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EVOLUTION OF THE THERIAN MAMMALS IN THE LATE CRETACEOUS OF ASIA. PART VI. ENDOCRANIAL CASTS OF EUTHERIAN MAMMALS

(Plates 29—31)

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The oldest eutherian endocranial casts belonging to *Kennalestes gobiensis*, *Asioryctes nemegetensis* and *Zalambdalestes lechei* from the Late Cretaceous of Mongolia are described and reconstructed. They represent the casts of primitive therian lissencephalic brains with very large olfactory bulbs, cerebral hemispheres widely separated posteriorly, large midbrain exposure on the dorsal side and a comparatively short and wide cerebellum. The rhinal fissure has not been found in *K. gobiensis*; it is tentatively recognized in *A. nemegetensis*, in which the neocortex is very small, while in *Z. lechei* the rhinal fissure is situated low down on the lateral side of the hemisphere, suggesting the presence of an extensive neocortex. The encephalization quotients are tentatively 0.36 for *K. gobiensis*, 0.56 for *A. nemegetensis* and 0.70 for *Z. lechei*. These Late Cretaceous eutherians were probably more macrosomatic than most Tertiary and recent mammals, and favoured nocturnal niches in which olfaction and hearing were important senses.

Key words: Paleoneurology, Endocasts, Insectivora, Eutheria, Mammalia, Cretaceous, Mongolia.

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EWOLUCJA SSAKÓW THERIA W PÓŻNEJ KREDZIE AZJI. CZĘŚĆ VI. ODLEWY JAMY CZASZKI SSAKÓW ŁOŻYSKOWYCH

Streszczenie. — W pracy opisano najstarsze znane odlewy jamy czaszki trzech ssaków łożyskowych: *Kennalestes gobiensis*, *Asioryctes nemegetensis* i *Zalambdalestes lechei*, z późnej kredy Azji. Jak można sądzić na podstawie tych odlewów, mózgi opisanych ssaków miały gładką korę, duże opuszki węchowe, półkule mózgowie w tyle silnie rozchodzące się na boki, śródmózgowie odsłonięte na stronie grzbietowej oraz krótki i szeroki mózdzek. Bruzda węchowa nie została znaleziona u *K. gobiensis*, lecz prawdopodobnie występowała u *A. nemegetensis*, u którego kora nowa zajmowała niewielką powierzchnię. Bruzda węchowa u *Z. lechei* położona była nisko na boku półkul mózgowych, sugerując obecność silnie rozwiniętej kory mózgowej. Obliczono w przybliżeniu współczynniki encefalizacji, które wynoszą 0.36 dla *K. gobiensis*, 0.56 dla *A. nemegetensis* i 0.70 dla *Z. lechei*. Wyżej wymienione cechy budowy mózgu tych ssaków oraz budowa ich czaszek (KIELAN-JAWOROWSKA 1981, 1983) wskazują, że węch i słuch były u nich silnie rozwinięte, w związku z czym można przypuścić, że zwierzęta te prowadziły nocny tryb życia.

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INTRODUCTION

In the collection of Late Cretaceous therian mammals from the Gobi Desert in Mongolia, housed in the Institute of Paleobiology, Polish Academy of Sciences in Warsaw (KIELAN-JAWOROWSKA 1969, 1975a, 1975b, 1981, 1984) a few of the eutherian specimens belonging to: *Kennalestes gobiensis*, *Asioryctes nemegetensis* and *Zalambdalestes lechei* have partially preserved endocranial casts.

K. gobiensis and *Z. lechei* derive from the Djadokhta Formation, *A. nemegetensis* from the Barun Goyot Formation or from its stratigraphic equivalent — the red beds of Khermeen Tsav. The age of the Djadokhta Formation has been determined by GRADZIŃSKI *et al.* (1977) as ?late Santonian and/or ?early Campanian, that of the Barun Goyot Formation as ?middle Campanian. Recently KARCZEWSKA and ZIEMBIŃSKA-TWORZYDŁO (1983) on paleobotanical evidence argued that the Nemegt Formation which overlies conformably the Barun Goyot Formation is not younger than the equivalent of the lower Campanian stage. It follows that the Barun Goyot Formation may be of ?late Santonian age, while the older Djadokhta Formation of ?early Santonian or even ?late Coniacian age. These estimates should be regarded as tentative.

An endocranial cast of Late Cretaceous eutherian *Barunlestes butleri* from the red beds of Khermeen Tsav has also been found; this is housed in the collection of the Palaeontological Institute, USSR Academy of Sciences, in Moscow and has been described by KIELAN-JAWOROWSKA and TROFIMOV (1980). Endocranial casts have not been preserved in members of the Deltatheridiidae (assigned to the order Deltatheroidea KIELAN-JAWOROWSKA within the Theria *incertae sedis*, see KIELAN-JAWOROWSKA 1975b, 1982) which occur in the same beds.

The purpose of the present paper is to describe the endocranial casts of *Kennalestes gobiensis*, *Asioryctes nemegetensis* and *Zalambdalestes lechei* and to evaluate their encephalization quotients.

The specimens described in the present paper are housed in the Institute of Paleobiology, Polish Academy of Sciences in Warsaw, abbreviated as ZPAL.

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DESCRIPTION

Kennalestes gobiensis KIELAN-JAWOROWSKA

(pl. 29; fig. 1A)

The endocast of *K. gobiensis* has been reconstructed on the basis of 3 specimens: ZPAL MgM-I/3 (the holotype), ZPAL MgM-I/2 and ZPAL MgM-I/1 from the Djadokhta Formation, Bayn Dzak locality in the Gobi Desert. The estimated length of the composite reconstruction of the endocast based on ZPAL MgM-I/3 and ZPAL MgM-I/2 is ca. 14.3 mm, for a skull length estimated as 29 mm. The index $\frac{\text{brain length} \times 100}{\text{skull length}}$ is 49.3. It should be mentioned that previously I estimated (KIELAN-JAWOROWSKA 1981) the skull length in *K. gobiensis* as 26 mm, however, after making the new measurements and reconstruction, this latter value seems an underestimate. It should be also remembered that the specimens of *K. gobiensis* in ZPAL collection belong to young individuals, so it is likely that the skull length in adult *K. gobiensis* is somewhat greater and may even measure 30 or 31 mm.

ZPAL MgM-I/3 is a skull without back of the brain case. The bone on the right side of

the cranial roof was originally missing exposing part of the right olfactory bulb (KIELAN-JAWOROWSKA 1969, pl. 22 : 1c). I intentionally removed the part of the bone from the cranial roof to expose the complete olfactory bulb (pl. 29 : 1). The bulb is 4.0 mm long, ca. 2.2 mm wide and ca. 2.5 mm high, and presumably of nearly equal height all along its length. A fragment of the left olfactory bulb is also seen on the left side of the same specimen.

ZPAL MgM-I/2 — small fragments of the right and left olfactory bulbs are preserved rostrally in this skull. In addition, in the same piece of rock an incomplete endocranial cast without olfactory bulbs has been preserved (KIELAN-JAWOROWSKA 1969, fig. 1E, pl. 24 : 1f and 1g) which is strongly compressed laterally. As originally preserved only parts of the hemispheres were visible, the colliculi and the preserved part of the cerebellum being obscured by the bone. A small piece of bone has been intentionally removed, in order to expose the colliculi. The specimen after this additional preparation is figured in pl. 29 : 2. The hemispheres diverge markedly posteriorly. They are ca. 7.4 mm long. As this specimen is strongly compressed laterally the width of the hemispheres is only 6.8 mm; they are also very deep in lateral view due to the deformation (pl. 29 : 2b).

The surface of the hemispheres is smooth and rather poorly preserved. The rhinal fissure is discernible neither in dorsal nor in lateral view. In lateral view, at the bottom part of the hemisphere there is a distinct ridge, interpreted as the trace of a venous sulcus (pl. 29 : 2b, ?VS). The colliculi are very large, each ca. 2.8 mm long and 1.8 mm wide, roughly triangular, widest in the middle of their length, closely pressed against each other, sharply narrowing anteriorly, not divided. Only the middle part of the cerebellum has been preserved and this is covered by bone. There is a poorly preserved cast of a transverse sinus. The ventral side of the endocast has not been preserved.

ZPAL MgM-I/1 is a juvenile skull, in which the endocranial cast has not been preserved (KIELAN-JAWOROWSKA 1981: figs. 4—6, pls. 12—15 and 16 : 3), but the endocranial cavity has been prepared. The size and shape of the endocranial cavity as well as the position and size of the fossa subarcuata have helped me in reconstruction of the endocast and the position of the paraflocculus, in fig. 1A. By comparison with ZPAL MgM-I/1 I estimated the width of the hemispheres (which are not preserved) in ZPAL MgM-I/3 as ca. 8.8 mm, for a skull length estimated as 29 mm.

Asioryctes nemegetensis KIELAN-JAWOROWSKA 1975
(pl. 30 : 1; fig. 1B)

In the holotype specimen ZPAL MgM-I/56 from the Barun Goyot Formation, Southern Mongolnocks of the Nemegt locality in the Gobi Desert, the bone from the roof of the posterior part of the brain case was originally missing. After having described and figured the skull of this specimen (KIELAN-JAWOROWSKA 1975a and 1981) I intentionally removed part of the right side of the cranial roof, exposing part of the casts of the nasal cavity, and of the paranasal sinuses, right olfactory bulb and right hemisphere. The cerebellum which had originally been exposed is badly damaged and its shape as well as the shape of the paraflocculi have been reconstructed in fig. 1B. The description that follows is based on this single specimen.

The interpretation of the cast of the nasal cavity is questionable. There is no doubt that the narrow medial compartment in fig. 1B₁, designated as the nasal cavity (see also pl. 30 : 1b), is the cast of the dorsal nasal meatus of the nasal cavity. The lateral compartments are situated somewhat higher than the dorsal nasal meatus, and therefore I believe that they may correspond to the paranasal (frontal) sinuses. Although it is less probable, it cannot be excluded that these are the casts of the lateral parts of the nasal cavity itself. To answer this question one should section the skull serially, which was considered inappropriate because of the uniqueness of this specimen.

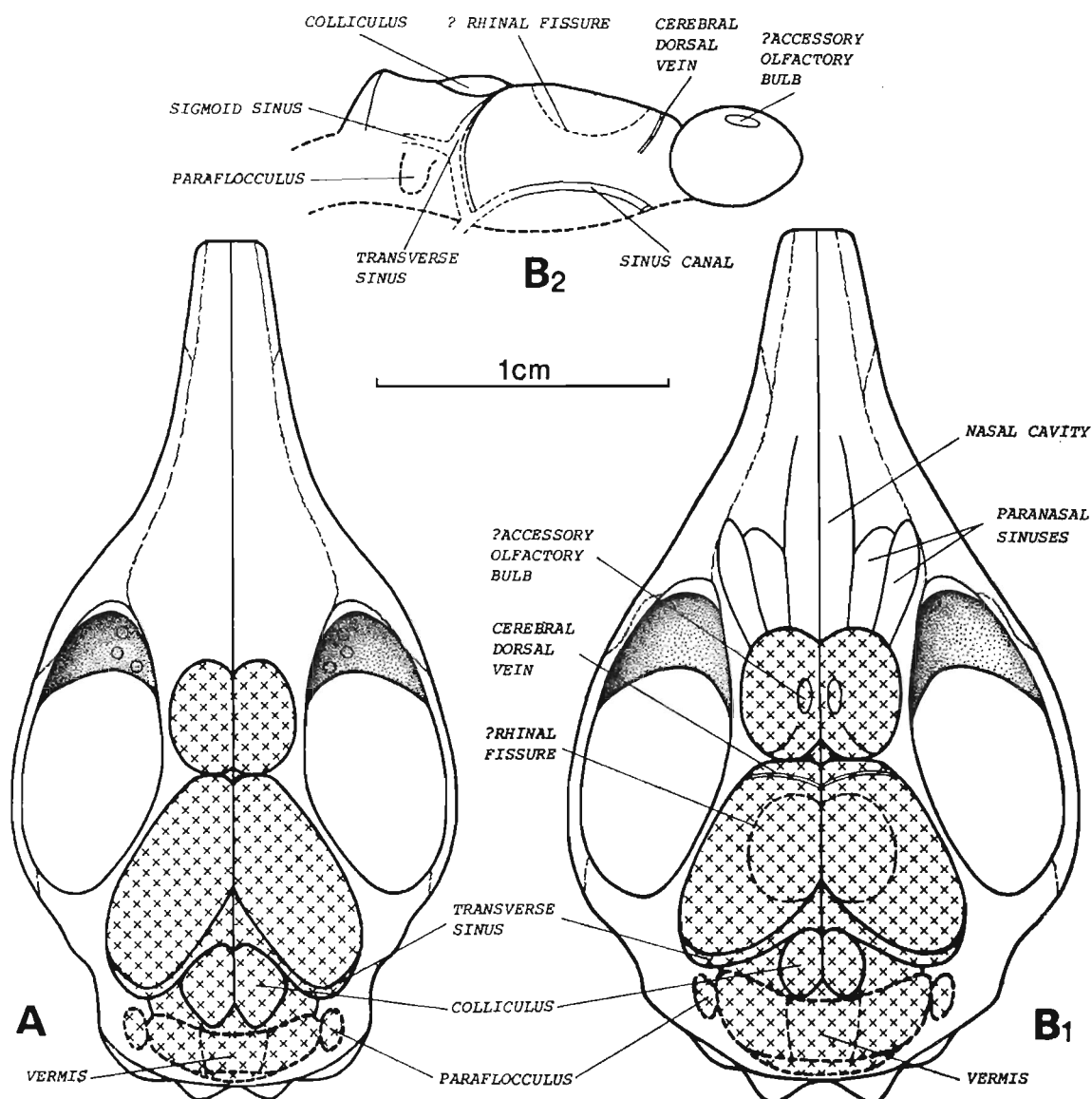


Fig. 1

Reconstructions. A *Kennalestes gobiensis*, the skull and endocast in dorsal view (based upon ZPAL MgM-I/1, ZPAL MgM-I/2 and ZPAL MgM-I/3). B *Asioryctes nemegetensis* (based upon ZPAL MgM-I/56), B₁ the skull and endocast in dorsal view, B₂ the endocast in lateral view. Sigmoid sinus and a part of the transverse sinus reconstructed in fig. B₂ have not been preserved. For the interpretation of the cast of the nasal cavity see p. 159.

ZPAL MgM-I/56. The endocast is ca. 15.4 mm long, and the skull length ca. 30 mm. The index $\frac{\text{brain length} \times 100}{\text{skull length}}$ is 51.3.

Viewed from above the endocast is characterized by notable development of the olfactory bulbs, which are very large, roughly oval, strongly inflated, and slightly divergent posteriorly. The olfactory bulb is 4.8 mm long, 2.8 mm wide and ca. 3.2 mm deep. The highest point of each bulb is close to the longitudinal fissure, at about the midlength of the bulb. In this place there is a cast of the small fusiform body ca. 1.2 mm long, recognized tentatively as an accessory olfactory bulb. A thin furrow extends postero-laterally from the accessory bulb toward the posterior margin of the olfactory bulb. In lateral view the dorsal margin of the olfactory bulb is strongly convex dorsally, while the posterior margin is convex posteriorly. The olfactory

bulb is deepest about its midlength; from this level the ventral margin slopes forwards and upwards (fig. 1 B₂).

The hemispheres are comparatively short and wide, strongly diverging posteriorly, leaving a place for the colliculi to be inserted between them. However, it should be stressed that the hemispheres shown in fig. 1 B, amounting to only ca. 6.5 mm, have been tentatively reconstructed, as the posterior margin of the hemispheres is badly damaged on both sides of ZPAL MgM-I/56. The maximum width of the hemispheres is 9.6 mm, centrally near the longitudinal fissure they are inflated. It is difficult to recognize the exact size of the inflated part, as it is somewhat differently shaped on each side. It is presumed that this inflated part may correspond to the neocortex, and that the boundary between it and the surrounding part corresponds to the rhinal fissure. The neocortex is lissencephalic. The lateral aspect of the hemisphere is not known and has been reconstructed in fig. 1 B₂ only on the basis of the shape of the brain case, as it was not considered appropriate to remove the bone from the lateral and ventral sides of the brain case in this unique specimen. Judging from the shape of the brain case, the maximum depth of the hemisphere was ca. 5.2 mm in front of the colliculus and gradually decreased anteriorly.

Extending subparallel and close to the anterior margin of the hemisphere (viewed from above) is a distinct ridge, interpreted as a trace of a cerebral dorsal vein (see DOM *et al.* 1970), which in lateral aspect continues for a short distance posteroventrally and vanishes. Extending longitudinally along the squamosal and parietal bones is a distinct ridge (KIELAN-JAWOROWSKA 1981, fig. 1), interpreted as a trace of a sinus canal, ending at a sinus canal opening. The posterior course of the sinus canal and its connection with the transverse sinus could not be traced and are reconstructed on the basis of a comparison with other mammals. The cast of the transverse sinus, is poorly preserved and has been reconstructed in fig. 1 B₂. The cast of the sigmoid sinus reconstructed in fig. 1 B₁ has not been preserved.

The colliculi are ca. 2.3 mm long, probably roughly oval, not divided into anterior and posterior ones. As originally preserved the lateral parts of both colliculi have been somewhat damaged which gives a false impression that they were cylindrical (pl. 30 : 1 B); it is however, not excluded that the colliculi were lower laterally than medially.

The cerebellum behind the colliculi is ca. 2.0 mm long and is badly damaged. The occipital surface is directed postero-ventrally and partly seen in dorsal view. The detailed structure of the cerebellum and paraflocculus have not been preserved and their shape is only tentatively reconstructed (fig. 1 B₁).

Zalambdalestes lechei GREGORY and SIMPSON

(pls. 30 : 2, 31; fig. 2)

Partial endocranial casts of *Zalambdalestes lechei* have been preserved in two specimens from the Djadokhta Formation, Bayn Dzak locality, Gobi Desert. In ZPAL MgM-I/14 the cast of the olfactory bulbs without the posterior portion of the endocast is preserved, while in ZPAL MgM-I/16 the endocast is nearly entire, but without olfactory bulbs. Both these specimens are juvenile (though not the smallest in the ZPAL collection), and belonged to individuals of similar size. On the basis of these two specimens a reconstruction of the endocast of *Z. lechei* (fig. 2) has been made, the length of which is ca. 20.1 mm, for a skull length of ca. 46 mm. The index

$\frac{\text{brain length} \times 100}{\text{skull length}}$ is 43.7. The skull of an adult *Z. lechei* (see GREGORY and SIMPSON 1926, SIMPSON 1928, SZALAY and MCKENNA 1971 and KIELAN-JAWOROWSKA 1981) measures ca. 50 mm.

ZPAL MgM-I/14 — The olfactory bulbs (pl. 31 : 2) are inflated posteriorly, more so than

anteriorly, which indicates, that they were not covered posteriorly by the cerebrum, as is also the case in *Barunlestes* (KIELAN-JAWOROWSKA and TROFIMOV 1980, pl. 1 : 1a). In dorsal aspect each bulb is 5.2 mm long and 3.5 mm wide and roughly oval in outline. The anterior and middle parts of the bulbs are closely pressed against each other and insignificantly diverge posteriorly. The latter feature may be due to post-mortem damage, as the inner margin of the left bulb forms a straight line, while the inner margin of the right diverges laterally. In lateral aspect the bulb is comparatively short anteriorly and becomes gradually deeper up to mid-length, where it measures 4.7 mm; it retains this depth along its entire posterior half.

ZPAL MgM-I/16 — *Dorsal aspect* (pl. 30 : 2). The hemispheres are ca. 10.3 mm long and 12.5 mm wide, narrowing anteriorly. Their dorsal surface is badly damaged and only posterolaterally has the original surface of the endocast been preserved (pl. 30 : 2). The hemispheres are probably lissencephalic; they diverge strongly posteriorly and the midbrain (colliculi) are exposed on the dorsal side. The length of the colliculus is ca. 2.8 mm, the width ca. 2.1 mm. They are roughly pear-shaped structures, with badly damaged dorsal surface. Because of this one cannot state whether they were separated into anterior and posterior colliculi. Extending transversely between the colliculi and the hemispheres on one side and the cerebellum on the other is a furrow. The cerebellum is ca. 9.5 mm wide and 3.0 mm long across the midline, the middle part is somewhat elevated and probably corresponds to the vermis. The cerebellar hemispheres which were probably present lateral to the vermis are poorly preserved and the details of their structure cannot be seen. Lateral to the cerebellum the cast of the para-flocculus is preserved on both sides of the specimen (see below). A cast of the transverse sinus, is well preserved on the right side. The sigmoid sinus branches from it, extending between the cerebellum and para-flocculus.

Lateral and ventral aspects (pl. 31). In lateral view the greatest depth of the endocast is across the cerebellum and the pyramid, where it measures 8 mm; across the colliculi and posterior part of the hemispheres the depth is 7.3 mm. The anterior part of the ventral side is partly damaged and deformed, the olfactory tract not being preserved. In the middle of the anterior part is an indistinct roughly triangular swelling, which is interpreted as a damaged cast of the optic chiasma, the roots of which diverge posteriorly. Extending parallel to the optic chiasma, near the outer margin is another furrow interpreted tentatively as a rhinal fissure. This is also seen on both sides of the specimen in lateral views at the lower part of the hemisphere. Because the area between the optic chiasma and the rhinal fissure is slightly compressed and damaged on both sides, one cannot determine the shape and the inflation of the olfactory tubercle. To the rear of the optic chiasma there is a rounded area of hypophysis cerebri, with badly damaged surface, the cast of hypophysis not being preserved. Lateral to the hypophysis area there are pyriform lobes, the surface of which is damaged on both sides; they are sharply delimited posteriorly. Behind the hypophysis the interpeduncular fossa enclosed between the posteromedial margins of the pyriform lobes is exposed. This is poorly preserved; in the middle of it small round structures, which might be casts of oculomotor nerves are recognizable. The pons is poorly defined, possibly very short. On the left side of the specimen is the calcite cast of the cochlea, forming a crescent-shaped roll, consisting of only one whorl. On the right side the broken fragments of the petrosal bone have been preserved showing the internal auditory meatus (pl. 31 : 1b); after the additional preparation the bone has been removed and the casts of facial and vestibulocochlear nerves have been exposed (pl. 31 : 1c). The cast of the trigeminal nerve is not discernible, it should be placed antero-medially to the facial and vestibulocochlear nerves, close to the posteromedial margin of the pyriform lobe. The corpus trapezoideum is poorly defined. The area of the medulla oblongata is poorly preserved, but the cast of the pyramid is visible. Postero-medial to the cochlea at the margin of the endocast on the right side of the specimen there is an elevation, which might correspond to the exits of glossopharyngeal or vagus, or accessory nerves, or to all of them. The para-flocculus is seen

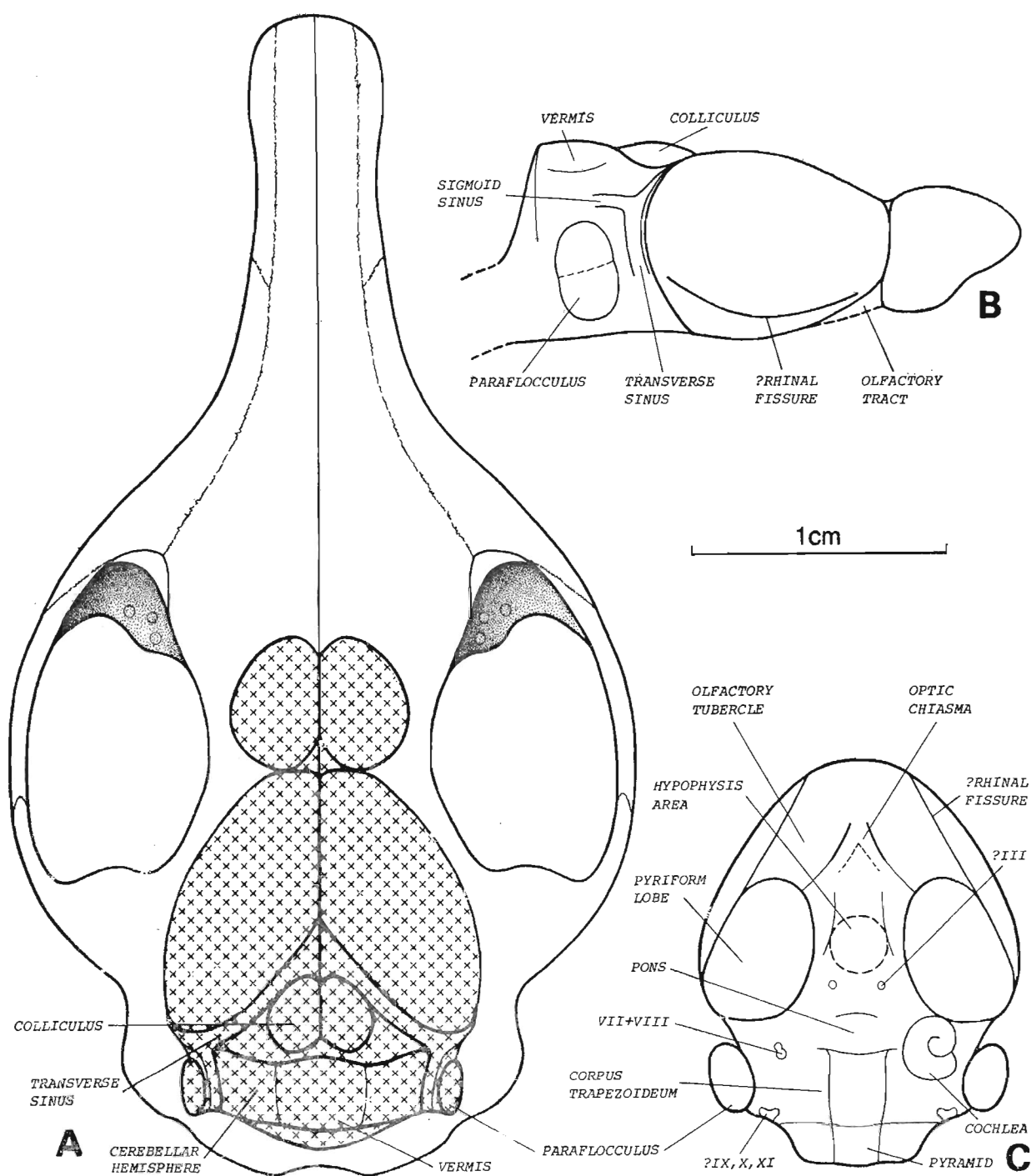


Fig. 2

Zalambdalestes lechei, A reconstruction of the skull and endocranial cast in dorsal view, B reconstruction of the endocranial cast in lateral view, C diagrammatic drawing of ZPAL MgM-I/16 endocranial cast in ventral view. A and B based upon ZPAL MgM-I/14 and ZPAL MgM-I/16.

in ventral view postero-lateral to the cochlea and is best exposed in right lateral view, where the cross section of the petrosal bone is visible, showing the area of the fossa subarcuata, entirely filled with calcite. As the cast of the brain is made of a fine red sandstone and that of the fossa subarcuata of calcite, the latter is easily distinguishable from the remaining portion of the endocranial cast. It is probable that the calcite cast of the fossa subarcuata which is preserved has

been enlarged in proportion to the size of the paraflocculus, due to the partial damage of the petrosal bone. The calcite cast of the fossa subarcuata consists of two portions: upper and lower, better seen on the right side of the specimen. This is interpreted as meaning that the filling of the fossa subarcuata with calcite took place in two stages.

LE GROS CLARK (1928: 253) stated that in *Elephantulus* the paraflocculus: „... is divided by a horizontal sulcus into two folia of which the upper is very slightly the larger”. The structure of the paraflocculus in *Elephantulus* (LE GROS CLARK l. c. fig. 1) bears a superficial resemblance to the cast preserved in *Z. lechei* and it is possible that the paraflocculus in *Z. lechei* consisted of two folia as in *Elephantulus*.

ENCEPHALIZATION QUOTIENT (EQ)

The preserved endocranial casts have allowed me to estimate tentatively the endocast volume and encephalization quotient for three described species (Table 1). JERISON (1973), in his classical work, estimated the brain volume in fossil mammals excluding the olfactory bulbs, while most authors (e. g. RADINSKY 1977, 1978 in Tertiary mammals, EISENBERG 1981 in recent mammals, and others) include the olfactory bulbs into the brain volume.

In the endocranial casts described here the olfactory bulbs are very large and protrude strongly anteriorly; they are also conspicuously narrower than the rest of the cast. Because of this the endocast shape is rather irregular. Therefore I have thought it better to measure the volume of the olfactory bulbs and that of the rest of the endocast separately, applying in each case the graphic double integration method described by JERISON (1973) and the equation for an ellipsoid. I regarded endocast volume as the total of the two values obtained. I have reconstructed both the dorsal and lateral aspects of the endocasts of *Asioryctes nemegetensis* and *Zalambdalestes lechei* and I evaluated the mean width and height from these reconstructions. In the case of *Kennalestes gobiensis*, because of the incompleteness of the material, I have reconstructed only the dorsal aspect of the endocast and calculated the mean height as equal to 0.8 of the mean width, as adopted by JERISON (1973).

In *K. gobiensis* and *A. nemegetensis* only fragments of the postcranial skeletons are known (KIELAN-JAWOROWSKA 1977) and it was impossible to measure body length. For these species I have followed JERISON and assumed that body length is 4 times the length of the skull.

I have reconstructed the postcranial skeleton of *Z. lechei* (KIELAN-JAWOROWSKA 1979, fig. 17) mostly on the basis of the juvenile specimen ZPAL MgM-I/43, the skull length of which is ca. 4.3 cm. Using JERISON's (1973, fig. 2.8) method the body length of this specimen is 14.0 cm. The partial endocasts of *Z. lechei* have been preserved in two specimens of similar size, the more complete of which ZPAL MgM-I/16 has a skull length of 4.6 cm. The body length of this specimen calculated by a comparison with that of the reconstructed one is 14.9 cm. From this it may be seen that the estimated body length in *Z. lechei* is somewhat less than 4 times the skull length. The reason may be self-evident: the elongated snout of *Z. lechei* makes the skull relatively longer than in other mammals of similar size.

To evaluate the body weight of the species studied I used JERISON's equation

$$Wt = 0.025 L^3 \quad (1)$$

in which Wt is body weight in grams and L length in centimeters. The coefficient (0.025) employed, is the same as JERISON used for lightly built mammals, such as small insectivores and rodents.

For evaluation of the EQ of mammals JERISON (1973) used the equation

$$EQ = \frac{E}{0.12 Wt^{0.66}} \quad (2)$$

Table 1

Endocast volume, body size and encephalization quotient in *Kennalestes*, *Asioryctes* and *Zalambdalestes*

Computations (lengths in cm, volumes in ml, weights in g)	<i>Kennalestes gobiensis</i> (based upon ZPAL MgM-I/2 and ZPAL MgM-I/3)			<i>Asioryctes nemegetensis</i> (based upon ZPAL MgM-I/56)			<i>Zalambdalestes lechei</i> (based upon ZPAL MgM-I/14 and ZPAL MgM-I/16)		
	Olfactory bulbs	Endocast exclusive of olfactory bulbs	Total endocast	Olfactory bulbs	Endocast exclusive of olfactory bulbs	Total endocast	Olfactory bulbs	Endocast exclusive of olfactory bulbs	Total endocast
Endocast									
Mean width (\bar{w})	0.36	0.64		0.48	0.948		0.59	1.20	
Mean height (\bar{h})	0.29	0.51		0.28	0.56		0.36	0.66	
Length (l)	0.38	1.05	1.43	0.45	1.09	1.54	0.52	1.49	2.01
Estimated volume ($E = \frac{1}{4} \pi l \bar{w} \bar{h}$)	0.03	0.269	0.299	0.047	0.454	0.50	0.086	0.93	1.02
Body									
Skull length (S)		2.90			3.00			4.60	
Body length (L)		11.60			12.00			14.90	
Body weight ($Wt = 0.025 L^3$)		39.00			43.20			82.69	
Encephalization quotient ($EQ = \frac{E}{0.055 Wt^{0.74}}$)		0.36			0.56			0.70	

in which E is brain weight in grams and Wt is body weight in grams. However, according to recent data (see EISENBERG and WILSON 1978, 1981, EISENBERG 1981, MARTIN 1981 and others) the allometric exponent for present-day mammals is ca. 0.74 (not 0.66), and the coefficient is 0.055 (not 0.12).

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

In Table 1 I give the estimates of the endocasts volume and body size of the described species and their encephalization quotients, computed from equation (3).

DISCUSSION

The *Kennalestes gobiensis*, *Asioryctes nemegetensis* and *Zalambdalestes lechei* endocasts are the oldest known endocasts for eutherian mammals and have allowed me to reconstruct the primitive lissencephalic therian brains that produced them. They are so different from the endocasts of therapsid reptiles (OLSON 1944, HOPSON 1979, QUIROGA 1979, 1980, KEMP 1979), triconodonts (SIMPSON 1927, see also reconstruction in KERMACK *et al.* 1981), multituberculates (SIMPSON 1937, KIELAN-JAWOROWSKA 1983) and from the brains of the monotremes (ELLIOT-SMITH 1899, GRIFFITHS 1968), that it is difficult to make any worthwhile comparisons.

They differ from each other in size, proportions and in the degree of the development of the neocortex, but they have several characters in common. These are: very large olfactory bulbs (the length of which amounts to more than one fourth of the endocast length); strong posterior divergence of the hemispheres (the point of divergence being about half way along the length of the hemispheres); an extensive midbrain exposure on the dorsal side and a comparatively short and wide cerebellum.

The most primitive is the endocast of *K. gobiensis*, the EQ for which has been calculated as 0.36, while the EQ for *A. nemegetensis* being 0.56 and for *Z. lechei* 0.70. The above EQ values (although tentative) agree with the general impression of the degree of development of these endocasts, based upon direct observation, and accord the conclusions that may be drawn from studies of the skull structure, dentition and postcranial skeleton (KIELAN-JAWOROWSKA 1969, 1975a, 1977, 1979, 1981, 1984, CROMPTON and KIELAN-JAWOROWSKA 1978).

The rhinal fissure is not visible on the endocast of *K. gobiensis*. QUIROGA (1980) recognized the existence of a large neocortex in the Middle Triassic therapsid reptile *Probainognathus jenseni*. If his interpretation is correct, one should expect a large neocortex in Late Cretaceous eutherians which, however, is not found in the specimens studied, except for *Zalambdalestes*. It is probable that in *Kennalestes*, which is the most generalized eutherian mammal thus far described, the neocortex has not yet developed. *Asioryctes* occurs in beds younger than those yielding *Kennalestes*, and is in various respects (e. g. in the structure of the dentition) more advanced than *Kennalestes*. In *A. nemegetensis* the central part of the dorsal aspect of the hemispheres is inflated and may correspond to the neocortex. If so, *Asioryctes* would have a small neocortex.

In *Z. lechei* there is a distinct furrow, tentatively interpreted as the rhinal fissure, situated low down and visible only in lateral and ventral views of the hemispheres. In numerous modern insectivores e. g. *Tenrec*, *Erinaceus*, *Talpa*, *Echinosorex* and others (see e. g. LE GROS CLARK 1932, DECHASEAUX 1964, STARCK 1962), as well as in numerous early carnivores (RADINSKY 1977) the rhinal fissure is present on the dorsal side of the hemispheres. If the identification of the rhinal fissure in *Z. lechei* given in this paper is correct, this Late Cretaceous species would be more advanced as far as the development of the neocortex is concerned than some modern insectivores and early Tertiary carnivores. *Zalambdalestes* occurs in the same beds as *Kennalestes*.

One should, however, remember that *Zalambdalestes* in contrast to *Kennalestes* is a derived genus. The dentition, brain case and postcranial skeleton all exhibit a mosaic of primitive and specialized characters. It is thus possible that in *Zalambdalestes* the neocortex was even more developed than in some recent mammals. One could argue that, as the dorsal side of the hemispheres is badly damaged in *Z. lechei*, it cannot be excluded that the rhinal fissure was present on the dorsal side and has not been preserved in the specimen studied. However, there is also no trace of the rhinal fissure in the closely related Late Cretaceous species *Barunlestes butleri*. The endocranial cast of this species (which has the dorsal side of the hemispheres partly preserved) does not differ much from that of *Z. lechei* (see KIELAN-JAWOROWSKA and TROFIMOV 1980, pl. 1 : 1a). It thus seems possible, that as far as the development of the neocortex is concerned, *Zalambdalestes* was as advanced as e. g. *Tupaia* (LE GROS CLARK 1924).

A common feature of the three endocasts is the extensive exposure of the midbrain on the dorsal side. This is also characteristic of some primitive recent insectivores and marsupials (STARCK 1962, BAUCHOT and STEPHAN 1967, VORIS and HOERR 1932). However, STARCK (1932) and EDINGER (1964) argued that the dorsal midbrain exposure is not always a primitive character. BAUCHOT and STEPHAN (1967) demonstrated that in *Rhynchocyon* the colliculi appear smaller on the artificial endocranial cast than on the brain itself, as they are partly obscured on the cast by the transverse sinus. The same holds for the artificial endocast of *Didelphis marsupialis* made by me, on which the colliculi appear smaller than they do on the brain (LENDE 1963). In the three endocasts described there is a distinct transverse sinus and very large colliculi. In all the specimens the colliculi appear undivided. This may be interpreted in one of two ways: either the anterior colliculi in all three species are overlapped by the transverse sinus and in part by the hemispheres and the exposed colliculi correspond to the posterior ones, or the furrow that divided the colliculi into anterior and posterior has not been preserved. If the first interpretation is the correct one, the exposed auditory colliculi would be enormous, which would agree with the skull structure of the studied species (KIELAN-JAWOROWSKA 1981, 1984). They have large promontoria, suggesting strongly developed auditory sense.

The whole cerebellum has been preserved only in *Zalambdalestes*. In *Asioryctes* it is partly preserved while in *Kennalestes* its shape had to be reconstructed on the basis of the skull structure. The extensive development of the cerebellum in the transverse axis that is characteristic of the Theria (see ARIËNS KAPPERS *et al.* 1960 for summary) is found in *Zalambdalestes*, and it has been possible to recognize the vermis and cerebellar hemispheres at least tentatively. The second feature characteristic of the mammalian cerebellum — the development of the cerebellar sulci — has not been observed in *Zalambdalestes*, but this may be due to the state of preservation. In all three species in question the cerebellum is relatively short compared to the long telencephalon. The paraflocculus has been preserved only in *Zalambdalestes*. It is very large, but as argued on p. 163, the preserved cast is probably an enlarged version of the actual paraflocculus, due to the partial damage of the petrosal.

It appears from Table 1 and from direct observation that the olfactory bulbs in the three species described formed a proportionally larger part of the brain than they do in most Tertiary and recent therian mammals, with possible exception of such primitive forms as *Tenrec ecaudatus* and *Didelphis marsupialis* (see e. g. LOO 1930, LE GROS CLARK 1924, 1932, STARCK 1962, STEPHAN and SPATZ 1962, RUSSELL and SIGOGNEAU 1965, BAUCHOT and STEPHAN 1962, JOHNSON 1977, RADINSKY 1977, 1978).

CONCLUSIONS

The endocasts of *Kennalestes gobiensis*, *Asioryctes nemegetensis* and *Zalambdalestes lechei* differ from those of various fossil and recent eutherian mammals, and of primitive marsupials, in having relatively larger olfactory bulbs, wider posterior divergence of the cerebral hemi-

spheres and possibly relatively larger auditory colliculi. They differ among themselves in the development of the neocortex, which was probably not developed in *Kennalestes*, incipiently developed in *Asioryctes* and relatively extensive in *Zalambdalestes*.

The EQ's for these Late Cretaceous mammals are not very low; the value for *Kennalestes gobiensis* (0.36) falls within the ranges (EISENBERG 1981) for *Tenrec ecaudatus* (0.345—0.486) and *Didelphis marsupialis* (0.353—0.573); 0.56 for *Asioryctes nemegetensis* falls within the range for *Solenodon paradoxus* (0.545—0.687), but is higher than for *Erinaceus europeus* (0.508); while 0.70 for *Zalambdalestes lechei* is higher than those for various recent marsupials and insectivores and corresponds roughly to that for *Marmosa robinsoni* (0.716) and *Mystromys albicaudatus* (0.710). It should, however, be remembered, that the EQ's obtained for the Late Cretaceous species discussed are to some extent tentative, as the endocasts studied had in part to be reconstructed. In the case of *K. gobiensis*, not only the endocasts but also the length of the skull has been reconstructed, and in all three, body weight is a derived figure from body length or assumed length.

As follows from the foregoing discussion, the eutherian mammals as early as during the Late Cretaceous developed typical eutherian brain and attained relatively high encephalization quotients. They were probably more macrosmatic than most Tertiary and recent Theria and favoured nocturnal niches, (as suggested by JERISON 1973 and CROMPTON *et al.* 1978), in which olfaction and hearing were very important senses.

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EXPLANATIONS OF THE PLATES 29—31

PLATE 29

Kennalestes gobiensis KIELAN-JAWOROWSKA

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

- 1a. Rostral part of the skull in dorsal view, ZPAL MgM-I/3, holotype.
- 1b. The same in right lateral view.
- 1c. The same in left lateral view.
- 2a. Partial endocast strongly compressed laterally, in dorsal view, ZPAL MgM-I/2.
- 2b. The same in right lateral view.

All stereo-photographs, $\times 4$

Abbreviations: COL colliculus, OB olfactory bulb TS transverse sinus, ?VS ?venous sinus.

Photo: E. Wyrzykowska

PLATE 30

Asioryctes nemegetensis KIELAN-JAWOROWSKA

- 1a. Skull in right lateral view, Upper Cretaceous, Barun Goyot Formation, Nemegt (Southern Monads), Gobi Desert, Mongolia, ZPAL MgM-I/56 — holotype.
- 1b. The same in dorsal view.

Zalambdalestes lechei Gregory and Simpson

- 2. Partial endocast in dorsal view, Upper Cretaceous, Djadokhta Formation, Bayn Dzak (Volcano), Gobi Desert, Mongolia, ZPAL MgM-I/16, (see also pl. 31).

All stereo-photographs, $\times 4$

Abbreviations: ?AOB ?accessory olfactory bulb, CDV cerebral dorsal vein, CER cerebellum, COL colliculus, NC nasal cavity, PS paranasal sinuses, SC sinus canal foramen, TS transverse sinus, VER vermis.

Photo: E. Wyrzykowska

PLATE 31

Zalambdalestes lechei GREGORY and SIMPSON

Upper Cretaceous, Djadokhta Formation, Bayn Dzak (Volcano), Gobi Desert, Mongolia.

- 1a. Partial endocast in right lateral view ZPAL MgM-I/16 (see also pl. 30 : 2).
- 1b. The same in ventral view as originally preserved.
- 1c. The same in ventral view, after additional preparation, covered with ammonium chloride.

1d. The same in left lateral view.

2a. Rostral part of the skull in dorsal view, showing olfactory bulbs, ZPAL MgM-I/14.

2b. The same in right lateral view.

All except 1d and 2a stereo-photographs, all $\times 4$

Abbreviations: COCH cochlea, CER cerebellum, COL colliculus, CT corpus trapezoideum, H area of the hypophysis, IAM internal auditory meatus, OCH optic chiasma, OT olfactory tubercle, P pons, PAR paraflocculus, PL pyriform lobe, PYR pyramid, ?RF ?rhinal fissure, III, VII, VIII, IX, X, XI cranial nerves.

Photo: E. Wyrzykowska

