MULTITUBERCULATE ENDOCRANIAL CASTS

by

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SUMMARY

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ABSTRACT

A reconstruction of a multituberculate endocranial cast is made on the basis of a complete natural cast prepared from the skull of *Chulsanbaatar vulgaris*, and other less complete endocasts, all from the Late Cretaceous of Mongolia. The multituberculate endocast is of mammalian pattern but it has retained a therapsid-like lateral profile with a deep rhombencephalon and a shallow telencephalon. It is characterized by: a heart-shaped cross-section of the telencephalon; an extensive lissencephalic neocortex; a very prominent pons placed far anteriorly; a lack of cerebellar hemispheres, and very large paraflocculi. Its structure, very different from the brains of other mammals, suggests thats the Multituberculata branched very early from the main mammalian stock. This supports Simpson's (1945) idea that the Multituberculata should be placed in a subclass of their own: Allotheria MARSH. The endocast and braincase structure show that the Multituberculata had strongly developed senses of smell and hearing. The encephalization quotient of approx. 0.55 evaluated for *Ch. vulgaris* is relatively high for a Mesozoic mammal.

RÉSUMÉ

L'auteur propose la reconstitution du moulage endocrânien d'un multituberculé, fondée sur l'étude d'un moulage endocrânien naturel complet, préparé à partir d'un crâne de *Chulsanbaatar vulgaris*, et d'autres moulages moins complets, tous du Crétacé supérieur de Mongolie. Bien que de type général mammalien, le moulage endocrânien a conservé un profil thérapside, avec un rhombencéphale élevé et un télencéphale bas. Il est en outre caractérisé par la section transversale du télencéphale, grossièrement en forme de cœur, par un néocortex très étendu mais lisse, par un pont de Varole très proéminent et situé très en avant, enfin par l'absence d'émisphères cérébelleux et la très grande taille des paraflocculi. Cette structure, qui apparaît donc très différente de celle connue chez les autres Mammifères, suggère que les Multituberculés se sont détachées très tôt du stock mammalien initial ; ceci vient appuyer l'idée de Simpson (1945) selon laquelle les Multituberculés devraient être rangés dans une sous-classe particulière : Allotheria MARSH. Ce moulage endocrânien comme la structure de la boîte crânienne témoignent, pour les Multituberculés, du fort développement des sens de l'ouïe et de l'olfaction. Le quotient d'encéphalisation, d'environ 0.55, qui fut calculé pour *Ch. vulgaris* est relativement élevé pour un Mammifère mésozoïque.

INTRODUCTION

Jerison (1973) reviewed the literature on the endocranial casts of all fossil vertebrates. An important result of his study is an outline of the changes in the relative size and proportions of the brain in the evolution of mammals and of the allometric relationships of brain to body weight. Since Jerison's book, numerous papers on mammalian paleoneurology have appeared which, however, exclusively concern Tertiary and Pleistocene mammals. Although the record of Mesozoic mammals has considerably increased during the last 30 years (Lillegraven *et al.*, 1979), their endocasts have been almost unknown. Three dorsal aspects of Mesozoic mammal endocasts have been described, but only one, that of the Late Jurassic *Triconodon* (Simpson, 1927), is reasonably completely preserved. The two remaining endocasts, one of the Liassic *Sinoconodon* (Patterson and Olson, 1961), referred to the Triconodonta *incertae sedis* by Jenkins and Crompton (1979), and one of the Late Jurassic dryolestid eupantothere *Amblotherium* (Edinger, 1964) are fragmentary.

In contrast with these few records, there is a collection of Late Cretaceous mammals from Mongolia (Kielan-Jaworowska, 1969, 1970, 1971, 1974, 1981) housed in the Institute of Paleobiology (Zaklad Paleobiologii) of the Polish Academy of Sciences in Warsaw (abbreviated as ZPAL) which contains more or less complete endocasts of three eutherian and two multituberculate species. The description of eutherian endocranial casts is published elsewhere (Kielan-Jaworowska, in press). The purpose of this paper is to describe a complete multituberculate endocast.

MATERIAL

Multituberculates are very common fossils in Mesozoic and Early Tertiary continental rocks (Clemens and Kielan-Jaworowska, 1979), but only one multituberculate endocast, that of Paleocene *Ptilodus montanus*, has been described. Simpson (1937) made a composite reconstruction of the dorsal surface of the *Ptilodus* endocast, based on four fragmentary specimens. In addition, Edinger (1964) mentioned the structure of the braincast of the Early Eocene *Ectypodus* (which is similar to that of *Ptilodus*) but did not describe or figure it, and Hahn (1969) made a reconstruction of the dorsal aspect of an endocast of the Late Jurassic *Paulchoffatia delgadoi*, based on the skull structure and on a comparison with Simpson's reconstruction. The ventral and lateral sides of a multituberculate endocast have not been described as yet.

In the above mentioned ZPAL collection of Late Cretaceous multituberculates are ten partial endocasts of *Chulsanbaatar vulgaris* KIELAN-JAWOROWSKA, 1974, and one poorly preserved endocast of *Nemegtbaatar gobiensis* KIELAN-JAWOROWSKA, 1974. These derive from the rocks of the Barun Goyot Formation or from its stratigraphic equivalent, the red beds of Khermeen Tsav. The ages of these rocks are uncertain. Gradzinski *et al.* (1977) argued that the Barun Goyot Formation may be of ?middle Campanian Stage. Recent paleobotanical evidence (Karczewska and Ziembińska-Tworzydlo, in press) suggests that the Nemegt Formation which conformably overlies the Barun Goyot Formation, is not younger than the Early Campanian Stage. It thus follows that the Barun Goyot Formation (and the red beds of Khermeen Tsav) may be of ?Late Santonian Stage. These estimates, however, should be regarded as tentative.

The specimen of *Nemegtbaatar gobiensis* (ZPAL MgM-I/57) is strongly compressed laterally and its endocast surface is badly damaged. As this endocast differs from those of *Chulsanbaatar vulgaris* only in being larger, and does not provide new data on the multituberculate brain structure, it is not described, nor figured in this paper.

Ten partial endocasts of *Ch. vulgaris* (four of which are illustrated in Pl. 1) belong to individuals at various ontogenetic stages and sizes. Three of these ten specimens have been figured by me as originally preserved (Kielan-Jaworowska, 1974, ZPAL MgM-I/61: Pl. XV, fig. 1a; ZPAL MgM-I/108: Pl. XIII, fig. 1a, and ZPAL MgM-I/88: Pl. V, fig. 7, the latter erroneously identified as ?*Kamptobaatar* sp.). In these specimens parts of the cranial roofs have been subsequently removed to show larger surfaces of the dorsal sides of the endocasts and partial casts of the nasal cavities. A nearly complete natural endocast of an adult (large) individual (ZPAL MgM-I/88), slightly compressed dorso-ventrally, was prepared by removing the braincase and cutting off most of the cast of the nasal cavity (Pl. 1, fig. 1). This has allowed me to examine the lateral and ventral sides of multituberculate endocast for the first time. The description that follows is based mainly on this specimen. Less complete endocasts of the same species, as well as skulls in which endocasts have not been preserved but which show parts of the inner sides of the braincases, have also been used for the reconstruction (fig. 1) and for comparisons.

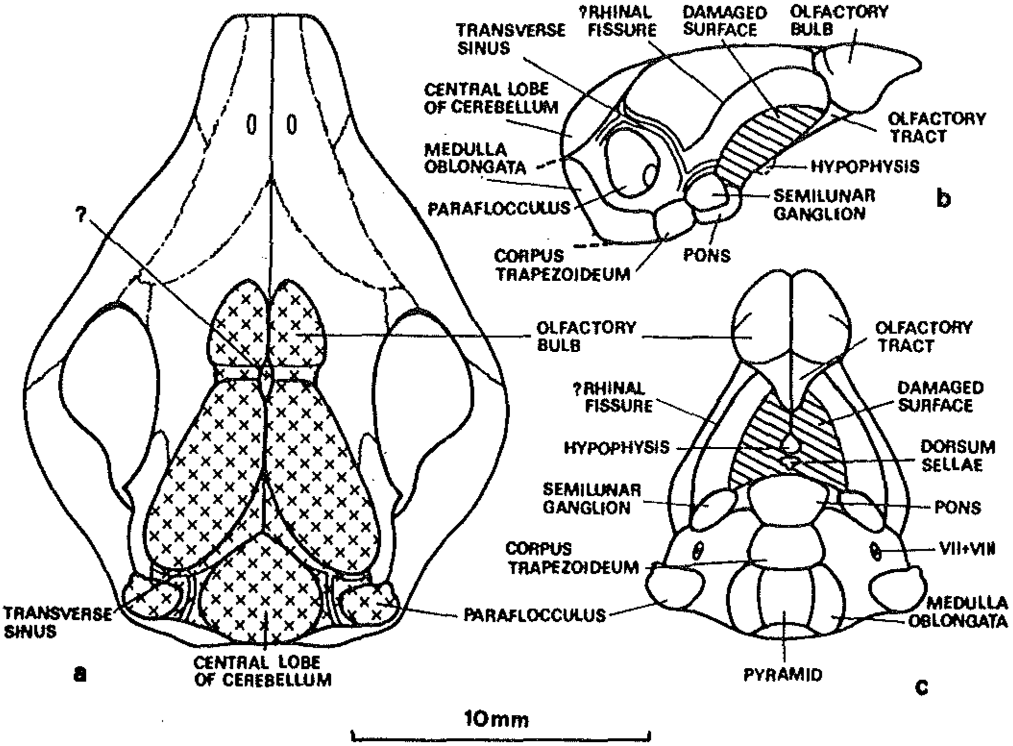

Fig. 1. — *Chulsanbaatar vulgaris* Kielan-Jaworowska, 1974, reconstructions; a: skull and endocast (hatched) in dorsal view, b: endocast in lateral view, c: the same in ventral view. Reconstruction of the skull based mostly on ZPAL MgM-I/61, that of the endocast on ZPAL MgM-I/88, the position of the hypophysis and dorsum sellae on ZPAL MgM-I/58.

THE ENDOCAST OF *CHULSANBAATAR VULGARIS*

The endocast of ZPAL MgM-I/88 (fig. 1 and Pl. 1, fig. 1) is 12.3 mm long, the skull length being about 21 mm. The greatest width of the endocast across the cerebral hemispheres is 8 mm and across the paraflocculi 9.8 mm. Viewed from above, it is characterized by a notable development of the telencephalon.

The olfactory bulbs are very large relative to the rest of the brain, 2.1 mm wide and 3.8 mm long, and taper slightly anteriorly. Extending parallel to the posterior margin of the olfactory bulb, at a distance of 0.7 mm from the margin, there is a shallow furrow. The part of the olfactory bulb behind this furrow measures 3.4 mm across both bulbs. It may correspond to the accessory olfactory bulb, being similar in shape to that of *Didelphis* (Loo, 1930, fig. 1). In *Didelphis*, however, the accessory olfactory bulbs are, in dorsal view, partly obscured by the cerebral hemispheres. As the recognition of an accessory olfactory bulb in *Ch. vulgaris* is not certain, it has not been marked in fig. 1. There is a single, median fusiform structure of unknown significance, approximately 1.5 mm long, interposed between the posterior parts of the olfactory bulbs and the anterior parts of the cerebral hemispheres. The olfactory bulb is about 1 mm deep anteriorly and 2.5 mm deep posteriorly. The cast of the nasal cavity extends onto the ventral side of the olfactory bulbs. Since the cribriform plate is not preserved, the structure of this region is not clear. The fissure between the olfactory bulb and the cerebral hemisphere extends anteroventrally in lateral view, and so the olfactory bulbs are shorter ventrally than dorsally.

Extending posteriorly from the inflated part of the olfactory bulbs is the olfactory tract which tapers posteriorly. The part of the olfactory telencephalon situated laterally and posterolaterally to the olfactory tract, corresponding to the olfactory tubercule, was probably insignificantly expanded. The cerebral hemispheres are about 6.7 mm long, and widen posteriorly. The neocortex is lissencephalic and slightly overhangs the paleocortex laterally. The tentatively recognized rhinal fissure is seen in lateral and ventral views, demarcating the boundary between the expanded neocortex and less expanded paleocortex. The surface of the pyriform lobe is damaged in all the specimens of *Ch. vulgaris*, as the ventral wall of the braincase was very thin in this region and was not preserved. The part of the pyriform lobe is visible only in the skull of *Kamptobaatar Kuczynskii* (ZPAL MgM-I/33) and is slightly inflated (in this specimen the whole endocast has not been exposed, see Kielan-Jaworowska, 1971, Pl. II, fig. 1a). In cross-section the telencephalon has a roughly heart-shaped outline. The casts of the nerves II-IV and VI are not preserved. The cast of the hypophysis is preserved only in ZPAL MgM-I/58 and has been reconstructed in fig. 1; it is bordered posteriorly by a deep depression made by the dorsum sellae. The midbrain is not exposed on the dorsal side; it appears to be overlapped by a very large central lobe (vermis) of the cerebellum, and possibly is also obscured by the transverse sinus, which is often the case in mammals (Bauchot and Stephan, 1967).

The rhombencephalon is about 5 mm deep and 5 mm long; it protrudes strongly ventrally and anteriorly. The central lobe of the cerebellum is relatively large, and extends rostrally between the cerebral hemispheres. There is no trace of cerebellar hemispheres. The paraflocculus is relatively enormous, being 2.5 mm wide and 1.9 mm long. It is directed postero-latero-ventrally, and has a small cuspule on its anterior surface. There is a cast of a transverse sinus which departs from the longitudinal fissure; lateral to the central lobe a vein branches from the transverse sinus in a posteroventral direction.

The pons is about 2.8 mm wide anteriorly and 1.7 mm long, narrowing posteriorly, very prominent, placed far anteriorly, sharply delimited anteriorly from the poorly preserved region of crus cerebri and laterally from the semilunar ganlion on the Vth nerve. The latter was exposed only on the right side of the specimen. The semilunar ganglion is situated obliquely; it is 1.9 mm long in posterolateral direction and very high in lateral view. Behind the semilunar ganglion a part of the petrosal (p in Pl. 1, fig. 1g) has been left for further studies. The promontorium has been removed on the right side; the cast of the internal auditory meatus is not visible, being obscured by the piece of petrosal (p); its position marked in fig. 1c (cranial nerves VII and VIII) has been reconstructed on the basis of other petrosals. The medulla oblongata is less prominent than the pons. A poorly defined corpus trapezoideum is 1 mm wide anteriorly, being about 1.3 mm long. The cast of the pyramid is also poorly preserved. Casts of cranial nerves IX-XII are lacking.

The less complete endocasts of *Ch. vulgaris* in ZPAL collection (Pl. 1, figs. 2-4, and Kielan-Jaworowska, 1974, Pl. XV, fig. 1a) differ from ZPAL MgM-I/88 in size and proportions, however, all are approximately the same size relative to skull length, with no apparent ontogenetic changes in the size series represented. The index: endocast length × 100 to skull length in six measured specimens (the skull lenght of which ranges between 16.2 and 21 mm) ranges between 55.83 and 58.64. It is the smallest (55.83) in ZPAL MgM-I/61, the skull length of which is 19.7 mm, and in which the olfactory bulbs do not taper anteriorly. These differences may be due to individual variation and in part also to the state of preservation.

ENCEPHALIZATION QUOTIENT

In estimates of the brain volume in fossil mammals, Jerison (1973) applied the formula for the volume of an ellipsoid. In cases where only the dorsal aspect of the endocast was known he accepted that the surface of the lateral side was 0.8 of that of the dorsal side, which is the case in primitive therian mammals. As demonstrated in the previous section, the multituberculate braincast has an irregular shape which hardly can be compared with that of an ellipsoid (fig. 1 and Pl. 1, fig. 1). Jerison measured the brain volume excluding the olfactory bulbs, while most authors (*e.g.* Radinsky, 1977, Eisenberg, 1981 and others) include the olfactory bulbs in the brain volume. In order to estimate the volume of the ZPAL MgM-I/88 endocast, I made a model with a linear magnification of 10 times. By water displacement of this model I obtained the endocast volume (with olfactory bulbs) of 0.22 ml.

In estimates of the body weight in fossil mammals Jerison used the equation

$$\mathrm{Wt} = \mathrm{k\,L}^3 \qquad (1)$$

where Wt is body weight in g, L is body length in cm, and k is an empirically determined coefficient. The value of coefficient applied by Jerison varies from 0.021 in mammals of light habitus, such as small insectivores and rodents, to 0.050 in heavily-built large mammals. Jerison regarded the multituberculates as "heavily built animals" and assumed that the value of k is 0.050. The undescribed postcranial skeletons of *Ch. vulgaris* studied by me are almost of the same size and stoutness as in smallest specimen of *Microtus arvalis* in ZPAL collection, the skull length of which is 21 mm. The average value of k in *M. arvalis* according to Prof. P.P. Gambarjan (personal communication), measured on four specimens is 0.025, whereas according to Eisenberg (1981) it is about 0.020. Using these two values of k, I obtained body weight estimates in *Ch. vulgaris* of 14.8 g and 11.8 g.

Evaluating the encephalization quotient in mammals, Jerison (1973) used the equation

$$\mathrm{EQ} = \frac{\mathrm{E}}{0.012\ \mathrm{Wt}^{0.66}} \qquad (2)$$

in which E is brain weight and Wt is body weight in grams. However, according to recent studies (*e.g.* Eisenberg and Wilson, 1978, 1981, Eisenberg, 1981, Martin, 1981) the allometric exponent value in measuring EQ in extant mammals is about 0.74 and the coefficient is not 0.012 but 0.055:

$$EQ = \frac{E}{0.055\ Wt^{0.74}} \qquad (3)$$

Nevertheless Radinsky (1981) used the exponent of 0.66 in estimates of the EQ of extinct South American ungulates.

In order to obtain the data comparable with those of extant mammals (Eisenberg, 1981), I used equation (3) and estimated the EQ for *Ch. vulgaris* to be 0.54-0.56. The above estimates are tentative, mostly because of the uncertainties of the endocast model, which was partly reconstructed.

Jerison (1973) evaluated the EQ for *Ptilodus montanus* as 0.26. Using Jerison's data, but applying equation (3) and measuring the brain volume including olfactory bulbs, the EQ for *Ptilodus* may be evaluated as 0.49. This value is only slightly lower than that for *Chulsanbaatar*, but the coincidence is surly occidental, as it is my opinion that Jerison used incorrect assumption for the evaluation of both the endocast volume and the body weight of *Ptilodus*, and highly overestimated its body weight (see also Radinsky, 1975 for criticism of Jerison's methodology). I assume that the EQ value for *Ptilodus* is much higher than 0.49. However, I am not able to estimate it even tentatively as this would require the evaluation of the coefficient k in equation (1) for *Ptilodus montanus*. Such an evaluation could be done on the basis of a direct comparison of *P. montanus* postcranial skeleton (housed in the United States National Museum in Washington and not available to me at this writing) with the skeletons of present-day mammals of similar size.

Jerison (1973) evaluated the EQ for the Late Jurassic *Triconodon*, one of the most primitive known mammals, to be 0.28. Correcting Jerison's data by including the olfactory bulbs in the brain volume and using equation (3), the EQ of *Triconodon* may be estimated as 0.49. This value may be too high as it is based on the assumption that the *Triconodon* brain had the shape of an ellipsoid which is rather unlikely. According to the tentative reconstruction of the brain of the Liassic *Morganucodon* (Kermack *et al.*, 1981), which is based on the structure of the skull, it appears that in the Triconodonta the brain was irregular in shape, possibly with a deep rhombencephalon, as in the Multituberculata.

COMPARISON OF ENDOCASTS AMONG MULTITUBERCULATES

All available material of multituberculate endocasts does not allow an outline of the main trends of brain evolution in the Multituberculata. Endocasts of two groups of genera have been described: Asian Late Cretaceous *Chulsanbaatar* and *Nemegtbaatar* (suborder Taeniolabidoidea) of Asian origin; and North American Paleocene *Ptilodus* and Eocene *Ectypodus* (suborder Ptilodontoidea) of North American origin (Kielan-Jaworowska, 1980). It cannot be even stated whether the differences observed between the casts of *Ptilodus* (Simpson, 1937) and *Chulsanbaatar* - *Nemegtbaatar*, *i.e.* the relatively larger and anteriorly widening olfactory bulbs, relatively smaller paraflocculi, and the lack of an unpaired structure between the olfactory bulbs in *Ptilodus*, are characteristic of the brains of the Ptilodontoidea and Taeniolabidoidea as a whole, or are variations at a lower taxonomic level. As the *Chulsanbaatar* endocast described herein is the most complete of all multituberculate endocasts so far described, I will refer to it as a representative multituberculate endocast in the discussion that follows.

COMPARISON OF THE MULTITUBERCULATE BRAIN WITH THAT OF THERAPSIDS AND PRIMITIVE MAMMALS

Although at that time he had little evidence, Simpson (1937, p. 752) stated: "... the cast thus reconstructed for *Ptilodus* is extraordinary different from those known in any other groups of mammals." The lateral and ventral aspects of the multituberculate endocast reconstructed herein show that the differences between this endocast and those of all other groups of mammals are greater than expected on the basis of dorsal aspect only.

The multituberculate endocast has an unusual combination of features. It resembles a typical mammalian brain and very large olfactory bulbs in having large cerebral hemispheres, possibly with a well developed lissencephalic neocortex. On the other hand, it is more therapsid-like (see Hopson, 1979 and Quiroga, 1980 for summaries) than are the brains in any other groups of mammals (except possibly the Triconodonta), in that it has retained a therapsid-like lateral profile, with a deep rhombencephalon and shallow telencephalon and large paraflocculi (which, however, are differently shaped than in the therapsids). The multituberculate endocast differs from those of the therapisids:

1/ in having a telencephalon that is wider relative to the lenght;
2/ in lacking a midbrain exposure on the dorsal side;
3/ in the shape of the cerebellum;
4/ in the shape of the pons.

The latter, if correctly reconstructed by Olson (1944) is bilobed in the therapsids and situated posteriorly not only to the Vth nerve insertion (as in the monotremes), but also posteriorly to the VIIth nerve insertion which does not occur in mammals. If Olson's interpretation is correct, the therapsid brains would differ sharply from those of all other reptiles.

In dorsal aspect the multituberculate endocast is most similar to that of the triconodonts (Simpson, 1927) which has long cerebral hemispheres, a central lobe of the cerebellum inserted between them, and probably no cerebellar hemispheres. The above mentioned reconstruction of the *Morganucodon* brain (Kermack *et al.*, 1981) shows large paraflocculi, a large semilunar ganglion of the Vth nerv and a deep rhombencephalon, as seen in the multituberculates. But other characteristic features of the multituberculate endocast, *viz.* a heart-shaped cross-section of the telencephalon and a very prominent pons, are not known in the triconodonts.

As the multituberculate and monotreme braincases share several common characters (Kielan-Jaworowska, 1971) it may be expected that these mammals could also have similar brains. This, however, is not the case. The multituberculate endocast differs from the brains of the monotremes (Elliot Smith, 1899, Griffiths, 1968) in having quite a different shape of the telencephalon, which in the monotremes is short, strongly expanded laterally, with a gyrencephalic neocortex in *Tachyglossus*, but lissencephalic in *Ornithorhynchus*. There is a similarity in the structure of multituberculate and *Ornithorhynchus* cerebellum in the common absence of the cerebellar hemispheres.

The differences between the multituberculate endocast and the brains of primitive marsupials (Loo, 1930, Voris and Hoerr, 1932, Johnson, 1978) and primitive eutherians (Ariëns Kappers *et al.*, 1960, Le Gros Clark, 1924, 1932, Starck, 1962, 1963, Bauchot and Stephan, 1967 and others) are conspicuous. They consist of: different proportions between the telencephalon and rhombencephalon, including a different cross-sectional shape of the telencephalon; a lack of the midbrain exposure on the dorsal side in the multituberculates which is characteristic of many, but not all, primitive therians (see Starck, 1963 and Edinger, 1964 for discussion); the structure of the cerebellum which even in the most primitive Theria is provided with cerebellar hemispheres and with cerebellar fissures. In the multituberculates, only the central lobe of the cerebellum is present and the cerebellar fissured have not been found. This latter feature may be, however, due to the state of preservation. It is interesting that the rhinal fissure in certain primitive insectivores and carnivores (Starck, 1963, Radinsky, 1977) is placed on the dorsal side of the brain, while in the multituberculates, if correctly recognized, it is visible only in lateral and ventral views. This would indicate that the neocortex has been relatively more expanded in multituberculates than in some primitive fossil and extant eutherians.

DISCUSSION

The structure of multituberculate endocast shows that they had strongly developed olfaction, while very large cochlea (Kielan-Jaworowska, 1971) suggests a well developed auditory sense. This supports the assumptions of Jerison (1973) and Crompton *et. al.* (1978) that Mesozoic mammals favored nocturnal niches.

The EQ of about 0.55 evaluated herein for *Chulsanbaatar vulgaris* appears high for a non-therian Mesozoic mammal. It is higher than that evaluated by me (Kielan-Jaworowska, in press), using equation (3), for the Late Cretaceous Asian insectivore *Kennalestes gobiensis* (0.36) and almost the same as that of a more specialized *Asioryctes nemegetensis* (0.56); for a derived Late Cretaceous insectivore *Zalambdalestes lechei* the EQ is (0.70). The EQ for *Ch. vulgaris* also appears high in comparison with those calcultated by Eisenberg (1981) for *Didelphis marsupialis* (0.35-0.57) and *Tenrec ecaudatus* (0.34-0.49). It is also possible, but far from proven, that the EQ for the Paleocene *Ptilodus* was higher than for the Cretaceous *Chulsanbaatar*.

The classification of the mammals at higher levels is a matter of argument. Hopson (1970) divided the class Mammalia into the subclasses Prototheria and Theria, and assigned to the Prototheria the orders: the Triconodonta, the Docodonta, the Multituberculata and the Monotremata. I showed (Kielan-Jaworowska, 1971) that the multituberculate braincase is similar to that of the monotremes and I followed the classification of Hopson. His classification has been subsequently accepted by many authors, including some zoologists (*e.g.* Eisenberg, 1981). However, in the book: "Mesozoic Mammals: the First Two-Thirds of Mammalian History" (Lillegraven *et al.*, 1979), we regarded the Prototheria as an informal taxonomic unit. Recently Presley (1981), on embryological evidence, challanged the division of the Mammalia into "therian" and "non-therian" groups, demonstrating that the ossification pattern of the braincase in extant monotremes, marsupials and placentals is essentially the same.

The present study of multituberculate endocranial casts, as well as data on their postcranial skeleton and mode of reproduction (Kielan-Jaworowska, 1979 and in preparation) induce me to change my previous opinion on the close relationship of multituberculates and monotremes. Multituberculates differ so much from monotremes and other mammals that they probably branched very early from the main mammalian stock. I now agree with Simpson (1945) and Hahn (1978) that the Multituberculata should be placed in a subclass of their own: Allotheria MARSH.

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EXPLANATION OF PLATE 1

Fig. 1-4 : *Chulsanbaatar vulgaris* KIELAN-JAWOROWSKA, 1974.

Fig. 1 : ZPAL MgM-I/88, 1a: the skull of a large individual, as originally preserved, in dorsal view, × 4, 1b: the same skull after additional preparation, showing dorsal surface of the endocast and part of the cast of the nasal cavity, × 4, 1c - 1h: natural endocast, with the proximal part of the cast of the nasal cavity, prepared from the same skull, all stereo-photographs × 2.5, 1c: posterior view, 1d: anterior view, 1e: right lateral view, 1f: left lateral view, 1g: dorsal view, 1h: ventral view. On the left side of the endocast the squamosal and petrosal bones have not been completely removed; on the right side a piece of petrosal (p) has been left between the semilunar ganglion and the paraflocculus. 1d-1h covered with ammonium chloride.

Fig. 2 : ZPAL MgM-I/142, rostral part of the skull of a small individual in dorsal view, showing anterior part of the endocast and cast of the nasal cavity, covered with ammonium chloride, × 4.

Fig. 3 : ZPAL MgM-I/108, skull of a small individual in dorsal view, showing the endocast and part of the cast of the nasal cavity, covered with ammonium chloride, × 4.

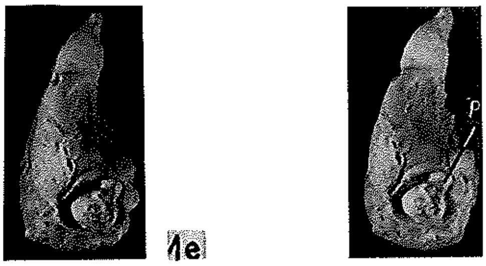
Fig. 4 : ZPAL MgM-I/140, skull of medium-sized individual, as originally preserved, in dorsal view, showing damaged endocast and cast of the nasal cavity, covered with ammonium chloride, × 4.

ZPAL MgM-I/88 and ZPAL MgM-I/108 are from the red beds of Khermeen Tsav, locality Khermeen Tsav II; ZPAL MgM-I/140 and ZPAL MgM-I/142 are from the Barun Goyot Formation, Khulsan locality, Nemegt Basin; all from the Gobi Desert, Mongolia.

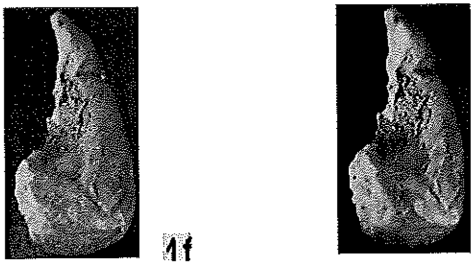
PLANCHE 1

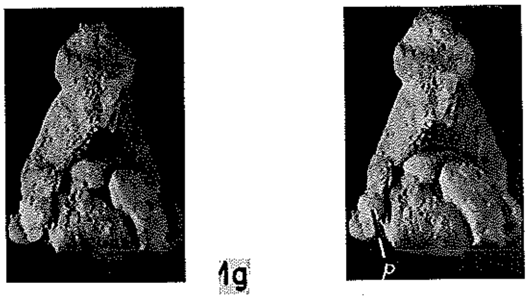

1c


1d

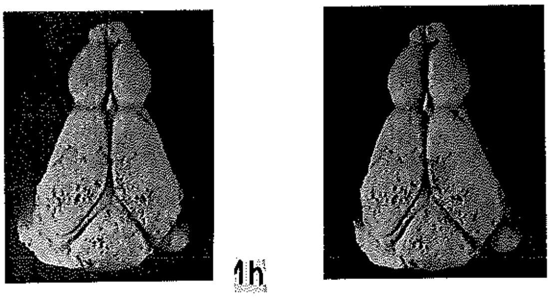


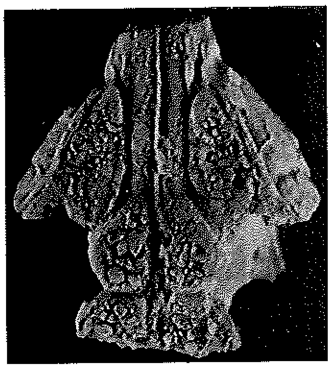
1e


1f



1g


1h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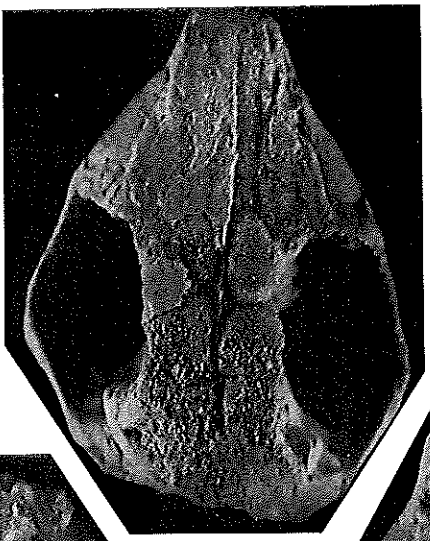
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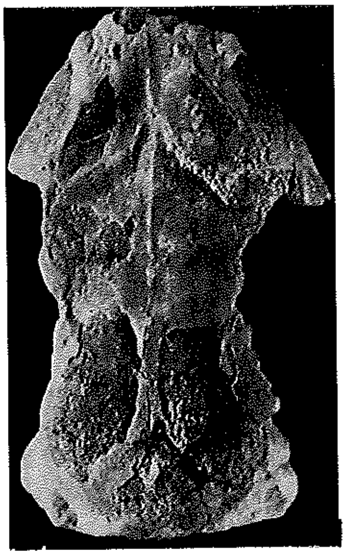
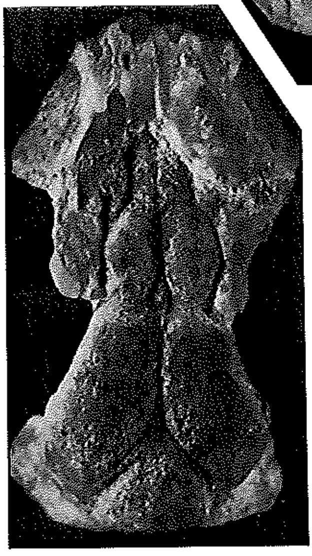

1a


1b


4