#### ZOFIA KIELAN-JAWOROWSKA

# SKULL STRUCTURE AND AFFINITIES OF THE MULTITUBERCULATA

(Plates I-V)

Abstract. — The skull structure of two Upper Cretaceous multituberculate genera from the Gobi Desert, Mongolia: Kamptobaatar KIELAN-JAWOROWSKA and Sloanbaatar KIELAN-JAWOROWSKA is described in detail. The lateral wall of the braincase and the occipital region of multituberculate skulls are described for the first time. The anterior lamina of the petrosal in the multituberculates consists of two parts: the ventral part and the ascending part. The ascending part of the anterior lamina, previously unknown in the multituberculates, is present in Kamptobaatar and it may be shown that the ascending part occupies most of the lateral wall of the braincase. The orbitosphenoid is large and not entirely ossified, whilst the alisphenoid is reduced to a comparatively small, ventral element, which is, however, more extensive than that of the monotremes. The following reptilian elements: ectopterygoid, tabular and post-temporal fossa are found in the studied skulls. The multituberculate braincase is compared with those of the Docodonta (Morganucodon), Triconodonta and Monotremata and it is shown that the general pattern of the braincase structure in these four orders is the same. However, the Multituberculata are more allied to the Monotremata than they are to the Docodonta and the Triconodonta. The opinion that the Docodonta, Triconodonta, Multituberculata and Monotremata form a subclass Prototheria, equivalent to the Theria, is supported.

## INTRODUCTION

Until recently the only known entire skulls of multituberculates have been the two Paleocene genera: *Ptilodus* GIDLEY and *Taeniolabis* COPE. However, the basicranial region was preserved only in *Ptilodus*, while the occipital region and the lateral wall of the braincase have so far not been described in any multituberculate. Recently, a mass of Cretaceous multituberculate material has been collected from various localities in the United States and Canada (RUSSELL, 1952, 1962; CLEMENS, 1963; SLOAN & VAN VALEN, 1965; CLEMENS & RUSSELL, 1965; SAHNI, MS; LILLEGRAVEN, 1969). Unfortunately, this rich material is fragmentary, yielding only skull fragments.

In the collection of Cretaceous mammals, collected recently by the Polish-Mongolian Palaeontological Expeditions in the Mongolian People's Republic (KIELAN-JAWOROWSKA & DOVCHIN, 1968/69; KIELAN-JAWOROWSKA, 1968/69), there are more than 30 multituberculate specimens. Some of these are partial skulls but there are a few entire skulls. This collection came from the locality of Bayn Dzak (referred to in American literature as Shabarakh Usu) in the Gobi Desert. The age of the Cretaceous sandstone occurring there has been estimated, on the basis of the multituberculate fauna, as Coniacian or Santonian (KIELAN-JAWOROWSKA, 1970a)<sup>1</sup>. The multituberculate material we collected from the Gobi Desert, is much less numerous

<sup>&</sup>lt;sup>1</sup>) McKENNA (1969) estimates that the age of the Djadokhta Formation is approximately Cenomanian (ca  $95 \times 10^{6}$  y.b.p.) He does not mention, however, the locality of the rocks investigated by radioactive methods. The nearest lava occurs about 20 km north of Bayn Dzak; the position of this lava, with regard to the sandstone of the Djadokhta Formation, is obscure. If it underlies the Djadokhta Sandstone, then the latter would be younger than  $95 \times 10^{6}$  y.b.p. On the other hand, the degree of diversification of the mammals yielded by the Djadokhta Formation indicates, in my opinion, that this formation is of Coniacian or Santonian age.

but more complete than that from the Cretaceous of North America. Recently (l. c.) I gave the diagnoses of four new multituberculate genera from Bayn Dzak, without, however, describing their skull structure in detail. The best preserved specimens studied in this multituberculate collection are: a tiny skull (without the lower jaws) — the type specimen of Kamptobaatar kuczynskii KIELAN-JAWOROWSKA (Taeniolabididae) and a complete skull associated with the lower jaws — the type specimen of *Sloanbaatar mirabilis* KIELAN-JAWOROWSKA (?Eucosmodontidae). The skull of *Kamptobaatar* is better preserved than that of *Sloanbaatar*, as it belongs to a young individual and almost all the sutures are recognizable. In the *Sloanbaatar* specimen the surface of the bone is covered with a mosaic of fine cracks, so it is difficult to recognize all sutures. Both specimens provide much information that is new about the skull structure in the Multituberculata. These are the first multituberculate skulls in which the occipital surface and the lateral wall of the braincase are preserved, and the basicranial region in Kamptobaatar is better preserved than in any multituberculate described so far. The present paper contains the descriptions of the skulls of Kamptobaatar and Sloanbaatar, with a discussion on the affinities of the Multituberculata. I hope that the information on these skulls may help in the interpretation of any isolated fragments of multituberculate skulls coming from other localities. The preliminary note on the skull structure in Kamptobaatar was published elsewhere (KIELAN-JAWO-ROWSKA, 1970b).

The specimens described in the present paper are housed in the Palaeozoological Institute of the Polish Academy of Sciences in Warsaw.

Abbreviations for the catalogues of specimens:

A. M. N. H. - American Museum of Natural History, New York.

B. M. — British Museum (Natural History), London.

Z. Pal. - Palaeozoological Institute of the Polish Academy of Sciences, Warsaw.

Abbreviations for text-figures:

A, B	- surfaces for muscle attachment on the zy-	Jn — jugular notch
	gomatic arch in Sloanbaatar	Lf — lateral flange
ΑI²	— alveolus for I <sup>2</sup>	Mipf — minor palatine foramen
Alpet	- anterior lamina of the petrosal	Mpf — major palatine foramen
Alsph	— alisphenoid	Mx — maxilla
Bo	- basioccipital	Mf — maxillary foramen
Bs	— basisphenoid	Na — nasal
Ce	— cavum epiptericum?	Oc — occipital
Ec	- ectopterygoid	Of — orbital fissure
Ept	Echidna pterygoid	Onf — orbitonasal foramen
Etf	— ethmoid foramen	Osph— orbitosphenoid
Exoc	— exoccipital	Pal — palatine
Fc	- fenestra cochleae (rotunda)	Par — parietal
Fm	- foramen magnum	Pet — petrosal
Fr	frontal	Pf — palatine fissure
F٧	- fenestra vestibuli (ovalis)	Pgf — postglenoid foramen (canalis prooticus)
Glf	— glenoid fossa	Pmx — premaxilla
Н	— hamulus	Pnf — palatonasal foramen
HF	— hiatus canalis Fallopii	Pp — paroccipital process
Ic	— internal carotid foramen	Ppt — postpalatine torus
Ip	— interparietal	Pt — pterygoid
Inf	— infraorbital foramen	Ptf — post-temporal fossa
Jf	— jugular foramen	Pv — palatal vacuity

- Scf scaphoid fossa Sf — sphenorbital fissure
- Sgf supraglenoid foramen (possibly anterior
- opening of post-temporal fossa)
- Soc supraoccipital
- Spf sphenopalatine foramen

- Sq squamosal
- Tb tabular
- V vomer
- Zr zygomatic ridge
- II, III, IV, V<sub>1</sub>, V<sub>2</sub>, V<sub>3</sub>, VI, VII foramina for respective cranial nerves

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## DESCRIPTIONS

#### Kamptobaatar kuczynskii Kielan-Jaworowska, 1970

(Pl. I, Figs. 2a, 2b; Pls. II-IV; Text-figs. 1-5, 12a, 13a, 14a)

1970a. Kamptobaatar kuczynskii n. sp.; Z. KIELAN-JAWOROWSKA, New Upper Cretaceous..., p. 46, Pls. 16, 17; Text-fig. 2. 1970b. Kamptobaatar kuczynskii KIELAN-JAWOROWSKA; Z. KIELAN-JAWOROWSKA, Unknown structures..., Figs. 1,2a.

Material. — The present description is based mainly on the type specimen (Z. Pal. No. MgM-I/33), which is an almost complete skull of a young individual. The lower jaws are missing as are parts of the zygomatic arches. This specimen has been figured by KIELAN-

JAWOROWSKA (1970*a* and 1970*b*) and is refigured in the present paper. In addition to the type specimen there are two incomplete skulls: Z. Pal. No. MgM-J/39 figured by KIELAN-JAWOROWSKA (*l. c.*) and Z. Pal. No. MgM-J/38 figured in the present paper. The latter is a partial skull and is associated with an incomplete left lower jaw and fragments of a right lower jaw.

The measurements of Z. Pal. No. MgM-I/33 and Z. Pal. No. MgM-I/39 are given by KIELAN-JAWOROWSKA (1970*a*, Tables 1 and 2).

The skull as a whole. The snout is comparatively wide and bluntly pointed. The zygomatic arches are directed at first laterally, then posterolaterally, giving this part of the skull a more rectangular than triangular appearance. The greatest width was probably across the posterior part of the zygomatic arches, but as they are broken off in all specimens, this cannot be stated with certainty. The postorbital process is prominent and situated far posteriorly; the orbit is very large and the interorbital constriction conspicuous. In lateral view, the snout is strongly tapered anteriorly; the occipital surface lies obliquely with regard to the plane of the teeth and the cranial roof is rounded posteriorly. In anterior view, the cranial roof is almost flat and the infraorbital foramina face anteriorly.

Snout and zygoma. The nasals are extensive, strongly expanded posteriorly. The frontonasal suture is convex posteriorly, with the median processes of the frontals deeply inserted between the nasals. In the transverse plane, the nasals are very slightly arched with a faint groove along the median suture. There are prominent "vascular" foramina, asymmetrically arranged, in the nasals, Z. Pal. No. MgM-I/33 has four small foramina in the left nasal and two in the right and the most posterior is the largest of all. The premaxilla is directed almost vertically and has a strongly elongated nasal process. The premaxillo-maxillary suture cuts the lateral wall of the snout very obliquely and appears vertical in anterior view. The maxilla is extensive, occupying more than two-thirds of the side of the snout. Anteriorly, the facial part of the maxilla is almost vertical and slightly convex. Posteriorly, the maxilla becomes flattened on the zygomatic arch. The infraorbital foramen, situated above  $P^2$ , is deep. This foramen is clearly seen in lateral and anterior views and is also visible in ventral view. The ventral wall of the maxilla, buccal to the row of premolars, is very small and roughly triangular. The anterior edge of that part of the zygomatic arch, formed by the maxilla, originates opposite P<sup>3</sup> and the posterior edge opposite the anterior part of P4. There is a prominent ridge on the zygoma (designated here as the zygomatic ridge) which, in ventral view, forms the anterior edge of the arch. In front of the ridge there is a distinct shallow fossa. The ridge is directed at first dorso-laterally and then bends to continue posteriorly. The ridge forms an arch, convex upwards, which delimits a crescent-shaped area for muscular attachment on the anterior part of the zygoma. In all specimens, the zygomatic arches are broken and neither the posterior part of the crescentic area nor the posterior part of the ridge are preserved. On the left side of Z. Pal. No. MgM-I/33 one can see that, opposite  $M^2$ , the ridge becomes very faint posteriorly. Anteriorly, the zygomatic arch is deep vertically and thin transversely.

Palate. The palatal processes of the premaxillae form extensive, concave surfaces occupying about two-fifths of the palatal length if measured from the anterior end of the skull. The margin between the ventral and lateral walls of the premaxilla is thickened and forms a sharp edge. On the premaxillae, to the rear of  $I^1$ , there are slight hollows from which indistinct, radial grooves extend towards the margin of the palate. On the lingual side of  $I^2$ , somewhat more anteriorly, there are the small, rounded, palatine fissures which are probably for the organs of Jacobson. The borders of these fissures reach the premaxillo-maxillary suture. In Z. Pal. No. MgM-I/38, the anterior part is broken along the median suture and can see a trace of the incisive canal on the broken wall. This canal extends towards the median suture. However, the incisive foramen is not recognizable in Z. Pal. No. MgM-I/33, in which the palatal processes of the premaxillae are well preserved.

The palatal processes of the maxillae are slightly concave. Palatal vacuities are absent. In front of the transverse palatine suture and about the middle of its course on either side, there is a small, oval major palatine foramen, the posterior edge of which reaches the transverse suture.



Kamptobaatar kuczynskii KIELAN-JAWOROWSKA, reconstruction of the skull in dorsal view. Abbreviations - see p. 6.

A palatine groove is lacking. Posterior to the transverse palatine suture, the maxilla hardly forms a definite palatal process but continues as a massive alveolar process. The suture between the maxilla and ectopterygoid extends parallel to  $M^1$  and  $M^2$  then turns laterally posterior to  $M^2$ .

The horizontal part of the palatine bone is rectangular; the transverse palatine suture is situated either opposite P<sup>4</sup>-M<sup>1</sup> embrasure, or the most anterior part of M<sup>1</sup>. Close to the palatino-maxillary suture, and about midway along, there are, on either side of each palatine, two minor palatine foramina of which the posterior is the larger. The choanae extend forwards to the level of the posterior cusps of M<sup>2</sup>. The postpalatine torus (McDOWELL, 1958) is wide and prominent and extends posteriorly as a long, medial process. The torus is delimited laterally by the palatino-maxillary suture, on which, opposite the torus, there is a longitudinally elongated, fissure-like foramen. This is the palatonasal foramen (TATARINOV, MS) which probably transmitted the palatonasal nerve. In ventral view the choanae are rounded and their lateral walls, formed by the ectopterygoids, are thickened and ridged. The entire palatal surface (premaxillae, maxillae and palatines) is pierced by numerous accessory palatine foramina, distributed at random. The choanae are separated by a vertical, median plate of bone, which lies in line with the direct prolongation of the median process of the postpalatine torus, and, in Z. Pal. No. MgM-I/33 seems to be almost coalesced with this process. This vertical median plate is identified here tentatively as the vomer.

The most peculiar feature of this region is the position of the pterygoids, which do not form part of the lateral walls of the choanae, but are situated between the vomer and the ectopterygoids. Thus the choanae are divided longitudinally by the vomer and the pterygoids into four channels. The outer channel, between the ectopterygoid and the lateral surface of the pterygoid, is more shallow than the inner channel, which is between the medial surface of the pterygoid and the vomer. The pterygoid is a vertical plate which posteriorly reaches the promontorium. Its posterior extremity is thickened and rounded, and is recognized here tentatively as a hamulus. Anteriorly, the pterygoid becomes more slender and changes its orientation from the vertical into the horizontal plane. Because of this change in orientation of the pterygoid, the inner channel of the choana becomes anteriorly very narrow and groove-like. In this anterior part the pterygoid is fused to the lateral wall of the choana, and forms the floor of the outer channel which appears to end blindly. The pterygoid still has a free inner border anteriorly, where there is a rounded incisure of unknown function.

Cranial roof. The frontals form the superior border of the anterior part of the orbit. The fronto-parietal suture forms a wide arc which is convex posteriorly. The fronto-parietal suture curves near the border of the orbit to cut the border of the skull roof to the rear of its maximal constriction. The dorsal surface of the frontals is featureless. The parietals are extensive and form the whole cranial roof posteriorly. The postorbital process is prominent. There are very faint parietal crests, which extend from the postorbital processes postero-medially. The parietal crests are hardly visible anteriorly, but become more distinct posteriorly where they meet to continue medially as a short, faint, sagittal crest. In lateral view, the parietal has a long, horizontal junction with the anterior lamina of the petrosal. The suture between the parietal and the orbitosphenoid extends dorsally and then turns anteriorly, parallel to the border of the orbit, to terminate at the fronto-parietal suture. The lambdoidal crests are faint medially and together form a gentle arc which is convex anteriorly. Laterally, the lambdoidal crests become convex posteriorly, very prominent and crescent-shaped. A shallow furrow delimits the crescent--shaped part of the lambdoidal crest anteriorly. It is difficult to determine the course of the parieto--occipital suture. In all probability, it extends along, or slightly in front of the lambdoidal crest. The parieto-occipital junction seems to be very short, as the squamosal is deeply inserted between the parietal and the occipital.

Occiput. The occiput is twice as wide as it is high, roughly semicircular in shape and surrounded from above and laterally by prominent lambdoidal crests. The occipital plate is situated

comparatively low, and lies obliquely, at an angle of about 110°, with regard to the plane of the palate. The region of the foramen magnum is damaged. Only the basal parts of the occipital condyles are preserved. The size of the basioccipital, the exoccipitals and the supraoccipital is obscure. The interparietal is absent from the cranial roof and it is impossible to state whether it was present on the occipital surface. Lateral to the foramen magnum, there is a deep, fusiform depression which is bordered laterally by a prominent, half-crescentic ridge. This ridge extends along the entire height of the occipital plate. The surface of the left depression is pierced by small foramina, seemingly distributed at random. The only sutures that can be recognized with certainty on the occipital plate, are those that separate the occipital bones from the tabulars.



Fig. 2

Kamptobaatar kuczynskii KIELAN-JAWOROWSKA, reconstruction of the skull in occipital view. The lower part of the snout is not shown in this figure. Abbreviations — see p. 6.

These sutures are present on both sides and start at the lambdoidal crests and extend downwards, parallel to each other, for about half the height of the occipital plate. The sutures then turn outwards to extend a short distance subtransversely before turning once more to extend subvertically, along the middle of the depression, to reach the ventral margin of the occipital plate between the occipital condyle and paroccipital process.

Laterally to the occipital bones there are extensive tabulars which occupy the entire surface between the occipital bone and the lambdoidal crest. As the sutures that separate the tabulars from the squamosals are hardly discernible, it is difficult to state the extent of the squamosal on the occipital plate. In the lower part of the tabular, lateral to the fusiform depression, there is a large, post-temporal fossa.

On the lower edge of the occipital surface, lateral to the occipital condyle, there is a triangular, paroccipital process, that lies in the ventral prolongation of the tabular. Above the paroccipital process there is a transverse depression. The suture separating the tabular from the paroccipital process is not discernible. A suture is present along the ventral edge of the paroccipital process; it is, however, difficult to state which bone forms the paroccipital process.

Orbit and temporal fossa. The orbit is very large and widely open posteriorly. Its anterior and lower boundaries are formed by the maxilla; the upper boundary is formed by the frontal and the parietal. The rim of bones which surround the orbit is somewhat thickened. The lacrimal bone and the lacrimal foramen are lacking. The orbit has no floor, but is roofed by the maxilla and the frontal anteriorly. Posteriorly, there is a narrow roof formed by the frontal and the parietal. In the lower part of the most anterior corner of the orbit, there is a foramen in the maxilla which leads to the infraorbital canal. The sphenopalatine foramen is readily recognizable in the interorbital wall and is situated at the level of the posterior half of M<sup>1</sup>. The sphenopalatine foramen is placed at the junction of four bones — the maxilla, the frontal, the orbitosphenoid and the palatine. A distinct groove, which becomes shallower posteriorly, extends from the sphenopalatine foramen along the lower part of the orbitosphenoid. Laterally the frontal has little exposure on the interorbital wall. The frontal tapers towards the sphenopalatine foramen and widens upwards to the orbital roof.

In the postero-dorsal corner of the interorbital exposure of the frontal, close to the junction with the orbitosphenoid, there is a deep, rounded depression situated above the sphenopalatine foramen. This depression is clearly visible in the ventral view of the skull.

In the posterior wall of the depression there is a distinct, small foramen, preserved only on the right side of the skull, which is obscured in ventral view and visible only in oblique view. It is called the orbitonasal foramen (JOLLIE, 1962).

The orbitosphenoid has a very large exposure in the orbit, occupying most of the interorbital wall. The orbitosphenoid is fan-shaped and has a junction with the palatine below, a well preserved junction with the frontal above and anteriorly, and a junction with the parietal above and posteriorly. In the central part of the orbit, exposed in lateral view, there is a large, rounded recess which is formed mostly by the orbitosphenoid, but a small ventral crescent is presumably formed by the palatine. This recess is deep, particulary posteroventrally. In the anterior margin of this recess within the orbitosphenoid, there is a small foramen which might be the ethmoid foramen. The anterior margin of the recess is delimited by a groove extending from the ethmoid foramen downwards to meet the horizontal groove, which extends from the sphenopalatine foramen posteriorly. In the central part of the recess (lying within the orbitosphenoid), the interorbital wall is slightly convex again. In this area the orbitosphenoid is thin and in the posterior part of the recess the bone is missing on both sides of the skull. It seems very probable that this part of the interorbital wall was membraneous in life. The shape of the unossified zone (orbital fissure) is reconstructed tentatively in Text-fig. 3. No definite foramina are recognizable in this region and it is presumed that through the large orbital fissure passed the following nerves: II, III, IV,  $V_{1-2}$  and VI.

The recognition of the limits of the alisphenoid in the studied skull is also to some extent tentative, as the bone is cracked in this region and 1 cannot be sure whether I am dealing with sutures or with cracks on the bone surface. The alisphenoid, as tentatively recognized here, is reduced to a small, ventral element which does not contribute to the lateral wall of the braincase. In lateral view the alisphenoid is inserted between the ectopterygoid and the anterior lamina of the petrosal. Anterodorsally, the alisphenoid reaches the recess described above in the orbitosphenoid. The ventral margin of the alisphenoid is slightly thickened and forms a "wing" which protrudes somewhat ventrally over the basicranial region. In ventral view, this wing is crescent-shaped and surrounds the foramina for  $V_3$  anterolaterally.

Speaking about the anterior lamina of the petrosal in the multituberculates I should make it clear, that this term, introduced by WATSON (1916) for the monotremes (processus anterior periotici) and accepted by K. A. KERMACK (1963) for the triconodonts, is not so applicable to the multituberculates. The element in the multituberculates that is homologous to the anterior lamina of the triconodonts and the monotremes, consists (due to the broadening of the skull) of two parts which are arranged at right angles to each other. Neither of the parts lie anterior to the cochlea. As, however, the term anterior lamina of the petrosal has been widely used in the relevant literature, I accept it for the multituberculates. One of the components of the anterior lamina in the multituberculates is the ventral part, which lies in the basicranial region, lateral to the lateral flange and antero-lateral to the cochlea. In ventral view, only this part of the anterior lamina is visible. The ventral part of the anterior lamina is pierced by the foramina for  $V_3$ , though it cannot be excluded that the two anterior foramina in *Kamptobaatar* lay in the line of fusion with the alisphenoid. The ventral part of the anterior lamina may be preserved in detached petrosals and is preserved in the petrosal of *Ptilodus*, figured by SIMPSON (1937, Fig. 8). K. A. KERMACK (1963, 1967) and HOPSON & CROMPTON (1969), when speaking about the anterior lamina of the petrosal in the multituberculates, refer only to this ventral part.



Fig. 3

Kamptobaatar kuczynskii KIELAN-JAWOROWSKA, reconstruction of the skull in lateral view. Abbreviations - see p. 6.

The second component of the anterior lamina is the ascending part, which forms in the multituberculates most of the lateral wall of the braincase and lies laterodorsal to the cochlea. This structure has not been described in the multituberculates so far and is found for the first time in *Kamptobaatar*. The ascending part of the anterior lamina is not visible in ventral view, but is well exposed in lateral view. It is difficult to imagine its preservation in the detached petrosals, as it is a fragile lamina, arranged at a right angle to the main body of the petrosal and which may easily be broken off.

The ascending part of the anterior lamina in *Kamptobaatar* is irregular in shape. Of all its junctions only that with parietal (a long, horizontal contact) may be traced with certainty on both sides of the skull. The suture with the squamosal appears to be directed obliquely and the posterodorsal corner of the ascending part is elongated into a narrow process. Posteriorly, the ascending part of the anterior lamina bears a ridge which is directed obliquely, tapers ventrally and runs subparallel to the junction with the squamosal. In the anterior part of the lamina there is another, less distinct ridge, parallel to the posterior margin of the orbitospenoid. Cranial nerve  $V_3$  left the braincase by way of five foramina, which lie in the ventral part of the anterior lamina of the petrosal. These foramina are exposed mostly on the ventral side of the skull.

Only the most lateral foramen is seen in lateral view. This region is described in detail in the next section. The ectopterygoid has little exposure in lateral view. It lies between the maxilla and the alisphenoid. It is very difficult to state the extent of the perpendicular part of the palatine in the interorbital wall. The suture between the ectopterygoid and the palatine is not recognizable. It seems probable that the triangular bone which tapers at the sphenopalatine foramen and is inserted between the maxilla and the orbitosphenoid, is the perpendicular part of the palatine. In lateral view the squamosal is very narrow, tapers upwards and is inserted as a narrow process between the parietal and occipital. The junction of the squamosal with the tabular is not known. The zygomatic process of the squamosal is broken off at the base on both sides, and both the glenoid cavity and the postglenoid process are not preserved.

Basicranium and ear. Though the state of preservation of the basicranium in Z. Pal. No. MgM-I/33 is very good, the small size of the specimen and the lack of comparative material do not permit identification of all the features in this region with any certainty. In ventral view, the basicranial region (as a whole) is wider than it is long. In front of the alisphenoid there is an ectopterygoid, which consists of a rectangular posterior part and a triangular, anterior process, which is inserted between the palatine and the maxilla. The ectopterygoid tapers at the palatonasal foramen. From this foramen a furrow extends posteriorly a short distance along the ectopterygoid. On the rectangular part of the ectopterygoid, lateral to the choanal region, there is a shallow fossa which is possibly for the median pterygoid muscle. The lateral margins of the ectopterygoids are slightly incurved. To the rear of the fossa for the pterygoid muscle lies the wing of the alisphenoid, which has been described above. In ventral view, the basioccipital is extensive, roughly triangular and narrows anteriorly. Its lateral sutures with the petrosal are filled with calcite and are clearly visible. The basioccipital-basisphenoid suture is not entirely clear; it seems that the suture is placed immediately behind two minute foramina, identified as the internal carotid foramina, in the basisphenoid. In front of the internal carotid foramina a large part of the basisphenoid is visible between the thickened, posterior parts of the pterygoids (hamulus). Lateral to the hamulus there is a comparatively large opening at the anterolateral corner of the promontorium, recognized here tentatively as a remnant of the anterior part of the cavum epiptericum. In the basioccipital, in front of the condyles, there are several small foramina. The condyles are not very prominent and are moderately convex. A very large and deep fossa, placed obliquely and parallel to the long axis of the condyle, separates the condyle from the basal part of the promontorium. In the middle of the floor of this fossa there is a distinct, rather small jugular foramen. The hypoglossal foramen which is lacking on the ventral wall of exoccipital, may be confluent with the jugular foramen, as it is in the monotremes. On the outer wall of fossa, which also forms the wall of the base of the promontorium, there is a comparatively small fenestra cochleae.

The promontorium has a narrow, posterolateral basal part, inserted between two fossae: the fossa described above for the jugular foramen and the much shallower recess of the tympanic cavity. The fenestra vestibuli lies at the base of the promontorium and faces anterolaterally. The fenestra cochleae is situated close to the fenestra vestibuli, is separated from it by a narrow tongue of the promontorium and faces the opposite direction to that of the fenestra vestibuli. The recess of the tympanic cavity extends laterally from the fenestra vestibuli and is here comparatively wide and deep but becomes shallower laterally, as it passes into the external auditory meatus. It is impossible to determine the position of the tympanum. The recess of the tympanic cavity and the external auditory meatus are delimited posteriorly by the paroccipital process, the tip of which is placed just lateral to the base of the promontorium. The posterior margin of the base of the promontorium and the fossa for the jugular foramen abut against the inner



Fig. 4 Kamptobaatar kuczynskii KIELAN-JAWOROWSKA, reconstruction of the skull in ventral view. Abbreviations — see p. 6.

ramus of the paroccipital process. The anterior wall of the recess of the tympanic cavity is formed by the posterior part of the lateral flange, which here forms a vertically directed edge. This edge separates the recess of the tympanic cavity from the ventral part of the anterior lamina. On the right side of the skull, which is better preserved, there is a triangular process on this part of the lateral flange, below which there is a distinct foramen for the canalis prooticus (postglenoid foramen — SIMPSON, 1937). Anterolaterally to this foramen there is another small foramen, situated in front of the external auditory meatus, which is the supraglenoid foramen of SIMPSON, 1937 (see p. 29).

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Anteromedially to the fenestra vestibuli there is a recess that delimits the promontorium anterolaterally. The outer wall of this recess is formed by the anterior part of lateral flange, which is here directed anteromedially. In this recess there is a foramen, which must be the facial foramen. In the small anterior wall of this recess there is a small foramen, through which might possibly pass a branch of the facial nerve. In front of the recess, along the anterolateral margin of the promontorium, there is another small foramen, the hiatus canalis Fallopii. In the anteromedial prolongation of this foramen, there is the comparatively large foramen described above as the cavum epiptericum.

On the ventral part of the anterior lamina of the petrosal, anterolateral to the lateral flange there is a shallow recess. In front of this recess there are five foramina for  $V_3$ . Four of these foramina are well seen in ventral view, but the fifth, which is less definite, faces more laterally than ventrally. The most internal foramen (see Text-fig. 4) is the largest of all the foramina. This foramen probably corresponds to the foramen ovale inferius in *Ptilodus*, and the four remaining foramina correspond to the foramen masticatorium (SIMPSON, 1937). The most posterior foramen is the smallest and faces both ventrally and laterally. On the right side, the foramina for  $V_3$  are somewhat differently arranged. In front of the recess, there is one, very large, oval foramen, corresponding to the foramen ovale inferius of the right side. It is, however, nearly twice as long as its counterpart. The remaining foramina are poorly preserved as the bone is broken off here. The suture between the alisphenoid and the ectopterygoid (in ventral view) is directed transversely. The suture between the alisphenoid and the petrosal is not well defined. The suture probably extends from the remnant cavum epiptericum towards the foramina for  $V_3$ .

Due to the difficulty in recognizing the suture between the alisphenoid and the petrosal it cannot be stated with certainty whether all the foramina for  $V_3$  pierce the ventral part of the anterior lamina of the petrosal or whether two of these foramina (more anterior) lay in the line of junction between the alisphenoid and the petrosal. If the tentative reconstruction of the suture between the petrosal and the alisphenoid, as figured in Text-fig. 4, is correct, the inner wall of the remnant cavum epiptericum is formed by the pterygoid and the petrosal, while the outer wall is formed by the alisphenoid.

Lower jaw. In Z. Pal. No. MgM-I/38 the right and left lower rami are preserved, while in Z. Pal. No. MgM-I/39 only the left lower ramus and two teeth from the right side are preserved. This left jaw MgM-1/39 is incomplete and has the posterior part missing, while in MgM-I/38 an impression of the posterior part of the right lower jaw is preserved. The lower margin of the jaws lies at an angle of about 35° with regard the plane of the teeth. The coronoid crest starts opposite the anterior root of  $M_1$ . In the anteroventral prolongation of the coronoid crest (beneath  $P_4$ ) there is a concavity in the wall of the mandible which may be seen in occlusal view. Beneath  $P_3$  there is a distinct swelling on the buccal side of the mandible and this forms the anterior apex of the masseteric fossa. The masseteric crest extends from this swelling posteriorly, nearly parallel to the plane of the teeth and reaches the lower margin of the jaw beneath the posterior root of  $M_2$ . The pterygoid fossa is large and deep and its anterior margin is situated opposite the posterior margin of  $M_2$  (or just to the rear of the posterior margin of  $M_2$ ). Entrance to the dental canal is afforded by a single, large foramen in the middle of the anterior wall of the fossa. The ramus separating the pterygoid and the masserteric fossae projects lingually to form the wide, horizontal floor of the pterygoid fossa. One mental foramen is discernible on the left mandible of MgM-I/39 at the level of the middle of the diastema. The surface of the symphysis is shaped like a comma.

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Dentition. Dental formula:  $\frac{2}{1} \frac{0}{0} \frac{2}{2} \cdot I^1$  is single cusped, comparatively short and sharply pointed. The enamel is very thick on the anterior surface of the tooth and sharply delimited by thickness and colour from the posterior surface, where the enamel is very thin or is lacking. The wear surface is as in *Taeniolabis*. I<sup>2</sup> is a small, peg-like tooth, directed somewhat obliquely towards the middle.



Fig. 5 Kamptobaatar kuczynskii KIELAN-JAWOROWSKA, reconstruction of the lower jaw in labial view.

 $P^1$ ,  $P^2$  and  $P^3$  are double rooted;  $P^1$  and  $P^2$  have 3 cusps (one buccal and two lingual) and  $P^3$  has 4 cups arranged symmetrically. In all the skulls  $P^1$  is the largest of the first three premolars and  $P^3$  the smallest. In Z. Pal. No. MgM-I/33, which has the teeth best preserved,  $P^1$  is twice as high and twice as long as  $P^3$ . In all the specimens the anterior root of  $P^1$  is placed strongly obliquely mesially. The cusp formula for  $P^4$  is 3 : 5 or 6. It is a comparatively slender tooth and kidney-shaped in occlusal view. The row of cusps is arranged obliquely across the tooth extending from the anterolingual to posterobuccal corner. In this row the cusps increase in size posteriorly and the penultimate cusp is larger and higher than the ultimate. Adjacent the two posterior, medial cusps there is, on the lingual side of the tooth, a smooth, rather triangular surface which slopes towards the palate.

The cusp formula for  $M^1$  is 5 : 5: ridge. In the outer row the first cusp is small and the next three cusps of equal size. The penultimate cusp has a long posterior ridge, on which the incipient but distinct fifth cusp is situated. The cusps of the medial row are symmetrically arranged and increase in height posteriorly, the first being almost flat. The inner ridge extends along the whole length of the tooth, forming a crescent-shaped convexity in the posterior half of the tooth and extending subparallel to the middle row of the cusps in the anterior half. In Z. Pal. No. MgM-I/33 the ridge appears smooth, but in MgM-I/38 it bears 3 (or 4) indistinct incipient cusps. The cusp formula for  $M^2$  is 1 : 2 : 3. The single cusp of the outer row is small, crescent-shaped, placed in the anterolateral corner of the tooth and obliquely faces the first cusp of the medial row. The first cusp of the medial row bears a ridge which extends anteromedially towards the anterior margin of the tooth. The second cusp is somewhat smaller. The three cusps of the inner row are subcrescentic and decrease in size posteriorly.

Both  $I_1$  are preserved in Z. Pal. No. MgM-I/39.  $I_1$  is a moderately curved tooth with a flat, inner wall. The enamel is thick on the ventrolateral surface, probably absent or very thin on the dorsomedial surface and with no sharp boundary between the two surfaces.  $P_3$  is a simple, peg-like tooth.  $P_4$  is arcuate with its highest point placed on a line with the lower molars. There are 6 (or 7) serrations, all with ridges. A small basal cuspule is present on the posterior part of the labial wall of the tooth. Cusp formula for  $M_1$  is 4 : 3; for  $M_2$  it is 3 : 2. Discussion — see p. 25.

## Sloanbaatar mirabilis KIELAN-JAWOROWSKA, 1970

(Pl. I, Fig. 1; Pl. V; Text-figs. 6-10, 11b, 12b)

1970a. Sloanbaatar mirabilis n. sp.; Z. KIELAN-JAWOROWSKA, New Upper Cretaceous..., p. 42, Pls. 10, 12, 13; Text-fig. 1

**Material.** — Only the type specimen (Z. Pal. No. MgM-I/20) — complete skull associated with lower jaws and part of the postcranial skeleton is known.

For measurements and additional figures — see KIELAN-JAWOROWSKA, 1970a.

The skull as a whole. The snout anteriorly is comparatively narrow, roughly rectangular and bluntly pointed. The zygomatic arches are strongly expanded laterally. The greatest width is across the posterior part of the zygomatic arches. The postorbital process is prominent and situated far posteriorly. The orbit is very large and the interorbital constriction is conspicuous. In lateral view, the rostrum is strongly tapered anteriorly, the cranial roof is rounded posteriorly, the occipital surface is situated very low and placed obliquely with regard to the plane of the teeth. In anterior view, the cranial roof is arched and the infraorbital foramina face anteriorly.

The snout and zygoma. The nasals are extensive and strongly expanded posteriorly. The fronto-nasal suture is convex posteriorly and sigmoid near the midline of the skull. Both frontals taper anteriorly in the middle to a rounded end which is inserted between the nasals. In the transverse plane the nasals are almost flat. There are very indistinct "vascular" foramina, probably asymmetrically arranged: two are visible in the left nasal and one in the right. The premaxilla is directed vertically and forms the lateral wall of the snout. The premaxillo-maxillary suture is indistinct; in the lateral view it is directed almost vertically in the ventral part and deflected posteriorly in the dorsal part. The maxilla extends over two-thirds of the side of the snout. Anteriorly the facial part of the maxilla is vertical, while posteriorly it becomes flattened at the zygomatic arch. The infraorbital foramen is situated above the P<sup>2</sup>-P<sup>3</sup> embrasure and is clearly seen in ventral, lateral, and anterior views, but entirely obscured in dorsal view. A furrow, with a prominent dorsal edge, extends from the infraorbital foramen anteriorly to fade out opposite P<sup>1</sup>. The ventral wall of the maxilla, buccal to the row of the premolars, is very small.

The suture between the maxilla and squamosal on the zygomatic arch is not discernible. The anterior edge of the zygomatic arch, formed by the maxilla, originates opposite  $P^2$ , while the posterior edge originates opposite the most anterior part of  $P^4$ . The anterior part of the zygomatic arch is wider vertically than transversely. The zygomatic ridge is very faint. In ventral view, it originates opposite the  $P^3$ - $P^4$  embrasure to form an arch convex anteriorly, and then continues posteriorly to form the lateral edge of the zygomatic arch. In lateral view, the ridge arches upwards and then extends for a long distance along the dorsal edge of the zygomatic arch. Thus the crescent-shaped area delimited by the ridge is strongly elongated. In the posterior part of the arch (which is much deeper than the anterior part), the ridge passes obliquely onto the lateral wall of the arch, dividing it into two areas. The anterior area, which is smaller, is



Fig. 6 Sloanbaatar mirabilis KIELAN-JAWOROWSKA, reconstruction of the skull in dorsal view. Abbreviations — see p. 6.

designated by the notation A, the posterior by the notation B. The maximal height of the zygomatic arch, in lateral view, is opposite the postorbital process. In ventral view, the zygomatic arch is slender anteriorly and becomes very wide in the posterior part. Most of the posterior part of the arch is occupied by a very large, almost flat, glenoid fossa which is roughly semicircular, and has a straight margin directed anterolaterally. Laterally, the fossa contacts the area A, which is placed obliquely with regard to the fossa, but is visible in ventral view. Posteromedially, the glenoid fossa almost contacts the lateral (lowermost) corner of the occipital plate. In dorsal view, the anterior part of the zygomatic arch is slender. In the posterior, wider part, one can recognize two surfaces, the posterior one is surface B, which in this view is crescent-shaped and directed obliquely posterolaterally. Anteromedially to surface B, there is a much larger, somewhat concave surface, which medially bends upwards to form the lateral wall of the squamosal. The edge which separates surface B from the anterior surface passes medially into the lambdoidal crest.

Palate. The palatal processes of the premaxillae form concave surfaces and occupy more than one-third of the palatal length. The margin between the ventral and the lateral walls of the premaxilla is thickened and forms a sharp ridge. On the lingual side of the alveoli for  $I_2$  and somewhat more anteriorly, there are rounded palatine fissures, which do not reach the median suture. As seen in ventral view, the premaxillo-maxillary suture extends a short distance posteriorly, subparallel to the outer border of the snout and then arches posteriorly around  $I^2$ . The suture almost reaches the palatine fissure and then extends as a short transverse line to reach its counterpart of the opposite side.

In the anterior part of the palate the two palatine processes of the maxillae meet to form a surface which is strongly concave. Posteriorly, a longitudinal ridge extends opposite M<sup>1</sup> and M<sup>2</sup> and along the median suture. Lateral to this ridge the palatine processes of maxillae are concave. There are two palatal vacuities. The anterior one is very narrow and extends from opposite  $P^2$  to opposite the middle of  $P^4$ . The posterior vacuity is much wider, oval, and extends from opposite the ultimate cusp of P4, to opposite the penultimate cusp of M1. The course of the maxillo-palatine suture is hardly discernible. It forms an arch to the rear of  $M^2$  and then turns anteriorly to run subparallel to M<sup>2</sup>. The position of the transverse palatine suture, however, cannot be established. The posterior rim of the horizontal part of the palatine bone is slightly thickened, but the true postpalatine torus is not developed. The middle ridge on the palatine bones is prolonged into a medial process, which is either very short or is broken off. On both sides of the process, the rim of the choanae is incurved anteriorly. It is impossible to establish which bones form the bottom or the lateral walls of the choanae, because the area is so strongly cracked. The morphology of the vomer and the pterygoids can not be determined. On the posterior part of the right, lateral rim of the choanae there is a ridge. On the left side this ridge is broken off.

*Cranial roof.* The frontals form the superior border of the anterior part of the orbit. Near the border of the orbit, to the rear of the maximal constriction of the skull, the frontoparietal suture forms a small arc, which is convex anteriorly and then extends posteriorly. Opposite the postorbital process the suture curves medially and extends transversely to meet its counterpart from the other side. The parietals are extensive and form the whole of the cranial roof posteriorly. The postorbital processes are very prominent. The parietal crests extend from the posterior border of the postorbital processes posteromedially and meet just in front of the lambdoidal crests. The parietal crests are very faint anteriorly, but become more prominent posteriorly. There is no sagittal crest. It is difficult to determine the shape of the parietal in lateral view, but it is very probable that the parietal is similar to that in *Kamptobaatar*. The lambdoidal crests medially are comparatively faint and slightly convex anteriorly. Laterally they curve to become convex posteriorly, much more prominent and crescent-shaped. It is impossible to determine the course of the parieto-occipital suture, but it probably extended along the lambdoidal crest. It is also probable that, as in *Kamptobaatar*, the squamosal is deeply inserted between the parietal and occipital.

Occiput. The occipital plate is situated comparatively low and lies obliquely with regard to the plane of the palate. The occipital plate is about 1.5 times wider than high. The border of the foramen magnum is preserved only in the upper part of the right side of the skull and the occipital condyles are not preserved. The supraoccipital is extensive. The suture between the supraoccipital and exoccipital is not preserved. Lateral to the foramen magnum, there is a longitudinal depression on the exoccipital, bordered laterally by a vertical ridge, which is slightly concave medially. The suture between the supraoccipital and tabular is probably as in *Kamptobaatar* (see Text-figs. 2 and 7). The sutures that separate the tabular from the squamosal and



Sloanbaatar mirabilis KIELAN-JAWOROWSKA, reconstruction of the skull in occipital view. The lower part of the snout is not shown in this figure. Abbreviations — see p. 6.

from the paroccipital process are not discernible. The post-temporal fossa is very large, roughly oval and tapers slightly upwards. The paroccipital process is triangular, longer and more prominent than in *Kamptobaatar*. Atransverse furrow extends along the upper part of the paroccipital process from the tabular. The suture along the ventral edge of the paroccipital process is not discernible.

Orbit and temporal fossa. The orbit is very large and widely open posteriorly. Its anterior and lower boundaries are formed by the maxilla; the upper boundary is formed by the frontal and the parietal. The orbit has no floor, but in the anterior part is roofed by the maxilla and frontal, while posteriorly there is a very narrow roof formed by the parietal. The rim of bones which form the roof of the orbit is thickened. The maxillary foramen (preserved on the right side of the skull) lies in the lower part of the most anterior corner of the orbit. The sphenopalatine foramen is preserved on the left side and lies at the level of the middle of  $M^1$ . A horizontal groove, shallowing posteriorly, runs from the sphenopalatine foramen. It is impossible to determine the extent of any particular bone in the interorbital wall. It seems probable that, as in Kamptobaatar, the orbitosphenoid is very large and fan-shaped, and that the anterior lamina of the petrosal occupies most of the temporal fossa. In the roof of the orbit there are three depressions to be seen in the ventral view of the skull (Text-fig. 9). The anterior one, the largest, lies above the sphenopalatine foramen and opposite M1. The second depression, separated from the first by a transverse ridge, is smaller and lies opposite M<sup>2</sup>. The most distinct is the third depression which is, however, very small and lies below the anterior part of the postorbital process. In the central part of the orbit, exposed in lateral view, there is a large, rounded recess (Text-fig. 8). On the anterior margin of this recess there is an ethmoid foramen. A deep

groove, slightly convex anteriorly, extends from the ethmoid foramen downwards. The recess is delimited ventrally by a horizontal bar. In the central part of the recess the wall of the orbit is slightly convex again. On both sides of the skull the bone is missing from most of the recess and is only partly preserved on the left side. The preserved part of bone forms a "tongue", which extends from the anterior margin of the recess posteriorly, in a way similar to the orbit in *Kamptobaatar*. The remaining foramina in the orbit are not preserved.



Fig. 8 Sloanbaatar mirabilis KIELAN-JAWOROWSKA, reconstruction of the skull in lateral view. Abbreviations — see p. 6.

In the lower part of the temporal fossa there is a ridge (probably on the anterior lamina of the petrosal), which extends parallel to the lambdoidal crest and tapers ventrally.

Basicranium and ear. The basioccipital is damaged. Along the medial border of both petrosals there are cracks filled with calcite, which might correspond to the sutures between the petrosals and basioccipital. The preserved part of the basioccipital lies deeper than the petrosals. No sutures are recognizable in this region. The promontorium has a narrow, posterolateral basal part. This part is bordered on the medial side by the jugular fossa and anterolaterally by the recess of the tympanic cavity. As the posterior part of the basicranium is missing, only the lateral walls of the jugular fossae are preserved on both sides. The fenestra cochleae lies at the base of the promontorium and faces posteromedially (into the jugular fossa). The fenestra vestibuli lies close to the fenestra cochleae, is separated from it by a narrow tongue of the promontorium base and faces in the opposite direction to that of the fenestra cochleae. The recess of the tympanic cavity becomes shallower laterally and passes into the external auditory meatus. Anteriorly, the recess of the tympanic cavity is bordered by the posterior part of the lateral flange, which forms a narrow, transversely directed ridge, and which overhangs the recess somewhat. In the lower part of the wall of this ridge, there is a poorly preserved foramen for the canalis prooticus (postglenoid foramen of Ptilodus; SIMPSON, 1937). Anterolaterally to this foramen, there is another small, poorly recognized foramen, which corresponds



Fig. 9

Sloanbaatar mirabilis KIELAN-JAWOROWSKA, reconstruction of the skull in ventral view. Abbreviations - see p. 6.

to the supraglenoid foramen in *Ptilodus* (SIMPSON, 1937). Anteromedially to the fenestra vestibuli, there is a narrow groove which borders the promontorium anteromedially. The lateral wall of this groove is formed by the anterior part of the lateral flange which, however, is not very prominent. In the groove there is a poorly preserved foramen, which I recognize as the facial foramen. Anteromedially to this groove, there is a small foramen, which might be an hiatus canalis Fallopii. A short furrow extends from this foramen posterolaterally. Anteromedially of the hiatus canalis Fallopii there is a third foramen, which lies more or less in the same place as the cavum epiptericum in *Kamptobaatar*. In *Sloanbaatar* this foramen is much smaller than in *Kamptobaatar*. As this area in *Sloanbaatar* is poorly preserved, it is very difficult to venture

an opinion as to whether the foramina in question, in *Kamptobaatar* and *Sloanbaatar*, are homologous or not.

In the region of the foramina for  $V_3$  there are two foramina and these may be compared with the foramen ovale (pseudoovale) inferius and the foramen masticatorium in *Ptilodus* as recognized by SIMPSON (1937). The foramen pseudoovale inferius is very large and faces ventrally. It is surrounded anterolaterally by the prominent, crescent-shaped wing of bone, which protrudes ventrally over the basicranial region. This wing of bone is recognized tentatively, by comparison with *Kamptobaatar*, as an alisphenoid. The foramen masticatorium is much smaller, lies on the edge of the petrosal and faces more laterally than ventrally. The recess on the ventral part of anterior lamina, which is easily recognizable in *Kamptobaatar*, is much less distinct here. The area which would correspond to it and which lies to the rear of the foramen pseudoovale inferius, is very small, almost flat and not bordered by distinct ridges on either side.



Fig. 10 Sloanbaatar mirabilis KIELAN-JAWOROWSKA, reconstruction of the lower jaw in labial view.

Lower jaw. The lower jaw is slender. The coronoid crest starts opposite the middle of  $M_1$ . The coronoid process is small, triangular and strongly deflected buccally. In the right lower jaw the coronoid process is almost complete. In the anteroventral prolongation of the coronoid crest (beneath  $P_4$ ) there is a concavity. On the buccal wall, beneath  $P_3$ , there is a swelling. The masseteric crest is very prominent. It starts opposite the anterior part of  $M_1$  and extends parallel to the plane of the teeth and reaches the lower margin of the jaw beneath the posterior edge of the coronoid process. The dorsal edge of the stem of the condyle is strongly incurved. The condyle is, in dorsal view, large and roughly circular. One mental foramen is discernible on the right jaw, in the anterior part of the diastema and opposite the lower part of the incisor. The pterygoid fossa is large and deep and its anterior margin lies opposite the posterior margin of  $M_2$ . There is a single, large opening (the entrance to the dental canal) in the upper part of the anterior wall of the fossa. The ramus separating the pterygoid and the masseteric fossae projects lingually to form the wide, horizontal floor of the pterygoid fossa.

Dentition. Dental formula:  $\frac{2042}{1022}$ . The upper tooth row is slightly curved outwards in an horizontal plane and is concave ventrally in a vertical plane. I<sup>1</sup> is single cusped, comparati-

vely straight and sharply pointed. Only the alveoli of  $I^2$  are preserved. P<sup>1</sup>, P<sup>2</sup> and P<sup>3</sup> are double rooted; P<sup>1</sup> and P<sup>2</sup> have three cusps (one external and two internal); P<sup>3</sup> has 4 cusps. P<sup>1</sup> is the highest of the first three premolars and P<sup>3</sup> is the shortest. In occlusal view, P<sup>3</sup> is elongated longitudinally and is rectangular. The cusp formula of P<sup>4</sup> is probably 2 : 4 or 5. As P<sup>4</sup> is poorly preserved on both sides, it is difficult to give a definite number of cusps for the inner row. P<sup>4</sup> is slender and becomes narrower posteriorly. The cusp formula of M<sup>1</sup> is 4 : 4: ridge. However, one cannot be certain if the number of cusps in the inner row was not 5. In both rows the cusps increase in size posteriorly. The inner ridge is not very prominent and extends along the two posterior cusps of the inner row. The cusp formula of M<sup>2</sup> is 1 : 2 : 3.

 $l_1$  is a curved tooth and has flat, inner wall. The enamel is thick and yellow on the ventrolateral surface and is not, however, delimited by a sharp boundary. The enamel is very thin and white (or absent) on the dorsomedial surface.  $P_3$  is not preserved but alveolus is present.  $P_4$  is arcuate and with its highest point placed on the line of lower molars. There are 9 serrations on  $P_4$ , all of which are provided with ridges. A very faint, basal swelling is present on the posterior part of the labial wall of the tooth. The cusp formula of  $M_1$  is 4:3.  $M_2$  is very short, rectangular in occlusal view and with a cusp formula of 2:2. The 4 cusps in  $M_2$  are arranged symmetrically.

## DISCUSSION

The systematic position of the genera *Kamptobaatar* and *Sloanbaatar* has been discussed elsewhere (KIELAN-JAWOROWSKA, 1970*a*). In the present paper, which is a study of the skull structure of these genera, the discussion that follows concentrates on the interpretation of the structure of the multituberculate skull and on comparisons of the skull in the Multituberculate with those in the Docodonta, the Monotremata and the Triconodonta.

### INTERPRETATION OF THE SKULL STRUCTURE IN THE MULTITUBERCULATA

The nasal bones of *Kamptobaatar* and *Sloanbaatar* bear asymmetrically arranged foramina referred to as vascular foramina by SIMPSON (1937) and others. They occur in all the Bayn Dzak multituberculates and are probably characteristic of the Multituberculata as a whole. Such foramina are quite unusual for mammals, but occur in various theriodonts (ATTRIDGE, 1956; BRINK, 1957; VAN VALEN, 1960; ESTES, 1961) and lizards (WATSON, 1931; OELRICH, 1956). OELRICH (1956) has shown that similar foramina, perforate the nasals in recent lizards and transmit the cutaneous branches of the lateral ethmoid nerve. These serve highly vascularized and richly innervated skin thickenings which surrounded the cartilaginous, nasal capsule. It is highly probable that the "vascular" foramina in the multituberculates transmitted the lateral ethmoid nerve.

In the palatal processes of the premaxillae there are, in *Kamptobaatar* and *Sloanbaatar*, large palatine fissures, which are characteristic of all the Bayn Dzak multituberculates. These are the fissures for Jacobson's organ. The incisive foramen is absent. In *Sloanbaatar*, the palatal vacuities are present, but this region is poorly preserved. In *Kamptobaatar*, as probably in all the Taeniolabididae, the palatal vacuities are lacking. In *Ptilodus*, where the palatal vacuities are present, there are no palatine foramina, and as shown by SIMPSON(1937), the palatal canal extends from the choanal rim to the posteroexternal rim of the palatal vacuity. In *Kamptobaatar*, on the other hand, there are distinct palatine foramina majora and minora, but the course

of the palatine canal is obscure. In the pterygopalatine fossa there is no opening which might be the dorsal orifice of the palatine canal; it is possible that this orifice was confluent with the sphenopalatine foramen (as is e.g. the case in *Tenrec*). Also it is not clear what the fissurelike foramen which is placed on the side of the postpalatine torus transmitted. The presence of such a foramen is unusual for mammals. Among multituberculates this foramen has not been found in *Ptilodus* and, as far as I know, in any other Tertiary multituberculate, but it occurs in all the Bayn Dzak genera in which this region is preserved. It is improbable that in *Kamptobaatar* (as in *Ptilodus*) the palatine canal opened into the choanae, as they are divided here by the pterygoid into two channels, and the outer channel which ends blindly, served probably as a fossa for muscle attachment. No foramen is visible in the walls of the outer channel.

A foramen, lying in the posterior corner of the palatine bone, either behind the last molar or lateral to it, is characteristic of various therapsids. KÜHNE (1956, Text-fig. 18, pp. 56—57) found such foramen in *Oligokyphus* and recognized it as an opening of a posterior branch of the suborbital canal. TATARINOV (1963, 1964) found a similar foramen in a therocephalian *Moschowhaitsia*, and later (1968), in a cynodont *Dvinia prima* AMALITZKY. He identified this foramen as the posterior, ventral foramen of the suborbital canal. Recently, TATARINOV (1969 and MS) changed his opinion and now regards this foramen as one for the palatonasal nerve, which in theriodonts usually lies at the junction of the maxilla, the palatine, the ectopterygoid and the jugal. Like TATARINOV, I call the fissure-like foramen which lies at the junction of the ectopterygoid, the palatine and the maxilla — the palatonasal foramen.

As has been stated above, the pterygoids in *Kamptobaatar* are placed in the middle of choanal channels, a position quite unusual for the therian mammals and unknown in the monotremes. Between the pterygoids there is a longitudinal, single bone, the vomer, which forms the middle ridge between the ridges of the pterygoid bones, giving to this region a triradiate pattern. This triradiate structure of the choanal region is so far known only in *Kamptobaatar* among the multituberculates. It must be, however, stressed that this region is extremely poorly known and is rarely preserved in the multituberculates, and the prominent ridges of the pterygoids are not easily preserved in normal conditions of fossilization. Thus, the triradiate structure of the choanal region may also have been characteristic of other multituberculates.

The thickened, posterior end of the pterygoid has been described here as the hamulus. It cannot be regarded, however, as entirely homologous with the hamulus of modern mammals, where the anterior end of the ventral extremity is turned slightly outwards and projects downwards to form the hamulus pterygoideus. In Kamptobaatar, it is the posterior end of the ventral extremity of this bone that is developed as a hamulus. There is, however, little doubt that this thickened, posterior margin of the pterygoid formed a pulley around which the tendon of the tensor palatine muscule was reflected. It seems also obvious that of the two choanal channels on each side, only the inner one served as an air channel, while the lateral one, which ends blindly, served as an area for muscle attachment and was separated from the air channel by a sheet of the pterygoid bone. I do not think that the lateral, choanal channel formed an area of attachment for the medial pterygoid muscle, as lateral to the choanae there is a shallow fossa (see Pl. J, Fig. 2b) which has the shape and the position of the fossa for the attachment of the medial pterygoid muscle in mammals and cynodonts. The lateral choanal channel is here regarded entirely tentatively as an equivalent of a scaphoid fossa for the attachment of the tensor veli palatini muscle. The structure of the choanal region in Kamptobaatar corresponds more or less to the hypothetical stage in the evolution of a mammalian palate, figured by PARRINGTON & WESTOLL (1940, Fig. 16D).

The interpretation of the skull foramina in the orbit and temporal fossa in Kamptobaatar is difficult, because this region is well preserved only in one specimen, Z. Pal. No. MgM-I/33, which is minute and the foramina are somewhat obscure. This difficulty is not helped by the fact that in the multituberculates this region has so far been described only roughly by SIMPSON (1937) for Ptilodus, and even there the interorbital wall was not figured. In Sloanbaatar this region is poorly preserved. There is no doubt at all that the lacrimal bone and the lacrimal foramen are lacking in all the studied Bayn Dzak multituberculate genera. The only multituberculate, in which the lacrimal bone and a lacrimal foramen have been described, is Paulchoffatia deldagoi KÜHNE (KÜHNE, 1961, 1968; HAHN, 1969) from the Kimmeridgian of Portugal, where the lactimal bone is extensive and the lactimal foramen large. Thus it may be presumed that the lack of the nasolacrimal duct in late Cretaceous Bayn Dzak multituberculates is secondary. The nasolacrimal duct is lacking amongst mammals in the Cetacea, the Sirenia, the Pinnipedia and the Hippopotamidae, but curiously enough it is also absent in some land mammals, such as the elephants and the South American peccary — Dicotyles (BOLK et al., 1936, p. 978; GIERSBERG & RIETSCHEL, 1967, p. 110). There is no reason to believe that the late Cretaceous multituberculates from Bayn Dzak were aquatic or semi-aquatic. It seems more reasonable to presume that, with regard to the secretion of tears and their removal, these multituberculates acquired adaptations similar to those in elephants and pecari.

A peculiar feature of the structure of the orbit in *Kamptobaatar* (which is unusually large), is the presence in that part of orbital roof, which is formed by the frontal, of a very large, rounded fossa. In *Sloanbaatar*, there are three fossae in the orbital roof. Similar structures are not known in modern mammals. Most probably the anterior fossa housed an Harderian gland. The minute foramen in the posterior part of this fossa in *Kamptobaatar*, is placed more or less in a similar position to that of a foramen in the interorbital wall in *Ornithorhynchus*, and called by JOLLIE (1962), the orbitonasal foramen. I give the same name to the minute foramen in *Kamptobaatar*. I presume that it may transmit the medial ethmoid nerve.

The interpretation of the structure of the interorbital wall in *Kamptobaatar* is to some extent tentative. The sutures that surround the large orbitosphenoid on both sides of the skull in Z. Pal. No. MgM-I/33 are very distinct, but there are doubts as to whether this area was entirely ossified in the multituberculates. As the missing parts of the orbitosphenoid are roughly of the same shape on both sides of the *Kamptobaatar* skull (see Pl. I) and on the left side of *Sloanbaatar* skull (Pl. V, Fig. 1), it is probable that the bone was lacking here in life and that the part of the sidewall of the braincase, below the interorbital constriction, was membraneous in the multituberculates. I have no doubts as to the position of the sphenopalatine and the ethmoid foramina. In this region in *Ptilodus*, SIMPSON (1937) recognized only one, large, sphenorbital fissure, which according to him, probably transmitted cranial nerves II, III, IV,  $V_{1-2}$  and VI. The optic foramen and the foramen rotundum are little or not differentiated from the sphenopalatine fissure. The interpretation of this region in *Kamptobaatar* given by me is similar to that given by SIMPSON for *Ptilodus*.

I identify the extensive bone, which forms the lower part of the braincase wall in Kamptobaatar — as the ascending part of the anterior lamina of the petrosal. SIMPSON (1937, Fig. 4) tentatively recognized an extensive squamosal in this region in *Ptilodus*, but as the squamosal in Kamptobaatar is differently shaped and very narrow, SIMPSON's interpretation may be doubted. Anteroventrally to the anterior lamina I identify in Kamptobaatar an alisphenoid. In all the Bayn Dzak multituberculate genera the alisphenoid probably forms a very characteristic, crescent-shaped wing, which protrudes somewhat ventrally over the basicranial region and in ventral view, surrounds the region of the foramina for  $V_3$  antero-laterally. The identification of this wing as an alisphenoid is tentative as the suture between the petrosal and alisphenoid is not easily distinguished. Another reason to regard this wing as belonging to alisphenoid is, that it is not preserved on the detached petrosals of *Ptilodus* (figured by SIMPSON, 1937) and on the Bug Creek multituberculates studied by Dr. MACINTYRE. As the alisphenoid wing is present in the Bayn Dzak multituberculate skulls, it is probably characteristic for the other multituberculates. The fact that the wing is never found in isolated petrosals speaks for the wing belonging to the alisphenoid.

The lower part of the lateral wall of the braincase in the therapsids is formed essentially by two bones: the anterior lamina of the petrosal (periotic) and an extensive alisphenoid (epipterygoid). The alisphenoid is usually broad, with a concave, free, anterior margin. In front of the alisphenoid is the unossified zone of the orbital fissure through which the cranial nerves II, III, IV, V<sub>1</sub>, VI and possibly also V<sub>2</sub> left the braincase. SIMPSON (1933) and BROILI & SCHROEDER (1934) have doubts as to whether the cranial nerve V<sub>2</sub> left the braincase through the orbital fissure, or through the foramen between the alisphenoid and the anterior lamina of the petrosal. PARRINGTON (1946) and HOPSON (1964) are of the opinion that the latter foramen transmits both the maxillary and mandibular branches of the trigeminal nerve, while MACINTYRE (1967) believes that it transmits only the mandibular branch.

The lateral wall of the braincase in the studied multituberculates generally resembles that of the therapsid reptiles and differs from them, in having a much more extensive anterior lamina of the petrosal (the alisphenoid being reduced to a comparatively small, ventral element). Moreover, the large orbital fissure, which is membraneous in the theriodonts, is, in the multituberculates, partly ossified. In the lateral wall of the braincase in the multituberculates, there is no opening between the anterior lamina of the petrosal and the alisphenoid, as in the cynodonts. The homologue of a foramen in the cynodonts is, in the multituberculates, divided into several (two or five) foramina, which face ventrally and are situated in the anteriolateral corner of the petrosal, presumably within the ventral part of the anterior lamina of the petrosal.

The interpretation of foramina is to some extent always open to doubt in fossil material. According to recent opinion (except MACINTYRE, 1967), the maxillary and the mandibular branches of the trigeminal nerve emerge from the skull in quite different ways in the advanced therapsids and in the primitive mammals, and this does not appear to me to be very convincing. In the multituberculates, in my opinion, the foramina for  $V_2$  and  $V_3$  are most probably, comparatively widely separated, as is the case in the monotremes.

The five foramina by which  $V_3$  leaves the braincase are only characteristic for Kamptobaatar. Any attempt at giving a detailed reconstruction as to which foramen transmitted a particular branch of the mandibular nerve would be pointless, as there are many possible interpretations. The division of the mandibular nerve into several branches before it leaves the skull appears to be characteristic of the Multituberculata as a whole. The fact that the foramina on the right side of the skull are differently arranged from those on the left side (this does not seem to be due to any damage), shows that there is great, individual variability in this respect within the multituberculates. In Sloanbaatar and in the other Bayn Dzak multituberculate genera in which this region is preserved, there are only two foramina for  $V_3$ , as is the case for *Ptilodus* (SIMPSON, 1937). A similar division of the mandibular nerve has been described in the therapsid *Ischignathus* (BONAPARTE, 1962) and in some rodents (HILL, 1935). In rodents there is great, individual variability in the development of the cranial foramina (BERRY & SEARLE, 1963) as in the multituberculates.

The basic ranium of Kamptobaatar and Sloanbaatar described in the present paper is of the same general pattern as the basic ranium in *Ptilodus*. Kampatobaatar differs from *Ptilodus*,

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in addition to the somewhat different structure of the region of the foramina for  $V_3$ , in that the condylar foramen as identified in Ptilodus by SIMPSON (1937), appears to be absent in Kamptobaatar (it is not preserved in Sloanbaatar). The hiatus canalis Fallopii, named by SIMPSON the dehiscientia canalis facialis, is placed in Kamptobaatar and Sloanbaatar more anteriorly with regard to the foramen for VII than in Ptilodus. The lateral flange is more conspicuous in Kamptobaatar than in Ptilodus and in Sloanbaatar. The two foramina, named by SIMPSON (1937) as the supraglenoid foramen and the postglenoid foramen and regarded by him as the openings of the prootic canal, occur in Kamptobaatar and Sloanbaatar in a similar position. The supraglenoid foramen is recognized here tentatively as an anterior opening of the posttemporal fossa (see below). SIMPSON (1937) has reconstructed the carotid foramen of Ptilodus in the anteromedial prolongation of the hiatus canalis Fallopii. In Kamptobaatar, 1 recognize this prolongation as the anterior end of cavum epiptericum. The cavum epiptericum is placed too far laterally in Kamptobaatar, to transmit the internal carotid artery. Moreover, in the basisphenoid of Kamptobaatar there are two minute foramina, which are identified here tentatively as the internal carotid foramina. Similar minute foramina occur in the basisphenoid of Ptilodus, which SIMPSON called: "probable nutritive foramina". Not having seen the original specimens of *Ptilodus* I cannot venture an opinion as to whether or not the structure described above are homologous in Kamptobaatar and in Ptilodus. It should also be mentioned that the similar, minute foramina in the anterior part of the basisphenoid in Diarthrognathus, have been tentatively recognized by CROMPTON (1958) as the internal carotid foramina. In general, the basicranial region of Ptilodus reminds me more of Sloanbaatar than of Kamptobaatar, but it must be stressed that the differences between the three genera are those of details and that the basic pattern of the basicranial region is the same in all of them.

The occipital plate in the multituberculates (Text — fig. 11) recalls that of Ornithorhynchus (WATSON, 1916) as well as that of the therapsid reptiles, especially the tritylodonts — see Oligokyphus (KÜHNE, 1956), and Likhoelia (GINSBURG, 1961, 1962); Likhoelia is probably congeneric with Tritylodon (HOPSON, 1964). In the tritylodonts the occipitals are not very large and most of the occipital plate is formed by the extensive tabulars, with large post-temporal fossae. Ventrally to the tabular lies a paroccipital process. All these elements are found in the multi-tuberculate skull. In the therapsids the post-temporal fossa opens anteriorly at the anterior end of the post-temporal bar, where the parietal, the petrosal and the squamosal meet (SIMPSON, 1933). In the multituberculates the posterior opening of the post-temporal fossa is placed as in the therapsids, but there is no foramen at the junction of the parietal, the petrosal and the squamosal, which would correspond to the anterior opening of the post-temporal fossa. The only foramen, which might be the anterior opening is the supraglenoid foramen (SIMPSON, 1937). It lies in front of the glenoid cavity and occupies the same position as the anterior opening of the post-temporal fossa in the monotremes.

In the therapsid reptiles the paroccipital process is formed by the opisthootic. It is difficult to state which bone forms the paroccipital process in the multituberculates. In *Kamptobaatar*, a distinct suture extends along the ventral edge of the paroccipital process. If the paroccipital process were to be made by the opisthootic, then a suture would separate the opisthootic from the prootic. This condition is very rare in therapsids (OLSON, 1944) and quite unusual in mammals. In the monotremes the paroccipital process (crista parotica) is formed by the petrosal, which is overlapped in part by the squamosal. The paroccipital process of the monotremes only differs from that of the multituberculates in that it lies somewhat obliquely with regard to the long axis of the skull, but otherwise occupies the same position. It is thus highly



Fig. 11

Diagrammatic drawings of the occipital plate in Ornithorhynchus (a), Oligokyphus (b) and Sloanbaatar (c). The lower part of the snout is not shown in this figure. The sutures in Fig. a after Watson, 1916, Fig. b after Kühne, 1956. Not to scale.

probable that the paroccipital process in the multituberculates is homologous to that of the monotremes.

In the studied collection, there are only single specimens of *Sloanbaatar* and *Kampto-baatar* in which the braincase is preserved. In both specimens the cranial roof is complete hence it was impossible either to destroy the cranial roof in order to examine the inner structure of the brain-cavity or to section one of the skulls serially. Both skulls are minute and strongly ossified and it also proved impossible to pass a bristle through any of the foramina. Therefore, the interpretation given above of the skull foramina in the multituberculates is based only on the external aspects of the studied skulls and must be regarded to some extent as tentative.

### COMPARISON WITH THE MORGANUCODONTIDAE

K. A. KERMACK (1963) has shown that the isolated petrosal of Morganucodon<sup>2</sup> from the Upper Triassic material from Wales resembles closely the petrosals of the Jurassic triconodonts. Since then new information on the braincase of the morganucodonts has been obtained by further preparation of the complete skull of Morganucodon from China, a preliminary description of which has been given by RIGNEY (1963). This skull is at present being described by Dr. K. A. KERMACK, Mrs. F. MUSSETT and Father RIGNEY in a paper that also includes a study of the new Welsh material. In ventral aspect, the skull of Morganucodon shows a close resemblance to those of Kamptobaatar and Sloanbaatar and the similarities concern both the

<sup>&</sup>lt;sup>2</sup> Morganucodon KÜHNE is regarded by PARRINGTON (1967) as a younger synonym of *Eozostrodon*. As, however, there is no general agreement about this (see D. M. KERMACK *et al.*, 1968), I regard, for the time being, Morganucodon as the valid name.

choanal and the basicranial regions. The choanae in *Morganucodon* are triradiate as in *Kampto-baatar*. As the new *Morganucodon* material has not yet been described, I cannot make a detailed comparison of the *Morganucodon* and multituberculate braincase. It may be, however, stated that the main difference between the multituberculates and *Morganucodon* concerns the lateral aspect of the braincase. In *Kamptobaatar* the lateral wall of the braincase is formed essentially by the anterior lamina of the petrosal and the alisphenoid is reduced to a small, ventral element. In *Morganucodon* there is a persistent alisphenoid in front of the anterior lamina. The alisphenoid is, in *Morganucodon* (K. A. KERMACK, 1967), much less broad than in cynodonts and is not crowded out from the lateral wall of the braincase as is the case in the multituberculates and the monotremes.

In the anterior lamina of the petrosal in Morganucodon are two foramina, which are better seen in lateral than in ventral view. K. A. KERMACK (1967) refers to them as the foramen pseudoovale and the foramen pseudorotundum. By comparison with the multituberculates one may suppose that these two foramina in Morganucodon are homologous with the two foramina in the region of the foramina for  $V_3$  in *Ptilodus* and *Sloanbaatar*. In these multituberculates the foramina for  $V_3$  lie either within the ventral part of the anterior lamina of the petrosal, or in the presumed suture between the petrosal and the alisphenoid (in the anterolateral corner of the basicranium) and face ventrally. In Morganucodon these foramina lie in the anterior lamina on the lateral wall of the braincase and face laterally. If the foramina in question are homologous in multituberculates and morganucodonts, one should presume that either in Morganucodon the foramen pseudoovale is divided into two foramina, or on the contrary, that in the multituberculates one of the foramina, referred to by SIMPSON (1937) as the foramina for  $V_3$  (foramen masticatorium and foramen ovale inferius), is in fact a foramen pseudorotundum. The homology of these foramina in multituberculates and morganucondonts does not seem to be very probable. In the monotremes, in the anterolateral corner of the basicranium there is a very large foramen for  $V_3$ , while the foramen for  $V_2$  lies comparatively distant from it and much more anteriorly. I presume that in Kamptobaatar V<sub>2</sub> was probably transmitted by the orbital fissure. If this be the case, in the multituberculates as in the monotremes, the foramina for  $V_2$  and  $V_3$  were widely separated and the foramina in the anterolateral corner of the basicranium probably passed branches of  $V_3$ .

The multituberculates differ distinctly from the morganucodonts in the structure of the lower jaw and the lower jaw suspensorium, which in all the known multituberculates, is entirely mammalian, while in *Morganucodon* both the dentary/squamosal and articular/quadrate joints are present. CROMPTON (1964) has shown that *Erythrotherium* described by him from the Upper Triassic of South Africa, shows much resemblance to *Morganucodon*. As, however, in the preliminary description of the *Erythrotherium* given by CROMPTON, only the lower jaw with teeth and the upper teeth are described, the comparison of this genus with the multituberculates cannot be made.

## COMPARISON WITH THE TRICONODONTA

Whole skulls of triconodonts have not yet been found <sup>3</sup> and any knowledge of their cranial structure is based on fragmentary material consisting of two petrosals and the sphenoid of a specimen of *Triconodon mordax* and two petrosals of a specimen of *Triconodon ferox*.

<sup>&</sup>lt;sup>3</sup> Sinoconodon rigneyi, which comes from the same beds as Morganucodon oehleri was assigned by PATTERSON & OLSON (1961) to the Triconodonta. According to K. A. KERMACK (1967), it is a younger synonym of Morganucodon, but now Dr. K. A. KERMACK tells me (personal communication) that it is more likely that Sinoconodon is a separate genus, belonging, however, to the Morganucodontidae.

Both specimens are from the English Upper Jurassic (Purbeck) and are housed in the British Museum (Natural History). K. A. KERMACK (1963) gave a detailed description of this material comparing the petrosal of the triconodonts with that of *Morganucodon*. He also mentioned (*l. c.*, p. 101) the similarities in the structure of the petrosal in triconodonts and multituberculates. I agree (see below) that the petrosals in triconodonts and multituberculates are of almost the same pattern and in my opinion the similarities between these two groups are even greater than has been presumed by K. A. KERMACK.

K. A. KERMACK (1963) gave a reasonable interpretation of the isolated petrosal of *Trio*racodon ferox (B. M. No. 47781). A comparison with the petrosals of *Sloanbaatar* and *Kampto*baatar enables me to emend this interpretation in some of the details (Text-fig. 12). The petrosals of *Sloanbaatar*, *Kamptobaatar* and *Trioracodon* are strikingly similar on first sight, and the similarity concerns the shape of the cochlear housing, the position of the fenestrae vestibuli and cochleae (which are somewhat larger in *Trioracodon*), the position of the paroccipital process, the presence of a longitudinal recess that extends along the lateral side of the cochlear housing, the shape of the lateral flange and the position of the foramen for  $V_3$ .



Fig. 12

Ventral view of the petrosals of a Kamptobaatar (Z. Pal.No.MgM-I/33), b Sloanbaatar (Z. Pal.No.MgM-I/20), c Trioracodon (B. M. No. 47782) Abbreviations --- see p. 6. Not to scale.

In Kamptobaatar and Sloanbaatar (as in Ptilodus) there are two venous foramina in the basicranial region, named by SIMPSON (1937) as the supraglenoid and postglenoid foramina. The supraglenoid foramen in Kamptobaatar is placed posterolaterally with regard to the foramen pseudoovale and in front of the posterior part of the lateral flange, while the postglenoid foramen is placed more ventrally and is on the inner (posterior) wall of the lateral flange. In Trioracodon there are two foramina similarly placed, for which the notations 3 and 5 were given by K.A. KER-MACK (1963, Pl. 2, Fig. 6). Foramen 5 has been recognized by K. A. KERMACK as the lateral opening of the canalis prooticus, while foramen 3 has been regarded by him tentatively as an opening for VII.

The foramen for VII lies, in the multituberculates, in the posterior part of a deep recess that extends along the lateral wall of the cochlear housing. In a similarly situated recess, at the posterior end there is a foramen in *Trioracodon*, to which K. A. KERMACK (*l. c.*) gave the notation 4 and tentatively recognized as a hiatus canalis Fallopii. In my opinion the foramen 4 in *Trioracodon* would correspond rather to the foramen for VII, while the hiatus canalis Fallopii — if it is as in the multituberculates, should be placed much more anteriorly and is not preserved in the specimen.

In the petrosal of *Trioracodon ferox* (B. M. No. 47781), described by K. A. KERMACK (1963, Pl. 2, Fig. 3) — see also Text-fig. 12*c* in the present paper, the foramen for  $V_3$  lies as in the multituberculates, but the crescent-shaped projection which surrounds the foramen anterolaterally, is directed less steeply downwards than in the multituberculates. K. A. KERMACK recognized only one (very large) foramen for  $V_3$  in *Trioracodon*. No certain, second foramen is present in this region in the petrosal examined by him. However, the crescent-shaped wing of the bone that surrounds the foramen for  $V_3$  is broken off in its posterior part, and there is a slight notch in it. It is possible that, as in the multituberculates, this notch corresponds to the second foramen for  $V_3$ . This statement must be regarded as entirely tentative. If this interpretation be correct, the basicranial region is of an essentially similar pattern in the triconodonts and the multituberculates; the only difference being the presence in the multituberculates of a distinct external auditory meatus, which is lacking in *Trioracodon*. K. A. KERMACK (1963) mentioned the presence of a foramen pterygoparoccipitale in the multituberculates.



Fig. 13

Comparison of the region of the internal nares in *a Kamptobaatar* (Z.Pal.No.MgM-I/33), *b Triconodon* (B.M.No.47763). Abbreviations — see p. 6. Not to scale.

In *Triconodon* there is a middle ridge formed by the vomer or parasphenoid (somewhat longer and less prominent than in *Kamptobaatar*), on both sides of which there are two channels, corresponding to the inner choanal channels in *Kamptobaatar* and surrounded laterally by longitudinal bones, recognized by me as pterygoids (Text-fig. 13). To the rear of the inner choanal channels in *Triconodon* there are the foramina for the internal carotid arteries, similarly situated as in *Kamptobaatar*, but much larger relatively than in the multituberculate genus.

As the specimen of *Triconodon* has been somewhat compressed in fossilization, the inner choanal channels are much less deep than in *Kamptobaatar* and the pterygoids much less prom-Palaeontologia Polonica No. 25

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inent. On the right side of the *Triconodon* specimen there are longitudinal ridges in the inner channel. These are most probably due to distortion. The posterior end of the pterygoid in *Triconodon* is somewhat extended laterally, and very strongly resembles the hamulus of *Kamptobaatar*, though it is changed by the distortion. The posterior end of the pterygoid in *Kamptobaatar* abuts laterally against a small opening recognized by me as the anterior end of the cavum epiptericum, as is the case in *Triconodon*. It seems that in *Triconodon* the opening of the cavum epiptericum was larger than in *Kamptobaatar*. Unfortunately, the lateral walls of the choanae are not known in *Triconodon* and one cannot be sure whether in this genus the pterygoid lies, in fact, along the middle of the choanal channel — as it is the case in *Kamptobaatar*, but this seems highly probable. The choanal region in *Sloanbaatar* is poorly preserved and one cannot state what the position of the pterygoid was in this genus.

### COMPARISON WITH THE MONOTREMATA

The possible affinities of the Multituberculata and the Monotremata were discussed by BROOM (1914), who, on little evidence, came to the conclusion that these groups are closely related and then by SIMPSON (1937, 1938) who came to the conclusion that the resemblance between the monotreme and the multituberculate braincase is only superficial. Consequently, SIMPSON described the multituberculate skull in terms of therian mammals.

The present study of the skull structure of *Kamptobaatar* and *Sloanbaatar* led me to the conclusion that the similarities in the braincase structure between the monotremes and multi-tuberculates are very great indeed and concern the following important characters. In both groups the dentary/squamosal joint is, in ventral view, lateral to the ear region. The squamosal is comparatively narrow and does not contribute to the structure of the lateral wall of the braincase. The posterior part of the lateral wall of the braincase is formed by the anterior lamina of the petrosal, in front of which is an extensive, fan-shaped orbitosphenoid. The alisphenoid is crowded out of the lateral wall of the braincase and reduced to a ventral element which is small in the monotremes but more extensive in the multituberculates (Text-fig. 14). In *Ornithorhynchus*, a wide groove extends posterolaterally from the ethmoid foramen towards an extensive foramen for II and III. In *Kamptobaatar*, there is a similar groove which extends from the ethmoid foramen towards the foramen for II. The orbitosphenoid is ossified. In *Ornithorhynchus*, there is an orbitonasal foramen (JOLLIE, 1962), which lies in the suture between the orbitosphenoid and the frontal.

The jugal is absent in both the monotremes and the multituberculates and the zygomatic arch is formed by the maxilla and squamosal only. The lacrimal is lacking in the monotremes but the nasolacrimal canal is present, while in the Cretaceous multituberculates the lacrimal and nasolacrimal canal are absent. The lack of a lacrimal in the Cretaceous multituberculates is evidently secondary, as in the Kimmeridgian multituberculates from Portugal (HAHN, 1969), an extensive lacrimal with a large lacrimal foramen is present. VANDEBROEK gave the notation lacrimal (1964, Fig. 6) to the orbital part of the maxilla in *Ornithorhynchus*, but such an interpretation is not commonly accepted.

In the monotremes, the foramen for  $V_3$  is single and very large, while in the multituberculates there are two or five foramina for  $V_3$ . In both groups the foramen (or foramina) for  $V_3$ is similarly situated in the anterolateral corner of the basicranium, and faces ventrally. In the multituberculates, there is a crescent-shaped wing, recognized tentatively as an alisphenoid,



Fig. 14

Diagrammatic drawings of the lateral aspects of the braincase in Kamptobaatar (a) and in Ornithorhynchus (b). Abbreviations — see p. 6. Not to scale.

which surrounds the region of the foramina for  $V_3$  anterolaterally and protrudes somewhat ventrally over the basicranial region. In the monotremes, the alisphenoid is less conspicuous and does not protrude ventrally, but is similarly placed. The multituberculates and the monotremes are the only known groups of mammals so far, in which the post-temporal fossa is present. However, while in the multituberculates the post-temporal fossa is associated with a persistent tabular, in the monotremes a tabular has not been recognized. The temporal canal in both groups probably has a similar course. The posterior opening is the post-temporal fossa and the canal opens anteriorly into the temporal fossa (in the multituberculates probably as a supraglenoid foramen). The paroccipital process has a similar position in both groups and is probably homologous (Text-fig. 11). One more character, which is common to the multituberculates.

culate and the monotreme braincase, is that the sutures in both groups are obliterated very early in life and therefore the identification of the bones becomes very difficult in both groups.

The above comparisons show that the braincase in the Multituberculata and the Monotremata is built according to the same general pattern. The postcranial skeleton of the multituberculates (GIDLEY, 1909; BROOM, 1914; SIMPSON & ELFTMAN 1928; GRANGER & SIMPSON, 1929; MCKENNA, 1961) is incompletely known. In the collection of Bayn Dzak multituberculates there are three incomplete postcranial skeletons (consisting of pelvic girdles and hind limbs). In the most complete specimen, *Kryptobaatar dashzevegi* KIELAN-JAWOROWSKA, well preserved marsupial bones were found *in situ* on both sides of the pelvis (KIELAN-JAWOROWSKA, 1969). The presence of marsupial bones in a multituberculate skeleton does not confirm their relationship to the monotremes. Marsupial bones have been found in tritylodonts (FOURIE, 1962, 1963) and so it is possible that this feature was characteristic also of all the early mammals. I should point out that the hind limbs associated with the pelvis of *Kryptobaatar dashzevegi*, not yet studied in detail, appear at first sight to be more of a therian pattern than of a monotreme pattern. It will be possible to discuss this question when the postcranial material of the Bayn Dzak multituberculates is described.

## CONCLUSIONS

The comparisons made above between the skull structure of the Multituberculata, the Monotremata, the Triconodonta and the Morganucodontidae, show that in these four groups the basic pattern of the braincase is essentially the same, however, the Multituberculata are more allied to the Monotremata, than they are to the Morganucodontidae and the Triconodonta. The present study contributes new data to support the opinion first expressed by K. A. KERMACK (1967), and later by HOPSON (1970) that the Morganucodontidae, the Triconodonta, the Multituberculata and the Monotremata are closely related and belong to one subclass the Prototheria which is equivalent to the Theria.

All students of the multituberculates after SIMPSON (1945) accepted that the Multituberculata should be placed in a subclass of their own — Allotheria MARSH, proposed by MARSH (1880) as an order and raised to a subclass by SIMPSON (1945). Recently, HOPSON (1970) proposed that the Allotheria be reduced from the subclass to the infraclass rank and assigned the Allotheria to the subclass Prototheria GILL. I tentatively accept in this paper, the classification of the Prototheria proposed by HOPSON (1970). When all the multituberculates from Bayn Dzak have been described, there will be more data to discuss both the structure and the affinities of the Multituberculata and the question of the classification of the Prototheria in more detail.

The main difference between the two mammalian subclasses Prothotheria and Theria concerns the structure of the braincase. In Prototheria the squamosal is comparatively small and does not contribute to the structure of the lateral wall of the braincase. The dentary/squamosal joint lies, in lateral view, in the posterior part of the braincase, while in ventral view it lies lateral to the petrosal. The lateral wall of the braincase is formed primarily by the extensive anterior lamina of the petrosal. The allisphenoid tends to be crowded out from the lateral wall of the braincase. The alisphenoid is still retained in the Triassic *Morganucodon* (see K. A. KERMACK, 1967, p. 243), but is reduced to a small ventral element in the multituber-culates and in the monotremes (the alisphenoid is unknown in the triconodonts). The anterior part of the lateral wall of the braincase is not ossified in the morganucodonts, is partly ossified in the Cretaceous multituberculates and is entirely ossified in the monotremes. The

orbitosphenoid (only known in the multituberculates and the monotremes) is very large and fan-shaped. The cochlea is nearly straight and the ear region opens ventrally. The foramen for  $V_3$  is situated either in suture between the petrosal and the alisphenoid, or pierces the petrosal. In all groups, except the morganucodonts, the foramen for  $V_3$  faces ventrally and lies in the anterolateral corner of the basicranial region. The remnant cavum epiptericum is retained in all the orders, except the monotremes. The jugal is absent in the monotremes and the multituberculates. The septomaxilla is retained in the monotremes. The ectopterygoid is retained in the monotremes and in the multituberculates. The occipital surface is known only in the Cretaceous multituberculates and in the monotremes. In the multituberculates it is therapsid-like with a persistent tabular, a large post-temporal fossa and a conspicuous paroccipital process (in the reptilian sense). In the monotremes the tabular is unknown, but the post-temporal fossa and the paroccipital process are present.

Of the groups assigned to the Prototheria, the Morganucodontidae are the most similar to the therapsids. The similarity concerns not only the structure of the lower jaw and the retention of the quadrate/articular suspensorium, but also the structure of the lateral wall of the braincase, the anterior part of which is not ossified, while the posterior is formed by the two bones: the alisphenoid and the anterior lamina of the petrosal. When stating that the morganucodonts are the most therapsid-like of the groups discussed here, one should take into account that the representatives of each group, on which the above comparisons are made, derive from very distant geological periods. While the morganucodonts are of late Triassic age (about 195 million years old), the triconodonts compared with them are of late Jurassic age (Purbeck) and are about 145 million years old. The multituberculates are of late Cretaceous age (Coniacian or Santonian) and are about 95 million years old, while the monotremes are Recent. If one could compare representatives of all the groups from the late Triassic, the differences, in their structure would be probably much less conspicuous. The Triassic representatives of the triconodonts, the multituberculates and the monotremes would be probably more therapsid-like than the representatives of the same orders from the later geological periods.

In the Theria the braincase has quite a different structure. The squamosal is more extensive and the dentary/squamosal joint lies, in lateral view, at the level of the middle of the braincase, while in ventral view the joint lies in front of the petrosal. The anterior lamina of the petrosal does not exist. The lateral wall of the braincase consists of an extensive squamosal, and a persistent alispehnoid. The anterior part of the lateral wall, in front of the alisphenoid, is entirely ossified. The orbitosphenoid is much less extensive than in the Prototheria. The foramen for  $V_3$  pierces the alisphenoid, faces laterally and lies on the lateral wall of the braincase. The cochlea is spiral and the middle ear tends to be closed ventrally. The occipital surface is of quite a different pattern from that in the therapsid reptiles. In the Theria the tabulars and the posttemporal fossa are absent, a mastoid is present and a new paroccipital process, formed by the exoccipital and not homologous with the reptilian one (characteristic of the Prototheria), is developed. A jugal is present and the septomaxilla has disappeared.

All recent students of the problem of the origin of mammals, except K. A. KERMACK (1967), HOPSON & CROMPTON (1969) and HOPSON (1970) accept that the class Mammalia is of polyphyletic origin (SIMPSON, 1959; OLSON, 1959). According to SIMPSON (*l. c.*), several lines (possibly nine and not less than four) independently crossed the reptilian-mammalian boundary in the late Triassic. One year later SIMPSON (1960) retracted this stating (p. 389) that: "a taxon may be considered monophyletic if derived from one of the next lower rank or still lower". By this definition the class Mammalia is monophyletic, as it arose from one of the lower categorical levels — from the order Therapsida. This formal definition, however, does not change Simpson's

opinion that the majority of the Mesozoic orders of mammals reached the mammalian level parallelly. Since 1959, this opinion has been regarded as a well established fact, and the discussion on the origin of mammals that had been going on, until recently was not concerned with the problem of whether the Mammalia were in fact a group of polyphyletic origin or not, but on how to avoid the inconvenient situation that the most important class of vertebrates was not clade, but a grade (HUXLEY, 1958). A suggestion was made by VAN VALEN (1960) to include the therapsids in the Mammalia. REED (1960) proposed that not only the Therapsida, but also the pelycosaurs immediately ancestral to them should be removed from the Reptilia and placed in the Mammalia. BRINK (1962) and CRUSAFONT-PAIRÓ (1962) independently suggested that the synapsids should be put in a separate class. According to MACINTYRE's (1967) proposal (see also Fox, 1969), only the Theria should be called mammals, while all the other groups of mammals, defined by him informally as the quasi-mammals, should either be left incertae sedis for the time being, or be added as families or subfamilies to the Therapsida. The proposal to include some, or all of the synapsids into the Mammalia, was rejected by SIMPSON (1960) and ROMER (1965) as were the proposals to erect a separate class for the synapsids (Romer, 1965, 1968).

It is quite evident to me that the Mammalia were regarded as a group of polyphyletic origin by most students, because, until recently, the skull structure of Mesozoic mammals was practically unknown and knowledge of these groups was based on the dentition. SIMPSON (1961), in his paper on the classification of Mesozoic mammals, discussed only the structure and the homology of the teeth. K. A. KERMACK (1963) was the first to draw attention to the cranial structure of the Mesozoic mammals. The elements of the skull structure of the Triconodonta and the Docodonta described by K. A. KERMACK (1963) and the new data on the skull structure of the Multituberculata given in the present paper show that there is no reason now to regard the mammals as a group of polyphyletic origin. Two different patterns of skull structure are recognized within the Mammalia (Prototheria and Theria); each possesses an extremely rich differentiation of dentition. Recently HOPSON & CROMPTON (1969) came to the conclusion that the mammals are of monophyletic origin. Their conclusion is based on the study of the molar pattern of Triassic mammals. They state (l. c., p. 66): "The Triconodonta and Docodonta were derived from late Triassic eozostrodontids, and the Jurassic symmetrodonts and pantotheres, and through them the later therians, were derived from late Triassic kuehneotheriids. The eozostrodontids and kuehneotheriids show a close similarity in dentition, suggesting a relatively recent separation from a common ancestor".

In my opinion, as long as we do not know the braincases of the kuehneotheriids and the Jurassic symmetrodonts and pantotheres, it is impossible to venture an opinion as to whether the division of the Mammalia into two branches (Prototheria and Theria) took place at the reptilian or at the mammalian level of evolution. The question of whether mammals are a group of monophyletic or diphyletic origin may be solved only when braincases of the early ancestors of the therians are found.

Palaeozoological Institute of the Polish Academy of Sciences Warszawa, February 1970

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PLATES

## Z. KIELAN-JAWOROWSKA: SKULL STRUCTURE OF MULTITUBERCULATA

## PLATE I

	Page	
Sloanbaatar mirabilis KIELAN-JAWOROWSKA	18	
(see also Plate V)		
Upper Cretaceous, Djadokhta Formation, Bayn Dzak, Ruins, Gobi Desert, Mongolia		
Fig. 1. Stereo-photograph of the skull in occipital view (Z. Pal. No. MgM-I/20); $\times$ 3.		
Kamptobaatar kuczynskii Kielan-Jaworowska	7	
(see also Plates II, 1II, and IV)		
Upper Cretaceous, Djadokhta Formation, Bayn Dzak, Main Field, Gobi Desert, Mongolia		
Fig. 2a. Stereo-photograph of the skull in occipital view. Type specimen (Z. Pal. Nor.MgM-I/33); $\times$ 3,5. Fig. 2b. Stereo-photograph of the same in ventral view; $\times$ 7.		

Photo: M. Czarnocka



Z. KJELAN-JAWOROWSKA: SKULL STRUCTURE OF MULTITUBERCULATA

Palaeontologia Polonica, No. 25, 1971

## Z. KIELAN-JAWOROWSKA: SKULL STRUCTURE OF MULTITUBERCULATA

## PLATE II

	Page
Kamptobaatar kuczynskii KIELAN-JAWOROWSKA	7
(see also Plates J, III and IV)	

Upper Cretaceous, Djadokhta Formation, Bayn Dzak, Main Field, Gobi Desert, Mongolia

Fig. 1a, 1b. Stereo-photographs of the skull in oblique views. Type specimen (Z. Pal. No. MgM-1/33); ×7.

Photo: M. Czarnocka



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## Z. KIELAN-JAWOROWSKA: SKULL STRUCTURE OF MULTITUBERCULATA

## PLATE III

Upper Cretaceous, Djadokhta Formation, Bayn Dzak, Main Field, Gobi Desert, Mongolia

Fig. 1*a.* Stereo-photograph of the skull in right lateral view. Type specimen (Z. Pal. No. MgM-I/33);  $\times$ 7. Fig. 1*b.* Stereo-photograph of the same in left lateral view;  $\times$ 7.

Photo: M. Czarnocka

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Z. KIELAN-JAWOROWSKA: SKULL STRUCTURE OF MULTITUBERCULATA

### Z. KIELAN-JAWOROWSKA: SKULL STRUCTURE OF MULTITUBERCULATA

### PLATE IV

Page

#### (see also Plates I, II and III)

Upper Cretaceous, Djadokhta Formation, Bayn Dzak, Ruins, Gobi Desert, Mongolia

- Fig. 1a. Stereo-photograph of the partial skull with root of left I<sup>1</sup>, alveolus of I<sup>2</sup>, P<sup>1</sup>, damaged P<sup>2</sup>, damaged P<sup>3</sup>, alveoli of P<sup>4</sup>, and M<sup>1</sup>; alveolus of right I<sup>2</sup>, P<sup>1</sup>, damaged P<sup>2</sup>, damaged P<sup>3</sup>, P<sup>4</sup>, placed obliquely M<sup>1</sup> and M<sup>2</sup>, in ventral view (Z. Pal. No. MgM-I/38); × 3.
- Fig. 1b. The same specimen in dorsal view;  $\times 3$ .
- Fig. 1c. The same specimen in left lateral view;  $\times 3$ .
- Fig. 1*d.* Incomplete left lower jaw of the same specimen, with P<sup>4</sup> in labial view;  $\times 5$ .
- Fig. 1e. The same in lingual view;  $\times 5$ .
- Fig. 1f. Stereo-photograph of the same specimen in ventral view;  $\times 5$ .
- Fig. 1g. Right  $P_4$ ,  $M_1$  and incomplete  $M_2$  of the same specimen, mounted on a piece of plastic in labial view;  $\times 5$ .
- Fig. 1*h*. The same specimen in lingual view;  $\times 5$ .
- Fig. 11. Stereo-photograph of the same specimen in ventral view; >5.

Photo: M. Czarnocka



1a

Z. KIELAN-JAWOROWSKA: SKULL STRUCTURE OF MULTITUBERCULATA

## Z. KIELAN-JAWOROWSKA: SKULL STRUCTURE OF MULTITUBERCULATA

## PLATE V

Upper Cretaceous, Djadokhta Formation, Bayn Dzak, Ruins, Gobi Desert, Mongolia

Fig. 1*a*. Stereo-photograph of the skull in left lateral view. Type specimen (Z. Pal. No. MgM-I/20);  $\times$ 4,5. Fig. 1*b*. Stereo-photograph of the same in ventral view;  $\times$ 4,5.

Photo: M. Czarnocka



1b