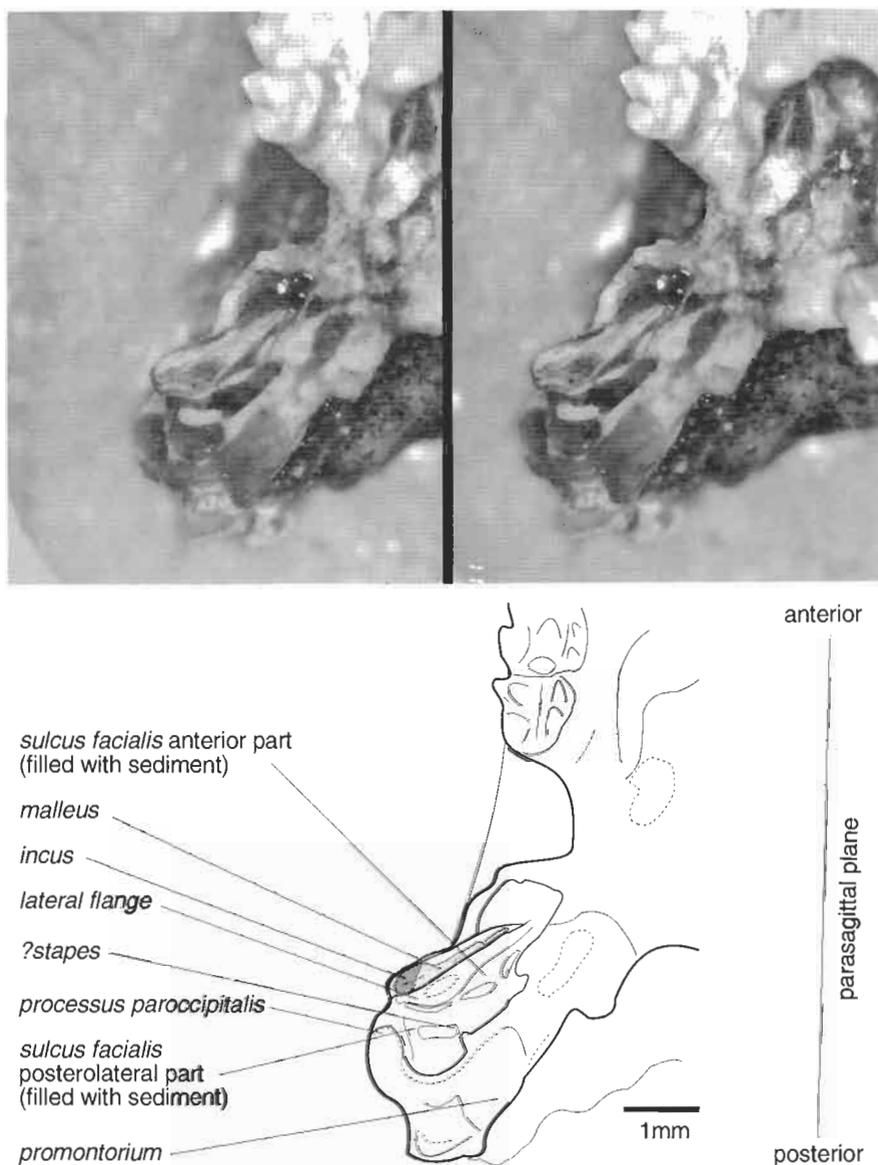


Fig. 5. *Chulsanbaatar vulgaris* ZPALMgM-I/160 from the Red beds of Khermeen Tsav (?middle Campanian), Khermeen Tsav II, Gobi Desert, Mongolia. Stereophotograph made in ultraviolet light of the right side of the basicranium in ventral view, showing part of the anterior process of the malleus and part of the incus in the epitympanic recess. Key to features mentioned in the text.

a part of the incus (crus breve). The incus is preserved in a similar place in the two other specimens described above (MgM-I/140 and MgM-I/86).

In Fig. 6 we present a tentative reconstruction of ear ossicles in *Chulsanbaatar vulgaris*, in comparison with *Didelphis*. Reconstruction of

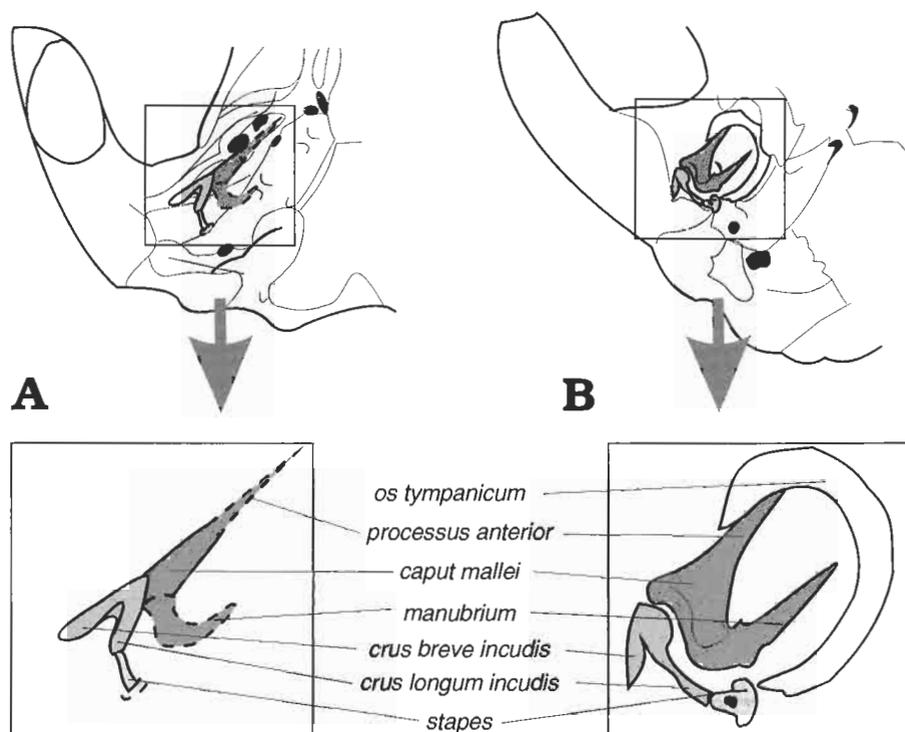


Fig. 6. Right part of basicranium showing arrangement of ear ossicles. **A.** *Chulsanbaatar vulgaris* — a highly hypothetical reconstruction — see text for the sources. Broken lines denote parts that have not been preserved and are reconstructed. Note that in this view the crus longum incudis is represented much foreshortened, its actual length is unknown. **B.** *Didelphis* (modified from Jollie 1962).

Chulsanbaatar is based on the specimens described in this paper, and partly on the reconstruction of the malleus in *Lambdopsalis* (Meng & Wyss 1995), on the partial malleus of *Kryptobaatar* (Rougier *et al.* in press) and on a comparison with embryos of some primitive mammals (e.g., Fleischer 1973, 1978 and Maier 1989).

Discussion

Promontorium and vestibule. — In the Paulchoffatiidae (Hahn 1988; Lillegraven & Hahn 1993) the promontorium is situated at about 45° to the sagittal plane. Similarly in the Ptilodontoidea, as drawn by Simpson (1937) and Sloan (1979), the promontorium is oriented obliquely to the longitudinal axis of the skull.

In Asian Taeniolabidoidea (the condition is unknown in the Plagiaulacidae) the anterior part of the promontorium is arranged as in the Paulchoffatiidae and Ptilodontoidea, but its posterior part, in which the fenest-

Table 1. Angles and dimensions (in mm) of basicranium in *Nemegtbaatar*, *Chulsanbaatar*, *Kamptobaatar*, and *Lambdopsalis*.

Species	Coll. number *)	Epitympanic recess/sagittal plane angle (1-1)	Anterior part of promontorium/sagittal plane angle (2-2)	Posterior part of promontorium/sagittal plane angle (3-3)	Estimated skull length
<i>N. gobiensis</i>	/82	62°	40°	60°	33
"	/81	59°	50°	65°	44
<i>Ch. vulgaris</i>	/168	55/60°	45°	65°	17
"	/160	—	42°	60°	15
"	/86	56°	55°	65°	19
"	/108	60/55°	40°	75°	17
"	/140	56/58°	45°	65°	19
"	/63	55°	45°	70°	15
"	/62	53°	50°	65°	19
"	/58	45°	40°	72°	20
"	/89	61/65°	45°	63°	19
"	/92	60°	50°	65°	15
"	/145	45/55°	45°	51°	17
"	/139	55°	46°	65°	17
"	/152	—	45°	71°	18
"	/156	48/50°	32°	65°	14
"	/157	49/51°	40°	70°	20
<i>K. kuczynskii</i>	/33	60/60°	45°	72°	17
<i>L. bulla</i> (cast)	IVPP V542	70/71°	55°	77°	47

*) *N. gobiensis*, *Ch. vulgaris* and *K. kuczynskii* belong to ZPAL collection MgM-1/. Where two numerals are given for the angles, they refer to right and left sides of the specimen respectively.

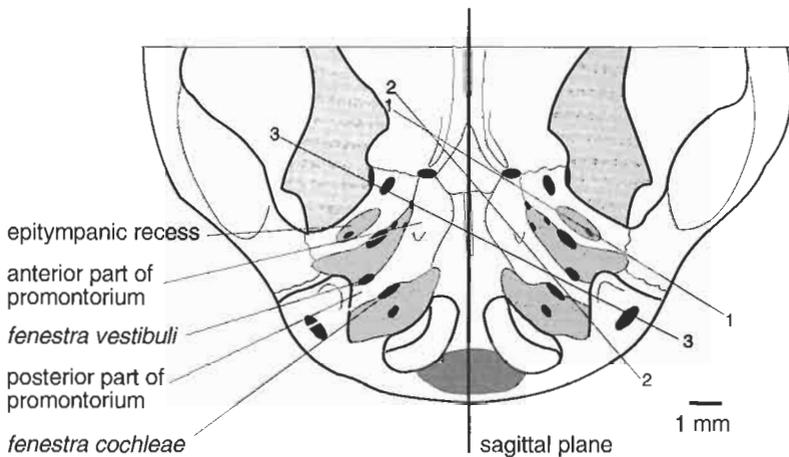


Fig. 7. Basicranial region of *Nemegtbaatar gobiensis*, modified from Kielan-Jaworowska *et al.* (1986) by lines (1-1, 2-2, 3-3) added. See Table 1 for explanation.

tra vestibuli and fenestra cochleae are placed, swings out to extend posterolaterally (Fig. 7, see also Kielan-Jaworowska 1971: fig. 4 and pl. 1: 2b; Kielan-Jaworowska *et al.* 1986: fig. 20c). This posterolateral part of the promontorium forms a bar that divides the cochlear fossula (jugular fossa) from the fossa for the stapedius muscle (posterolateral part of the facial sulcus). A similar prolongation of the promontorium to the rear of fenestra vestibuli and fenestra cochleae is also present in *Sinoconodon*, *Morganucodon*, *Dinnetherium*, triconodontids, and monotremes (Wible 1990) and is termed the crista interfenestralis by Wible *et al.* (1995). In these mammals, in contrast to multituberculates where this bar is long, relatively wide and extends posterolaterally, the bar is shorter, narrower and extends more posteriorly (e.g., Wible 1990: fig. 7A; Crompton & Luo 1993: fig. 4.12). In marsupials, eutherians, and *Vincelestes*, this bar is not developed and the two fossae are confluent, forming the post-promontorial tympanic sinus (Wible 1990: figs 5 and 7B). Additionally the breadth of the promontorium between the fenestra vestibuli and fenestra cochleae is relatively much greater in the multituberculates described in this paper than in *Morganucodon* (K.A. Kermack *et al.* 1981); the posterolateral part appears in ventral view about half as narrow as the anterior part. In the taeniolabidoid *Nemegtbaatar*, the anatomy is very similar to that of *Kamptobaatar*: the promontorium swings out at about half-way along its total length (Table 1 and Fig. 7). The anterior portion lies at 40–50° to the sagittal plane, the flared portion carrying the fenestra vestibuli at about 60–65°.

Kielan-Jaworowska *et al.* (1986) suggested that the orientation of the taeniolabidoid petrosal was primarily related to braincase changes reflecting specialization in the masticatory muscles and that it varied with size. Miao (1988) showed that the expansion of this region in *Lambdopsalis* is related to an enormously inflated vestibule. Luo & Ketten (1991), using computer tomography, suggested a sizeable vestibule in isolated petrosals from two taeniolabidoids (*Catopsalis* and *Meniscoessus*). According to them, the vestibule in both genera is enormous with respect to a relatively narrow and small cochlea. Considering their specimens and those of Miao (1988), they concluded that this enlarged vestibule is probably a synapomorphy of Multituberculata.

We disagree. Comparison of the reconstructions of Luo & Ketten (1991) with the sections of the skull of *Nemegtbaatar* here (Fig. 8), and in sections published by Kielan-Jaworowska *et al.* (1986) and of *Chulsanbaatar* (Hurum in preparation) shows that the vestibule is not so large in these two Late Cretaceous Mongolian genera. In both *Nemegtbaatar* and *Chulsanbaatar*, the cross-sectional diameter of the vestibule is only about 1.5–2 times that of the cochlea (as is the ratio of vestibular to proximal cochlear diameter in neonatal therians available to us) and not 5 or 7 times larger, as illustrated by Luo & Ketten (1991) for *Meniscoessus* and *Catopsalis* respectively (as measured from their fig. 3). Comparison of the scans figured by Luo & Ketten (1991) with the sections figured by Kielan-Jaworowska *et al.* (1986) and the complete serial sections of *Nemegtbaatar* and

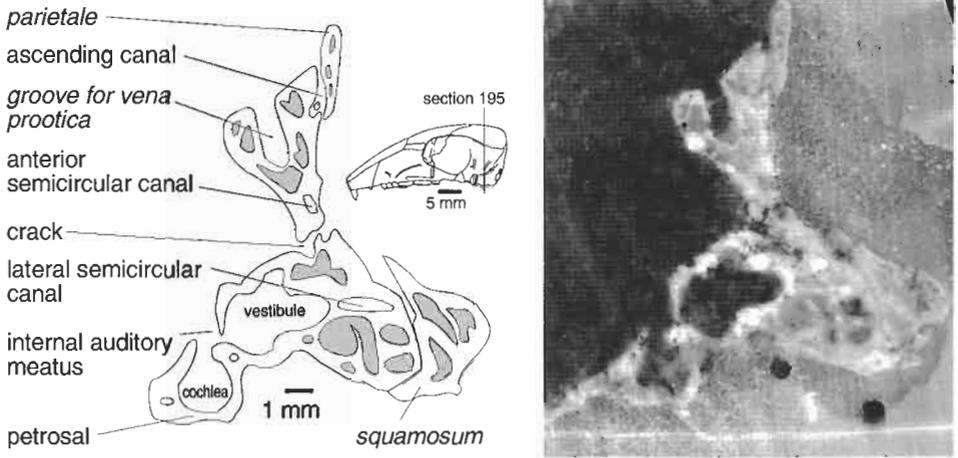


Fig. 8. *Nemegtbaatar gobiensis* ZPAL MgM-1/76 section 195, from the Late Cretaceous Barun Goyot Formation, Khulsan locality, Gobi Desert, Mongolia. Contour drawing of right side and photograph made in ultraviolet light, showing the vestibule and cochlea. Light grey — sinuses filled with marrow.

Chulsanbaatar skulls available to us shows that in the region of the expanded vestibule demonstrated by Luo & Ketten (1991) in their specimens, there lie, in our smaller forms, multiloculated cavities, interpreted from our serial sections as sinuses filled with marrow, and clearly demarcated from the vestibule and from the large subarcuate fossa. Similarly, photographs of the unidentified Hell Creek petrosals published by Kielan-Jaworowska *et al.* (1986: figs 8a, 9a) show posterolateral to the promontorium, a large cavity in the paroccipital process in addition to smaller multiloculated cavities nearby in the same region. These forms also had a large subarcuate fossa.

Thus we cannot support the concept that the inflation of this region is always, in all multituberculates, due to an expanded vestibule. There was certainly a great degree of variation in the expansion of sinuses, as well as in the size of the vestibule and subarcuate fossa among multituberculates. Following Kielan-Jaworowska *et al.* (1986) and Gambaryan & Kielan-Jaworowska (1995), we prefer to explain the characteristic laterally expanded shape of the posterior part of the basicranial region in taeniolabidoids as an adaptation for their unique specializations in jaw-action and the masticatory muscles, and the lateral expansion of their zygomatic arches.

Ossicles and epitympanic recess. — The material studied by us does not permit direct observations on the orientation of the ectotympanic and the tympanic membrane in multituberculates. Wible (1991), starting from an assumption that the plane of the fenestra vestibuli parallels that of the ectotympanic, argued that the ectotympanic must have had considerable vertical inclination in those multituberculates in which the petrosal could

be studied. Given, however, that the tympanic membrane does not always lie exactly plane-parallel to the fenestra vestibuli in specialized modern mammals (personal observations of RP), we believe that the inclination of the multituberculate ectotympanic cannot be precisely reconstructed using the orientation of the fenestra vestibuli alone. Nevertheless, the steep slope of the medial wall of the epitympanic recess and the fit of the broken fragment of malleus into it in ZPAL MgM-1/86 suggest to us that there must have been a significant vertical component in the plane of the manubrium and therefore of the tympanic membrane.

The fenestra vestibuli in multituberculates does not face laterally (as it does in e.g., *Morganucodon* and in therian mammals), but anterolaterally. One would therefore expect a corresponding alteration in the orientation of the stapes, with its axis directed anterolaterally, rather than laterally (Fig. 6). In *Lambdopsalis*, because of the enormous expansion of the post-promontory region (Miao & Lillegraven 1986; Meng 1992), the stapes was apparently oriented vertically and more anteriorly than in the Late Cretaceous Asian taeniolabidoids studied by us.

We have not had an opportunity to examine the original material of the Paulchoffiidae and Ptilodontoidea, but it appears to us that because of the oblique orientation of the promontorium in these groups, the fenestra vestibuli (and in consequence the stapes) was arranged roughly as in the Taeniolabidoidea (Table 1, Figs 6 and 7).

The incus of *Chulsanbaatar* which, besides the uncertain fragment described by Miao & Lillegraven (1986), is the first almost complete multituberculate incus found, shares with therians the possession of crus breve and crus longum. The transformation of the incus from the therapsid quadrata has been reviewed by Luo & Crompton (1994). In comparison with their interpretation of the morganucodontid incus, both crura in *Chulsanbaatar* are relatively long, slender processes, and are thus more therian-like. In therians (Fleischer 1973, 1978) the malleus and incus meet with groove-and-ridge facets so that the malleus can push the incus (and stapes) inwards but cannot pull them out beyond the point of elastic return, thus protecting the stapedia footplate from possible disarticulation. The articular facets between incus and malleus are not clear or complete in our specimens, and it is not possible to say whether there was any similar groove-and-ridge feature. The anterior region or body of the incus seems slender and convex in *Chulsanbaatar*, unlike the robust and concave form in most therians.

In *Chulsanbaatar*, the anterior process of the malleus points along the long axis of the epitympanic recess, at nearly 55° to the sagittal plane (Fig 6). This has the following implications. The long axis of the crus breve incudis should be roughly parallel to that of the axis around which the malleus moves during vibration of the tympanic membrane. This axis is usually determined in mammals by the orientation of the anterior process and the suspensory ligaments of the malleus anteriorly and by the suspensory ligament of crus breve posteriorly (Fleischer 1978). From our

specimens we believe that crus breve lay subparallel to the long axis of the epitympanic recess. We would therefore expect the epitympanic recess to be an approximate guide to the axis of vibration of the malleus and incus working together.

It should be noted, however, that this has developmental implications. In Recent mammals the malleus is derived (Starck 1975) partly from the hind end of Meckel's cartilage, and its anterior process also in part from the gonial (= prearticulare). These, the chorda tympani nerve, and the line of the anterior crus of the ectotympanic follow the line of Meckel's cartilage as they develop. The incus and the fossa incudis lie at the rear of Meckel's cartilage, in the epitympanic region. The incus articulates with Meckel's cartilage somewhat caudally in therians. Zeller (1993) stated that the incus of monotremes articulates medial to the malleus, but inspection of his figures and the specimens available to us indicates that the articulation is dorsal as much as medial. In all these living mammals the line through the incus and malleus is approximately parallel to and closely medial to the line of the mandibular ramus and condylar process. This is to be expected because the mandible develops as a membrane bone immediately lateral to Meckel's cartilage, and encloses the more rostral part of it within the mandibular canal. In the embryo, Meckel's cartilage guides the chorda tympani nerve forward through and beyond the developing epitympanic recess towards the point where it joins the lingual nerve medial to the mandible. The orientation we reconstruct for the incus and the anterior process of the malleus in the adult *Chulsanbaatar* implies that the line of these structures, associated embryonically with Meckel's cartilage, diverges at nearly 55° from the sagittal plane and in *Lambdopsalis* the divergence may be more extreme (Miao 1988; Meng & Wyss 1995). We therefore expect that the chorda tympani nerve, running forward, must have followed this very oblique course when leaving the tympanic region. Similarly, the anterior crus of the ectotympanic should be expected also to have followed this line. We have not seen this arrangement among Recent mammals. On the other hand, it seems to be characteristic of all multituberculates, as Hahn (1988) described the epitympanic recess in Paulchoffatiidae with a similar inclination to that found in taeniolabidoid multituberculates.

The fragments described in this paper, although poorly preserved, indicate the presence of a malleus with a long anterior process similarly arranged to those in *Lambdopsalis* (Meng & Wyss 1995), *Kryptobaatar* (Rougier *et al.* in press), monotremes and in embryos of extant therian mammals (Fleischer 1973; Maier 1989, 1990). Rougier *et al.* (in press) compiled a matrix of 63 characters of the ossicles and basicranium for 19 mammal (mostly early mammal) taxa and analyzed it using PAUP. They obtained 5 equally parsimonious trees, differing in the relationships of multituberculates, monotremes, and triconodonts with respect to the prototribosphenidan lineage. According to their results Monotremata is either the sister group of Theriiformes (Multituberculata + Theria) or

united with Multituberculata in a monophyletic grouping. In spite of the fact that the ossicles are poorly or wholly unknown for most of the taxa considered and their phylogenetic bearing is limited, cladistic analysis allowed the authors to draw the conclusion that the suspended ear ossicles evolved in the last common ancestor of multituberculates, monotremes, triconodonts and trechnotherians (symmetrodonts + therians).

Our data agree with the conclusion of Rougier *et al.* (in press) that multituberculate ear ossicles are not different in arrangement from those in modern mammals. This may be taken as an argument in favour of the monophyletic origin of mammals.

Acknowledgements

We thank our colleagues and friends James A. Hopson, John R. Wible, Guillermo W. Rougier and Edgar F. Allin for reading the manuscript and providing useful comments, and Michael J. Novacek and Guillermo W. Rougier for showing us the specimen of *Kryptobaatar*. Hopson and Wible first noticed the presence of the incus in ZPAL MgM-1/140 and drew our attention to it. We thank Jan Kihle (Institut for Energiteknikk, Kjeller, Norway) for making the equipment for ultraviolet photography available to us. The work of JHH and ZKJ has been supported by Norges Forskningsrd, grant no. ABC/LR 441.95/004 to ZKJ.

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Ucho środkowe multituberkulatów

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Streszczenie

Kostki słuchowe ssaków (strzemiączko, kowadełko i młoteczek), mieszczące się w uchu środkowym i przekazujące drgania błony bębenkowej do ucha wewnętrznego, bardzo rzadko zachowują się w stanie kopalnym. Niekompletne kostki słuchowe multituberkulatów zostały po raz pierwszy opisane u paleoceńskiego rodzaju *Lambdopsalis* z Chin przez Miao & Lillegravena (1986). Autorzy ci, oraz Miao (1988) zrekonstruowali młoteczek z rękojeścią skierowaną ku tyłowi, a nie skośnie ku przodowi i dośrodkowo jak u wszystkich innych ssaków. Niekompletne kostki słuchowe zostały następnie odkryte w czterech okazach maleńkiego multituberkulata *Chulsanbaatar vulgaris* z późnej kredy Mongolii, w materiałach zebranych przez Polsko-Mongolskie Wyprawy Paleontologiczne do Mongolii, znajdujących się w zbiorach Instytutu Paleobiologii Polskiej Akademii Nauk. Jeden z tych okazów został krótko opisany w poprzedniej naszej pracy (Hurum *et al.* 1995), a trzy w niniejszej pracy. Opisane kostki słuchowe *Chulsanbaatar vulgaris* obejmują trzy prawie kompletne kowadełka (po raz pierwszy znalezione u multituberkulatów) i dwa fragmenty młoteczka. W poprzedniej pracy opisano również kowadełko oraz strzemiączko, jednakże identyfikacja tego ostatniego elementu nie jest całkowicie pewna. Kowadełko ma w przybliżeniu kształt litery A. W związku z bocznym rozszerzeniem puszek mózgowych multituberkulatów, promontorium ustawione jest u nich nieco bardziej skośnie w stosunku do osi czaszki niż u innych ssaków, co powoduje, że okienko przedsionka jest zwrócone w bok i ku przodowi, a nie tylko w bok, jak u innych ssaków. Położenie okienka przedsionka wpływa na zmianę ustawienia strzemiączka. Zachy-

łek nadbębenkowy jest położony bardziej ku przodowi w stosunku do okienka przedsionka niż u innych ssaków i jest głęboki, dlatego kowadełko musiało być ustawione prawie pionowo, z odnogą krótką skierowaną równoległe do osi drgań młoteczka. Zachowane fragmenty młoteczka wykazują obecność długiego wyrostka donosowego, co zgadza się z rekonstrukcją młoteczka u paleoceńskiego *Lambdopsalis* (Meng & Wyss 1995), z odkrytymi ostatnio fragmentami kostek słuchowych multituberkulata *Kryptobaatar* z późnej kredy Mongolii (Rougier *et al.* w druku), a także z budową młoteczka u stekowców oraz u zarodków prymitywnych ssaków (Fleischer 1973, 1978; Maier 1989, 1990). Dane te (mimo że rękojeść młoteczka nie została dotychczas znaleziona u multituberkulatów) wskazują, że kostki słuchowe multituberkulatów miały taką samą orientację jak u ssaków współczesnych (Fig. 6). Rekonstrukcja kostek słuchowych multituberkulatów przedstawiona w niniejszej pracy nie zgadza się z rekonstrukcją Miao & Lillegravena (1986) i przemawia przeciw wyodrębnieniu się multituberkulatów z gadów ssakokształtnych oddzielnie od pozostałych ssaków, a więc stanowi argument na korzyść monofiletyzmu ssaków.

Ponadto, na podstawie szlifów seryjnych czaszek multituberkulatów *Chulsanbaatar vulgaris* i *Nemegtbaatar gobiensis*, wykazano (Fig. 8), że średnica przedsionka u tych multituberkulatów jest około dwukrotnie większa niż średnica ślimaka, tak samo jak to ma miejsce u osesków współczesnych ssaków. Luo & Ketten (1991), na podstawie niejasnych przekrojów tomograficznych kości skalistej multituberkulatów *Catopsalis* i *Moensicoessus*, stwierdzili, że średnica przedsionka jest u nich odpowiednio 5 i 7 razy większa niż średnica ślimaka i zasugerowali, że silnie powiększony przedsionek stanowi synapomorfie multituberkulatów. Na podstawie danych opublikowanych w niniejszej pracy, wniosek ten odrzuciliśmy.