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CRANIAL MORPHOLOGY OF THE CRETACEOUS EUTHERIAN MAMMAL *BARUNLESTES*

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Skull and lower jaw of Late Cretaceous (?middle Campanian) eutherian zalambdalestid genus *Barunlestes* from the Gobi Desert in Mongolia is described and figured. It is characterized by: maxilla extending backwards along the choanae, the presphenoid with a prominent median process, very large pterygoid process of basisphenoid, a fissura Glaseri, postglenoid process extending only opposite the medial part of glenoid fossa, large promontorium, foramen arteriae stapediae, sulcus arteriae stapediae, no sulcus arteriae promontorii. Large promontoria and large olfactory bulbs indicate strong development of auditory and olfactory senses in *Barunlestes*. Basicranial structure of *Barunlestes* supports Presley's (1979) idea that the primitive mammalian morphotype with two vessels (medial internal carotid and promontory), should be revised.

K e y w o r d s: Arteria carotis interna, *Barunlestes*, braincase, Cretaceous, endocranial casts, Mongolia.

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INTRODUCTION

Barunlestes Kielan-Jaworowska 1975 is a member of the Late Cretaceous, specialized eutherian family the Zalambdalestidae Gregory and Simpson 1926, which includes also *Zalambdalestes* Gregory and Simpson 1926. Both genera are monotypic, *Zalambdalestes* is represented by *Z. lechei* Gregory and Simpson 1926, *Barunlestes* by *B. butleri* Kielan-Jaworowska 1975 and both are known only from Asia (Gregory and Simpson 1926, Simpson 1928, Kielan-Jaworowska 1969, 1975, 1979, Szalay and McKenna 1971). *Zalambdalestes* occurs in the Late Cretaceous Djadokhta Formation, the age of which has been estimated as ?late Santonian and/or ?early Campanian, *Barunlestes* is known from the Late Cretaceous Barun Goyot Formation, which is of ?middle Campanian age, and from its stratigra-

phic equivalent known as red beds of Khermeen Tsav (Gradzinski *et al.* 1977).

The specimens of *Barunlestes* collected by Polish-Mongolian Paleontological Expeditions (Kielan-Jaworowska and Barsbold 1972) are housed in the Institute of Paleobiology in Warsaw, and those collected by Soviet-Mongolian Paleontological Expeditions (Beliajeva *et al.* 1974) are housed in the Institute of Paleontology of the USSR Academy of Sciences in Moscow.

So far only the preliminary description of *Barunlestes* skull (Kielan-Jaworowska 1975), and the detailed description of the postcranial skeleton (Kielan-Jaworowska 1979) have been published. As the skulls of *Barunlestes* housed in Warsaw and in Moscow complement each other it was thought desirable to describe all of them together in a joint paper. The Russian version of this paper will be published in Paleontologitsheskij Zhurnal.

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Abbreviations used

PIN Institute of Paleontology USSR Academy of Sciences, Moscow
ZPAL Institute of Paleobiology, Polish Academy of Sciences, Warsaw.

MATERIAL

ZPAL MgM-I/77, holotype, Barun Goyot Formation, Khulsan, Nemegt Basin, Gobi Desert, incomplete skull associated with right and left lower jaws and part of postcranial skeleton. Skull and lower jaws figured by Kielan-Jaworowska 1975, pls. 5 and 6, postcranial skeleton figured by Kielan-Jaworowska 1979, pls. 1, 2, 4—11 and text-figs. 2, 4—8, 11—14.

ZPAL MgM-I/90, red beds of Khermeen Tsav, Khermeen Tsav II, Gobi Desert, right lower jaw with root of I_1, alveoli for P_1—P_2, one root of P_3 and P_4—M_3 strongly worn out.

ZPAL MgM-I/94, red beds of Khermeen Tsav, Khermeen Tsav II, Gobi Desert, incomplete, badly damaged face, associated with partial right and left lower jaws, figured in this paper on pl. 5 : 2.

ZPAL MgM-I/104, red beds of Khermeen Tsav, Khermeen Tsav II, Gobi Desert, incomplete face of an old individual, associated with partial

right and left lower jaws, humerus and scapula. Postcranial skeletal parts figured by Kielan-Jaworowska 1979, pls. 7 and 8, and text figs. 9 and 10, skull and lower jaws figured in this paper on pls. 5:1 and 6.

ZPAL MgM-I/107, red beds of Khermeen Tsav, Khermeen Tsav II, Gobi Desert, incomplete damaged face, associated with right and left damaged lower jaws, figured in this paper on pl. 7:1 and 8.

ZPAL MgM-I/135, Barun Goyot Formation, Nemegt, Eastern Sayr, Nemegt Basin, Gobi Desert, incomplete right lower jaw with alveoli for P_1—P_2 and P_3—M_3, figured in this paper on pl. 7:2.

PIN 3142-701, red beds of Khermeen Tsav, Khermeen Tsav II, Gobi Desert, nearly complete very well preserved skull, with cast of the nasal cavity and incomplete cast of the braincase, and somewhat damaged dentition, associated with right and left incomplete lower jaws, figured in this paper on pls. 1—4.

DESCRIPTION

Skull as a whole. — The length of the skull varies between 35 and 40 mm. The snout is very narrow anteriorly, strongly elongated into a narrow tube, ca. 12 mm long, with roughly parallel margins, extending between I^1 and P^2. Opposite P^2 the snout widens abruptly. There is an interorbital constriction, but no postorbital process. Zygomatic arches are slender, strongly expanded laterally. The occipital surface lies at an angle of ca. 85° to the plane of the teeth. The lower jaw is deep and robust.

Snout and anterior part of zygomatic arch. — The nasals, preserved in ZPAL MgM-I/77 and ZPAL MgM-I/94 are narrow anteriorly, greatly widen behind and contact the lacrimals. The naso-frontal suture is convex posteriorly on each side. The anterior margin of the premaxilla is not preserved. The lateral wall of the maxilla is concave, the infraorbital foramen is ca. 1.5 mm deep, placed very low, immediately above the P^2—P^3 embrasure. The facial wing of the lacrimal is extensive and roughly triangular. The anterior margin of the orbit is placed above M^1. The suture between the jugal and maxilla is not preserved and it is impossible to state whether the maxilla contributes to the zygomatic arch. The posterior margin of the anterior root of zygomatic arch lies opposite M^2 or opposite M^2—M^3 embrasure.

Palate. — The palatal part of the premaxilla is preserved only in ZPAL MgM-I/107, where it is slightly concave, and very damaged. The hardly discernible premaxillary-maxillary suture is situated ca. 2.5 mm in front of the canine. The palatal part of the maxilla is concave on either side. The greater palatine foramen is situated far in front of the palatino-maxillary suture, opposite P^3. A distinct palatine groove extends from it

anteriorly. In addition the whole surface of the palatal process of the maxilla is pierced by small foramina, distributed irregularly. In the posterior part of the maxilla there is a large (ca. 2 mm long), oval posterior palatine foramen, arranged obliquely, with the anterior margin situated opposite M^1 and the posterior opposite the margin of the choanae. The palatino-maxillary suture is well preserved in PIN 3142-701. The horizontal part of the palatine bone is very narrow just in front of the choanae, where the palatino-maxillary suture skirts the posterior palatine foramen. The horizontal part becomes the widest opposite M^2 and narrows gradually again to a short transverse end, situated opposite P^4. Immediately to the rear of the palatino-maxillary suture, opposite P^4—M^1 embrasure there is a small lesser palatine foramen. The posterior part of the horizontal plate is strongly thickened, to form a distinct postpalatine torus, ca. 2.5 mm long.

Cranial roof. — The bones of the cranial roof are either missing or badly damaged in all available specimens. Also the posterior part of the zygomatic arch is missing. The fronto-parietal suture cannot be discerned. In PIN 3142-701 the sagittal crest is preserved in the badly damaged part of the cranial roof, to the rear of the endocranial cast. The sagittal crest is similarly prominent as in *Zalambdalestes* (see Szalay and McKenna 1971: fig. 31).

Occiput. — The occipital plate is preserved in PIN 3142-701 and in ZPAL MgM-I/77, in both specimens badly damaged. It is roughly semicircular. The occipital condyles are prominent, extending to about mid-height of the foramen magnum. Dorsolaterally the foramen is surrounded by weak protuberances of the exoccipitals. In the PIN specimen the occipital plate on the right side appears to be cracked and displaced along the suture between the supraoccipital and exoccipitals; this suture extends dorsolaterally from the foramen magnum, above the protuberances of the exoccipitals. The suture between the exoccipital and the mastoid is well preserved on the right side of the PIN specimen. The mastoid seen from behind is large and roughly rectangular, with an extensive ventral mastoid process. In both specimens the central part of the wall of the mastoid is lacking and the subarcuate fossa is visible. In ZPAL MgM-I/77 the mastoid, preserved only on the right side of the specimen, is displaced laterally and visible in the lateral view of the skull (see Kielan-Jaworowska 1975: pl. 5:1a). In this specimen above and below the missing part of the mastoid the ridge of the lateral mastoid flange (MacIntyre 1972) is present. The mastoid foramina are not preserved.

Orbit and temporal fossa (see fig. 1). — The orbit is confluent with temporal fossa and there is no trace of postorbital process. The upper rim of the orbit is thickened; it is made by the lacrimal and nasal. The orbital wing of the lacrimal appears extensive, but its shape is poorly known. The lacrimal foramen is placed just below the rim which surrounds the orbit.

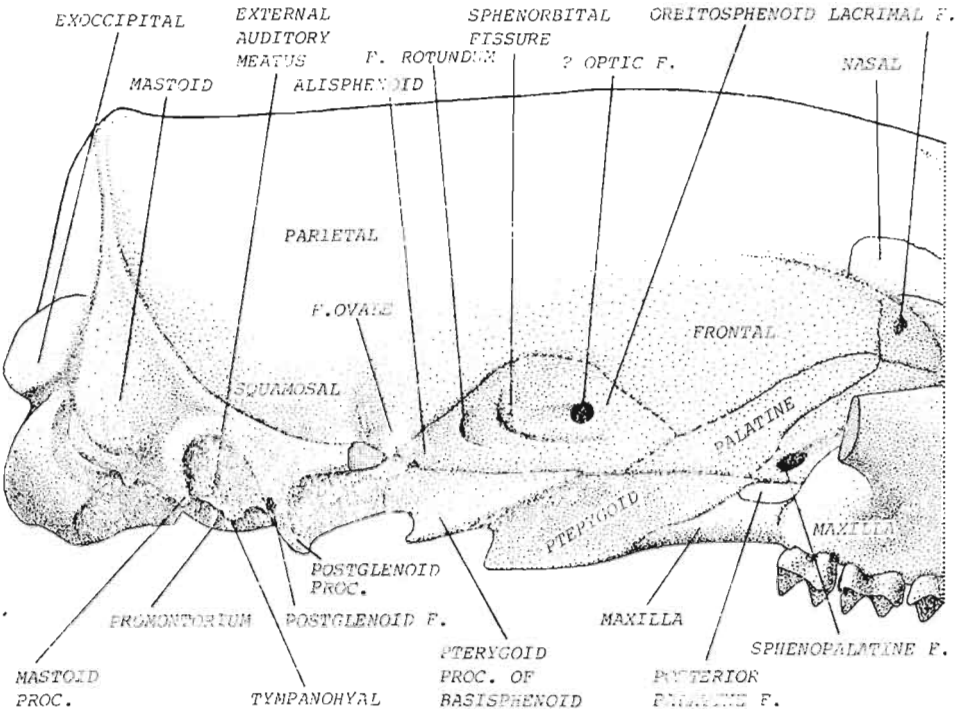

Fig. 1. *Barunlestes butleri* Kielan-Jaworowska. Reconstruction of the braincase in lateral view, based mostly upon PIN 3142-701.

The sutures in the orbital and temporal regions are only tentatively recognized. The maxillary foramen is poorly seen, placed medially and below the lacrimal foramen. Extending posteriorly from the maxillary foramen through the floor of the orbit to a sphenopalatine foramen is a deep groove. The sphenopalatine foramen is well preserved in ZPAL MgM-I/77, near the large, oval opening of the posterior palatine foramen. The suture between the maxilla and palatine within the orbit extends parallel to the groove described above.

The perpendicular part of the palatine is rectangular, pierced by two minute foramina. The suture between the frontal and the palatine extends in the anterior part parallel to the palatino-maxillary suture, posteriorly it is not discernible. The floor of the orbit is comparatively large. The pterygoid bone appears very large, somewhat concave when viewed from the side and the hamulus is not prominent. The size and shape of the orbitosphenoid and alisphenoid are only tentatively recognized: the orbitosphenoid is probably fan-shaped; the alisphenoid roughly triangular, pointed posteriorly. At the boundary between the orbitosphenoid and

alisphenoid and along the ventral part of the orbitosphenoid the bone is strongly incurved medially, but the foramina in this region are hardly discernible. There is a sphenorbital fissure, in front of which is a foramen possibly the optic. The foramen rotundum is placed to the rear of the sphenorbital fissure. At the postero-ventral corner of the alisphenoid there is a large foramen ovale, similarly placed as in *Asioryctes* (Kielan-Jaworowska 1980). On the left side of PIN 3142-701 the orbitosphenoid is pierced in the middle by a large, rounded foramen, which is regarded as an artefact, but might be as well a suboptic foramen (see Butler 1956). The pterygoid process of basisphenoid extends ventrolaterally from the alisphenoid. It is described in the next section.

Choanae and basicranium (well preserved in PIN 3142-701, fragmentarily in ZPAL MgM-I/77), (see fig. 2). — The horizontal part of the palatine bone prolongs behind forming the lateral walls of the anterior part of the choanal channel. The maxilla has also a backward extension along the side of the palatine. Both maxilla and the palatine have pointed ends situated at the same level, some 3.5 mm to the rear of the anterior margin of the choanae. The pterygoid bone has a pointed anterior end, inserted between the prolongations of the maxilla and the palatine. The pterygoid extends for a distance of ca. 4.2 mm, measured from the anterior. Its posterior end is incurved and slightly overhangs the presphenoid. The posterior tip of the pterygoid is pointed forming a small hamulus. The vomer is not discernible at the anterior part of the choanal channel. From the middle of the length of the choanal channel a single bone, with an indistinct median suture protrudes strongly ventrally, forming a prominent hook-like projection situated to the rear of the pterygoids, opposite the pterygoid process of the basisphenoid. This bone overhangs ventrally the central part of the basisphenoid. It is placed too far posteriorly to be a vomer and is regarded as a median process of the presphenoid, which protrudes ventrally, the structure not known to our knowledge in other mammals. Lateral to the anterior part of the hook-like projection extends the presphenoid, the anterior part of which cannot be defined. The posterior boundary of the presphenoid is discernible as an uncertain suture, tentatively recognized on both sides of PIN 3142-701. In *Asioryctes*, at the boundary between the presphenoid and basisphenoid (Kielan-Jaworowska 1980) is a distinct Vidian foramen. No foramen in this region is discernible in *Barunlestes*.

The basisphenoid is wide, gently concave and provided with a very extensive, roughly triangular lateral pterygoid process, the posterior margin of which is concave and the postero-ventral tip protrudes ventrolaterally as a pointed tip. Between the posterior margin of the pterygoid process and the postglenoid process there is a deep groove for chorda tympani. Across the middle of the basisphenoid there extends a rounded ridge, 0.7 mm wide, which ends as a rounded knob at the place which might be

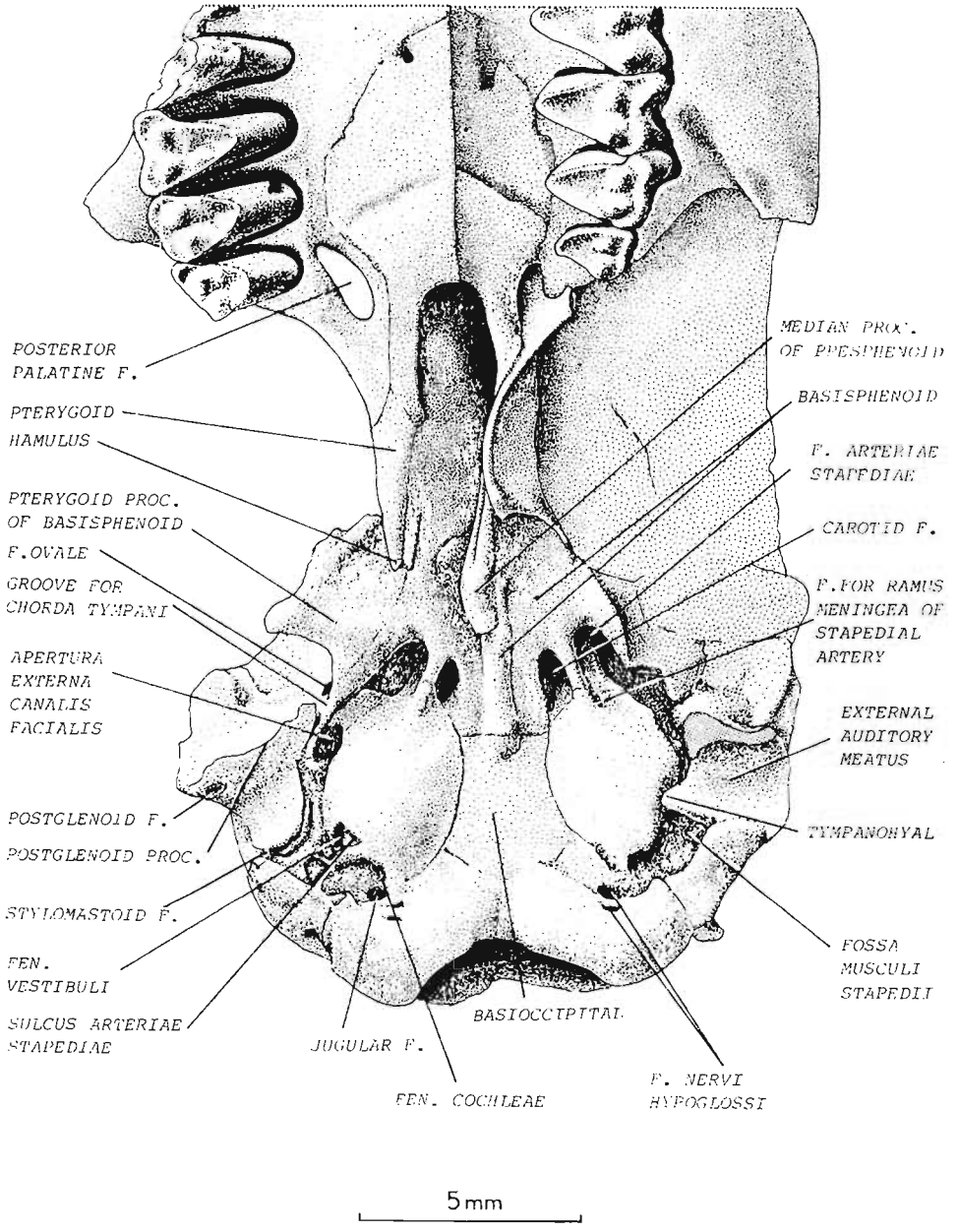

Fig. 2. *Barunlestes butleri* Kielan-Jaworowska, PIN 3142-701. Ventral view of the braincase.

a basisphenoid-basioccipital suture. The suture is not preserved, but the bone is cracked in this place and the crack is filled with calcite — it is possible that it was cracked along the suture. At the posterior margin of the basisphenoid, at the boundary between it and the promontorium there are two distinct foramina, the medial one, smaller, recognized as

a carotid foramen and a more lateral one probably enlarged somewhat on the left side of PIN 3142-701 by preservation or by preparation — a foramen arteriae stapediae for the ramus inferior of stapedial artery. On the rod of bone, which extends between the two foramina on both sides of PIN specimen an indistinct suture between the basisphenoid and the petrosal is discernible. A small foramen at the anteromedial corner of the promontorium, behind the foramen arteriae stapediae, present on the left side of PIN specimen (fig. 2 and pl. 2:2) is interpreted as a foramen for ramus meningea of stapedial artery.

The basioccipital, not distinguishable from exoccipitals, consists of an anterior, roughly rectangular part, inserted between the promontoria, and a very wide posterior part, with large and prominent occipital condyles. The foramina nervi hypoglossi consist of two openings situated to the rear and somewhat medially to the jugular foramen. The condyloid fossae are apparently absent. The basioccipital is clearly separated from the petromastoid by a distinct suture, well preserved on both sides of PIN 3142-701. The suture is situated close to the occipital condyle and extends anteromedially, reaching the sulcus which houses the jugular foramen. The paroccipital process is absent.

The promontorium is very large, pear-shaped, very strongly convex and highest in the posteromedial part, with a narrow rostral apex inserted between the two foramina and passing into the narrow rod of the basisphenoid. The promontorium bulge slopes gradually toward the rostral apex; more steeply, posterolaterally, toward the mastoid apex and very steeply, posteromedially, toward the occipital apex. The promontorium is bounded posteromedially by a very narrow rim. The fenestra vestibuli is a comparatively large, oval opening on the lateral face of the promontorium, only partly exposed in ventral view. Extending medially from the fenestra vestibuli is a short and shallow triangular sulcus arteriae stapediae, appearing very short in ventral view (as it lies on a steep slope). The fenestra cochleae is situated at the posterior margin of the promontorium and faces posteriorly towards the sulcus which houses the jugular foramen. The latter is rounded, faces entirely downwards and adheres the occipital condyle.

Of the sulci for the arteries only the above described sulcus arteriae stapediae is discernible. The sulcus arteriae promontorii is absent as is the sulcus medialis. Judging from the position of the carotid foramen, the arteria carotis interna probably extended along the lateral margin of the basioccipital, at the boundary with promontorium. The sulcus for the inferior petrosal vein has not been discerned.

The surface of the promontorium is somewhat undulating, and the shallow, irregular grooves, present on both sides of PIN 3142-701, are regarded as artefacts. The lateral side of the petrosal is preserved on the right side of PIN specimen, where the apertura externa canalis facialis is

discernible. The hiatus Fallopii cannot be discerned, but it seems that it was placed at the anterior end of facial canal bridge (MacIntyre 1972), immediately posteriorly to the stapedial foramen. The length of the facial canal bridge between these apertures is 1.3 mm. Extending posteriorly from the aperatura externa canalis facialis is a well defined, narrow groove for the facial canal (sulcus facialis, MacIntyre 1972), to the rear of which is a fossa musculi stapedii. The latter is roughly rectangular in shape, partly covered ventrally by the tympanohyal. The foramen stylomastoideum (developed rather as a sulcus) is placed between the tympanohyal and mastoid process.

The squamosal. The glenoid fossa is situated lateral to the anterior part of the promontorium. It is nearly flat, the postglenoid process is thin and prominent, extending only posteromedially, to about the mid-width of the glenoid fossa and is absent postero-laterally. The postglenoid foramen is tentatively recognized behind the lateral end of the postglenoid process. To the rear of the postglenoid process there is a large concave area of the external auditory meatus, at the posteromedial corner of which there is a triangular process — the tympanohyal, preserved only on the left side of PIN 3142-701. To the rear of the external auditory meatus a suture between the squamosal and the mastoid, well seen on the right side of PIN specimen, is preserved.

The mastoid as seen in ventral view is not very extensive. The tympanic process of the petromastoid (which is very extensive in *Kennalestes*, see Kielan-Jaworowska 1980) is not preserved in *Barunlestes*. The anterolateral part of the mastoid is developed as a prominent mastoid process, better preserved in ZPAL MgM-I/77 than in PIN 3142-701, where on both sides it is partly damaged.

Nasal cavity. — In PIN 3142-701 a partial cast of the nasal cavity has been preserved. On both sides of the specimen in front and somewhat lateral to the cast of olfactory bulbs, casts of sinuses frontales have been preserved. These sinuses evidently contained complicated turbinals. On the right side one can recognize a cast of the sinus frontalis medialis, separated transversely into a larger, oval posterior compartment and a smaller anterior one. Lateral to the sinus frontalis medialis is a cast of the sinus frontalis lateralis, divided longitudinally into two narrow, tubular compartments both subdivided transversely into two parts. On the left side of the specimen the cast of the sinus frontalis medialis is not present, as the bones (anterior part of the frontal and posterior part of the nasal) have been preserved in this region; the cast of the sinus lateralis although less completely exposed shows similar division into compartments as on the right side. In front of the frontal sinuses the bone is partly preserved on both sides and the details of the cast of the anterior part of nasal cavity cannot be discerned.

Endocranial cast. — A partial endocranial cast has been preserved in

PIN 3142-701. This consists of well preserved olfactory bulbs, which are very large, oval and measure (each) ca. 5.5 mm in length and 3.8 mm in width, and of very damaged cerebral hemispheres and partial cerebellum. The hemispheres strongly diverge posteriorly, but the anterior and posterior colliculi, which were evidently well exposed on the dorsal side are not seen, as the bone (parietal) has been preserved in this region. The right hemisphere which is better exposed is badly damaged. The rhinal fissure is not visible. The cast of the cerebellum is strongly deformed.

Lower jaw. — The anterior part of the lower jaw is most complete on the right side of ZPAL MgM-I/107, where all the teeth, although damaged, are preserved; in both jaws of ZPAL MgM-I/104 the rami are nearly completely preserved. The lower jaw consists of a relatively robust body and a large ramus. The alveolar border is concave upwards between P_3 and M_2 and nearly straight anteriorly, the dentary is the deepest below P_4. The lower margin is convex opposite the alveolar border and very slightly concave below the masseteric fossa. The depth of the lower jaw strongly increases with the growth of the animal, it is 4 mm deep below P_4 in ZPAL MgM-I/107, which is a juvenile individual in which the M_3 and permanent P_4 are just erupting and 5 mm deep in ZPAL MgM-I/104. The coronoid process slopes steeply upwards. The greatest estimated depth of the ramus is ca. 13 mm. The masseteric crest starts below the middle of the height of the body where it is provided with a knob-like projection (see Kielan-Jaworowska 1975, fig. 2B) and is very stout and prominent, particularly in the lower part. It is provided with an internal prominence, well seen from the front, wide at the base of the crest and tapering upwards. The coronoid fossa is divided into a deep triangular upper part, the lower boundary of which extends obliquely downwards from the condyle, and a shallower lower part. The angular process when seen from the side is bent upwards. The posterior margin forms two concavities, separated from each other by the condyle, which is situated above the level of the teeth. The condyle is very wide transversely when viewed from the top. There is one mental foramen situated below the posterior root of P_3.

The symphysis forms a crescent-shaped area which sends posteriorly a ridge, reaching back as far as P_3. The coronoid process in medial view is separated by a roughly transverse rounded ridge into upper and lower parts, the lower more concave than the upper. There is a rounded swelling at the base of the ascending ramus of coronoid process, however, no remnant of the coronoid bone is discerned (present in *Kennalestes* and *Asioryctes*, see Kielan-Jaworowska 1980, figs. 10 and 11). The mandibular foramen is placed at the anterior part of the ramus, 4 mm in front of the posterior margin. To the rear of the mandibular foramen there is a shallow, barely defined fossa. The angular process is in medial view roughly rectangular, bent medially. From its posteroventral corner starts thread-

like ridge which extends anterodorsally for ca. 5 mm along the mandibular ramus.

Dentition. — Dental formula: ?,1,3,3,/3,1,3,3. The upper incisors are not preserved, except for the root of I^3 in ZPAL MgM-I/107. The canine is placed 4.7 mm behind I^3 and is single-rooted. P^1 is absent. Between C and P^2 is a diastema 3 mm long; along the diastema the maxilla is distinctly concave upwards. P^2 is a small two-rooted tooth, compressed laterally, when viewed from the side it has an appearance of a scalene triangle, without a cingulum. The anterior basal cusp present in this tooth in *Zalambdalestes* does not occur in *Barunlestes*. P^3 is roughly triangular in

Table 1

Barunlestes butleri Kielan-Jaworowska

Measurements of the dentition in mm.*)

Mus. cat. nos.	PIN 3142—701		ZPAL MgM-I/77		ZPAL MgM-I/104		ZPAL MgM-I/ /135
	Left	Right	Left	Right	Left	Right	Right
P^2 ant.-post. ext.				1.00			
P^3 ant.-post. ext.				1.75			
P^3 tr.				2.98			
P^4 ant.-post. ext.	1.83			2.00			
P^4 tr.	3.20			3.50			
M^1 ant.-post. ext.	1.95	1.83		1.84			
M^1 tr.	3.49	3.58		3.50			
M^2 ant.-post. ext.	2.00	1.75		1.75			
M^2 tr.	3.00	2.90		3.00			
M^3 ant.-post. ext.	1.56	1.58		1.25			
M^3 tr.	2.10	2.15		2.25			
P_1 ant.-post. ext.			1.75				
P_3 ant.-post. ext.	2.30		2.00		2.00		
P_4 ant.-post. ext.	2.17	2.22	2.25		2.20	2.25	2.35
M_1 ant.-post. ext.	2.30	2.25	2.25		2.15	2.00	2.20
M_2 ant.-post. ext.	2.16	2.05	2.05		1.75	2.00	2.10
M_3 ant.-post. ext.	2.30	2.30	1.90				

*) Damaged teeth have not been measured. As all the lower teeth are strongly worn, their transverse dimensions cannot be given.

occlusal view, strongly transverse, with a paracone situated close to the external border and an incipient metacone in form of a small cuspule, situated at the posterior crest of the paracone (as in *Zalambdalestes*). The protocone is spur-like. The metastyle present in P^3 of *Zalambdalestes* is also discernible in *Barunlestes*. P^4 is similarly shaped as in *Zalambdalestes*, differing only in this that an incipient metacone is here somewhat larger and more strongly pronounced. M^1 — M^3 are strongly worn or damaged in all the specimens. They do not differ in any details from those of *Zalambdalestes* (see Kielan-Jaworowska 1969: 188) and thus do not merit a separate description.

The first lower incisor is a very large tooth, directed nearly horizontally, in a prolongation of the lower margin of the jaw, measuring ca. 1.9 mm in a vertical diameter and 1 mm in a transverse diameter, covered with a very thick layer of enamel. The entire tooth is not preserved and there is only a root, reaching back below P_3. I_2, I_3 and C are small teeth, semi-procumbent, styliform, one-rooted, similar to each other. P_1 is situated after a diastema of 0.7 mm behind the canine, it is trenchant, very slightly procumbent, with a prominent main cusp and a minute posterior basal cusp. P_2 is absent and there is a diastema between P_1 and P_3, 1 mm long. P_3 is a large tooth, consisting of a main cusp and a small un-basined heel with one low cusp. An anterior basal cusp characteristic of P_3 of *Zalambdalestes* is absent. P_4 appears to be somewhat more molarized than in *Zalambdalestes*. The protoconid is higher than in *Zalambdalestes*, and the trigonid as far as can be judged from the worn specimens is shaped as in the molars, whereas the talonid is somewhat larger than in *Zalambdalestes*. M_1—M_3 are best preserved in ZPAL MgM-I/135, where they are, however, somewhat worn. They do not differ from those in *Zalambdalestes* (see Kielan-Jaworowska 1969: 189) and thus do not merit description.

DISCUSSION

Barunlestes is very close to *Zalambdalestes*, from which it differs in having a single-rooted upper canine, in the lack of P_2 and P^1 and in having a somewhat more robust and shorter skull and lower jaw (see also Kielan-Jaworowska 1975: 11). The details of the palate and braincase structure as far as can be judged from the incomplete material of *Zalambdalestes* are identical in two genera.

Skulls of the Late Cretaceous Asian genera *Asioryctes* and *Kennalestes* have been recently described in detail (Kielan-Jaworowska 1980). The skull of *Barunlestes* differes from *Asioryctes* and *Kennalestes* in addition to the differences in the dentition (see Kielan-Jaworowska 1969, 1975 and

Crompton and Kielan-Jaworowska 1978): in its greater size; in having a more elongated and tubular snout and a relatively shorter mesocranial region; in the presence of a large posterior palatine foramen (only a notch occurs in *Asioryctes* and *Kennalestes*); in the presence of a median process of presphenoid and a very large pterygoid process of basisphenoid; in a different structure of basisphenoid (without a basisphenoid wing); in differently shaped postglenoid process and in lack of a flange which extends anteromedially from the postglenoid process. In spite of these differences concerning the dentition, skull proportions and details of skull structure there are several characters in common, such as large olfactory bulbs, lack of paroccipital process, very large and similarly shaped promontoria, general arrangement of skull foramina and the same pattern of the internal carotid circulation, although a Vidian foramen characteristic of *Asioryctes* has not been encountered in *Barunlestes*.

Presley (1979) demonstrated on embryological evidence that in present-day mammals the internal carotid artery at the level of the auditory capsule is a single vessel, which may move medially or laterally during the growth of the promontorium and may be placed either along its medial border or cross the middle or lateral side of the promontorium and lie within the tympanic cavity. Thus the possession of two main vessels of the internal carotid in primitive Eutheria, usually referred to as medial internal carotid and promontory arteries, accepted until recently by paleontologists (McDowell 1958, McKenna 1966, Van Valen 1966, MacIntyre 1972, Szalay 1975, Archibald 1977 and others) should be revised.

One of us (Kielan-Jaworowska 1980) supported Presley's idea, demonstrating that in the oldest known skulls of eutherian mammals from the Late Cretaceous of Mongolia: *Kennalestes* and *Asioryetes*, no trace of a groove for the promontory artery has been encountered. The structure of *Barunlestes* skull gives further support for Presley's idea. In *Barunlestes*, which derives from the same beds as *Asioryctes*, the promontory artery was evidently absent. The position of a carotid foramen, well preserved in PIN 3412-701 shows that the internal carotid artery probably extended along the basisphenoid at the boundary with promontorium.

In the Bug Creek petrosals from the Late Cretaceous Hell Creek Formation of Montana, described by MacIntyre (1972) and in the Leptictidae (Butler 1956, Kielan-Jaworowska 1980) the sulci arteriae stapediae and promontorii are present, which (accepting Presley's hypothesis) indicates that in these groups the carotid artery has moved laterally over the promontorium.

Barunlestes is reminiscent of the Leptictidae in some details of the skull structure such as the presence of large posterior palatine foramen and fissura Glaseri. It is reminiscent of the Tenrecidae in having a backward extension of the maxilla along the choanae, but otherwise the basicranial region of *Barunlestes* is very different from that in the Ten-

recidae (e.g. the tympanic process of basisphenoid is absent). The skulls of the Erinaceidae (Butler 1948) and other modern insectivores (McDowell 1958) do not invite a close comparison with *Barunlestes*.

It follows from the foregoing description and discussion as well as from the study of the postcranial skeleton (Kielan-Jaworowska 1979) and dentition (Crompton and Kielan-Jaworowska 1978) of the Zalambdalestidae, that *Barunlestes* is an advanced genus, which, however, has retained in basicranial structure several primitive features, indicating a relatively recent separation from a common ancestor with the primitive Asian eutherian genera *Asioryctes* and *Kennalestes*.

Large promontoria, large olfactory bulbs and probably also complicated turbinals in *Barunlestes* support Jerrison's (1973) view that the auditory and olfactory senses were strongly developed in Mesozoic mammals.

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ZOFIA KIELAN-JAWOROWSKA i BORYS A. TROFIMOV

MORFOLOGIA CZASZKI KREDOWEGO ŁOŻYSKOWEGO SSAKA *BARUNLESTES*

Streszczenie

W pracy opisano czaszkę górno-kredowego ssaka łożyskowego *Barunlestes butleri* Kielan-Jaworowska 1975, należącego do rodziny Zalambdalestidae. Okazy *B. butleri* pochodzą z formacji Barun Gojot, która jest przypuszczalnie wieku środkowo-kampańskiego, z miejscowości Nemegt i Chulsan w Dolinie Nemegetańskiej, oraz z czerwonych warstw Chermin Caw, które są tego samego wieku co formacja Nemegt, z miejscowości Chermin Caw na pustyni Gobi w Mongolii. *B. butleri* różni się od *Zalambdalestes lechei* Gregory and Simpson 1926, który należy do tej samej rodziny brakiem P^1 i P_2 oraz krótszą i bardziej masywną czaszką i żuchwą. Zęby trzonowe *B. butleri* i *Z. lechei* są nie do odróżnienia. Czaszka *Barunlestes* charakteryzuje się następującymi cechami: bardzo duże płaty węchowe mózgu, obecność wyrostka kości szczękowej, skierowanego ku tyłowi wzdłuż nozdrzy wewnętrznych, równolegle do kości podniebiennej, obecność na kości przedklinowej dużego wyrostka, skierowanego

dobrzusznie, występowanie dużych wyrostków skrzydłowatych kości przedklinowej, obecność szczeliny Glazera, bardzo duże promontorium, krótki wyrostek zapanewkowy, rozciągający się tylko na przeciw środkowej części dołu żuchwowego, brak wyrostka przypotylicznego, obecność szczeliny klinowo-oczodołowej, otworu okrągłego, otworu owalnego, otworu dla arteria carotis interna oraz otworu dla dolnego odgałęzienia arteria stapedia, obecność na promontorium sulcus arteriae stapediae oraz brak sulcus arteriae promontorii, zagięcie wyrostka kątowego żuchwy dośrodkowo.

Brak sulcus arteriae promontorii u *Barunlestes* (nie występującego również u kredowych ssaków łożyskowych *Kennalestes* i *Asioryctes*) potwierdza pogląd Presley'a (1979) oparty na danych embriologicznych, że należy poddać rewizji morfotyp uznany powszechnie w literaturze paleontologicznej za prymitywny dla ssaków, w którym występują dwa niezależne naczynia krwionośne: arteria carotis interna i arteria promontorii. Brak arteria promontorii u *Kennalestes, Asioryctes* i *Barunlestes* wskazuje że u prymitywnych ssaków łożyskowych występowała tylko arteria carotis interna, która, jak sugeruje Presley (1979) mogła w ewolucji różnych grup ssaków przemieszczać się ku bokowi i biec przez środek lub z boku promontorium.

Duże rozmiary płatów węchowych mózgu i duże promontorium sugerują, że zmysły węchu i słuchu były u *Barunlestes* silnie rozwinięte.

Praca była częściowo wykonana w ramach problemu MR II/6 finansowanego przez Polską Akademię Nauk i w ramach umowy o współpracy między PAN i AN ZSRR, temat 30.1.

ЗОФИЯ КЕЛЯН-ЯВОРОВСКА, БОРИС А. ТРОФИМОВ

МОРФОЛОГИЯ ЧЕРЕПА МЕЛОВОГО ПЛАЦЕНТАРНОГО МЛЕКОПИТАЮЩЕГО *BARUNLESTES*

Резюме

В статье описан череп верхнемелового плацентарного млекопитающего сем. Zalambdalestidae — *Barunlestes butleri* Kielan-Jaworowska 1975. Образцы происходят из свиты Барун-Гойот (?средний кампан) местонахождений Нэмэгт и Хульсан в Нэмэгетинской котловине, а также из красной толщи Хермин-цав, имеющей тот же возраст. *B. butleri* отличается от *Zalambdalestes lechei* Gregory et Simpson 1926 отсутствием P^1 и P_2, а также более коротким и массивным черепом и нижней челюстью. Коренные зубы *B. butleri* и *Z. lechei* не отличаются. Череп *B. butleri* характеризуется следующими чертами: очень большие обонятельные доли мозга; наличие максилярного отростка, направленного назад вдоль внутренних ноздрей параллельно нёбу; присутствие на пресфеноиде длинного выроста, направленного вентрально; наличие больших крыловидных отростков пресфеноида; щели Глазера; очень крупного промонториума; короткий заднесочленовный отросток, про-

стирающийся до уровня средней части гленоидной ямы; отсутствие предтеменного отростка; наличие сфеноорбитальной щели; округлого и овального отверстий, а также отверстия для внутренней сонной артерии и отверстия для нижней ветви артерия стапедиа; присутствие на промонториум борозды для артериа стапедия, а также отсутствие борозды артериа промонториа; изгибание углового отростка челюсти вовнутрь.

Отсутствие sulcus arteriae promontorii у *Barunlestes*, которого также нет у меловых плацентарных *Kennalestes* и *Asioryctes* подтверждает мнение эмбриолога Присли (1979) о том, что следует ревизовать морфотип, который в морфологической литературе принято считать примитивным для млекопитающих. В этом морфотипе два независимых кровеносных сосуда arteria carotis interna и a. promontori. Отсутствие a. promontori у *Kennalestes*, *Asioryctes* и *Barunlestes* показывает, что у примитивных плацентарных существовала только a. carotis interna, которая, как считает Присли (1979) могла в эволюции разных групп млекопитающих смещаться вбок и проходить через середину или край промонториума. Большие размеры обонятельных долей мозга и промонториума дают основание предполагать, что обоняние и слух у *Barunlestes* были сильно развиты.

EXPLANATION OF THE PLATES 1—8

Plate 1

Barunlestes butleri Kielan-Jaworowska

Upper Cretaceous, red beds of Khermeen Tsav, Khermeen Tsav II, Gobi Desert, Mongolia, PIN 3142-701 (see also plates 2—4)

1a. Stereo-photograph of the skull associated with lower jaws, showing the cast of the nasal cavity and incomplete cast of the braincase, in dorsal view, covered with ammonium chloride. CER — cerebellum, HEM — cerebral hemisphere, OB — olfactory bulb, SFL — sinus frontalis lateralis, FSM — sinus frontalis medialis.

1b. Stereo-photograph of the incomplete right lower jaw of the same specimen in outer view.

1c. Stereo-photograph of left lower jaw of the same specimen in outer view.

All × 3

Plate 2

Barunlestes butleri Kielan-Jaworowska

Upper Cretaceous, red beds of Khermeen Tsav, Khermeen Tsav II, Gobi Desert, Mongolia, PIN 3142-701 (see also plates 1, 3 and 4)

1a. Stereo-photograph of the skull, after the separation of the lower jaws, in occipital view.

1b. Stereo-photograph of the same skull, after the separation of the lower jaws, in ventral view.

Both × 3

Plate 3

Barunlestes butleri Kielan-Jaworowska

Upper Cretaceous, red beds of Khermeen Tsav, Khermeen Tsav II, Gobi Desert, Mongolia, PIN 3142-701 (see also plates 1, 2 and 4)

1a. Stereo-photograph of the skull, after the separation of the lower jaws, in right lateral view.
1b. Stereo-photograph of the same in left lateral view.

Both × 3

Plate 4

Barunlestes butleri Kielan-Jaworowska

Upper Cretaceous, red beds of Khermeen Tsav, Khermeen Tsav II, Gobi Desert, Mongolia, PIN 3142-701 (see also plates 1—3)

1a. Stereo-photograph of the incomplete left lower jaw in occlusal view.
1b. Stereo-photograph of the same in inner view.
1c. Stereo-photograph of the incomplete right lower jaw of the same specimen in occlusal view.
1d. Stereo-photograph of the same in inner view.

All × 3

Plate 5

Barunlestes butleri Kielan-Jaworowska

Upper Cretaceous, red beds of Khermeen Tsav, Khermeen Tsav II, Gobi Desert, Mongolia

1. Stereo-photograph of the incomplete face of an old individual, with strongly worn dentition, in ventral view, ZPAL MgM-I/104, (see also plate 6).
2a. Incomplete, damaged right lower jaw in inner view, ZPAL MgM-I/94.
2b. The same in outer view.
2c. Strongly damaged face of the same specimen in ventral view.
2d. The same in dorsal view.

All × 3

Plate 6

Barunlestes butleri Kielan-Jaworowska

Upper Cretaceous, red beds of Khermeen Tsav, Khermeen Tsav II, Gobi Desert, Mongolia, ZPAL MgM-I/104

1a. Incomplete face associated with both lower jaws, as it has been found, in right lateral view.
1b. Incomplete right lower jaw of the same in inner view.
1c. The same in outer view.
1d. Stereo-photograph of the same in occlusal view.
1e. Incomplete left lower jaw of the same in outer view.
1f. The same in inner view.
1g. Stereo-photograph of the same in occlusal view.

All × 3

Plate 7

Barunlestes butleri Kielan-Jaworowska

Upper Cretaceous, red beds of Khermeen Tsav, Khermeen Tsav II, Gobi Desert, Mongolia, ZPAL MgM-I/107 (see also plate 8)

1a. Damaged face, after the separation of the lower jaws, in right lateral view.
1b. Stereo-photograph of the damaged left lower jaw of the same specimen in occlusal view.
1c. Stereo-photograph of the damaged right lower jaw of the same specimen in occlusal view.

Barun Goyot Formation, Nemegt, Eastern Sayr, Nemegt Basin, Gobi Desert, Mongolia, ZPAL MgM-I/135

2a. Stereo-photograph of incomplete right lower jaw in inner view.
2b. Stereo-photograph of the same in outer view.
2c. Stereo-photograph of the same in occlusal view.

All × 3

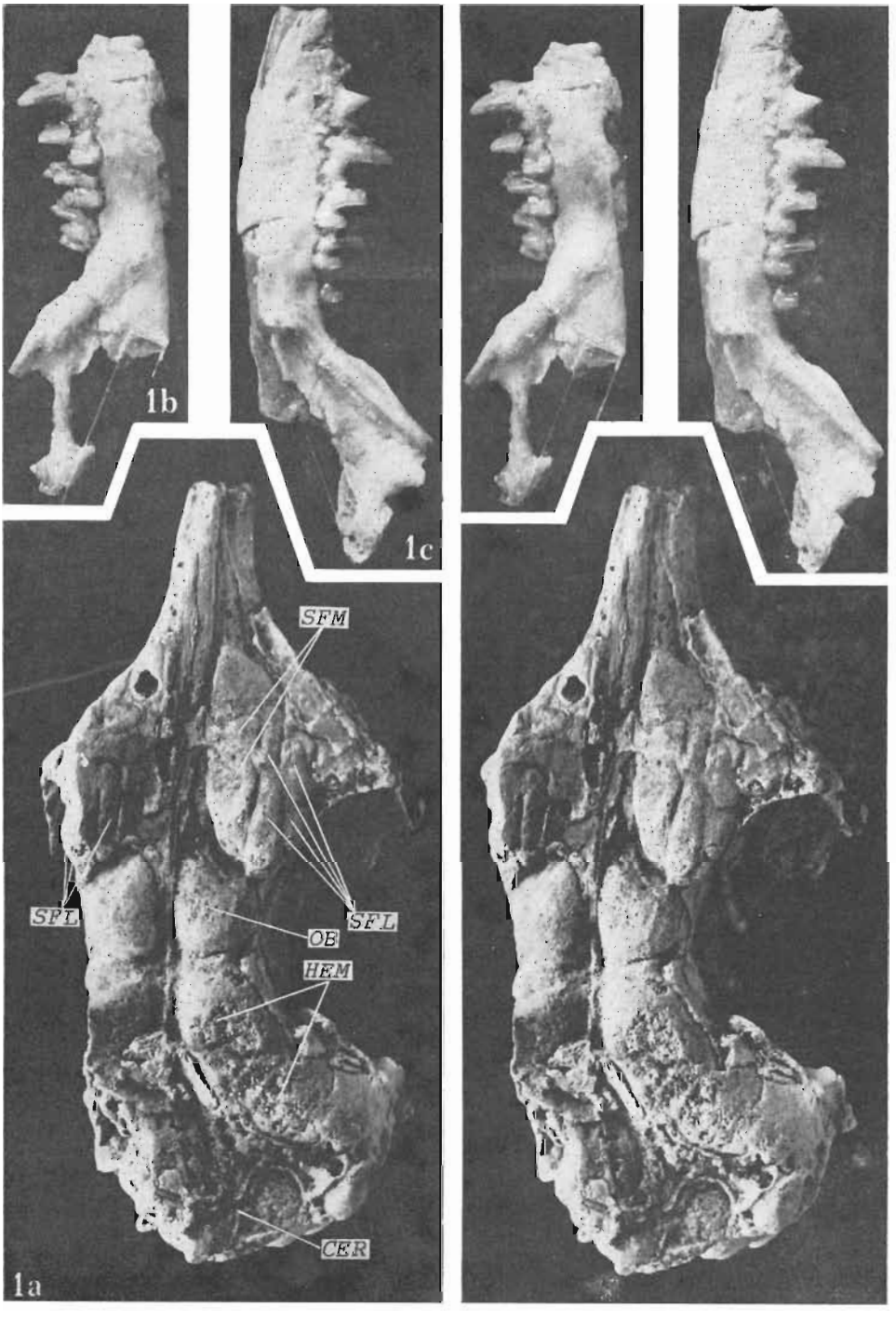
Plate 8

Barunlestes butleri Kielan-Jaworowska

Upper Cretaceous, red beds of Khermeen Tsav, Khermeen Tsav II, Gobi Desert, Mongolia, ZPAL MgM-I/107

1a. Incomplete face, associated with right and left lower jaws, as it has been found, in right lateral view.
1b. The same, after separation of the lower jaws, showing strongly damaged denition, in ventral view.
1c. Incomplete right lower jaw of the same specimen in inner view.
1d. The same in outer view.
1e. Stereo-photograph of the incomplete left lower jaw of the same specimen in inner view.
1f. Stereo-photograph of the same in outer view.

All × 3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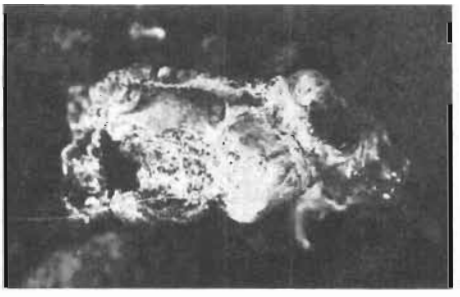

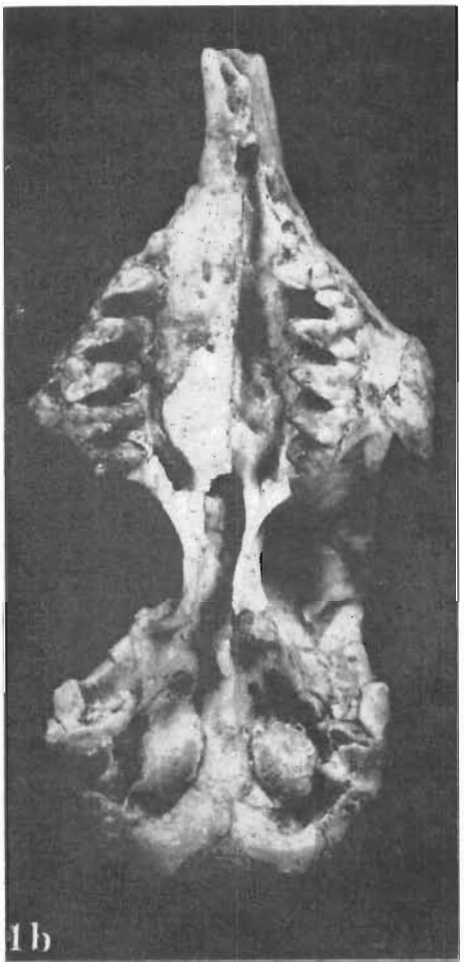

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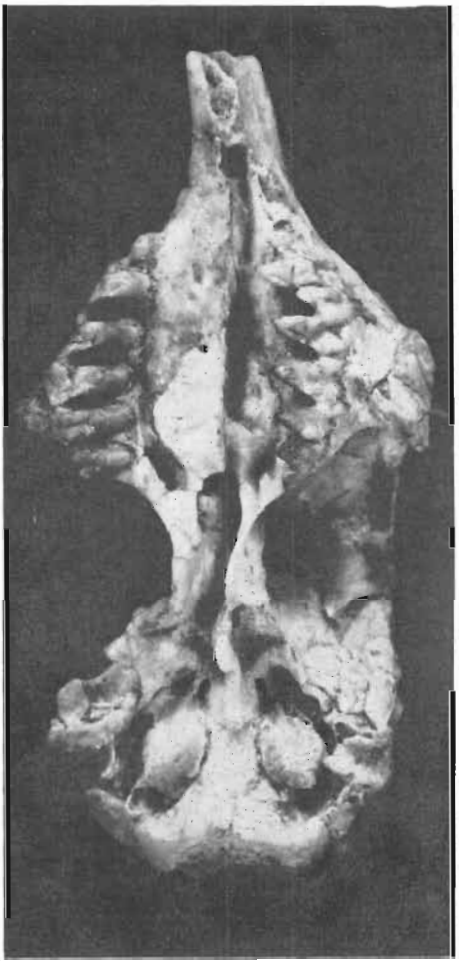

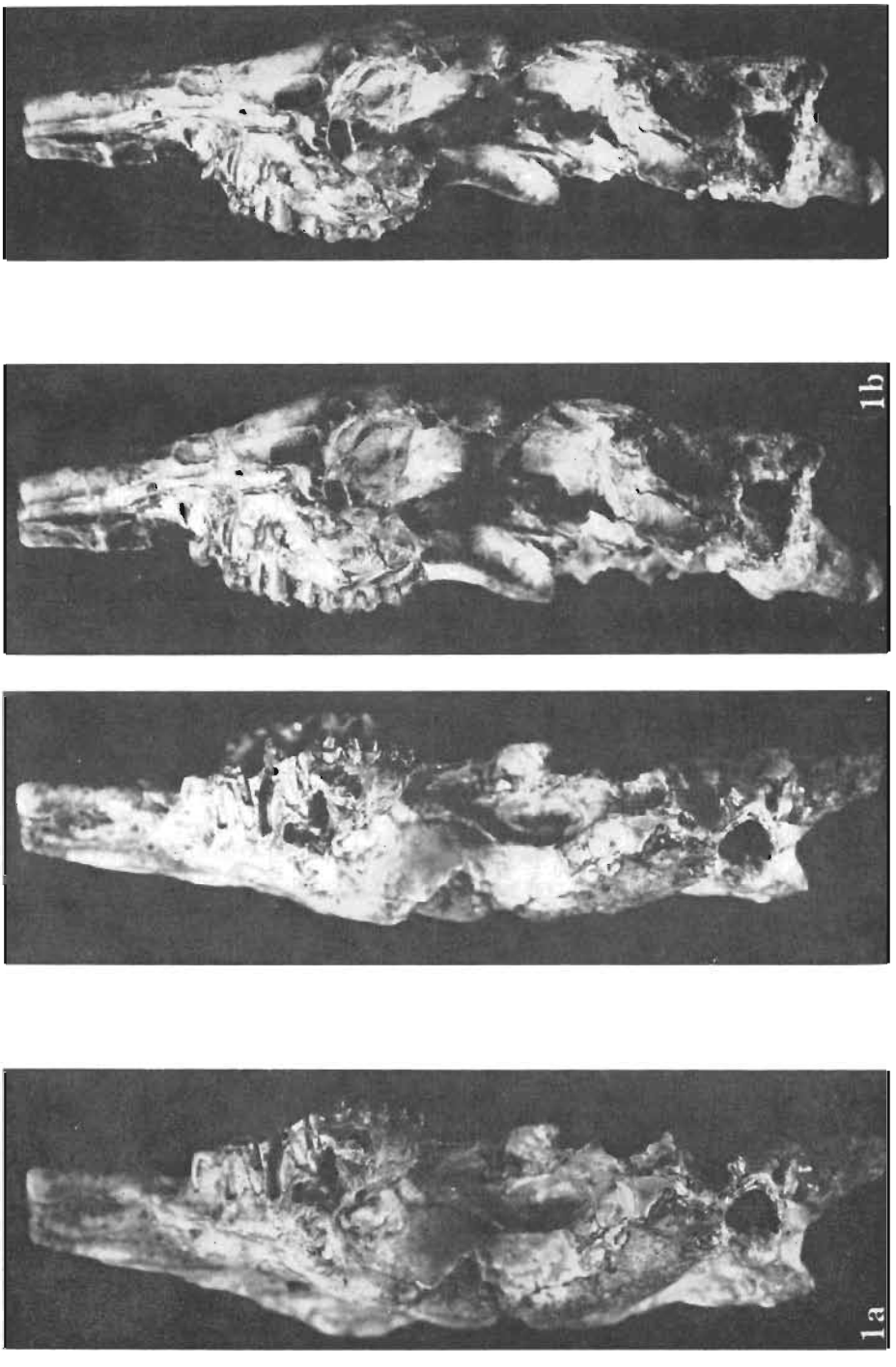
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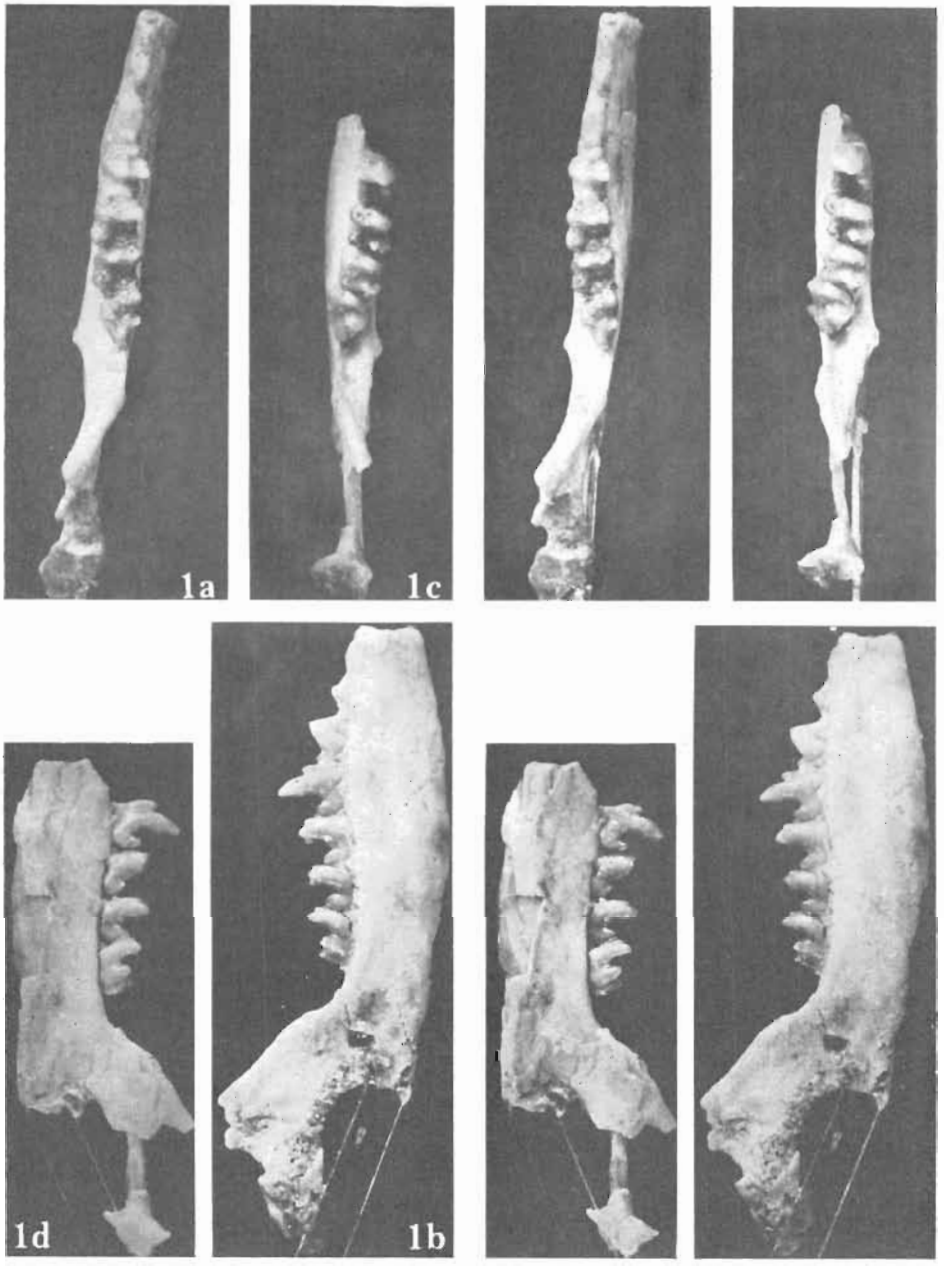
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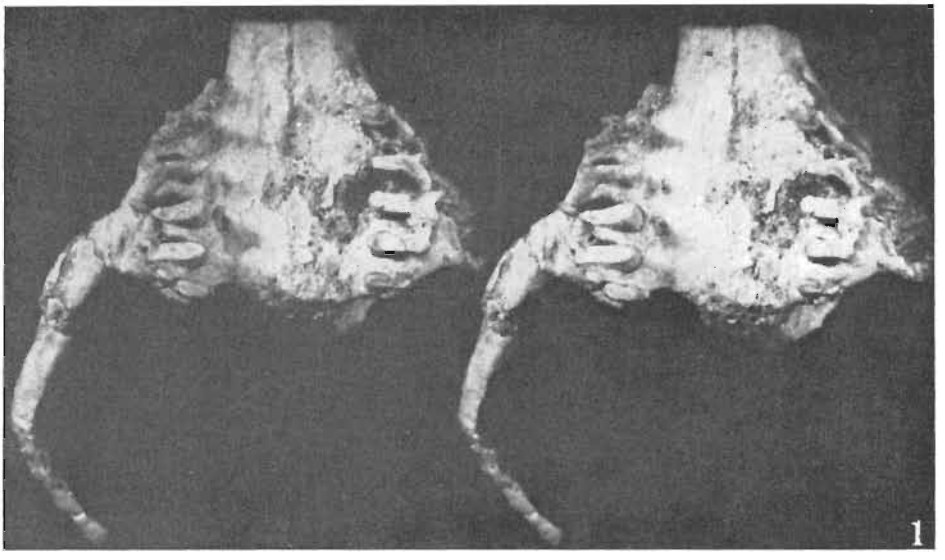
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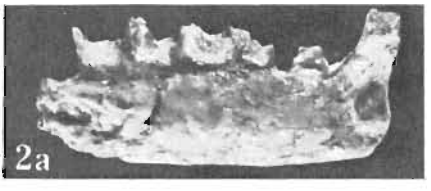
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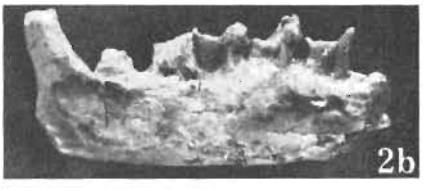
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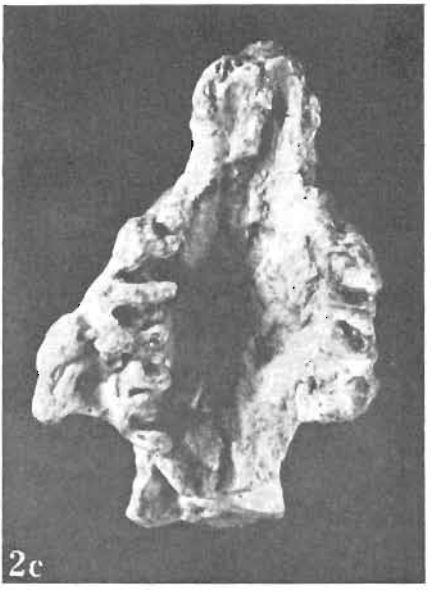
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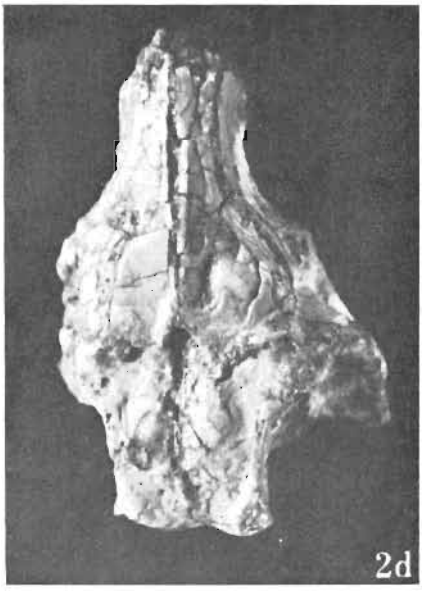
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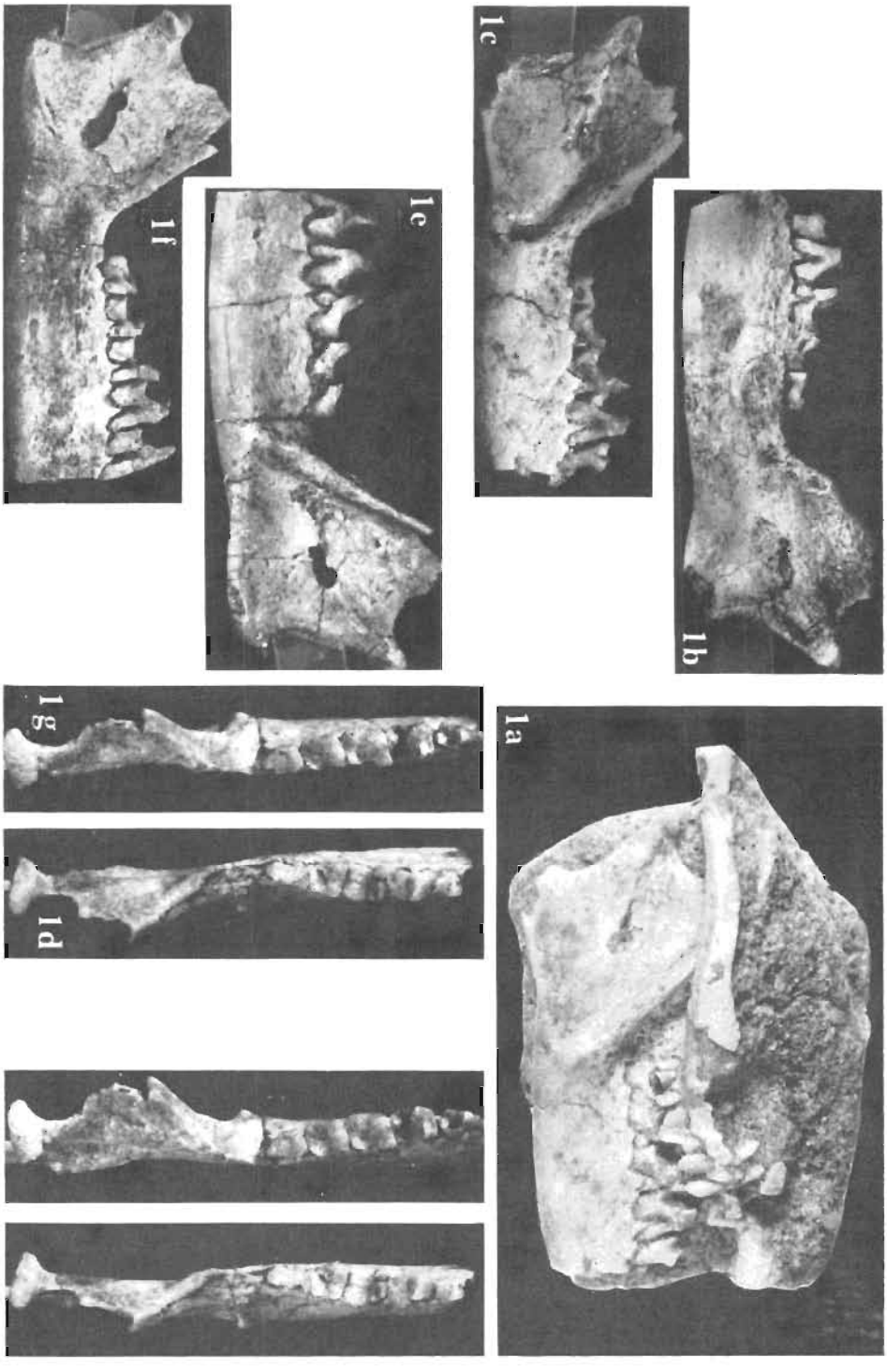
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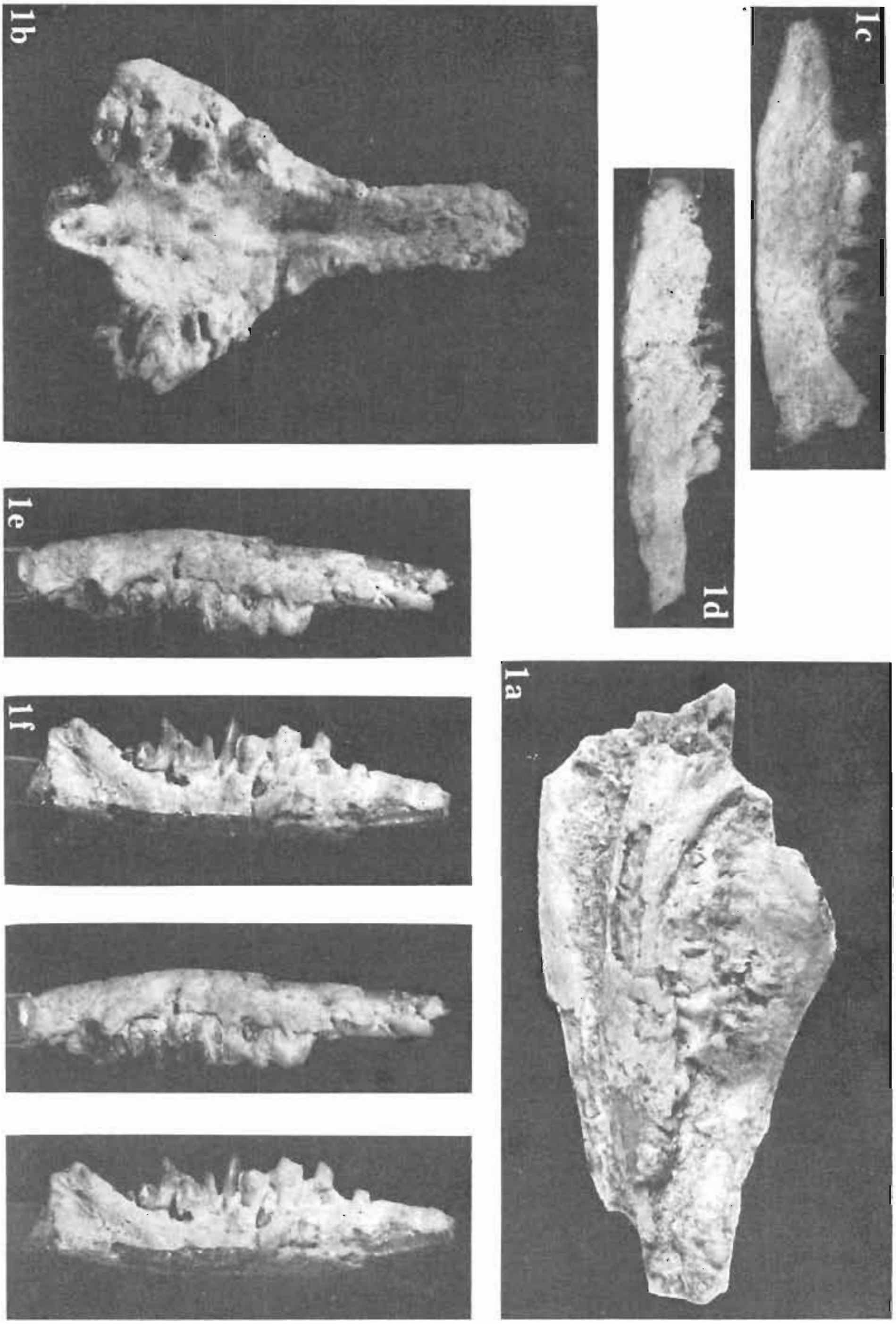
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